Conf., Worldwide Furbearer Conf. Inc., Frostburg, Md.
———. 1985. Wolf predation on caribou: the Nelchina herd case history. J. Wildl. Manage. 49: 711–720.
———. 1988. Wolf predation on Nelchina herd caribou: a comment. 1988. J. Wildl. Manage. 52: 243–250.
WALTERS, C. J., M. STOCKER, AND G. C. HABER. 1981. Simulation and optimization models for a wolf-ungulate system. Pages 317–337 *in* C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley and Sons. New York, N.Y.

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SURVIVAL OF MALE BIGHORN SHEEP IN SOUTHWESTERN ALBERTA

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Abstract: I monitored the survival of 86 tagged adult male bighorn sheep (*Ovis canadensis*) in southwestern Alberta from 1981 to 1988. Yearly mortality averaged 33% for yearlings and 18% for 2-year-olds; 7 of 16 deaths in these age classes occurred during a pneumonia epizootic. Yearling males were more likely to die during the epizootic than yearling females. Overwinter survival of male lambs varied among years and was lower after the epizootic than before it. Hunting accounted for 68% of the 28 deaths of males ≥5 years old. Natural mortality of males ≥3 years old averaged 10% yearly. The mortality of young males was higher than reported by studies based on skull collections. Skull collections may provide a biased estimate of natural mortality. The assumption of high survival of young males may not always be correct.

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Most hunted populations of mountain sheep (*O. canadensis* and *O. dalli*) are managed for trophy production (Heimer and Watson 1986). Management strategies usually involve the setting of a minimum (legal) horn size for males, at times coupled with limited female and lamb harvests (Wishart 1978, Winkler 1987). Under this management scheme, males are protected from 1 year of age until they reach legal horn size, which depends on the species, population, and definition of legal male. Information on survival to legal horn size is therefore needed by managers to forecast numbers of legal males based upon lamb survival or counts of yearling or sublegal males.

Murie's (1944) data on age-specific mortality of Dall sheep (*O. dalli*) males are widely known and often exemplify the use of life tables to summarize demographic data (Caughley 1966, Ricklefs 1973). Hoefs and Cowan (1979) obtained similar results for another Dall sheep population, while Woodgerd (1964), Geist (1971), and Hansen (1980) found the same pattern of mortality among Rocky Mountain (*O. c. canadensis*) and desert bighorn males (*O. c. mexicana*). These studies suggested that natural survival was high from 1 to about 7 or 8 years of age, and mortality increased in later years.

Geist (1971) postulated that strenuous physical exercise, possible fighting injuries, and little feeding during the rut may leave older, socially dominant males in poor condition. These males may then be more likely to succumb to predators or harsh winter weather. However, no data have been published showing that during the rut subordinate males are less active or spend more time feeding than dominant males. Data suggesting a correlation between participation in breeding and increased mortality are available for males of other large mammals (LeBoeuf 1974, Wilkinson and Shank 1976, Clutton-Brock et al. 1982). Among bighorn sheep, mature males may suffer high mortality during some pneumonia epizootics (Onderka and Wishart 1984).

Earlier studies of male mortality relied on skull collections, the assumption that the population studied had a stable age distribution, and that skulls of different age classes were equally likely to be recovered. Both assumptions are unjustified (Geist 1971, Murphy and Whitten 1976).

My objective was to quantify the age-specific

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Table 1. Number of tagged bighorn males ≥1 year old that did and did not survive from May of 1 year to May of the following year at Sheep River, Alberta. All males tagged up to 30 June each year are included.

	Yr						
	1981–82	1982–83	1983–84	1984–85	1985–86	1986–87	1987–88
No. surviving	15	28	29	31	25	22	21
No. not surviving	3	4	11	9	17	4	4
% mortality	16.7	12.5	27.5	22.5	40.5	15.4	16.0
Hunting deaths[a]	3	1	7	7	3	1	1
% natural mortality	0.0	9.7	12.1	6.1	35.9	12.0	12.5

[a] Includes those assumed to have been shot.

survival of male bighorn sheep. By monitoring marked individuals, I tested the hypothesis that young adults experience little natural mortality.

