Effects of body size, population density, and maternal characteristics on age at first reproduction in bighorn ewes

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The factors affecting variation in age at first reproduction of bighorn ewes (*Ovis canadensis*) were investigated in two marked populations in Alberta. One population was studied for 20 years, the other for 11 years. As yearlings, females that lactated at 2 years of age were on average heavier and larger, and had longer horns than females that did not lactate at 2 years. However, there was wide overlap in body mass between early and late producers, and increases in body mass over the threshold for reproduction had little effect on the probability of early lambing. The body mass of females at 4 months of age explained less than half of the variance in female body mass at 1 year or at 15 months. In one population, the proportion of 2-year-old ewes lactating was not correlated with density and declined after a pneumonia epizootic. In the other population, the proportion of 2-year-old ewes lactating was higher during an experimental reduction of density, and dropped to near zero as density increased. There was a significant interaction effect of body mass and population density upon the probability that a ewe would lactate at 2 years of age. Independently of body mass, yearlings were less likely to lactate at 2 years of age at high population density than at low density. The number and age distribution of rams did not affect the proportion of 2-year-old ewes lactating. The mothers of lactating 2-year-olds were not older or heavier than the mothers of ewes that did not lactate at 2 years. Although some of the variation in age at first reproduction was due to differences in mass and population density, much of it remained unexplained and could be due to genetic factors.

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Cette étude porte sur les facteurs responsables de la variabilité de l'âge à la première reproduction des femelles de deux populations marquées du Mouflon d'Amérique (*Ovis canadensis*) en Alberta. Une population a été étudiée pendant 20 ans, l'autre pendant 11 ans. À l'âge de 1 an, les femelles qui allaitaient à 2 ans étaient en moyenne plus lourdes, de plus grande taille et munies de cornes plus longues que les femelles qui se sont reproduites pour la première fois à un âge plus avancé. Cependant, il y avait un chevauchement important entre la masse corporelle des femelles à reproduction hâtive et celle des femelles à reproduction tardive et, chez les femelles pesant plus que le minimum nécessaire à la reproduction, les augmentations de masse avaient peu d'effet sur la probabilité de grossesse hâtive. La masse corporelle des femelles à l'âge de 4 mois expliquait moins de la moitié de la variance de la masse corporelle des femelles à l'âge de 1 an ou de 15 mois. Chez une population, la proportion des femelles nourricières de 2 ans n'était pas en corrélation avec la densité et elle a diminué après une épidémie de pneumonie. Chez l'autre population, la proportion de femelles de 2 ans nourricières était plus élevée à la suite d'une réduction expérimentale de la densité de population et était presque nulle après la remontée de la densité. On a relevé une interaction significative entre les effets de la masse corporelle et ceux de la densité de la population sur la probabilité qu'une femelle allaite ou non à l'âge de 2 ans. Indépendamment de leur masse corporelle, les jeunes femelles de 1 an avaient une probabilité moindre d'allaiter à 2 ans lorsque la densité de la population étaient élevée que lorsqu'elle était faible. Le nombre de béliers et leur distribution d'âges n'ont eu aucun effet sur le nombre de femelles de 2 ans qui allaitaient. Les femelles qui se sont reproduites à un jeune âge n'étaient pas issues de mères particulièrement âgées ou de masse élevée. Bien qu'une partie de la variabilité de l'âge à la première reproduction soit attribuable à des différences de masse et de densité de la population, une grande partie de cette variabilité reste inexpliquée et pourrait être attribuée à des facteurs génétiques.

Introduction

The age at which females first reproduce is of considerable interest to those developing life-history theories and can profoundly affect population dynamics (Cole 1954; Stearns 1992). Females face a trade-off between selection to reproduce as early as possible and the potential reproductive costs of early breeding (Huber 1987; Reiter and LeBoeuf 1991). Natural selection should favor a reproductive strategy that takes into account the average chances of successful reproduction at any age and the consequences of early breeding for subsequent survival and reproduction (Gadgil and Bossert 1970). For example, when the chances of survival are low, animals should breed as early as possible (Harvey and Zammuto 1985). On the other hand, early breeding may negatively affect survival (Kozlowski 1992), so that it may be difficult to interpret a correlation between early reproduction and survival: poor survival could be a selective pressure for early breeding but it may also be its consequence (i.e., a selective pressure against).

If early maturation affects subsequent survival and repro-

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duction by depleting body resources, individual differences in body size or in maternal condition should play an important role in determining which females mature early. Some studies of wild mammals reported that early reproduction is costly for females, lowering their survival or subsequent reproductive success compared with females that postpone their first breeding attempt (Huber 1987; Miura et al. 1987; Reiter and LeBoeuf 1991). Other studies, however, have found that precocious breeders have the same or better survival and reproductive success than females that breed at a greater age (Festa-Bianchet 1989*a*; Green and Rothstein 1991*b*; King et al. 1991; Ozoga and Verme 1986). In the latter studies, early breeders were often larger or in better body condition than late breeders.

Like our study, those quoted above were conducted on seasonally breeding mammals that take more than 1 year to achieve adult body size. In these species, differences in age at first reproduction between early and late breeders are substantial (1 year or more), as are the differences in body mass between females of different ages. The seasonality of reproduction should play an important role in the evolution of reproductive strategy. For example, a young female in mediocre body condition during the breeding season will be faced with conflicting selective pressures. If she breeds, she will risk compromising her survival and body growth. The chances that her offspring will survive may be low (Festa-Bianchet 1988*a*; Huber 1987). If she does not breed, however, she will forgo reproduction for an entire year, possibly lowering her total reproductive success and facing the risk of dying before the next breeding season.

