

# Early development, adult mass, and reproductive success in bighorn sheep

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Despite considerable empirical and theoretical work on the individual and population consequences of early development, little is known about the correlations between early mass and adult size or lifetime reproductive success of free-ranging mammals. Using a 26-year study of bighorn sheep (*Ovis canadensis*), we examined how mass as a lamb and mass gain as a yearling affected adult mass for both sexes, horn length of males and lifetime reproductive success of females at different population densities. Mass as a 3-week-old lamb was either weakly or not correlated with adult mass, horn length of adult males, or the number of lambs weaned over a ewe's lifetime. Weaning mass was correlated with most of these variables when the number of ewes in the population was taken into account. When weaning mass was controlled through partial correlation, mass as a yearling was correlated with adult mass of ewes but not with ewe reproductive success or with adult mass or horn length of rams. Lamb mass and number of ewes explained more of the variance in adult characteristics for males than for females. Our results suggest that mass gain during lactation, possibly but not necessarily related to the amount of maternal care received, affects adult mass and reproductive success. Females appear better able than males to compensate for poor early development, likely by postponing their first reproduction. Mass gain over several years and the number of ewes in the population strongly affect adult mass of both sexes and therefore can have profound effects on reproductive success of this long-lived species with a multi-year growth period. *Key words*: maternal expenditure, maternal effects, early development, population density, *Ovis canadensis*, bighorn sheep, lifetime reproduction, body mass, horn size. [*Behav Ecol* 11:633–639 (2000)]

Early development is thought to play a key role in affecting individual reproductive success and population ecology of mammals. In ungulates, cohort variations in birth mass or juvenile growth affect life-history traits and population dynamics (Clutton-Brock et al., 1987, 1992; Post et al., 1997; Rose et al., 1998). Sæther (1997) suggested that variables affecting early development could affect the reproductive performance of different cohorts, regardless of whether or not they were density-dependent. Lindström (1999) found pervasive effects of early development on life-history and population dynamics of birds and mammals.

Despite the apparent importance of early development, most studies of mammals have been limited to making comparisons among cohorts: little is known about the consequences of early development for adult mass and reproductive success of individuals. Large mammals are difficult to capture, and it is unusual for researchers to weigh individuals repeatedly. Most published information compares early mass to mass as an older juvenile or as a very young adult. For 13 captive white-tailed deer (*Odocoileus virginianus*) males, Schultz and Johnson (1995) found a strong correlation ( $r = .81$ ) between birth mass and mass at 2.5 years of age, while Birgersson and Ekvall (1997) found that weaning mass of captive fallow deer (*Dama dama*) was correlated ( $r \geq .72$ ) with mass at 23 months of age. A correlation between birth mass and first-winter mass ( $r \geq .72$ ) was also reported by Pélabon (1997) for captive fallow deer. Captivity, however, removes many environmental sources of variation in growth, and the effects of early devel-

opment on adult mass for captive animals may differ from those for wild animals. For wild roe deer (*Capreolus capreolus*) in a population with abundant resources, there was no correlation between birth mass and first-winter mass (Gaillard et al., 1993). In feral sheep, birth mass only explained 8% of the variance in mass at 16 months, and 14% at 28 months (Clutton-Brock et al., 1992). For 11 red deer (*Cervus elaphus*) females, Clutton-Brock et al. (1988) found a correlation of birth and adult mass ( $r = .62$ ), but adult mass was not adjusted for either season or age. Birth mass is often used as an index of early development (Byers and Hogg, 1995; Clutton-Brock et al., 1992; Fairbanks, 1993; Smith et al., 1997), but it does not account for differences in postnatal maternal care and environmental effects. The frequent use of birth mass may be due more to its availability than to its suitability as an index of early development.

Correlations between early development and adult size and reproductive success are particularly relevant to the study of maternal investment. It is generally assumed, but seldom quantified, that differences in maternal expenditure that affect early development also have long-term effects on offspring fitness (Clutton-Brock, 1991). Clearly, the strength of the relationship between early development and lifetime reproductive success has a major effect on the cost-benefit trade-offs of alternative strategies of maternal investment. For example, the theory of parent-offspring conflict (Trivers, 1974) assumes that an increase in maternal investment will increase offspring fitness. For mammals, this theory must assume a correlation between size or condition at weaning and lifetime reproductive success. A similar assumption is fundamental to theories of adaptive sex-ratio variation (Trivers and Willard, 1973).

