Ecology, 76(3), 1995, pp. 871–881

LIFE HISTORY CONSEQUENCES OF VARIATION IN AGE OF PRIMIPARITY IN BIGHORN EWES[1]

MARCO FESTA-BIANCHET
Groupe de recherche en écologie, nutrition et énergétique, Département de biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada J1K 2R1

JON T. JORGENSON
Alberta Fish and Wildlife Division, 5920 1A Street Southwest, Calgary, Alberta, Canada T2H 0G3

MAURO LUCHERINI
Groupe de recherche en écologie, nutrition et énergétique, Département de biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada J1K 2R1

WILLIAM D. WISHART
Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

Abstract. We investigated the life history consequences of age at primiparity in two marked populations of bighorn sheep (*Ovis canadensis*), studied for 19 and 12 yr. Some ewes first lambed at 2 yr of age, others at 3 or 4 yr. Lambs of 2-yr-old ewes were smaller and less viable than lambs of older ewes. Lactation at 2 yr did not affect survival to 3 yr, but in one population it was associated with reduced survival from 3 to 4 yr. Two yr olds that weaned lambs gained less mass during summer than other 2 yr olds. Overwinter mass loss from 2 to 3 yr was correlated with autumn body mass, and was lower for parous than for nonparous ewes. Reproductive success at 3 yr was independent of reproductive status at 2 yr. At 4 yr, ewes that lactated as 2 yr olds were smaller than ewes that had not lactated as 2 yr olds. In one population, negative effects of early maturation upon mass gain and subsequent reproductive success became evident at high density, and very few 2 yr olds lambed when population density was high. The lifetime reproductive success of early-maturing ewes was not lower than that of late-maturing ewes. To account for individual variation in initial reproductive potential, we controlled body mass as a yearling, a variable that affected reproductive success. Mass as a yearling, however, did not interact with age of primiparity to affect survival, growth, or reproductive success. Uncertainties about resource availability and possible effects of genotype and body fat may explain why many ewes postponed their first reproduction despite apparently low life history costs of early maturation.

Key words: age of primiparity; bighorn sheep; cost of reproduction; density dependence; lifetime reproductive success; mass changes; Ovis canadensis.

INTRODUCTION

Variation in age of first reproduction can greatly affect individual fitness (Bell 1980) and population dynamics (Reiter and LeBoeuf 1991), but for wild mammals few studies have assessed the effects of age of primiparity upon lifetime reproductive success. Selective pressures for early maturation include a shorter period during which animals risk dying before reproducing and a greater contribution to the gene pool of future generations, particularly in expanding populations (Cole 1954, Bell 1980, Harvey and Zammuto 1985). Early reproduction, however, may reduce residual reproductive value (reviewed in Stearns 1992).

Some studies of mammals show that early reproduction can reduce survival and subsequent fecundity (Huber 1987, Miura et al. 1987, Bailey 1991, Reiter and LeBoeuf 1991). Other studies, however, suggest that early-maturing females have the same or better survival and reproductive success than females that first breed at a later age (Clark et al. 1986, Ozoga and Verme 1986*a*, Festa-Bianchet 1989, Green and Rothstein 1991, King et al. 1991, Lunn et al. 1994). Failure to detect a cost of early reproduction could be due to an absence of cost or to differences in reproductive potential: early-maturing individuals may be in better condition than late-maturing individuals (Noordwijk and de Jong 1986). Among ungulates, body size is usually thought to affect reproductive potential: early-maturing females are often larger than late-maturing females (Reimers 1983, Green and Rothstein 1991, Gaillard et al. 1992, Sæther and Heim 1993).

Seasonally reproducing mammals cannot fine-tune the timing of their first reproduction to body condition, because breeding seasons are limited in time. In a variable environment, uncertainties about resource availability may play an important role in reproductive strat-

[1] Manuscript received 20 March 1994; revised 30 March 1994; accepted 30 July 1994; final version received 26 August 1994.

egy. There is little information on the consequences of variation in age of primiparity for subsequent growth and development of females. Green and Rothstein (1991) found that adult bison (*Bison bison*) cows that first calved at 2 yr were smaller than cows giving birth for the first time at 3 or 4 yr.

Here, we analyze the consequences of variation in age of first reproduction for body mass, survival, and reproductive success of bighorn sheep ewes (*Ovis canadensis*). Four characteristics make bighorns ideal for this study. First, ewes are limited to producing one lamb per year and can live up to 18 yr; therefore, variations in longevity should have a strong effect on lifetime reproductive success (Clutton-Brock et al. 1988). If early maturation affects survival, then the age of primiparity should be under strong selective pressure. Second, because ewes can lamb as 2 yr olds but continue to grow until 4 or 5 yr of age (Jorgenson and Wishart 1984), early reproduction may affect body growth. Third, several studies suggest that large mammals are "capital breeders" (sensu Stearns 1992), and reproductive effort in one year should have negative consequences upon subsequent reproductive success, because reproduction in different years is expected to draw upon a shared pool of resources (Clutton-Brock et al. 1983, Sydeman et al. 1991, Lunn et al. 1994) (but see Festa-Bianchet 1989, LeBoeuf et al. 1989). Thus, early maturation in bighorn sheep should be associated with a reproductive cost. Finally, we previously reported wide overlap in mass of yearling females that subsequently did and did not lactate at 2 yr. Many yearlings heavier than the "threshold" for reproduction postponed lambing until age 3, and increases in mass beyond this threshold did not affect the probability of lambing at 2 yr (Jorgenson et al. 1993*a*). Therefore, the occurrence of early reproduction appears to be somewhat independent of body mass and, presumably, of initial reproductive potential.

Many studies of large mammals have reported lower survival of offspring from young mothers (Reiter et al. 1981, Ozoga et al. 1982, Ozoga and Verme 1986*b*, Festa-Bianchet 1988*a*, Lunn et al. 1994). Because the fitness consequences of early maturation should vary with the reproductive success of young females, we compared the size and survival of lambs of 2-yr-old ewes with lambs of older ewes.

We predicted that by late summer nonparous 2 yr olds would be heavier than parous 2 yr olds. We expected that ewes that had lambed at 2 yr would be smaller as 3-yr-olds than other ewes, and possibly suffer a reduction in reproductive success. We also tested whether, similarly to bison (Green and Rothstein 1991), body mass of adult bighorn ewes was negatively affected by early maturation. Finally, we tested whether early reproduction led to a reproductive cost the following year or over the lifetime.

We stimulated early maturation by lowering adult female density, but we could not directly control the age of primiparity of individual females. Therefore, we faced the potential problem of variation in individual reproductive potential (Lessels 1991). If most early-maturing bighorn ewes are high-quality individuals, they may not experience any reproductive costs, as suggested by some studies of ungulates (Green and Rothstein 1991, Gaillard et al. 1992, Sæther and Heim 1993). In one population, we used body mass at 12 mo of age to control for differences in reproductive potential. Body mass during early development should affect reproductive potential (Albon et al. 1987, Clutton-Brock et al. 1992); therefore, we expected that the costs of early reproduction would be particularly evident for parous 2 yr olds that were small as yearlings.