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STUDY AREA AND METHODS

The study was conducted from March 1981 to May 1988 in and near the Sheep River Wildlife Sanctuary in southwestern Alberta. The study area and the methods used to capture, mark, and census bighorn males have been described (Festa-Bianchet 1986*a*). Data reported here refer to males that wintered in the wildlife sanctuary and areas to the east. Age of males tagged when >1 year old was estimated at capture by counting the horn annuli (Geist 1966). Sheep were considered dead when remains were found, reports were received of hunter harvest, or individuals were not seen for 7 months. In no case was assumed mortality proved wrong.

Estimates of time of death were aided by the predictability with which males congregated in the wildlife sanctuary (where they could be easily seen) in June (100% fidelity) and October (98% fidelity) (Festa-Bianchet 1986*a*). If a male failed to appear for either congregation, I assumed it was dead. No evidence of emigration was found, despite compulsory registration of shot males, helicopter surveys by Alberta Fish and Wildlife of all bighorn winter ranges in southwestern Alberta outside the national parks in 1983 and 1988, and studies of bighorn sheep (including capture and marking) approximately 100 km south and 80 and 200 km northwest of the study area. No reports of tagged males outside the study area were received from hunters or fish and wildlife staff. Emigration cannot be ruled out, but it was not documented.

Hunting was allowed in September and October outside the wildlife sanctuary. Males with horns ≥4/5 of a curl could be harvested. Over 50% of males reached legal horn size by 5 years, and on average <30% of legal males were harvested each year (Festa-Bianchet 1986b). In most cases hunters reported shooting tagged males. Because hunters were not required to report tags, 8 legal males that disappeared between 15 July and the end of October were assumed to have been shot. Some of these males may have been wounded and died without being recovered.

A pneumonia epizootic occurred in the population from November 1985 to April 1986 (Festa-Bianchet 1988*a*). Carcasses recovered during the epizootic were frozen and later necropsied in the veterinary laboratory of Alberta Agriculture in Edmonton.

Most lambs are born in late May (Festa-Bianchet 1988*b*), and survival was calculated from May to the following May. Males were not included in the calculation of age-specific survival for years they lived through before being marked. Those that survived several years after tagging were included in the calculation of survival for several year classes. Survival rates were compared with *G*-tests using Williams's correction, or Fisher's exact test when sample size was <30 (Sokal and Rohlf 1981).

RESULTS

Eighty-six resident males were marked that lived to 1 year or were tagged when >1 year. Sixteen were shot by hunters, 8 were assumed to have been shot, 14 were recovered dead, 3 were poached, 1 was captured for a game farm,

Table 2. Age-specific survival of tagged bighorn males, 1981–88, at Sheep River, Alberta. Survival was calculated from May to the following May, including all males tagged up to 30 June each year.

Age interval	Surviving	Not surviving	Hunter kills[a]	Died during 1985–86 epizootic	% survival	% natural survival[b]
1–2	20	10	0	6	67	67
2–3	27	6	0	1	82	82
3–4	31	2	0	0	94	94
4–5	29	6	3	1	83	91
5–6	32	4	2	1	89	94
6–7	18	11	7	1	62	82
7–8	10	7	5	0	59	83
8–9	7	3	2	0	70	88
>9	5	3	3	0	62	100

[a] Includes known and suspected hunter kills.
[b] Excludes known and suspected hunter kills.

1 was suspected to have lost its ear tag, and 15 disappeared and were presumed dead. Those that were poached, collected, or thought to have lost tags were excluded from subsequent analysis. Ten deaths or disappearances occurred during the epizootic, accounting for 34% of the losses not attributed to hunting. Causes of death other than hunting could not be determined, except for 4 males that died of pneumonia and whose carcasses were recovered in time for necropsy (Festa-Bianchet 1988*a*), and 2 that fell to their deaths (Festa-Bianchet 1987*b*).