Here we use long-term data on bighorn sheep (*Ovis canadensis*) to investigate correlations between early development and adult mass. Because most of our study animals were re-

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captured every year, we could compare mass for the same individual at different ages. We also investigated the effects of early development on lifetime reproductive success. For females, we used the number of lambs weaned during lifetime. Because we had no data on paternity, for rams we used horn length at five years of age as an indirect measure of reproduction, assuming that horn size was correlated with reproductive success (Geist, 1971). Because we suspected that population density affected individual development, we included in our analyses the number of adult ewes in the population in the year of birth. We addressed three specific questions: (1) Is mass during early development correlated with adult mass and other fitness-related adult traits? (2) Do these correlations vary with the stage of early development when mass is measured? (3) Do these relationships differ according to sex?

## METHODS

### Study area and population

The study population inhabits Ram Mountain, Alberta, Canada (52°N, 115°W, elevation 1080 to 2170 m). Data used in this article were collected from 1973 to 1998. Sheep were captured in a corral trap from late May to early October and weighed to the nearest 250 g with a Detecto spring scale. Adjustments in body mass of adult ewes, rams aged 2 or 3 years, and lambs and yearlings of both sexes were made using each individual's own rate of mass gain, determined through repeated captures. Most rams 4 years of age and older were only caught from late May to July, and many were only caught once a year. For rams 4 years of age and older, therefore, mass was only adjusted to 5 June using age-specific linear regressions of mass on capture date for all rams combined.

We adjusted mass of individual lambs to 15 June and to 15 September. By 15 June, most lambs are about 3 weeks old (Festa-Bianchet, 1988a), therefore we refer to them as "3-week-old lambs." We chose 15 June because few lambs were weighed before the first week in June. September 15 corresponds approximately to weaning (Festa-Bianchet, 1988b), therefore we refer to this age group as "weaned lambs." Experimental weaning in early September did not affect yearling mass for females and had a moderate (7–8% mass reduction) effect for males (Festa-Bianchet et al., 1994). It is therefore likely that by 15 September lactation is almost over. For yearlings of both sexes, adult ewes and young rams, we adjusted mass to 5 June and to 15 September. More details about mass adjustment procedures are reported elsewhere (Festa-Bianchet et al., 1996). We measured horn length of all sheep captured. Here we limited our analyses to horn length of 5-year-old males. We chose that age as a compromise between assessing the effects of early development on horn size of full-grown rams [aged eight years and older (Jorgenson et al., 1998)] and the strong age-related decrease in sample size, as adult rams are subject to high natural and hunting mortality (Jorgenson et al., 1993b; Loison et al., 1999). We used the length of the longer horn for each ram, adjusted to 5 June through linear regression using the slope of horn length on capture date for all five-year-old rams from 24 May to 15 July. We measured lifetime reproductive success of ewes as the number of lambs weaned, including only ewes born before 1987 that died of natural causes and a 13-year-old ewe still alive in September 1999.

At first capture, lambs received numbered Ketchum metal ear tags that held a colored strip of Safeflag plastic. As yearlings, males received color-coded Allflex ear tags, females were fitted with canvas or plastic collars with unique patterns.

From 1973 to 1981, ewe removals maintained the popula-

tion at an average of 34 adult ewes (Jorgenson et al., 1993b). After 1981, the population increased, peaking at 104 ewes in 1992 and declining to 75 ewes in 1997, when a further 11 adult and 3 yearling ewes were removed. Density-dependence was evident through delayed primiparity (Jorgenson et al., 1993a), decreased lamb survival (Portier et al., 1998) and lower mass gain and horn growth for young sheep (Festa-Bianchet and Jorgenson, 1998; Jorgenson et al., 1998).

### Data analyses

As in previous publications (Festa-Bianchet and Jorgenson, 1998), we measured population density as the number of adult ewes in June in the year of birth. Substituting the average number of ewes during the first 3 years of life led to very similar results to those reported here. We previously reported that the number of rams in the population did not affect horn development of rams (Jorgenson et al., 1998) possibly because much horn growth occurs before young rams leave the ewe groups at 2–4 years of age (Festa-Bianchet, 1991). The number of adult ewes is therefore a better measure of population density than the number of rams. All bighorn habitat on Ram Mountain was utilized at all levels of population size, therefore population size and density are equivalent.

