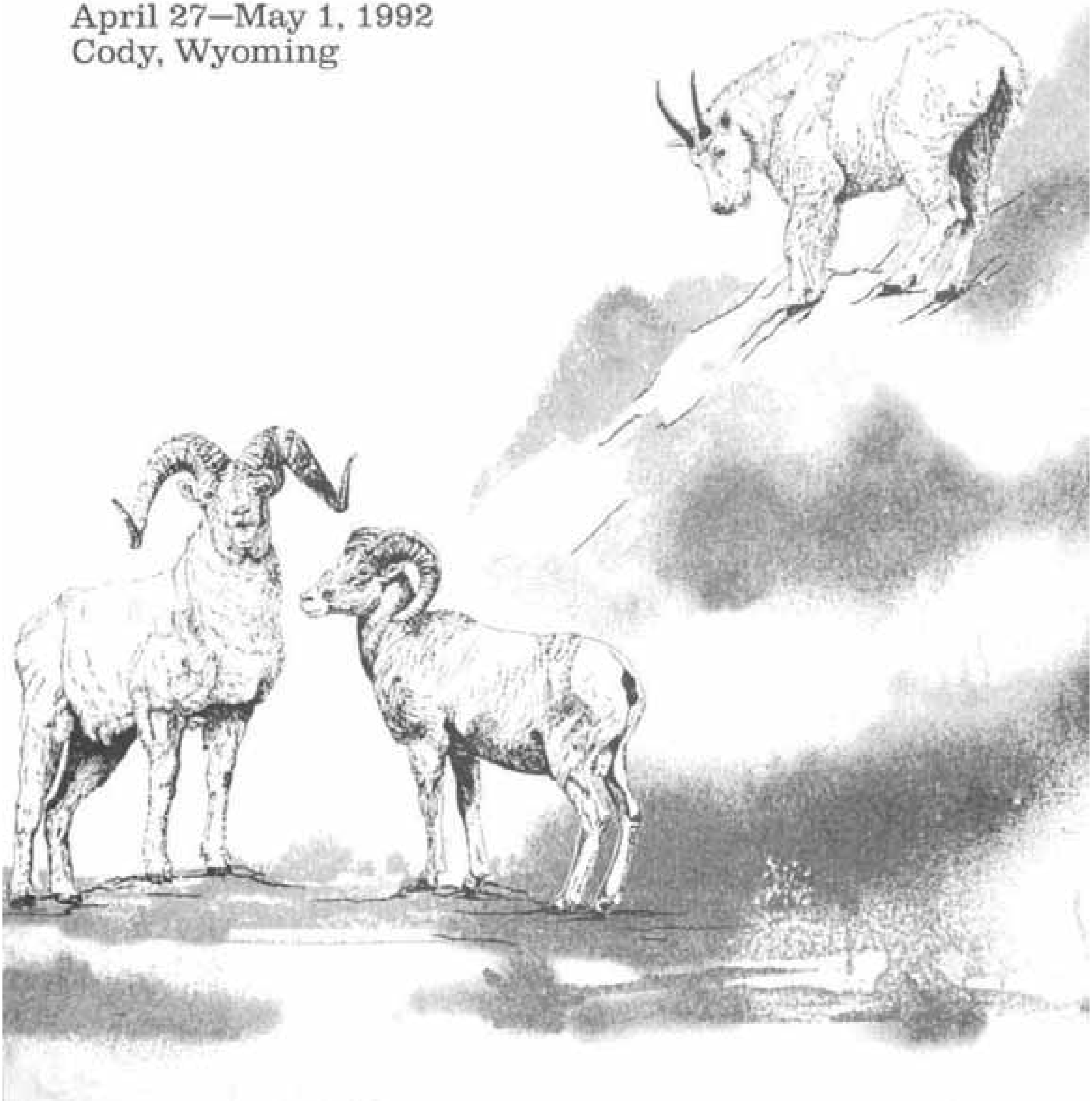
Northern Wild Sheep and Goat Council

Proceedings of the Eighth Biennial Symposium

April 27—May 1, 1992
Cody, Wyoming



NORTHERN WILD SHEEP
AND GOAT COUNCIL

PROCEEDINGS OF THE EIGHTH BIENNIAL SYMPOSIUM

APRIL 27 - MAY 1, 1992

CODY, WYOMING

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W. G. Hepworth

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Kevin Hurley, 1992 NWSGC Conference Chair

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Without the contributions and hard work of these people, especially our publications coordinator and editor John Emmerich, the 1992 conference would not have been so successful. They have my personal thanks, and those of the membership of the Northern Wild Sheep and Goat Council.

IN MEMORIAM

Kay Bowles, Game Warden with the Wyoming Game and Fish Department died from a heart attack in February, 1992 while conducting routine enforcement and survey activities near his home in Dubois, Wyoming. These proceedings are dedicated to Kay and his accomplishments in managing bighorn sheep.

Kay served the Wyoming Game and Fish Department in west-central Wyoming for 25 years. He was a skilled wilderness horseman with a keen interest and intimate knowledge of Wyoming's wilderness and the bighorn sheep it supports. His dedication was instrumental in the acquisition and management of important wintering areas for bighorn sheep in the Whiskey Basin area. He was a member of the Whiskey Basin Bighorn Sheep Interagency Management Committee and a key player in the Whiskey Basin bighorn sheep trapping and transplanting program that has made reintroduction of bighorn sheep possible in many western states. His enthusiasm and joyful attitude helped all who met Kay, more deeply appreciate Wyoming's wildlife resource. Generations to come will benefit from Kay's efforts.

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FOREWORD

Papers and poster abstracts in these proceedings were presented during the Eighth Biennial Symposium of the Northern Wild Sheep and Goat Council held April 27 - May 1, 1992 at Cody, Wyoming.

These papers and abstracts have been reviewed, but not refereed. Each manuscript was read carefully by at least two peer biologists, and suggestions were submitted to each author. No papers were rejected based on peer review, although several papers were revised as a result of review suggestions. Final versions of all papers reflect author responses to review comments. This review process is designed to enhance the timely dissemination of useful information. However, the reader is responsible for critically evaluating the information contained in these papers. This is always the responsibility of a professional biologist.

POPULATIONS AND MANAGEMENT

Bienn. Symp. North. Wild Sheep
and Goat Counc. 8:1-7.

EFFECTIVE POPULATION SIZES FOR BIGHORN SHEEP

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Abstract: Determination of effective population size allows conceptualization of the effects of population size and demography on rates of genetic drift and inbreeding. To better understand the extent to which genetic factors may be affecting population viability, we estimated effective population size for bighorn sheep (*Ovis canadensis*) with varied population histories. For 13 populations of bighorn sheep in Wyoming, Montana and South Dakota, we found ratios of effective population size to actual population size ranging from 0.23 to 0.42, and averaging 0.33. This suggests that bighorn sheep populations should be kept at total sizes of over 150 to avoid short-term loss of genetic variability. Effective population size provides a conceptual framework for considering the managment of bighorn sheep populations, especially those that are small or isolated.

The importance of genetic factors in the management of free-ranging wildlife populations is being increasingly recognized (Soulé 1986), especially where populations are small, have undergone bottlenecks, or are isolated (Leberg 1991). Genetic variability is important in contributing to population viability, and assumes 2 forms: allelic variability and heterozygosity. Allelic variability refers to the kinds and frequencies of genes that occupy specific positions (loci) on chromosomes. Allelic variability is important in part because it provides the basis for adaptation to local environments; without it, selection cannot occur. Heterozygosity refers to the ways in which dissimilar alleles are paired at loci, and reflects an intrinsic taxon-specific value as well as recent breeding history. Examples of factors that affect recent breeding history are genetic exchange among populations, and the breeding system within a population (Falconer 1981).

In very small populations, variability often is reduced. More specifically, variability is lost at low values of effective population size (N_e), the size of an idealized population (one with panmictic breeding, an even sex ratio, and no variation in size over time) that has the same rate of drift as the population of concern (Falconer 1981). In these populations, heterozygosity is reduced primarily by inbreeding, or breeding among close relatives, whereas allelic variability is

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reduced primarily by drift, or the changes in allele frequencies that occur as a result of the ramdom sampling of gametes to form zygotes (Falconer 1981). Both allelic variability and heterozygosity undergo reductions at increased rates at low levels of N_e, and these reductions are undesirable from the standpoint of population persistence.

Genetic variability has been alleged to affect population performance of bighorn sheep (DeForge et al. 1979, Skiba and Schmidt 1982) because of the high insularity and low N_e of many populations (Schwartz et al. 1986). In captive-born bighorn sheep, lamb survival was 34% less in inbred lambs than in non-inbred lambs (Sausman 1984). Horn growth has been correlated with population history in bighorn sheep by Stewart and Butts (1982), who found that herds in Montana that had undergone bottlenecks of population size (N) < 60 had lower cumulative horn growth to age 3.5 years than did herds that had maintained $N \geq 150$. In other ungulate species, allozyme variability has been shown to be positively correlated with reproductivity (Johns et al. 1977), fetal growth rate (Cothran et al. 1983), longevity (Chesser et al. 1982), and antler size (Scribner et al. 1989). Others have dismissed the importance of loss of genetic variability to bighorn sheep populations because interpopulation movements are difficult to detect and may be relatively common (Schwartz et al. 1986).

Predictions of population viability rely on species-specific knowledge of N_e. However, estimation of N_e is problematic, particlularly for polygamous species hunted for only one sex, such as the bighorn sheep. This paper attempts to estimate N_e for bighorn sheep using aerial survey data for 13 populations from Wyoming, Montana, and South Dakota, and discusses the potential conceptual importance of effective population size in managing bighorn sheep.

Funding for this study was provided by the Wyoming Game and Fish Department, and the Foundation for North American Wild Sheep.

