

EFFECTS OF AGE, SEX, DISEASE, AND DENSITY ON SURVIVAL OF BIGHORN SHEEP

JON T. JORGENSEN,¹ MARCO FESTA-BIANCHET,² JEAN-MICHEL GAILLARD,³ AND WILLIAM D. WISHART⁴

¹Alberta Department of Environmental Protection, Natural Resources Service, Suite 201,
800 Railway Avenue Canmore, Alberta, Canada T1W 1P1

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

³UMR 5558, Laboratoire de Biométrie- Génétique et Biologie des Populations Université Claude-Bernard Lyon 1,
43 Boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France

⁴Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

Abstract. Longitudinal studies of survival are valuable because age-specific survival affects population dynamics and the evolution of several life history traits. We used capture–mark–recapture models to assess the relationship between survival and sex, age, population, year of study, disease, winter weather, and population density in two populations of bighorn sheep (*Ovis canadensis*) in Alberta, Canada. The Ram Mountain population, monitored for 20 yr, more than doubled in density; the Sheep River population, monitored for 13 yr, experienced a pneumonia epizootic. Yearling survival varied among years and was lower than that of older sheep of the same sex, except for yearling males at Ram Mountain. Yearling females at Ram Mountain were the only sex-age class exhibiting density dependence in survival. Senescence was evident for both sexes in both populations. Female survival from age 2 to age 7 was very high in both populations, but males aged 2 and 3 yr enjoyed better survival than males aged 4–6 yr. Our data support the suggestion that where hunters remove many males older than 5 yr of age, the natural mortality of males increases at 3–5 yr, possibly because young males suffer a mortality cost of participating in rutting activity. The decline in survival for sheep older than 7 yr was greater for males than for females. Survival was lower for males than for females, both among prime-aged sheep (0.896 vs. 0.939 at Sheep River; 0.837 vs. 0.945 at Ram Mountain) and among older sheep (0.777 vs. 0.859 at Sheep River; 0.624 vs. 0.850 at Ram Mountain), but not among yearlings. Survival of sheep aged 2–7 yr was not significantly different between the two populations. Winter weather did not affect survival. Survival of sheep 2 yr of age and older did not vary significantly between years, except at Sheep River where survival of prime-aged sheep of both sexes was lower in the year of the pneumonia epizootic. Studies of survival of mountain sheep based upon skull collections may have overestimated survival of young rams. Our results underline the need for accurate information on age-specific survival.

Key words: age-specific survival; bighorn sheep; capture–recapture; cost of reproduction; disease; model selection; population dynamics; senescence; sexual dimorphism.

INTRODUCTION

Variations in survival with sex and age are thought to affect the evolution of mammalian reproductive strategies (Partridge and Harvey 1988, Stearns 1992) and have direct effects on population size (Larsen et al. 1989, Garrott 1991). Accurate measures of age- and sex-specific survival, however, are difficult to obtain because they require long-term monitoring of individuals of known age. In particular, very few longitudinal survival data exist for long-lived mammals (Clutton-Brock et al. 1991, Gaillard et al. 1993, Owen-Smith 1993a) and references therein). Because of the scarcity of studies comparing different species and populations, the general validity of single-population estimates of

natural survival rates is unknown, making it difficult to test predictions of life history models (Gaillard et al. 1994). Some studies have analyzed life history strategies of mammals by assigning “typical” adult and juvenile survival rates to each species (Promislow and Harvey 1990, Promislow 1991), but the degree to which age-specific survival varies between years or between populations remains largely unknown. Variability in survival probability is likely to be as important as average expected survival in affecting life history evolution (Stearns 1992), therefore, limited knowledge of variability in survival is an important gap in our understanding of reproductive strategies.

Studies of large mammals suggest that adult survival in general is less sensitive than juvenile survival to population density or weather (Sauer and Boyce 1983, Skogland 1985, Fowler 1987, Owen-Smith 1990), but adult survival decreases at high population density in

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some species (Clutton-Brock and Lonergan 1994). Few studies of large mammals have experimentally manipulated population density (Choquenot 1991). Density may not be correlated with changes in survival either because there is no relationship between density and survival, or because the effects of density and resource availability are confounded: if low density and scarce resources co-occur, survival may be low despite low density (Caughley and Sinclair 1994).

Owen-Smith recently suggested that most information on the survival of ungulates comes from populations where large predators have been eliminated (Owen-Smith 1993a, b). He argued that such populations may experience mortality rates very different from those prevalent during their evolution, when they were subjected to predation. It is therefore useful to examine survival rates in natural ungulate populations with large predators, where survival should resemble that experienced during recent evolutionary history.

Here we present the results of two long-term studies of individually marked bighorn sheep (*Ovis canadensis*). Our data set is unique because of the long-term nature of our studies (20 and 13 yr), the large sample (over 600) of marked individuals, the comparison of two natural populations, and the precision of survival estimates due to a sighting probability close to 100%. Both populations varied in density during our study: one was experimentally kept at low density for 9 yr (Jorgenson et al. 1993), the other declined by $\approx 30\%$ during a pneumonia epizootic (Festa-Bianchet 1988a).

Previous research on survival of wild sheep suggested that male mortality was very low for young adults but that it increased after 6–8 yr of age, when males were thought to take part in the rut (Murie 1944, Geist 1971, Hansen 1980). More recently it has been suggested that younger males may also be reproductively active (Hogg 1987, Singer et al. 1991). The age at which males participate in the rut is crucial to an understanding of male mortality patterns. Although there are no data correlating the rutting behavior of individual males with their subsequent survival, it has been proposed that the age-related increase in male mortality is due to their participation in the rut (Geist 1971). If mortality and rutting activity are associated, removal of old males could favor the participation of younger males in the rut and therefore increase the mortality of males aged 4–6 yr (Heimer et al. 1984). In Soay sheep, rutting activity by very young males carries a survival cost (Stevenson and Bancroft 1995).

The studies of survival of male sheep mentioned above were based upon skull collections and their reliability has been questioned because of biases in the probability of finding skulls of sheep of different ages and because the assumptions of life table analysis (in particular a stable age distribution) were not respected (Murphy and Whitten 1976). The only available data on age-specific survival of female wild sheep come from skull collections (Murie 1944) and from a kill

sample of Dall sheep (*Ovis dalli*) (Simmons et al. 1984). No longitudinal data on survival of marked female wild sheep have been published.

Our goals were to compare survival of different sex-age classes in two populations at different densities. We also wanted to assess interpopulation variability in survival of individuals of the same sex-age class. A third objective was to determine whether or not bighorn sheep showed evidence of senescence. Promislow (1991) suggested that senescence was more evident in short- than long-lived mammals. He also claimed that among long-lived mammals, mortality increased immediately after the first reproduction and then again for older age classes, as shown for red deer (*Cervus elaphus*) (Clutton-Brock et al. 1983). Some studies report an increase in mortality for older ungulates of both sexes (Gaillard et al. 1993, Owen-Smith 1993a), but others do not (Loison et al. 1994), and Promislow's methods and conclusions have been challenged (Gaillard et al. 1994).

