

Early weaning in bighorn sheep, *Ovis canadensis*, affects growth of males but not of females

Theories of parental investment and parent-offspring conflict assume that investment involves a cost to the parent and a benefit to the offspring, but for herbivorous mammals, behavioral and nutritional weaning are gradual processes that are difficult to define, and little is known about the consequences of individual variation during weaning. To study the effects of late maternal care on offspring fitness, we removed female bighorn sheep (*Ovis canadensis*) from a marked population in Alberta, Canada, and monitored the survival, growth, and reproductive success of orphan and nonorphan lambs. Mothers were removed when lambs were 3.5–4.0 months, about 2–4 weeks before the suspected time of nutritional weaning. Female orphans and nonorphans had the same weight as yearlings, the same probability of producing their first lamb at 2 years of age, the same lifetime reproductive success (lambs produced or lambs that survived to early autumn), and the same longevity. Male orphans from most cohorts were smaller as yearlings compared to nonorphans from the same cohort. They were unable to compensate for this early weight difference in later life: at 4 years, orphan males had smaller horns and were lighter than nonorphans. Small horn and body size likely lowered the reproductive success of orphaned males compared to nonorphans from the same cohort. We suggest that in this sexually dimorphic species late maternal care is more important for males than for females. Because late maternal care had no measurable benefit for daughters, we suggest that parent-offspring conflict over the duration of maternal care may not exist for mother-daughter pairs. For mother-son pairs it remains to be shown whether late maternal care involves a cost to the mother, but the assumption of a benefit to the son was met. *Key words*: bighorn sheep, maternal care, weaning, sexual dimorphism, orphaning, lactation, reproductive success, body growth, parent-offspring conflict. [*Behav Ecol* 5:21–27 (1994)]

In an influential paper, Trivers (1974) hypothesized that conflict between parents and offspring would arise over the duration of parental investment because the offspring should be selected to demand investment for longer than the parent should be selected to give. This hypothesis rests on two assumptions: that late parental care should increase the offspring's fitness, and that it should impose a fitness cost on the parent, lowering its future ability to reproduce. For most herbivorous mammals, parental (or maternal) care can best be measured by the amount of milk provided to the offspring, although other forms of care are possible. Therefore, parent-offspring conflict in mammals may exist over the timing of weaning (Trivers, 1974), and offspring may continue to demand milk beyond the optimal weaning time for the mother. However, despite all the attention paid to Trivers's model, there have been no experimental investigations of the effects of variation in timing of weaning upon either offspring fitness or subsequent maternal reproductive success for wild mammals. Therefore, neither of the two assumptions of Trivers's hypothesis has been tested.

Weaning is a difficult process to study or even to define (Clutton-Brock and Harvey, 1984; Martin, 1984). It is often unclear when weaning occurs, particularly in species where the transition from reliance upon mother's milk to solid foods is very gradual, such as in ungulates (Berger, 1979; Festa-

Bianchet, 1988b). For example, in bighorn sheep (*Ovis canadensis*), if weaning were defined as the very last suckle, then it would occur when lambs are 7–8 months old, yet suckles are so short and rare (less than 12 s and probably less than once/day) after about 5 months of age that this definition would clearly not reflect the nutritional importance of milk transfer for lambs or its potential costs to the mother. On the other hand, Martin's (1984) definition of weaning as the time of most rapid change in maternal investment is also unsatisfactory. Suckle duration declines most rapidly when lambs are 3–5 weeks old, yet milk is likely to have a nutritional function for at least 3 months after that time, as the proportion of time lambs feed on vegetation increases gradually (Festa-Bianchet, 1988b). Changes in the rate of maternal investment, defined as care that involves a fitness cost to the mother (Clutton-Brock, 1991), have not been measured in any wild mammal during lactation. For the present study, weaning was defined as the time when milk ceased to play a nutritional role for lambs. Even though we could not determine precisely when it occurred, we assumed that weaning occurred after our manipulation of maternal care.

