

The development of sexual dimorphism: seasonal and lifetime mass changes in bighorn sheep

Marco Festa-Bianchet, Jon T. Jorgenson, Wendy J. King, Kirby G. Smith, and William D. Wishart

Abstract: Individually marked bighorn sheep (*Ovis canadensis*) were monitored to determine how seasonal and lifetime changes in mass affected the development of sexual dimorphism, and to what extent mass at a given age could predict mass of the same sheep at a later age. We trapped sheep from late May to early October each year from 1971 to 1985 in a population artificially kept at low density. Lambs and yearlings gained mass linearly from June to September, while absolute mass gain of older sheep was faster in June–July than in August–September. Males gained more mass than females each summer up to at least 3 years of age. Relative summer mass gain, calculated as a proportion of body mass at the beginning of June, was the same for male and female lambs but was greater for male than for female yearlings and 2-year-olds. With the exception of lambs, all age-classes lost mass during winter. Mass loss between September 15 and June 5 was greater for females than for males, possibly because ewes lost mass through parturition in late May. For both sexes, asymptotic mass was not reached until at least 7 years of age. Mass at 4 and 12 months of age was correlated with mass at 4 years. For all sex–age classes, mass on June 5 was negatively correlated with summer mass gain. For lambs and yearlings, winter mass loss was positively correlated with mass on September 15. Our results suggest that at low population density, sheep optimize rather than maximize summer mass accumulation. Most sexual dimorphism develops after weaning, through faster mass gain by males than by females at 1 and 2 years of age and possibly a longer season of mass gain each year for males than for females after females reach puberty.

Résumé : Nous avons étudié les changements de masse corporelle chez des Mouflons d'Amérique (*Ovis canadensis*) marqués individuellement au sein d'une population d'Alberta. Nous avons capturé les mouflons entre la fin mai et le début octobre, de 1971 à 1985. Le gain de masse des agneaux et des jeunes de 1 an était linéaire de juin à septembre, tandis que les mouflons plus âgés présentaient des gains de masse plus rapides en juin et juillet qu'en août et septembre. Les mâles ont gagné plus de masse que les femelles à chaque année, jusqu'à l'âge de 3 ans. Le gain relatif de masse, calculé par rapport à la masse corporelle au début de juin, était le même chez les agneaux et les agnelles, plus élevé chez les mâles de 1 an que chez les femelles de 1 an, et plus élevé chez les mâles de 2 ans que chez les femelles du même âge. En hiver, à l'exception des agneaux, les mouflons de toutes les classes d'âge ont subi des pertes de masse. Les femelles ont subi des pertes plus importants que les mâles entre le 15 septembre et le 5 juin, vraisemblablement à cause de l'agnelage à la fin mai. La masse moyenne a augmenté chez les deux sexes au moins jusqu'à l'âge de 7 ans. Il y avait une corrélation entre la masse des mouflons à 4 mois et à 12 mois et leur masse à l'âge de 4 ans. Pour toutes les classes de sexe et d'âge, la masse au 5 juin était en corrélation négative avec le gain de masse pendant l'été chez agneaux et les jeunes de 1 an, la perte de masse en hiver était en corrélation positive avec leur masse au 15 septembre. Nos résultats indiquent qu'à une faible densité de population les mouflons optimisent leur gain de masse plutôt que de le maximiser. C'est après le sevrage qu'apparaît le dimorphisme sexuel et on observe un gain de masse plus rapide chez les mâles que chez les femelles, à l'âge de 1 an et à l'âge de 2 ans. Il semble aussi que la période annuelle de gain de masse soit plus longue chez les mâles que chez les femelles après que celles-ci aient atteint la maturité sexuelle.

Introduction

Most ungulates in northern environments face a short growing season and a long season when forage is dormant and

inadequate to maintain body mass (Albon and Langvatn 1992; Blood et al. 1970; Crête et al. 1993; Houston et al. 1989; Leader-Williams and Ricketts 1982; Miura 1986). As a result, northern ungulates undergo annual fluctuations in body mass, often complicated by reproductive cycles (Houston et al. 1989; Leader-Williams and Ricketts 1982; Parker et al. 1993) and potentially adaptive seasonal changes in metabolic rate or food requirements (Bandy et al. 1970; Chappel and Hudson 1978).

There are few studies on long-term changes in body mass of individual wild ungulates, and little is known of how growth patterns vary among sex–age classes. Sex- and age-specific differences in seasonal mass changes are of interest from both a theoretical and a practical viewpoint (Stamps 1993). Different growth patterns (seasonal and lifetime) may reflect differences in reproductive strategies or in the relative

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importance of different selective pressures. For example, if early development has a strong effect upon adult mass (and, therefore, upon reproductive success), there might be stronger selective pressure favoring high maternal investment (especially for male offspring) than if adult body mass was largely dependent upon postweaning development.

Most temperate ungulates are sexually dimorphic, but it is unclear how much dimorphism originates from differences in age-specific growth rates (do males grow faster than females?) and how much from differences in growth period (do males grow for longer than females, either within a year or over several years?). Previous studies of mass changes in wild ungulates have relied on either small samples or on single measurements of individuals, and could not address individual variation in growth rate or in the shape of seasonal and lifetime growth curves.

Bighorn sheep (*Ovis canadensis*) are among the most sexually dimorphic of ungulates. At birth, however, males are only 10% heavier than females (Hogg et al. 1992) and little is known of how sexual dimorphism develops with age. Here we describe age- and sex-specific seasonal mass changes for bighorn sheep and examine individual variability in growth rate and age-specific body mass. Our objectives were to determine how sheep of different sex–age classes gain mass in summer, at what age each sex achieves its asymptotic mass, and to what extent individual sheep vary in mass from one year to the next.

For some ungulates, early development plays a major role in determining adult size and lifetime reproductive success (Clutton-Brock et al. 1987; Clutton-Brock et al. 1992). Other studies have found weak relationships between body masses of the same individual over intervals of 1 year or less, and no studies have compared mass at weaning with adult body mass. Mass of calf moose (*Alces alces*) explained 45% of the variance in mass in the same individuals 1 year later (Sæther and Heim 1993). In roe deer (*Capreolus capreolus*), birth mass was not correlated with mass at 8 months of age (Gaillard et al. 1993). In female bighorn sheep, mass at 4 months of age explains only 34% of the variance in mass 1 year later (Jorgenson et al. 1993a). Whether early development affects adult body mass has important implications for maternal investment strategy. Theories of parent–offspring conflict and parental investment assume that mass at weaning affects adult mass and reproductive success (Clutton-Brock and Godfray 1991; Trivers 1974). To test this assumption, we compared individual body mass during early development with adult body mass.

Materials and methods

We studied bighorn sheep at Ram Mountain, Alberta (52°N, 115°W, elevation 1082–2173 m). The techniques used to capture, mark, measure, and monitor individual sheep have been described previously (Jorgenson et al. 1993a) and will only be briefly summarized here. Most data were collected between 1973 and 1985, when the population was artificially limited to 30–51 adult ewes. Up to 24% of adult ewes were removed in September each year between 1972 and 1981, as explained in Jorgenson et al. (1993a). We captured sheep in a corral trap baited with salt. Trapping effort and success increased during the study; for example, captures of ewes 2 years and older increased from 1.1 captures per ewe each year in 1973–1974 to 2.0 in 1976–1977 to 3.2 in 1982–1983. Captured sheep

were weighed with a Detecto spring scale to within 125 g. The accuracy of the scale was tested every few weeks with known weights. Trapping began each year in late May or early June and ended in late September or early October.