We used backward stepwise multiple regressions and partial correlations to assess the relationships between early mass and adult mass, horn length and lifetime reproductive success. For adult ewes, adult mass was the average mass adjusted to 15 September at 5 to 7 years of age (Festa-Bianchet et al., 1996). For adult rams, we used the average mass at 4 and 5 years of age, adjusted to 5 June. We could not use the same measure of adult mass for both sexes for two reasons. First, very few males aged 4 years and older were caught after July, therefore we could not adjust the mass of rams to mid-September. Second, high male mortality led to a small sample of rams older than 6 years. The measure we used for ewes (average mid-September mass at 5 to 7 years of age) was probably a better indicator of adult mass than the measure we used for rams (average early-June mass at 4 and 5 years of age), because mass in September is less affected than mass in June by year-to-year changes in weather (Festa-Bianchet et al., 1996; Réale et al., 1999). For both sexes, we found results similar to those reported here when we repeated univariate analyses for body mass at each age from 3 to 6 years for males and from 3 to 8 years for females. We excluded male lambs orphaned during the early years of the study, because orphaning had a weak but significant effect on their development (Festa-Bianchet et al., 1994). We include orphans, however, in the comparison of adult mass and horn length with mass gain as a yearling, because we were interested in any factors (maternal and environmental) that may have caused variation in postweaning mass gain. Statistical analyses were performed using SPSS for the Macintosh (SPSS, 1994).

## RESULTS

### Mass as a 3-week-old lamb

Multiple regressions including the number of adult ewes suggested that mass as a 3-week-old lamb had a weak, positive, and density-dependent effect on adult mass of both ewes and rams. Mass as a 3-week-old lamb was not correlated with ewe lifetime reproductive success and had a weak positive effect on horn length of adult rams through its interaction with number of ewes (see Table 1).

### Weaning mass and mass gain as a yearling

Mass at weaning affected adult mass of sheep of both sexes, reproductive success of ewes and horn length of rams (see

**Table 1**

**Multiple regressions comparing mass as a 3-week-old lamb and number of ewes in the year of birth to mass as an adult, horn length for rams at 5 years of age and lifetime reproductive success for ewes**

Variable	Slope ( <i>b</i> )	<i>p</i>	Partial <i>r</i>
Adult mass of ewes: $R^2 = .170$ ; $F_{2,37} = 3.794$ ; $p = .032$			
Number of ewes	-0.104	.009	-.41
Lamb mass * number of ewes	0.008	.056	.31
Rejected term			
Lamb mass at 3 weeks, $p = .35$			
Adult mass of rams: $R^2 = .750$ ; $F_{2,18} = 27.045$ ; $p < .0001$			
Number of ewes	-0.429	.000	-.87
Lamb mass * number of ewes	0.012	.051	.55
Rejected term			
Lamb mass at 3 weeks, $p = .90$			
Ewe lifetime reproductive success ( $n = 30$ )			
Rejected terms			
Number of ewes, $p = .95$			
Lamb mass at 3 weeks, $p = .81$			
Lamb mass * number of ewes, $p = .89$			
Horn length of rams at 5 years of age: $R^2 = .708$ ; $F_{2,24} = 29.13$ ; $p < .0001$			
Number of ewes	-0.355	.000	-.83
Lamb mass * number of ewes	0.007	.059	.38
Rejected term			
Lamb mass at 3 weeks, $p = .13$			

Data are from the Ram Mountain bighorn sheep population, 1972 to 1998, and exclude orphan males. Adult mass for ewes is the average mass on 15 September at ages 5 through 7; adult mass for rams is the average mass on 5 June at ages 4 and 5. We used the backward stepwise multiple regression procedure and included in the final models all variables with  $p < .10$ . See text for further explanations.

Table 2, Figures 1 and 2). The number of adult ewes had negative effects on the same variables. The interaction of weaning mass and number of ewes was negative when retained in models including weaning mass as a main effect, and positive in models including number of ewes as a main effect (see Table 2), because density had a negative effect on the dependent variables, while weaning mass had a positive effect. For the sample of lambs included in the analyses, the number of ewes was not correlated with weaning mass (males:  $r = -.25$ ,  $n = 21$ ,  $p = .28$ ; females:  $r = .03$ ,  $n = 40$ ,  $p = .83$ ).

