

Selfish mothers: reproductive expenditure and resource availability in bighorn ewes

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When resources are scarce, iteroparous females may value their subsequent survival and reproduction over their current offspring's development and survival. Field data to test this hypothesis are scant because it is difficult to determine whether reduced development of juveniles when resources are scarce is due to maternal restraint or constraint. During a 24-year study of bighorn sheep (*Ovis canadensis*), lamb mass near the time of weaning was very weakly correlated with maternal mass. A weak maternal mass effect persisted for body mass of yearlings of both sexes. As the number of adult ewes tripled, summer mass gain by lambs decreased about 22%, while summer mass gain by mothers decreased only 9%. Maternal expenditure (the residual of the regression of lamb mass and maternal mass in mid-September) was much lower at high than at low population density. For individual females, maternal expenditure was correlated with winter mass loss, but had no other overt short-term costs. Our results suggest that most bighorn ewes adopt a conservative maternal care strategy and reduce maternal care when resources are scarce to favor their own mass gain over the development of their lambs. *Key words*: bighorn sheep, body mass, maternal care, maternal effects, maternal expenditure, *Ovis canadensis*, population density, reproductive strategy, seasonal mass gain. [*Behav Ecol* 9:144–150 (1998)]

When resources are scarce, mothers face a trade-off between caring for their offspring and their own maintenance and survival. If the potential for future reproduction is low, maternal care is expected to increase when resources decrease because the reproductive value of the offspring should be greater than the mother's reproductive value. If, on the other hand, resource scarcity affects juvenile survival and reproductive value more than maternal reproductive value, maternal care should decrease when resources are scarce because mothers should favor their own survival and subsequent reproduction over that of their offspring (Clutton-Brock, 1991). In large mammals, food limitation usually affects juvenile survival more than adult survival (Douglas and Leslie, 1986; Fowler, 1987; Moorcroft et al., 1996; Owen-Smith, 1990), and therefore mothers should provide less care when resources are scarce than when resources are abundant.

When environmental conditions are difficult, juveniles often exhibit reduced mass or low survival (Byers and Hogg, 1995; Clutton-Brock et al., 1987a; Fowler, 1987; Illius et al., 1995). In wild and feral sheep (*Ovis* spp.), maternal behaviors such as nursing, nuzzling and licking the lamb diminish when resources are scarce (Berger, 1979; Festa-Bianchet, 1988b; Rachlow and Bowyer, 1994; Robertson et al., 1992). White-tailed deer (*Odocoileus virginianus*) mothers take more risks in defending their fawns against predators in years when they are in better condition than in years when they are in poor condition (Smith, 1987). Without a measure of how mothers partition resources between themselves and their offspring, however, it is difficult to determine whether small offspring size, low juvenile survival, and poor maternal behavior when resources are scarce result from an adaptive strategy of lower maternal care or are simply a nonadaptive consequence of low

food availability and poor maternal condition. Field data on how mammalian maternal expenditure varies with resource availability are extremely limited, making it difficult to test evolutionary hypotheses. In otariid seals, the proportion of the maternal energy budget devoted to lactation appears fixed at about 30% despite wide fluctuations in resource availability (Trillmich, 1990).

Many female ungulates in temperate environments rely on the short growing season for both fat storage and lactation: in several species mothers gain mass during lactation and lose mass during winter (Festa-Bianchet et al., 1996; Hudson and Adamczewski, 1990). Body mass of juveniles often has a positive effect on survival (Clutton-Brock et al. 1987; Clutton-Brock et al., 1992; Festa-Bianchet et al., 1997; White et al., 1987). No information is available on body mass effects on survival of adult females, except for bighorn sheep (*Ovis canadensis*), in which body mass had a weak positive effect on survival of females beyond 7 years of age (Festa-Bianchet et al., 1997). On the other hand, adult female mass usually has a positive effect on reproductive success (Bérubé, 1997; Cameron and Hoef, 1994; Clutton-Brock et al., 1996). In mammals with seasonal mass cycles, comparison of mass changes of mothers and offspring could lead to valuable insights into strategies of maternal care (Dobson and Michener, 1995). If mothers limit their reproductive expenditure because they place higher priority on their own survival and subsequent reproduction than on that of their offspring, then as resource availability decreases, the proportional mass gain of offspring during lactation should decrease more than the proportional mass gain by mothers. If, on the other hand, mothers do not change their level of maternal expenditure in response to resource availability, as resources become scarce, both maternal and offspring mass accumulation should be equally affected.

Bighorn sheep in the Canadian Rocky Mountains follow a marked seasonal mass cycle. Individual adult ewes fluctuate in mass by as much as 35% during the year (Festa-Bianchet et al., 1996). Mass loss occurs from November to April, while

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most mass gain is from late May to early August, coincident with lactation. Lambs are born in late May and weaned by late September or early October. From mid-June to mid-September, lamb mass can more than triple. Lamb survival over the winter is positively related to mid-September mass, whereas mid-September mass has no effect on the survival of ewes aged 2–7 years and a weak positive effect on the survival of older ewes (Festa-Bianchet et al., 1997).

In this study, we first determined whether maternal and offspring size are correlated, as has been reported in reindeer (*Rangifer tarandus*; Kojola, 1993), and in two species of seals (Arnbohm et al., 1997; Iverson et al., 1993). A strong correlation between maternal and offspring mass would suggest that light mothers are unable to provide as much maternal care as heavy mothers during summer. We then compared maternal expenditure to population density. Following Clutton-Brock (1991), we hypothesized that as food resources became scarcer, mothers should favor their own mass accumulation over maternal care. We predicted that as population density increases, summer mass gain of lambs should decrease more than the summer mass gain of mothers. The late-summer mass of lambs relative to their mothers' mass should therefore decrease as population density increases. We also tested for potential effects of lamb mass after mid-September on maternal mass loss during winter, because if maternal care continued after mid-September, lamb mass changes during winter should be negatively correlated with maternal mass changes. To test these predictions, we used 24 years of data from a marked population of bighorn sheep for which we had accurate information on seasonal mass changes for mother–lamb pairs and where we experimentally induced a wide variation in population density (Jorgenson et al., 1993b).