METHODS

We analyzed demographic data for bighorn sheep herds in Wyoming, Montana, and South Dakota obtained from aerial surveys (Wyoming Game and Fish Department completion reports 1975-1990) and from periodic surveys by other agencies to estimate N_e. We adjusted for unequal sex ratios of breeders with the formula:

$$N_e = \frac{4N_f N_m}{N_f + N_m}$$

where N_f is the number of breeding females and N_m is the number of breeding males (Crow and Kimura 1970). We adjusted for the effect of changes in N over time with the formula:

$$\frac{1}{N_e} = \frac{1}{t}\left(\frac{1}{N_{e_1}} + \frac{1}{N_{e_2}} + \frac{1}{N_{e_t}}\right)$$

which uses a harmonic mean of estimates of N_e over time to emphasize years of low population size (Crow and Kimura 1970). The number of breeding females was estimated by multiplying the number of adult ewes observed by the post-harvest proportion of ewes accompanied by lambs. The number of males was estimated by multiplying the number of adult rams (with $\geq$ 1/2 curl horns) by 0.66. This proportion represents the midrange between the value (0.33) reported by Hogg (1987) to be the dominant breeders of estrous ewes, and 100%, which is possible given that sub-dominant rams also mate (Hogg 1987). From these calculations, we obtained estimates of N_e/N for each year. N_e may be reduced by overlapping populations, but we had too few data on age-specific reproduction and mortality to address this issue. We assumed no significant gene flow among native herds, which likely is violated for some herds we studied. Such gene flow would tend to increase N_e to an extent influenced by the gender of dispersers in polygamous species (Chesser 1991). To assess the effect of changes in the number of breeding rams or in lamb/ewe ratios, N_e also was estimated by reducing the number of breeders of each sex by 50%. Inbreeding coefficients (F) were estimated by the formula of Crow and Kimura (1970):

$$F = \frac{1}{2N_e}$$

RESULTS AND DISCUSSION

We estimated that the mean N_e/N for all populations was 0.33 (range = 0.23 - 0.42), which resulted in N_e values from 36 to 326 in native herds (Table 1). All introduced herds had $N_e < 50$. In calculating N_e/N, if the number of breeding rams or the lamb/ewe ratio was reduced by 50%, mean N_e/N decreased to 0.21. Rate of inbreeding was < 1% in all native herds except in a small remnant herd in the Teton Mountains, where it was 1.4% (Table 1). Reintroduced herds had inbreeding rates ranging from 1.0 - 4.6%. Because our estimated N_e/N ratios varied by a factor of almost 2, herd-specific estimates should be used to address any herd-specific question. Importantly, estimates of N_e from aerial observations may be confounded by herd-specific biases in locating ewe/lamb or ram cohorts.

Our estimates of herd-specific N_e values suggest that the transplanted herds and the Teton herd are at risk of losing genetic variability over the short-term, and that several native herds may be at long-term risk. To manage for the maintenance of genetic variability over the short term, Franklin (1980) recommended an $N_e \geq 50$, which would keep the inbreeding rate <1%. For bighorn sheep, this requires $N \geq 150$, given a mean N_e/N of 0.33. Therefore, herds that have $N < 150$ should be expected to lose variability over generational time. Persistently small populations may fail to grow, even in the presence of adequate habitat, if their reproductivity becomes impaired by the phenotypic changes

Table 1. Population histories of native and transplanted bighorn sheep herds from Wyoming and neighboring states. Population estimates are from records of the Wyoming Game and Fish Department and the South Dakota Department of Fish, Parks and Wildlife. N_e represents the effective population size, N the population size and F the inbreeding coefficient. The N_e/N ratio is the average value derived from aerial survey data 1975-1990.

Location	Year of Transplants	Founder N	1990 N	N_e	N_e/N	F
Native						
Clark's Fork, WY	n.a.	n.a.	520	129	0.33	0.004
Trout Peak, WY	n.a.	n.a.	668	79	0.39	0.006
Wapiti Ridge, WY	n.a.	n.a.	968	154	0.27	0.003
Yount's Peak, WY	n.a.	n.a.	827	130	0.23	0.004
Franc's Peak, WY	n.a.	n.a.	1146	326	0.39	0.002
Jackson, WY	n.a.	n.a.	525	184	0.40	0.003
Tetons, WY	n.a.	n.a.	100	36	0.36	0.014
Founder						
Whiskey Mtn., WY	n.a.	n.a.	1070	207	0.28	0.002
Transplant						
Bighorn Canyon, WY/MT	1973	8	90	11	0.42	0.046
Douglas Creek, WY	1970	41	131	48	0.27	0.010
Custer State Parker, SD	1965	12	145	21	--	0.024
Encampment River, WY	1976-77	69	60	25	0.31	0.020
Laramie Peak, WY	1964-82	129	53	25	--	0.020

caused by inbreeding (Sausman 1984). Franklin's (1980) suggested $\underline{N}_e$ > 500 to reduce genetic loss over the long term would necessitate maintaining bighorn populations of over 1530, an estimate larger than any herd size in Wyoming. This assumes little or no exchange of animals among these herds.

The objective of genetic management of bighorn sheep populations should be to minimize the loss of naturally-occuring genetic variability, rather than to maximize genetic variability through outcrossing to distant herds. For the large native herds, this may be most effectively accomplished by maintaining habitat corridors to permit continued migration between adjacent herds, which will increase the $\underline{N}_e$ of both populations involved. Habitat improvements to increase carrying capacity also should be considered. Maintaining or restoring genetic variability should be considered for persistently small or reintroduced herds. Theoretically, an immigration rate of 1 per generation can prevent allele fixation (Wright 1978). However, Lacy's (1987) models showed that 5 immigrants per generation were required to retain at least 90% of long-term genetic variability. These values provide a range for managers to consider in planning supplemental transplants. Chesser (1983) found that inbreeding in polygynous species is more rapidly countered when males that can impregnate several females are introduced. This suggests the importance of rams of breeding age in both initial and supplemental transplants. Transplant size also is important because it determines initial inbreeding levels and the time necessary to expand to population sizes with high persistence probabilities.

Genetic factors should be considered along with vegetation, topography, weather, disturbance and disease when assessing and managing bighorn sheep populations. Management of small or isolated herds to achieve goals of $\underline{N}_e$ rather than of $\underline{N}$ would place the management of these herds into the theoretical framework of conservation biology, which could suggest new solutions to old problems. For example, the effects of hunting only large-horned rams may warrant further consideration. In simulations of grizzly bear (Ursus arctos) populations, different hunting regimes resulted in values of $\underline{N}_e/\underline{N}$ ranging from 0.24 to 0.32 (Harris and Allendorf 1989). Similarly, Ryman et al. (1981) estimated that $\underline{N}_e/\underline{N}$ of moose (Alces alces) would range from 0.24 to 0.36 under different hunting regimes.

The role of genetic variability within and among populations of bighorn sheep should be considered if populations are to persist, expand, and have long-term viability with low management costs. Management decisions may need to rely on genetic theory because diagnostic tools are not yet available. If habitat fragmentation and herd isolation are not offset by corridors for dispersal or supplemented gene flow, then genetic variability and population viability may be compromised.

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and Goat Counc. 8:8-13.

WHY IS MONTANA THE LAND OF GIANT RAMS?

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Abstract: Montana has been producing Boone and Crockett (B&C) record book bighorn (*Ovis canadensis canadensis*) rams in ever increasing numbers. Each year seems better than the last, and 1991 was no exception. These high scoring rams are coming mostly from introduced populations with the same genetic source (Sun River). There is much variation in horn growth among the introduced populations: the phenomenon of superior horn growth is explored and several hypotheses are brought forth that are intended to stimulate thinking among bighorn sheep managers.

As the 20th century draws to a close, a hunter would hardly expect to find large numbers of outstanding big game trophies being harvested. Such a phenomenon is occurring with Montana bighorn sheep. In 1990, a new official state record ram was taken by Lester Kish. It is the largest recorded ram killed by a hunter in the United States, with a B&C score of 200 7/8, and a left horn length of 49 2/8 inches.

In 1974, Jack Atcheson spoke before the Northern Wild Sheep and Goat Council. He explained that during the previous few years about 500 North American rams had been mounted in his shop. Of those 500 rams, he stated that less than 1% had horn lengths of 39 inches or more (Atcheson 1974). During mid-December of 1991 I visited Atcheson's Taxidermy. Record book bighorn rams were everywhere. They had just finished mounting a ram with a score of 196 4/8. Another had a score of 191 6/8. Others safely made the B&C minimum of 180. A couple of weeks later I returned to visit once again. There was a new set of horns on the floor with a reported score of 185 and horn lengths of nearly 44 inches. Have times changed!

Forty-eight bighorn rams from Montana have been officially scored 190 B&C points or more (Table 1). Others will score above 190 but have not been officially scored or have been disqualified for various reasons. Of these 48 rams, 38 (79%) have been taken since 1980. It is likely that at least 11 more rams were taken during the 1992 hunting season that will officially score over 190 points.

For the past decade and a half, Montana has produced up to 20 or more record book rams each year. In some management units half the kill, or more, is comprised of "Book" sheep (pers. records). Growth rates are phenomenal with many high-scoring sheep only being 4 1/2 years old. One ram measured from the East Fork of the Bitterroot, that had perished from pneumonia, was only 3 1/2 years old and had a 38 inch horn length and 17 inch bases.

In the 1990 Montana state record book, 34 of 139 registered rams are from Sun River. Most were taken many years ago. Gail Joslyn (Mont. Dep. Fish Wildl. and Parks, pers. commun.) feels that the Sun River herd produced its highest scoring rams following fires a generation ago. Fires no doubt stimulated forage growth with a possible reduction of lungworm larva (L.S. Nielsen, Mont. Dep. Fish Wildl. and Parks, pers. commun.).

Most "Record Book" sheep are coming from introduced herds that are genetically from Sun River stock. On new range, trophies tend to reach their maximum size until the population reaches the capacity for the range (Geist 1971, Shackleton 1973, Heimer and Smith 1975). Geist (1971) has theorized that quality rams are most likely to occur on new ranges where there is a low population density. Most of Montana's introduced bighorn populations are still expanding, so carrying capacities have not been reached (L.S. Nielsen, Mont. Dept. Fish Wildl. and Parks, pers. commun.). The Thompson Falls area is apparently an exception to this criterion (B. Sterling, Mont. Dep. Fish Wildl. and Parks, pers. commun.). Sterling told me in an interview that the population had probably reached a maximum level and that horn growth rates had drastically declined.

Stewart and Butts (1982) studied mean cumulative horn volume for the first 4 growth periods. It was found that all introduced herds demonstrated greater average horn volumes than native herds. They postulated that inbreeding has contributed to the small horns common in native herds. They feel that inbreeding will occur in a population of 50 animals or less, with a corresponding reduction in horn size. Additionally they feel inbreeding may also contribute to the eventual demise of the herd.

Stewart and Butts (1982:77) state, "It appears that when sheep are put into a new and relatively unexploited habitat, the rate of horn growth is exceptional-far surpassing that of the parent stock. As a population expands, the rate of horn growth declines. Eventually, carrying capacity is reached and horn growth is reduced to a level similar to that of the parent stock with minor differences, due to differences in productivity between the ranges." This same phenomenon has been demonstrated in New Zealand with red deer (*Cervus elaphus*) where antlers grew larger after transplanting than found in parent stock coming from England and Scotland. When red deer numbers grew to beyond the carrying capacity of the range, trophy antlers were not found within the population (Banwell 1986).