STUDY AREAS AND METHODS

We studied two populations in Alberta, Canada. Here we provide a brief description of the study areas and of the techniques used to mark and census sheep. Further details have been published elsewhere (Festa-Bianchet 1988b, Jorgenson et al. 1993). We monitored the natural survival of marked individuals. Sheep that were collected, died during capture attempts, were shot, or were hit by vehicles were withdrawn from the sample in the year of their death. In this paper, we consider the survival of sheep 1 yr of age and older.

Natural causes of death were seldom known, except for some sheep that died of pneumonia and whose carcasses were recovered in time to undergo veterinary examination. Occasionally, we were able to ascertain the cause of death by finding fresh carcasses with obvious signs of predation (predator tracks, predator sightings, signs of struggle) or accidents [broken bones and internal injuries (Festa-Bianchet 1987)]. We never found any sheep that appeared to have starved.

Rams with horns of at least four-fifths of a curl were hunted. Hunting resulted in considerable mortality (not included in this paper) for rams older than 5 yr; most rams attained four-fifths of a curl at 5–6 yr (Festa-Bianchet 1989). In both study areas about half of the rams whose horns reached "legal" size were shot by hunters, although some survived 1–7 yr after becoming "legal." Hunters must register their kills; therefore we knew the identity, location, and date of death for legally killed sheep. Hunter registrations also provided us with some information on shot rams that had emigrated from our study areas.

In both study areas we monitored some sheep with radio collars and relocated them at least once every 2 mo, mostly to document seasonal dispersion and dispersal (Festa-Bianchet 1986a). Additional information on dispersal was obtained from reports of tagged sheep

from hunters, other members of the public, and Alberta Fish and Wildlife or Forest Service staff.

Ram Mountain.—Ram Mountain (52° N, 115° W, elevation 1082–2173 m) is a habitat island for bighorn sheep, separated from the main Rocky Mountain range by ≈30 km of foothills covered with coniferous forests. The North Saskatchewan River cuts Ram Mountain from Shunda Mountain, a smaller outcrop with ≈30 resident sheep. Bighorns (almost exclusively males) marked on Ram Mountain occasionally moved to Shunda, either temporarily or permanently. Shunda was searched on foot at least once each summer from 1980 to 1992. Information on marked males emigrating to Shunda Mountain was also obtained from registrations of hunter kills.

Potential predators included wolves (*Canis lupus*), cougars (*Felis concolor*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), and Golden Eagles (*Aquila chrysaetos*). Rams were hunted by humans from late August through October.

Live-trapping of bighorn sheep at Ram Mountain began in 1971, and since 1975 we have precise data on herd size and individual survival because in most years over 95% of the population was marked. A corral trap baited with salt allowed multiple captures of most sheep between late May and early October each year. We censused the study area at least once per week during the trapping period and noted the identity of all sheep seen. Most marked sheep missed in any 1 yr had moved to Shunda Mountain. Some of these individuals were later sighted either on Ram or on Shunda Mountain. Survival data presented here were collected from marked sheep between 1975 and 1994.

Between 1972 and 1981, yearly removals of 12–24% of adult ewes kept the population at 95–110 sheep (Jorgenson et al. 1993). After 1981, the population increased, peaking at 210 individuals in 1992. Data presented here were collected from 222 ewes and 199 rams that survived to 1 yr and were marked as lambs or as yearlings. Sheep first caught when older than 1 yr were excluded because their small number (15 females and 43 males, mostly caught in 1975 or earlier) relative to our overall sample did not justify the technical complexities of analyzing data for animals with different ages at first capture (Loison et al. 1994). In 1982–1986, we installed radio transmitters on 20 males aged 2–13 yr, and monitored them for periods ranging from 2 mo to 2 yr.

Sheep River.—The Sheep River population (50° N, 114° W, elevation 1420–2550 m), 160 km south of Ram Mountain, has been studied since 1981. The proportion of marked sheep increased from 54% in 1982 to an average of 92% in 1990–1993. Most sheep were captured by darting (Jorgenson et al. 1990). This population experienced pneumonia epizootics in 1978 and 1986 (Festa-Bianchet 1988a). The number of sheep in March (from total counts of marked and unmarked individuals) increased from 140 in 1982 to 153 in 1985,

then declined to 99 following the epizootic in 1986. Numbers recovered to 121 by 1993. Survival of marked sheep was monitored by censusing the winter range 1–5 times per month from April 1981 to September 1987. In 1988–1993 the winter range was censused each year in April, June, September, and November, with census effort in other months varying from year to year. Monitoring of survival at Sheep River was facilitated by the accessibility and openness of the winter range (on average, 97% of marked females were seen during each winter census) and by the strong site fidelity of both sexes (Festa-Bianchet 1986a, b).

Bighorns at Sheep River frequently contacted neighboring herds (Festa-Bianchet 1986a, b). Potential predators were cougars, wolves, black bears, coyotes, and eagles. Because of ongoing cougar research in the area (Ross and Jalkotzy 1992), we had better information about predation by cougars than by other predators. Wolves had been extirpated but returned to the area in 1987. Rams were hunted in September and October (Festa-Bianchet 1989). Five marked ewes were also legally harvested during the study. Data presented here were collected from 96 ewes marked when aged 0–2 yr, and 103 rams marked when aged 0–3 yr. All sheep included in the sample survived to 1 yr of age, and data analysis included the years 1981–1993.

In 1982–1986, we radio collared seven males aged 2–7 yr and seven adult females older than 3 yr. Sheep with radios were monitored for periods ranging from 3 mo to 3 yr. Most radio-collared sheep were nonresidents, which spent most of the winter outside the range of the main study group (Festa-Bianchet 1986b, c).

Data analysis.—Most lambs are born in the last 2 wk of May and the 1st wk of June (Festa-Bianchet 1988c), thus we calculated yearly survival from 1 June each year. The word “capture” refers to actual captures at Ram Mountain and sightings of marked sheep at either study site.

We obtained weather records for Ram Mountain from the Environment Canada weather station at Nordegg, ≈20 km from Ram Mountain. We used the precipitation and temperature data for December–March to calculate a modified Lamb's index of weather severity as described by Picton (1984). We related survival to one index with five classes of winter severity and one with two classes of severity. Winter weather varied widely during our study, for both average daily temperature ($\bar{X} \pm 1 \text{ SD} = 8^\circ \pm 2.8^\circ\text{C}$, range -3°C to -13°C , $\text{CV} = 36\%$) and total snowfall ($\bar{X} \pm 1 \text{ SD} = 86 \pm 33.3 \text{ cm}$, range 49–145 cm, $\text{CV} = 39\%$). We did not have equivalent weather data for Sheep River.