Babbitt and Packard (1990) suggested that in collared peccaries (*Tayassu tajacu*), weaning involved little overt conflict and that most maternal investment (beneficial to the young and costly to the mother) probably occurred by mid-lactation. In

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bighorn sheep, correlations between nursing behavior and maternal condition, as well as offspring survival, were strongest in mid-lactation (Festa-Bianchet, 1988b). Based on these and similar observations for other ungulates (Green, 1990), it may be reasonable to predict that the latter part of lactation in ungulates involves little fitness cost to the mother and little fitness benefit for the offspring. The amount of milk transferred may be negligible, as suggested by the low frequency and short duration of suckles. Occasional nursing may continue to maintain contact between mother and offspring, possibly to protect the latter from predation or intraspecific aggression (Green et al., 1989), or in association with other forms of care such as assistance in social interactions or transmission of information about resources. These forms of care should not be considered maternal investment if they benefit the offspring but do not involve a fitness cost for the mother (Clutton-Brock, 1991).

In some ungulates, lactating females that do not conceive in the following breeding season may continue to nurse their offspring through the winter. Clutton-Brock et al. (1982) suggested that such prolonged nursing in red deer (*Cervus elaphus*) increased calf growth rate and survival. Similarly, Green and Rothstein (1991) reported that bison (*Bison bison*) mothers that did not conceive again weaned their daughters at 17–21 months of age, much later than the 8.5–12 months of age at which daughters were weaned if the mother conceived again. The reproductive success of bison daughters that received such prolonged nursing increased. In both studies, differences in duration of care were due to differences in maternal reproductive status. Mothers that failed to conceive did not simply prolong maternal care within the range seen for mothers that conceived, but doubled its duration. Neither study addressed directly the effects of individual variation in duration of maternal care without the confounding factors of differences in reproductive status.

One way to examine the consequences of late lactation would be to compare time of weaning and some measure of growth or reproductive performance for offspring weaned at different times in the same population. However, such an approach may not produce reliable results because individual differences among mothers may mask the real effects of the time of weaning. An experiment in which weaning is controlled by the researcher, and early- and late-weaned offspring are randomly selected, would be a more powerful test of whether late lactation has any effect on offspring fitness.

Hölzenbein and Marchinton (1992) showed that orphaned male white-tailed deer (*Odocoileus virginianus*) had higher survival than nonorphans, apparently because orphans were less likely to disperse, and dispersal increased the risk of death. In that study, however, lactation was probably over by the time most orphaning took place. Derrickson (1988) artificially weaned litters of white-footed mice (*Peromyscus leucopus*) between 19 and 25 days of lactation in the laboratory and found that early weaning had little effect on pup growth rate. By 42 days of age, the effects of early weaning were non-existent for males, and for females growth was greater for those weaned earlier.

Here we report the results of a long-term ex-

periment involving the removal of lactating bighorn sheep females from a marked population during 9 years, followed by the monitoring of survival, growth, and, for females, reproductive success of orphans and nonorphans over 11 or more years. We have already shown that survival did not differ between orphans and nonorphans of either sex (Jorgenson et al., 1993). In the present experiment we first tested whether late maternal care affected lamb growth and reproduction. Lambs start feeding on vegetation at about 2 weeks of age but continue suckling regularly until they are almost 5 months old, and sporadic suckling continues for 2 or 3 months afterward (Festa-Bianchet, 1988b). Yearling males do not associate with their mothers, and yearling females have only a slight tendency to be in the same group as their mothers (Festa-Bianchet, 1991). Second, we examined whether any effects of orphaning differed between male and female offspring. Adult bighorns are sexually dimorphic. In our study population, the average weight of 7 year olds in June is about 58 kg for females and 96 kg for males (a ratio of about 1.7). The same ratio in yearling sheep is only about 1.1: males weigh about 34 kg and females about 31 kg (Jorgenson and Wishart, 1984). Because access to estrous females depends on male–male combat, body size is likely a more important determinant of reproductive success for males than for females (Geist, 1971), and, similarly to red deer (Clutton-Brock et al., 1988), it is possible that early development of bighorn sheep would have a greater effect on growth and reproduction of males than females. The role of maternal care in affecting the postweaning development of either sex, however, is unknown. Sexual difference in growth and development may alternatively result from differences in foraging behavior (Verme, 1989), rather than from differences in rate or duration of milk delivery.