This paper explores some of the possible reasons why Montana is growing so many high scoring rams. It is hoped that it will stimulate some thinking among game managers on the production of "Super Rams."

FACTORS AFFECTING HORN GROWTH

Forage

Areas that are producing high numbers of large horned rams from introduced herds have an abundance of good forage, such as rough fescue

(Festuca scabrella). Rough fescue has a high protein content as dry winter food, far exceeding most other plants that are natural foods of bighorn sheep (Wishart 1969, Johnson et al. 1968). Rough fescue is abundant only on range not overgrazed by domestic livestock or wildlife (L.S. Nielsen, Mont. Dep. Fish Wildl. and Parks, pers. commun.).

It seems appropriate to compare forage quality among herds in Montana, as all sheep with fast growing horns come from the same genetic source, the Sun River. It appears that all the best Montana rams are coming from areas that are producing a large volume of rough fescue or other super food (L.S. Nielsen and D. Hook, Mont. Dep. Fish Wildl., and Parks, pers. commun.). Nielsen has observed large amounts of rough fescue in areas noted for large horned sheep like Rock Creek and the South Flint Creek range. I have observed rough fescue in the bighorn ram summer range of the Highlands, which is another area noted for its large horned rams. Wishart (1969) noted that in Alberta large horned rams appear to be the result of an optimum combination of climate, soil, and vegetation. Rough fescue is the dominant grass in those portions of alberta producing large horned rams.

Hunting Seasons

In western Montana, introduced sheep herds have relatively small home ranges. Rams use dense timber for security except during the rut. Sheep seasons often run until the Sunday after Thanksgiving, which includes some of the rut period. A few units such as Upper Rock Creek and the Anaconda area close at the end of October before the rut. The original intention of this regulation was to protect some rams, allowing them to reach old age (L.S. Nielsen, Mont. Dep. Fish Wildl. and Parks, pers. commun.). This hunting season seems to work as intended since these units produce a high percentage of trophy rams. Over the past 2 seasons, nearly half the rams harvested in Upper Rock Creek have scored in excess of 190 B&C points. Anaconda produced the U.S. record in 1990 and has produced numerous other record book rams under this type of season.

THE ROCK CREEK HERD

The area of Upper Rock Creek between Philipsburg and Missoula was the home of a native bighorn herd that reached low levels several times during this century (L.S. Nielsen, Mont. Dep. Fish Wildl. and Parks, pers. commun.). In 1975 wild sheep from the Sun River were released in the area. It has been stated that only 3 native sheep remained when the release was made (L. Clark, local guide, pers. commun.). Horns from mature rams before the release were small, seldom exceeding 30 inches in length (pers. observation). Since the season was reopened in 1983, record book rams have been taken with regularity, including the Larry Smith ram taken in 1984 scoring 199 0/8 (Table 1). Since 1990, rams with high scores have appeared in larger numbers in the harvested segment. In 1990, 4 of 10 rams had scores exceeding 190 points and in 1991, 2 exceeded 190 points (Table 1).

It has also been noted that ram body sizes in the area are exceptional. Boone (letter to R. Dimarchi, B.C. Fish and Wildl.

Branch, Cranbrook, 1985) wrote concerning the Gingras ram harvested in 1984, "What impresses me most is the size of the ram's body. The ram was brought out in pieces and weighed the next day, minus the lower legs, much of the back cape and some trimmed meat and bone, and of course the entrails. The weight was 255 pounds. The live weight is estimated at 350 plus pounds."

Butts (1980:69) had this to say about the Rock Creek herd: "Berwick reported that horn size of original Rock Creek rams was exceptionally small and tight. He attributed that to a lack of phosphorus (P), calcium (Ca) and other minerals, though he pointed out that horn size was larger shortly before the population crash. The availability of minerals on the Rock Creek range has probably not changed since the mid-1960's. The forage quality and the genetics of the population have changed."

In the mid to late 1960's, the range was considered in poor condition. As a result, cattle numbers were reduced and rest rotation grazing systems initiated on public lands. By the mid-1970's, the range was improving and ranked good to excellent according to the Bureau of Land Management (Butts 1980). Rams from the herd established after the 1975 release leave traditional wintering areas, allowing better utilization of forage including abundant rough fescue (Butts 1980). In a February 1992 telephone conversation, Rock Creek rancher and bighorn guide Larry Clark said that sheep were continuing to establish new splinter herds. The herd, which the state estimates at 300 individuals, appears to still be expanding and continuing to produce large horned rams.

MANAGEMENT SUGGESTIONS

The upper Rock Creek habitat should be studied to determine whether the area possesses unique properties that contribute to the growth of large horned rams. A comparison of forage types and quality among various bighorn sheep ranges may shed light on the role quality forage, such as rough fescue, plays in the growth of large horns.

In addition more detailed analysis of the effects of supplemental transplants of desirable genetic stock on sheep herd productivity, survival, and horn growth should be undertaken. A better understanding of these factors may help managers duplicate the current Montana phenomenon of extraordinary ram horn growth in other sheep herds.

Table 1. Montana bighorn sheep with an official Boone and Crockett score of 190 or greater.

Score	Locality	Year	Hunter
200 7/8	Unit 213	1990	Lester Kish
200 3/8	Unit 680	1991	Eugene Knight
199 0/8	Unit 216	1984	Larry Smith

Table 1. Continued.

Score	Locality	Year	Hunter
197 5/8	Unit 213	1987	Art Dubs
197 1/8	Unit 121	1979	Armand Johnson
197 1/8	Unit 216	1990	Lee Hart
197 0/8	Unit 340	1989	Gene Riordan
196 7/8	Unit 216	1990	Keith Koprivica
196 5/8	Sun River	1961	Don Anderson
196 4/8	Unit 340	1991	Vern Barnett
196 2/8	Unit 340	1989	Guy Miller Jr.
196 0/8	Unit 203	1984	Claude Burlingame
195 7/8	Unknown	1890	Dole and Bailey, Inc.
195 5/8	Park Co.	pick up	Rodney Lawrence
195 4/8	Unit 213	1988	Tom Matosich
195 3/8	Unit 203	1990	Leonard Thompson
195 0/8	Sun River	1911	Gold White
194 5/8	Unit 213	1987	Mitch Thornson
194 4/8	Unit 216	1990	Bill Pelc
194 3/8	Unit 213	1987	Norman Lesh
193 4/8	Unit 216	1986	Michael Girard
193 4/8	Unit 340	1990	Thomas Webster
193 2/8	Unit 121	1989	Jerry Landa
193 1/8	Unit 203	1982	Bonnie Ford
192 6/8	Unit 216	1991	John Steel
192 7/8	Unit 216	1989	Ray Dvorak
192 5/8	Sun River	pick up	Robert Gabbert
192 3/8	Unit 216	1991	John Sandman
192 2/8	Sanders Co.	1968	Richard Browne
192 2/8	Sanders Co.	1978	Michael Jorgenson
191 7/8	Unit 216	1984	Steve Gingras
191 7/8	Unit 203	1989	Carl Schmidt
191 7/8	Wildhorse Is.	1961	U of M (stolen)
191 6/8	Unit 340	1991	Jim Dennehy
191 5/8	Unit 121	1982	Bryan Nelson
191 4/8	Lincoln Co.	1961	Ed Boyes
191 1/8	Unknown	1985	Mike Gesuale
190 7/8	Sanders Co.	1988	Terri Stoneman
190 6/8	Unit 122	1991	Gene Warren

Table 1. Continued.

Score	Locality	Year	Hunter
190 6/8	Unit 216	1990	Scott Campbell
190 6/8	Unit 203	1986	Art Dubs
190 5/8	Unit 203	1985	John Ottman
190 5/8	Unit 203	1986	Chris Mostad
190 4/8	Unit 340	1988	Quinn Ness
190 4/8	Unit 121	1991	Bob Blenker
190 3/8	Sun River	1957	F. P. Murray
190 1/8	Unit 203	1987	Joe Turner
190 0/8	Unit 210	1991	Rick Williams

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BIGHORN SHEEP MOVEMENTS AND SUMMER LAMB MORTALITY IN CENTRAL IDAHO

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Abstract: Rocky Mountain bighorn sheep (Ovis canadensis canadensis) wintering on Big Creek, in central Idaho experienced 5 years of low lamb:ewe ratios, 1987-91, and an all-age die-off in 1990. Twelve ewes were radio instrumented on the winter range in 1989 and 1990, and monitored to locate lambing areas and summer ranges and to determine causes of mortality. Ewes from different parts of the winter range used 4 different drainages for lambing and had 3 separate summer ranges. Ewes migrated from 1 to 40 km from winter ranges to lambing areas. All lambing areas were in steep south facing cliffs; elevations ranged from 1,150 to 2,450 m. Summer ranges were located within the same drainages as the lambing areas, but at higher elevations. Two summer ranges were in alpine areas, while the low elevation Big Creek summer range was within the winter range. Lamb production was consistently high in all areas (79-85 lambs:100 ewes). By July, all 4 lambing areas experienced a major decline in lamb numbers, for a ratio of 7:100 when lambs were 4 to 6 weeks old. Nine lambs and 6 ewes were found dead and necropsied. Tissue samples from 6 dead lambs and 1 dead ewe were cultured and examined for diseases. Pasteurella haemolytica was cultured from 5 of 6 dead lambs and Pasteurella multocida was cultured from 1 of 6 lambs. Pneumonia caused by P. haemolytica was a significant source of early summer bighorn lamb mortality. The record high bighorn population and recent drought conditions may have caused these sheep to be more susceptible to pneumonia.

Bighorn sheep populations can experience large fluctuations in size. A decrease in population size can be caused by a sudden die off, a long-term decline in lamb production or survival, or an increase in adult sheep mortality. Diseases are often implicated as the cause of bighorn population declines, although disease agents and parasites are found in healthy herds as well as declining populations. Factors such as adverse weather conditions, poor range quality or quantity, intraspecific competition, interspecific competition with other wild ungulates or livestock, contact with domestic livestock, human disturbance, constriction of habitat, or a combination of factors have been cited as causes of bighorn mortality or susceptibility to diseases (Cowan 1947, Buechner 1960, Constan 1972,

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Trefethen 1975, McCollough et al. 1980, Mackie 1981, Wakelyn 1987, Coggins 1988, Foreyt 1990, Spraker and Adrian 1990). Lamb survival has been correlated with nutrient quality of summer food for bighorns (Cook et al. 1990) and fall and winter precipitation for desert bighorns (O. c. nelsoni) (Douglas and Leslie 1986, Wehausen et al. 1987). Although disease was a proximate cause of lamb mortality, food ultimately limited an introduced population of bighorns in Wyoming in a classical density dependent regulation (Cook et al. 1990).