Study Areas and Methods

In Alberta, bighorn sheep rut in late November and early December. Singleton lambs are born in late May and early June, most births normally occurring over a 12-d period (Festa-Bianchet 1988*b*). We studied two populations: Ram Mountain from 1975 to 1993 and Sheep River from 1981 to 1993. Our studies are based upon monitoring marked individuals. In both study areas we can measure survival with great precision: at Sheep River there has never been a ewe missed in one year and later resighted, at Ram Mountain there have been only two cases out of ≈1350 ewe-years.

Definition of variables

Early producer.—A ewe that lactated at 2 yr of age.

Late producer.—A ewe not known to lactate at 2 yr of age.

Neonatal mortality.—Death of lambs that were never seen, but whose birth was indicated by lactation in the ewe. Distended udders are clearly visible in lactating ewes. Most neonatal deaths probably occurred when lambs were between 0 and 7 d of age, because we saw or caught most ewes within a week of lambing.

Successful early producer.—An early producer whose lamb survived to October, the approximate time of weaning.

Unsuccessful early producer.—An early producer whose lamb died during its first summer.

Ram Mountain

At Ram Mountain (52° N, 115° W, elevation 1082–2173 m), a corral trap allowed multiple captures of almost all ewes each year, and over 95% of the population was individually marked in most years. Trapping took place from late May to late September or early October. Captured sheep were weighed to within 125 g with a spring scale that was regularly checked with known masses. The lactation status of captured ewes (milk, colostrum, or flaccid udder) was recorded.

Between 1972 and 1981, the population was kept at 95–110 sheep by removing adult ewes (Jorgenson et al. 1993*b*). Removals ceased in 1981 and the population increased (Table 1). Only ewes born before 1987 are

TABLE 1. Changes in composition and in average body mass (kg) of yearling ewes on 5 June for the Ram Mountain study population, 1975–1993. In parentheses is the number of yearling ewes whose mass was adjusted to 5 June each year.

Year	Adult ewes (≥2 yr)	2-yr-old ewes	2-yr-old ewes lactating	Body mass of yearling ewes on 5 June
1975	33	6	1	28.0 (5)
1976	30	6	1	31.1 (5)
1977	30	8	5	29.9 (10)
1978	33	12	7	30.7 (5)
1979	34	6	0	31.2 (11)
1980	33	11	9	30.0 (5)
1981	31	8	4	28.7 (3)
1982	36	7	3	29.9 (6)
1983	38	7	0	28.9 (8)
1984	47	11	1	31.2 (7)
1985	51	6	1	32.3 (7)
1986	58	8	0	28.1 (8)
1987	61	9	0	33.1 (9)
1988	65	10	3	30.3 (9)
1989	72	11	0	28.1 (15)
1990	83	17	0	25.7 (18)
1991	97	21	1	26.0 (10)
1992	102	12	0	27.4 (9)
1993	97	9	0	22.5 (3)

considered here, because during the last 4 yr of study the body mass of young ewes declined and only 1 of 59 2 yr olds produced lambs (Table 1). We obtained total counts for all sex age classes during the summer. In most years, over 80% of lambs were caught and tagged.

Ewe mass gain over the entire summer is best described by a linear regression of body mass on the square root of date, taking 25 May as day 1 (Fig. 1). To compare mass changes for different groups of ewes we adjusted mass to 5 June (day 12) and 15 September (day 114). These dates were chosen because in some years, few captures were available in late September, and in some years trapping began in early June. We adjusted each ewe's body mass using her individual growth rate. For ewes caught only once in a summer (6% of ewes), we used the growth rate calculated for all captures of ewes of the same age and reproductive status. Ewes not captured within 50 d of the adjustment date were excluded. The average (± 1 SE) time between adjusted and measured mass was only 8.8 d ± 0.7 for 5 June, and 27.4 ± 1.3 d for 15 September. The longer period of adjustment in late summer is unlikely to affect the results because ewes gain little mass after mid-

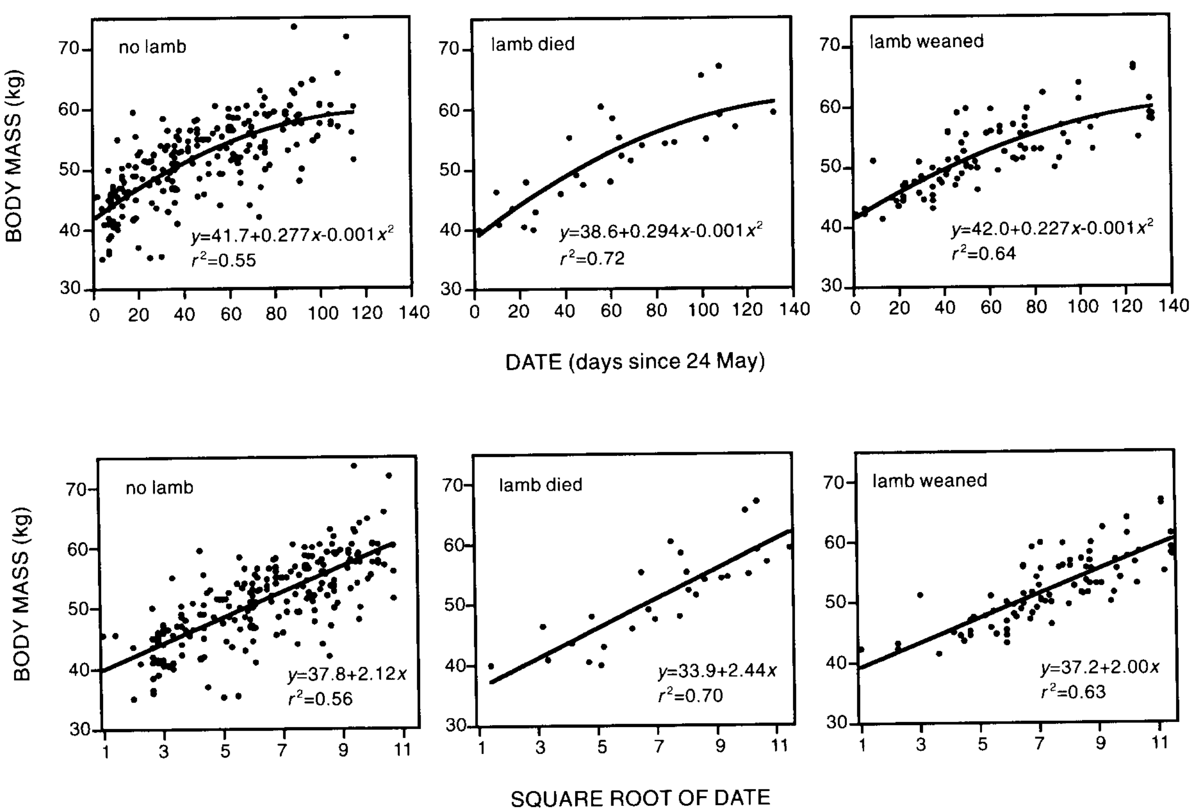

FIG. 1. Body mass of 2-yr-old ewes of different reproductive status at Ram Mountain from 25 May (day 1) to 6 October (day 135) in 1975–1988, with square-root transformed (linear regressions) and untransformed (curvilinear regressions) capture dates.