For seasonally breeding ungulates, a female's mass, independently of her age, is a major determinant of whether or not she will reproduce in a given year: there are population-specific threshold body masses above which most females reproduce and below which females do not reproduce (Albon et al. 1983; Sæther and Haagenrud 1983; Thomas 1982). Other than carcass mass of pregnant and nonpregnant females, however, there are few data comparing females that differ in age at first reproduction. Studies of red deer (*Cervus elaphus*) and feral sheep (*Ovis aries*) suggest that early development has major effects on subsequent reproductive success and body size (Albon et al. 1987; Clutton-Brock et al. 1987, 1992). Female yearling moose (*Alces alces*) that matured at 2.5 years were heavier than females that matured at 3.5 years (Sæther and Heim 1993). Bison (*Bison bison*) cows that produced their first calf at 2 years of age weighed about 30% more as yearlings than cows that had their first calf at an older age (Green and Rothstein 1991*b*). In roe deer (*Capreolus capreolus*), nonpregnant yearlings weighed about 12% less on average than pregnant yearlings, and all yearling females above the threshold mass of 20 kg were pregnant (Gaillard et al. 1992). In wild reindeer (*Rangifer tarandus*), pregnant yearlings had 32% more mass at the time of the rut than nonpregnant ones (Reimers 1983). We expected similar relationships of body mass and age of first reproduction for bighorn sheep ewes and predicted that early breeders should have been larger on average than other females of the same age.

The relationship between body mass and age at first breeding may vary with population density. In red deer, the minimum mass at which females of any age reproduce is greater at high than at low population density (Albon et al. 1983). Albon et al. (1983) suggested that because the mortality of small females and lactating females increases with density, a small female that calves in a high-density population faces a high risk of death. Similarly, at high population density females may postpone their first reproduction even if they reached a high body mass early in life.

In Dall sheep (*Ovis dalli*), it was proposed (Heimer and Watson 1982) that the number and age distribution of rams may affect the frequency of breeding among yearling ewes, because many young rams may induce ovulation in young ewes through persistent courtship. Alternatively, a low ram:ewe ratio may reduce the changes for young females to breed.

Here we examine the correlates of variation in age of first lambing in bighorn ewes (*Ovis canadensis*) in two populations in Alberta, Canada, with widely different population dynamics: one population was affected by a pneumonia epizootic (Festa-Bianchet 1988*b*), while the other was first subjected to 10 years of experimental ewe removals, and then more than doubled in size with no signs of pneumonia (Jorgenson et al. 1993). Primiparous ewes ranged in age from 2 to 6 years, but because only 13% of ewes did not reproduce until 4 years of age or later, we focused on two groups of ewes: those that produced their first lamb at 2 years of age (therefore bred at 18 months of age), and those that did not. We predicted that, compared with late producers, early producers would have been larger as lambs and as yearlings. We predicted that high population density would decrease the proportion of ewes that produced lambs at 2 years of age. We also compared age at first reproduction for the daughters of early and late producers, and tested for correlations between ram numbers, ram age structure, and the frequency of lambing among 2-year-old ewes.

Study areas, populations, and methods

General

The reproductive status of 2-year-old ewes was assessed by checking for the presence of a suckling lamb or the development of the udder (either visible during observations or found to contain milk at capture). We could not detect pregnancies in ewes that failed to show any sign of lactation, or in ewes that did not carry their pregnancy to term. In this paper, we refer to ewes that showed signs of lactation at 2 years of age as early producers, and to other ewes as late producers. For statistical analyses we utilized the SPSS package, and probability values are two-tailed unless otherwise indicated. Means are reported with standard deviations.

Ram Mountain

Ram Mountain is an isolated outcrop in western Alberta (52°N, 115°W), separated from the main Rocky Mountain range by about 30 km of coniferous forest. Elevations range from 1082 to 2173 m and the sheep use approximately 38 km^2 of alpine and subalpine habitat. Data were collected between 1974 and 1991. A corral trap baited with salt allowed multiple captures of almost all ewes in the population each year, and over 95% of individuals in the population were marked with plastic ear tags and canvas collars in most years of the study. At each capture, sheep were weighed with a spring scale to within 125 g and their horns measured with a tape to within 1 mm. Trapping usually began in late May and continued until late September or early October. Further details can be found in Jorgenson et al. (1993). Between 1972 and 1980 we kept the population at low density (95–110 sheep) by removing 12–24% of the adult ewes each year through shooting or transplants. Ewe removals ceased in 1981. Rams with horns over 4/5 of a curl were hunted from late August to October,

Because almost all sheep were individually recognizable and the study area was easy to census, we obtained total counts for all sex- and age-classes during the summer. Lambs were more difficult to capture, but in most years over 80% were caught and tagged. We identified the mothers of over 90% of tagged lambs from suckles and associations with marked ewes. Unmarked lambs that survived the winter were caught as yearlings. Sheep that disappeared were assumed to have died, and it was rare for sheep recorded as missing one year to reappear in a subsequent year (2 ewes and 5 rams out of approximately 2500 sheep-years). Permanent emigration to other populations was possible, but reports of Ram Mountain tagged sheep in other populations were rare (one ram and four yearlings).

Body mass in all sex- and age-classes increased during the trapping season (Jorgenson and Wishart 1984). For most analyses we wanted to compare the body mass of different groups of ewes at the beginning and end of summer. Linear regression was used to adjust the mass of female lambs to a common date. Date of capture was coded from 0 to 140, with May 25 as day 1. September 15 (day 114) was chosen as the date for our late-summer lamb mass comparisons because the growth of lambs was linear every year up to the end of September (Fig. 1), but few captures were available in late September in some years. Only lambs captured later than day 64 (July 27, fifty days before September 15) were used in the analysis. For lambs with multiple captures, and with at least 40 days between first and last capture, we calculated individual growth rates and used them to adjust lamb mass to day 114. For lambs that were only caught once in a summer, we used the slope of mass on date calculated for each year as follows: we first fitted a linear regression on date for all female lamb captures. Standardized residuals were calculated, and points that were more than 2 SD off the regression were dropped. The regression was recalculated and the resulting slope was used to adjust individual body mass to September 15. The average time between adjusted and measured mass was 22 days (±14). On average, lambs were captured 1.4 times each during the summer. We caught 225 female lambs between 1974 and 1991, for a total of 323 captures.