Bighorn sheep wintering in the Big Creek drainage had abnormally low April lamb:ewe ratios from 1987 to 1991 (Fig. 1). Idaho Fish and Game Department spring (Apr) aerial counts averaged 43 lambs per 100 ewes from 1973-82, and repetitive ground counts were 32:100 in 1985 and 46:100 in 1986. Lamb-ewe ratios from both aerial and ground counts were 16:100 in 1987 and 1988. Lamb-ewe ratios in adjacent populations remained stable at 35-45 per 100. Small coughing lambs with nasal discharge were observed on Big Creek since the spring of 1986. This period of low lamb:ewe ratios coincided with summer drought conditions and mild winters. The Big Creek bighorn population increased significantly in the 1980's and reached record high numbers in 1989 (M. Schlegel, Id. Dep. Fish and Game, unpubl. data). Elk also markedly increased in the 1980's.

Little was known about lambing areas and summer movements of Big Creek sheep. This study was initiated in 1988 to: (1) locate and describe lambing areas and summer ranges, (2) compare lamb production and survival for each lambing area, and (3) assess the potential causes of lamb mortality.

The Foundation for North American Wild Sheep provided the primary financial support for this study. Idaho Department of Fish and Game and the University of Idaho provided additional support. We express special thanks to M. Schlegel who provided advice in all phases of the study, to L. Oldenburg for his efforts coordinating the project, and R. DiGrazia for his enthusiasm for the study and sincere concern for these sheep. We appreciate the dedication of R. Guse and D. Tomlinson for their exceptional efforts in the field and D. Hunter and M. Dunbar who provided expertise in all disease aspects. Pilots T. Keogh and R. Arnold made aerial tracking safe and productive.

STUDY AREA

This study was conducted on a native population of Rocky Mountain bighorn sheep in central Idaho, which winter in the lower 20 km of the Big Creek drainage, a tributary of the Middle Fork of the Salmon River. Big Creek and all of the seasonal ranges of these sheep were located within the 920,000 ha Frank Church River of No Return Wilderness (Fig. 2). Research on this population of bighorns was conducted from the University of Idaho's Taylor Ranch Field Station, on the Big Creek winter range. Access to Taylor Ranch is via backcountry airplanes. Big Creek is in Game Management Unit 26, where there have been 15 bighorn ram hunting permits allocated each fall. The Big Creek sheep are a subpopulation of the 2,500 Rocky Mountain bighorn sheep in the central Idaho Salmon River Mountains. In 1989 the Big Creek sheep population peaked; 200 sheep were observed during the spring aerial survey (Id. Dep. Fish and Game, unpubl data). They declined during

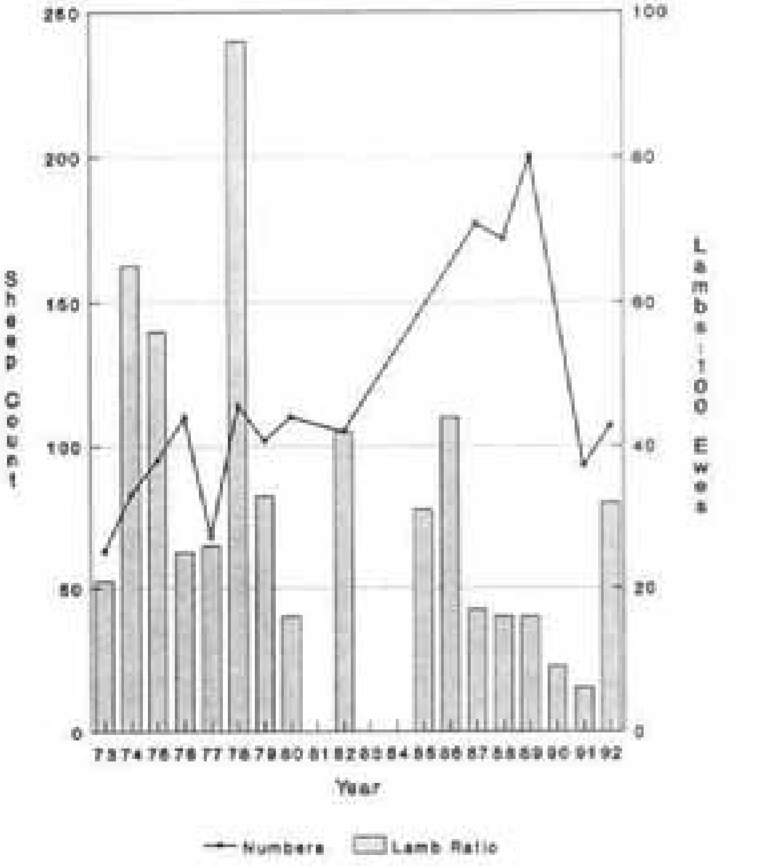

Fig. 1. Spring bighorn sheep counts and April lamb:ewe ratios, Big Creek, Idaho, 1973-92 (Fixed wing surveys, Idaho Dep. Fish and Game).

Fig. 2. Location of the Big Creek study area in central Idaho.

the next 2 years and appeared to be recovering in 1992 with a spring count of 107 sheep.

Elk were at record levels on Big Creek in the 1980's. Elk and mule deer are potential competitors of bighorns on the winter range, however, elk use of the sheep winter range was light and competition did not appear to be significant in 1985 and 1986 (Akenson 1992). Below normal precipitation was recorded at the Taylor Ranch weather station since 1986 (U.S. Weather Service Monthly Data Records, 1986-90). Winter weather in the late 1980' was more mild and snow-free than in the early 1980's.

Bighorns use the south aspects of the steep narrow lower Big Creek canyon for winter range. The terrain is rugged and broken. Bluffs with mountain mahogany (Cercocarpus ledifolius) are interspersed with talus slides and grassy slopes containing bluebunch wheat grass (Agropyron spicatum), Idaho fescue (Festuca idahoensis), and a variety of forbs. One third of the Big Creek sheep winter on the grass slopes of the Cliff Creek benches and adjacent bluffs. A fire burned 23,000 ha on the north edge of the upper winter range in 1988.

METHODS

Bighorn ewes were radio instrumented and monitored during 2 field seasons, from April to August 1989 and 1990. Twenty-one ewes were captured during late winter using the immobilizing drug carfentanil and a dart gun. Blood, fecal samples, and nasal and tonsil swabs were collected. These samples were processed by the University of Idaho Caine Veterinary Teaching Center. Twelve ewes were radio instrumented by the 1990 field season. We instrumented ewes from distinctly different herds to increase the chance of finding several lambing areas.

Ewe movements were monitored by both fixed-wing aircraft and ground tracking techniques. Aerial tracking for sheep locations and herd composition intensified after spring migration began on 1 May. Flights were conducted on a weekly basis, until mid-August. A field crew monitored herds containing radio-instrumented ewes on the ground in lambing areas and summer ranges. Observers were constantly alert for indications of sheep mortality, including increased activity of ravens, eagles, and magpies or erratic behavior of a ewe, which involved bleating, running, and traversing an area constantly in search of the missing lamb. When lamb or ewe carcasses were located, a preliminary cause of death was determined and nasal and tonsil swabs were done. Carcasses or tissue samples (tonsil, lung, eye, femur) were collected and transported to the State Veterinarian for examination, necropsy, and disease culturing at the Caine Veterinary Teaching Center.

Population dynamics were determined through composition counts conducted weekly while aerial radio tracking. Supplemental lamb:ewe ratios were obtained during ground monitoring.

RESULTS

Lambing Areas

Six lambing areas were identified which were used by Big Creek sheep. Cliff Creek, Lobauer, and the Gorge lambing areas are in lower Big Creek; West Monumental is in upper Big Creek; and Big Cottonwood and Dynamite are in the Marble Creek drainage (Fig. 3).

All lambing areas have similar physical features. They were in precipitous cliff formations with narrow ledges, bluffs, crevices, and steep talus slides and had southern aspects. Springs or streams were available adjacent to lambing areas. Heavily browsed mountain mahogany occurred at most sites and grasses and forbs were sparse, indicating that food was scarce in lambing cliffs. Agropyron spicatum, Festuca idahoensis, Bromus tectorum, Balsamorhiza sagitatta, and a variety of forbs were more abundant outside of these cliff formations.

Lambing areas were scattered geographically (Fig. 3) and varied in elevation, distance from winter range, size, and amount of use (Table 1). The greatest difference between these areas was proximity to the winter range. Ewes used lambing areas 1-40 km from their respective winter ranges. Lower Big Creek lambing areas, including Cliff, Lobauer, and Gorge were mid-elevation cliffs within the Big Creek winter range, while the other lambing areas were high elevation canyons 40 km southwest of the winter range. The size of lambing cliffs was determined as the entire extent of a small isolated cliff where ewes were consistently observed with newborn lambs, or the area within a cliff complex that encompassed all observations of ewes with newborn lambs. Mountain goats (Oreamnos americanus) were observed in the three distant lambing areas.

Table 1. Lambing area characteristics, Big Creek bighorn sheep in central Idaho.