Date of capture was coded with May 25 as day 1: this is the earliest date when sheep were caught and corresponds to the mean birthdate of bighorn sheep lambs in Alberta (Festa-Bianchet 1988a). Individual rates of mass gain were calculated for sheep caught at least twice with more than 30 days between captures. Mass was adjusted to June 5 (day 12) and September 15 (day 114) using individual growth rates, provided that an actual measurement was available within 50 days of these dates. When there were fewer than 30 days between first and last captures, but either day 12 or day 114 occurred between the two captures, we used the sheep's individual growth rate to adjust body mass but did not use that growth rate for other analyses. We chose to use individual rates of mass gain rather than classic growth curves such as logistic, Gompertz, or von Bertalanffy curves because growth curves are prone to error when fitted to only a few data points (Leberg et al. 1989; Zach 1988). By using adjusted masses for individual sheep rather than pooling all data for a given sex–age class, we were able to analyze interindividual variability.

When the mass of lambs first caught in July or later was adjusted to June 5, we often obtained estimates lower than 4 kg (the average birth mass of bighorn sheep (Hogg et al. 1992)), and sometimes obtained negative masses, possibly because mass gain of lambs during the first 2 weeks of life was not linear. We therefore adjusted lamb mass to June 15 (day 22), excluding three lambs whose mass adjusted to June 15 was less than 4 kg. Lambs of 2-year-old ewes were excluded from analyses because they were smaller than other lambs and their number varied greatly from year to year (Festa-Bianchet et al. 1995).

For each sex–age class, we tested whether mass gain during the trapping season was curvilinear by the significance of a quadratic term in a regression of mass on capture date, pooling all data for individuals caught 4 or more times. For sex–age classes where individuals grew linearly during the capture period we used individual linear regressions of mass on date to adjust body mass to standard dates at the start and end of summer. For classes where most individuals exhibited curvilinear mass gain, the regression of body mass on the square root of capture date was approximately linear and was used for adjusting body mass. We assessed other transformations, (ln, log₁₀, square root of square root), but square root provided the best fit. For adult sheep caught 5 or more times in the same summer, log transformations tended to have a slightly higher r^2 value but resulted in unrealistically low estimates of mass on June 5, except for sheep captured before that date. Potential biases in mass adjustments were reduced by excluding sheep not caught within 50 days of either adjustment date.

Masses of ewes first caught when pregnant were excluded from analyses of mass adjusted to June 5. Pregnancy was detected by the presence of colostrum or when ewes without signs of lactation at first capture lactated later in the summer.

Except for rams 3 years of age and older, most sheep caught only once in a summer were excluded from analyses. For sheep captured within 3 days of either June 5 or September 15, however, we used the mean individual rate of mass gain for that sex–age class to adjust body mass. When an individual growth rate was not available for a sheep 2 years of age or older captured within 6 days of September 15, we adjusted its body mass using the mean sex- and age-specific individual growth rate. By using the mean growth rate and adjusting individual body mass over 3 or 6 days, the greatest possible error in estimate was similar to the scale error of 0.125 kg.

We calculated individual growth rates for eight 3-year-old rams that were caught at least twice with more than 30 days between captures. For other rams 3 years of age and older, we adjusted body mass to June 5 using age-specific linear regressions of mass on date

Table 1. Frequency of captures of bighorn sheep at Ram Mountain, Alberta, 1973 to 1985.

	No. caught	No. of captures per sheep each year	% caught of those seen
Lambs			
Males	115	1.6	78
Females	115	1.4	79
Yearlings			
Males	94	2.9	91
Females	104	2.9	87
2-year-olds			
Males	82	2.3	84
Females	92	2.8	88
3-year-olds			
Males	58 ^a	1.6 ^a	55
Females	88	2.9	92
4-year-olds			
Males	55 ^a	1.2 ^a	75
Females	63	2.6	86
5-year-olds and older ^b			
Males	83 ^a	1.2 ^a	50
Females	158 ^b	2.3	79

^aIncludes 1971 and 1972.

^bFor sheep older than 4 years, refers to sheep-years because many individuals were caught in more than 1 year.

for captures before July 25 (day 62). Body mass was adjusted only for rams caught within 20 days of June 5. The mass of rams older than 3 years was not adjusted to September 15 because none was caught later than August 1 (day 69). To increase the sample size, for rams 3 years of age and older we included data from 1971 and 1972. We did not use those years for other sex-age classes because almost all sheep were captured only once each year and did not fit our criteria for adjusting body mass.

Some lactating ewes were removed from the study population in 1972–1981 (Jorgenson et al. 1993b), so some lambs were orphaned just before weaning. Male orphans were smaller than non-orphans (Festa-Bianchet et al. 1994) and were excluded from analyses, except for relative mass changes that were independent of orphan status (t test, $P > 0.9$).

Over-winter mass change was calculated by subtracting mass on September 15 from mass on June 5 the following year. Relative mass gain of individual sheep was calculated as the ratio of summer mass gain to June 5 mass. Use of relative mass gain takes into account the expectation that a large individual will gain more mass than a small individual and expresses summer mass accumulation as a proportion of body mass on June 5. We calculated relative winter mass change (usually a loss) as the mass change from September 15 to June 5 divided by the mass on September 15.

We analyzed the data with parametric statistics, including regression and analysis of variance. All probability values are two-tailed unless otherwise specified, with $\alpha = 0.05$. Means are reported with standard deviations. For sheep aged 2 years or less, we also performed two-way ANOVAs with year and sex effects to test whether differences between sexes could be affected by year-to-year variations. Not all data could be included from these analyses because some yearly samples for some sex-age classes were insufficient for testing year effects. Therefore, the number of degrees of freedom for year effects varies among analyses.

Results

Trapping success and selection of age-specific mass-adjustment methods

Adult ewes and rams 2 years of age were generally caught twice or more each summer, but many lambs and rams older than 2 years were only caught once each year (Table 1). Of rams older than 3 years, none were captured later than August 1.

Linear regression provided a good approximation of mass gain for lambs from early June to early October (Fig. 1). For six lambs captured 4 times each, the r^2 values of linear regressions of mass on date averaged 0.988 (range 0.959–0.999). When sex was taken into account, there were no significant year-to-year differences in rate of mass gain ($F_{[10,47]} = 1.71$, $P = 0.11$), but samples for some years consisted of only two or three lambs of each sex.

Linear regression provided a good fit to the pattern of mass gain of yearling sheep from late May to early October (Fig. 1). For 20 non-orphaned yearlings captured 5 or more times each, the linear r^2 value averaged 0.982 (range 0.955–0.999). For the same sample of yearlings, however, mass gain was slower in late summer than in early summer (paired test of slopes over the first and second halves of available captures, $t = 3.45$, $P = 0.002$; mean change in mass gain -0.043 kg/day). There were no significant yearly differences in growth rates of yearlings in summer when sex was taken into account ($F_{[11,123]} = 1.43$, $P = 0.17$).