TABLE 2. Changes in composition and in lamb survival to weaning of the Sheep River population, 1982–1993. In parentheses is the number of individually marked lactating ewes used to calculate lamb survival to weaning.

Year	Adult ewes (≥2 yr)	2-yr-old ewes	2-yr-old ewes lactating	Percent lamb survival to weaning
1982	55	5	3	71 (38)
1983	63	11	7	70 (43)
1984	62	9	6	69 (49)
1985	71	14	9	48 (52)
1986	57	7	0	84 (38)
1987	49	3	1	57 (40)
1988	51	6	3	87 (40)
1989	53	5	4	71 (42)
1990	59	6	0	64 (47)
1991	59	4	0	50 (48)
1992	61	7	3	79 (52)
1993	57	6	0	49 (45)

August (day 85, Fig. 1). Between 1975 and 1989, 125 2-yr-old ewes were weighed on average 3 times each (range 1–6), for 369 mass measurements. Overwinter mass loss was calculated by subtracting mass on 15 September from mass on 5 June the following year.

We adjusted body mass of ewes older than 2 yr using the same methods outlined above. Analyses of overwinter mass loss included only ewes that were lactating the following spring.

Occasionally, pregnant ewes were caught in late May or early June. Pregnancy was detected because the ewe had colostrum or had a flaccid udder but later nursed a lamb or had milk when recaptured. These ewes (n = 8) typically lost mass between their first and second capture, and the first capture while pregnant was not used for analyses of body mass.

For ewes born before 1983 that were not removed, we calculated lifetime reproductive success (lambs produced and lambs weaned) and reproductive success up to age 10. Lifetime reproductive success is a minimum estimate for nine ewes (four early producers and five late producers) still alive in 1994 and aged 12 yr or more. The data set includes 116 ewes of known reproductive status at age 2 from 1975 to 1988, whose subsequent survival and reproductive success were monitored between 1976 and 1993.

Sheep River

Sheep River (50° N, 114° W, elevation 1420–2550 m) is 160 km south of Ram Mountain. Bighorns in this herd are larger than at Ram Mountain (Jorgenson et al. 1993*a*) and reproduction among 2-yr-old ewes is common (Table 2). Pneumonia in 1978 and in 1985–1986 (Festa-Bianchet 1988*d*) led to declines in numbers and in lamb survival (Table 2). Most captures were made with immobilizing drugs (Jorgenson et al. 1990). The proportion of marked ewes increased from 40% in 1981 to 95% in 1984–1992. Heart girth was measured at capture, but <1% of the bighorns at Sheep River were recaptured and few were weighed. Over 85% of captures since 1983 were of lambs, mostly from late August to early November, and we could not make the same body mass comparisons that we made at Ram Mountain. Reproductive status at 2 yr was known for 81 ewes.

At Sheep River, we followed six cohorts to 8 yr of age. To assess the long-term effects of age of primiparity, we compared the total number of lambs born and weaned and the number of lambs produced and weaned by 8 yr of age for 47 ewes that were born before 1986 and by May 1994 were either dead (n = 38) or aged at least 8 yr (n = 9, including three early producers and six late producers).

STATISTICAL ANALYSES

Differences in body mass (Ram Mountain) or heart girth (Sheep River) of lambs according to maternal age (2 yr or older) were tested with ANOVA using capture date as a covariate. Mass gain in lambs was linear from early June to late September.

At Ram Mountain, we used ANOVA to compare body mass changes of three groups of ewes: late producers, unsuccessful early producers, and successful early producers. Sex of lambs reared by 2-yr-old ewes has no effect upon maternal mass changes (Bérubé 1993), and was therefore not considered. Scheffé tests were used to detect pairwise differences (Sokal and Rohlf 1981). The sample of unsuccessful early producers was small, especially for ewes older than 2 yr, because some were lost through natural deaths or experimental removals. Some comparisons, particularly for ewes 3 yr of age and older, were therefore limited to t tests between successful early producers and late producers. To study the effects of early reproduction upon body mass of adult ewes (aged 3, 4, and 5 yr), we used repeated-measures analysis of covariance (Potvin et al. 1990) for adjusted 5 June body mass for ewes that were caught at appropriate times in all 3 yr, with body mass at 12 mo of age as a covariate. Because this analysis could only be performed on a subset (n = 41) of our total sample, we also performed separate ANOVAs for body mass on 5 June at 3–6 yr of age, again with mass at 12 mo as a covariate.

We used G tests and Fisher's exact tests (for small sample sizes) to compare survival of lambs born to ewes of different ages, to test for differences in ewe survival according to age of primiparity and to see whether reproduction at 2 yr affected reproduction at 3 yr.

Measures of reproductive success (longevity, number of lambs produced and of lambs weaned) were not expected to be normally distributed (Clutton-Brock 1988) and comparisons between ewes of different age of primiparity were made with Mann-Whitney U tests. For the Ram Mountain data, body mass at 12 mo was included as a covariate in an ANOVA comparing lifetime reproductive success of early and late producers.

Statistics were performed using SPSS for the Mac-

TABLE 3. Survival of lambs born to 2-yr-old and to older ewes at Sheep River, 1982–1992, and at Ram Mountain, 1975–1991. Only years in which at least one 2-yr-old ewe reproduced are included.

		Survival to							
		Weaning (October)				One year			
Study area	Mother age	n	%	G*	P*	n	%	G*	P*
Sheep River	2	35	51.4	6.66	0.01	32	25.0	3.77	0.06
	>2	306	73.2			262	42.4		
Ram Mountain	2	35	77.1	1.60	>0.1	33	54.5	4.01	0.04
	>2	280	85.7			275	72.0		

* G and P values refer to a comparison of each row with the previous row.

intosh (SPSS 1990). Probability values are two tailed unless otherwise indicated. Data are reported as means ± 1 SE.

RESULTS

Reproductive success of 2-yr-old ewes

Lambs of 2 yr olds were less viable (Table 3) and smaller than lambs of older ewes (Fig. 2). Analysis of covariance showed that mother age affected body mass of lambs (males: $F_{1,305} = 20.49$, $P < 0.001$; females: $F_{1,293} = 11.89$, $P = 0.001$). By 15 September, daughters of 2 yr olds had ≈12% less mass than daughters of older ewes (24.1 vs. 27.5 kg, predicted by regressions of all lamb captures) and sons of 2 yr olds had ≈14% less mass than sons of older ewes (25.9 vs. 30.2 kg).