Yearlings were captured more frequently than lambs, therefore a mass estimate for mid-September (that normally requires at least two captures; see Festa-Bianchet et al., 1996) was available for almost all yearling sheep. When we repeated the analyses reported in Table 2 using mass as a yearling on 15 September, we found very similar results. Weaning mass and mass as a yearling, however, are not independent (females:  $r = .47$ ,  $n = 62$ ,  $p < .001$ ; males:  $r = .69$ ,  $n = 60$ ,  $p < .001$ ; test for equality of correlation coefficients,  $t = 1.82$ ,  $0.1 > p > .05$ ), therefore correlations of yearling mass and adult characteristics may be simply an inevitable consequence of their correlation with weaning mass. To test whether mass gain as a yearling had in itself any effects on adult mass and reproductive success, we used the residuals of the regression of yearling mass on weaning mass. For females, those residuals were correlated with adult mass ( $r = .43$ ,  $n = 33$ ,  $p = .015$ ), but not with lifetime reproductive success ( $r = .27$ ,  $n = 21$ ,  $p = .24$ ). In both cases, adding the effects of population size at birth within a multiple regression did not change the results as population size did not have a significant effect. For males, however, the residuals of the regression of yearling mass on weaning mass were not correlated with either adult mass ( $r = .23$ ,  $n = 20$ ,  $p = .35$ ) or with horn length at 5 years ( $r = .22$ ,  $n = 25$ ,  $p = .31$ ).

### Sex differences

Because of differences in capture timing and frequency, we could not use the same measure of adult body mass for both sexes. However, the results of multiple regressions including the effects of the number of ewes (see Tables 1 and 2) suggest that the explanatory power of mass as a 3-week-old lamb and at weaning was much greater for males (coefficients of multiple determinations of 0.75) than for females (coefficients of determinations of 0.17 and 0.18), despite the fact that post-weaning mass gain (relatively and absolutely) is greater for rams than for ewes (Festa-Bianchet et al., 1996).

### DISCUSSION

Mass during early development is correlated with adult mass and reproductive success in bighorn sheep. The strength of the correlations between early development and adult mass increased as "early development" was measured at a later age, and lamb mass appeared to be a better predictor of ram adult mass and horn size of males than of ewe adult mass.

Mass as a 3-week-old lamb (on 15 June most lambs are between 15 and 25 days old) had a marginally significant effect on ewe adult mass through its interaction with the number of ewes in the population (see Table 1), suggesting an increasingly positive effect of mass as a 3-week-old lamb on adult mass as population size increased. Our data do not suggest that mass at 3 weeks of age affects ewe reproductive success. Mass as a 3-week-old lamb also affected adult mass and horn length of males through its interaction with population density (see Table 1). Both adult mass and horn length are likely correlated with reproductive success in bighorn rams (Geist, 1971), therefore it is possible that mass as a 3-week-old lamb plays a small role in affecting reproductive success of males.

Table 2

Multiple regressions comparing weaning mass and number of ewes in the year of birth to mass as an adult, horn length for rams at 5 years of age and lifetime reproductive success for ewes

Variable	Slope ( <i>b</i> )	<i>p</i>	Partial <i>r</i>
Adult mass of ewes: $R^2 = .185$ ; $F_{1,39} = 8.825$ ; $p = .0051$			
Lamb weaning mass	0.418	.005	
Rejected terms			
Number of ewes, $p = .19$			
Lamb mass * number of ewes, $p = .14$			
Adult mass of rams: $R^2 = .748$ ; $F_{2,19} = 28.226$ ; $p < .0001$			
Lamb weaning mass	1.161	.000	.81
Lamb mass * number of ewes	-0.010	.000	-.83
Rejected term			
Number of ewes, $p = .53$			
Ewe lifetime reproductive success: $R^2 = .307$ ; $F_{2,24} = 5.319$ ; $p = .012$			
Number of ewes	-0.385	.003	.52
Lamb mass * number of ewes	0.009	.006	-.55
Rejected term			
Lamb weaning mass, $p = .25$			
Horn length of rams at 5 years of age: $R^2 = .719$ ; $F_{2,24} = 30.768$ ; $p < .0001$			
Lamb weaning mass	0.491	.009	.50
Number of ewes	-0.277	.000	-.81
Rejected term			
Lamb mass * number of ewes, $p = .93$			

Data are from the Ram Mountain bighorn sheep population, 1972 to 1998 and exclude orphan males. Adult mass for ewes is the average mass on 15 September at ages 5 through 7; adult mass for rams is the average mass on 5 June at ages 4 and 5. See text for further explanations.