We estimated survival rates and tested hypotheses using recent developments of capture–recapture methods (see Lebreton et al. 1992 for details about the methods) and Gaillard et al. 1993 for an application to ungulates). Data analysis followed two steps. First, we looked for a general model fitting the data. We used the Cormack–Jolly–Seber (CJS) model because a good-

ness-of-fit test of this model can be directly performed using the program Release (Burnham et al. 1987). From the CJS model, we checked whether a constant capture probability (assuming no year-to-year changes in capture probability) would provide a more parsimonious model than one based upon different capture probabilities. In all cases we found no yearly changes in capture probabilities, and these always approached 100%, the lowest being (mean \pm 1, SD) $95.5 \pm 1\%$ for males at Ram Mountain and the highest 100% for females at Sheep River. Therefore, we do not present the analyses that led us to reject models based upon year-specific capture probabilities. All models are based upon constant capture probabilities.

Subsequently, we tested for effects of yearly variation and age on survival as well as for additivity or interactions between these effects. Because the typical survival curve of mammals generally is a three-stage process (Caughley 1966), we used a three-age-class model (the Caughley-like model, Gaillard et al. 1993) with a yearling stage (survival from 1 to 2 yr), a prime-age adult stage (between 2 and 7 yr of age), and a senescent stage (individuals older than 7 yr of age). The cut-off point between prime-age and senescent stages was chosen from previous knowledge of survival curves for bighorns (Festa-Bianchet 1989). We first checked the suitability of the Caughley-like model to account for age effects on survival. We then compared the Caughley-like model to a model with complete age dependence (a separate parameter for each year of age) to see how much of the total variability in age-specific mortality was captured by the Caughley-like model. Finally, we tested for the significance of each of the three stages in the Caughley-like model by comparing it with models combining each two adjacent age groups. Model selection was based on the Akaike Information Criterion (AIC; Sakamoto et al. 1986) as recommended by Burnham and Anderson (1992) and Lebreton et al. (1992). AIC can be calculated for any model as deviance plus twice the number of identifiable parameters. The model with the lowest AIC value is the best compromise between accuracy and precision. When two models had very close AIC values (difference less than 1), model selection was based on biological considerations (as recommended by Burnham and Anderson 1992). To test particular biological hypotheses, we also used the more classical likelihood ratio tests.

The second step started from the model retained from the first step. We looked for a more precise model using information on population density (Sheep River and Ram Mountain), occurrence of pneumonia (Sheep River), and weather records (Ram Mountain). AIC values and likelihood ratio tests were used to select the final model. All calculations were performed using the program SURGE4 (Pradel and Lebreton 1991). To avoid higher order interactions, which are usually very difficult to interpret, we considered four separate data sets

according to sex and study site. In addition, for sexually dimorphic ungulates like bighorn sheep, it is reasonable to expect that survival patterns vary according to sex (Clutton-Brock et al. 1982). We already knew that males did not live as long as females in our study populations, that pneumonia only affected the Sheep River population, and that variations in density were much greater at Ram Mountain than at Sheep River. Therefore, separating data sets by sex and population was justified both biologically and statistically. With separate data sets, we only had to cope with two-way interactions between age and year of study. Comparisons of survivorship across data sets were performed using Wald's tests (Rao 1973; see Blondel et al. [1992] for an example in capture-mark-recapture context). The symbols used for the different models compared in our analyses are summarized in the Appendix.

In bighorn sheep, it is possible to measure age precisely until ≈ 10 yr of age in rams, but only until ≈ 4 yr in ewes (Geist 1966), by counting the horn annuli. Therefore, young animals could be reliably aged at first capture. For the Sheep River population, we included in our analysis females marked when 2 yr old ($N = 19$) as well as those marked as yearlings or younger ($N = 77$) and males marked when 3 yr old ($N = 11$), 2 yr old ($N = 16$), and yearling ($N = 76$). Too few animals were marked at older ages to be considered (consistently < 10 individuals), given the increased practical difficulties of analyzing data sets with different ages at first capture. To analyze the survival pattern at Sheep River, we used the flexibility allowed by SURGE4 to include into the same analysis animals from the same cohort captured at different ages (see Loison et al. 1994 for details about this procedure and application to chamois (*Rupicapra rupicapra*)). Survival estimates are reported as means \pm 1 SE. We use the symbol ϕ to refer to apparent survival, because in most cases we could not ascertain that animals that disappeared had actually died.

RESULTS

Ram Mountain

Males.—The model selection process for Ram Mountain males is summarized in Table 1. The Cormack-Jolly-Seber model provided a satisfactory fit to the data and was used as a starting point ($\chi^2 = 65.02$, $df = 104$, $P > 0.99$). There was no evidence of between-year changes in survival. We could not find any overall difference in survival as a function of age when each year class (from yearlings to 10-yr-olds) was included as a distinct category in the model. When we considered a Caughley-like model with three age groups (yearlings, 2 to 7 yr old, which we refer to as "prime-age" adults and animals aged ≥ 7 yr that we refer to as "older") to study simultaneously the effects of age and year of study, we found no significant interaction between year and age and no significant ef-

TABLE 1. Modelling survival probability of male bighorn sheep at Ram Mountain. The model selected at each step (lowest Akaike Information Criterion) occurs in boldface. The final model is boldfaced and underlined.

Biological hypothesis	Models to be compared	AIC	χ^2	df	P †
Time dependence of survival	$[\phi, p]$	874.34	22.72	18	0.20
	$[\phi p]$	861.06			
Age dependence of survival	$[\phi_a p]$	874.77	22.29	18	0.22
	$[\phi p]$	861.06			
Interaction between age and time effects on survival	$[\phi_{ac+t}, p]$	901.91	27.17	29	0.56
	$[\phi_{ac+tt}, p]$	871.08			
Time dependence of survival	$[\phi_{ac+t}, p]$	871.08	22.72	18	0.20
	$[\phi_{ac} p]$	857.80			
Age dependence in survival	$[\phi_{ac+t}, p]$	871.08	7.26	2	0.03
	$[\phi_t, p]$	874.34			
Occurrence of a senescent stage	$[\phi_{ac} p]$	857.80	6.29	1	0.01
	$[\phi_y, p]$	862.09			
Occurrence of a yearling stage	$[\phi_{ac}, p]$	857.80	0.39	1	0.53
	$[\phi_t, p]$	856.19			
Effect of winter severity (five classes) on age-dependent survival‡	$[\phi_{ac-w5}, p]$	840.24	8.27	12	0.76
	$[\phi_{ac} p]$	804.51			
Effect of winter severity (two classes) on age-dependent survival‡	$[\phi_{ac-w2}, p]$	807.26	3.25	3	0.35
	$[\phi_{ac} p]$	804.51			
Density dependence (number of males) on survival	$[\phi_{densM}, p]$	862.41	0.65	1	0.42
	$[\phi_p]$	861.06			
Density dependence (population size) on survival	$[\phi_{densT}, p]$	862.15	0.91	1	0.34
	$[\phi_p]$	861.06			
Density dependence (three classes) on age-dependent survival	$[\phi_{ac-dc}, p]$	868.99	4.07	6	0.67
	$[\phi_{ac} p]$	857.80			
Effect of breeding status on survival	$[\phi_{br}, p]$	853.74	6.06	1	0.01
	$[\phi_{ac}, p]$	857.80			
Effect of breeding status on survival	<u>$[\phi_{rs}, p]$</u>	<u>851.99</u>	6.20	1	0.01
	$[\phi_t, p]$	856.19			

† Model selection was based on minimum AIC values rather than probability values.

