

Body mass and survival of bighorn sheep

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Abstract: In ungulates, body mass is often positively correlated with juvenile survival, but little is known of whether body mass affects survival of other age-classes. We studied two marked populations of bighorn sheep (*Ovis canadensis*) in Alberta, Canada, to determine if body mass affected the survival of different sex-age classes. Chest girth at weaning was correlated ($P < 0.0001$) with survival of bighorn lambs in the Sheep River population. In the Ram Mountain population, body mass in mid-September had a stronger effect upon survival than mass in early June, mass gain in summer, or mass loss in winter. Body mass at weaning was correlated with lamb survival ($P = 0.004$). In both study areas, relationships between size and survival of lambs were similar for the two sexes. At Ram Mountain, survival of yearling and adult males seemed to be independent of body mass. Light yearling females were less likely to survive than heavy yearling females. Among females aged 3–6 years, body mass had no effect on survival. Among females 7 years of age and older, mass in mid-September had a weak but significant ($P = 0.03$) effect on survival. Females were slightly lighter in mid-September in their last year of life than in the rest of their adult life. Maternal expenditure is unlikely to affect the survival of prime-age ewes, but may have a detrimental effect on the survival of older ewes.

Résumé : Chez les ongulés, la survie des juvéniles dépend de la masse corporelle, mais les effets de la masse sur la survie chez les autres classes d'âge sont mal connus. Pour déterminer si la masse corporelle a un effet sur la survie des différentes classes de sexe et d'âge, nous avons étudié deux populations de Mouflons d'Amérique (*Ovis canadensis*) marqués en Alberta, Canada. La circonférence thoracique au sevrage était en corrélation ($P < 0,0001$) avec la survie des agneaux dans la population de Sheep River. Chez la population de Ram Mountain, la masse corporelle à la mi-septembre a eu un effet plus marqué sur la survie que la masse corporelle au début de juin, le gain estival ou la perte hivernale de masse. La masse au sevrage était en corrélation avec la survie des agneaux ($P = 0,004$). Aux deux sites de l'étude, les relations entre la masse et la survie étaient semblables pour les agneaux et pour les agnelles. À Ram Mountain, la survie des mouflons mâles âgés de 1 an et des mâles adultes semblait être indépendante de la masse corporelle; par contre, parmi les jeunes femelles de 1 an, celles qui étaient plus légères avaient moins de chance de survivre que celles qui étaient plus lourdes. Chez les femelles âgées de 3 à 6 ans, la masse corporelle est restée sans effet sur la survie. Chez les femelles âgées de 7 ans et plus, la masse à la mi-septembre a eu un effet limité mais significatif ($P = 0,03$) sur la survie. De plus, les femelles étaient un peu plus légères à la mi-septembre lors de leur dernière année de vie qu'au cours des autres années de leur vie adulte. Les soins maternels ne devraient pas affecter la survie des femelles âgées de 3 à 7 ans, mais ils pourraient avoir un effet négatif sur la survie des femelles plus âgées.

Introduction

It is important to identify factors that affect survival because the survival of different sex-age classes plays a major role in the evolution of life-history strategies (Stearns 1992) and affects changes in population size. Body mass affects survival in many taxonomic groups (Hutchings 1994; Sedinger et al. 1995; Williams et al. 1993). In small mammals and birds, large

size is often associated with increased survival (Murie and Boag 1984; Richner et al. 1993). For small birds, daily mass accumulation can affect overnight survival, and small variations in mass are under very strong selective pressures (Gosler et al. 1995). In larger animals, differences in body mass among individuals could affect survival on a seasonal basis.

For large mammals, individuals in poor condition (usually associated with low mass) are generally at greater risk of

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mortality, regardless of the cause of the poor condition (Crête and Huot 1993; Gulland 1992; Owen-Smith 1990). No studies, however, have examined how the effects of body mass on survival change with an individual's age. Low birth mass increases the risk of perinatal mortality in several species of ungulates (Cassinello and Alados 1996; Clutton-Brock et al. 1987b; Clutton-Brock et al. 1992; White et al. 1987), but little is known of the effects of body mass on survival for older ungulates, despite suggestions that energy reserves accumulated during summer should affect adult winter survival (Parker et al. 1996).

In temperate environments, body mass of ungulates fluctuates seasonally; in some species, individuals can lose over 25% of their mass during winter (Festa-Bianchet et al. 1996; Leader-Williams and Ricketts 1982). In these species, survival may be affected by body mass seasonally. For example, mass at the end of summer should be correlated with the amount of lipid reserves that each individual has accumulated (Rumpler et al. 1987). These reserves should increase survival during winter, when forage is scarce and of low nutritional quality (Parker et al. 1996). If the main effect of mass on survival is through the use of summer-accumulated energy reserves, then late-summer mass should affect survival more than mass at the beginning of the summer, when high-quality forage is readily available.