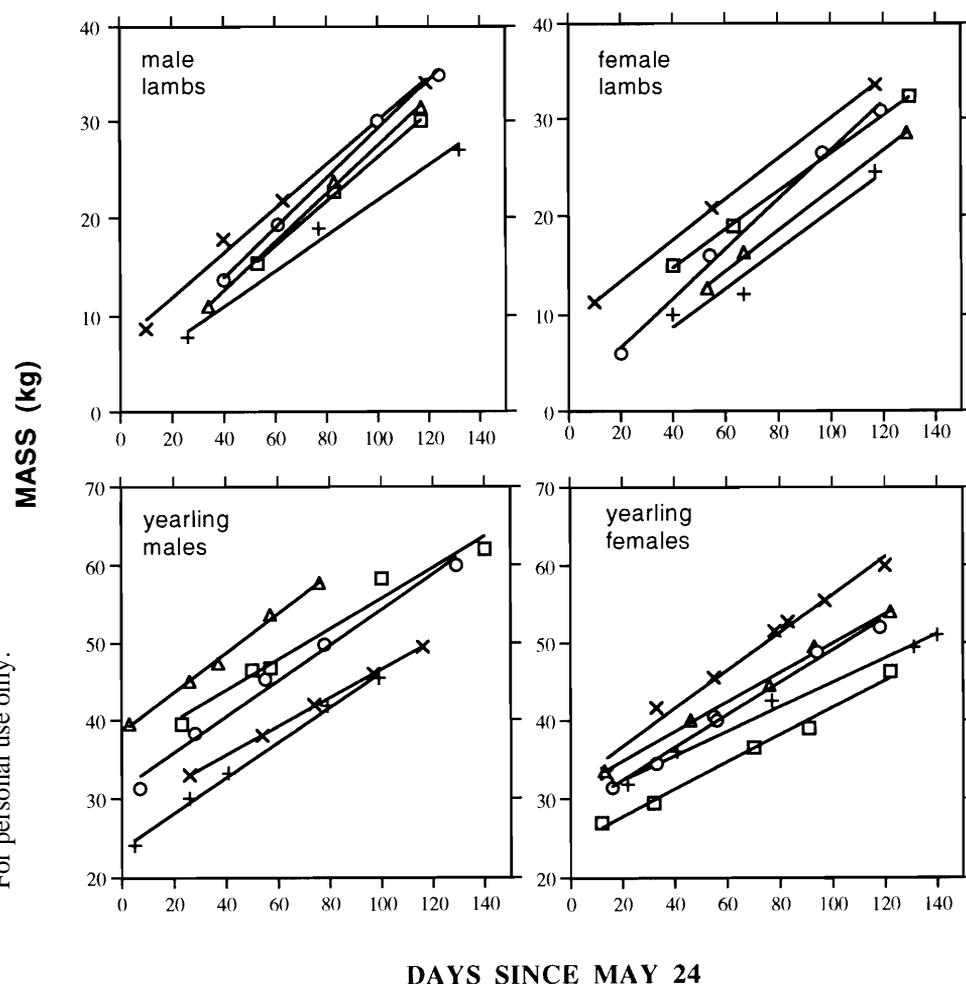
Older sheep of both sexes gained mass in a quadratic fashion from late May to early October (Fig. 2). For 18 females aged between 2 and 6 years that were caught a minimum of 5 times each during the same summer, the r^2 value of linear mass gain averaged 0.919 (range 0.816–0.995), while when a second-degree polynomial was fitted to the same data, the r^2 value averaged 0.973 (range 0.843–0.999). Despite the small sample size, the second-order term was significant in 5 of these 18 polynomial regressions. For fourteen 2-year-old males caught 4 or more times, the r^2 value of linear mass gain averaged 0.969 (range 0.891–1.0), while when a second-degree polynomial was fitted to the same data, the r^2 value averaged 0.991 (range 0.952–1.0). Only 1 of the 14 curves had a significant second-order term.

Mass gain of adult sheep over the 140-day trapping period was approximately linear when plotted against the square root of capture date. For rams 3 years of age and older, mass gain from late May to late July appeared linear (Figs. 2 and 3). We could not confirm linearity by looking at individual growth curves in early summer because no ram older than 2 years was caught more than twice over this period. For most ewes 2 years of age and older, little gain in body mass appeared to occur after mid-August (day 80; Fig. 2). Ten ewes caught twice after August 25 (day 93) gained only 0.07 ± 0.06 kg/day.

Sex differences in summer mass gain

Despite considerable individual variability, male lambs gained mass faster than female lambs (Table 2). There was no sex difference in mass on June 15 (at about 3 weeks of age), but by September 15, male lambs were heavier than female lambs. Yearling males gained mass faster than yearling females and were 9–10% heavier than females throughout the summer (Table 2). All the significant sex differences

Fig. 1. Mass gain of representative individual bighorn sheep lambs and yearlings at Ram Mountain, Alberta, 1973–1985, with fitted linear regressions. The individuals shown were chosen from those with the greatest number of captures and to minimize point overlap in the figure.



reported in Table 2 were confirmed with two-way ANOVAs including year and sex effects.

Sexual dimorphism in mass on June 5 increased gradually from 18% at 2 years to 65% at 6 years (Fig. 4). At 2 years of age, lactating ewes gained less mass than nonlactating ewes (Festa-Bianchet et al. 1995). Most (64%) 2-year-olds did not lactate (Jorgenson et al. 1993a), while 91% of older ewes lactated.