‡ Tested between 1975 and 1993 only (no climatic data available in 1994).

fects of year. Age group, however, had a marked effect on survivorship.

Following the overall analysis, the Caughley-like model emerged as the best descriptor of male survival at Ram Mountain, with a yearling survival rate (mean \pm 1 SE) of 0.857 ± 0.026 , "prime-age" survival of 0.837 ± 0.017 , and "older" survival of 0.624 ± 0.095 . From this model, the yearly survival probability of yearlings and prime-aged adults could not be distinguished, and a significant decline in survival occurred after 7 yr of age. We know of no male at Ram Mountain that survived beyond 13 yr of age.

We then considered two variables that might have affected survival: winter severity and population density. Winter severity (tested from 1975 to 1993 because weather data for 1994 were not available) had no apparent effect on male survival. Because males and females often use different habitats and even different parts of the study area, we considered separately the potential effects of total population size and of the number of males two years of age and older in the population. We found negative trends but no significant effects of density (male population: slope = -0.0028 ± 0.0097 ; total population: slope = -0.0035 ± 0.0027). Even when reduced to three levels to account for suspected nonlinearity (<100, 100–150, and >150 sheep), density was not correlated with the yearly survival of males.

Because we suspected that males in hunted populations may take part in the rut beginning at ≈ 3 yr of age (Heimer et al. 1984), we divided "prime-age" males into two age classes. Males aged 4 to 7 yr had lower annual survival ($\phi = 0.785 \pm 0.030$) than males aged 2–3 yr ($\phi = 0.872 \pm 0.020$; Wald's $\epsilon = 2.42$, $P = 0.009$). An age-dependent model with three classes, young males (<4 yr of age), males 4–7 yr of age, and old males (>7 yr of age) was therefore selected as the final model to describe survival pattern in males at Ram Mountain (Tables 1 and 2).

Females.—The model selection process for Ram Mountain females is summarized in Table 3. The Cormack-Jolly-Seber model provided a satisfactory fit to the data and was used as a starting point ($\chi^2 = 67.46$, $df = 104$, $P > 0.99$). Survival did not change between years, but there was a highly significant variability in survival according to age. The Caughley-like model with the same three age classes initially used for males accounted satisfactorily for this variability: from this model survival was estimated at 0.833 ± 0.025 for yearlings, 0.945 ± 0.009 for prime-age females, and 0.850 ± 0.022 for older females.

When the effects of age and year were considered together, there was no interaction between them and survival did not change between years. As expected from previous results, survival varied according to age. Similarly to what we found for males, the Caughley-

TABLE 2. Survival estimates for bighorn sheep in two study areas, based on the final models selected for each sex and each population.

Sex	Age group	Study area	Survival (± 1 SE)
Male	yearling	Sheep River	year dependent (see Fig. 1)
		Ram Mountain	0.855 ± 0.026
	prime age	Sheep River	0.896 ± 0.022 except year of pneumonia 0.691 ± 0.094 in year of pneumonia
		Ram Mountain	0.872 ± 0.020 (2–3 yr olds) 0.785 ± 0.030 (4–6 yr olds)
			0.777 ± 0.101
	older	Sheep River	0.628 ± 0.095
Female	yearling	Sheep River	year dependent (see Fig. 1)
		Ram Mountain	0.939 ± 0.026 (<100 sheep)
			0.786 ± 0.055 (100–150 sheep) 0.762 ± 0.047 (>100 sheep)
	prime age	Sheep River	0.939 ± 0.015 except year of pneumonia 0.758 ± 0.071 in year of pneumonia
		Ram Mountain	0.945 ± 0.009
	older	Sheep River	0.859 ± 0.040
		Ram Mountain	0.850 ± 0.022

like model emerged as the best descriptor of female survival at Ram Mountain. From this model, a decline in survival occurred after age 7 and survival of yearlings was lower than adult survival.

Considering what factors could explain variability in yearly survival, an overall density dependence was apparent (using the number of females: slope = -0.011 ± 0.0095 [$P > 0.2$]; using total population size: slope = -0.0072 ± 0.002 [$P = 0.008$]). Winter severity from 1975 to 1993, on the other hand, had no effect on ewe survival. As expected, given that we found independent age and density effects, a better model for the survival of Ram Mountain ewes included three age classes, each with density dependence. From this latter model, it was evident that the apparent overall density dependence in ewe survival was explained by the density-dependent survival of yearling females.

To determine if the age-specific patterns of survival of males and females were the same, we divided prime-age females into the same two age groups used for males. The mostly primiparous females aged 2–3 yr of age survived at a very similar rate as the mostly multiparous females aged 4–6 yr ($\phi = 0.948 \pm 0.012$ and $\phi = 0.941 \pm 0.014$, $\varepsilon = 0.39$, $P = 0.35$).

The final model had yearling survival negatively affected by density, a constant "prime-age" survival and a constant survival for older ewes (Table 2). No ewe was known to survive beyond 18 yr of age during our study at Ram Mountain.

Sheep River

Males.—The model selection process for Sheep River males is summarized in Table 4. The Cormack-Jolly-Seber model provided a satisfactory fit to the data ($\chi^2 = 48.99$, $df = 62$, $P = 0.89$). There was a strong interaction of year and age effects. The best model to describe the survival pattern of Sheep River males, therefore, included that interaction.

To reduce the number of model parameters, we at-

tempted to explain the high yearly variability in survival of the three male age classes as a function of density (using three classes of density: <110 sheep, 110–140, and >140 sheep) and of the pneumonia epizootic of winter 1986. Such a model, however, did not explain the variability in yearly survival of the three male age classes. The latter result seemed due mostly to a very high yearly variability in yearling survival, independently of density and of the pneumonia epizootic (Fig. 1). The best model to represent the survival pattern of males at Sheep River included a year-dependent yearling survival, an effect of the pneumonia epizootic upon the survival of prime-aged adults, and a year-independent survival of older rams. It should be noted, however, that our sample included few older rams in the year of the pneumonia epizootic: there were only two rams aged ≥ 8 yr, and both survived.

When prime-age males were divided into the same two age classes we had identified at Ram Mountain according to suspected breeding status, survival did not differ between the two groups, but the trend was the same as that found at Ram Mountain, as males aged 2–3 yr tended to survive better than those aged 4–7 yr ($\phi = 0.919 \pm 0.027$ vs. $\phi = 0.859 \pm 0.041$, $\varepsilon = 1.21$, $P = 0.11$) (Fig. 2).

According to the final model (Tables 2 and 4), yearling survival varied greatly from year to year (Fig. 1), survival of prime-aged males was constant through the years of the study except during the pneumonia epizootic, and the survival of males aged >7 yr was stable through the study. At Sheep River as at Ram Mountain, no male was known to live >13 yr.