METHODS

We carried out the study between 1972 and 1992 at Ram Mountain, Alberta, Canada (52° N, 115° W). The study area is a mountainous complex about 30 km east of the main range of the Rocky Mountains, ranging in elevation from 1082 to 2173 m and including approximately 38 km² of alpine and subalpine habitat used by the sheep.

Weather data were collected by Environment Canada about 20 km west of Ram Mountain. We analyzed three weather parameters that we suspected a priori may influence body growth: winter (January–March) temperature and snowfall (measured in mm of water equivalent) and summer (May–August) rain and snow (combined as mm of water equivalent). We reasoned that low winter temperatures and high snowfalls should have a negative effect on body size, whereas summer precipitation should have a positive effect by favoring forage growth. The weather varied considerably between years. For example, average winter temperatures varied from –13.3°C to –1.7°C, and average monthly summer precipitation from 42 mm to 152 mm.

Beginning in 1971, we captured sheep in a corral trap baited with salt and marked them with plastic ear tags or canvas collars for individual identifi-

cation. Since 1976, over 90% of the population has been individually marked each year, and more than 95% has been marked in most years. Sheep born since 1972 were first captured as lambs or yearlings, so we knew their exact ages. We recorded body weight and horn measurements at each capture. Lambs and adult rams were difficult to catch and were typically captured only once or twice each summer, but most ewes and yearlings of both sexes were captured twice or more during each trapping season, between late May and early October.

The study area was easily censused on foot, and sheep were regularly seen at the trap several times each summer. We calculated survival based on the assumption that marked sheep not seen during a summer had died during the previous winter. It was extremely rare for sheep recorded as missing to reappear in a subsequent year (two ewes and five rams, out of approximately 2500 sheep-years).

We removed ewes during the last 3 weeks of September. Removals began in 1972 and ended in 1980, but one lactating ewe died during trapping in September 1981. All orphan and nonorphan comparisons refer to cohorts born between 1972 and 1981. Until 1978, we randomly selected ewes to be removed among those more than 3 years old and shot them. Between 1978 and 1980, we trapped ewes and transplanted them to the main Rocky Mountains range, about 40 km away. Orphaned lambs were between 3.5 and 4 months old.

To compare differences in weight and in weight changes of orphaned and nonorphaned sheep, we compared adjusted weights at three different dates: 15 September (late summer) for lambs and 5 June (late spring) and 5 September (late summer) for yearlings. For each year, we calculated separate linear regressions of weight on date for sheep of each sex and age class, using 25 May as day 0. Repeated captures of the same sheep were excluded when standardized residuals were greater than 2 SD (see Festa-Bianchet, 1988b). We then calculated adjusted weights using the capture of each sheep closest to the desired date, excluding sheep not captured within 50 days of that date. The average time difference between actual weight and adjusted weight was 14 days for yearlings and 30 days for lambs. Growth of lambs was linear during the summer, but after about 15 September the growth of yearlings reached a plateau. The regression of yearling weight on date over the entire summer was quadratic; therefore, we used 5 September for the late-summer weight of yearlings. For those sheep for which we had an adjusted lamb weight on 15 September and as a yearling the following 5 June, we also calculated overwinter weight change, the difference between these two weights. Because trapping success was lower in the first 2 years of the study, we could not include the 1972 and 1973 cohorts in the analysis of yearling body weight.

We analyzed weights with ANOVA using SPSS (Berkeley, CA). For lambs, we checked for differences among orphans and nonorphans to ensure that ewe removals were random with respect to lamb weight at orphaning. For yearlings, we first analyzed both sexes together to see if there was an interaction between orphan status and sex. Later we analyzed differences in weight separately for males and females, with year of birth and orphan status as main effects. We also attempted to include

weather variables as covariates: winter weather for June weight, and winter and summer weather for September weight. Body weights and measurements were normally distributed.