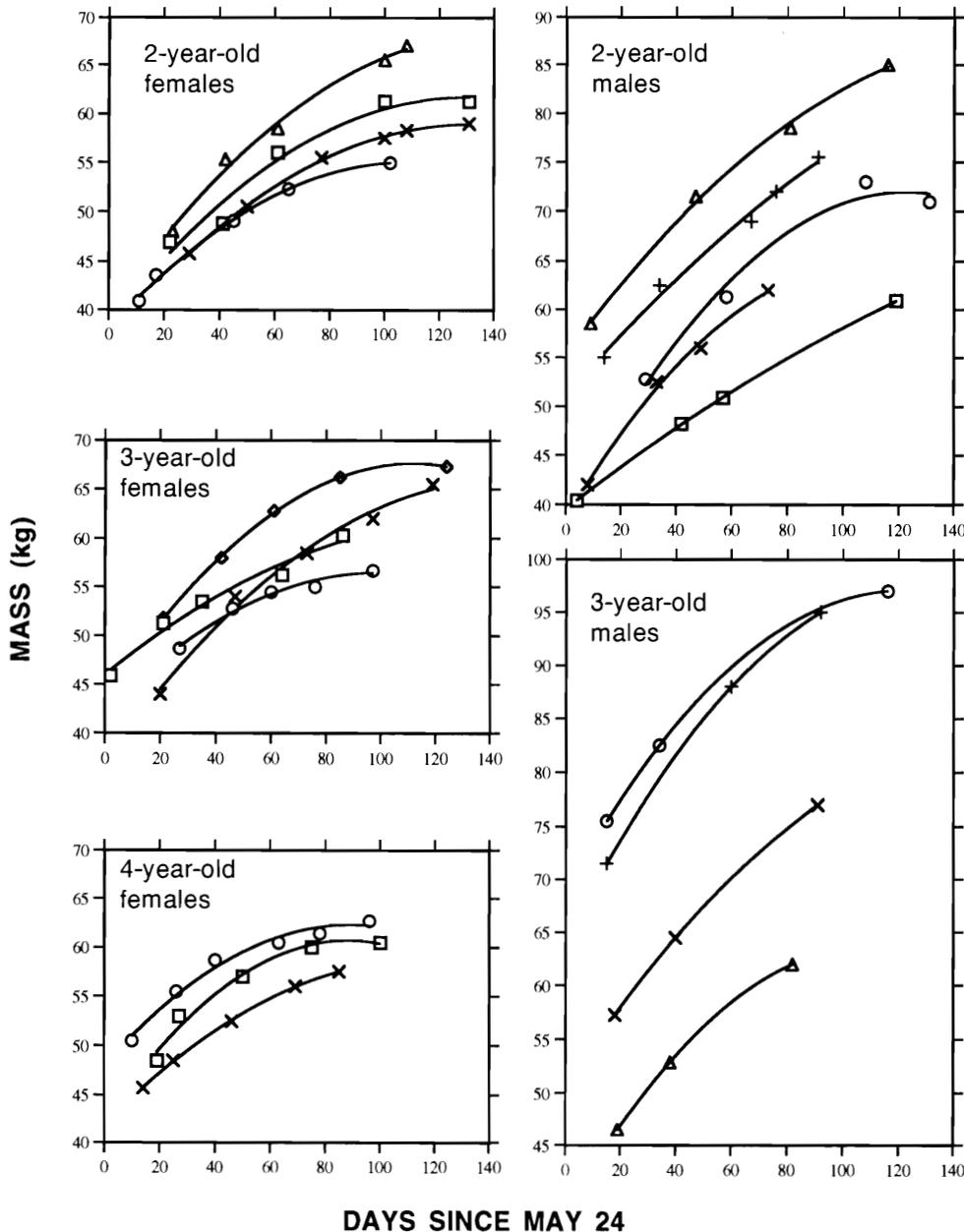
During summer, males accumulated significantly more relative mass than females only as 2-year-olds (Table 3). When year effects were included, sex had a significant effect on the relative mass gain of yearlings ($F_{[1,99]} = 4.23$, $P = 0.04$) and a highly significant effect on the relative mass gain of 2-year-olds ($F_{[1,74]} = 12.15$, $P = 0.001$). There was no sex difference in relative summer gain of lambs ($F_{[1,41]} = 0.62$, $P = 0.4$) or 3-year-olds (Table 3; data for 3-year-olds were insufficient for a two-way ANOVA). Year of birth also had a significant effect on relative mass gain by lambs ($F_{[9,41]} = 2.81$, $P = 0.01$) and 2-year-olds ($F_{[10,74]} = 2.37$, $P = 0.02$) but not by yearlings ($F_{[11,99]} = 1.10$, $P = 0.4$). There were no significant year–sex interactions.

We could not determine whether relative mass gain differed according to sex for sheep older than 3 years because we had no data on mass of adult rams in late summer. Ewes 4 years of age and older gained an additional 26–36% of their June 5 mass over the summer (Table 3).

Over-winter mass changes

Lambs of both sexes gained mass between September 15 and the following June 5, but sheep of all other ages lost mass during this period (Fig. 5). Among lambs, males appeared to gain more mass over-winter than females, but the difference was not significant ($F_{[1,29]} = 0.72$, $P = 0.4$). Among yearlings, females lost more mass than males ($F_{[1,65]} = 10.64$, $P = 0.002$). We have previously shown (Festa-Bianchet et al. 1995) that pregnant yearlings lost more mass than nonpregnant ones. If the comparison of winter mass loss for yearlings included only females that did not lactate as 2-year-olds, there was no difference between males and females ($F_{[1,49]} = 0.96$, $P = 0.3$). Yearling males (excluding orphans) lost 2.5 ± 4.7 kg ($n = 29$) and nonreproductive yearling females lost 2.2 ± 3.2 kg ($n = 30$). Between September 15 and June 5,

Fig. 2. Mass gain of representative individual adult bighorn sheep at Ram Mountain, Alberta, 1973–1985. Data for each sex–age class are plotted against capture date. The individuals shown were chosen from those with the greatest number of captures and to minimize point overlap in the figure.



2-year-old males lost less mass ($\bar{x} = 6.3 \pm 4.2$ kg; $n = 15$) than females of the same age ($\bar{x} = 10.9 \pm 3.7$ kg; $n = 47$) ($F_{[1,49]} = 27.53$, $P < 0.001$). Winter mass loss of females between 2 and 3 years of age was not affected by reproduction: mean loss was 10.6 kg for both lactating and nonlactating 3-year-olds. Winter mass loss of females aged 3–7 ranged from 13.0 ± 4.9 kg for 3-year-olds ($n = 33$) to 16.2 ± 5.3 kg for 5-year-olds ($n = 14$).

Males lost a smaller proportion of their September mass (or regained more of it before June 5) than females (Table 4). The difference between male and female yearlings appeared to be due to the greater mass loss incurred by yearling ewes

that lactated as 2-year-olds. When lactating 2-year-olds were excluded, there was no sex difference in relative mass loss of yearlings ($t_{57} = 0.25$, $P = 0.81$): nonlactating females ($n = 30$) lost $5 \pm 7\%$ of their September 15 mass. Unlike the results obtained for yearlings, the greater relative mass loss by 2-year-old females than by males was not explained by reproductive status. Whether or not they were lactating as 3-year-olds, 2-year-old ewes lost similar proportions (18 and 17%) of their previous summer's body mass. Overall, adult ewes lost about one-fifth of their mid-September body mass during winter (Table 4).

Our data showed no clear sex difference in winter mass

Table 2. Comparison of body mass (kg) and summer linear rate of mass gain (kg/day) from June 5 to September 15 for male and female bighorn sheep at Ram Mountain, Alberta, 1973–1985 (lambs of 2-year-old ewes are excluded).

	Males			Females			% difference	<i>t</i>	<i>P</i>
	\bar{x}	SD	<i>N</i>	\bar{x}	SD	<i>N</i>			
Lambs									
Mass on 15 June	9.8	2.0	30	9.2	2.0	31	6.5	1.18	0.24
Mass on 15 Sept.	30.5	3.5	32	27.5	3.8	30	10.9	3.28	0.002
Rate of mass gain	0.22	0.03	29	0.20	0.04	26	10.0	2.39	0.020
Yearlings									
Mass on 5 June	33.6	4.9	55	30.6	3.2	81	9.8	4.30	0.0001
Mass on 15 Sept.	54.6	7.0	48	49.1	4.2	61	11.2	5.11	0.0001
Rate of mass gain	0.21	0.05	54	0.18	0.04	76	16.7	3.23	0.002
2-year-olds									
Mass on 5 June	51.7	6.9	54	44.0	4.7	73	17.5	7.39	0.0001
Mass on 15 Sept.	74.7	8.1	44	60.0	4.7	61	24.5	11.69	0.0001
Summer gain	22.6	5.4	42	16.5	4.4	58	37.0	6.18	0.0001
3-year-olds									
Mass on 5 June	67.3	7.6	45	49.0	5.0	65	37.3	15.22	0.0001
Mass on 15 Sept.	85.9	12.2	8	64.8	4.7	63	32.6	9.52	0.0001
Summer gain	19.8	8.9	8	15.8	4.8	61	25.3	1.96	0.055
4-year-olds									
Mass on 5 June	76.8	7.8	45	51.1	5.2	44	50.3	18.13	0.0001

loss for lambs and yearlings. Among older sheep, we found a trend for greater winter mass loss by females than by males.