Mass at the end of summer may reflect the amount of resources available to an individual, but relative changes in body mass may affect survival independently of absolute mass. In particular, changes in body mass of full-grown adults may be closely associated with changes in lipid reserves (Parker et al. 1993). For example, in mule deer (*Odocoileus hemionus*), fawns that starved during winter lost almost twice as much mass as fawns that survived (Bartmann et al. 1992). It is rare to obtain repeated captures of the same individuals because wild ungulates are often difficult or costly to capture. In one of our bighorn sheep (*Ovis canadensis*) study areas, however, we recaptured most individuals several times each year (Festa-Bianchet et al. 1996). Here we analyze detailed long-term data on marked individuals to explore the relationships among mass, changes in mass, and survival of bighorn sheep of different sex and age classes. We expected that heavier sheep would have a higher survival rate than lighter sheep, and that the correlation between mass and survival would weaken with age, as adult sheep should mostly be individuals that had sufficient mass to survive the juvenile stage. Because bighorn sheep accumulate mass until they are at least 7 years old (Festa-Bianchet et al. 1996), however, we expected that mass would affect survival of young adults.

Material and methods

We studied two populations of bighorn sheep in Alberta, Canada. Both studies are based upon monitoring of marked individuals. In this paper we consider only individuals that either survived or died of natural causes; sheep that were removed or died through human actions were withdrawn from the sample in the year of their removal or death.

In over 80% of cases of assumed death, marked animals simply disappeared. Natural causes of death tentatively determined from sheep remains included predation by coyotes (*Canis latrans*) ($N = 8$) or cougars (*Felis concolor*) ($N = 29$)

(Ross et al. 1997), accidents ($N = 9$), and disease ($N = 37$). We found no sheep that appeared to have starved. We know of only one male emigrant at Sheep River despite compulsory registration of males killed by hunters and aerial surveys by the Alberta Natural Resources Service of all sheep winter ranges near Sheep River every 2–4 years. We documented 21 cases of emigration (7 females and 14 males) at Ram Mountain, less than 1 per year of study. The probability of resighting a marked sheep that was alive in any one year was over 99% for females and over 95% for males (Jorgenson et al. 1997).

Ram Mountain

Ram Mountain (52°N, 115°W, elevation 1082–2173 m) is an isolated outcrop about 30 km from the main Rocky Mountain range. A mark–recapture program began at Ram Mountain in 1971. After 1975, over 90% of the sheep were marked in most years; females were marked with canvas collars and males with Allflex ear tags. Lambs were marked with numbered metal Ketchum tags with attached colored strips of Safeflag plastic. From late May to early October, we trapped bighorn sheep in a corral trap and searched the study area on foot 5–15 times each month, noting the identity of each sheep seen. Captured sheep were weighed to the nearest 250 g with a Detecto spring scale whose accuracy was frequently checked with known weights. Data used in this paper were collected between 1973 and 1995 and include only sheep-years for which we had data on body mass. We address other factors that may affect survival (sex, age, population density, and reproduction) only with regard to their relationship to body mass.

Between 1972 and 1981, yearly removals kept this population at 30–33 adult ewes. After 1981, the population increased, peaking at 104 ewes in 1992 and declining to 79 ewes by 1995. Data presented here were collected from 276 females and 246 males. We adjusted individual mass to June 5 (except for lambs, whose mass was adjusted to June 15) and September 15. Lambs and yearlings gain mass linearly from early June to late September. Mass gain of older sheep during summer is quadratic, but becomes linear when plotted against the square root of capture date (coded with May 24 as day 0) (Festa-Bianchet et al. 1996). We adjusted body mass of most sheep using their individual rate of mass gain each year, determined by repeated weighings each summer. For males older than 2 years, however, we used age-specific linear regressions of body mass on capture date to adjust individual mass to June 5 because most males older than 2 years were only captured once each year. Mass of males that were captured only once was adjusted only if they were caught within 30 days of June 5: mass gain of adult males from late May to early July is linear (Festa-Bianchet et al. 1996). We used the number of ewes in June each year as an index of population size. We had an accurate estimate of the number of ewes because over 95% were marked in almost all years (100% since 1976). Sheep at Ram Mountain did not expand their range as the population increased, therefore population size and population density were highly correlated.