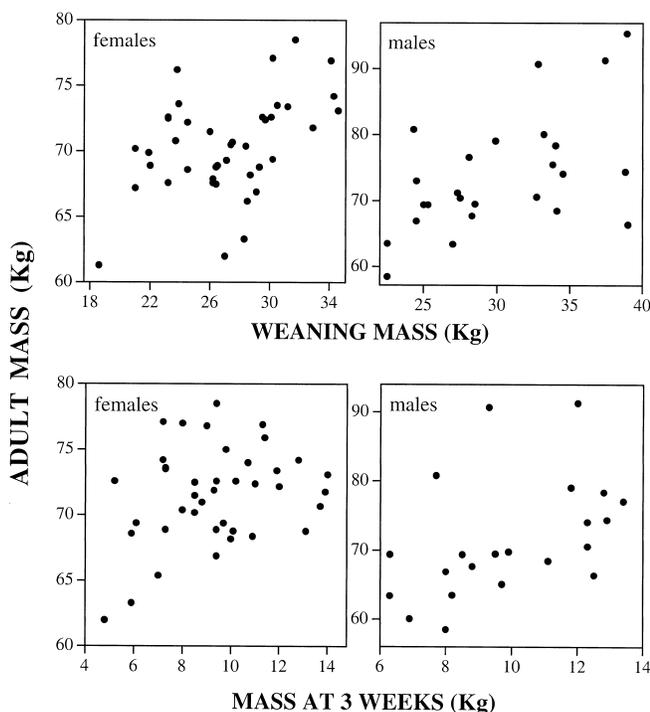
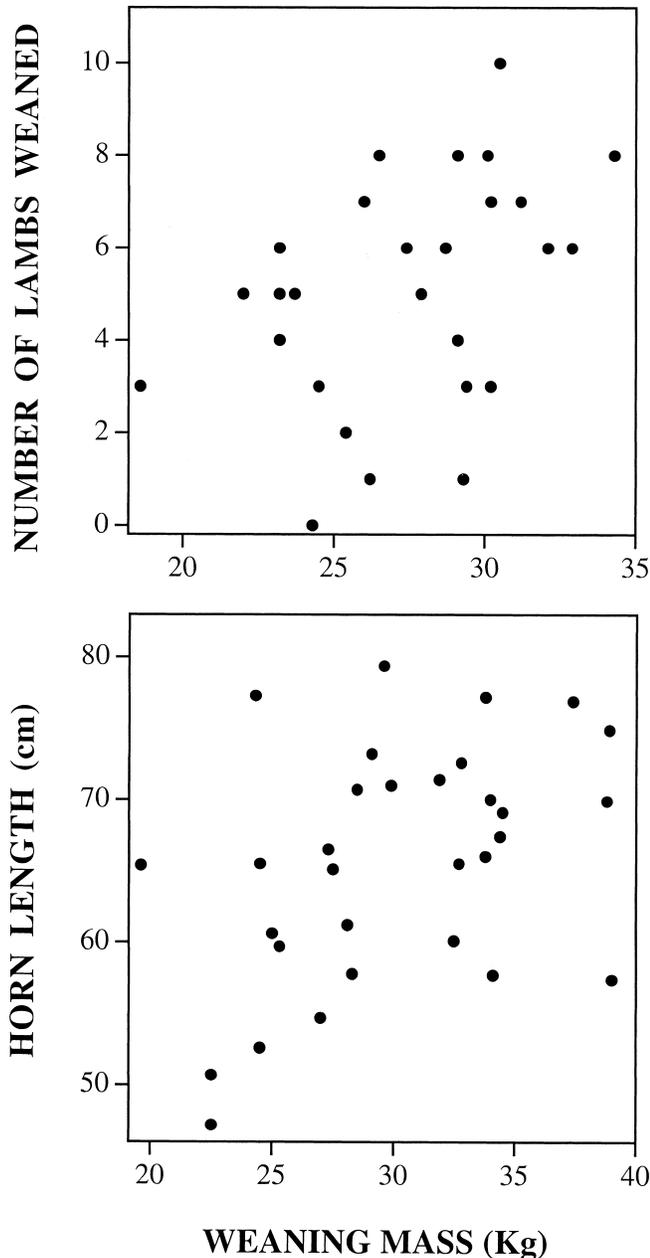


Figure 1

Correlations between mass at about 3 weeks of age (lamb mass adjusted to 15 June), weaning mass (mass adjusted to 15 September) and adult mass (average mass on 15 September at 5 to 7 years of age for ewes; average mass on 5 June at 4 and 5 years of age for rams) for bighorn sheep at Ram Mountain, Alberta, in 1972–1998.