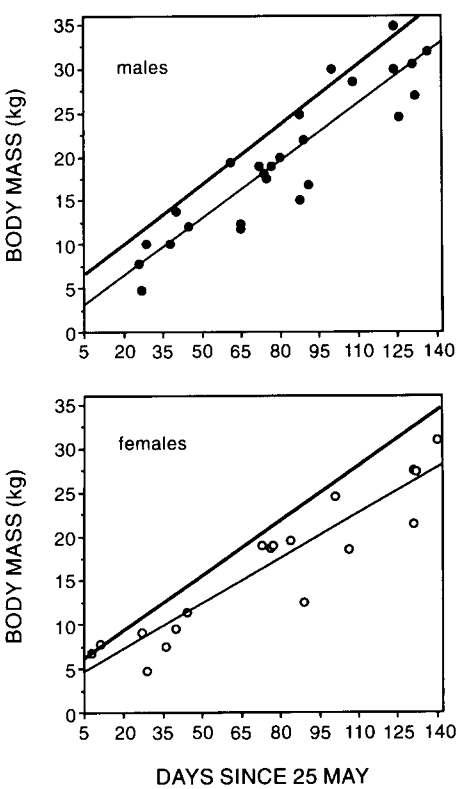

FIG. 2. The body mass of male and female lambs born to 2-yr-old ewes at Ram Mountain, Alberta, 1973–1988. Thin lines show linear regressions for the data in the figure, while thicker lines show linear regressions for body mass of lambs of older ewes.

Offspring of 2 yr olds that survived to 1 yr, however, were not smaller than offspring of older ewes on 5 June at 1 yr of age (males: 32.2 ± 1.8 kg for 8 sons of 2 yr olds and 33.1 ± 0.5 kg for 116 sons of older ewes; females: 30.6 ± 1.4 kg for 4 daughters of 2 yr olds and 30.1 ± 0.4 kg for 109 daughters of older ewes (t tests, both $P > 0.5$). This result suggested that only the largest lambs of 2 yr olds were likely to survive. A two-way ANOVA of all masses of lambs of 2 yr olds with date of capture as a covariate did not reveal significant effects of either sex or survival to 1 yr, but showed a significant interaction of sex and survival ($F_{1,39} = 8.17$, $P = 0.007$). When lambs of 2 yr olds were considered separately according to sex, summer mass affected survival to 1 yr for males ($F_{1,23} = 8.46$, $P = 0.008$) but not for females ($F_{1,15} = 0.69$, $P = 0.4$).

At Sheep River, despite the limited sample (four sons and six daughters of 2 yr olds), mother age affected heart girth when lamb sex and capture date were considered ($F_{1,194} = 13.85$, $P < 0.001$). Adjusted to 15 September, lambs of 2 yr olds had ≈9% smaller girth (65.0 ± 1.1 cm) than lambs of older ewes (71.5 ± 0.3 cm). At the same date, male lambs had an average heart girth of 72.2 ± 0.51 cm, ≈3% greater than for females ($\bar{X} = 70.2 \pm 0.4$, $t_{238} = 3.08$, $P = 0.002$).

Some lambs of 2-yr-old ewes reproduced successfully. At Ram Mountain, of 14 known daughters of 2-yr-old ewes, at least 5 produced at least one lamb that survived to yearling age. At Sheep River, the corresponding figure was three of eight daughters of 2-yr-old ewes. The reproductive success of sons is unknown.

Short-term consequences of early primiparity

At Ram Mountain, early producers lost more mass overwinter as yearlings than late producers ($F_{2,65} = 8.09$, $P = 0.0007$). Mass loss between 15 and 24 mo of age averaged 0.8 ± 0.6 kg for late producers (n = 45), 4.3 ± 1.0 kg for successful early producers (n = 16), and 6.6 ± 1.6 kg for unsuccessful early producers (n = 5). Pairwise differences existed between late producers and both groups of early producers.

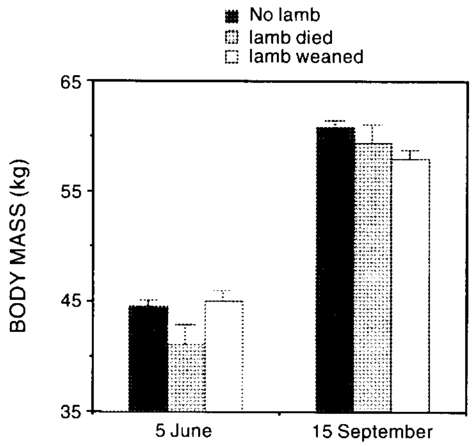

FIG. 3. Adjusted body mass of 2-yr-old bighorn ewes of different reproductive status at Ram Mountain, Alberta, 1975–1989.

Reproductive status did not affect body mass of 2 yr olds on 5 June (Fig. 3; $F_{2,110} = 2.0$, $P = 0.14$), but affected summer mass gain ($F_{2,91} = 6.22$, $P = 0.003$) (Fig. 3). Scheffé tests revealed that successful early producers gained less mass over the summer ($\bar{X} = 12.4$ kg) than either unsuccessful early producers ($\bar{X} = 19.6$ kg) or late producers ($\bar{X} = 16.4$ kg). Body mass on 15 September differed among the three groups ($F_{2,92} = 3.03$, $P = 0.05$). There were no pairwise differences, but there were only seven unsuccessful early producers and a *t* test comparing late producers and successful early producers suggested that the latter were smaller ($t_{86} = 2.41$, $P = 0.02$). By 15 September, successful early producers were ≈3 kg (5%) lighter than late producers (Fig. 3). Analysis of variance of September body mass as a 2 yr old with mass a year earlier as a covariate confirmed the negative effect of reproduction ($F_{2,51} = 6.37$, $P = 0.003$); mass a year earlier had a significant effect ($F_{1,51} = 16.4$, $P < 0.001$).

Late producers lost more mass overwinter between 2 and 3 yr than successful early producers (Table 4; $F_{2,76} = 5.49$, $P = 0.006$) and mass of lactating 3 yr olds did not vary according to age of primiparity (Table 4; $F_{2,92} = 0.42$, $P = 0.4$). Large ewes lost more mass overwinter than small ewes: mass loss was correlated with mass on 15 September (Fig. 4), especially for early producers ($n = 24$, $r = 0.60$, $P = 0.002$). For late producers, the correlation between September mass and overwinter mass loss was significant ($n = 55$, $r = 0.40$, $P = 0.002$), even if the outlier circled in Fig. 4 was excluded ($n = 54$, $r = 0.29$, $P = 0.03$). The correlation coefficients for early and late producers (outlier excluded) were not significantly different ($t_s = 1.52$, $P > 0.1$).

Survival to 3 yr did not vary with age of primiparity in either population ($P > 0.5$). At Sheep River, survival to 3 yr was the same, 92%, for 35 early producers and for 38 late producers. At Ram Mountain, survival to 3 yr was 97% for 79 late producers and 94% for 36 early producers.

TABLE 4. Overwinter mass loss and body mass (kg) on 5 June at 3 yr of age for ewes with different reproductive status at 2 yr of age, Ram Mountain 1975–1988. Only ewes that produced a lamb at 3 yr of age are included.

	Overwinter mass loss			Mass at 3 yr		
Status at 2 yr	n	$\bar{X}$	SE	n	$\bar{X}$	SE
Not lactating	55	−11.9	0.6	68	49.3	0.7
Lamb died	6	−12.8	1.3	7	46.7	1.5
Lamb weaned	18	−7.8	1.1	20	49.6	0.8

At Sheep River, the probability of producing a lamb at 3 yr was independent of reproductive status at 2 yr (Table 5). Festa-Bianchet (1989) reported that in 1982–1988 lactation at age 3 was positively associated with lactation at age 2. When the latest 5 yr of data were included, reproductive status at 2 yr no longer affected reproduction at 3 yr but the trend remained opposite to the prediction of the cost of reproduction hypothesis. At Ram Mountain, there was no effect of age of primiparity upon lamb production at 3 yr. In both study areas, the survival of lambs of 3 yr olds was independent of the mother's age of primiparity (Table 5).