The reproductive success of males could not be measured directly because during the rut the study area is only accessible by helicopter. Body and horn size, however, are likely correlated with reproductive success for males (Geist, 1971). To test whether orphaning in late lactation had an effect on adult body and horn size, we compared orphan and nonorphan males 4 and 5 years old. Rams are hunted and suffer high natural mortality, therefore the sample of rams older than 5 years was very small. Rams must have a minimum horn size to be legally shot, and the largest rams reach that size by 4.5 years of age. Therefore, the sample of 5 year olds available for measurement was biased in favor of small-horned rams, because large ones are at risk of being shot at 4.5 years of age. This bias appeared to favor orphans: Of seven rams shot by hunters at 4.5 years of age, six were nonorphans. All ram captures used for analysis were made between 25 May and 5 July. We used ANOVA with year of birth and orphan status as main effects and capture date as a covariate to test for differences in horn size and body weight of 5-year-old males because date of capture was significantly correlated with body and horn size. For 4 year olds there was no significant correlation between capture date and weight or horn size. Therefore, date was not used as a covariate.

Ewes can produce their first lamb at 2 years of age, but many start to reproduce later. We used a G test to see if the probability of producing a lamb at 2 was the same for orphan and nonorphan ewes. We determined lactation status each year for all marked ewes by examining the udder at capture or by observing the ewe nurse a lamb. We measured ewe reproductive success as the number of lambs produced (i.e., the number of years in which the ewe was lactating) and the number of lambs surviving to late September. The latter variable corresponds closely to the number of lambs weaned (Festa-Bianchet, 1988b). Many ewes born in the first 6 years of the study were removed at ages of 3–6 years and were excluded from analyses of reproductive success beyond 2 years of age. Because some (16 of 49, all more than 11 years old) were still alive at the end of summer 1992, we computed two measures of reproductive success: number of lambs produced or weaned by 11 years of age (including ewes that died of natural causes before that age) and over the lifetime. The latter variable was a minimum estimate of reproductive success for the 16 surviving ewes, which were present in about the same proportion of orphans and nonorphans (3 orphans and 13 nonorphans) as the ewes that had died. Reproductive success and longevity were not normally distributed; therefore, they were compared with Mann-Whitney *U* tests. Data are reported as means \pm SE, and all probability values are two-tailed.

RESULTS

Orphan and nonorphan lambs did not differ in body weight on 15 September (30.4 ± 0.5 kg for 38 orphan and 30.5 ± 0.4 kg for 67 nonorphan

Table 1

Overwinter weight increase (percentage of late summer weight) for orphan and nonorphan bighorn sheep lambs, from 15 September of year 1 to 5 June of year 2, 1975–1981

Sex	Status	N	Weight change (kg)			F ^a	p ^a
			Mean	SD	%		
Male	Orphan	11	1.29	4.67	4.7	2.63	.12
	Nonorphan	21	2.89	2.50	9.4		
Female	Orphan	4	0.45	3.87	3.7	0.93	.35
	Nonorphan	19	2.57	2.58	11.1		
Both	Orphan	15	1.07	4.35	4.4	4.09	.05
	Nonorphan	40	2.74	2.51	10.2		

^a F and p values refer to two-way ANOVA with year effects.

male lambs, 27.8 ± 0.7 kg for 29 orphan and 27.2 ± 0.5 kg for 68 nonorphan female lambs, all $p > .4$). The sample of sheep with information on overwinter weight change was limited by the conservative criteria we set for adjusting weight at common dates. Between 15 September of one year and 5 June of the next year, lambs ($n = 55$) on average gained 2.3 ± 0.4 kg. Nine lambs lost weight during this period. Individual changes varied from a loss of 6.5 kg to a gain of 7.6 kg. There were no differences according to sex (males gained 2.3 ± 0.6 kg, females gained 2.2 ± 0.6 kg; $F_{1,53} = 0.24$, $p = .88$): therefore, the sexes were pooled to examine the effects of orphaning. Orphans gained less weight than nonorphans (Table 1), and there was a year effect ($F_{5,36} = 2.65$, $p = .04$). When the sexes were considered separately, the trend was the same, but the effects of orphaning were not significant for either sex (Table 1).