Lambing area	Aspect	Elev. (m)	Dist. from winter range (km)	Size (ha)	Number of ewes (1989/90)
Cliff Creek	S	1,600-1,900	6	150	20/14
Gorge	S	1,150-1,300	1	5	-/6
Lobauer	S	1,250-1,300	2	3	2/1
Dynamite	S	2,050-2,450	40	100	-/20
Big Cottonwood	S	2,050-2,300	35	130	21/21
Monumental	S	2,200-2,400	35	25	-/16

Movements of Radio Instrumented Ewes

Winter Range.--The largest winter concentration of bighorns along Big Creek occurred on the bunch grass slopes of lower Cliff Creek. The maximum number of bighorns in Cliff Creek occurred in late November during rutting activities, when 80-100 bighorn sheep were present on this

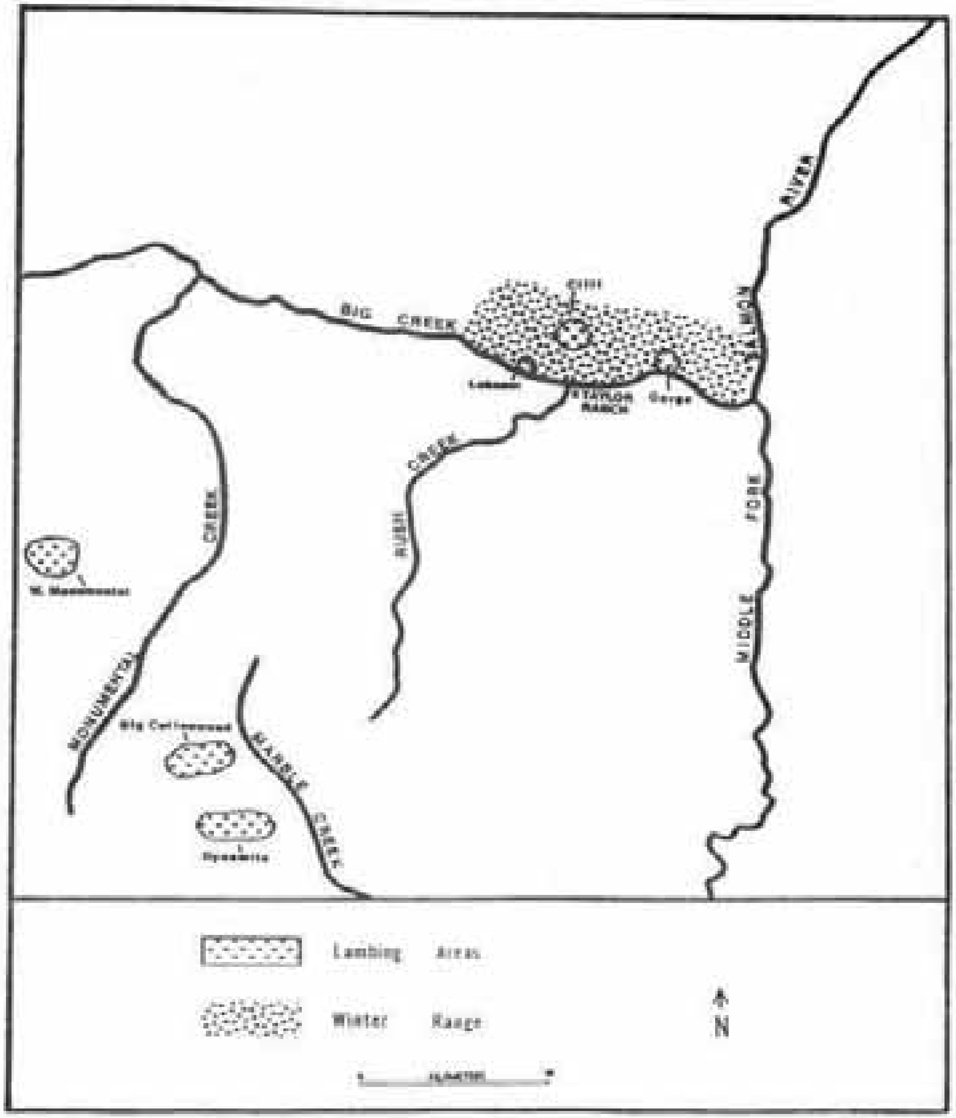

Fig. 3. Big Creek bighorn sheep winter range and lambing areas.

130 ha area. With the arrival of winter snow cover, sheep dispersed to rugged bluffs and outcrops with mountain mahogany and less snow.

Winter Range Segregation.--In January, mature rams separated from ewe groups. At this time ewes broke into small groups. Radio-instrumented ewes tended to winter with sheep from the same lambing areas. Bighorns wintering on the western portion of the winter range lambed on Cliff Creek. Ewes wintering on Cliff Creek, the central portion of the winter range migrated to Big Cottonwood and Dynamite Creek to lamb. Those ewes that spent late winter on the eastern segment of the winter range near the Gorge used either the West Fork of Monumental Creek or the Gorge for lambing.

Spring Migration.--In April bighorn ewes used the bunch grass hillsides of Cliff Creek as a staging area. May migration to lambing areas was rapid. Ewes travelled more than 40 km from Cliff Creek to the Marble Creek drainage in less than 3 days. Pregnant ewes were observed swimming Big Creek during flood stage to begin migration. Ewes followed rock outcrops and broken open terrain, but the migration corridor also included forested ridges and a snow covered 2,400 m pass.

Some ewes did not migrate from the winter range to lamb. Three radio instrumented ewes moved less than 5 km from where they spent the winter and lambed within the winter range. In both years a herd of barren ewes, yearling ewes, and young rams remained on the winter range.

Summer Movements.--Ewe movements were localized from mid-May through early June within respective lambing areas. In late June ewe-lamb groups expanded their movements out of the lambing cliffs, but remained near escape terrain. By early July ewes from the higher elevation lambing areas shifted 4-8 km to high elevation basins at the heads of the drainages in which they lambed. Ridge-tops at elevations above 2,700 m were preferred for travelling. Ewes that used lambing areas on the winter range remained on the winter range throughout the summer.

Unusual Long Distance Movements.--After lambing, some long distance movements were observed by ewes which had lambs that died. In 2 successive years an instrumented ewe left Big Cottonwood Creek after her lamb died and returned to Cliff Creek. In 1989 she made this journey twice. When she returned to Big Cottonwood she was accompanied by another radio-collared ewe which had lost her lamb earlier in the Cliff Creek lambing area. Three other instrumented ewes made migratory-type movements from lambing areas. One had a lamb that died before she left, the other 2 presumably had lambs that died.

Summer Ranges

The Big Creek summer range was very different from the Big Cottonwood, Dynamite, and Monumental summer ranges. Plants matured early in the season in this arid, low elevation range. During summer forage quality was probably significantly lower and insect harassment greater than in the alpine summer ranges. Ewes utilized the recent burn heavily during summer.

Summer ranges for Big Cottonwood, Dynamite, and Monumental ewes were 2,500-2,700 m elevation. Ewe-lamb herds used cirque basins and ridges with nearby springs and highly nutritious vegetation at the highest elevations available.

Few observations were made of other ungulates on the bighorn sheep summer ranges. Summer ranges were more than 30 km from domestic sheep grazing allotments.

Lamb:Ewe Ratios

Ewes were observed with newborn lambs from 12 May to early June. Peak lamb numbers occurred in the first week of June. Lamb production was high in all lambing areas during both years (Table 2). Early June lamb:ewe ratios were 70:100 in 1989 and 86:100 in 1990. Most lambs died between 4 and 6 weeks after birth, which was from mid-June to mid-July (Fig. 4). By mid-July lamb:ewe ratios had dropped to 15:100 in 1989 and 6:100 in 1990. Mortality occurred at a similar rate in all lambing areas (Table 2). Radio-instrumented ewes showed the same patterns of production and survival. In 1989, 5 of 6 instrumented ewes gave birth to lambs, but only 1 lamb was alive in mid-July. In 1990, 10 of 12 instrumented ewes were observed with live lambs; by late July none of the instrumented ewes had lambs with them. Summer lamb mortality was the source of low lamb:ewe ratios observed in April.

Mortality

Samples including organs, tissue, and blood were collected from 2 dead lambs, 3 dead ewes, and 4 hunter killed rams in 1989 and 7 dead lambs and 3 dead ewes in 1990. Tissue samples from 6 dead lambs and 1 dead ewe were cultured and examined for diseases. *Pasteurella haemolytica* was cultured from 5 of 6 dead lambs and *Pasteurella multocida* was cultured from 1 of 6 lambs (Table 3). Clinical examinations and culturing indicated that pneumonia due to *P. haemolytica* was a significant cause of summer lamb mortality. *P. haemolytica* (type A and T) and *P. multocida* were opportunistic in Big Creek lamb populations and present throughout the lambing environment (D. Hunter, Id. Dep. Fish and Game, unpubl. report) . Lambs were infected prior to weaning (D. Hunter, Id. Dep. Fish and Game, unpubl. report).

Of the 10 live ewes that were sampled on Big Creek in spring 1989, *P. haemolytica* T_{10} (hemolytic) and T_4. T_{10} (hemolytic) were isolated from 3 tonsils, but no nasal swabs (Dunbar 1990). Serum antibody analysis of respiratory disease viruses including: respiratory syncytial virus, parainfluenza virus, bovine virus diarrhea, and infectious bovine rhinotracheitis were all negative (M. Dunbar, Id. Dep. Fish and Game, unpubl. data). Ewes sampled in spring 1989 and 1990 had extremely low serum selenium, with a mean of 0.01 PPM (M. Dunbar, Id. Dep. Fish and Game, unpubl. data; D. Hunter, Id. Dep. Fish and Game, unpubl. data). This value was much lower than the mean selenium level in an adjacent population (Morgan Creek) and the normal value for selenium, which should be greater than 0.08 PPM (M. Dunbar, Id. Dep. Fish and Game, unpubl. report; Dierenfeld and Jessup 1990).

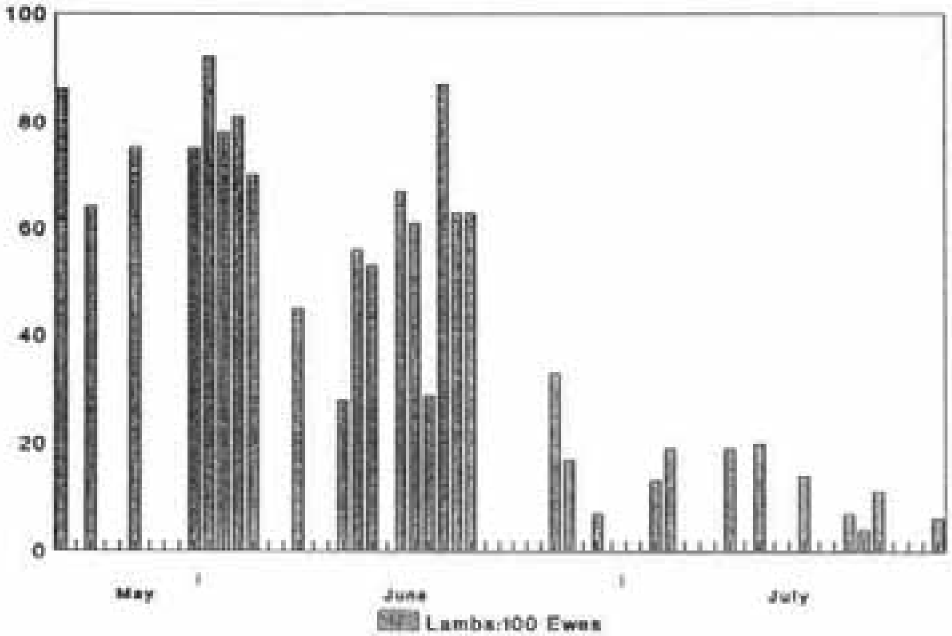

Fig. 4. Lamb:ewe ratios for all Big Creek, Idaho lambing areas, 1990.