Lifetime mass gain

Individual rams did not increase significantly in mass after 5 years of age, while individual ewes continued to gain mass until they were at least 7 years old (Table 5). We first used pairwise *t* tests of mass adjusted to June 5 to find the age at which individuals stopped gaining mass from one year to the next. This procedure avoided the risk of spurious changes in average mass caused by mass-related mortality.

A comparison of all ram captures available, however, suggested that rams may gain mass throughout life: when June masses of all rams aged 2–13 years were compared and those 7 years of age and older pooled in a single age group, there were significant age differences ($F_{[5,204]} = 147.9$, $P < 0.001$). Five-year-old rams (86.4 ± 7.1 kg (mean \pm SD); $n = 25$) were smaller than rams 7 years of age and older (94.6 ± 11.4 kg (mean \pm SD); $n = 23$) by about 9%, a significant difference according to Scheffé comparisons. The largest ram caught was an 11-year-old, in 1978, that weighed 111 kg on June 7 (day 14) and 127.5 kg on July 25 (day 62).

Our data indicate that ewes accumulate mass until at least 7 years of age, and that rams probably gain mass until 7 years of age, but our captures of rams were insufficient to confirm that age-specific differences in ram body mass were independent of mass-specific mortality.

Correlations between mass during early development and adult mass

The mass of a 4-month-old lamb or yearling was generally correlated with its mass as an adult, but the mass of a

1-month-old lamb was not significantly correlated with its adult mass (Table 6). We chose 4 years of age as ‘‘adult’’ size to retain an adequate sample size. For males there were significant correlations between the mass of a yearling and its mass as a 4-year-old. For females, mass at 16 months was not correlated with adult mass. The correlation between mass at 4 months and at 4 years for males was based upon only six individuals. Generally, mass as a yearling or lamb explained one-third or less of the variance in mass as an adult (Table 6).

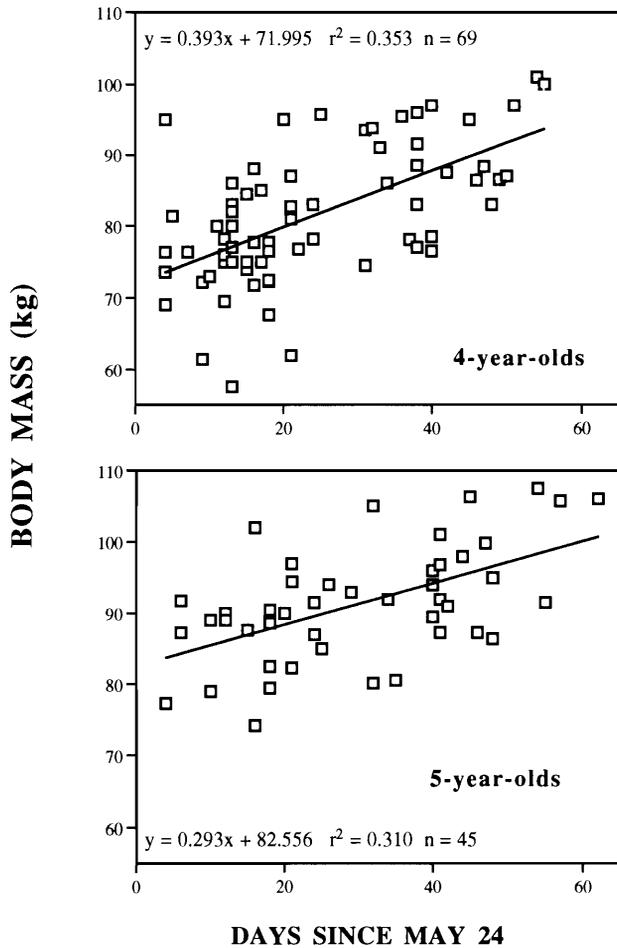
Given the apparent importance of mass gain at age 2 for the development of sexual dimorphism, we tested whether mass at the end of summer at age 2 affected adult mass for both sexes. For males, mass on September 15 at age 2 was correlated with mass on June 5 at age 4 ($n = 21$; $r = 0.77$, $P < 0.01$) but not at age 5 ($n = 13$; $r = 0.41$, $P > 0.05$). For females, mass on September 15 at age 2 was correlated with mass on June 5 at age 4 ($n = 26$; $r = 0.45$, $P < 0.05$) and age 5 ($n = 20$; $r = 0.53$, $P < 0.01$).

Year-to-year individual mass changes

From ages 2 to 7, mass on June 5 was usually correlated with the mass of the same individual 1 year later, but not all correlations were significant and, particularly for females, tended to be weak (Table 7). Correlation coefficients averaged 0.38 for ewes and 0.64 for rams.

Correlations between masses of the same individual on September 15 in successive years seemed to be stronger than similar correlations for June 5 mass (Table 7). For ewes, correlation coefficients averaged 0.64. For rams, we could only compare mass on September 15 between 2 and 3 years of age, and found a strong correlation with a small sample.

Fig. 3. Mass of 4- and 5-year-old bighorn sheep males captured at Ram Mountain, Alberta, from May 25 to July 25 in 1971–1985. Lines are the fitted overall linear regressions.



Relationships between absolute mass and mass changes

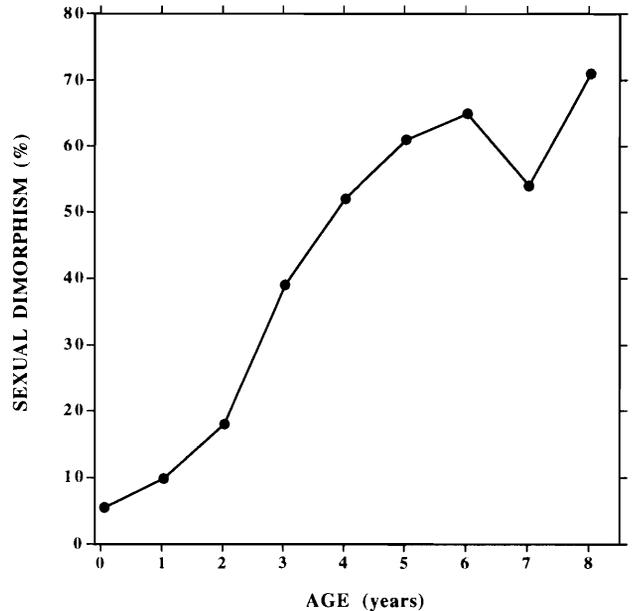
Seasonal mass changes were generally negatively correlated with absolute mass. The relative summer mass gain of heavier sheep of any sex–age class was less than that of lighter sheep (Table 8). Over-winter mass change was negatively affected by mass on September 15 for lambs and yearlings of both sexes. For sheep 2 years of age and older there were no significant correlations between mass in mid-September and relative mass loss to the following June 5, but there was a consistent negative trend (Table 8).

