HARVESTING BIGHORN EWES: CONSEQUENCES FOR POPULATION SIZE AND TROPHY RAM PRODUCTION

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Abstract: We wanted to test whether ewe hunting would cause a decline in population size or in trophy ram production, and whether a reduction in ewe density would increase the size of ram horns. Thus, we examined the consequences of a bighorn sheep (*Ovis canadensis*) ewe hunting season through an experimental manipulation of an isolated population in Alberta, 1972–91. The number of ewes remained stable during 9 years despite yearly removals of 12–24% of the total ewe population. The removals did not affect ($P > 0.5$) ewe mortality due to other causes, lamb production by adult ewes, or lamb survival. The prevalence of lactation among 2-year-old ewes was higher ($P < 0.001$) during the removal than afterwards. The survival of orphan and non-orphan lambs was similar ($P > 0.1$). The number of trophy rams in the population and the number shot by hunters were independent ($P > 0.5$) of ewe numbers. A threefold increase in ewe numbers over the 10-year post-removal period did not affect the number of trophy rams ($P > 0.5$), but rams born during the removal years had larger horns at 4 and 5 years of age than rams born in the post-removal years ($P < 0.05$). Our study illustrates that ewe hunting seasons have the potential to limit population increase and can increase trophy ram size. In the absence of significant predation, about 12% of the ewes could be harvested annually, based upon conservative estimates of herd size in summer. We caution against ewe removals in populations with a history of pneumonia, because in these herds, population growth following die-offs appears slow and density-independent, and hunting mortality would likely be additive.

J. WILDL. MANAGE. 57(3):429–435

Over most of their geographical distribution, bighorn sheep, Dall's sheep (*O. dalli*), and other wild sheep are either fully protected or managed for the harvest of trophy males (Wishart 1978, Hoefs 1984, Wehausen et al. 1987, Heimer 1988). Hunting is usually limited to mature males that have reached a pre-determined minimum horn size measured by the degree of curl. Females (ewes) are actually protected under the assumption that a reduction in female numbers may reduce the number of trophy rams.

A major problem in the management of bighorn sheep is their susceptibility to pneumonia, which can have devastating consequences (Feuerstein et al. 1980, Onderka and Wishart 1984, Coggins 1988). The etiology of pneumonia in bighorns is unclear but in many cases, overpopulation and other sources of stress appear to be predisposing factors (Feuerstein et al. 1980, Spraker et al. 1984, Festa-Bianchet 1988*a*). In the absence of predation, bighorn populations may increase in density until a decline in the amount of forage available may affect body condition, lower immunity, and precipitate disease outbreaks. The potential role of predators in limiting historic sheep populations is unclear, but effective predators such as wolves (*Canis lupus*) have been extirpated in most of the present range of bighorn sheep.

Given the risk of pneumonia die-offs, and the reasonable suspicion that high population density may facilitate the outbreak of pneumonia, some form of population control may be desirable. Because of sexual segregation in habitat use (Shank 1982) the ram and ewe sectors of the population should be considered independently of each other; removal of a few mature rams (usually <4% of a bighorn population) may have no effect on the amount of resources available to nursery herds (ewes, lambs, and young rams).

Ewe harvests could stabilize populations and reduce the likelihood of pneumonia outbreaks. Epizootics are a particularly serious threat in areas such as Alberta where bighorns inhabit almost all their original range, and an outbreak in 1 population could spread to many other populations because of the large area of continuous bighorn habitat (Onderka and Wishart 1984). Harvesting ewes could also theoretically increase the horn growth rate and body size of trophy rams. The rationale for this untested expectation is the assumption that lowered competition in nursery groups would allow young males to grow more rapidly and to reach a larger size before they join ram groups (Festa-Bianchet 1991*a*).