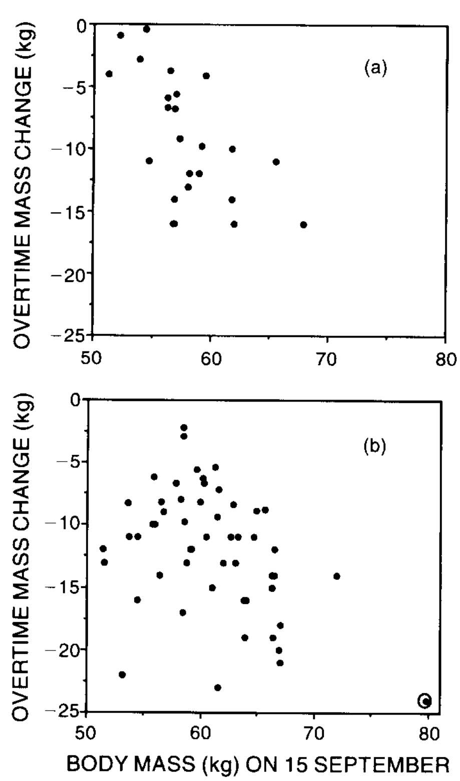

FIG. 4. Mass change from 15 September to 5 June for 2-yr-old bighorn sheep ewes at Ram Mountain, Alberta, 1975–1988. (a) Early producers. (b) Late producers. If the circled point is excluded, the correlation for late producers becomes weaker.

TABLE 5. Lamb production by 3-yr-old bighorn ewes according to their reproductive status as 2 yr olds at Sheep River (1982–1993) and Ram Mountain (1975–1988).

Study area	Lamb at 2	Produced lamb at 3 yr Yes	No	% yes	G^*	P^*
Sheep River	Yes	28	6	82	2.66	0.1
	No	27	14	66		
Ram Mountain	Yes	28	5	84	0.59	0.4
	No	64	7	90		
		Lamb at 3 yr survived to weaning				
		Yes	No	% yes	G^*	P^*
Sheep River	Yes	14	14	50	0.02	0.9
	No	13	14	48		
Ram Mountain	Yes	22	6	79	0.74	0.4
	No	55	9	86		

* G and P values refer to a comparison of each row with the previous row.

Effects of population density

At Sheep River, the frequency of early maturation appeared independent of population density (Table 2), but most years of low density followed the pneumonia epizootic, when lamb survival was low (Festa-Bianchet 1988*b*). Any effect of density could be confused by the effects of the disease. The number of ewes only varied by 45%, compared to 240% at Ram Mountain.

At Ram Mountain after the population was allowed to increase, few 2 yr olds lambed, except for 1988 (Table 1). The number of ewes in 1988 was more than twice the average for the years of artificially low density, therefore we used that year to test for effects of population density, even though the available sample size was very small. Parous 2 yr olds in 1988 gained less than half as much mass as nonparous ones during summer (6.2 ± 1.0 kg vs. 14.1 ± 1.1 kg, t_8 = 4.26, P = 0.003) and by 15 September were about 10% lighter (53.6 ± 0.1 kg vs. 58.2 ± 2.0 kg, t_6 = 2.27, one-tailed P = 0.03). The summer mass gain of nonparous 2 yr olds did not vary with density but mass gain for parous 2 yr olds was lower at high density (Table 6).

The lambs produced by 2 yr olds in 1988 survived to October, but none of their mothers weaned a lamb the following year. In contrast, of the six surviving late producers of the same cohort, all but one weaned lambs as 3-yr-olds. Despite the small sample, the probability of weaning a lamb at 3 yr was greater for ewes that had not lambed at 2 yr (Fisher's exact test, P = 0.05). Comparing the years of low population density to the population increase from 1983 to 1989, the probability of weaning a lamb as a 3 yr old declined significantly for early producers but not for late producers (Table 7).

TABLE 7. Reproductive success (production of a lamb that survives to weaning) for 3-yr-old ewes at Ram Mountain, according to the ewe's reproductive status at 2 yr of age and to population density. Low density includes data from 1976 to 1982, high density includes data from 1983 to 1989.

Reproductive status at 2 yr	Weaned lamb as a 3 yr old: Low density Yes	No	% yes	High density Yes	No	% yes	G	P
Lactating	21	7	75	1	4	20	5.51	0.02
Not lactating	26	7	79	39	23	63	2.61	0.11

Long-term consequences of early primiparity

Age of primiparity did not appear to affect either body mass beyond 4 yr of age or lifetime reproductive success. Repeated-measures analysis of covariance for ewes 3–5 yr of age showed that body mass was affected by age ($F_{2,90}$ = 4.24, P = 0.02), mass at 12 mo ($F_{1,38}$ = 9.33, P = 0.004) and age of primiparity ($F_{1,38}$ = 4.64, P = 0.04). There was no interaction between reproductive status at 2 yr and age ($F_{2,90}$ = 1.14, P = 0.33). When data on body mass on 5 June at ages 3–6 yr were analyzed separately for each age, reproductive status at age 2 affected mass only for 4 yr olds ($F_{1,53}$ = 13.88, P < 0.001), while mass at 12 mo affected mass at ages 3 ($F_{1,76}$ = 5.09, P = 0.03) and 4 ($F_{1,53}$ = 8.8, P = 0.005) (Fig. 5).

Age of first reproduction had no effect on ewe survival at Ram Mountain (Fig. 6). At Sheep River, more early producers (8 of 32) than late producers (2 of 32) died between 3 and 4 yr (G = 4.52, P = 0.04), but there were no differences in survival for other age classes (Fig. 6). At Ram Mountain, yearly survival between 2 and 8 yr was 96% for early producers and 95% for late producers. At Sheep River, excluding survival from 3 to 4 yr, yearly survival between 2 and 8 yr averaged 94% for early producers and 92% for late producers.

TABLE 6. Mass gain (kg) of 2-yr-old bighorn sheep ewes between 5 June and 15 September at Ram Mountain, Alberta, according to their reproductive status and to population density. In 1975–1982 the population included, on average, 32.5 ewes; in 1988 it had increased to 65 ewes.