Discussion

Duration of yearly mass gain

Because we trapped bighorns only from late May to early October, we cannot describe their entire yearly cycle of mass changes. With the possible exception of lambs, all sex–age classes appeared to be gaining mass at their maximum rate in late May, suggesting that they had already gained some mass by that time. Thus, mass on June 5 was clearly not the annual nadir. Sheep are probably unable to gain mass until the onset of vegetation growth in spring (Hebert 1973). In most years, forage growth at 1700–2200 m

Fig. 4. Sexual dimorphism of bighorn sheep of different ages on June 5 (June 15 for lambs) at Ram Mountain, Alberta. The graph indicates the percentage of mass by which males were larger than females. Sample sizes for males from ages 0 to 8 were 36, 55, 37, 35, 34, 20, 10, 7, and 2; corresponding samples for females were 34, 81, 73, 65, 44, 31, 25, 18, and 10.



elevation is only beginning by late May (personal observation). At the lower elevations (1100–1200 m) used by bighorns in our study area, new forage is probably available by late April, and mass accumulation may start at that time. Except for yearlings and lambs, the September 15 mass estimates were likely very close to the peak mass achieved by sheep during their yearly cycle, although some sheep gained small amounts of mass as late as early October.

Age differences in the yearly mass-gain pattern

Mass gain soon after birth was likely not linear because adjusting lamb mass to June 5 often resulted in masses well below the average birth mass for this species, even though most lambs were likely born before June 1 (Festa-Bianchet 1988a). Our captures of very young lambs were insufficient to demonstrate a curvilinear pattern, but newborn lambs may gain mass very slowly or even lose mass.

Lambs and yearlings gained mass linearly until early autumn. In contrast, older sheep of both sexes gained mass rapidly until late July, when their mass gain slowed considerably. Some adults, especially females, appeared to reach their maximum yearly mass by August (Fig. 2). Age-specific differences in seasonal mass gain may reflect different growth strategies rather than constraints imposed by resource availability: if yearling sheep gained mass in a near-linear fashion in August and early September, it is reasonable to suppose that other sheep could do the same. Lambs and yearlings are in female groups and therefore feed in the same sites as adult females (Festa-Bianchet 1991). It is important to note that during the period when the data were collected, the popu-

Table 3. Relative summer mass gain (kg/kg; mass accumulated from June 5 to September 15 divided by mass on June 5) for individual bighorn sheep of different ages and sexes at Ram Mountain from 1973 to 1985.

	Mean	SD	N	t	P
Lambs					
Males	2.21	0.55	33	0.11	0.91
Females	2.23	0.83	25		
Yearlings					
Males	0.66	0.19	65	1.61	0.11 ^a
Females	0.61	0.15	61		
2-year-olds					
Males	0.44	0.12	42	2.02	0.05
Females	0.39	0.13	58		
3-year-olds					
Males	0.32	0.17	8	0.26	0.79
Females	0.33	0.12	59		
4-year-olds					
Females	0.33	0.12	40		
5-year-olds					
Females	0.29	0.10	28		
6-year-olds					
Females	0.36	0.12	18		
7-year-olds					
Females	0.26	0.15	15		
8-year-olds					
Females	0.27	0.11	10		

Note: For lambs to 3-year-olds, *t* tests were used to compare males and females. For lambs, relative mass accumulation was calculated from June 15 to September 15.

^aFor yearlings, the difference between the sexes was significant when year effects were included (see the text).

lating was artificially kept at low density and sheep were unlikely to face severe resource shortages, particularly during summer (Festa-Bianchet et al. 1995; Jorgenson et al. 1993a; Jorgenson et al. 1993b). The summer mass-change patterns reported here, therefore, probably reflect sex- and age-specific differences in growth strategies rather than summer food limitation.

Young males should be selected to gain as much mass as possible in order to increase their chances of gaining access to estrous females through intrasexual competition (Geist 1971; Hogg 1984). As expected, 2-year-old males gained mass faster than females of the same age and appeared to be still gaining considerable mass until August (Fig. 2). Non-lactating 2-year-old females might also have been expected to gain mass for a longer period during summer in order to achieve their asymptotic body mass more quickly. Instead, they appeared to concentrate most of their yearly mass gain in the first 2 months of summer, when the protein content of the forage is at its peak (Festa-Bianchet 1988c). By age 3, there was no difference in mass between ewes that had lactated and those that had not lactated as 2-year-olds (Festa-Bianchet et al. 1995), suggesting that nonlactating 2-year-olds did not gain body mass from lack of investment in reproduction.

Table 4. Relative winter mass change (kg/kg; mass gained or lost from September 15 to June 5 the following year divided by mass on September 15) for individual bighorn sheep of different ages and sexes at Ram Mountain from 1973 to 1985.

	\bar{x}	SD	n	t	P
Lambs					
Males	0.15	0.13	20	1.20	0.24
Females	0.10	0.12	23		
Yearlings					
Males	-0.02	0.09	42	3.57	0.001
Females	-0.09	0.09	46		
2-year-olds					
Males	-0.08	0.06	20	6.14	0.0001
Females	-0.18	0.06	47		
3-year-olds					
Females	-0.20	0.07	33		
4-year-olds					
Females	-0.21	0.06	25		
5-year-olds					
Females	-0.23	0.08	14		
6-year-olds					
Females	-0.21	0.05	10		

Note: All significant differences were confirmed with ANOVAs including year and sex effects. For lambs to 2-year-olds, *t* tests were used to compare males and females.

Table 5. Pairwise comparison of mass (mean \pm SD) on June 5 in successive years for individual adult bighorn sheep rams and ewes at Ram Mountain, Alberta, 1973–1985.

	Age interval (years)	n	Mass change (kg)	Paired t	P
Males	2–3	28	16.2 \pm 4.2	20.50	0.0001
	3–4 ^a	20	9.2 \pm 6.3	6.52	0.0001
	4–5 ^a	17	9.3 \pm 6.6	5.85	0.0001
	5–6 ^a	8	4.7 \pm 8.4	1.56	0.16
	6–7 ^a	6	-4.0 \pm 5.3	1.86	0.12
Females	2–3	53	5.1 \pm 5.8	6.42	0.0001
	3–4	34	2.5 \pm 6.2	2.39	0.02
	4–5	26	2.7 \pm 5.9	2.38	0.02
	5–6	16	2.0 \pm 8.6	0.93	0.36
	6–7	12	4.6 \pm 5.8	2.73	0.02
	7–8	4	2.9 \pm 10.4	0.56	0.62

^aIncludes 1971 and 1972.