Survival varied among years (Table 1) if hunting mortalities were ignored ($G = 18.67$, 6 df, $P < 0.005$), but not when all causes of death were considered ($G = 10.98$, 6 df, $P > 0.05$). Of 41 males tagged at 3–6 months of age, 28 (68%) survived to 1 year. Survival to 1 year of tagged male lambs was 89% ($n = 19$) in the 4 years before the epizootic, and 57% ($n = 14$) in the 2 years after the epizootic ($G = 4.35$, 1 df, $P < 0.05$). Three of 8 tagged male lambs survived the epizootic.

Of the 29 deaths and assumed deaths not attributed to hunting, 21 (72%) and 8 (28%) occurred in November–May and in June–October, respectively. Hunting was the greatest source of mortality for males >4 years old (Table 2). Yearling and 2-year-old males, however, did not have the high rate of survival that had been expected. If hunting mortality was excluded, the mean yearly survival of males aged 1–4 years (84%, $n = 128$ M-years) was almost identical to that of males >5 years (85%, $n = 47$ M-years).

Survival from 1 to 4 or 5 years was calculated for males tagged when <2 years old that would have been >4–5 years old had they survived to May 1988. Nineteen of 35 (54%) survived to 4 years, and 12 of 28 (43%) survived to 5 years. The latter figure excludes 3 4-year-olds shot by hunters.

During the epizootic, mortality of yearling males (4 found and 2 disappeared of 8 tagged) exceeded that of yearling females (none dead of 7 tagged) (Fisher's exact test, $P = 0.01$). No dead untagged yearling females and 4 dead, untagged yearling males were found. It is possible that not all yearling males that died during the epizootic were killed by pneumonia. If data collected during the epizootic were excluded, mortality would decrease to 18% for yearlings and 17% for 2-year-olds, compared to the mean of 2% reported by skull collections (Table 3).

DISCUSSION

The pattern of mortality during this study is not similar to that described in studies based on skull collections, but resembles that found by other studies of marked males (Table 3). Possibly, the difference in survival of young males simply results from the ineffectiveness of skull collections as a technique to estimate survival. Skulls of young males may deteriorate faster than skulls of older males, and are more likely to be carried away by predators (Geist 1971) or to lose the horn sheaths and teeth. If the horn sheaths and teeth are missing, accurate aging is not possible and the skull would probably be excluded from the sample. In addition, skulls of young males may be less likely to be found than skulls of older males with larger horns. Life tables calculated from skull collections are valid only if the population had a stable age distribution during the time collections were made, an assumption known to be violated during Murie's (1944) study (Geist 1971, Murphy and Whitten 1976).

Few long-term studies of marked ungulates

Table 3. Age-specific percent yearly natural mortality of mountain sheep males in North America.

Species	Area	Method[a]	Age interval 1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	Source
Ovis canadensis dalli	Alas.	1	1	2	1	4	6	7	11	23	43	Murie (1944)[b]
O. c. canadensis	Alta.	1	0	3	4	8	13	13	21	28	39	Geist (1971)
O. c. dalli	Yukon	1	4	4	4	6	5	11	14	24	39	Hoefs and Cowan (1979)
O. c. canadensis	Nev.	1	1	2	1	2	2	7	11	13	30	Hansen (1980)
O. c. dalli	Alas.	2	3	1	12	28	23	39	45	75	[c]	Heimer et al. (1984)
O. c. canadensis	Alta.	2	19	3	14	10	14	26	30	17	41[d]	Jorgenson and Wishart (1986)
O. c. canadensis	Alta.	2	33	18	6	9	6	18	17	12	0[d]	This study

[a] 1 = skull collections, 2 = monitoring marked individuals.
[b] From Ricklefs (1973).
[c] Not available.
[d] Includes older age classes.

have been published. Smith (1986) monitored the survival of 62 radio-collared mountain goats (*Oreamnos americanus*) of both sexes in a hunted population, and found that yearly natural mortality from 2 to 8 years was about 1%, but it was 29% for yearlings and 32% for goats >8 years old. Clutton-Brock et al. (1982) found that mortality of unhunted red deer (*Cervus elaphus*) males was 13% for yearlings, averaged 3% yearly from 2 to 8 years, and increased to 24% for older males. The considerable mortality among yearlings revealed by these studies was not detected by skull collections. The low mortality rate of mountain goats and red deer aged 2–8 years is in agreement with skull-collection data, but other studies of marked bighorn and Dall sheep males have produced different results (Table 3).