METHODS

Study area and population

We studied bighorn sheep at Ram Mountain, Alberta, Canada (52° N, 115° W, elevation 1082–2173 m). Each year, sheep captured in a corral trap from late May to late September or early October were weighed to the nearest 250 g with a Detecto spring scale. Data used in this paper were collected from 1973 to 1996 and include only cases for which the lamb was captured at least twice as a lamb or as a yearling, so that we could adjust its body mass to the beginning of the summer mass accumulation period (5 June for yearlings, 15 June for lambs) or to 15 September (Festa-Bianchet et al., 1996). A few lamb–ewe pairs were excluded because we did not capture the ewe twice and therefore could not adjust her mass to 5 June and 15 September. Ewe–lamb associations were determined in the field by observing marked lambs suckle from marked ewes (more than 80% of ewes were marked in 1973; all ewes were marked from 1976 onward). In most years, more than 80% of the lambs were captured. Lambs were marked with numbered Ketchum metal ear tags and a small strip of colored Safeflag plastic, which was replaced the following year by either color-coded Allflex ear tags (for males) or canvas collars with unique color and symbol patterns (for females).

From 1973 to 1981, the population was maintained at low density (average of 34 ewes) through yearly removals of 12–24% of ewes (Jorgenson et al., 1993b). After 1981, the population increased, peaking at 104 ewes in 1992 and declining to 73 ewes in 1996. As the number of ewes increased, the population showed clear evidence of resource limitation, including delayed age of primiparity (Jorgenson et al., 1993), lower survival of lambs and of yearling females (Festa-Bianchet et al., 1997, Jorgenson et al., 1997), and reduced mass gain and horn growth for young sheep (this study; Festa-Bianchet et al., unpublished data).

Data analyses

We adjusted mass of lambs to 15 June instead of 5 June because for some lambs, mass adjusted to 5 June was much less than the average birthweight for this species (Hogg et al., 1992), even including a few negative values, probably because mass gain of very young lambs was not linear and because some lambs were born later than 5 June (Festa-Bianchet et al., 1996). Summer mass gain was calculated as the difference between mass in September and mass in June of the same year (Festa-Bianchet et al., 1996). We calculated mass change during winter by subtracting mass adjusted to mid-September from mass adjusted to 5 June the following year.

Our measure of reproductive expenditure was the residual of the linear regression of lamb and ewe masses adjusted to 15 September. We also performed most of the analyses reported here using the ratio of lamb to ewe mass on 15 September as a measure of reproductive expenditure and obtained similar results to those presented here. By mid-September ewes have nearly completed their summer mass accumulation, but lambs have not (Festa-Bianchet et al., 1996). Because we did not trap after early October and because capture frequency decreased after early September, we could not adjust individual masses to a later date. We assumed that lamb mass on 15 September was representative of the end of the period of maternal care. As in many other ungulates (Lavigne and Barrette, 1992), weaning in bighorn sheep is a gradual process. By mid-September, suckles are rare and lambs appear to rely on foraging for most of their nutrition (Festa-Bianchet, 1988b). Experimental early weaning in early September had no effect on yearling mass for females and a moderate (7–8%) negative effect for males (Festa-Bianchet et al., 1994). It is therefore reasonable to assume that by 15 September the period of maternal care was almost finished.

We used the number of adult ewes in the population in June to measure population density. Bighorn sheep are sexually segregated for most of the year (Geist, 1971), so the amount of resources available to ewes and lambs should not be affected by the number of rams in the population. Bighorn females have a traditional area-use pattern and do not usually expand the size of their group's home range in response to increases in population size (Festa-Bianchet, 1986; Geist, 1971). Therefore, population size and population density are largely equivalent. For some analyses (for example, comparisons of reproductive expenditure by the same ewe at different population densities) it was preferable to consider population size as a categorical rather than as a continuous variable. In these cases we considered 1973–1987 to be low-density years (average of 40 ewes and 120 total sheep in June) and 1988–1996 to be high-density years (average of 85 ewes and 203 total sheep).

We used parametric statistics (linear and multiple regression; partial correlation; *t* test) to analyze data on body mass. Logistic regression (Trexler and Travis, 1993) was used to test associations of survival with mass variables. We used nonparametric statistics to compare variables that were unlikely to be normally distributed, such as ewe age. Our analyses were affected to a slight extent by pseudoreplication (Machlis et al., 1985) because several ewes were sampled in more than one year. For example, for the comparison of ewe and lamb mass, 121 ewes contributed an average of 1.9 observations (ewe-years) each. However, many important variables changed for the same ewe from year to year, including lamb sex, lamb and ewe mass, ewe age, population density, and lamb birthdate. For ewes sampled over several years, we used paired *t* tests to compare reproductive expenditure, mass changes, or lamb mass for the same ewe under different circumstances. For ewes that were sampled at least twice, we compared maternal