Sheep River

The Sheep River population (50°N, 114°W, elevation 1420–2550 m) has been studied since 1981. The Sheep River drainage is about 240 km southeast of Ram Mountain and is part of a large area of continuous bighorn sheep habitat (Festa-Bianchet 1986). The number of adult ewes varied between 41 and 54 during the study. The proportion of marked sheep was 54% in 1982 and averaged 94% in 1991–1995. Bighorn sheep of both sexes at Sheep River were marked with Allflex ear tags. A dart gun was used for most captures (Jorgenson et al. 1990).

We only consider survival of lambs at Sheep River, because most bighorn sheep were captured once, at less than 6 months of

age. Body mass was seldom measured, therefore we used chest girth (measured to the nearest half-centimetre) to assess body size. We used sex-specific linear regressions to adjust individual chest girth of lambs captured from late August to late November to the average capture date (October 6), and compared survival to 1 year of age with adjusted girth for 158 female and 130 male lambs caught in 1981–1994.

Data analysis

We measured yearly survival to June 1. We used logistic regressions to compare survival of different sex–age groups in order to simultaneously examine the effects of several variables and, when possible, the interactions among variables (Glantz and Slinker 1990). For adult females, we also assessed the effects of reproductive status (whether they weaned a lamb or not).

We used the stepwise backward procedure in SPSS (SPSS Inc. 1994): final logistic regression models included only variables that had a significant effect on survival and whose removal significantly decreased the model's explanatory power. We also report the partial correlation (R) statistic, which measures the relative effect of each independent variable upon the dependent variable. Averages are reported with standard deviations unless otherwise indicated.

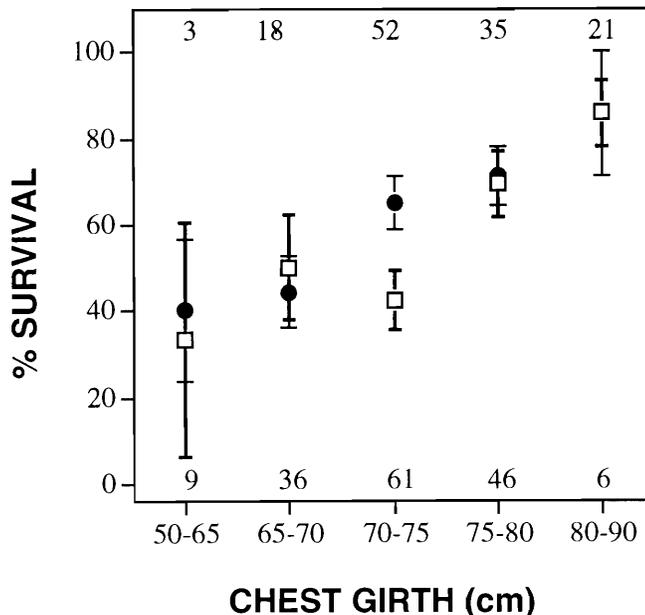
For sheep at Ram Mountain, we analyzed the effects of body mass on survival separately for lambs and for sex and age classes that we had previously identified as having different levels of survival: yearlings of both sexes, adult ewes, and adult rams. We excluded 2-year-olds because we only had mass data for 6 females and 5 males that died at 2 years and because there were wide yearly fluctuations in the proportion of 2-year-old ewes that lactated (Jorgenson et al. 1993). For sheep aged 3 years and older, we could not simply use individual adjusted mass because of the considerable age-related variation in mass found in this species. For example, while 3-year-old ewes average 65 kg in September, 7-year-old ewes average 72 kg (Festa-Bianchet et al. 1996). To obtain an age-independent measure of mass for all adult sheep, we first calculated age-specific means for each mass variable considered, then subtracted this mean value from individual adjusted mass. For ewes, we calculated mean values for each age from 3 to 9 years and pooled together ewes aged 10 years and older. For rams, we calculated mean values for each age from 3 to 5 years and pooled into a single class rams aged 6 years and older. Our analyses for adult sheep were therefore based upon individual mass after age effects were eliminated: the age-specific residuals that were used for statistical analyses were positive for individuals heavier than the average mass for their age-class and negative for individuals lighter than the average.

We first considered all adult females together, then we separated them into two age-classes (3–6 and 7–18 years) because the probability of survival is higher for ewes aged 3–6 years (about 94%) than for older ewes (about 85%) (Jorgenson et al. 1997). We could not do the equivalent analysis for adult males because we had very few data for rams older than 6 years.