Capture frequency for yearlings was greater than for lambs. Between 1975 and 1991, 141 yearling ewes were caught on average 2.7 times each during summer, for a total of 387 captures. Only body mass measurements collected up to September 6 (day 105) were considered, because in most years the growth of yearling females was linear until then but became quadratic after about day 109–115 (Fig. 1). Together with the low number of captures after mid-September in some years, the quadratic growth in late summer made it less reliable to adjust mass for later than about September 3 (day 102). Individual growth rates were calculated for each yearling female that had been caught twice or more, with at least 40 days between first and last capture. The individual growth rate was used to adjust mass for June 5 and September 3, provided that in each case a body mass measurement was available within 50 days of these dates. For the other yearling females, an overall regression of mass on date for all yearling female captures for the same year was calculated and the slope used to adjust mass to June 5 or September 3, provided that one of these dates was within 50 days of her capture. These regressions were calculated with the same criteria for dropping outliers used for lambs. The average time between adjusted and measured mass was only 9.6 days (±9.0) for June, and 18.6 (±12.1) days for September. Over-winter mass change was calculated by subtracting mass as a lamb on September 15 from mass as a yearling on June 5 the following year. June 5 was chosen as early summer mass because in some years few captures were available before the first few days of June.

We first compared body and horn size of early and late producers using parametric statistics; then we tested the effects of population density and body mass at 4, 12, and 15 months using logistic regressions (Cox 1970) to see if the probability of lambing at 2 years of age (coded as a binary variable: 0 for no and 1 for yes) changed significantly with variation in body mass, population density, and weather variables (Clutton-Brock et al. 1987; Green and Rothstein 1991*a*).

To test the hypothesis that early lambing is affected either by the number or the age distribution of rams (Heimer and Watson 1982), we compared the total number of rams, the number of young (2–4

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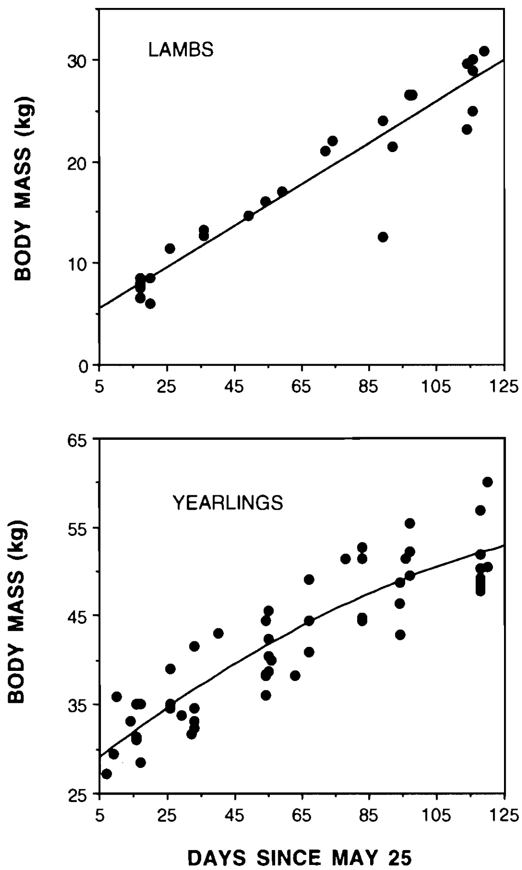

FIG. 1. Seasonal increase in body mass for female lambs in 1982, and for female yearlings in 1979, at Ram Mountain, Alberta. These years were chosen as representative because they had the largest sample sizes. The increase in body mass of lambs was linear (mass = 4.1 ± 0.20(date); r^2 = 0.91); the increase in body mass of yearlings was quadratic (mass = 27.5 + 0.30(date) − 0.001(date)^2; r^2 = 0.80) but was linear up to day 105 (mass = 28.8 + 0.23(date); r^2 = 0.78).

years of age) rams, and the number of mature (5 years and older) rams with the number and percentage of 2-year-old ewes that produced lambs the following year. We also repeated these analyses looking at the ram:ewe ratio to see if the number of rams available per ewe affects the probability of early lambing.

Sheep River

The Sheep River population was studied from 1981 to 1992. Descriptions of the study area and details of data collection techniques have been published elsewhere (Festa-Bianchet 1986*a*, 1986*b*, 1988*c*). This migratory herd winters in the Sheep River Wildlife Sanctuary and summers in the Rocky Mountains, 10–16 km west of the Sanctuary. A pneumonia epizootic in 1985–1986 killed approximately 40% of the sheep (Festa-Bianchet 1988*b*). Rams are hunted outside the Wildlife Sanctuary (Festa-Bianchet 1989*b*) and a limited entry ewe hunt results in an average kill of less than one ewe/year. About 40 sheep were caught in a corral trap but most were darted free-ranging (Jorgenson et al. 1990). At capture, we measured horn length, horn base circumference, heart girth, and hind foot length. The proportion of ewes marked with plastic ear tags increased from 40% (19 of 48) in 1981 to 85% (47 or 55) in 1982 and to 100% (49 of 49) in 1987. Data on reproductive success at 2 years of age were available for 75 marked ewes.

Because most sheep were captured only once, we could not calculate individual growth rates and we had insufficient data to calculate

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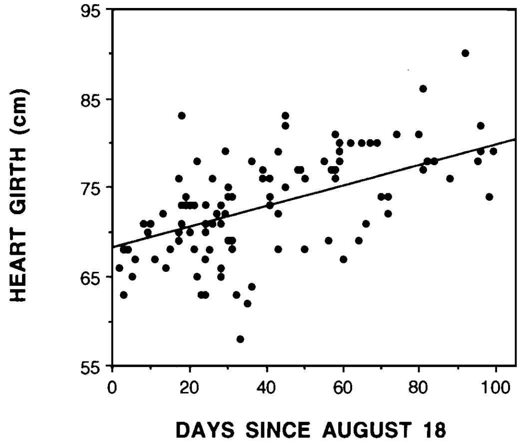

FIG. 2. Increase in heart girth for female lambs captured between August 18 and November 30 at Sheep River, Alberta, from 1981 to 1991. Heart girth increased linearly with date (girth = 68.2 + 0.11(date); r^2 = 0.29).