Mass at 3 weeks of age is presumably affected by a combination of prenatal and early postnatal maternal care, because at that age lambs are entirely dependent on milk (Festa-Bianchet, 1988b). At 3 weeks of age, lambs are about one-third their weaning mass, therefore the measurement error (assuming that our error in reading the scale was independent of sheep mass) is proportionately greater for lambs at 3 weeks than at weaning. In addition, age differences of a few days may have a greater effect on lamb mass at 3 weeks of age than at weaning. Compared to other ungulates, bighorn sheep produce relatively small neonates (Byers and Hogg, 1995), and bighorns appear to have a very conservative maternal investment strategy, postponing primiparity (Jorgenson et al., 1993a) and decreasing maternal effort in response to increasing population density (Festa-Bianchet and Jorgenson, 1998). The results presented here show that the low level of maternal care provided by some ewes may have a negative effect on offspring fitness, because larger lambs tend to become larger adults with high reproductive success. For both sexes, lamb mass at weaning had a stronger effect on subsequent development than mass at 3 weeks of age. Therefore, our data suggest that bighorn sheep may experience parent-offspring conflict: increased maternal investment leads to a fitness cost by reducing fecundity the following year (Festa-Bianchet et al., 1998) but it may also increase offspring fitness because larger lambs at weaning tend to develop into larger adults. Large adult ewes have a longer life expectancy (Bérubé et al., 1999) and experience lower costs of reproduction (Festa-Bianchet et al., 1998). Ewes curtail maternal care at high density, a tactic that allows them to maintain high survival and high summer mass gain regardless of population density, but leads to small lambs with low viability at high population density (Festa-Bianchet et al., 1998; Festa-Bianchet and Jorgenson, 1998; Jorgenson et al., 1997). Parent-offspring conflict in bighorn sheep is likely more intense at high than at low population density, and likely more intense for sons than for daughters, as we previously speculated (Festa-Bianchet et al., 1994).



**Figure 2**  
Correlations between weaning mass and lifetime number of weaned lambs for ewes, and horn length at 5 years of age for rams, for bighorn sheep at Ram Mountain, Alberta, 1972–1998.

Our results give a limited picture of the total fitness effects of early development because our analysis was restricted to individuals that survived to adult age. We have reported elsewhere (Festa-Bianchet et al., 1997) that mass at weaning affects lamb survival to one year of age, and that the effects of weaning mass on overwinter survival increase with population density, similarly to results for feral domestic sheep (Milner et al., 1999). Therefore the effects of the density-dependent reduction of maternal care in bighorn sheep include lower survival of lighter lambs, in addition to the possible impacts on adult mass and reproductive success reported here.

Bighorn sheep have a complex pattern of mass changes: both sexes gain mass until at least 7 years of age, and individuals gain 20–35% of their late-winter mass each summer then

lose most of that mass during the following winter (Festa-Bianchet et al., 1996). At weaning, females have achieved about 40% of their adult mass, but males less than 30%; one year later, the corresponding figures are 70% for females and 50% for males. Therefore, during their development individuals could compensate for poor early mass gain, but may also experience events that negatively affect their growth, such as harsh weather, low resource availability due to high population density, injuries, parasites, and diseases (L'Heureux et al., 1996).