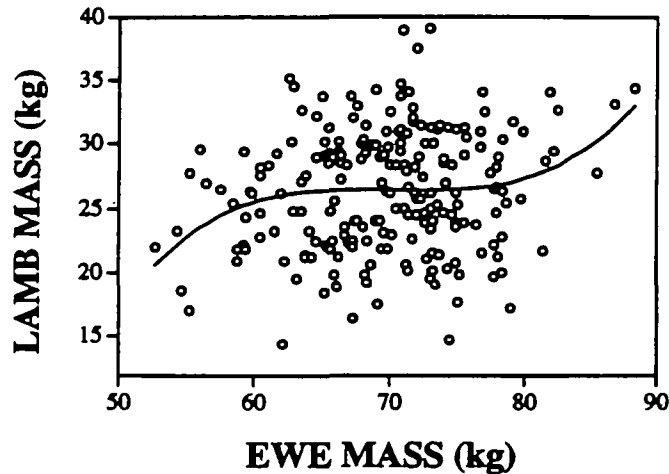


Figure 1
Relationship between maternal and offspring mass adjusted to 15 September for bighorn ewe-lamb pairs at Ram Mountain, Alberta, Canada, in 1975-1996 ($y = 17.39x - 0.248x^2 + 0.001x^3 - 379.3$, $r^2 = .05$, $p = .016$, $n = 207$; all terms in the third-degree polynomial: $p < .04$). Only ewes aged 3-14 years are included.

mass in the years when they produced their heaviest and their lightest lambs. To determine whether ewe mass in mid-September affected winter lamb survival, we used paired *t* tests comparing September mass of the same ewe in years when her lamb did and did not survive the winter.

We excluded data from 2-year-old ewes because they only reproduced at low population density, and their lambs were lighter than those of older ewes (Festa-Bianchet et al., 1995). We also excluded data from ewes older than 14 years because none was sampled at low density, they undergo senescence-related changes in mass, and they appear to adopt different reproductive strategies from younger ewes (Bérubé, 1997). For 17 ewes sampled during years of different population densities, we used paired *t* tests to compare mass, reproductive expenditure, and lamb mass in years of high and low density.

Statistical analyses were performed using SPSS for the Macintosh (SPSS, 1994). Means are reported \pm SD, and all probabilities are two-tailed except where indicated.

RESULTS

Maternal effects on offspring mass

Ewe mass on 5 June was weakly correlated with mass of her lamb on 15 June [lamb mass = $0.074(\text{mother's mass}) + 4.99$, $r^2 = .05$, $p = .0031$, $n = 173$ lambs]. Summer mass gain by the lamb was not correlated with maternal mass on 5 June ($r^2 = .004$, $p = .4$, $n = 155$).

Overall, maternal mass was weakly positively correlated with lamb mass on 15 September [lamb mass = $0.12(\text{mother's mass}) + 17.9$, $r^2 = .027$, $p = .017$, $n = 207$ lambs]. This relationship was better described by a third-degree polynomial because over most of the range, ewe and lamb mass were not correlated, but the lightest ewes tended to produce light lambs, and the heaviest ewes tended to produce heavy lambs (Figure 1). Using multiple regression, 29% of the variance in lamb mass on 15 September could be explained by maternal mass, number of ewes in the population, and lamb sex (Table 1). Ewe age (coded as 2 classes: 3-year-olds in one class and older ewes in the other class) did not explain any additional variance in lamb mass ($p = .3$). Ewe mass on 15 September was not related to mass of the lamb weaned the following year ($r^2 = .01$, $p = .15$, $n = 178$).

Table 1

Multiple regression analyses of the effects of sex, maternal mass on 15 September in the year of lamb birth, and number of ewes in the population on mass (kg) of bighorn lambs and yearlings on 15 September at Ram Mountain, Alberta, Canada, 1975 to 1996

Variable	Coefficient	Partial r	t	p
Lambs ($n = 231$, $R^2 = .293$, $p < .0001$)				
Ewes	-0.091	-.460	7.76	<.0001
Sex	-1.985	-.212	3.70	.0003
Mother's mass	0.202	.289	4.90	<.0001
Constant	21.75			
Yearlings ($n = 199$, $R^2 = .421$, $p < .0001$)				
Ewes	-0.134	-.424	7.57	<.0001
Sex	-6.026	-.428	7.81	<.0001
Mother's mass	0.285	.281	5.03	<.0001
Constant	45.51			
Yearling males ($n = 92$, $R^2 = .226$, $p < .0001$)				
Ewes	-0.148	-.460	4.69	<.0001
Mother's mass	0.356	.328	3.35	.0012
Constant	35.52			
Yearling females ($n = 107$, $R^2 = .345$, $p < .0001$)				
Ewes	-0.124	-.532	6.65	<.0001
Mother's mass	0.235	.329	4.11	.0001
Constant	36.05			

Sex was entered as a dummy variable coded as 1 for males and 2 for females.

Maternal mass affected offspring mass a year later: multiple regression explained 42% of the variance in mass of yearlings on 15 September when maternal mass, number of ewes in the population, and lamb sex were used as independent variables (Table 1). As sexual dimorphism increases with age (Festa-Bianchet et al., 1996), the variance in mass explained by sex increased with offspring age. To see whether long-term effects of maternal mass existed for both sexes, we performed separate analyses for males and females: for both sexes yearling mass was correlated with maternal mass (Table 1).

Summer mass gains by mother and lamb were positively correlated, but the relationship was weak [lamb gain = $0.14(\text{ewe gain}) + 16.1$, $r^2 = .05$, $n = 160$, $p = .03$] and was not significant if years of high and low density were considered separately [low density: lamb gain = $0.14(\text{ewe gain}) + 17.9$, $r^2 = .04$, $n = 50$, $p = .18$; high density: lamb gain = $0.11(\text{ewe gain}) + 15.7$, $r^2 = .02$, $n = 112$, $p = .12$].