Geist (1971) suggested that if mortality of older males was related to their participation in the rut, younger males should be expected to suffer greater mortality if allowed to take part in the rut. Heimer et al. (1984) and Heimer and Watson (1986) suggested that such may be the case when most older males are removed by hunters. Heimer et al. (1984) reported that natural survival of Dall sheep males aged 4–8 years was lower in areas with greater hunting pressure and a less restrictive definition of legal male. The studies based on monitoring marked individuals summarized in Table 3 were conducted on hunted populations. Of skull collections, only Hansen's (1980) was conducted on a population that was hunted for trophy males. Murie (1944), Geist (1971), and Hoefs and Cowan (1979) worked in national parks.

Does hunting of trophy males affect survival of younger males? The hypothesis is appealing because it relates survival to reproductive effort, and is supported by correlative evidence. If the hypothesis is correct, the present management strategy of mountain sheep in most of North America is biologically unsound and more restrictive definitions of legal male should be adopted, to prevent harvest of males <8 years old (Heimer and Watson 1986). However, several assumptions of this hypothesis remain to be tested. There are no data available showing that young males expend less energy during the rut than older ones. Younger, subordinate males are likely denied access to estrous females, but they may spend much of their time trying to gain access (Hogg 1984). In this study, most deaths and disappearances of sublegal males occurred among yearlings and 2-year-olds. According to the hypothesis proposed by Geist (1971) and Heimer and Watson (1986), these males should not experience high mortality, because males aged between 3 and 6 years should prevent them from participating in the rut.

Alternatively, mortality of young males may be independent of hunting regime and common to most sheep populations. In some cases, it may be due to insufficient forage resources and greater susceptibility to disease. Clutton-Brock et al. (1985) pointed out that immature male ungulates have greater forage requirements than immature females, and are more likely to die during periods of resource shortages. I suggest that they are also more vulnerable to parasites and pathogens. Young males may use most metabolic resources for growth, to achieve the large body size required to compete successfully for access to females (Geist 1971). They may store less fat (Clutton-Brock et al. 1982) and possibly channel fewer resources into their immune system, adopting a more risky strategy than females. The sexual difference in yearling mortality during the pneumonia epizootic appears to support this hypothesis, as does the greater fecal output of lungworm (*Protostrongylus* spp.) larvae by male than by female bighorns at 10–11 months of age (Festa-Bianchet 1987*a*). Bighorn males do not complete body growth until >3 years old (Jorgenson and Wishart 1984). It is therefore possible that they may be exposed to increases in mortality by resource shortages and diseases in their first 3 years of life.

Information on causes of death, behavioral observations of rutting males, and experimental manipulations of hunting regimes are necessary to determine if survival of young males can be affected by the proportion of older males present during the rut. Age-specific differences in vulnerability to predation and disease are 2 areas that require particular attention.

LITERATURE CITED

CAUGHLEY, G. 1966. Mortality patterns in mammals. Ecology 47:906–918.

CLUTTON-BROCK, T. H., S. D. ALBON, AND F. E. GUINNESS. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature 313:131–133.

———, F. E. GUINNESS, AND S. D. ALBON. 1982. Red deer: behavior and ecology of two sexes. Univ. Chicago Press, Chicago, Ill. 378pp.

FESTA-BIANCHET, M. 1986*a*. Site fidelity and seasonal range use by bighorn rams. Can. J. Zool. 64:2126–2132.