For adult females, we tested whether mortality was associated with a decrease in individual body mass. For ewes that survived until at least 6 years of age, we used pairwise t tests to compare average mass on September 15 from 4 years of age to 1 year before death with mass on September 15 in the year of death, and average winter mass loss from 4 years of age to 1 year before death with winter mass loss in the year of death. In the case of a ewe that died at age 8, for example, we compared her mass in September at 8 years of age with her mean mass in September at ages 4–7, and her winter mass loss between 7 and 8 years of age with her mean mass loss at ages 4–7.

For adults of both sexes we used G tests (Sokal and Rohlf 1981) to compare survival of the smallest 10% with that of larger animals. This comparison was partly affected by the problem of pseudo-replication (Machlis et al. 1985) because we used animal-years

Fig. 1. Survival of bighorn lambs to 1 year of age at Sheep River, Alberta, as a function of chest girth adjusted to October 6. Percent survival values (mean \pm SE) of lambs are grouped by 5-cm intervals in chest girth. Male lambs are represented by squares and thick error bars and females by circles and thin error bars. Sample sizes for males are listed at the top and those for females at the bottom.



rather than individual animals as our sample units. No individual sheep, however, contributed more than 3% of the data set.

Results

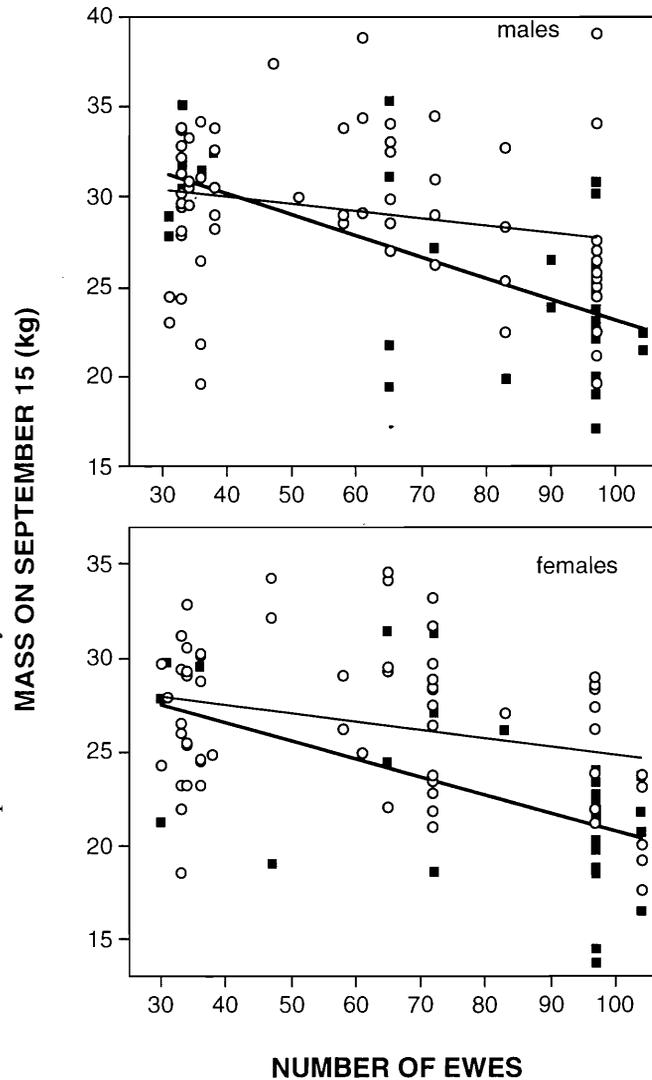
Lambs

At Sheep River, girth affected lamb survival (logistic regression coefficient = 0.138, $P < 0.0001$, $R = 0.24$) (Fig. 1). In 1985–1986, lamb mortality was high because of a pneumonia epizootic (Festa-Bianchet 1988a). Pneumonia did not have a significant effect on survival when included in a logistic regression ($P = 0.076$), but chest girth was available for only 17 lambs in the year of the pneumonia outbreak. Average chest girth adjusted to October 6 for 61 female lambs that died was 70.7 ± 4.81 cm. For 97 female lambs that survived, adjusted girth averaged 73.6 ± 4.74 cm, a 4% difference. For males, 55 that died in winter averaged 72.7 ± 4.86 cm in adjusted chest girth, 5% less than that of the 75 survivors ($\bar{x} = 76.4 \pm 5.32$ cm). Chest girth and body mass for Sheep River lambs were correlated ($r = 0.94$ for 19 males and $r = 0.83$ for 39 females, both $P < 0.01$).

At Ram Mountain, large body mass in mid-September was associated with increased survival for lambs of both sexes, but only at high population density (Fig. 2 and Table 1). At high population density (more than 60 ewes in the population), male lambs that survived the winter were 18% heavier by mid-September than those that died. Among female lambs, survivors were 23% heavier than those that died. Mass on June 15 had no significant effect on lamb survival (logistic regression, $P = 0.2$).