In early June, when both sexes were considered in an ANOVA that included sex, orphaning, and year effects, orphan status did not have a significant effect on body weight ($F_{1,92} = 2.54$, $p = .11$). Sex had a significant effect ($F_{1,92} = 9.04$, $p = .003$), and there was a significant (sex \times orphan) interaction term ($F_{1,92} = 7.44$, $p = .008$), indicating that males and females differed in both weight and the effects of orphaning. Yearly differences were not significant ($F_{7,92} = 1.71$, $p = .12$). When the sexes were considered separately, we found no effect of orphaning on females, regardless of whether we included year effects as factors or weather variables as covariates. Orphan male yearlings appeared to be smaller than nonorphans, and the weight difference was almost significant ($F_{1,44} = 3.697$, $p = .06$, ANOVA with year effects). The 5 June weight for orphan yearling males was 30.6 kg ($n = 21$), 2.3 kg (or 7%) less than for nonorphans ($n = 41$, $\bar{X} = 32.9$ kg; Figure 1). If we analyzed yearling male weights in June with winter temperature and winter

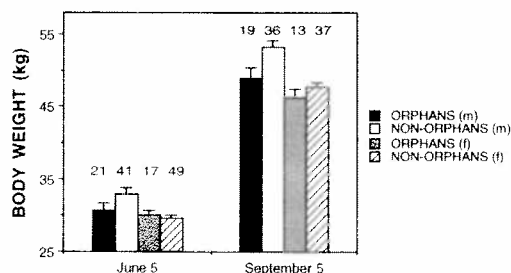
precipitation as covariates, we obtained similar results: weather had no effect ($p > .6$), and orphan status had a nearly significant effect ($p = .09$).

For weight on 5 September, when both sexes were considered in an ANOVA that included sex, orphaning, and year, all factors had significant effects (year: $F_{7,79} = 3.06$, $p = .007$; orphaning: $F_{1,79} = 10.52$, $p = .002$; sex: $F_{1,79} = 27.09$, $p < .001$), and there was a significant (sex \times orphan) interaction ($F_{1,79} = 8.32$, $p = .005$), indicating again a difference in weight between the sexes and a difference in the way orphaning affected males and females. When the sexes were considered separately, orphaning had no effect on weight of yearling females ($p > .7$), which was affected by winter weather (temperature, $F_{1,45} = 8.9$, $p = .005$; precipitation, $F_{1,45} = 5.51$, $p = .02$). It should be noted that these two weather variables were correlated with each other ($r = -.53$, $n = 19$, $p < .05$), suggesting that cold winters had high snowfall. In contrast, weather did not affect the 5 September weight of yearling males (all $p > .15$), but orphans were smaller than nonorphans: the difference in weight was significant when year effects were included ($F_{1,37} = 8.464$, $p = .006$; Figure 1). Nonorphans even appeared to gain slightly more weight than orphans over the summer: by 5 September orphan yearling males weighed, on average, 49.0 kg ($n = 19$), 4.2 kg (or 8%) less than nonorphans ($n = 36$, $\bar{X} = 53.2$ kg).

Other body measurements of yearling sheep appeared to follow a pattern similar to that for body weights. For example, the horns of orphan males were smaller than those of nonorphan males, according to ANOVA with year effects and capture date as a covariate. The horns of orphans were about 2 cm (18%) shorter than those of nonorphans ($F_{1,177} = 18.93$, $p < .001$) and about 1.6 cm (15%) smaller in base circumference ($F_{1,177} = 16.72$, $p < .001$). In contrast, the horns of orphan and nonorphan yearling females were not different. Analyses of horn size may have been slightly affected by repeated measurements of the same individuals (Machlis et al., 1985), but no individual contributed more than 4 data points (2.1% of the total).