Females.—The model selection process for Sheep River females is summarized in Table 5. The Cormack-Jolly-Seber model provided a satisfactory fit to the data on female survival at Sheep River ($\chi^2 = 18.22$, $df = 62$, $P > 0.99$). The interaction between age and year effects was significant, but the AIC of the model in-

TABLE 3. Modelling survival probability of female bighorn sheep at Ram Mountain. The model selected at each step (lowest Akaike Information Criterion) occurs in boldface. The final model is boldfaced and underlined.

Biological hypothesis	Models to be compared	AIC	χ^2	df	P†
Age dependence of survival	$[\phi_{ac+1}p]$	716.96	32.86	2	0.00
	$[\phi, p]$	745.82			
Interaction between age and time effects on survival	$[\phi_{ac+1}p]$	719.89	55.07	29	0.00
	$[\phi_{ac+1}p]$	716.96			
Time dependence of survival	$[\phi_{ac+1}p]$	716.96	32.84	18	0.02
	$[\phi_{ac}p]$	713.80			
Age dependence of survival accounted for by three age classes	$[\phi_{ac}p]$	732.13	13.67	16	0.62
	$[\phi_{ac}p]$	713.80			
Age dependence of survival	$[\phi_{ac}p]$	713.80	32.28	2	0.00
	$[\phi p]$	742.08			
Occurrence of a senescent stage	$[\phi_{ac}p]$	713.80	19.91	1	0.00
	$[\phi, p]$	731.71			
Occurrence of a yearling stage	$[\phi_{ac}p]$	713.80	23.33	1	0.00
	$[\phi, p]$	735.13			
Density dependence (number of females) of survival	$[\phi_{densF}p]$	742.77	1.31	1	0.25
	$[\phi p]$	742.08			
Density dependence (population size) of survival	$[\phi_{densT}p]$	737.33	6.75	1	0.01
	$[\phi p]$	742.08			
Effect of winter severity (five classes) on age-dependent survival‡	$[\phi_{ac+w5}p]$	656.35	9.44	12	0.66
	$[\phi_{ac}p]$	641.79			
Effect of winter severity (two classes) on age-dependent survival‡	$[\phi_{ac+w2}p]$	644.47	3.32	3	0.34
	$[\phi_{ac}p]$	641.79			
Density dependence (three classes) on age-dependent survival	$[\phi_{ac+dc}p]$	709.32	16.48	6	0.01
	$[\phi_{ac}p]$	713.80			
Density dependence (three classes) of survival accounted for by density dependence for yearlings only	$[\phi_{ac+dc}p]$	709.32	4.51	4	0.34
	$[\phi^*_{dc}\phi\phi'p]$	705.83			
Effect of breeding status on survival	$[\phi_{ac}p]$	715.64	0.16	1	0.69
	$[\phi_{ac}p]$	713.80			

† Model selection was based on minimum AIC values rather than probability values.

‡ Tested between 1975 and 1993 only (no climatic data available in 1994).

cluding an age \times year interaction was greater than for the additive model.

We subsequently tried to reduce the number of model parameters to see if we could model yearly differences in survival using the same three levels of population density we used for males and the effects of the pneumonia epizootic. This new model provided an acceptable fit to the survival pattern of females (Table 5). Similarly to our findings for males, the difference between the model with interactive effects and the model using each year as a parameter appeared to be explained by high yearly variability in survival of yearling fe-

males. As expected, a model with year-dependent yearling survival, adult survival affected by the pneumonia epizootic, and year-independent survival for older ewes provided the best fit to the survival data for Sheep River females. The survival of females aged 2–3 yr was not significantly different from the survival of females aged 4–6 yr ($\phi = 0.916 \pm 0.026$ vs. $\phi = 0.958 \pm 0.018$, $\varepsilon \pm 1.32$, $P = 0.09$), therefore a single “prime-age” class of females aged 2–6 yr was included in the final model.

According to the final model, yearling female survival varied greatly during the study (from 0.0 to 1.0;

TABLE 4. Modelling survival probability of bighorn sheep males at Sheep River. The model selected at each step (lowest Akaike Information Criterion) occurs in boldface. The final model is boldfaced and underlined.

Biological hypothesis	Models to be compared	AIC	χ^2	df	P†
Interaction between age and time effects on survival	$[\phi_{ac+1}p]$	317.18	41.26	18	0.00
	$[\phi_{ac+1}p]$	322.44			
Time dependence of age-dependent survival accounted for by density dependence (three classes) and effect of pneumonia on survival	$[\phi_{ac+1}p]$	317.18	44.53	21	0.00
	$[\phi_{ac+pneu+dc}p]$	319.71			
Time dependence of age-dependent survival accounted for by time dependence in yearling survival and effect of pneumonia on prime-age survival	$[\phi_{ac+1}p]$	317.18	30.79	17	0.02
	$[\phi^*_1\phi_{pneu}\phi'p]$	313.97			
Effect of breeding status on survival	$[\phi^*_1\phi_{pneu}\phi^0_{pneu}\phi'p]$	317.71	0.26	2	0.88
	$[\phi^*_1\phi_{pneu}\phi'p]$	313.97			

† Model selection was based on minimum AIC values rather than probability values.

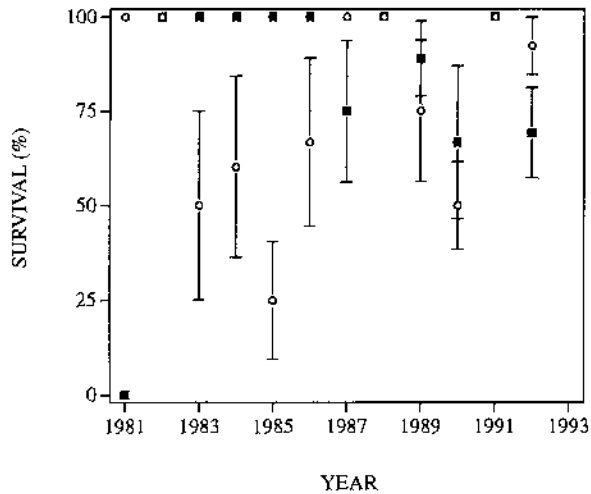


FIG. 1. Yearly survival (± 1 SE) of yearling male (\circ) and female (\blacksquare) bighorn sheep at Sheep River, Alberta; \square indicates years when survival was 100% for both sexes. No standard error could be calculated when survival was 100 or 0% (females in 1981).

Fig. 1), prime-aged female survival was constant except for the year of the epizootic, and survival of older females was stable during all years of the study (Tables 2 and 5). However, our sample included few females aged 7 yr in the year of the epizootic. Ewes aged ≥ 7 yr in winter 1986 would have been aged at least 3 yr in 1981, the 1st yr of our study. Beyond that age, ewes cannot be aged reliably from horn rings (Geist 1966), and therefore were not included in the analyses presented here. Of 19 females estimated to be ≥ 8 yr at the outbreak of the epizootic, only 13 (68.4%) survived, suggesting that pneumonia had a negative effect on the survival of old females. At Sheep River as at Ram Mountain, no female was known to survive beyond 18 yr of age.