We also analyzed the effect of rate of mass gain during

Fig. 2. Mass adjusted to September 15 for bighorn lambs that survived to 1 year of age (\circ) and that died during winter (\blacksquare), according to the number of adult ewes in the Ram Mountain population, 1975–1994.



summer and of summer mass gain relative to mass on June 15 to see whether changes in mass had a stronger relationship with lamb survival than did absolute mass. Measures of mass accumulation, however, were either not significantly associated with survival or had lower partial correlations with survival than mass in mid-September.

Yearlings

The survival of yearlings at Ram Mountain appeared to be independent of mass in early June (logistic regression, $P = 0.1$), but large mass in September was associated with greater survival; this effect was independent of the number of ewes (Table 1). The significant mass–sex interaction (Table 1) suggests that September mass had a stronger effect on survival of yearling females than of yearling males. In mid-September, female yearlings that died were lighter than survivors by about 11%, while yearling males that died were only 2% lighter than survivors.

Fig. 3. Frequency distribution of body masses adjusted to September 15 for bighorn ewes aged 5–6 years and 9 years or more at Ram Mountain, Alberta, 1975–1994. Most individual ewes are represented more than once, as they were weighed at each age.

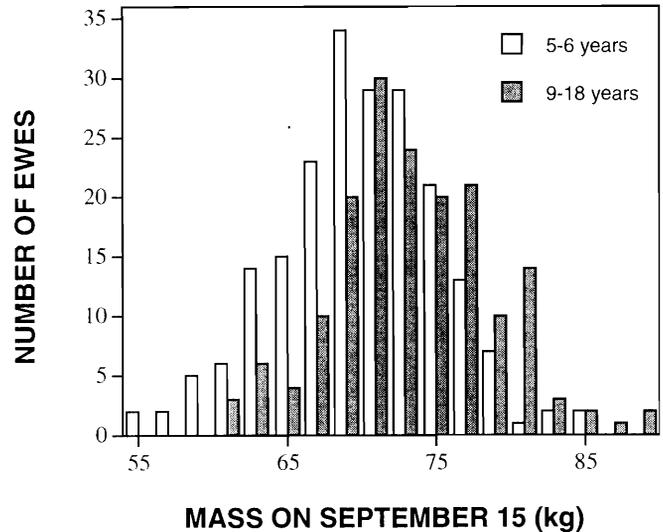


Table 1. Logistic regression analysis of survival to 1 year of age of bighorn lambs and yearlings at Ram Mountain, Alberta, as a function of body mass adjusted to September 15, the number of ewes in the population, and sex.

Term	Coefficient	P	R
Lambs			
Number of ewes	-0.028	0.000	-0.220
Mass	0.119	0.004	0.160
Rejected terms			
Lamb sex		0.3	
Sex \times number of ewes		0.5	
Sex \times mass		0.3	
Yearlings			
Mass	0.142	0.003	0.185
Sex	5.324	0.060	0.089
Sex \times mass	-0.123	0.046	-0.101
Rejected terms			
Number of ewes		1.0	
Sex \times number of ewes		0.9	

Note: All terms have 1 degree of freedom.

The rate of mass gain during summer had no relationship with the survival of yearling males, but surviving females accumulated mass faster than those that died during winter (167 ± 48 vs. 136 ± 58 g/day). The rate of mass gain, however, was not a better predictor of survival than mid-September mass (logistic regression, $P = 0.02$, $R = 0.184$). Relative mass gain (mass on September 15 divided by mass on June 5) was not related to yearling survival (logistic regression, $P > 0.3$).

Adult females

Despite varying considerably among individuals (Fig. 3), body mass did not have a strong effect on ewe survival: when

Table 2. Logistic regression analysis of survival of bighorn ewes at Ram Mountain, Alberta, as a function of age-specific residual body mass on September 15, age ("young" ewes were those aged 3–6 years and "old" ewes those aged 7–18 years), and weaning success (ewes that weaned lambs compared with ewes that did not wean lambs).