Ewe harvests could present several potential problems. For example, the effects of ewe harvests on population growth are unknown, and there are no data to predict what proportion of ewes could be removed to maintain a stable population. An increase in productivity following a reduction in numbers could be expected if the population was limited by food, but if the population was limited mostly in a density-independent manner, for example by disease (Wehausen et al. 1987) or weather, ewe removals may cause a decline in numbers. The survival of orphaned lambs also could play an important role in population dynamics; poor orphan survival could further impede population growth.

Recently, wildlife scientists have emphasized the need for long-term studies (Gavin 1991) and manipulative experiments (Sinclair 1991) to answer important questions in wildlife management. We conducted a long-term manipulation of a marked population of bighorn sheep during 1972–91. Nine years of ewe removals were followed by 10 years of ewe protection. Herein, we report the effects of our removal experiment upon herd size, productivity, size, number and harvest of trophy rams, and survival of orphaned lambs. We tested the hypotheses that a ewe hunting season would prevent overpopulation, would not reduce the availability of trophy rams, and would lead to increased horn growth rates in rams.

We thank the many individuals who have assisted with data collection over the 20 years of this project. At the beginning of the study, G. L. Erickson built the corral trap that we still use today. We offer particular thanks to K. G. Smith, W. H. Hoffman, D. MacDonald, D. Blumer, J. Samson, and B. Fougère. Financial support was provided by the Alberta Fish and Wildlife Division, the Alberta Recreation Parks and Wildlife Foundation, the Natural Sciences and Engineering Research Council of Canada, the Fonds pour la Formation de Chercheurs et l'Aide à la Recherche, and the Craighead Wildlife-Wildland Institute, particularly J. T. Hogg, G. Luikart, M. Shields, and S. Tardiff. The logistical support of the Alberta Forest Service is much appreciated. A. W. Todd, E. Bruns, and T. Nette provided constructive reviews of earlier drafts of this manuscript.

STUDY AREA AND METHODS

Ram Mountain (52°N, 115°W) is a mountainous outcrop about 30 km east of the main range of the Rocky Mountains in westcentral Alberta, Canada. The study area ranges in elevation from 1,082 to 2,173 m, with treeline at about 1,830 m, and includes approximately 38 km^2 of alpine and subalpine habitat used by bighorn sheep. It is surrounded on 3 sides by foothills covered with coniferous forest. On the fourth side, the North Saskatchewan River separates Ram Mountain from Shunda Mountain, a similar isolated outcrop that supports a population of about 30 bighorns. Movement across the river is mostly limited to a few rams that cross back and forth, although at least 1 ewe emigrated from Ram to Shunda. Shunda Mountain is regularly censused by winter helicopter surveys and has been searched on foot at least once each summer since 1980.

Potential bighorn predators observed in the area include wolves, cougars (*Felis concolor*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), and golden eagles (*Aquila chrysaetos*). Hunting of rams with horns of at least ⅘ of a curl is permitted on an unlimited entry basis (any Alberta resident can buy a tag and hunt trophy sheep) between the last week of August and the end of October. Ewe hunting by the public was permitted on Ram Mountain only in 1966 and 1967, when 4 ewes were taken each year.

Beginning in 1971, sheep were captured in a corral trap baited with salt, and they were marked with colored plastic ear tags or canvas collars for individual identification. Since 1973, over 80% of the herd has been marked, and since 1976 the proportion marked each summer has been over 90%, with a peak of 98% in 1980. Most unmarked animals were lambs which, if not captured in the year of their birth, were captured and marked as yearlings the following year. Therefore, population estimates since 1975 were actual counts of marked individuals. Since most sheep were first captured as lambs or yearlings, the exact ages of almost all individuals were known. Body mass and horn measurements were recorded for each animal captured, and most sheep were usually captured more than once between late May and early October.

The study area was easily censused by foot, and most sheep were regularly seen at the trap site several times each summer. We calculated

Table 1. Demography of a population of bighorn sheep in westcentral Alberta during an experimental ewe removal.