———. 1986*b*. Bighorn ram survival and harvest in southwestern Alberta. Symp. North. Wild Sheep and Goat Counc. 5:102–109.

———. 1987*a*. Individual reproductive success of bighorn sheep ewes. Ph.D. Thesis, Univ. Calgary, Alta. 229pp.

———. 1987*b*. Bighorn sheep, climbing accidents, and implications for mating strategy. Mammalia 51:618–620.

———. 1988*a*. A pneumonia epizootic in bighorn sheep, with comments on preventive management. Symp. North. Wild Sheep and Goat Counc. 6:In Press.

———. 1988*b*. Age-specific reproduction of bighorn ewes in Alberta, Canada. J. Mammal. 69: 157–160.

GEIST, V. 1966. Validity of horn segment counts in aging bighorn sheep. J. Wildl. Manage. 30:634–635.

———. 1971. Mountain sheep: a study in behavior and evolution. Univ. Chicago Press, Chicago, Ill. 383pp.

HANSEN, C. G. 1980. Population dynamics. Pages 52–63 *in* G. Monson and L. Sumner, eds. The desert bighorn. Univ. Arizona Press, Tucson.

HEIMER, W. E., AND S. M. WATSON. 1986. Harvest strategy panel: maximizing ram harvests. Symp. North. Wild Sheep and Goat Conc. 5:24–33.

———, ———, AND T. C. SMITH. 1984. Excess ram mortality in a heavily hunted Dall sheep population. Symp. North. Wild Sheep and Goat Counc. 4:425–432.

HOEFS, M., AND I. M. COWAN. 1979. Ecological investigation of a population of Dall sheep (*Ovis dalli dalli* Nelson). Syesis 12 (1, Suppl.):1–83.

HOGG, J. T. 1984. Mating in bighorn sheep: multiple creative male strategies. Science 225:526–529.

JORGENSON, J. T., AND W. D. WISHART. 1984. Growth rate of Rocky Mountain bighorn sheep on Ram Mountain, Alberta. Symp. North. Wild Sheep and Goat Counc. 4:270–284.

———, AND ———. 1986. Ram Mountain bighorn sheep project. Progress report—1984 and 1985. Alta. Energy Nat. Resour., Fish and Wildl. Div., Edmonton. 72pp.

LEBOEUF, B. J. 1974. Male-male competition and reproductive success in elephant seals. Am. Zool. 14:163–174.

MURIE, A. 1944. The wolves of Mount McKinley. Fauna of the National Parks of the United States. Fauna Ser. 5. 238pp.

MURPHY, E. C., AND K. R. WHITTEN. 1976. Dall sheep demography in McKinley Park and a reevaluation of Murie's data. J. Wildl. Manage. 40: 597–609.

ONDERKA, D. K., AND W. D. WISHART. 1984. A major bighorn sheep die-off from pneumonia in southern Alberta. Symp. North. Wild Sheep and Goat Counc. 4:356–363.

RICKLEFS, R. E. 1973. Ecology. Chiron Press, Newton, Mass. 861pp.

SMITH, C. A. 1986. Rates and causes of mortality in mountain goats in southeast Alaska. J. Wildl. Manage. 50:743–746.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Second ed. W. H. Freeman and Co., San Francisco, Calif. 859pp.

WILKINSON, P. F., AND C. C. SHANK. 1976. Rutting-fight mortality among musk oxen on Banks Island, Northwest Territories, Canada. Anim. Behav. 24:756–758.

WINKLER, C. K. 1987. Desert bighorn sheep hunting regulations and methodology for determining harvest quotas. Desert Bighorn Counc. Trans. 31:37–38.

WISHART, W. D. 1978. Bighorn sheep. Pages 161–171 *in* J. L. Schmidt and D. L. Gilbert, eds. Big game of North America. Stackpole Books, Harrisburg, Pa.

WOODGERD, W. 1964. Population dynamics of bighorn sheep on Wildhorse Island. J. Wildl. Manage. 28:381–391.

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