TABLE 1. Comparisons of body measurements (cm) for bighorn sheep females as lambs (4 months old) and yearlings (15 months old) that subsequently did (early producers) or did not (late producers) produce a lamb at 2 years of age at Sheep River, Alberta, 1981–1990

	Early producers			Late producers		
Measurement	Mean	SD	*N*	Mean	SD	*N*
Lambs						
Heart girth	74.8	5.42	11	73.7	4.92	27
Horn base circumference	8.2	0.37	11	7.9	1.23	26
Horn length	5.9	0.87	11	5.9	1.68	25
Hind foot	37.4	1.15	11	36.6	1.97	25
Yearlings						
Heart girth*	92.3	3.10	14	87.6	5.29	6
Horn base circumference	12.7	0.82	15	12.5	2.13	7
Horn length**	17.3	0.86	15	14.4	1.44	7
Hind foot	41.6	1.50	15	40.5	1.10	7

*P < 0.05.
**P < 0.01, t tests.

separate regressions for each year. Therefore, to compare body size of early and late producers, we calculated a single regression for all lambs caught between August 18 (day 0) and November 30 (day 104) and adjusted individual measurements to September 29 (day 42), the average date of female lamb captures. Body measurements increased linearly during this period, although there was considerable scatter in the data (Fig. 2). No lambs were caught before August 18.

Our sample of body measurements of yearling females from Sheep River was limited to 22 individuals. We fitted a linear regression through these data and adjusted measurements for August 16, the average date of yearling female capture.

Results

Effects of body size

Body size differed between study areas; the Ram Mountain sheep are small and the Sheep River sheep are among the largest in North America (Blood et al. 1970). Yearling ewes at Sheep River in early September had longer horns (14.7 ± 3.0 cm vs. 13.0 ± 2.5 cm; t_{132} = 3.00, P = 0.003) and greater heart girths (99 ± 7.6 cm vs. 89 ± 4.3 cm; t_{89} = 7.68, P = 0.0001) than yearling ewes at Ram Mountain.

TABLE 2. Comparisons of body mass (kg) and change in body mass during winter for bighorn sheep females that subsequently did (early producers) or did not (late producers) produce a lamb at 2 years of age at Ram Mountain, Alberta, 1973–1991

	Early producers			Late producers		
Age	Mean	SD	*N*	Mean	SD	*N*
4 months	29.2	3.36	13	27.5	4.57	78
4 to 12.5 months[a]	1.8	3.19	11	0.9	3.50	61
12.5 months***	31.3	2.98	33	28.9	4.09	109
15.5 months***	48.8	4.24	23	44.1	5.61	94

[a]Average overwinter mass change for individual ewes weighed in late summer one year and in late spring the following year.
***P < 0.001, t test.

At Ram Mountain, heart girth and horn length were correlated with body mass. The correlation of heart girth and mass for yearling ewes was 0.87 (N = 237, P < 0.001), and between mass and horn length was 0.42 (N = 308, P < 0.001). Therefore, even though we analyzed differences in heart girth at Sheep River and in body mass at Ram Mountain, our comparisons between early and late producers likely reflected related measures of body size.

As lambs, early producers at Sheep River were not significantly different in body measurements from late producers (Table 1), and there were no differences in body size of lambs with respect to age at first lambing when comparisons were limited to the five cohorts with at least one early producer. Among yearlings (15 months), early producers had longer horns and greater heart girth than late producers (Table 1).

At Ram Mountain, early producers were on average heavier than late producers as yearlings at 12 and 15 months of age (Table 2). At 4 months, however, the difference between early and late producers was not significant (Table 2). Mass change over the first winter was not different for ewes that did and did not breed at 18 months (Table 2). Most of the ewes that lambed at 2 years (28 of 34) were born during the experimental ewe removal (Jorgenson et al. 1993), and limiting the analysis to those years resulted in the same significant differences reported in Table 2.

Although early producers were on average heavier than late producers, there was considerable overlap in mass between the two groups. For example, considering only the years of ewe removal, very few late producers were lighter than the smallest early producer (Fig. 3). The probability of early lambing was 0% (N = 25) for ewes under 26 kg in early June, 26% (N = 50) for ewes between 26 and 30 kg, and 30% (N = 67) for ewes of more than 30 kg. If comparisons were limited to ewes at least as heavy as the smallest early producer, early and late producers did not differ significantly in mass at any of the three ages above, according to t tests.

Early development may affect the age of first reproduction if body masses of the same ewes at different ages are closely correlated. Masses at different ages were correlated, but more than half of the variance was left unexplained (Fig. 4). For example, mass at 4 months explained 46% of the variance in mass at 12 months (N = 79, P < 0.001), and the mass of yearlings in June explained 47% of the variance in mass only 3 months later (N = 122, P < 0.001). Mass at 4 months explained only 34% of the variance in mass 1 year later (N = 68, P < 0.001). Similar relationships were found when early and late producers were considered separately, but the corre-