Reproductive status	Years: 1975–1982 $\bar{X}$	SE	n	1988 $\bar{X}$	SE	n	t	P
Nonparous	15.4	0.9	24	14.1	1.1	7	0.70	0.5
Parous, lamb survived to weaning	14.4	1.0	18	6.2	1.0	3	3.20	0.005

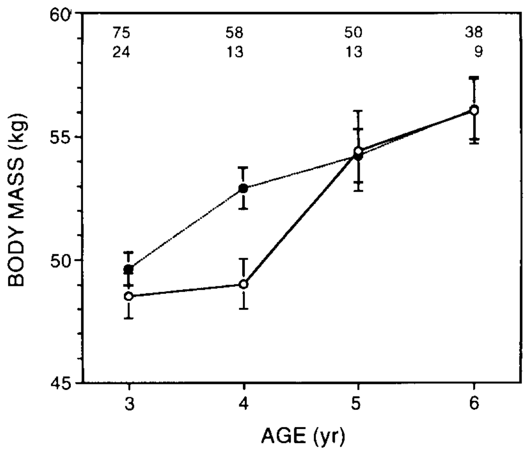

FIG. 5. Body mass on 5 June from 3 to 6 yr of age for bighorn ewes at Ram Mountain, according to their reproductive status at 2 yr of age: (●) no lamb produced; (○) lamb weaned. Sample sizes are reported along the top, with numbers for ewes that did not produce lambs as 2 yr olds on the first line.

At Ram Mountain, data on lifetime reproductive success did not support the hypothesis of a cost of early reproduction. Early producers tended to live longer and produce and wean more lambs than late producers, but the only significant difference was in lamb production by 10 yr of age (Table 8). At Sheep River, there were no differences in reproductive success according to age of primiparity but except for longevity all trends were opposite to the predictions of the cost hypothesis (Table 8).

Size as a yearling at Ram Mountain did not interact with age of primiparity to affect lifetime reproductive success. Mass at 12 mo had significant effects as a covariate upon all five measures of reproductive success in Table 8 (P values ranged from 0.01 for lambs produced by age 10 to 0.04 for longevity, while regression coefficients ranged from 0.25 for lambs weaned by age 10 to 0.44 for total lambs produced), but lactation at 2 yr had no significant effects (all $P > 0.5$).

DISCUSSION

Reproductive success of 2-yr-old ewes

Our primary goal was to test the hypothesis that early primiparity involved a life history cost. It is also important, however, to assess the potential benefits of early maturation. In both study areas, lambs of 2 yr olds were smaller and less viable than lambs of older ewes. At Sheep River, 2 yr olds lamb later and allow shorter suckles to their lambs relative to older ewes (Festa-Bianchet 1988*a, c*). Therefore, 2 yr olds appear less capable mothers than older ewes. Nevertheless, for some ewes, lambing at 2 yr resulted in viable grandchildren in both study areas. At Ram Mountain, many small lambs of 2 yr olds died overwinter, and survivors included mainly relatively large lambs.

By reproducing at 2 yr, a female may obtain maternal experience and improve her subsequent reproductive success (Ozoga and Verme 1986*b*, Reiter and LeBoeuf 1991). That was not the case for bighorns: weaning success was not different for primiparous and multiparous 3 yr olds (Table 5). Our data contrast with other studies of mountain ungulates, that report lower subsequent short-term reproductive success for early producers (Miura et al. 1987, Bailey 1991).

Life history consequences of early maturation

Our results suggest that early maturation involves reproductive costs only during stressful periods, such as at high density or during pneumonia epizootics. At Sheep River, early producers were more likely to die than late producers during a pneumonia epizootic (Festa-Bianchet 1989), suggesting that risk of mortality in particularly stressful years may select for a delay in the production of the first lamb. We confirmed the existence of a survival cost of early reproduction at Sheep River, but found no such cost at Ram Mountain. Unlike elephant seals (*Mirounga angustirostris*), where early

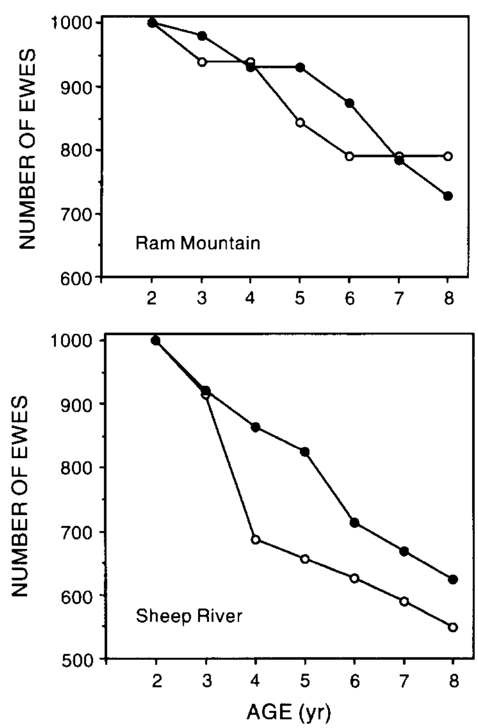

FIG. 6. Age-specific survival from 2 to 8 yr of bighorn ewes that first reproduced at 2 (○) and at >2 (●) yr at Ram Mountain (1975–1992) and at Sheep River (1982–1992). Sample sizes for early producers averaged 24 (range 15–35) at Sheep River and 20 (range 15–32) at Ram Mountain. For late producers, sample sizes averaged 24 (range 15–38) at Sheep River and 36 (range 27–50) at Ram Mountain.

TABLE 8. Longevity and reproductive success of bighorn ewes born in the Ram Mountain population before 1983 and in the Sheep River population before 1986, according to their age of primiparity. At Ram Mountain, sample size was 19 early producers and 33 late producers. Longevity and lifetime reproductive success data are incomplete for nine ewes, all aged 12 yr and older ($\bar{X}$ = 13.9 yr), still alive in 1994. At Sheep River, sample size was 25 early producers and 22 late producers. Longevity and lifetime reproductive success data are incomplete for nine ewes, aged 9–13 yr ($\bar{X}$ = 11.4).

	Age of first lambing					
	2 yr		>2 yr			
Variable	$\bar{X}$	SE	$\bar{X}$	SE	Z*	P
Ram Mountain						
Longevity (yr)	10.3	1.1	9.2	0.6	1.05	0.29
Lambs produced	8.5	1.0	6.8	0.6	1.45	0.15
Lambs weaned	6.5	0.8	5.5	0.5	1.11	0.27
Lambs produced by age 10	6.8	0.7	5.9	0.4	2.15	0.03
Lambs weaned by age 10	5.4	0.6	4.9	0.4	1.19	0.23
Sheep River						
Longevity (yr)	6.8	0.7	7.6	0.5	0.53	0.60
Lambs produced	5.2	0.7	4.5	0.7	1.05	0.29
Lambs weaned	3.2	0.6	3.0	0.5	0.08	0.94
Lambs produced by age 8	4.4	0.5	3.7	0.5	1.40	0.16
Lambs weaned by age 8	2.7	0.4	2.6	0.4	0.08	0.93

* Z transformation of Mann-Whitney U test.

producers had low survival up to 8 yr of age (Reiter and LeBoeuf 1991), in bighorns the survival cost of early reproduction was limited to the interval between 3 and 4 yr, and in only one population.

The lower mass gain associated with early reproduction should affect survival in the following winter, yet a survival cost of reproducing at 2 yr occurred between 3 and 4 yr of age and not between 2 and 3 yr. Interestingly, however, at Ram Mountain early reproduction affected mass at age 4 but not at age 3. Early reproduction may have a delayed effect upon both body mass and survival.