Table 2. Summer lamb:ewe ratios in lambing areas of Big Creek, Idaho bighorn sheep, 1989 and 1990.

Year	Lamb area	June peak			late July		
		Ewes	Lambs	Lamb:Ewe	Ewes	Lamb	Lamb:Ewe
1989	Cliff Creek	16	14	88:100	15	3	20:100
1989	Lobauer	2	1	50:100			
1989	Big Cottonwood	21	12	57:100	26	3	12:100
1989	TOTAL	39	27	70:100	41	6	15:100
1990	Cliff Creek	14	12	86:100	22	0	0:100
1990	Lobauer	1	1	100:100			
1990	Gorge	5	3	60:100			
1990	Big Cottonwood	10	8	80:100	20	2	10:100
1990	Dynamite	20	17	85:100	8	0	0:100
1990	Monumental	13	11	85:100	12	2	17:100
1990	TOTAL	63	52	82:100	62	4	6:100

Table 3. Results of disease sampling of bighorn sheep from the Big Creek winter range, 1989-90 (M. Dunbar, Id. Dep. Fish and Game, unpubl. data; D. Hunter, Id. Dep. Fish and Game, unpubl. data).

Sample year	Sex	Age	Pasteurella cultured	Clinical symptoms	Cause of mortality	Veterinarian
1989		10 ewes	3 P. haemolytica (T)	no external symptoms	(live sampled)	Dunbar
1989	lamb	12 weeks	P. haemolytica (T)	necrotizing pneumonia	pneumonia due to P. haemolytica	Dunbar
1989	ram	mature	none	severe pneumonic lesions typical of Mycoplasma spp.	hunter kill	Dunbar
1989	ram	mature	P. multocida	normal lung tissue	hunter kill	Dunbar
1990	lamb	1 week	P. haemolytica (T)	organs normal	exposure	Hunter
1990	lamb	1 week	P. haemolytica (T)	good body condition no organ samples	exposure	Hunter
1990	lamb	3 week	none	autolyzed, no organ samples	unknown	Hunter
1990	lamb		P. haemolytica	pneumonia, tracheitis	emaciation	Hunter
1990	ewe	mature	P. multocida and P. haemolytica	autolyzed	pneumonia due to P. multocida	Hunter
1990	lamb	7 weeks	P. multocida and P. haemolytica		orphaned	Hunter

Cold wet weather during the early lambing period was also a mortality factor. Temperatures of -10 C with new snow accumulations of 25 cm occurred at lambing areas in both years during late May. Two dead newborn lambs were recovered after a snowstorm and necropsied. They cultured positive for P. haemolytica, but organs were normal with no indication of pneumonia. These lambs apparently died from exposure. Many dead lambs were robust and in good body condition. Most of these lambs tested positive for the presence of P. haemolytica.

Ewes displayed a strong maternal bond. Distraught ewes frequently cued us to search for a dead lamb. One was observed alone for 3 days at the site where its lamb died. Several ewes aggressively defended the dead lamb from human and raven intervention. One ewe was observed protecting a dead lamb by horn threatening a coyote on a ledge.

Predation did not appear to be a significant lamb or ewe mortality factor. Most dead lambs were found intact. Golden eagles were observed in the vicinity of lambing sites, but only 1 dead lamb had been fed on by an eagle. Coyotes were observed in the Cliff Creek lambing area, but the terrain made access for most land predators difficult. Lambs appeared to be most vulnerable to predation during the migration from lambing areas to summer range. This time coincided with the June drop in lamb numbers. However, of the 7 dead lambs recovered in 1990, none appeared to have died from predation. Bears scavenged 2 ewe carcasses.

Recent Events

The Big Creek sheep population experienced an all-age die-off in 1990. The population plummeted from a spring count of 200 in 1989 to 93 in 1991. The April lamb-ewe ratio remained low, at 16:100 in 1989, 11:100 in 1990, and 6:100 in 1991. In 1992 the April lamb-ewe ratio showed a considerable improvement at 32:100. Adjacent populations have experienced similar declines in lamb:ewe ratios, but did not decline until several years after the Big Creek lamb mortality. In 1992 adjacent populations continued to have low lamb-ewe ratios of 11:100 (M. Schlegel, Id. Dep. Fish and Game, unpubl. data).

DISCUSSION

We expected to find different mortality rates between the high and low elevation lambing and summer ranges due to differences in forage quality. Instead, we found that lamb production was similar in all areas, summer mortality occurred at the same time, and lamb survival was consistently poor. These factors indicate that summer lamb mortality was not restricted to a single subpopulation or lambing or summer range.

Most lamb mortality had occurred by early July. The repetitive intensive surveys of lambing areas were essential for verifying whether this population was experiencing low lamb production or early summer lamb mortality. If intensive surveys are not conducted within a week after the peak of lambing, low lamb production may be incorrectly designated as the cause of low lamb:ewe ratios in a population, rather than early summer lamb mortality.

The primary cause of summer lamb mortality in the Big Creek population was pneumonia due to P. haemolytica. The chronology of this epizootic was as follows: Coughing, nasal discharge, and poor body condition, noted in spring 1986, were the fist signs that the Big Creek population had a problem. Lambs were the first to be affected by mortality. Early summer lamb mortality occurred in 1986-90. An all-age die-off occurred in 1990-91, decreasing the population by 54%. In 1992 the spring lamb:ewe ratio was much higher than in earlier years and the population appeared to have increased.

Complex spatial and temporal range use patterns were observed among sub-populations of sheep from the Big Creek winter range. These complex dispersion patterns occur in other native bighorn sheep populations (Geist 1971, Festa-Bianchet 1986). The use of a range in winter and summer by multiple groups of sheep may be detrimental to the sheep. Summer residents on the winter range cause a reduction in the amount of available winter forage, while concentrated use of an area is likely to increase vulnerability to disease and parasite transmission, particularly during periods when there is a high bighorn sheep population.

Before this investigation, it was not known whether Big Creek sheep mixed with other bighorn populations. Big Creek sheep in the Big Cottonwood and Dynamite summer ranges on Marble Creek used the same range as bighorns from a different winter range. Hickey (1982) documented a ewe migrating 32 km to the summer ranges on Marble Creek from a winter range on the Middle Fork of the Salmon River. The Marble Creek drainage was the primary lambing area for the Big Creek sheep, although they wintered approximately 50 km from the Middle Fork of the Salmon River sheep. The winter ranges are geographically separate, but the shared summer range can facilitate disease transfer between sub-populations within the Salmon River Mountains.

Aerial counts of the Big Creek sheep population indicated it was at a record high in 1989 (Fig. 1). The high number of sheep and the severe lamb mortality problem suggest that these sheep have exceeded their ecological carrying capacity.

An important factor which likely contributed to the lamb mortality due to pneumonia was the long-term drought. Drought conditions result in a decrease in plant production. Bighorn sheep in poor condition due to a limited food supply are more susceptible to diseases. It is unknown whether the selenium level measured in these sheep is "typical" for this population or if the drought may have affected mineral uptake in vegetation.

In summary the summer lamb mortality which occurred for 5 years on Big Creek, in central Idaho was likely caused or exacerbated by the high bighorn population and a decrease in available food caused by drought. Natural patterns of socialization and migration may have facilitated the transmission of diseases within and between populations.

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TROPHY HUNTING OF DALL SHEEP IN ALASKA; AN EVALUATION OF THE BIOLOGICAL IMPLICATIONS

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Abstract: Several hypotheses were investigated concerning the possible negative effects of trophy hunting removal of large-horned Dall sheep (Ovis dalli dalli), including the social disruption, magnet, depressed survivorship, and immature ram incompetence hypotheses. Observations on production, breeding behavior, and survival of hunted and unhunted populations were made from 1970-84 in the Kenai Peninsula, and from 1981-85 in central and north-central Alaska. No evidence was obtained that legal harvests of all or most ≥ 3/4-curl (1968-1979) or ≥ 7/8-curl (1979 to end of study) reduced production or recruitment rates in Dall sheep. The depressed ram survivorship hypothesis was not supported by the data, young ram (< 3/4-curl:100 ewes) versus old ram (> 3/4-curl:100 ewes) were not correlated. Limited evidence was gathered that breeding occurred later and young rams courted ewes more aggressively in hunted populations (juvenile ram incompetence). Ewes accepted mounts at a higher rate in the unhunted versus hunted central Alaska herd. Observations concerning the magnet hypothesis were equivocal; mid-sized rams departed rut groups an equivalent amount in both populations in central Alaska, but more young rams associated with ewe-young groups outside of the rut in the hunted herd. No short-term effects of trophy hunting under the 7/8-curl regulation were observed on productivity, or ram survival of Dall sheep in Alaska, but the implications of more aggressive courtship, fewer accepted mounts per ewe-hour of observation and greater association of rams with ewes in winter in hunted herds needs to be investigated. Further, research involving greater replication of treatments study sites and greater use of control and manipulated populations is suggested.

Trophy hunting, the harvest of only older males, in mountain sheep has been hypothesized to result in a number of undesirable population and behavioral consequences (Morgan 1973, 1974, Geist 1971, 1974, Heimer and Watson 1982, Heimer and Watson 1990, Festa-Bianchet 1989). These hypotheses may be characterized (Hogg 1983, Murphy et al. 1990) as:

1. The social disruption hypothesis: Young rams are observed to be more socially disruptive than are dominant, large-horned rams. Younger rams, in the absence of large-horned rams, wastefully court anestrus ewes (Geist,

1971, 1974, Nichols 1972), more wildly chase estrus ewes (Morgan 1973, 1974, Geist 1971), guard estrus ewes less (Geist 1974, Nichols 1972), and court anestrus ewes year-round (Geist 1974). Young rams are more overtly aggressive and more likely to attempt to mount any ewe (Geist 1971:171). Older rams control the activity of younger rams and prevent the excessive harassment of ewes (Geist 1974). Although age-specific differences in rut behavior were documented by Geist (1968), quantitative behavior differences are needed between populations under differing hunting regimes (Festa-Bianchet 1989, Murphy et al. 1990, Shackleton 1991).