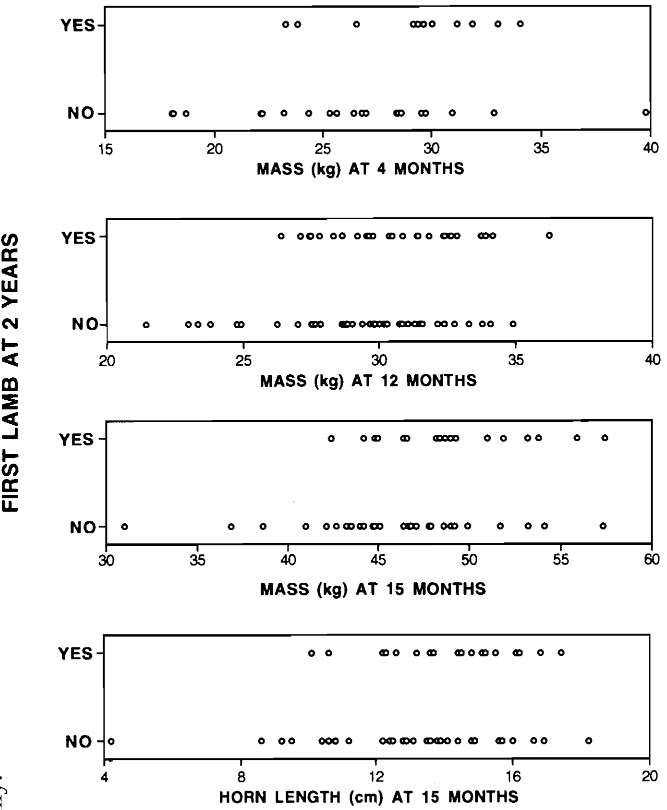

FIG. 3. Mass at different ages of female bighorn sheep that did (YES) and did not (NO) produce their first lamb at 2 years of age at Ram Mountain, Alberta. Cohorts born between 1974 and 1982.

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lations between the mass of lambs and yearlings for early producers were not significant, possibly because of the small sample (mass at 4 and 12 months; r^2 = 0.34, N = 11, P = 0.06; mass at 4 and 15 months: r^2 = 0.27, N = 10, P = 0.12).

To determine whether summer growth as a yearling affected the probability of early lambing, we compared the residuals from the regression of mass at 12 and 15 months for early and late producers (Fig. 4). When all years of the study were considered, early producers grew faster than late producers because their residuals were greater (2.16 ± 3.42 cm vs. −0.12 ± 4.06 cm; t_{100} = 2.35, P = 0.02). This result, however, was biased by the lower summer growth of yearlings in high-desity years when the proportion of early producers was lower than at low density. If the comparison is limited to years when most of the early lambing took place (1974−1984), the difference is not significant (0.84 ± 3.14 cm vs. −0.36 ± 3.68 cm, t_{50} = 1.19, P = 0.24).

At Ram Mountain there was a significant difference in horn length between early (N = 22, $\bar{X}$ = 14.1 ± 1.8 cm) and late producers (N = 83, $\bar{X}$ = 12.4 ± 2.6 cm) (t = 2.92, P = 0.004). Using only cohorts born during the removal experiment, the trend remained (early producers: $\bar{X}$ = 14.1 ± 1.9 cm, N = 20; late producers: $\bar{X}$ = 12.9 ± 2.7 cm, N = 38) and the difference was significant if a one-tailed test was used (t = 1.74, P = 0.04).

Effects of population density and yearly differences

At Sheep River there was no relationship between the number of ewes 2 years of age and older and the prevalence of lactation among 2-year-olds the following year (Fig. 5; N = 11, r = 0.38, P = 0.27). The prevalence of lactation ranged from 60 to 67% while the population increased in the 4 years before the pneumonia (in 1981 no 2 year olds were marked before lambing). In the 6 years after the epizootic the prevalence of lactation among 2-year-olds ranged from 0 (3 years) to 80%. Overall, 25 of 39 two-year-olds (64%) produced lambs before the epizootic, but only 8 of 31 (26%) did so afterwards (G = 10.49, df = 1, P < 0.005). The average number of ewes was 60 before the pneumonia and 55 afterwards. It is unlikely that changes in body size caused the decline in lactation at 2 years of age, as there were no differences in heart girth or horn length between female lambs born up to 1983 (2 years old in 1985) and those born later (t tests; all P > 0.3).

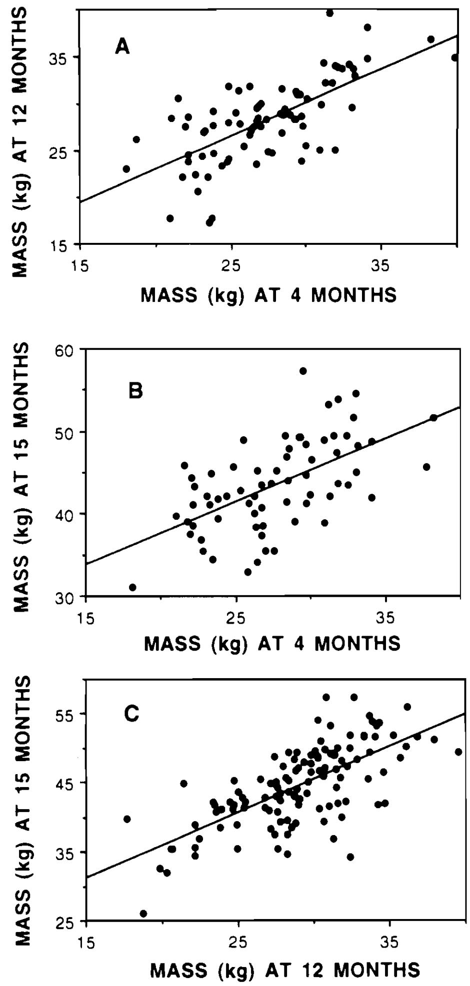

FIG. 4. Correlations between body masses of the same bighorn ewes at different ages at Ram Mountain, Alberta, 1975−1991. A. Four months and 1 year (y = 8.8 + 0.71x). B. Four months and 15 months (y = 22.3 + 0.76x). C. One year and 15 months (y = 16.9 + 0.95x).