Comparisons between sexes and populations

Prime-age survival was higher for females than for males at Ram Mountain (Wald's test $\epsilon = 5.67$, $P < 0.0001$) (Table 6). At Sheep River there was a similar trend (9% difference in the year of the pneumonia ep-

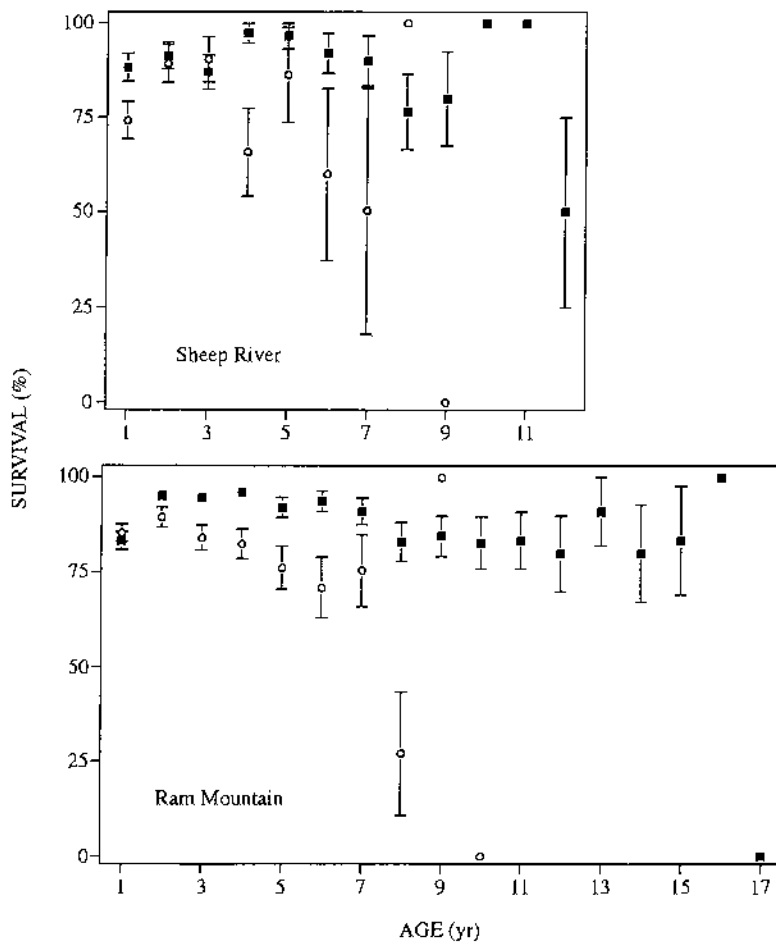


FIG. 2. Estimated survival (± 1 SE) of male (\circ) and female (\blacksquare) bighorn sheep at Ram Mountain and at Sheep River, Alberta. Standard errors were too small to be shown for Ram Mountain females aged 2, 3, and 4 yr and cannot be calculated for age classes with survival of 0 or 100%.

TABLE 5. Modelling survival probability of bighorn sheep females at Sheep River. The model selected at each step (lowest Akaike Information Criterion) occurs in boldface. The final model is boldfaced and underlined.

Biological hypothesis	Models to be compared	AIC	χ^2	df	P †
Interaction between age and time effects on survival	$[\phi_{ac+}, p]$ $[\phi_{ac+}, p]$	292.73 286.97	28.24	17	0.04
Time dependence of age-dependent survival accounted for by density dependence (three classes) and effect of pneumonia on survival	$[\phi_{ac+}, p]$ $[\phi_{ac+}, p_{pneu}, dc, p]$	292.73 285.39	34.66	21	0.03
Time dependence on age-dependent survival accounted for by time dependence in yearling survival and effect of pneumonia on prime-age survival	$[\phi_{ac+}, p]$ $[\phi_{ac+}, \phi_{pneu}, \phi', p]$	292.73 279.59	18.86	16	0.28
Effect of breeding status on survival	$[\phi^*, \phi_{pneu}, \phi_{pneu}^o, \phi', p]$ $[\phi^*, \phi_{pneu}, \phi', p]$	282.94 279.59	0.65	2	0.72

† Model selection was based on minimum AIC values rather than probability values.

izootic; 5% difference in other years) but the difference in survival between sexes was not significant ($\varepsilon = 0.57$, $P = 0.28$ in epizootic year, $\varepsilon = 1.63$, $P = 0.10$ in the other years, Table 6).

When differences in the likely breeding status of "prime-aged" males were considered, a clearer picture emerged. Survival of 2- to 3-yr-olds of different sexes did not differ at Sheep River, but young females survived better than young males at Ram Mountain (Table 6). On the other hand, in both populations, 4- to 6-yr-old females survived much better than males of the same age. Among sheep ≥ 7 yr, there was a consistent trend for lower survival of males than of females, but the difference was significant only at Ram Mountain, where the survival of older females decreased by 10% compared to that of prime-aged females, and the survival of older males decreased by 25% compared to that of prime-aged males. At Sheep River, survival of older females was 8.5% lower than that of prime-aged females and survival of older males was 13% lower than that of prime-aged males, but the survival of older males and females was not significantly different (Table 6).

For comparisons between study areas, we excluded survival during the year of the pneumonia epizootic at Sheep River and limited comparisons to sheep aged 2–6 yr. The estimated survival rate of females in the two

populations differed by <1% ($\varepsilon = 0.34$, $P = 0.73$). For males, we compared survival for the 2–3 years and the 4–6 yr age classes, because our final model for Ram Mountain retained these two classes, and results from Sheep River, although not significant, suggested a trend toward higher survival of 2- to 3-yr-olds than of 4- to 6-yr-olds. The survival of males at Ram Mountain was 5–7% lower, but neither difference was significant (2- to 3-yr-olds: $\phi = 0.919$ for Sheep River, 0.872 for Ram Mountain, $\varepsilon = 1.40$, $P = 0.08$; 4- to 6-yr-olds: $\phi = 0.859$ vs. 0.785, $\varepsilon = 1.45$, $P = 0.075$).

Emigration

It appeared that very few sheep left one of our study populations to join another population. No female at Sheep River was ever known to emigrate. Three females emigrated from Ram to Shunda Mountain, one each at ages 1, 2, and 3. Three female yearlings and one 2-yr-old emigrated elsewhere.

Only one male was known to emigrate from Sheep River: he was last seen as a yearling and was shot 4 yr later in another population. Emigration from Ram Mountain to Shunda Mountain was documented for 13 males, and one 2-yr-old male moved to the main Rocky Mountain range. The age of emigrant males in the year when they were last seen on Ram Mountain varied from 1 to 6 yr and averaged 2.4 yr.

DISCUSSION

Population and age effects

Recent comparative studies of life history evolution (Harvey and Zammuto 1985, Promislow and Harvey 1990, Promislow 1991) have assumed that a single species-specific adult survival rate can be identified. Our results indicate caution about uncritical acceptance of that assumption, suggesting that it is important to distinguish specific age classes for interspecific comparisons.

The survival of yearling sheep varied considerably between years in both study areas, and appeared to differ among populations, making it almost meaningless to assign a "typical" survival rate for this age

TABLE 6. Comparison of survival of male and female bighorn sheep of different age classes in two study areas.