Age differences in winter mass loss

We could not detect mass loss by lambs in winter, and yearlings of both sexes lost less mass over winter than older sheep. It is unlikely that the winter mass-change patterns of lambs were due to feeding on milk, because suckles are rare by mid-September and weaning appears complete by October (Festa-Bianchet 1988b). Other studies of ungulates have reported lower winter mass loss for juveniles than for older animals (Bandy et al. 1970; Houston et al. 1989; Leader-

Fig. 5. Body mass (\pm SD) on June 5 and September 15 from ages 0 to 8 for bighorn sheep at Ram Mountain, Alberta. Sample sizes for males were 36, 38, 55, 48, 37, 30, 35, 7, 34, 20, 10, 7, and 2. No data were available for mass of males aged 4 years and older on September 15. Sample sizes for females were 34, 34, 81, 61, 73, 61, 65, 63, 44, 40, 31, 29, 25, 18, 18, 15, 10, and 10.

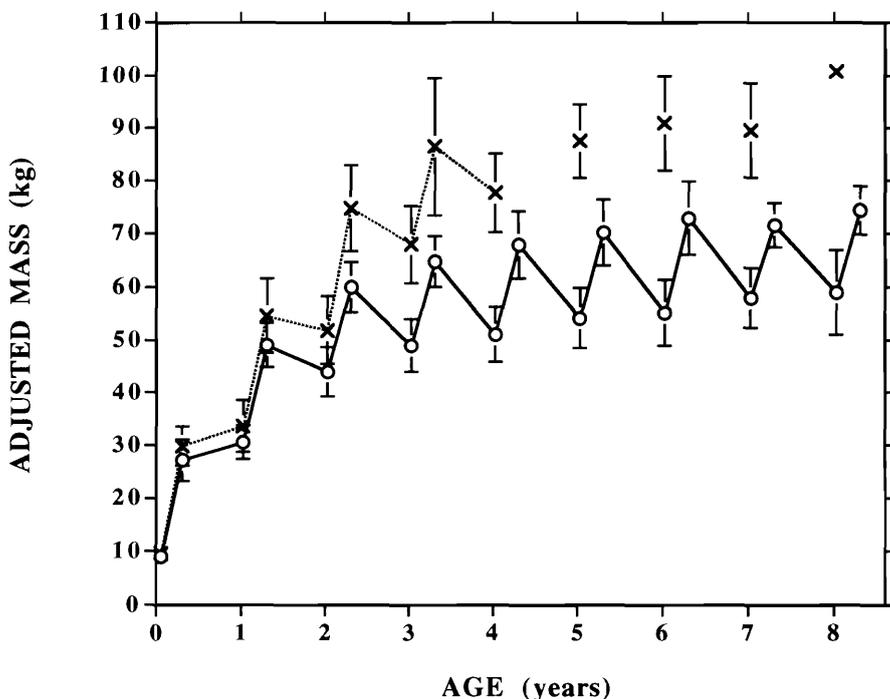


Table 6. Correlations of body mass during early development and on June 5 at 4 years of age for bighorn rams and ewes at Ram Mountain, Alberta, 1973–1985 (orphaned males are included).

	Age (months)	<i>r</i>	<i>n</i>	<i>P</i>
Males	1	0.18	7	0.70
	4	0.88	6	0.02
	12	0.46	28	0.01
	16	0.50	27	0.07
Females	1	0.24	11	0.48
	4	0.58	14	0.03
	12	0.42	32	0.02
	16	0.27	24	0.21

Table 7. Correlations of body mass on June 5 and on September 15 in successive years for individual bighorn rams and ewes of different adult ages at Ram Mountain, Alberta, 1973–1985 (orphaned males are included).

	Date of mass adjustment	Ages compared (years)	<i>r</i>	<i>n</i>	<i>P</i>
Males	June 5	2 and 3	0.83	28	0.001
		3 and 4	0.78	20	0.001
		4 and 5	0.46	17	0.031
		5 and 6	0.36	8	0.189
		6 and 7	0.78	6	0.033
		September 15	2 and 3	0.98	5
Females	June 5	2 and 3	0.33	53	0.008
		3 and 4	0.22	34	0.106
		4 and 5	0.47	26	0.007
		5 and 6	0.24	16	0.183
		6 and 7	0.63	12	0.014
		September 15	2 and 3	0.68	46
	3 and 4	0.74	31	0.001	
	4 and 5	0.72	24	0.001	
	5 and 6	0.86	10	0.001	
	6 and 7	0.22	7	0.318	

Williams and Ricketts 1982; Miura and Maruyama 1986). Miura (1986) found no significant winter mass loss for lambs of the Japanese serow (*Capricornis crispus*). Lambs were still accumulating mass linearly by late summer, and probably accumulated considerable mass after September 15. Therefore, lambs may have undergone some winter mass loss that we could not detect because we did not trap throughout the year.

Possibly, lambs and yearlings simply had little mass that they could lose in winter, and those that lost mass did not survive. In red deer (*Cervus elaphus*), nonlactating females were fatter at the end of the summer and lost more mass over winter than lactating females, but the latter also had higher

winter mortality (Clutton-Brock et al. 1983; Mitchell et al. 1976). At Ram Mountain, lactating 2-year-old ewes lost less mass over winter than nonlactating 2-year-olds (Festa-Bianchet et al. 1995).

Seasonal mass loss in temperate ungulates occurs also

Table 8. Pearson's correlations (r) between absolute mass and mass changes of bighorn sheep of different sex and age classes at Ram Mountain, Alberta, 1973–1985.

Variable	Sex	Age	n	r
June 22 mass and relative mass gain from June 22 to Sept. 15	Female	Lamb	25	-0.83 ^a
	Male	Lamb	33	-0.78 ^a
June 5 mass and relative mass gain from June 5 to Sept. 15	Female	1	61	-0.65 ^a
		2	58	-0.76 ^a
		3	59	-0.72 ^a
		4	40	-0.55 ^a
		5	28	-0.54 ^a
		6	18	-0.59 ^a
		7	15	-0.85 ^a
	Male	8	10	-0.91 ^a
		1	65	-0.56 ^a
		2	42	-0.62 ^a
September 15 mass and relative mass change from Sept. 15 to June 5	Female	Lamb	23	-0.76 ^a
		1	46	-0.47 ^a
		2	47	-0.16
		3	33	-0.28
		4	25	-0.14
		5	14	-0.13
	Male	Lamb	10	0.13
		1	20	-0.44 ^b
	Male	Lamb	20	-0.41 ^a
		2	20	-0.25

^a $P < 0.01$ (one-tailed test).

^b $P < 0.05$ (one-tailed test).

among captive individuals provided with food ad libitum (Parker et al. 1993), and does not necessarily indicate a lack of adequate forage. Adult ewes at Ram Mountain regularly sustained losses of over 20% of their autumn body mass, yet in most years over 90% produced lambs.

The development of sexual dimorphism

Male lambs are heavier at birth than female lambs (Hogg et al. 1992), and by June 15, males at Ram Mountain were 5% heavier than females (Table 2). Differences in birth date may have affected mass and mass gain of lambs, but we have no reason to suspect that birth date differed according to lamb sex. Male lambs gained more mass than female lambs, but there were no significant differences in relative mass gain. Other studies of sexually dimorphic ungulates found either no difference in relative mass gain of male and female offspring during lactation, or a tendency for females to grow faster (Bandy et al. 1970; Leader-Williams 1988).