The weakness of the relationship between maternal mass and lamb mass was confirmed by an analysis of individual ewes in the years when they weaned their heaviest and lightest lambs. Despite a mean difference in mid-September lamb mass of 6.4 ± 4.8 kg (about 24% of the mean mass of all lambs), mothers were not significantly heavier in the year they weaned the heavier lamb than in the year they weaned the lighter lamb (mean difference of 0.8 ± 5.2 kg, or about 1% of mean ewe mass, $t_{44} = 1.17$, $p = .25$). There was also no difference in ewe mass on 15 September the year before weaning the heavier and the lighter lamb (mean difference of 0.7 kg, $t_{42} = 0.71$, $p = 0.5$). On average, the 55 ewes in this sample were aged 7.6 ± 3.0 years when they produced the lighter lamb and 6.3 ± 2.4 years when they produced the heavier lamb (Wilcoxon matched-pairs test, $z = 2.96$, $p = .003$).

Reproductive expenditure, maternal mass, and population density

The weak correlation between lamb and ewe mass meant that heavy lambs required more expenditure than light lambs and

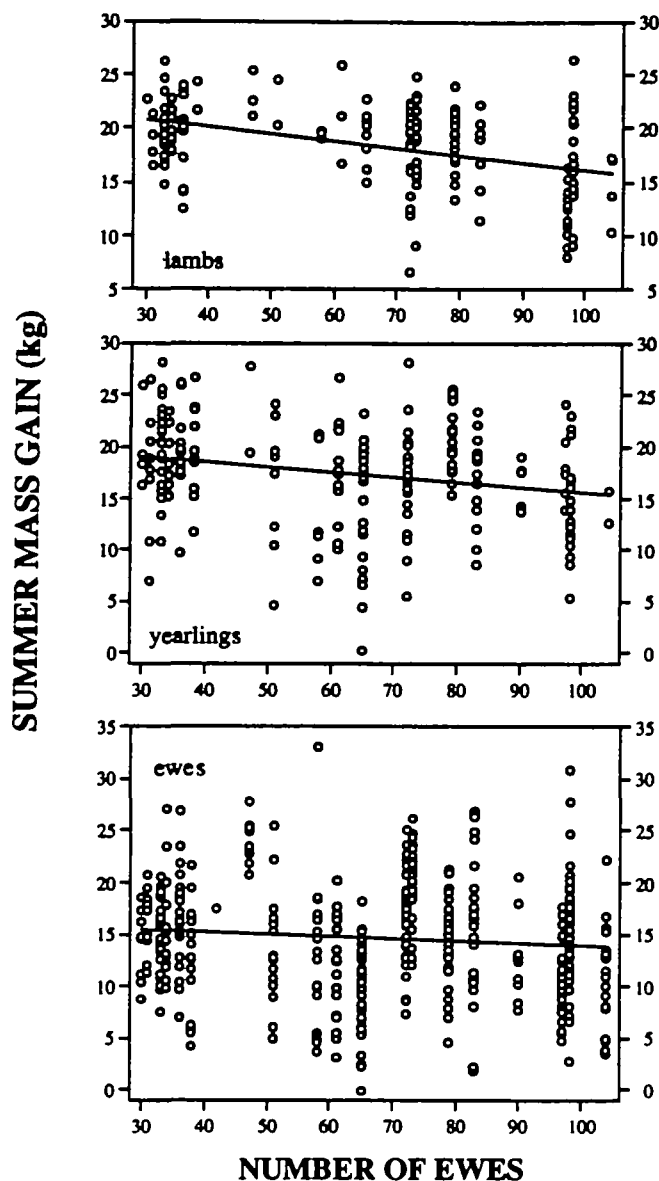


Figure 2
Number of adult ewes in June and summer mass gain by bighorn lambs ($y = 22.9 - 0.068x$, $r^2 = .164$, $n = 168$, $p = .0001$), yearlings ($y = 20.6 - 0.049x$, $r^2 = .048$, $n = 206$, $p = .001$) and lactating ewes ($y = 16.1 - 0.022x$, $r^2 = .009$, $n = 463$, $p = .04$) in the Ram Mountain population, 1973–1996.

light mothers expended more than heavy mothers. Because male lambs were heavier than female lambs, reproductive expenditure for sons (residuals from regression of lamb mass on ewe mass, $\bar{x} = 1.27 \pm 4.83$) was greater than for daughters ($\bar{x} = -1.17 \pm 4.21$; $t_{206} = 3.90$, $p < .001$).

Although summer mass gain was negatively affected by population density for all age classes, ewes were less affected than younger sheep (Figure 2). The regression equations in Figure 2 suggest that as the population increased from 35 to 100 ewes, summer mass gain by lambs decreased by about 22%, mass gain by yearlings decreased by 17%, and mass gain by lactating ewes decreased by only 9%. Population density explained less than 1% of the variance in mass gain by lactating ewes.

To determine if the poor mass gain of lambs at high population density was due to differences in forage intake rather

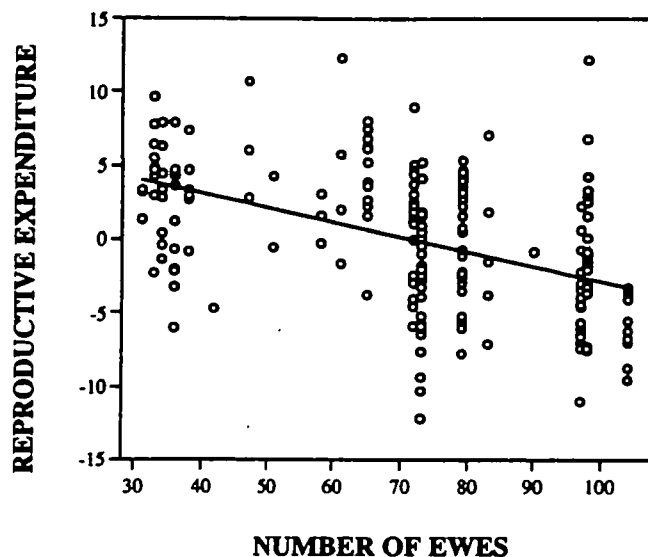


Figure 3
Relationship between the number of adult ewes and reproductive expenditure in bighorn sheep at Ram Mountain, Alberta, Canada, 1973–1996. Reproductive expenditure is the residual of the linear regression of lamb mass on maternal mass, both adjusted to 15 September ($y = 7.03 - 0.098x$, $r^2 = .22$, $n = 207$, $p < .0001$). Only ewes aged 3–14 years are included.