2. The magnet hypothesis: In the absence of large-horned rams, young rams are more likely to remain with ewe-young groups throughout the year (Dunbar and Dunbar 1981, Hogg 1983). The largest-horned rams are followed away from ewe groups by younger rams; older rams tend to draw younger rams away with them (Geist 1974, Dunbar and Dunbar 1981). Adult male mountain sheep (Ovis canadensis) segregate spatially and by habitat from ewe-young groups (Geist and Petocz 1977, Shank 1982). Spatial segregation of rams outside of the rut may enhance individual fitness of rams by reducing sexual-agonistic behavior at a time when reproduction is not possible (Morgantini and Hudson 1981).

3. The immature ram incompetence hypothesis: Depressed production and recruitment have been hypothesized in Dall sheep populations in Alaska subjected to intense cropping of trophy rams (Heimer and Watson 1982, 1990). Predictions were that conception rates in yearling ewes would be higher in hunted than unhunted populations, resulting in smaller body size and reserves, and subsequently in alternate year or intermittent reproduction in ewes (Heimer and Watson 1982).

Breeding may be later and pregnancy rates lower in populations where all the breeding is done by young males. Bubenik (1971, cited in Stringham and Bubenik 1974) suggested that when young males assume breeding in hunted populations, the rut is later and young may subsequently be born later than the optimum birth date. Dall sheep lambs born late in the lambing period are smaller by the onset of winter and they survive at lower rates (Bunnell 1982). Young rams may be less competent in breeding ewes. In domestic sheep, young rams were less able to detect estrus ewes and estrus ewes were more likely to recognize and display their receptivity to older, sexually active rams (Orgeur 1991). Hogg (1983) speculated that ewes were less receptive to young rams since young rams might be less competent at intromission, and since older rams possess, on the average, superior genotypes and produce superior young (Trivers 1972).

Scarcity of rams in intensely cropped populations might result in lower pregnancy rates, since estrus in ewes is less pronounced when insufficient number of rams are present (Nichols 1972). Weakly estrus ewes, such as those coming into estrus for the first time are less likely to be bred when insufficient rams are present (Fraser 1968, Grubb and Jewell 1966).

4. Depressed ram survivorship hypothesis. Young rams in the absence of older rams, participate more heavily in the rut, and as a result they may acquire the higher natural mortality rate typical of mature (> 8 years old) rams (Geist 1971, Heimer and Watson 1984). Young rams are reported to court estrus ewes more aggressively and to court anestrus ewes more than do mature rams (Geist 1971, 1974; Nichols 1978). Young rams that are allowed to rut after larger rams are harvested may acquire even higher mortality rates than 8+ year-old rams, since juvenile rams have smaller body size and are *a priori* metabolically disadvantaged to survive the winter (Heimer et al. 1984).

These concerns over the possible effects of trophy hunting of rams in Alaska resulted in progressively more restrictive harvests; in 1968 $\geq$ 3/4-curl restriction was instituted, in 1979 the limit was raised to $\geq$ 7/8-curl, and in 1989 the limit was raised to full-curl. The purpose of this paper is to review the effects of trophy hunting removals of Dall sheep on productivity, survival, and breeding behavior. The results reported were obtained from the authors' intense classification and behavioral data from hunted and unhunted populations in the Kenai Peninsula, from 1974-84, and in central and north-central Alaska, from 1981-85.

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STUDY AREAS AND METHODS

Population demography and breeding behavior were studied on the Kenai Peninsula 1970-84 (Nichols 1971, 1972, 1978). The Dall sheep at Cooper Landing were unharvested, while the Surprise Mountain herd was subjected to $\geq$ 3/4-curl harvest. Nichols (1971, 1972, 1978) describes the Kenai study areas, where he classified sheep annually from fixed-wing aircraft each of the 15 years. The Kenai Peninsula study populations were located only 8 km (5 miles) from each other, although the Sterling Highway separated them and apparently minimized interchange, based upon observations of marked animals (Nichols 1978). Breeding behavior studies were conducted 11 or 16 November - 17 or 20 December 1971 and 1972. All checking, breeding, and guarding interactions between Dall sheep were recorded following Geist (1968, 1971). An interaction was defined as when 2 sheep come together and perform behavioral displays toward each other (Geist 1971:156). Guarding, breeding, and checking interactions (Geist 1971) were recorded each day. During 1970-78 all or nearly all $\geq$ 3/4-curl rams were harvested from the Surprise Mountain study area, from 1980-89, all or nearly all >7/8-curl rams were harvested, and in 1989 the regulation was raised to full-curl in the hunted area. Lamb:ewe ratios were gathered during fixed-wing (Super Cub) surveys by the junior author, 1970-92, as described in Nichols (1978).

The Savage River (unhunted) and Usibelli Mine (hunted) study areas in the central Alaska Range where repeated ground and helicopter classifications were made in 1983 and 1984 are described in Singer et al. (1991). Apparently all legal ($\geq$ 7/8-curl) rams were harvested from the area each hunting season, although during the late-rut each year (21 Nov 1983, 9 Dec 1984), 1 or 2 7/8-curl rams were observed in the breeding groups. These animals either were not harvested or they moved onto the study area. Breeding observations were made between 15 November-16 December of 1983 and 1984. Two teams of 2 people each hiked over and observed sheep on each study area each day. All ram-ewe and ram-ram interactions observed were recorded. All behavioral displays (Geist 1968, 1971) were recorded during each interaction.

Mounts were expressed as no./ewe-hour, where ewe-hour = no. ewes x no. hours of observation, to correct for observation effort. More limited observations, primarily on activity, were made on a second unhunted population in Denali National Park at Igloo Creek in 1984 (see Singer et al. 1991); only classification data from Igloo Creek in 1984 are presented. Group classifications were obtained from the Savage River (unhunted) and Usibelli Mine (hunted) study populations during March-April of each winter. Helicopter classifications were conducted in June of 1984 and 1985.

Comparisons of population composition from aerial surveys were made between the hunted and unhunted Kenai and central Alaska study areas in order to test for lowered survivorship of young rams in the hunted herds. Comparisons were also made in portions of Gates of the Arctic National Park and Lake Clark National Park just after closure to sport hunting and several years later. The hypothesis that harvests of $\geq$ 3/4-curl rams resulted in depressesed survivorship of younger rams (< 3/4-curl) was additionally tested from 25 general surveys throughout Alaska, 1974-84. This hypothesis was tested with linear regression under the assumption that the ratios of young (< 3/4-curl:100 ewes) rams would be directly correlated with ratios of older (> 3/4-curl:100 ewes) rams if the depressed survivorship hypothesis held. Differences in ratios were tested with the Kolomogorov-Smirnov test using each complete aerial survey as a sample.

Rut behavior was observed in the Kenai Peninsula study areas for 21 days in 1970, and for 22 days in the unhunted area and 25 days in the hunted area in

1971. Observation conditions were good in 1970 on both areas, although low clouds limited visibility on the hunted area during the late rut in 1970.

Rutting behavior of Dall sheep groups was observed for 74 hours in the hunted central Alaska area and 55 hours in the unhunted area in 1983 (n = 28 days) and 1984 (n = 29 days). Plowed road access was available right to the study areas in 1983 and 1984 and visibility was unrestricted in the treeless terrains: typically 2-5 rutting groups might be visible at any time. We hiked to different points in the study areas each day and we attempted to observe different groups each day.

RESULTS

Comparability of Study Populations

The Kenai Peninsula study populations of Dall sheep were very similar in terms of density and productivity. Dall sheep density in the hunted area was 3 sheep/km^2 and density in the unhunted area was 2.2 sheep/km^2. Lamb ratios did not differ between the hunted and unhunted areas, 1970-92 (t-tests, P = 0.07, Fig. 1). Lamb ratios in the hunted herd were higher in 1980-92 ($\bar{x}$ = 53 ± 14.1 lambs/100 ewes) than during 1970-79 ($\bar{x}$ = 27 ± 14.5, t = -4.0, P = 0.001). Lamb ratios were also higher in 1980-92 in the unhunted area, ($\bar{x}$ = 39) than during 1970-79 ($\bar{x}$ = 30), but the difference was not significant (P = 0.18). A 4th degree polynomial fit suggested upward trend in productivity for both areas through about 1986, followed by a downward trend. Lamb/ewe ratios fluctuated a great deal annually, apparently in relation to weather, but the fluctuations were highly synchronous between the hunted and unhunted areas. Synchrony, when both populations increased or decreased together, was observed in 15 year intervals, while asynchrony was observed in 4 intervals (sign test, P = 0.01, n = 19 intervals with data). Considerably fewer rams per 100 ewes were present in the hunted area (23.2 ± 7.2) than in the unhunted population (54.0 ± 12.7), 1970-84, due to the removal of nearly every legal sized ram each hunting season.

In the central Alaska study, population characteristics were similar for Dall sheep in both study areas. Densities ($\bar{x}$ = 2.5 ± 0.4 sheep/km^2, $\bar{x}$ ± standard deviation) and group sizes (summer $\bar{x}$ = 7 ± 6, winter $\bar{x}$ = 12.9 ± 9.9 sheep/group) did not differ between the 2 study areas (t-tests, P > 0.05). Slightly fewer rams per group were observed in the hunted (rams/group, median = 3.5) than in the unhunted area (rams/group, median = 2.9), but the difference only approached significance (median test, x^2 = 2.16, d.f. = 5, P = 0.14). Lambs per 100 ewes ($\bar{x}$ = 36 lambs/100 ewes) and yearlings ($\bar{x}$ = 15/100 ewes) did not differ between the 2 study areas either in 1984 or 1985 (Mann-Whitney U tests, P > 0.05).