At Ram Mountain very few ewes were lactating at 2 years after the population was allowed to increase (Fig. 5). The correlation between ewe numbers and the prevalence of lactation among 2 year olds the following year was significant (r = −0.57, P < 0.05). It was clear, however, that the relationship between these variables was not linear (Fig. 5). Attempts to fit polynomial or exponential curves were unsuccessful, likely because of the distribution of years when no 2-year-olds lactated. During the low-density years (30−50 adult ewes), the

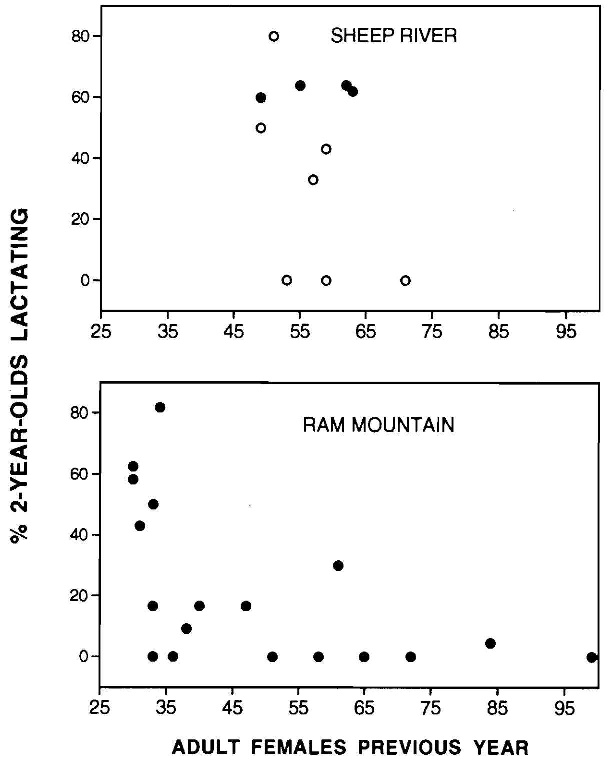

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FIG. 5. Proportion of 2-year-old bighorn sheep females lactating at Sheep River and at Ram Mountain, Alberta, plotted against the number of adult ewes in the population during the previous summer. At Sheep River, solid circles (●) refer to years before the pneumonia epizootic (1982–1985) and open circles (○) refer to years after the epizootic (1986–1992). Yearly samples ranged from 3 to 14 and averaged 7. At Ram Mountain (1975–1992), yearly samples of 2-year-old females ranged from 6 to 22 and averaged 10.

frequency of lactation among 2-year-olds varied from 0 to 82% and averaged 32%. After the population increased beyond 50 ewes, no 2-year-olds lactated in 5 of 7 years, and the yearly average was 5%.

Winter weather affects the growth of yearling females (J.T. Jorgenson and M. Festa-Bianchet, unpublished data), and we attempted to explain additional variance in the prevalence of lactation among 2-year-olds through multiple regression with ewe population size and weather variables. None of the variables considered (winter precipitation, winter temperature, summer precipitation), however, contributed significantly to the regression models.

Effects of ram numbers

The number of rams 2 years of age and older in the Ram Mountain population varied from 26 to 61 ($\bar{X} = 38 \pm 10$) in 1974–1991 (age distribution of rams in earlier years was not accurately known). Rams aged 2–4 years ranged in number from 8 to 45 ($\bar{X} = 24 \pm 10$) and older rams from 8 to 20 ($\bar{X} = 13 \pm 4$). Generally, there were more rams per ewe at low than at high population density because the number of ewes increased more rapidly than the number of rams (Jorgenson et al. 1993). For example, the ratio between rams older than 4 years and ewes averaged 0.41 in 1974–1983, but only 0.19 in 1984–1991. The proportion of ewes producing lambs at 2 years of age was negatively correlated with the number of young rams, opposite to the prediction of Heimer and Watson (1982) ($r = -0.49$, $N = 18$, $P = 0.03$). There was a correlation between the ratio of rams older than 4 to adult ewes and the percentage of 2-year-old ewes that produced lambs the following year ($r = 0.50$, $N = 18$, $P = 0.03$). However, when we limited comparisons to 1974–1983 (to remove the effects of increasing ewe density) none of the correlations was significant.

When all years of data were analyzed, with ewe numbers controlled by partial correlation, none of the relationships between ram numbers and lactation among 2-year-old ewes remained significant (partial correlation of the percentage of 2 year olds lactating with older rams per ewe: $r = 0.22$, df = 15, $P = 0.2$; with the number of young rams: $r = -0.11$, $P = 0.3$). The partial correlation between the number of ewes and the percentage of 2-year-olds lactating, controlling for variation in the ram:ewe ratio, was also not significant ($r = -0.33$, $P = 0.1$). We could not repeat these tests for Sheep River because we did not have sufficiently accurate information on ram age distribution.

Interaction of population density and body mass

Ewes may breed at 18 months if they are heavier than a threshold value, but the wide range and overlap in mass of early and late producers argues against a fixed threshold. Therefore, we considered how the relationship between body mass and age at first reproduction varied with changes in population density at Ram Mountain.

As density increased, the summer growth rate of yearling females declined, from 0.20 ± 0.04 kg/day during the removal years to 0.16 ± 0.05 kg/day in the last 2 years of the study (comparing average yearly summer growth rate; $N = 17$ years, $r = -0.63$, $P = 0.007$). Therefore, ewe density could have affected the frequency of early lambing by lowering the yearling female growth rate. This was not the case: the regression of early September mass of yearling females on ewe number was significant ($r = -0.43$, $N = 116$, $P < 0.001$), but logistic regression indicated that both body mass at 15 months and adult ewe density had independent effects upon the probability that a ewe would be an early producer. Density improved the logistic regression model containing a constant alone ($\chi^2 = 60.45$, df = 1, $P < 0.001$), and yearling mass improved the model with a constant and ewe density ($\chi^2 = 7.65$, df = 1, $P = 0.006$). Attempts to better predict whether individual ewes would or would not lamb early by including weather variables in logistic regressions, or by simple correlations between weather and proportion of 2-year-olds that lactated, were unsuccessful.