than to differences in milk supply, we compared the relative summer mass accumulation of lambs (that both nurse and feed on vegetation) and of yearlings (that only feed on vegetation). Because relative mass gain during summer is negatively correlated with mass at the beginning of the summer (Festa-Bianchet et al., 1996), we compared the residuals of the regression of relative summer mass gain (kg gained/mass in early summer) on early-summer mass with the number of ewes for both lambs and yearlings. Both relationships were significant (yearlings: $y = 0.102 - 0.002x$, $r^2 = 0.05$, $p = .002$, $n = 206$; lambs: $y = 0.522 - 0.008x$, $r^2 = .14$, $p = .0001$, $n = 168$), suggesting that as population density increased young sheep accumulated less mass during summer than would have been expected from their early-summer mass. The steeper slope found for lambs compared to yearlings (the 95% confidence intervals of the two slopes do not overlap) suggests that population size had a greater effect on lambs than on yearlings, contrary to what was expected if the effects of population density on mass gain were primarily through reduced forage availability.

The relative summer mass gain of lactating ewes after accounting for individual early-summer mass was independent of population density ($r^2 < .001$, $p = .9$, $n = 442$), providing further evidence that density had little effect on how much energy lactating ewes allocated to themselves. The average age of lactating ewes increased with population density ($y = 3.1 + 0.049x$, $r^2 = .16$, $p = .0001$, $n = 478$) and so did their average 5 June mass ($y = 54.2 + 0.59x$, $r^2 = .04$, $p = .0001$, $n = 459$).

Reproductive expenditure decreased as the number of ewes increased (Figure 3). In a multiple regression, 28% of the variance in reproductive expenditure was explained by the number of ewes ($p < .0001$) and lamb sex ($p = .002$), but ewe mass on 15 September did not explain any additional variance ($p = .3$).

Individual-level analysis of 17 ewes that reproduced during years of low and high density confirmed the results reported above. Because the years of high density followed those of low density, the ewes were older at high than at low population

Table 2
Multiple regression analysis of mass (kg) of bighorn yearlings on 5 June at Ram Mountain, Alberta, Canada, 1973–1996

Variable	Coefficient	Partial r	t	p
Mother's adjusted overwinter mass loss	0.181	.175	2.65	.01
Mass as a lamb on 15 September	0.691	-.655	9.78	<.0001
Number of ewes	-0.064	-.321	4.89	<.0001
Sex	-1.203	-.135	2.02	.047
Constant	16.38			

Adjusted maternal overwinter mass loss is the residual of the regression of winter mass loss on mass on 15 September for individual ewes. Sex was entered as a dummy variable coded as 1 for males and 2 for females; $n = 80$, $R^2 = .69$, $p < .0001$.

density (by 5 ± 2.6 years), but their mass on 15 September was not significantly different at high and at low density (mean difference of -0.8 ± 5.0 kg, paired $t_{16} = 0.65$, $p = .5$). The lambs produced at high density were 6.6 ± 3.9 kg lighter on 15 September than the lambs produced at low density (paired $t_{16} = 6.94$, $p = .0001$), a difference of about 21%.

Reproductive expenditure, reproductive costs and lamb survival

Reproductive expenditure did not have a short-term negative effect on ewe survival because ewes that died during the winter had lower reproductive expenditure (-2.76 ± 3.96 , $n = 15$) than ewes that survived to the following spring (0.70 ± 4.54 , $n = 166$; $t_{170} = 2.86$, $p = .005$). Considering only years when they weaned lambs, individual ewes were lighter in mid-September when their lamb died during the following winter than in years when their lamb survived to 1 year (mean difference of -1.18 ± 2.8 kg or about 2% of the mean mass of adult ewes, paired $t_7 = 2.64$, $p = .012$). We next considered the relationship between reproductive expenditure and ewe mass loss over the following winter. Winter mass loss was negatively affected by reproductive expenditure ($y = -12.8 - 0.38x$, $r^2 = .10$, $n = 132$, $p = .0002$). Multiple regression confirmed the negative effect of reproductive expenditure on winter mass loss when lamb sex and population size were taken into account, although neither of the two latter variables affected mass loss ($p > .1$).

If maternal investment continued after 15 September, winter mass loss by mothers should be correlated with either mass of the lamb as a yearling or overwinter survival by the lamb. However, winter mass loss by ewes was not independent of mass on 15 September because heavy ewes lost more mass overwinter than light ewes [winter mass loss = $12.1 - 0.36(\text{mass on 15 September})$, $n = 317$, $r^2 = .19$, $p = .001$]. Therefore, rather than comparing lamb survival to absolute mass loss by its mother, we compared lamb survival to the residuals of the regression of winter mass loss on ewe mass on 15 September ("adjusted mass loss"). Adjusted mass loss by the mother did not affect lamb survival ($p = .3$) when entered in a logistic regression including the number of ewes and lamb mass on 15 September, two variables known to affect winter lamb survival (Festa-Bianchet et al., 1997). In multiple regression, however, adjusted winter mass loss had a weak positive effect on yearling mass the following 5 June (Table 2), suggesting that the less mass ewes lost during winter, the heavier their yearlings on 5 June. Therefore, rather than a positive effect of ewe winter mass loss on offspring mass (expected if

ewe mass loss was caused by maternal investment), we found a negative effect. When we entered the same variables listed in Table 2 in a stepwise regression to predict yearling mass on 15 September, only mass as a lamb 1 year earlier had a significant effect ($r^2 = .46$, $p < .0001$).