Gestation during the second winter of life involved a cost in body mass, because overwinter mass loss from 15 to 24 mo was greater for early producers than for late producers. As expected, summer mass gain of 2 yr olds nursing lambs was less than for nonlactating 2 yr olds. There was a short-term trade-off between reproduction and growth: lactating ewes were unable to accumulate body mass at the same rate as nonlactating ewes. Results for reindeer (*Rangifer tarandus*) are comparable to ours: yearlings that conceived were 8% heavier during rut than yearlings that did not conceive, but lactating 2 yr olds were 14% lighter than nonlactating ones in late summer (Reimers 1983).

Overwinter mass loss between 2 and 3 yr was greater for late producers than for early producers. As a result, age of primiparity had no effects upon body mass at age 3. Mitchell et al. (1976) obtained similar results for red deer (*Cervus elaphus*): lactating hinds were lighter and leaner than nonlactating hinds at the beginning of winter but the difference disappeared by the end of winter. We suspect that the lower September mass of lactating 2 yr olds compared to late producers was due mostly to differences in fat accumulation, and that somatic growth was relatively unaffected by reproduction. Fat stores of late producers were apparently depleted over winter and by the following spring, early and late producers had the same average mass. This interpretation would explain the positive correlation between mid-September mass and overwinter mass loss. In contrast, young nonparous reindeer did not accumulate more fat during summer compared to parous females of the same age, but increased their somatic growth (Leader-Williams and Ricketts 1982). In *Rangifer*, a sharp threshold of both body mass and condition determines which females will conceive and which will not (Leader-Williams and Ricketts 1982, Thomas 1982). In bighorns, mass is not an accurate predictor of the age of first reproduction (Jorgenson et al. 1993*a*). Early reproduction seems to affect growth in bighorn ewes less than in other ungulates (Leader-Williams and Ricketts 1982, Green and Rothstein 1991), and bighorns may recover the energy cost of reproduction by exploiting summer forage.

Lactating 2 yr olds may accumulate mass later than nonlactating ewes, reaching a similar mass by the onset of winter. There might be an optimum amount of either fat or somatic growth and nonparous 2 yr olds appear to stop accumulating mass sooner than parous 2 yr olds (Fig. 1). For all groups of ewes, however, mass gain reached a plateau in September (Fig. 1 and *unpublished data* of J. T. Jorgenson and M. Festa-Bianchet on older ewes). Studies of northern ungulates indicate that forage quality is poor by September (Seip and Bunnell 1985, Festa-Bianchet 1988*e*) and it is unlikely that lactating ewes could compensate in autumn for low mass gain during summer.

At high density, early maturation lowered body growth and subsequent short-term reproductive success of bighorn ewes, confirming the results obtained for seals (Reiter and LeBoeuf 1991). These results may explain why many ewes postponed their first lambing even though their body mass was higher than average (Jorgenson et al. 1993*a*). If increases in population density (and, presumably, other factors that may affect resource availability) can increase the fitness costs of early maturation, ewes should adopt a conservative reproductive strategy when changes in population density are unpredictable. This prediction is supported by the strong density-dependent decline in lamb production among 2 yr olds at Ram Mountain (which left us with a small sample of early producers at high population density) (Jorgenson et al. 1993*a*) and by the heavier mortality of early producers during the pneumonia epizootic at Sheep River (Festa-Bianchet 1989). Apparently, the life history costs of early maturation are much greater at times of resource scarcity.

There is controversy about how to measure the life history costs of reproduction (Reznick 1985, 1992, Lessels 1991, Partridge 1992). One problem of studies that measure individual variation in life histories and compare it with reproductive costs is that when individuals vary in reproductive potential fitness components tend to be positively correlated (Smith 1981, Bell and Koufopanou 1986, Noordwijk and de Jong 1986, Festa-Bianchet 1989, Stearns 1992). In large mammals, body mass has a positive effect upon reproductive potential (Mitchell et al. 1976, Thomas 1982, Albon et al. 1983, Sæther and Haagenrud 1983, LeBoeuf et al. 1989, Green and Rothstein 1991, Gaillard et al. 1992), and we found that mass at 12 mo affected reproductive success. Even when we controlled for differences in body mass at 12 mo, however, we found few life history consequences of early primiparity.

There are two possible interpretations of our results. First, and despite several studies on ungulates that suggest the contrary, early development (in our case, mass at 12 mo) may not be a good predictor of reproductive potential in this species. Body mass during early development may interact with either fat reserves (Thomas 1982) or genotype (Pemberton et al. 1991) to affect both the probability of early maturation and subsequent reproductive success. According to this interpretation, accounting for prepubertal body mass would not control for individual differences in reproductive potential. To test this possibility, one would need information on body fat content and on genetic differences among individuals.

Alternatively, when their populations are below carrying capacity bighorn sheep may be "income breeders" (Stearns 1992): for reproduction, they may rely more on resources obtained during each summer than on a pool of somatic resources shared between years. Early reproduction may not be very costly if summer forage is abundant and of high protein content (Festa-Bianchet 1988*e*). This interpretation is supported by the scarcity of short-term effects of early reproduction on reproductive success or of long-term effects on body mass.

ACKNOWLEDGMENTS

Financial support was provided by the Natural Sciences and Engineering Research Council of Canada (scholarships and operating grant to M. Festa-Bianchet), the Fonds pour la Formation de Chercheurs et l'Aide à la Recherche (Québec) (Programme établissement de nouveaux chercheurs, M. Festa-Bianchet), the Alberta Recreation Parks and Wildlife Foundation (grants to J. T. Jorgenson and M. Festa-Bianchet), and the Alberta Fish and Wildlife Division. M. Lucherini was supported by an international fellowship from the Ministero della Publica Istruzione (Italy). We thank the many people that helped us capture and observe bighorn sheep over 20 years. Earlier drafts of the manuscript were constructively reviewed by S. D. Albon, J. Berger, J. T. Hogg, W. J. King, N. Lunn, and S. C. Stearns. This is contribution number 86 of the Groupe de recherches en écologie, nutrition et énergétique.

LITERATURE CITED

Albon, S. D., T. H. Clutton-Brock, and F. E. Guinness. 1987. Early development and population dynamics in red deer. II. Density-independent effects of cohort variation. Journal of Animal Ecology **56**:69–81.

Albon, S. D., B. Mitchell, and B. W. Staines. 1983. Fertility and body weight in female red deer: a density-dependent relationship. Journal of Animal Ecology **52**:969–980.

Bailey, J. A. 1991. Reproductive success in female mountain goats. Canadian Journal of Zoology **69**:2956–2961.

Bell, G. 1980. The costs of reproduction and their consequences. American Naturalist **116**:45–76.

Bell, G., and V. Koufopanou. 1986. The cost of reproduction. Pages 83–131 *in* R. Dawkins and M. Ridley. Oxford surveys in evolutionary biology. Oxford University Press, Oxford, England.

Bérubé, C. 1993. L'investissement maternel différentiel en fonction du sexe du jeune chez le mouflon des Rocheuses (*Ovis canadensis*). Thesis. Université de Sherbrooke, Sherbrooke, Quebec, Canada.