	Year										
	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
No. of ewes removed previous Sep	0	7	6	7	9	6	7	5	11	10	1[a]
% of previous years' ewes removed	0	13	12	15	22	16	17	13	24	24	3
No. of ewes in Jun	52	49	48	40	38	42	39	45	42	40	43
% ewe survival[b] from previous year		93	98	80	100	92	91	100	96	100	97
No. of lambs produced	24[c]	25[c]	15[c]	23	23	24	27	25	30	25	31
% of ewes lactating[d]				70	77	80	82	74	91	81	86
No. of lambs surviving to 1 year	14	18	11	12	17	12	20	17	23	17	22
% of lambs surviving to 1 year				52	74	50	74	68	77	68	71

[a] Trapping mortality.
[b] Excluding artificial removals, calculated from June to June.
[c] Excluding neonatal lamb mortality (not known for these 3 years).
[d] Ewes 2 years of age and older.

survival based on the assumption that marked sheep not seen during a given field season had died during the previous winter. The incidence of sheep recorded as missing in one year but reappearing in a subsequent year was very low (2 ewes and 5 rams). Ten rams left the study area and were regularly seen on Shunda Mountain; these rams were still considered part of the Ram Mountain population for purposes of calculating harvest and survival statistics. Causes of death were rarely known, because most disappearances occurred in winter (Nov–May) when access to the study area was difficult. We obtained the number of rams shot during the hunting season from compulsory registrations.

Ewe removals began in 1972 and continued until 1980. A single ewe died during trapping in each of 1981 and 1982. In addition, 5 lambs were collected in 1984 for an investigation of lungworm parasitism (Samson et al. 1987). Until 1978, ewes aged ≥3 years were randomly selected and shot during the last 3 weeks of September. Between 1978 and 1980, ewes were trapped and transplanted about 41 km west of Ram Mountain. Ewes removed from Ram Mountain either had identified, marked lambs ($n = 56$) or no lamb alive at the time of removal ($n = 12$).

Lactation was determined each year for all marked ewes by examining the udder at capture or by observing the ewe suckle a lamb. Ewes that were lactating in early June but were never seen suckling a lamb were assumed to have lost their lamb at or soon after birth, and this type of lamb loss was classified as neonatal mortality. Ewes can produce their first lamb when 2 years old. Therefore, we use the term "ewes" to refer to all females ≥1 year old, and the term "mature ewes" to refer to females ≥2 years.

We analyzed the data with parametric statistics and with G-tests for frequency distributions (1 df) unless otherwise indicated. The G-test comparing lamb survival in different years was adjusted by Yates' correction factor because of the small sample of lambs that failed to survive (between 2 and 8 each year, $\bar{x} = 4.1$). We knew the exact number of ewes removed and the total number of ewes in the population, because all ewes were marked in most years. Therefore, relationships between ewe population size, numbers of ewes removed, reproductive performance, harvest, and availability of trophy rams were tested with linear regression. To test for the effects of the removal upon ram horn size we first regressed horn lengths upon capture date, then we compared horn lengths of rams born during the removal with other rams by a t-test and by analysis of covariance using date of capture as a covariate if the regression of horn length on capture date was significant (Sokal and Rohlf 1981).

RESULTS

Experimental Removals, Numbers of Ewes, and Productivity

The proportion of adult ewes removed each year varied from 12 to 24% of the total number of ewes ≥1 year old. The removal of 5–11 adult ewes/year was associated with a relatively stable population during the experimental phase of the study (Table 1). These removals were equivalent to a harvest rate of 12 to 24% of the total summer ewe population, or 14 to 33% of the previous

Table 2. Survival (%) of orphaned and non-orphaned bighorn sheep lambs born at Ram Mountain, Alberta, during an experimental ewe removal, 1972–81.