Term	Coefficient	P	R
All ewes			
Age	-1.761	0.000	-0.199
Mass × age	0.034	0.035	0.076
Weaning success × age	0.363	0.043	0.077
Rejected terms			
Mass		0.6	
Mass × weaning success		0.7	
Weaning success		0.8	
Old ewes			
Mass	0.076	0.032	0.107
Weaning success	0.706	0.058	0.084
Rejected term			
Mass × weaning success		0.6	

Note: All terms have 1 degree of freedom. Results of analyses for young ewes are not reported, as none of the variables considered was significant. Age-specific residual body mass was calculated by subtracting from each ewe's mass the average mass of all ewes of her age.

all ewes were considered, age-specific residual mass on September 15 or on June 5 was not related to survival (logistic regression, $P = 0.09$ and $P = 0.18$, respectively). When ewes were classed in two age-groups, however, we found an interaction between mass on September 15 and age (Table 2). Mass on September 15 had a positive relationship with survival for ewes aged 7 years or more (Table 2). In this latter age group, survivors were heavier than ewes that died by about 1.8 kg (Table 3), or 2.5% of the average mass (Festa-Bianchet et al. 1996).

To determine whether reproduction affected survival when body mass was accounted for, we tested whether weaning a lamb decreased ewe survival. Weaning success did not affect survival (Table 2), but there was a positive interaction between weaning success and age. When ewes were separated by age-class, we found that reproductive status had no effect on the survival of young ewes, but among old ewes, those that weaned lambs were more likely to survive than those that did not wean lambs. Body mass, however, did not interact with weaning success in affecting survival (Table 2).

After accounting for age effects, loss of body mass during winter did not affect ewe survival, when measured either as mass lost from September 15 to June 5 or as a proportion of body mass on September 15, regardless of whether the analysis included all ewes or was limited to either of the two age-classes considered above (logistic regression, all $P > 0.14$). Similarly, mass on June 5 was not correlated with survival even when the two age-classes were considered separately (logistic regression, $P = 0.2$).

Individual ewes were lighter in mid-September in the last summer before they died than they were, on average, in mid-September since the age of 4 (a difference in mass of 1.34 ± 4.56 kg, $N = 44$, paired $t = 1.947$, one-tailed $P = 0.03$; 14 ewes were heavier in the year of death and

Table 3. Mean age-specific residual body masses (kg) of adult bighorn ewes of different ages at Ram Mountain, Alberta, according to whether or not they survived to the following year.

	Age (years)	Survived?	\bar{x}	SD	N
June 5	3–6	Yes	0.164	5.409	467
		No	0.084	5.042	26
	7–18	Yes	0.393	5.634	246
September 15	3–6	Yes	0.106	5.304	440
		No	-0.106	5.581	23
	7–18	Yes	0.255	4.947	239
		No	-1.549	5.596	39

Note: Age-specific residual body mass was calculated by subtracting from each ewe's mass the average mass of all ewes of her age.

30 were lighter), but mass loss in the final winter was similar to the mean winter loss since the age of 4 (an average difference of -0.34 ± 5.63 kg, paired $t = 0.37$, $P = 0.79$; 12 ewes lost more mass in the year of death and 27 lost less mass). The age at death of ewes included in this analysis was 9.8 ± 3.1 years (range 6–17 years). For ewes aged 3–6 years, mortality of the smallest 10% was similar to that of other ewes (6.5% compared with 4.8%, $N = 463$ ewe-years, $G = 0.26$, $P = 0.6$). For ewes aged 7 years or more, however, the smallest 10% suffered over twice the mortality of heavier ewes, a nearly significant difference (25.9% compared with 12.7%, $N = 278$ ewe-years, $G = 3.00$, $P = 0.08$).

Adult males

Mass did not affect the survival of all adult rams or of rams aged 3–6 years (logistic regression, all $P > 0.4$). The inclusion of age and population size failed to reveal any significant effects of body mass on ram survival.

If heavier young rams are more likely than lighter rams to take part in the rut, they may suffer a survival cost of reproduction (Stevenson and Bancroft 1995). If that was the case, mortality may have been higher for rams that were either larger or smaller than the mean. To visually assess this possibility, we plotted June mass against survival for rams aged 3 and 4 years (Fig. 4). No bimodal pattern was evident.

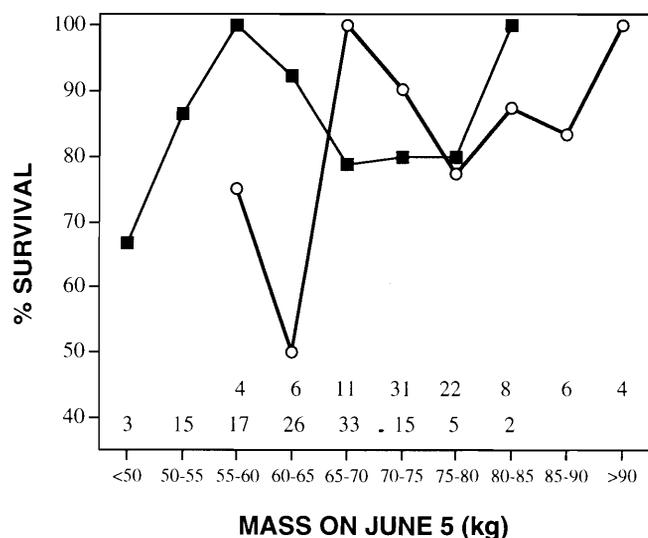
Finally, we examined the possibility that the smallest adult males may suffer high mortality. For ages 3–5 years, we compared the smallest decile of males within each age-class with all other males. Although the smallest males were almost twice as likely to die (25% of 28) than other males (13.6% of 236), the difference was not significant ($G = 2.28$, $P > 0.1$).