Once year effects were accounted for by ANOVA, our analyses revealed an effect of orphaning on the weight of male (but not female) yearlings on 5 September. For males, there was no significant (orphan \times year) interaction ($F_{5,37} = 1.84$, $p = .13$) and a t test including all years revealed an overall effect of orphaning ($t_{53} = 2.5$, $p = .015$). However,

Figure 1
Average body weight (kg \pm SE) for orphan and nonorphan bighorn sheep yearlings, near the beginning (5 June) and the end (5 September) of the summer growth period at Ram Mountain, Alberta, from 1973 to 1982. Numbers above bars indicate sample sizes.



it would still be interesting to consider the possibility that orphaning may have an effect on yearling male body weight only in some years, such as those of poor growth. Similarly, female orphans may be affected in some years, even though the overall analysis suggested that they were not. Therefore, we considered in greater detail the yearly variation in the effects of orphaning on weight of yearlings in early September (Figure 2). Orphaning seemed to have a strong and consistent effect on males except for the years 1978–1980. However, non-orphans were not heavier in those years ($\bar{X} = 54.2 \pm 1.7$ kg, $n = 10$) than in other years ($\bar{X} = 52.9 \pm 1.2$ kg, $n = 26$; $t_{34} = 0.59$, $p = .56$), so 1978–1980 were not generally “good” years. There were no clear differences in weather, and the weight of yearling females in those 3 years was not different from other years (Figure 2). These results may have been due to chance: in 1977–1979, male lambs that were orphaned appeared to be larger in mid-September ($\bar{X} = 32.0 \pm 1.3$ kg, $n = 7$) than lambs whose mothers were not removed ($\bar{X} = 29.6 \pm 1.1$ kg, $n = 9$; $t_{14} = 1.39$, $p = .19$). Although the 2.4-kg difference was not significant, it may explain why the effect of orphaning was not as evident in those 3 years as in other years.

Possibly, orphaning only affected those males that were relatively small when their mother was removed. The total sample of orphan males with known weight both as lambs on 15 September and as yearlings on 5 September was too small ($n = 11$) to reliably test this idea, but the limited data suggested otherwise: Of 6 orphans smaller than average as lambs, 4 gained more weight than the average for all 11 in the year after orphaning.

The effects of orphaning could also be detected among 4-year-old males, and orphans were still smaller than nonorphans (Table 2). The same trends persisted among 5 year olds despite the bias against large-horned nonorphans caused by hunting (see Methods). The only significant difference for 5 year olds was horn length ($p = .01$); the horns of orphans ($n = 10$) were about 3 cm (or 4%) shorter than those of nonorphans ($n = 19$). The effect of orphaning became evident only when year effects were included in the ANOVA. That was because orphan rams from two cohorts (1978 and 1979) grew to large sizes, larger than most nonorphans from other cohorts. With the exception of the 1978 cohort (from which only one nonorphan survived to 4 years of age), orphans always had smaller horns than nonorphans born in the same year.

Table 2
Effects of orphaning on horn and body size of bighorn sheep rams at 4 years of age

Variable	Status	N	Mean	SE	p^a	Difference ^b
Body weight (kg)	Orphan	15	78.4	1.7	.047	6.2%
	Nonorphan	28	83.6	1.5		
Horn length (cm)	Orphan	15	62.0	1.0	.001	5.5%
	Nonorphan	29	65.6	0.6		
Horn base (cm)	Orphan	15	35.4	0.4	.003	3.8%
	Nonorphan	29	36.8	0.3		

Measurements were collected between 28 May and 5 July, 1976–1985, and are adjusted for year effects.

^a p values refer to two-way ANOVA with orphan status and year as main effects.

^b Difference in size or weight between orphans and nonorphans.