DISCUSSION

Our investigation of maternal expenditure produced three major results: maternal and offspring mass were weakly but significantly correlated, maternal expenditure decreased as numbers of sheep increased, and despite a wide mass-independent variability in maternal expenditure, that expenditure had few short-term costs. Together, these results suggest that the maternal expenditure of most bighorn ewes is generally well below the maximum expenditure possible (see also Byers and Hogg, 1995) and is further reduced at high population density. When resources are scarce, female bighorn sheep appear to favor their own mass accumulation over their lambs'. An analysis of adult female survival patterns in this population and in the Sheep River population (Jorgenson et al., 1997) revealed that female survival is high (about 94% for ewes aged 2–7 years and about 85% for older ewes) and independent of population density. Bighorn ewes therefore appear to have a conservative reproductive strategy, minimizing reproductive expenditure while maximizing their own survival.

Bernardo (1996) suggested that long-term studies of marked individuals are particularly valuable for analyzing how maternal characteristics affect offspring condition and subsequent life history through multiple environments. In our study, although maternal mass was weakly correlated with offspring mass, maternal mass nevertheless affected offspring mass up to 1 year after weaning. Therefore, some maternal effects on adult morphology and reproductive behavior may exist in bighorn sheep, particularly when other factors such as population density and offspring sex are taken into account.

If mothers devoted a high reproductive effort to their lambs, heavy ewes should produce heavier lambs than light ewes. Thus, maternal and offspring mass should be correlated, particularly given the wide range of maternal body masses: the heaviest ewes were about 30 kg (or 50%) heavier than the lightest ewes. Although the very lightest ewes produced lambs that were generally lighter than average and the heaviest ewes produced lambs that tended to be heavier than average, ewe body mass appeared to have little or no effect on lamb mass for ewes weighing from 60 to 80 kg (Figure 1); a 33% increase in ewe mass had no detectable effect on lamb mass. The weak correlation between maternal and offspring mass suggests that many ewes were not expending the maximum possible amount of energy to nurse their lambs, with the likely exception of the lightest ewes in our sample. A weak correlation between maternal and lamb mass was also found for feral sheep (Clutton-Brock et al., 1996) and low levels of maternal investment may be a common characteristic of ovids.

Individual differences in ewe body mass in mid-September could be due to differences in skeletal size and differences in body condition, especially the amount of fat. If heavy ewes were simply larger than light ewes and not necessarily in better body condition, then it would be unreasonable to expect a strong effect of maternal mass on lamb mass: a large ewe in poor condition may be unable to provide as much maternal care to her lamb as a small ewe in good condition. The lamb of a small, fat ewe may be heavier than the lamb of a large, lean ewe. Our within-individual comparisons, however, suggest that individual ewes did not produce heavier lambs in years when they were heavier. Individual ewes gain mass until at least 7 years of age (Festa-Bianchet et al., 1996), but because in the individual-level analysis we found that ewes were older when they produced their

smaller lamb, we argue that year-to-year differences in mass of the same ewes were mostly due to differences in fat stores. These results suggest that factors other than body size or body condition appear to affect maternal expenditure.

Age-related differences in body mass (Festa-Bianchet et al., 1996) and an aging population may explain why absolute mass gain of lactating ewes during summer declined slightly as the number of ewes increased (Figure 2), but when mass on 5 June was accounted for, relative summer mass gain by ewes was unaffected by population density. Therefore, the decline in summer mass accumulation of lactating ewes is probably not due to their inability to obtain sufficient forage during summer, but rather to the negative correlation between 5 June mass and summer mass gain. This result underscores the importance of accounting for population age distribution. The apparently counterintuitive positive correlation of population density and average mass of lactating ewes in June is probably due to a changing age structure. Ewes gain mass until about 7–8 years of age (Festa-Bianchet et al., 1996). At low density most lactating ewes considered in this analysis were aged 3–7 years, but as population density increased the average age increased to about 8 years.

The discussion above assumes that lamb mass in mid-September is determined mostly by the amount of milk received during summer. If lamb mass was determined by factors independent of maternal care, such as the quality and quantity of forage consumed or the weather, differences in lamb mass and in our measure of reproductive expenditure would not necessarily indicate differences in maternal care. Bighorn lambs appear to spend much of their time grazing from about 1 month of age onward, but we do not have data on their foraging behavior during the entire study. The relative contributions of forage and milk to lamb mass accumulation are not known, but it is reasonable to assume that the importance of forage increases as lambs age (Lavigneur and Barrette, 1992; Robbins, 1993). Experimental early weaning in early September at low population density had no effect on the development of females and a moderate effect (about 7–8% lower body mass as yearlings) on the development of males. Therefore, it appears that by September lambs rely mostly on forage rather than on milk, and we cannot exclude that differences in forage availability were involved in density-dependent changes in lamb mass. However, if differences in summer mass gain were mostly determined by forage availability (and therefore affected by weather and population density independently of the amount of maternal care), then yearlings should show the greatest effects of population density on summer mass gain because yearlings do not receive any milk from their mothers (with a few exceptions at high density, see L'Heureux et al., 1995) and are still undergoing considerable body growth (Festa-Bianchet et al., 1996). Instead, we found that summer mass gain by yearlings was less sensitive to population density than mass gain by lambs. In addition, adult ewes were able to gain about as much mass at high density as at low density, suggesting that forage availability was not severely affected by high population density. Therefore, we argue that density-dependent differences in summer mass gain of lambs and in our measure of reproductive expenditure at least partly reflect differences in maternal care. We suggest that at high population density, lambs receive less maternal care, and as a consequence they are lighter in mid-September than at low population density. Low mid-September mass in lambs is associated with poor survival at high population density (Festa-Bianchet et al., 1997) and therefore the restraint in maternal care could have serious negative effects on offspring fitness. It is reasonable to predict that at high population density lambs should increase their forage intake to compensate for lower milk supply, but we do not have the data to test that prediction. Horejsi (1976) reported that in the Sheep River population lambs spent more time feeding on vegetation in a year when they appeared to receive less milk from their

mother and when lamb survival was low compared to 2 years when they received longer suckles and their survival was high.