Age interval	Sex	Orphaned[a]	*n*	Non-orphaned[a]	*n*
4 months–1 yr	M	76	33	84	63
	F	83	24	85	75
	Both	79	57	85	138
4 months–2 yr	M	61	33	71	62[b]
	F	83	24	79	75
	Both	70	57	75	137[b]
1–2 yr	M	80	25	85	52
	F	100	20	92	64
	Both	89	45	89	116

[a] There were no differences ($P > 0.1$, G-tests) between those orphaned and non-orphaned.
[b] One trapping death excluded.

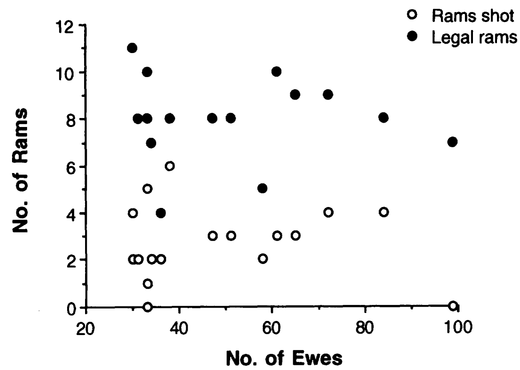

Fig. 1. The number of trophy-sized (with horns of more than ⅘ of a curl) bighorn sheep rams alive at the beginning of each hunting season (Aug) and the number shot by hunters at Ram Mountain, Alberta, compared with the number of adult ewes in the population in June of the same year, 1975–91.

winter's ewe population (5–13% of the total winter sheep population). There was an average of 50 ewes in June during the first 3 years of the experiment, and 41 in the last 7 years. The decline of 9 ewes appeared due mostly to unusually high natural losses between 1974 and 1975 (20% vs. 4% in the other years of the removal, $G = 14.49$, $P < 0.001$).

After the end of the removal phase of the study, the number of mature ewes increased, and by June 1991 it had tripled to 99. The survival of adult ewes during the removal was independent of either the number or the proportion of ewes collected the previous year ($r^2 < 0.04$, $P > 0.5$).

The removals did not affect productivity the following year (Table 1). The number of lambs surviving to 1 year of age was independent ($r^2 = 0.02$, $P > 0.5$) of the number of ewes removed the previous September, and neither the proportion of ewes ≥2 years old that produced lambs nor the proportion of lambs surviving to 1 year were dependent upon the number of ewes removed the previous year ($r^2 < 0.11$, $P > 0.5$). The removal experiment affected the proportion of 2-year-old females that produced lambs. Lactation by 2 year olds dropped from 47% ($n = 64$) in 1973–82 to only 6% ($n = 102$) in 1982–91 ($G = 39.5$, $P < 0.001$).

Survival of Orphan Lambs

Lambs orphaned by ewe removals had the same survival as non-orphans up to 2 years of age, regardless of their sex (Table 2). During the period considered, lamb survival from 4 months to 1 year did not vary between years ($G_{adj} = 4.25$, 7 df, $P > 0.5$).

Harvest, Production, and Size of Trophy Rams

Ram survival was not affected by changes in ewe population size. During the removal phase of the study, the harvest of trophy rams averaged 2/year (range = 0–5). Rams in this population can attain legal status at age 4. Survival from 4 months to 4 years was the same ($G = 0.04$, $P > 0.9$) for rams born during the removal period (53%, $n = 81$) and for those born later (51%, $n = 85$).

There was no relationship between the number of ewes in the population in June and the number of rams available to, or shot by, hunters in the following hunting season (Fig. 1). The increase in ewe numbers was not accompanied ($r^2 = 0.005$, $P > 0.5$) by an increase in the availability of legal rams. This result was somewhat surprising because of the large increase in the number of mature ewes that followed the cessation of ewe removals. The proportion of legal rams shot each year did not change between the experimental (36%) and control (35%) phases of the study. The number of legal rams harvested was independent ($r^2 = 0.005$, $P > 0.5$) of the number of ewes in the population.