Discussion

In general, large body mass was associated with an increase in the probability of survival of bighorn sheep. The effects of body mass, however, varied considerably with age, sex, and population size, being strongest for lambs at Sheep River and at high population density at Ram Mountain, least for older ewes, and not significant for prime-age ewes and adult rams. In both populations, small lambs suffered higher mortality than large lambs. At Ram Mountain, however, this effect

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Fig. 4. Survival of male bighorn sheep aged 3 (□) and 4 years (●) at Ram Mountain, Alberta, as a function of their body mass adjusted to June 5. Sample sizes are listed along the bottom of the graph, with 4-year-olds above 3-year-olds.



became evident only at high population density. At low population density, lamb mortality was apparently not affected by mass in late summer: for both sexes, many lambs that survived at high density were lighter than most lambs that died at low population density (Fig. 2). At high population density, there were many more small lambs than at low population density, and these small lambs were particularly vulnerable to winter mortality. Therefore, population density must be taken into account when assessing the effects of body mass upon lamb survival. At Ram Mountain, the increase in density apparently prevented some lambs from accumulating sufficient mass to survive their first winter. In ungulates, high population density is often associated with decreased juvenile survival (Clutton-Brock et al. 1987a; Clutton-Brock et al. 1987b; Douglas and Leslie 1986; Fowler 1987; Illius et al. 1995). At Ram Mountain, high density apparently led to low juvenile survival by affecting mass gain of specific individuals: lambs that survived had almost the same mass at low and at high population density (Fig. 2).

In both populations we found that small lambs were at greater risk of mortality than larger lambs. Because we seldom knew the cause of death, we ignore whether small lambs were more easily taken by predators or were more likely to die of other causes (White et al. 1987). At Ram Mountain, until population density increased, there was no detectable effect of lamb mass upon survival: light lambs appeared to be able to survive at low density (Fig. 2). Our results therefore underline the importance of long-term monitoring in ecological studies of large mammals (Derocher and Stirling 1995; Pelton and Manem 1996): at Ram Mountain we would have found no effect of body mass on lamb survival had our study ended after 13 years (Fig. 2). At Sheep River, body size appeared to have a positive effect on lamb survival over the entire range of chest girths that we measured (Fig. 1), possibly because of unknown differences in the causes of mortality in the two study areas.

For lambs, mass at the end of summer was more impor-

tant for winter survival than mass at the beginning of summer. On June 15, most lambs were 3–4 weeks old and depended upon maternal milk for nutrition, while by September, 15 lambs were within 2–4 weeks of weaning. Lambs that were light on June 15 had high relative rates of summer mass gain (Festa-Bianchet et al. 1996). Small mass deficiencies during early development could be compensated for to some extent by summer mass gain, but a small mass at the end of summer decreased over-winter survival.

Mass adjusted to June 15 is not comparable to data on birth mass reported for other ungulates (Clutton-Brock et al. 1992; Fairbanks 1993) because only lambs that survived long enough to be caught were weighed. By June 15, most lambs were 3–4 weeks old (Festa-Bianchet 1988b). It is possible that lambs that were small at birth suffered heavy neonatal mortality. Guinness et al. (1978) reported that in red deer (*Cervus elaphus*), small neonates experienced high summer mortality but winter mortality was mostly independent of birth mass. Birth date, however, had a strong effect on winter survival, presumably because late-born calves were smaller than other calves at the onset of winter. Although no data comparing winter survival with mass at weaning are available for red deer, the data reported by Guinness et al. (1978) are consistent with the idea that small calves which survive their first few days may be able to gain mass faster than other calves during summer. Calves that are born late and presumably are small at the end of summer, however, are less likely than early-born calves to survive the winter. A late birth date lowers the survival of bighorn lambs, and the proportion of late-born lambs increases with population size (Festa-Bianchet 1988b). We do not know the exact birth dates of most Ram Mountain lambs, but as the population size increased, the number of ewes still pregnant when first caught in late May and early June also increased (unpublished data). It is likely that many of the smaller lambs seen at high population density were born late and were therefore unable to gain sufficient mass to survive the winter.