Bighorn ewes appear to adopt a cautious maternal care strategy, limiting the amount of care devoted to their lamb, possibly to avoid reducing their residual reproductive potential. In our study, the only short-term reproductive cost related to different levels of reproductive expenditure was that winter mass loss increased with reproductive expenditure. The costs of reproduction in bighorn ewes may increase with population density: negative effects of early reproduction on summer mass accumulation and subsequent reproductive success were evident only at high population density (Festa-Bianchet et al., 1995). As population density increases, female ungulates tend to adopt a more conservative reproductive strategy by delaying primiparity or lowering the mass-specific probability of conception (Albon et al., 1983; Jorgenson et al., 1993a). Our study suggests that ungulate females that reproduce at high population density limit maternal expenditure so as to minimize the negative consequences of poor resource availability on their own body condition. At high population density, lactating ewes accumulated about as much mass during summer as at low density, but their lambs gained almost a quarter less mass at high than at low population density. Survival of adult bighorn ewes is high, varies little from year to year, and is density independent (Jorgenson et al., 1997). Furthermore, beyond age 4, more than 90% of ewes give birth every year, even at high population density (Festa-Bianchet, 1988a; Festa-Bianchet and Jorgenson, unpublished data). In contrast, lamb survival is variable and density dependent (Bérubé et al., 1996). It is therefore predictable that when resources are scarce mothers will reduce the amount of care because they favor their own residual reproductive value over that of their offspring (Clutton-Brock, 1991).

Our contention that small lamb body mass in mid-September relative to maternal mass was due to reproductive restraint rather than to nutritional constraints is further supported by within-individual comparisons that show that individual ewes did not produce larger lambs in years when they were heavier and produced lighter lambs at high population density even though density had no effect on their body mass. The weak but positive correlation between maternal and lamb summer mass gain further suggests that ewes did not produce heavier lambs at the expense of their own summer mass accumulation.

The within-individual analyses reported here reveal a considerable amount of phenotypic plasticity in the maternal care strategy of individual ewes. The same ewes weaned larger lambs at low than at high population density, even though there were no differences in their own body mass. Therefore, the changes in maternal care that we documented were due to phenotypic plasticity and not to selection for different types of individuals, as might be expected for animals that reproduce over several years (up to 14 years in the study population) during which environmental conditions can vary considerably.

Lambs born at high population density should be less valuable to their mothers than lambs born at low population density because at high density lambs experience greater winter mortality (Festa-Bianchet et al., 1997), and, as they age, female offspring have a later age of primiparity and male offspring have smaller horns (Jorgenson et al., 1993b) than offspring born at low density. Lambs born at low density likely have higher lifetime reproductive success than lambs born at high density and therefore should be more valuable to their mothers. Bighorn sheep populations can vary considerably in density over a few years because of disease or predation (Ross et al., 1997; Wehausen, 1996; Wehausen et al., 1987); therefore, a ewe could face very different population densities over her life span. If short-term density fluctuations were a characteristic of bighorn sheep populations during their evolution, we would expect ewes to have been selected

to vary maternal expenditure in response to different levels of population density, as suggested by our results.