The relative mass gain of yearling males was greater than that of yearling females. The wide variation in individual gain may explain why the difference was significant only when year effects were included in the analysis. The difference in relative summer mass gain between males and females was about the same for yearlings and 2-year-olds (Table 3). By age 3, relative gains of males and females were the same, but because by then males were much larger than females (Fig. 5), the absolute mass gain of males was still greater than that of females.

Sexual dimorphism increased with age up to 6 years (Fig. 5), which contradicts our finding of similar relative females (Fig. 5), the absolute mass gain of males was still greater than that of females.

summer mass gain for males and females at age 3. This discrepancy could be explained by the timing of our captures if males accumulated more mass than females before June 5. Sex differences in mass accumulation over the first 2 years of life appeared less important for the development of sexual dimorphism than mass accumulation between 2 and 3 years. The latter age-classes correspond to a behavioral shift of males from ewe groups to ram groups (Festa-Bianchet 1991). It is therefore likely that age-related changes in social and foraging behavior play an important role in the development of sexual dimorphism. Possibly, young males exploit areas far from escape terrain, where they might find better forage but where they might also be at greater risk of predation. Females, on the other hand, tend to use areas safer from predators, particularly when accompanied by lambs (Festa-Bianchet 1988c).

Differences in winter mass loss contributed to the development of sexual dimorphism because, contrary to the results of a study of reindeer (*Rangifer tarandus*) (Leader-Williams and Ricketts 1982), our results suggest that young males undergo smaller relative fluctuations in body mass than young females. For example, 2-year-old males lost only 8% of their body mass from mid-September to early June compared with 18% for females of the same age. Unfortunately, we do not

have comparable data for older males. It should also be pointed out that because we did not trap sheep in winter, we cannot exclude the possibility that young males actually lost as much (or more) mass as young females, but recovered much of their lost mass by the time we began trapping.

Sex-related differences in relative mass changes were most likely affected by differences in reproductive cycle. Three-year-old females were captured for the first time that season after they had given birth, therefore some of the food resources they obtained before June 5 would have been used for production of fetal mass and milk. Some mass accumulated by females before we began capturing sheep was presumably converted into reproductive tissues and lost at parturition. By early June, males likely had accumulated more mass than females above their yearly minimum. Several lines of evidence support this suggestion: adult males molt earlier than adult females (personal observation) and most males have visible new horn growth by late May. In addition, there was no difference in winter mass loss between male and nonreproductive female yearlings, suggesting that the June 5 mass of adult ewes was negatively affected by reproduction. Changes in reproductive biology contribute substantially to the development of sexual dimorphism in bighorn sheep. By not investing in reproductive tissues in late spring, males probably accumulate mass each year over a longer period than females, leading to increased sexual dimorphism with age.

Ewes continued to gain mass until they were at least 7 years of age. Although the yearly mass increase beyond 4 years of age was small (4–8% annually), it was significant. The results of other studies of similar-sized ungulates also suggest that some age-related mass gain may continue until several years after puberty, although small mass increments are difficult to establish from data on single measurements of each individual (Houston et al. 1989; Mech and McRoberts 1990; Solberg and Sæther 1994).

Sexual dimorphism in adult bighorn sheep seems to originate mostly from the multiplicative effects of a small initial body mass advantage of males over females with greater relative mass gain for males at 1 and 2 years of age and from investment of mass into reproduction for young females. Differences in relative growth rates at ages other than 1 and 2 years and differences in the age at which asymptotic mass is reached play a limited role in the ontogeny of sexual dimorphism. Our results contrast, for example, with those obtained for mountain goats (*Oreamnos americanus*): in that species, adult males are about 70% heavier than adult females, a degree of dimorphism similar to that of bighorn sheep. Sexual dimorphism in mountain goats, however, originated mostly from continued mass gain of males, but not of females, beyond 3 years of age (Houston et al. 1989). Sexual dimorphism in ungulates has previously been explained mostly by a longer lifetime mass gain period for males than for females: females are thought to reach asymptotic body mass at an earlier age than males (Bandy et al. 1970; Berger and Peacock 1988; Leader-Williams and Ricketts 1982; Solberg and Sæther 1994). Our results suggest that sexual dimorphism in different species or populations of ungulates follows different developmental routes, with important implications for ecology and evolutionary biology (Stamps 1993). For example, rapid growth of males between 1 and 3 years of age

suggests a selective pressure for a relatively risky growth strategy to quickly reach a size that would allow males to compete for breeding opportunities. Slower development, as in mountain goats, may indicate a selective advantage for a more conservative strategy, where survival to old age, rather than rapid growth, may be the most important factor affecting male reproductive success (Owen-Smith 1993).

Correlations between mass and mass changes at different ages

Few studies have compared the body mass of individual wild ungulates at different ages, yet it is commonly believed that early development plays a key role in growth and reproductive success (Albon et al. 1987; Clutton-Brock et al. 1992). For bighorn sheep, mass at 1 month of age was not correlated with adult mass, a result similar to that obtained for roe deer (Gaillard et al. 1993). Mass at 4 and 12 months had significant correlations with adult mass, suggesting that mass accumulation during lactation and up to 1 year of age affects adult size. These correlations support the assumption that differences in the quality or amount of maternal care can affect adult body mass and, ultimately, reproductive success (Clutton-Brock 1991). Body mass during the first year, however, generally explained less than one-third of the variance in adult mass (Table 6), indicating that events beyond the first year of age can have profound effects on adult size. This result is not surprising, given that over half (for males) and almost half (for females) of the lifetime gain in body mass occurs after 1 year of age.

For summer relative mass gain, there was a general tendency to regress towards the mean: sheep that were heavier at the beginning of the summer gained less mass than smaller ones relative to their body mass. This pattern suggests that sheep may adjust their foraging behavior according to their body mass. Bighorns seem to attempt to grow to an individual-specific late-summer body mass, as suggested by the much stronger correlations between successive mid-September masses than between successive early June masses for the same sheep. Sheep likely have more control over their summer mass gain than over their winter mass loss. If sufficient forage is available, changes in foraging behavior should allow a sheep to regulate its mass gain. In winter, forage is not growing and its accessibility is affected by snow cover. Winter mass changes likely depend upon variable weather patterns, such as temperature, wind, and snow depth, explaining the relatively weak correlations found between successive early-June masses for the same sheep.

There could be a cost to excessive summer mass accumulation. If most mass gain is in the form of fat reserves for winter, there may be an amount beyond which further accumulation does not increase survival or subsequent reproduction sufficiently to offset possible negative effects upon agility, ability to avoid predators, and increased locomotory costs. If mass gain included substantial somatic growth, then a potential cost would be an increase in food required to sustain the extra mass during winter.

Relative mass loss in winter, except for lambs and yearlings, was weakly related to mass in mid-September. All adult sheep lost considerable mass, but relative individual differences in mass that existed in mid-September appeared to persist through the winter, suggesting that differences in

body composition (e.g., the amount of body fat to be mobilized in winter) may be more important than absolute mass in determining winter mass loss. Future research should investigate whether differences in body mass at different seasons and ages affect individual survival and reproductive success, and how summer and winter weather affects mass changes of sheep of different sex-age classes.

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