Rams born while population density was low grew larger horns by 4 or 5 years of age than rams born in years of high population density (Table 3). We excluded from this analysis rams born in 1982 (the first year of no ewe removal,

Table 3. Horn size (cm) of 4- and 5-year-old rams born during the period of artificial ewe removals (1972–80) and after it (excluding those born in 1982), measured at Ram Mountain, Alberta, between 27 May and 12 July.

	Rams born			
	During removal	*n*	After removal	*n*
4 year olds				
$\bar{x}$ base circumference	36.5	43	35.2	47*
$\bar{x}$ horn length	64.0	43	59.6	47***
5 year olds				
$\bar{x}$ base circumference	38.3	28	37.4	33
$\bar{x}$ horn length	73.7	28	68.8	33**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; *t*-tests.

before the sheep population increased). When rams born in 1982 were included in the post-removal sample all significant differences remained significant. One consequence of the difference in horn size was a change in the proportion of young rams of legal size at risk of harvest. The proportion of legal 4-year-old rams tended to decline ($G = 1.689$, $P = 0.2$) following the cessation of ewe removals, from 12% (n = 51) in 1976–85 to 4% ($n = 50$) in 1986–91. The proportion of legal 5 year olds also showed a non-significant decline ($G = 0.618$, $P > 0.5$), from 36% to 27%.

Horn size comparisons may be complicated by the range in dates of ram captures (27 May–12 Jul), because horns grow during that period. To evaluate this problem, we first looked for correlations between date of capture (using 25 May as day 0 and 12 Jul as day 48) and horn size (length and base circumference) for rams born during the ewe removal period. For 4 year olds, the regression was not significant ($r^2 < 0.05$, $P > 0.1$), but for 5 year olds ($n = 31$) date of capture affected horn length ($r^2 = 0.26$, $P < 0.01$) and base circumference ($r^2 = 0.14$, $P < 0.05$). However, there were no differences in average date of capture of 5 year olds during the removal and control phases of the study, and the experimental effect on horn length of 5-year-old rams was confirmed (ANCOVA, $F_{1,58} = 10.718$, $P = 0.002$).

DISCUSSION

Removal of 12–24% of the adult ewes did not lead to a decline in either the total population size or in the number of rams available to hunters. Our results suggest that increases in the number of ewes in an established population will not necessarily lead to an increase in the number of rams available for harvest. Similarly, Clutton-Brock et al. (1987) found that a doubling of the number of female red deer (*Cervus elaphus*) was not accompanied by an increase in the number of males. These somewhat counterintuitive results are partly due to the higher natural mortality rate of males compared with that of females: for example in 1972–84, the average mortality of ewes excluding removals was 5%, that of rams excluding hunting was 21%. Female-biased survival is typical of sexually dimorphic ungulates (Clutton-Brock et al. 1982, Leader-Williams 1988). In addition, a few rams were removed by hunters, and since most rams are legal by 5 or 6 years of age, their chances of survival were small. Between 1975 and 1991, only 5 rams reached 10 years in our study area; the probability of survival to 10 years was 3.4% for 88 yearling rams born between 1971 and 1981. Therefore, there is little evidence that more trophy rams would be made available by an increase in ewe density in established bighorn populations. Furthermore, the horn growth of rams was greater during years of ewe removals. Slower horn growth limits the number of available trophy rams, because rams require more years of growth to reach legal horn size, and are exposed to mortality during the additional time (Festa-Bianchet 1989). That may explain in part why the number of trophy rams did not increase following cessation of ewe removals.

We suspect that most disappearances were due to death and not emigration, which appears to be a rare event among bighorn sheep (Festa-Bianchet 1991*a*). During this study, 20 rams (aged 2–13 yr) were radiocollared and monitored for a total of approximately 39 ram-years. None of these rams were ever relocated off the study area, except for movements to Shunda

Mountain. All rams eventually died on the study area or on Shunda Mountain.