Clark, M. M., C. A. Spencer, and B. G. Galef. 1986. Reproductive life history correlates of early and late sexual maturation in female Mongolian gerbils (*Meriones unguiculatus*). Animal Behaviour **34**:551–560.

Clutton-Brock, T. H., editor. 1988. Reproductive success. University of Chicago Press, Chicago, Illinois, USA.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1988. Reproductive success in male and female red deer. Pages 325–343 *in* T. H. Clutton-Brock, editor. Reproductive success. University of Chicago Press, Chicago, Illinois, USA.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1983. The costs of reproduction to red deer hinds. Journal of Animal Ecology **52**:367–383.

Clutton-Brock, T. H., O. F. Price, S. D. Albon, and P. A. Jewell. 1992. Early development and population fluctuations in Soay sheep. Journal of Animal Ecology **61**:381–396.

Cole, L. C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology **29**:103–137.

Festa-Bianchet, M. 1988*a*. Age-specific reproduction of bighorn ewes in Alberta, Canada. Journal of Mammalogy **69**: 157–160.

———. 1988*b*. Birthdate and survival in bighorn lambs (*Ovis canadensis*). Journal of Zoology **214**:653–661.

———. 1988*c*. Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate and sex. Animal Behaviour **36**:1445–1454.

———. 1988*d*. A pneumonia epizootic in bighorn sheep, with comments on preventive management. Biennial Symposium of the Northern Wild Sheep and Goat Council **6**: 66–76.

———. 1988*e*. Seasonal range selection in bighorn sheep:

conflicts between forage quality, forage quantity, and predator avoidance. Oecologia **75**:580–586.

———. 1989. Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). Journal of Animal Ecology **58**:785–795.

Gaillard, J.-M., A. J. Sempéré, J.-M. Boutin, G. V. Laere, and B. Boisaubert. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). Canadian Journal of Zoology **70**:1541–1545.

Green, W. C. H., and A. Rothstein. 1991. Trade-offs between growth and reproduction in female bison. Oecologia **86**: 521–527.

Harvey, P. H., and R. M. Zammuto. 1985. Patterns of mortality and age at first reproduction in natural populations of mammals. Nature **315**:319–320.

Huber, H. R. 1987. Natality and weaning success in relation to age of first reproduction in northern elephant seals. Canadian Journal of Zoology **65**:1311–1316.

Jorgenson, J. T., M. Festa-Bianchet, M. Lucherini, and W. D. Wishart. 1993*a*. Effects of body size, population density and maternal characteristics on age of first reproduction in bighorn ewes. Canadian Journal of Zoology **71**:2509–2517.

Jorgenson, J. T., M. Festa-Bianchet, and W. D. Wishart. 1993*b*. Harvesting bighorn ewes: consequences for population size and trophy ram production. Journal of Wildlife Management **57**:429–435.

Jorgenson, J. T., J. Samson, and M. Festa-Bianchet. 1990. Field immobilization of bighorn sheep with xylazine hydrochloride and antagonism with idazoxan. Journal of Wildlife Diseases **26**:522–527.

Jorgenson, J. T., and W. D. Wishart. 1984. Growth rate of Rocky Mountain bighorn sheep on Ram Mountain, Alberta. Biennial Symposium of the Northern Wild Sheep and Goat Council **4**:270–284.

King, W. J., M. Festa-Bianchet, and S. E. Hatfield. 1991. Determinants of reproductive success in female Columbian ground squirrels. Oecologia **86**:528–534.

Leader-Williams, N., and C. Ricketts. 1982. Seasonal and sexual patterns of growth and condition of reindeer introduced into South Georgia. Oikos **38**:27–39.

LeBoeuf, B. J., R. Condit, and J. Reiter. 1989. Parental investment and the secondary sex ratio in northern elephant seals. Behavioral Ecology and Sociobiology **25**:109–117.

Lessels, C. M. 1991. The evolution of life histories. Pages 32–68 *in* J. R. Krebs and N. B. Davies, editors. Behavioural ecology. Third edition. Blackwell, Oxford, England.

Lunn, N. J., I. L. Boyd, and J. P. Croxall. 1994. Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. Journal of Animal Ecology **63**:827–840.

Mitchell, B., D. McCowan, and I. A. Nicholson. 1976. Annual cycles of body weight and condition in Scottish red deer. Journal of Zoology **180**:107–127.

Miura, S., I. Kita, and M. Sugimura. 1987. Horn growth and reproductive history in female Japanese serow. Journal of Mammalogy **68**:826–836.

Noordwijk, A. J. v., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist **128**:137–142.

Ozoga, J. J., and L. J. Verme. 1986*a*. Initial and subsequent maternal success of white-tailed deer. Journal of Wildlife Management **50**:122–124.

Ozoga, J. J., and Verme, L. J. 1986*b*. Relation of maternal age to fawn-rearing success in white-tailed deer. Journal of Wildlife Management **50**:480–486.

Ozoga, J. J., L. J. Verme, and C. S. Bienz. 1982. Parturition behavior and territoriality in white-tailed deer: impact on neonatal mortality. Journal of Wildlife Management **46**:1–11.

Partridge, L. 1992. Measuring reproductive costs. Trends in Ecology and Evolution **7**:99–100.

Pemberton, J. M., S. D. Albon, F. E. Guinness, and T. H. Clutton-Brock. 1991. Countervailing selection in different fitness components in female red deer. Evolution **45**:93–103.

Potvin, C., M. J. Lechowicz, and S. Tardif. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. Ecology **71**:1389–1400.

Reimers, E. 1983. Reproduction in wild reindeer in Norway. Canadian Journal of Zoology **61**:211–217.

Reiter, J., and B. J. LeBoeuf. 1991. Life history consequences of variation in age at primiparity in northern elephant seals. Behavioral Ecology and Sociobiology **28**: 153–160.

Reiter, J., K. J. Panken, and B. J. LeBoeuf. 1981. Female competition and reproductive success in northern elephant seals. Animal Behaviour **29**:670–687.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos **44**:257–267.

———. 1992. Measuring the costs of reproduction. Trends in Ecology and Evolution **7**:42–45.

Sæther, B.-E., and H. Haagenrud. 1983. Life history of the moose (*Alces alces*): fecundity rates in relation to age and carcass weight. Journal of Mammalogy **64**:226–232.

Sæther, B.-E., and M. Heim. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. Journal of Animal Ecology **62**:482–489.

Seip, D. R., and F. L. Bunnell. 1985. Nutrition of Stone's sheep on burned and unburned ranges. Journal of Wildlife Management **49**:397–405.

Smith, J. N. M. 1981. Does high fecundity reduce survival in song sparrows? Evolution **35**:1142–1148.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Freeman, San Francisco, California, USA.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, England.

Sydeman, W. J., H. R. Huber, S. D. Emslie, C. A. Ribic, and N. Nur. 1991. Age-specific weaning success of northern elephant seals in relation to previous breeding experience. Ecology **72**:2204–2217.

Thomas, D. C. 1982. The relationship between fertility and fat reserves of Peary Caribou. Canadian Journal of Zoology **60**:597–602.