Among yearlings, mass had a stronger effect upon the survival of females than of males. We had expected the contrary, because in sexually dimorphic species young males are generally thought to be more sensitive to resource shortages than young females (Clutton-Brock et al. 1985). In bighorn sheep, yearling males are more susceptible than yearling females to parasite infection (Festa-Bianchet 1991). However, mortality was density-dependent for yearling females but not for yearling males (Jorgenson et al. 1997). Possibly, at high population density there was stronger selection for individual quality among male lambs than among female lambs, so the sample of males that survived to yearling age was more biased towards high-quality individuals than the sample of females. Within the sample of lambs for which data on body mass were available, however, there was no evidence that mortality of males increased with density more than mortality of females (Table 1). There is some evidence of sex-biased investment in this species (Bérubé et al. 1996; Hogg et al. 1992) and at high population density mothers appear to increase their investment in sons relative to daughters (Bérubé et al. 1996). Therefore, increased maternal care may mask potentially sex-biased effects of resource shortage on lamb survival.

Jorgenson et al. (1997) reported that survival of yearling

females decreased at high population density. Within the subsample of yearlings for which we had data on body mass, density did not seem to affect survival once mass was included in the analysis (Table 1), suggesting that the low survival rate of yearling females at high population density could probably be explained by a density-dependent decrease in body mass.

By the time bighorn sheep reach age 2, they may have already undergone a selective process so that only relatively high-quality individuals have survived. The wide individual variability and seasonal fluctuations in adult mass in this species seem to be mostly unrelated to risk of mortality. Therefore, it appears that, at least for ewes aged 3–6 years, most individuals accumulate sufficient reserves during summer to survive the winter period, when forage quality is insufficient to maintain body mass (Parker et al. 1996).

Measurements of body mass do not take into account potential differences in body composition (Adamczewski et al. 1993), therefore we cannot assess the relative effects of lean mass and fat reserves upon survival. Ewes were lighter than their individual average mass in the September preceding their death, suggesting that failure to accumulate adequate mass, including sufficient fat reserves, increased the risk of mortality. Winter mass loss in temperate-zone ungulates is due largely to depletion of fat stores (Parker et al. 1993).

Winter mass loss and summer mass gain were either unrelated to individual survival or were less powerful predictors of survival than mass in mid-September. Measurements of mass and seasonal mass changes for the same individual are not independent of each other: large sheep gain relatively less (and absolutely more) mass during summer than small sheep, and there is a nonsignificant trend for larger sheep to lose more mass during winter than smaller sheep (Festa-Bianchet et al. 1996). Our data do not imply that over-winter mass loss is unimportant in affecting survival, because we compared survival with mass loss during the second-last winter for each individual. Animals that lost large amounts of mass in winter may have died before we resumed trapping the following May. Indeed, if the accumulation of lipids during summer is an important factor affecting survival, it is not surprising that there would be no link between mass loss during one winter and survival the following winter.

In this paper, we did not consider population size when analyzing the survival of adult sheep because a previous analysis considering all adults (rather than only those for which mass data were available) failed to reveal any density dependence in survival for either sex (Jorgenson et al. 1997). For ewes, the effects of density and age were confused because there were very few old ewes during the years of the experimental removal, therefore the average ewe age increased with population size.

The weak but significant positive association of weaning success with survival for older ewes (Table 2) suggests that there are individual variations in individual quality which are independent of body mass: some ewes that were able to wean lambs were also more likely to survive than ewes that failed to wean lambs. It is likely that old females that weaned lambs were in particularly good condition. Possibly, they had good fat reserves relative to their body mass, which allowed them to wean a lamb and survive the following winter.

Our results have implications for understanding the repro-

ductive strategy of female bighorn sheep, and suggest that the costs of reproduction vary with ewe age. Adult ewes enjoy a very high survival rate (about 95%) up to about 7 years of age (Jorgenson et al. 1997), and we could not find a relationship between late-summer body mass and survival for young ewes. It therefore appears that ewes aged 3–6 years run little risk of compromising their short-term survival by investing heavily in reproduction. Older ewes, on the other hand, may be subject to greater constraints in maternal investment because lower summer mass gain may carry a survival cost. Data on body mass comparable to those we have presented here are not available for other ungulates, but the high survival rate typical of females aged 2–6 years (Gaillard et al. 1993; Loison et al. 1994; Toïgo et al. 1997) suggests that in other species, increased investment in reproduction may also have a limited survival cost for female ungulates in this age group.

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