Our attempts to test the hypothesis that the average mass of early producers increases with density were somewhat inconclusive because few 2-year-old ewes lambed at high population density (Fig. 5) and our results differed depending on whether we analyzed yearling mass in late summer (September 3) or in early summer (June 5). In the logistic regression comparing the probability of early lambing with ewe number and mass as a yearling on June 5, both variables improved the model significantly, and so did their interaction term ($\chi^2 = 4.04$, df = 1, $P = 0.04$), suggesting that the effect of body mass on the probability of early lambing changed with population density. The interaction between mass on September 3 and density was not significant at the 0.05 level ($P = 0.09$). Comparing the differences in mass between late and early producers at high and low population density, we found no effects of density on September mass. In early June the average mass of future early producers was only 5.7% more than that of late pro-

TABLE 3. Number of bighorn sheep ewes that produced their first lamb at 2 years of age, according to the age at which their mothers produced their first lamb

	Age at first lambing		
		Daughter	
Study area	Mother	2 yr	>2 yr
Sheep River	2 yr	5	10
	>2 yr	1	4
Ram Mountain	2 yr	4	13
	>2 yr	8	12

NOTE: Sheep River data are for 1983–1992, Ram Mountain data are for 1976–1983. None of the differences are significant relative to the age of the mother (*G* tests).

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ducers at low population density, but at high density it was 17.4% more than that of late producers. Among those born during the removal experiment, 53% of 30 ewes weighing more than 30 kg on June 5 were lactating at age 2. For ewes born later, only 11% of 37 that weighed more than 30 kg on June 5 were lactating at age 2 ($G = 14.88$, df = 1, $P < 0.001$).

Maternal effects

We hypothesized that the mothers of early producers would be mostly ewes 4 years of age and older that had completed body growth (Jorgenson and Wishart 1984). Our data did not support this expectation. At Sheep River, early producers included 3 of 10 (30%) ewes born to mothers aged 2–3 years, and 12 of 32 (37%) ewes whose mothers were 4 years and older ($G = 0.188$, df = 1, $P > 0.5$).

At Ram Mountain, we also found no evidence that maternal age affected age at first lambing. Early producers included 7 of 29 (24%) ewes born to mothers aged 2 or 3 years and 17 of 101 (17%) ewes whose mothers were 4 years of age and older ($G = 0.76$, df = 1, $P > 0.2$). This result is biased because during the years of low density, when most of the reproduction among 2-year-olds occurred, many ewes were removed and few remained in the population past the age of 6 or 7 years. Therefore, older mothers made up a greater proportion of the population in the years of high density later in the study. Nevertheless, it was clear that early producers were not all daughters of mature ewes.

Pooling all years, at Ram Mountain early producers actually had lighter mothers (49 ± 8 kg, $N = 11$) than late producers (54 ± 7 kg, $N = 76$; $t_{85} = 2.0$, $P = 0.05$). The mass of mothers was adjusted to June 5 by using individual growth rates for ewes that were caught at least twice between days 0 and 60, when growth of adult ewes was linear (J.T. Jorgenson, M. Festa-Bianchet, and M. Lucherini, unpublished data). Maternal mass, however, was only available for 11 early producers, all from the low-density phase of the study. When the comparison is restricted to the years when data on lactating 2-year-olds were available, the average mass of mothers of late producers (49 ± 6 kg, $N = 23$) is similar to that of the 11 mothers of early producers reported above ($t_{32} = 0.09$, $P = 0.9$).

We had a small sample for our investigation of whether early reproduction was inherited. For Ram Mountain we limited the analysis to ewes born up to 1983 because early lambing was rare for ewes in later cohorts. We found no evidence in either study area that daughters of ewes that produced their first lamb at 2 years of age were more likely to breed early than daughters of ewes that postponed their first reproduction (Table 3).

Discussion

Body size during early development

In female bighorn sheep, mass during early development explained only a small part of individual variation in age at first reproduction. On average, ewes that first produced a lamb at 2 years were larger as yearlings and tended to be larger as lambs than ewes that postponed their first reproduction. At Ram Mountain there was no difference in the mass of yearlings according to age at first reproduction when the analysis excluded the few ewes smaller than the smallest reproducing yearling. Surprisingly, several yearling females with mass above the average for early producers did not lamb as 2-year-olds. Therefore, the effect of body mass on age at first reproduction in bighorn sheep was not as strong as reported by studies of early- and late-maturing females in bison, roe deer, reindeer, and moose (Gaillard et al. 1992; Green and Rothstein 1991*b*; Reimers 1983; Sæther and Heim 1993).

Rather than finding a close relationship between mass during early development and age at first reproduction, our analyses identified an age-specific minimum mass below which young females did not breed. Above this minimum, variation in mass had no significant effect on age of first lambing: at low population density, a 55-kg yearling was about as likely to produce a lamb the following spring as one with 20% less mass. Body mass did not have a major effect on age at first reproduction in bighorn sheep ewes: the only firm conclusion that we can draw from our analyses of body mass data is that very small yearling females do not lactate in the following year.

The results from Sheep River demonstrated a wide overlap in body size between early and late producers. There were no significant differences according to age at first lambing among lambs, and among yearlings differences were small. Although we did not measure body mass at Sheep River, we suggest that results from the two study areas are comparable because heart girth and horn length are correlated with body mass at Ram Mountain and in Dall sheep (Bunnell 1980). Therefore body mass, horn length, and heart girth can all be considered measurements of body size.

Body condition may be an important determinant of age at first reproduction: a small fat yearling may be more likely to breed at 18 months than a large but lean one. We suspect that heavy yearling females were both larger and fatter than light ones, but it is possible that differences in fat content may partly explain the wide overlap in mass between yearlings that first bred at 18 months and those that did not.