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REFERENCES

- Albon SD, Mitchell B, Staines BW, 1983. Fertility and body weight in female red deer: a density-dependent relationship. *J Anim Ecol* 52:969-980.
- Arnomb T, Fedak MA, Boyd IL, 1997. Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology* 78:471-483.
- Berger J, 1979. Weaning conflict in desert and mountain bighorn sheep (*Ovis canadensis*): an ecological interpretation. *Z Tierpsychol* 50:188-200.
- Bernardo J, 1996. Maternal effects in animal ecology. *Am Zool* 36:83-105.
- Bérubé CH, 1997. Les stratégies d'adaptation vitale chez les brebis du mouflon d'Amérique (*Ovis canadensis*): la reproduction en fonction de l'âge (PhD dissertation). Sherbrooke, Canada: Université de Sherbrooke.
- Bérubé CH, Festa-Bianchet M, Jorgenson JT, 1996. Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. *Behav Ecol* 7: 60-68.
- Byers JA, Hogg JT, 1995. Environmental effects on prenatal growth rate in pronghorn and bighorn: further evidence for energy constraint on sex-biased maternal expenditure. *Behav Ecol* 6:451-457.
- Cameron RD, Hoef JMV, 1994. Predicting parturition rate of caribou from autumn body mass. *J Wildl Manage* 58:674-679.
- Clutton-Brock TH, 1991. The evolution of parental care. Princeton, New Jersey: Princeton University Press.
- Clutton-Brock TH, Albon SD, Guinness FE, 1987. Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. *J Anim Ecol* 56:857-871.
- Clutton-Brock TH, Major M, Albon SD, Guinness FE, 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *J Anim Ecol* 56:53-64.
- Clutton-Brock TH, Price OF, Albon SD, Jewell PA, 1992. Early development and population fluctuations in Soay sheep. *J Anim Ecol* 61:381-396.
- Clutton-Brock TH, Stevenson IR, Marrow P, MacColl AD, Houston AI, McNamara JM, 1996. Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. *J Anim Ecol* 65:675-689.
- Dobson FS, Michener GR, 1995. Maternal traits and reproduction in Richardson's ground squirrels. *Ecology* 76:851-862.
- Douglas CL, Leslie DM, 1986. Influence of weather and density on lamb survival of desert mountain sheep. *J Wildl Manage* 50:153-156.
- Festa-Bianchet M, 1986. Site fidelity and seasonal range use by bighorn rams. *Can J Zool* 64:2126-2132.
- Festa-Bianchet M, 1988a. Age-specific reproduction of bighorn ewes in Alberta, Canada. *J Mammal* 69:157-160.
- Festa-Bianchet M, 1988b. Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate and sex. *Anim Behav* 36: 1445-1454.
- Festa-Bianchet M, Jorgenson JT, Bérubé CH, Portier C, Wishart WD, 1997. Body mass and survival of bighorn sheep. *Can J Zool* 75:1372-1379.
- Festa-Bianchet M, Jorgenson JT, King WJ, Smith KG, Wishart WD, 1996. The development of sexual dimorphism: seasonal and lifetime mass changes of bighorn sheep. *Can J Zool* 74:330-342.
- Festa-Bianchet M, Jorgenson JT, Lucherini M, Wishart WD, 1995. Life-history consequences of variation in age of primiparity in bighorn ewes. *Ecology* 76:871-881.
- Festa-Bianchet M, Jorgenson JT, Wishart WD, 1994. Early weaning in bighorn sheep, *Ovis canadensis*, affects growth of males but not of females. *Behav Ecol* 6:21-27.
- Fowler CW, 1987. A review of density dependence in populations of large mammals. In: Current mammalogy (Genoways HH, ed), New York: Plenum Press; 401-441.
- Geist V, 1971. Mountain sheep. Chicago: University of Chicago Press.
- Hogg JT, Hass CC, Jenni DA, 1992. Sex-biased maternal expenditure in Rocky Mountain bighorn sheep. *Behav Ecol Sociobiol* 31:243-251.
- Horejci BL, 1976. Suckling and feeding behavior in relation to lamb survival in bighorn sheep (*Ovis canadensis canadensis* Shaw) (PhD dissertation). Calgary, Canada: University of Calgary.
- Hudson RJ, Adamczewski Z, 1990. Effect of supplementing summer ranges on lactation and growth of wapiti (*Cervus elaphus*). *Can J Anim Sci* 70:551-560.
- Illius AW, Albon SD, Pemberton J, Gordon IJ, Clutton-Brock TH, 1995. Selection for foraging efficiency during a population crash in Soay sheep. *J Anim Ecol* 64:481-492.
- Iverson SJ, Bowen WD, Boness DJ, Oftedal OT, 1993. The effects of maternal size and milk energy output on pup growth in grey seals (*Halichoerus grypus*). *Physiol Zool* 66:61-88.
- Jorgenson JT, Festa-Bianchet M, Gaillard J-M, Wishart WD, 1997. Effects of age, sex, disease and density on survival of bighorn sheep. *Ecology* 78:1019-1032.
- Jorgenson JT, Festa-Bianchet M, Lucherini M, Wishart WD, 1993a. Effects of body size, population density and maternal characteristics on age of first reproduction in bighorn ewes. *Can J Zool* 71:2509-2517.
- Jorgenson JT, Festa-Bianchet M, Wishart WD, 1993b. Harvesting bighorn ewes: consequences for population size and trophy ram production. *J Wildl Manage* 57:429-435.
- Kojola I, 1993. Early maternal investment and growth in reindeer. *Can J Zool* 71:753-758.
- L'Heureux N, Lucherini M, Festa-Bianchet M, Jorgenson JT, 1995. Density-dependent mother-yearling association in bighorn sheep. *Anim Behav* 49:901-910.
- Lavigueur L, Barrette C, 1992. Suckling, weaning, and growth in captive woodland caribou. *Can J Zool* 70:1753-1766.
- Machlis L, Dodd PWD, Fentress JC, 1985. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. *Z Tierpsychol* 68:201-214.
- Moorcroft PR, Albon SD, Pemberton JM, Stevenson IR, Clutton-Brock TH, 1996. Density-dependent selection in a fluctuating ungulate population. *Proc R Soc Lond B* 263:31-38.
- Owen-Smith N, 1990. Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. *J Anim Ecol* 59:893-913.
- Rachlow JL, Bowyer RT, 1994. Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy? *J Mammal* 75:328-337.
- Robbins CT, 1993. Wildlife feeding and nutrition. San Diego, California: Academic Press.
- Robertson A, Hiraiwa-Hasegawa M, Albon SD, Clutton-Brock TH, 1992. Early growth and sucking behaviour of Soay sheep in a fluctuating population. *J Zool* 227:661-671.
- Ross PI, Jalkotzy MC, Festa-Bianchet M, 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. *Can J Zool* 75:771-775.
- Smith WP, 1987. Maternal defense in Columbian white-tailed deer: when is it worth it? *Am Nat* 130:310-316.
- SPSS, 1994. SPSS 6.1 Macintosh version. Chicago, Illinois: SPSS Inc.
- Trexler JC, Travis J, 1993. Nontraditional regression analyses. *Ecology* 74: 1629-1637.
- Trillmich F, 1990. The behavioral ecology of maternal effort in fur seals and sea lions. *Behaviour* 114:3-20.
- Wehausen JD, 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. *Wildl Soc Bull* 24:471-479.
- Wehausen JD, Bloish VC, Blong B, Russi TL, 1987. Recruitment dynamics in a southern California mountain sheep population. *J Wildl Manage* 51:86-98.
- White GC, Carrott RA, Bartmann RM, Carpenter LH, Alldredge AW, 1987. Survival of mule deer in northwest Colorado. *J Wildl Manage* 51:852-859.