Males are more strongly affected by early development than females. When the number of ewes in the population was included in multiple regressions, the multiple coefficients of determination obtained for rams were generally more than twice those obtained for ewes (see Tables 1 and 2). Indeed, our results suggest that over 70% of the variance in adult male mass and horn length is explained by population density in the year of birth and by weaning mass, while less than 20% of the variance in adult ewe mass is explained by the same variables. These results may at first appear counterintuitive, given that postweaning growth is much greater for rams than for ewes (Festa-Bianchet et al., 1996), and therefore the potential for compensatory growth should also be greater for rams. Differences in plasticity of resource allocation between growth and reproduction, however, potentially explain this paradox. By varying their age of primiparity, females can allocate resources to growth or to reproduction, and affect their mass gain between 2 and 4 years of age (Jorgenson et al., 1993a). Males, however, cannot redirect resources to growth from reproduction, even though young bighorn rams can reproduce (Hogg and Forbes, 1997). Energy expenditure during the early-winter rut likely affects the timing of consumption of fat reserves and possibly over-winter survival, but is unlikely to affect skeletal growth and mass accumulation over the following summer. Therefore, young females have greater flexibility than young males in redistributing resources between somatic growth and reproduction. Compensatory growth would weaken correlations between mass during early development and adult mass, and the potential for compensation appeared stronger in ewes than in rams. Rams are likely selected always to gain as much mass as possible, because large adult males may enjoy high reproductive success (Hogg, 1988). Rams that are small early in life appear generally unable to compensate for their initial disadvantage by increasing their growth rate later on. This conclusion is strengthened by our analysis of the residual effects of yearling mass on adult mass: For rams, it appeared that individual differences in mass accumulation during the first year after weaning had little or no effect on fitness. For young ewes, on the other hand, individual differences in mass accumulation as yearlings had a significant effect on adult mass and suggested a compensatory pattern of mass gain. Similar results were reported for Alpine ibex (*Capra ibex*), where females but not males were able to compensate for poor horn growth in their first year (Toïgo et al., 1999).

Because we found that weaning mass affected fitness-related adult characteristics, a possible interpretation of our results is that variations in the level of maternal care affect offspring fitness. If that interpretation is correct, females that curtail maternal care when resources are scarce (Festa-Bianchet and Jorgenson, 1998) would suffer a fitness cost through reduced offspring survival or lowered quality of surviving offspring. That cost would presumably be compensated by an increase in the ewe's survival and future reproductive potential. Theories of sex-differential maternal investment have been concerned with whether additional investment leads to different fitness returns according to offspring sex (Clutton-Brock et al., 1986, 1991). The apparent absence of postweaning com-

pensatory growth for males suggests that a reduced level of maternal care should have a greater impact on the fitness of sons than of daughters. One could then predict that the density-dependent decrease in maternal care seen in this population would have a stronger effect on young males than on young females, yet yearling survival was density-dependent for females but not for males (Jorgenson et al., 1997) and we have no evidence of sex-differential effects of density on lamb survival (Festa-Bianchet et al., 1997).

The assumption that a correlation between early development and adult fitness traits is due to differences in maternal expenditure, however, remains untested. A positive phenotypic correlation between early mass and adult traits could arise in the absence of maternal effects on adult traits. Phenotypic correlations of mass at different ages could be due to pleiotropic genes that influence both traits (Falconer and Mackay, 1996). For instance, individuals that are genetically large early in life also tend to be genetically large later in life (Cheverud et al., 1983). To quantify the effects of maternal care on adult characteristics, other factors that affect the relation between early development and adult size must be accounted for. Cross-fostering experiments are a potential solution (Lindström, 1999), but they are impractical or impossible with most wild mammals. Another alternative is a quantitative genetic analysis based on pedigrees. Because fathers were unknown in the Ram Mountain population, however, we could not estimate maternal effects on the phenotypic correlation between early mass and adult traits. Although maternal effects can have important consequences on offspring fitness, little is known about the persistence of maternal effects over an offspring's lifetime. Generally, maternal effects have a strong effect on offspring early traits, but their influence decreases with offspring age and may become negligible for adult traits (Cheverud, 1984; Wolf et al., 1998). Previous studies of the Ram Mountain population suggest that small mothers may compensate for potentially negative genetic effects on lamb mass by increasing maternal expenditure, because the phenotypic relationship between maternal mass and lamb mass is very weak (Festa-Bianchet and Jorgenson, 1998; Réale et al., 1999). Maternal expenditure likely affects pre-weaning development and survival, but lamb survival from weaning to one year was unrelated to maternal mass while increasing with weaning mass (Festa-Bianchet et al., 1997, 1998). In the study population, more than 50% of the variability in adult mass appears due to additive genetic variance (Réale et al., 1999), therefore it would not be surprising if only a small part of the variance in adult mass was caused by differences in maternal expenditure.

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