Population density

At Ram Mountain, lamb production by 2-year-old ewes declined after the population was allowed to increase (Fig. 5). The decline in early lambing among ewes could not be explained by a density-dependent decrease in body mass among yearling females because differences in body mass could not fully account for the great difference in the prevalence of lactation among 2-year-olds at high and at low density. Instead, the interaction between body mass and population density suggests that at high density ewes of any given mass are less likely to be lactating at 2 years compared with ewes of the same mass at low

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population density. At high density, many yearling ewes surpassed the threshold mass for reproduction, but few of these heavy ewes produced lambs at 2 years of age. At high population density ewes may be selected to conserve body resources to ensure their own growth and survival, rather than using resources for reproduction. Albon et al. (1983) found that increases in population density reduced the probability that a female red deer of a given mass would be pregnant and suggested that at high density females avoided risky reproductive strategies. One prediction that follows from this hypothesis is that the cost of early reproduction should increase with high density, as reported for northern elephant seals (*Mirounga angustirostris*) (Reiter and LeBoeuf 1991). One potential alternative for bighorn sheep is that the cost of early lambing may not change with increasing population density, but the benefit may be lower if the probability of successfully rearing a lamb at 2 years of age declines at high density.

We do not know whether females that did not produce lambs at 2 years of age failed to conceive at 18 months, or if gestation was interrupted. The explanation we propose for the relationship between lambing at 2 years and population density, however, would still be valid if reduction of lactation among 2-year-olds was caused by termination of pregnancy rather than failure to conceive. In either case females would avoid the costs of late gestation and of lactation.

Population density had an effect on the proportion of ewes producing lambs at 2 years at Ram Mountain but not at Sheep River. The larger size of Sheep River ewes compared with Ram Mountain ewes may have facilitated early lambing, even at high population density. The number of adult ewes (excluding yearlings) at Sheep River changed by 45% during our study (from 49 to 71), while at Ram Mountain it changed by 230% (from 30 to 99). Therefore, population density at Sheep River may not have reached a level where intraspecific competition affected the development of young ewes. Another possibility is that of a time lag: the probabilitiy of maturing early was perhaps not affected by density in the year of yearling age but by density 1 or 2 years earlier. However, we found no evidence to support this alternative. For example, none of the ewes born in 1988 and 1989 (N = 12) produced a lamb at 2 years, even though they were conceived, born, and raised at relatively low population density.

Number of rams

The number of rams did not seem to affect the proportion of yearling ewes that matured. Among domestic sheep, rams can induce estrus in ewes (Watson and Redford 1960), and it has been proposed that in wild sheep, young rams may court otherwise anestrous young ewes and induce ovulation (Heimer and Watson 1982). Our results from Ram Mountain do not support this hypothesis because the number of young rams was negatively correlated with the prevalence of lactation among 2-year-old ewes.

We found a correlation between the ratio of rams older than 4 years to the number of ewes, and the percentage of 2-year-old ewes that lactated. We suspect that this correlation was due to the slow increase in the number of mature rams after ewe removals ceased; when ewe density was high there were few older rams per ewe. The correlation was not evident (r = 0.03) when the analysis was restricted to the early years of the study during which ewe density varied little. The partial correlation of ewe density and the percentage of 2-year-old ewes lactating (controlling for variation in ram availability) was not quite significant, but the sample size was limited (18 years), and, more importantly, there were no years combining high ewe desity and high mature ram availability, or low ewe density and low ram availability. Therefore, there was limited statistical power to assess variation in the occurrence of early lambing with respect to one of these two variables while holding the other one constant. Because the partial correlation was not significant, however, our data cannot falsify the hypothesis that the availability of mature rams may interact with ewe density to affect the age at first lambing of bighorn ewes.

Maternal effects

Our studies did not reveal strong maternal effects upon age at first reproduction, similar to findings on moose (Sæther and Heim 1993). Two- and 3-year-old ewes have 5–20% less mass than older ewes (Jorgenson and Wishart 1984), but their daughters were as likely to lamb at 2 years as the daughters of older ewes, and maternal mass in June did not affect the daughter's age at first lambing. The overall trend for mothers of late producers to be heavier disappeared when analyses were limited to years of low density, and was probably due to a change in population age structure. Young (therefore light) mothers were less common in the later years, after ewe removals ceased. The inclusion of a greater proportion of old ewes in the sample of maternal mass for the high-density years (when very few 2-year-old ewes had lambs) may result in higher average mass. Nevertheless, the data suggest that maternal age and mass did not have a strong effect upon age at first reproduction.

Differences in maternal care that may be related to maternal mass may affect the mass of lambs, but the mass, as a lamb, of early and late producers did not differ significantly (Table 2). Correlations between masses of the same ewe as a lamb and as a yearling were weak (Fig. 4), possibly explaining in part the absence of maternal effects upon age at first reproduction. The slopes of regressions between body mass of ewes as lambs and as yearlings were less than 1 (Fig. 4), suggesting that some compensatory growth may have taken place among ewes that were small as lambs. Sæther and Heim (1993) compared mass as a calf and as a yearling for 13 female moose and found a correlation similar to that for bighorn sheep (r^2 = 0.45).

Removal of the mother when lambs were aged 3.5 to 4 months had no effect on the probability of producing the first lamb at 2 years (Festa-Bianchet et al. 1994); therefore maternal care at the end of lactation does not seem to affect age at first lambing. Differences in maternal care should have a greater effect upon daughters as lambs than as yearlings, and given the weak relationship between mass as a lamb and as a yearling, and between mass as a yearling and age at first reproduction, it is not surprising that maternal age and mass had no measurable effect upon age at first reproduction.

In our study we did not measure genetic differences among individuals. Comparing mothers and daughters did not reveal a strong inheritance of age at first reproduction, but the limited sample available did not allow us to account for year-to-year differences or differences in mass of individual females. Pemberton et al. (1991) found that genotype affected the age of first reproduction in female red deer once the effects of population density and weather were accounted for.

In conclusion, our studies suggest that body mass is not the sole determinant of when a young female will reproduce for the first time, and underline the importance of population density and individual characteristics as factors affecting age at primiparity. Compared with other ungulates, age at first reproduction in bighorn sheep seems to be less predictable on the basis of body size. Therefore, we hypothesize that the fitness consequences of variation in age at first reproduction may also be independent of body size during the first two years of life, and we are currently attempting to test this hypothesis.

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