Ewe removals likely lowered competition in nursery herds, allowing young rams to grow faster during their first 2 years of life. The effect was more pronounced among 4 year olds than among 5 year olds. That was not surprising, because the largest 4 year olds were legal and less likely to survive the hunting season, and were not available for measurement at 5 years of age. Ewe harvests could increase ram horn size, but may not result in the harvest of larger rams unless the harvests were combined with either a limit in the number of ram permits or a more restrictive definition of legal horn size. Otherwise, greater horn size of young rams may simply mean that some are killed at only 4 years of age, several years before reaching maximum horn size.

The survival of orphaned lambs was not different from that of non-orphan lambs, therefore a ewe hunting season beginning when lambs are >15 weeks old should not affect lamb survival. This result was not unexpected, given that by that age lambs appear to obtain little milk (Festa-Bianchet 1988*b*) and relationships among mothers and weaned offspring seem to play a limited role in this species (Festa-Bianchet 1991*a*).

One rationale for harvesting ewes was to stabilize the population in the hope of reducing risk of pneumonia epizootics. Our experiment at Ram Mountain was successful in stabilizing the population. This herd, however, had no history of pneumonia, and no evidence of pneumonia was encountered despite a major increase in density. Therefore, we cannot say that ewe removals prevented pneumonia. Our work at Sheep River suggests that demographic variables, such as survival or lamb production, are not useful predictors of pneumonia die-offs (Festa-Bianchet 1988*a*). Lungworm (*Protostrongylus* spp.) fecal larval counts appear to be equally useless as predictors of pneumonia (Festa-Bianchet 1991*b*). We suggest that in established bighorn herds with a history of pneumonia, increases in density should be considered a threat to the population.

The increase in population size at Ram Mountain following the cessation of ewe removals occurred despite the presence of several potential predators. Predation pressure appears to vary greatly among populations of bighorn sheep (Hebert and Harrison 1988, Berger and Wehausen 1991). Managers should avoid harvesting ewes in populations with considerable natural mortality that may be independent of population density.

MANAGEMENT IMPLICATIONS

Our experiment evaluated the consequences of a limited-entry (<25% of the summer ewe population) hunting season for bighorn sheep ewes. The drop in ewe numbers between 1974 and 1975 may have been due to a severe winter. That decline suggested that ewe harvests at the level of our study could stabilize a population but may not allow recovery from high non-hunting losses. In those circumstances, hunting mortality may be additive. Therefore, we recommend a conservative strategy of harvesting about 12% of the estimated summer ewe population ≥1 year old, or about 5% of the total winter population ≥1 year old. The number of permits should be increased if censuses indicate that the population continues to grow. In our study, removal losses were partially compensated by lamb production from 2-year-old ewes. After ewe removals were stopped and the population increased, this source of recruitment disappeared. In other populations, whether or not 2 year olds will produce lambs following ewe hunting seasons would have profound effects on population growth; during the removal, 2 year olds typically made up over 25% of the mature ewe population.

We suggest that ewe hunting seasons could be used conservatively within herds that are healthy and that would likely increase if unharvested. Clearly, a major task facing managers is the determination of a safe population density, in the absence of reliable information on historic population size. For populations that have recently experienced pneumonia die-offs, we recommend against ewe hunting seasons for 5 years, and possibly longer. These populations will likely experience density-independent mortality, particularly among lambs, as a consequence of the disease (Spraker and Hibler 1982). Under these circumstances, population increases may be slow or non-existent even at low density (Wehausen et al. 1987, Festa-Bianchet 1988*a*), and ewe removals could further reduce population size.

LITERATURE CITED

BERGER, J., AND J. D. WEHAUSEN. 1991. Consequences of a mammalian predator-prey disequilibrium in the Great Basin desert. Conserv. Biol. 5:244–248.

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

———, G. R. IASON, AND F. E. GUINNESS. 1987. Sexual segregation and density-related changes in habitat use in male and female red deer (*Cervus elaphus*). J. Zool. 221:275–289.