Study area	Age	Difference†	Wald's ε	P
Ram Mountain	2–3	7.6	3.28	<0.001
	4–6	15.6	4.74	<0.001
	>6	22.2	2.27	0.013
Sheep River (no pneumonia)	2–3	-0.3	1.12	0.144
	4–6	9.9	4.46	<0.001
	>6	7.7	0.91	0.182
Sheep River (pneumonia)	2–3	-0.5	0.04	0.494
	4–6	4.2	0.26	0.398

† Percentage female survival minus percentage male survival.

class to use in interspecific comparisons. Yearling survival appeared to be more sensitive than adult survival to environmental factors that may vary between years.

For adult rams, differences in survival between populations approached significance, but because these differences were rather small, the use of either estimate should not have a noticeable effect upon the results of interspecific comparisons. For prime-aged females, survival rates in the two populations were within 1% of each other if the year of the pneumonia epizootic at Sheep River was excluded. Also with the exception of the pneumonia year at Sheep River, survival rates of prime-aged females varied little among years. Our results therefore suggest that within the adult age groups we identified, there were strong similarities in the survival of bighorn sheep in different populations. Catastrophic events such as epizootics, however, can have a great impact on survival.

Perhaps because of their efficient antipredator strategy (Geist 1971), during our studies bighorn sheep enjoyed high survival, despite the presence of predators. Adult survival in our study populations was comparable to the survival of adult ungulates in Europe, where predation is minimal (Clutton-Brock et al. 1982, Skogland 1985, Gaillard et al. 1993, Loison et al. 1994), and lower than reported for some African ungulates (Owen-Smith 1993a) where predators are common. Populations of 100–200 sheep, such as those we studied, may be unable to support populations of large predators, which probably rely mostly on other ungulates. Alternative prey species in our study areas included moose (*Alces alces*), wapiti (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and smaller herbivores. Because of the small size of most bighorn sheep populations, and changes in availability of alternative prey, however, predation rates could vary among populations and among years for the same population.

A recent discussion of the methodological problems involved in detecting senescence in natural populations of mammals stressed the need for long-term studies of marked individuals (Gaillard et al. 1994), therefore our results are very relevant to understanding senescence. In both populations and for both sexes we found clear evidence of senescence: the survival of sheep aged ≥ 7 yr was lower than for sheep aged 2–6 yr. Most female bighorns have their first lamb at 2 or 3 yr of age, but contrary to Promislow's (1991) suggestion, reproductive maturity did not have a strong negative effect on survival. In a previous analysis of individual life histories, we showed that early maturation did not affect female survival at Ram Mountain but may have had a delayed effect on survival at Sheep River (Festa-Bianchet et al. 1995).

We do not know the proximate reason for the increase in mortality of ewes older than 7 yr. Increased tooth wear may lower feeding efficiency, as suggested by Gaillard et al. (1993) for roe deer, yet there is no ev-

idence of a decrease in body mass or in summer mass gain at that age (Festa-Bianchet et al. 1996). Senescence may be related to cumulative effects of reproductive activities as suggested by Sydean et al. (1991) for elephant seals (*Mirounga angustirostris*), or to deleterious mutations having their effects later in life (Rose 1991). All of these hypotheses predict an accelerating increase in mortality with age beyond the onset of senescence. Our data, however, suggest that ewe survival did not progressively continue to decline as ewes aged well beyond 7 yr. Survival may further decrease for very old ewes (Fig. 2), but because our sample included only four individuals that survived beyond 15 yr of age, we could not adequately describe mortality patterns of very old females. Future research should investigate the possibility that long-lived individuals are not a random sample of the population, and attempt to identify factors that may explain individual differences in longevity. For males, we only followed eight animals at Ram Mountain and six at Sheep River beyond 8 yr of age and could not determine how survival may vary beyond that age.

The onset of reproduction did not depress female survival, but in both populations participation in the rut may have lowered male survival. Male bighorns are usually thought to begin active participation in the rut at ≈ 6 yr of age (Geist 1971), and skull-collection studies have suggested that mortality of male *O. canadensis* and *O. dalli* increases at ≈ 6 –8 yr of age (Festa-Bianchet 1986c). These results have been interpreted as evidence of a survival cost of reproduction: male survival appears to decline at the age when males begin to participate actively in the rut. Younger rams are sexually mature but prevented from breeding by older males (Geist 1971), which are much larger as body growth in males continues through at least 6 yr of age and possibly through life (Festa-Bianchet et al. 1996).

In feral sheep, chemically castrated male lambs did not rut and had higher survival than intact lambs, who took part in breeding (Stevenson and Bancroft 1995). For wild sheep, it has been proposed (Geist 1971, Heimer et al. 1984) that in hunted populations where most mature rams are removed by hunters, the survival of younger rams may decline because in the absence of older rams, younger rams participate actively in the rut and suffer greater mortality as a result of their reproductive effort. This suggestion is noteworthy because it underlines a potential implication of life history theory for wildlife management. Our data appear to support this suggestion, because hunters removed many rams aged ≥ 4 yr (Festa-Bianchet 1989), and mortality increased among rams aged 4–6 yr compared to those aged 2–3 yr. We did not observe the rut at Ram Mountain, but at Sheep River males aged 3–5 yr were regularly seen courting ewes and involved in social interactions during the rut. In some populations, rams aged 2–4 yr take part in the rut via alternative mating tactics (Hogg 1988). The relatively high mortality of

males as young as 4 yr may therefore represent a survival cost of reproduction. Geist (1971) and Hejmer et al. (1984) suggested that if hunter removal of older rams allows younger rams to take part in the rut, mortality should increase for rams aged 4–6 yr compared to unhunted populations. Because the results of skull-collections studies have been questioned (Murphy and Whitten 1976), a direct comparison of the rutting behavior of marked individuals with their subsequent survival is necessary to determine whether investment in reproduction increases mortality in males. It would also be interesting to compare our results with data from males in unhunted populations. At least four mature rams died from rut-related injuries at Sheep River (Festa-Bianchet 1987), and reproductively active rams may suffer increased predation after the rut, as suggested by Geist (1971). A recent study of elephant seals reported that male mortality increased following participation in reproductive activities but that some highly successful males also had very high survival (Clinton and LeBoeuf 1993).

Studies of ram survival in mountain sheep based on skull collections (see Festa-Bianchet 1989 for a review) are commonly used as an example of life table analysis (Ricklefs 1990), but these studies likely overestimated survival of yearlings (assigned survival rates of 0.96–1.0) and of prime-aged males (assigned survival rates of 0.87–0.99). The high yearly variability in survival of yearling sheep violates the strict assumptions of life table analysis for bighorn sheep, and other problems with applying life table analyses to skull collections have been discussed (Murphy et al. 1990). Therefore, it is unclear that our results can be compared with skull-collection studies. Differences in results may be due either to real differences in survival or to the numerous methodological problems associated with skull collections. If the results of skull-collections studies were reliable and the survival of young adult males was indeed higher in unhunted populations than in our study areas, then our data would strongly support the hypothesis that removal of older males through hunting leads to an increase in mortality of younger males (Hejmer et al. 1984).