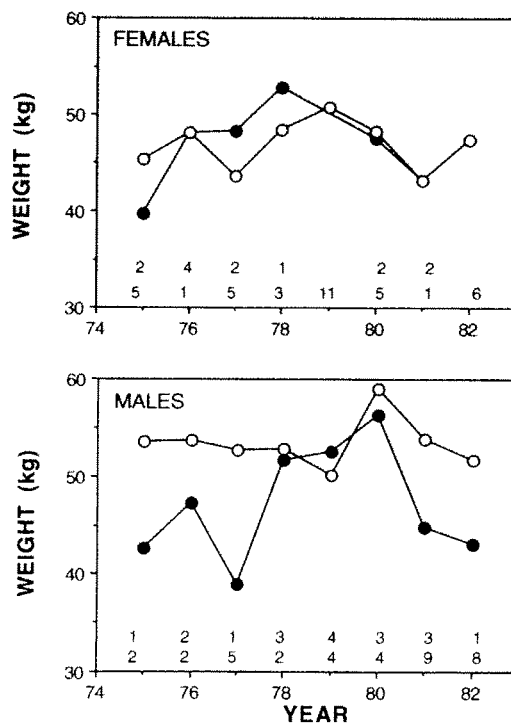


Figure 2
Average body weight on 5 September for orphan (filled circles) and nonorphan (open circles) bighorn yearlings at Ram Mountain, Alberta, 1975 to 1982. Yearly sample sizes are indicated along the bottom of each graph, with orphans above and nonorphans below.

Orphaning did not affect the reproductive success of females. The proportion of ewes producing their first lamb at 2 years of age was the same for orphans (42%, $n = 19$) and nonorphans (37%, $n = 60$; $G = 0.18$, $p > .5$). There were no differences in the numbers of lambs produced or weaned, nor in longevity, among orphan and nonorphan ewes (Table 3). The average age of the 13 surviving ewes was 13.2 years, and because only three ewes ever survived more than 15 years during our study, we expect that most of these 13 will die over the next 1–3 years.

DISCUSSION

Late maternal care did not appear to have any benefit for daughters during our study: neither the growth nor the reproductive success of female orphans was different from those of nonorphans. Therefore, one of the two assumptions of weaning conflict theory, that late maternal care should benefit the offspring, was not supported, and we sug-

Orphan males were unable to compensate for their initial loss of weight relative to nonorphans, even after both groups had lived for 3 or 4 years completely independent of their mothers. For wild mammals, small initial differences between individuals can have profound effects on growth and, ultimately, reproductive success (Albon and Clutton-Brock, 1988). That conclusion should be particularly important for males of sexually dimorphic ungulates, if differences in body size play a greater role than for females in determining reproductive success (Clutton-Brock et al., 1988; Geist, 1971). Ewe removals likely maintained the population below carrying capacity: After removals ceased the population almost tripled, and growth rates decreased for yearlings of both sexes (Jorgenson JT and Festa-Bianchet M, unpublished data). Therefore, the sexual difference in the importance of maternal care revealed by our manipulation was evident even though intraspecific competition was not very strong. It is interesting to note that orphaning appeared to lower overwinter weight gain in both sexes, yet any relative disadvantage for yearling females disappeared during the summer. For males, the difference between orphans and nonorphans seemed to increase during the summer. At high population density, differences in the duration of maternal care may play a more important role, and even females may be unable to recover from any potential effects of early weaning.

For parent-offspring conflict (Trivers, 1974) to exist during weaning, late lactation must involve a cost to the parent and a benefit to the offspring. In this study we demonstrated a benefit to male offspring, but we did not investigate the reproductive costs of late maternal care. A nonmanipulative study of bighorn sheep, however, was unable to detect a significant cost of reproduction (Festa-Bianchet, 1989). In that study, sons appeared to require greater energetic investment because they increased their mother's parasite load, but the survival and reproductive success of mothers did not differ in years after the weaning of a son or of a daughter. If differences in total care (from conception to weaning) are not enough to cause detectable differences in subsequent reproductive success, it is reasonable to assume that differences in late care are even less likely to do so. Therefore, the assumption of a cost of late maternal care has yet to receive any support for this species.

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