COGGINS, V. 1988. The Lostine Rocky Mountain bighorn sheep die-off and domestic sheep. Proc. Bienn. Symp. North. Wild Sheep and Goat Counc. 6:57–64.

FESTA-BIANCHET, M. 1988*a*. A pneumonia epizootic in bighorn sheep, with comments on preventive management. Proc. Bienn. Symp. North. Wild Sheep and Goat Counc. 6:66–76.

———. 1988*b*. Nursing behavior of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate, and sex. Anim. Behav. 36:1445–1454.

———. 1989. Survival of male bighorn sheep in southwestern Alberta. J. Wildl. Manage. 53:259–263.

———. 1991*a*. The social system of bighorn sheep: grouping patterns, kinship, and female dominance rank. Anim. Behav. 42:71–82.

———. 1991*b*. Numbers of lungworm larvae in feces of bighorn sheep: yearly changes, influence of host sex, and effects on host survival. Can. J. Zool. 69:547–554.

FEUERSTEIN, V., R. L. SCHMIDT, C. P. HIBLER, AND W. H. RUTHERFORD. 1980. Bighorn sheep mortality in the Taylor River-Almont Triangle area, 1978–1979: a case study. Colo. Div. Wildl. Spec. Rep. No. 48. 19pp.

GAVIN, T. A. 1991. Why ask "why": the importance of evolutionary biology in wildlife science. J. Wildl. Manage. 55:760–766.

HEBERT, D. M., AND S. HARRISON. 1988. The impact of coyote predation on lamb mortality patterns at the Junction Wildlife Management Area. Proc. Bienn. Symp. North. Wild Sheep and Goat Counc. 6:283–291.

HEIMER, W. E. 1988. Toward a working hypothesis for mountain sheep management. Proc. Bienn. Symp. North. Wild Sheep and Goat Counc. 6:39–46.

HOEFS, M., editor. 984. Wild sheep. Spec. Rep. of the North. Wild Sheep and Goat Counc. Yukon Wildl. Branch, Whitehorse, Yukon Territ. 218pp.

LEADER-WILLIAMS, N. 1988. Reindeer on South Georgia. Cambridge Univ. Press, U.K. 319pp.

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

SAMSON, J., J. C. HOLMES, J. T. JORGENSON, AND W. D. WISHART. 1987. Experimental infections of free-ranging Rocky Mountain bighorn sheep with lungworms (*Protostrongylus* spp.; Nematoda: Protostrongylidae). J. Wildl. Dis. 23:396–403.

SHANK, C. C. 1982. Age-sex differences in the diets of wintering Rocky Mountain bighorn sheep. Ecology 63:627–633.

SINCLAIR, A. R. E. 1991. Science and the practice of wildlife management. J. Wildl. Manage. 55: 767–773.

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

SPRAKER, T. R., AND C. P. HIBLER. 1982. An overview of the clinical signs, gross and histological lesions of the pneumonia complex in bighorn sheep. Proc. Bienn. Symp. North. Wild Sheep and Goat Counc. 3:163–172.

———, ———, G. G. SCHOONVELD, AND W. S. ADNEY. 1984. Pathologic changes and microorganisms found in bighorn sheep during stress-related die-off. J. Wildl. Dis. 20:319–327.

WEHAUSEN, J. D., V. C. BLEICH, B. BLONG, AND T. L. RUSSI. 1987. Recruitment dynamics in a southern California mountain sheep population. J. Wildl. Manage. 51:86–98.

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.

———, J. T. JORGENSON, AND M. HILTON. 1980. A minor die-off of bighorns from pneumonia in southern Alberta (1978). Proc. Bienn. Symp. North. Wild Sheep and Goat Counc. 2:229–245.

Received 3 February 1992.
Accepted 19 February 1993.
Associate Editor: Woolf.