Sex effects

The survival of adult males was generally lower than the survival of females of the same age classes. Most other studies of polygynous ungulates have reported greater survival of females than of males (Clutton-Brock et al. 1982, Anderson 1985, Skogland 1985, Gaillard et al. 1993), but exceptions exist (Berteaux 1993). Because males are larger than females, they have greater energy requirements and may be subject to greater mortality during periods of resource shortages (Clutton-Brock et al. 1985). In support of this hypothesis, Owen-Smith (1993a) reported that in kudu (*Tragelaphus strepsiceros*) sexual dimorphism in body mass and in mortality are correlated. However, he found

no clear correlation between sexual dimorphism and adult sex ratio among African bovids. Roe deer (*Capreolus capreolus*) males suffer higher mortality than females (Gaillard et al. 1993), despite limited sexual dimorphism ($\approx 10\%$ for adults).

At 2–3 yr of age, bighorn sheep males are $\approx 20\text{--}40\%$ heavier than females (Festa-Bianchet et al. 1996), yet in only one of our two study areas was male mortality higher than female mortality at 2–3 yr of age. Even at Ram Mountain, where the difference was significant, male mortality at 2–3 yr of age exceeded female mortality by only 7.6% (Table 6). At 4–6 yr of age, the sexual difference in mortality more than doubled at Ram Mountain, and became significant at Sheep River. Although sexual dimorphism also increased (to $\approx 50\text{--}60\%$) as sheep aged from 2 to 6 yr, our results suggest that participation in reproduction by young males likely had a greater role than dimorphism in body mass in determining sexual differences in survival. Yearling males at Sheep River are more susceptible than yearling females to parasites and pathogens (Festa-Bianchet 1991). Therefore, as suggested by Clutton-Brock et al. (1985), young males may suffer greater mortality than young females when faced with stressful events such as epizootics. However, contrary to the suggestion of Clutton-Brock et al. (1985), high population density at Ram Mountain was associated with an increase in mortality of yearling females and not of yearling males. Possibly, density led to increased mortality of male lambs, so that the sample of males surviving to one year at high population density was biased in favor of relatively high-quality individuals. For example, none of the males born in 1992 survived to yearling age.

In both study areas the effects of senescence appeared stronger for males than for females. The sex difference in rate of senescence could be explained by several alternative hypotheses, including sex differences in immediate age-specific costs of reproduction (supposing that older males make a great investment in reproductive activities), sex differences in the long-term costs of reproduction (supposing that older males suffer high mortality because of the great investment in reproduction they made over several years), or reasons not directly related to reproductive strategies: for example, the rate of tooth wear may be faster in males than in females, or older males may be more susceptible than older females to diseases and parasites.

Density and year effects

The survival of females at Ram Mountain was negatively affected by population density, but when age groups were considered separately, the negative effect of density was significant only for yearlings. The survival of yearling females decreased at intermediate population density, and did not show much further decrease when density peaked in the last few years of the study. Young females seem to be particularly sensitive to changes in population density in this population. The

age of first reproduction for Ram Mountain females increased almost as soon as the population began to increase after the cessation of ewe removals, before we could detect any other demographic signs of resource limitation (Festa-Bianchet et al. 1995).

We had expected that the Ram Mountain data would show a negative effect of density upon male survival because as population density increased, the adult sex ratio became more biased in favor of females (Jorgenson et al. 1993). Similar results have been obtained for red deer, another sexually dimorphic ungulate where density had a negative effect on the survival of males, both yearlings and adults (Clutton-Brock and Lonergan 1994). However, the negative effect of density on adult male survival was not significant. Therefore, increased mortality of males at high density is unlikely to be the main factor explaining the density-dependent increase in female bias of the adult sex ratio at Ram Mountain. We suspect that at high density lamb sex ratio was biased in favor of females soon after birth (J. T. Jorgenson et al., unpublished data). Our results therefore suggest that survival of adults of either sex is little affected by changes in population density. Therefore, population limitation should mostly depend upon changes in either the production or the survival of lambs, as suggested, for example, by the density-dependent increase in age of first reproduction among females at Ram Mountain (Festa-Bianchet et al. 1995).

In the Sheep River population, the pneumonia epizootic of 1986 had a major effect upon the survival of prime-aged adults, but its impact was limited to 1 yr. Survivors of the disease likely developed immunity to it, as continued high summer mortality of lambs following this and other pneumonia epizootics (Festa-Bianchet 1988a) suggests that the pathogens that led to the die-off were still present in the population for at least two more years. There was no effect of population density on survival of bighorn sheep of any sex-age class at Sheep River, possibly because the epizootic prevented the population from reaching a density at which resource scarcity would have affected adult survival (see Van Sickle [1990] for a similar viewpoint).

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APPENDIX

Variables used to model survival in bighorn sheep. Notation follows Lebreton et al. (1992).

Notation for survival and capture models	Biological significance
ϕ	Constant survival probability (no age or year effects)
ϕ_{ac}	Caughley-like model with three age classes (yearlings, "prime-age" [2-7 yr] and "older" sheep [>7 yr])
ϕ_y	Two age classes (yearlings and adults [>2 yr])
ϕ_s	Two age classes (adults 1-7 yr and "older" [>7 yr])
ϕ_{ac*}	Interaction between age (three classes) and year effects
ϕ_a	Age dependence
ϕ_t	Time dependence
ϕ_{ac*w5}	Five classes of winter severity in each of the three age classes of the Caughley-like model
ϕ_{ac*w2}	Two classes of winter severity in each of the three age classes of the Caughley-like model
ϕ_{densM}	Density dependence (density measured as the total number of males)
ϕ_{densF}	Density dependence (density measured as the total number of females)
ϕ_{densT}	Density dependence (density measured as the total population size)
ϕ_{ac*dc}	Density dependence (three classes of total population size) in each of the three age classes of the Caughley-like model
ϕ_{ar}	Four age classes (yearlings, young adults [2-4 yr], "breeding" adults [4-7 yr], and older [>7 yr])
ϕ_{rs}	Three age classes (young adults [1-4 yr], "breeding" adults [4-7 yr] and "older" [>7 yr])
$\phi_{dc}\phi\phi'$	Density dependence in yearling survival and constant survival for "prime-age" and "older" individuals
$\phi_{ac*pnou*dc}$	Density dependence (three classes of total population size) and effect of pneumonia on each of the three age classes of the Caughley-like model
$\phi^*\phi_{pneu}\phi'$	Year dependence in yearling survival, effect of pneumonia on "prime-age" individuals, constant survival of "older" individuals
$\phi^*\phi_{pneu}\phi_{pneu}^o\phi'$	Year dependence in yearling survival, effect of pneumonia on young adults and on "breeding" adults, constant survival of "older" individuals
ϕ_{ac*}	Additive effects of age (three classes) and year dependence

Note: Asterisks indicate interactions among variables in the model (as opposed to additive effects), not multiplicative function.