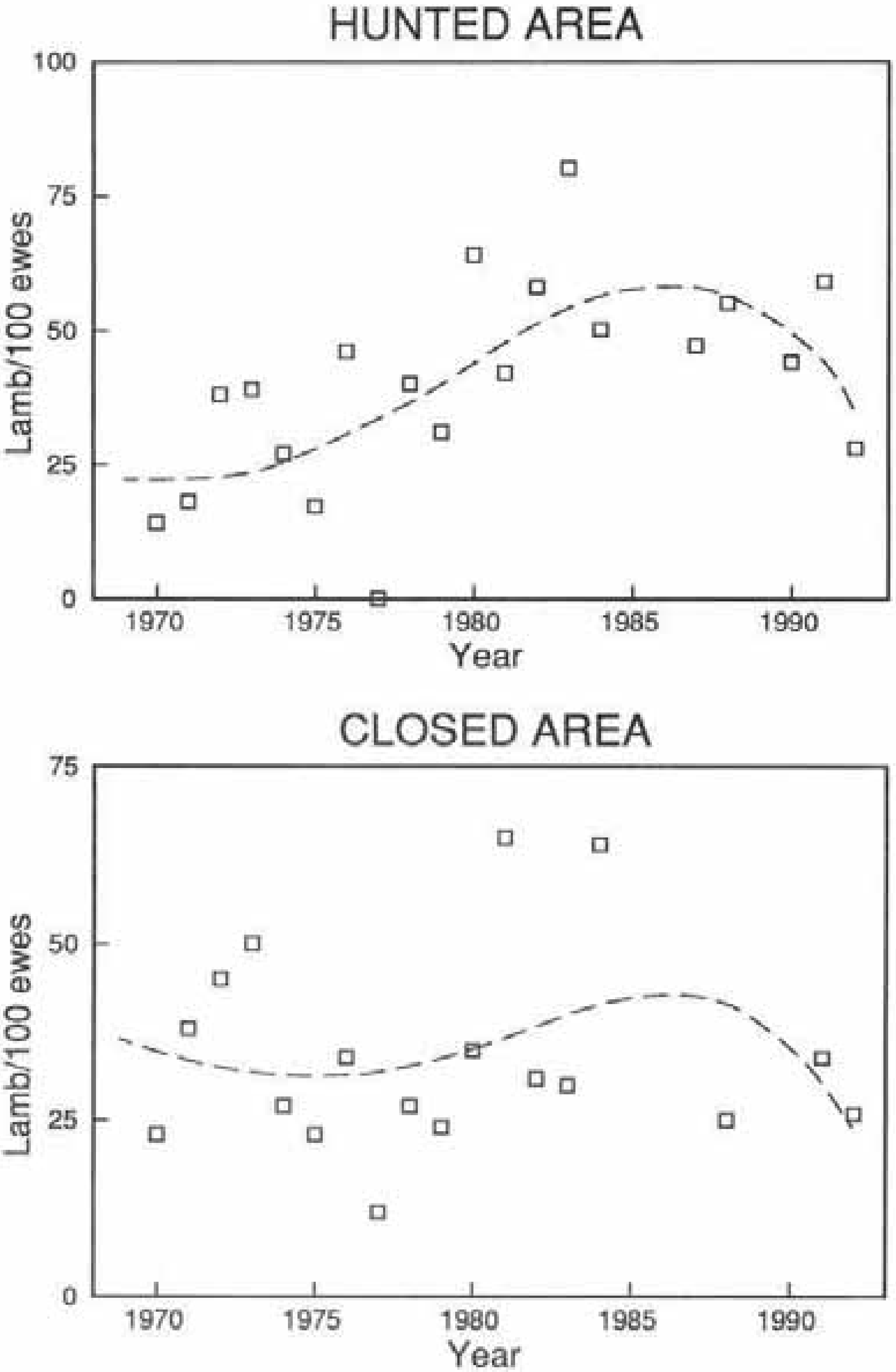


Fig. 1. Lambs per 100 ewes observed on the hunted and unhunted study areas on the Kenai Peninsula, 1970-1992.

Both pairs of hunted and unhunted study areas were highly similar with regard to Dall sheep population characteristics. Direct comparisons of rutting behavior between these pairs of hunted and unhunted areas appeared justified.

Social Disruption

Young rams approached ewes differently in the hunted and unhunted areas in central Alaska herd (Table 1); younger rams in the hunted herd performed one-half as many twists, twice as many butts, and seven times as many sniffs urine ($\underline{P} < 0.05$). Other behavior displays were performed in equivalent proportions ($\underline{P} > 0.05$). Interactions observed per day were lower in the hunted Kenai population both in 1970 and 1971 (Nichols 1971, 1972), the opposite predicted by the social disruption hypothesis. Ewes accepted an equivalent proportion of mount attempts by rams in the hunted and unhunted central Alaska populations during the early rut, but during late rut (when more ewes were in estrous) ewes in the unhunted population accepted a higher rate of mount attempts, about 2 times as many, as in the hunted area (Fig. 2).

Guarding or tending of ewes, the cooperative close association of a ram and an estrus ewe during the ewe's cycle, was observed less in the hunted central Alaska population, although the rate of guarding was low in both hunted and unhunted Dall sheep populations. Guarding by younger rams in the hunted Kenai population was weaker and more confused; ewes were guarded for 1-2 hours at the most during the 1-2 day estrus period in Dall sheep (Nichols 1972). We observed only 1 tending pair in the hunted central Alaska herd, and 5 tending pairs in the unhunted herd during 2 rut seasons. Only 0.3% of all interactions in the hunted herd and 1% in the unhunted herd involved guarding behavior displays. Tending pairs involved mostly the largest-horned rams (the only 7/8-curl observed in the hunted herd during 1 rut; 4 full-curl plus rams and 1 3/4-curl ram in the unhunted population).

Magnet Effect of Older Rams

Evidence for the magnet effect of older rams varied. Ratios of mid-sized rams declined significantly during the late rut from both the hunted (Usibelli) and 2 unhunted (Savage River, Igloo Creek) herds in the central Alaska Range, suggesting the leadership of older rams was not required for young rams to depart from ewe-young groups (Fig. 3). We observed several ram-only groups of mid-sized horn classes 1-3 km (0.6-2 miles) from the rutting groups, suggesting the drop in ratios was due to the departure of mid-sized rams from the rut groups and not to movements of the other age classes. Mid-sized rams lost considerable opportunities for breeding by departing the rut groups, since most of the breeding of ewes occurred during the second half of the rut (Fig. 3).

All rams (mostly younger rams), however, associated more with ewe-young groups during late winter in the hunted population ($\underline{P} < 0.05$, Fig. 4) in comparison

Table 1. Ram displays by all rams in each herd towards ewes during ram-ewe interactions in an unhunted and hunted herd of Dall sheep, central Alaska Range, 1983 and 1984.

Behavior displays/ 100 displays by all rams	Unhunted (Savage River)	Hunted (Usibelli Mine)
Low stretch	13	13
Twist	43	25
Rush	5	5
Horn threat	1	0.3
Sniff rear	15	16
Sniff urine	3	21
Lip curl	4	4
Butt	6	11
Front kick	5	3
Mount	2	2
Guard	1	0.3
Sample size (No. displays observed)	1,940	2,388

to the unhunted population, providing evidence for the magnet hypothesis during late winter period. More rams were also seen in ewe-young groups during summer in the hunted population, but the difference was not significant ($\underline{P} > 0.05$). The higher ram:ewe ratios in the hunted herd were even more significant in that rams per 100 ewes were less in the hunted herd during summer aerial classifications (45 rams versus 71 rams per 100 ewes, $\underline{P} < 0.05$).

Immature Ram Incompetence

Later breeding dates were observed in the hunted central Alaska area populations, and less breeding activity was observed in the hunted Kenai area in comparison to the unhunted areas. On the Kenai Peninsula, fewer total interactions were observed per day of observation per sheep group in the hunted population than in the unhunted population both in 1970 (7.5 versus 17) and in 1971 (18.7 versus 31) (Nichols 1971, 1972). Breeding was initiated nearly 2 weeks later in the hunted Kenai population in 1971 (Nichols 1972). Rutting

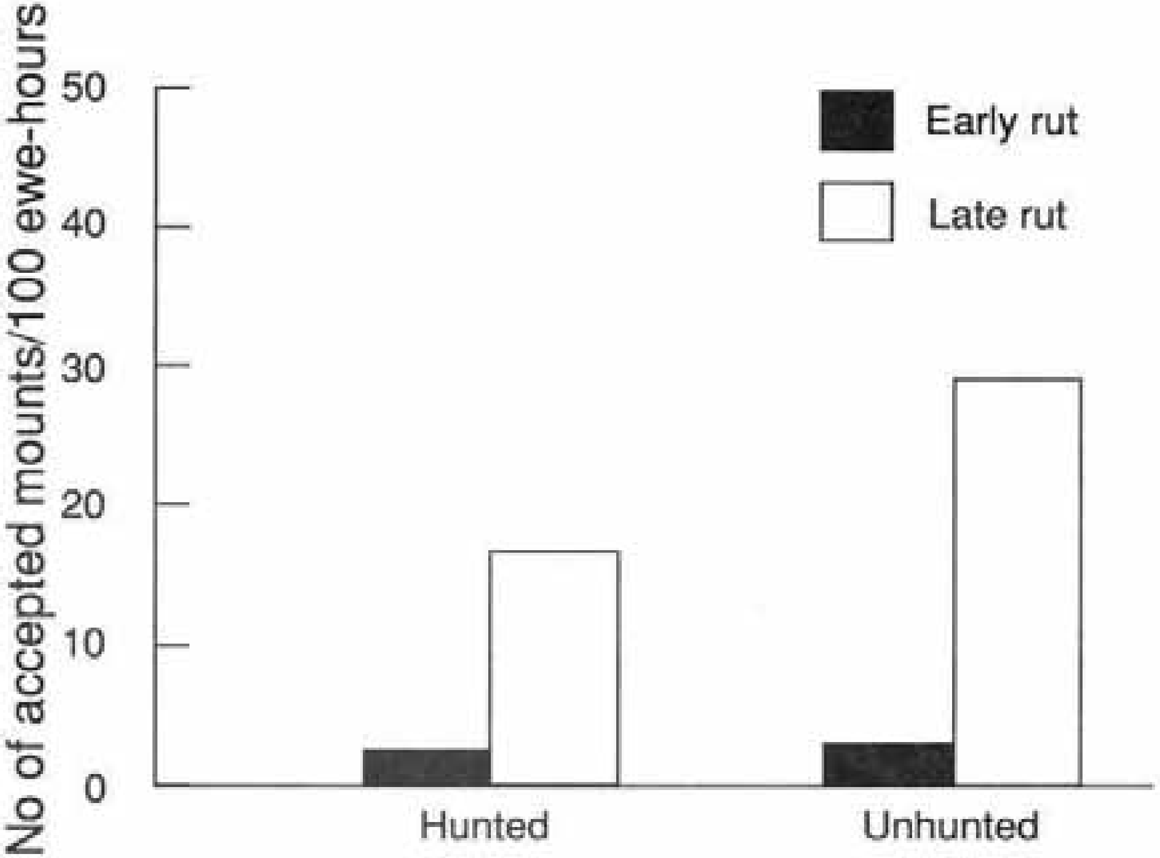
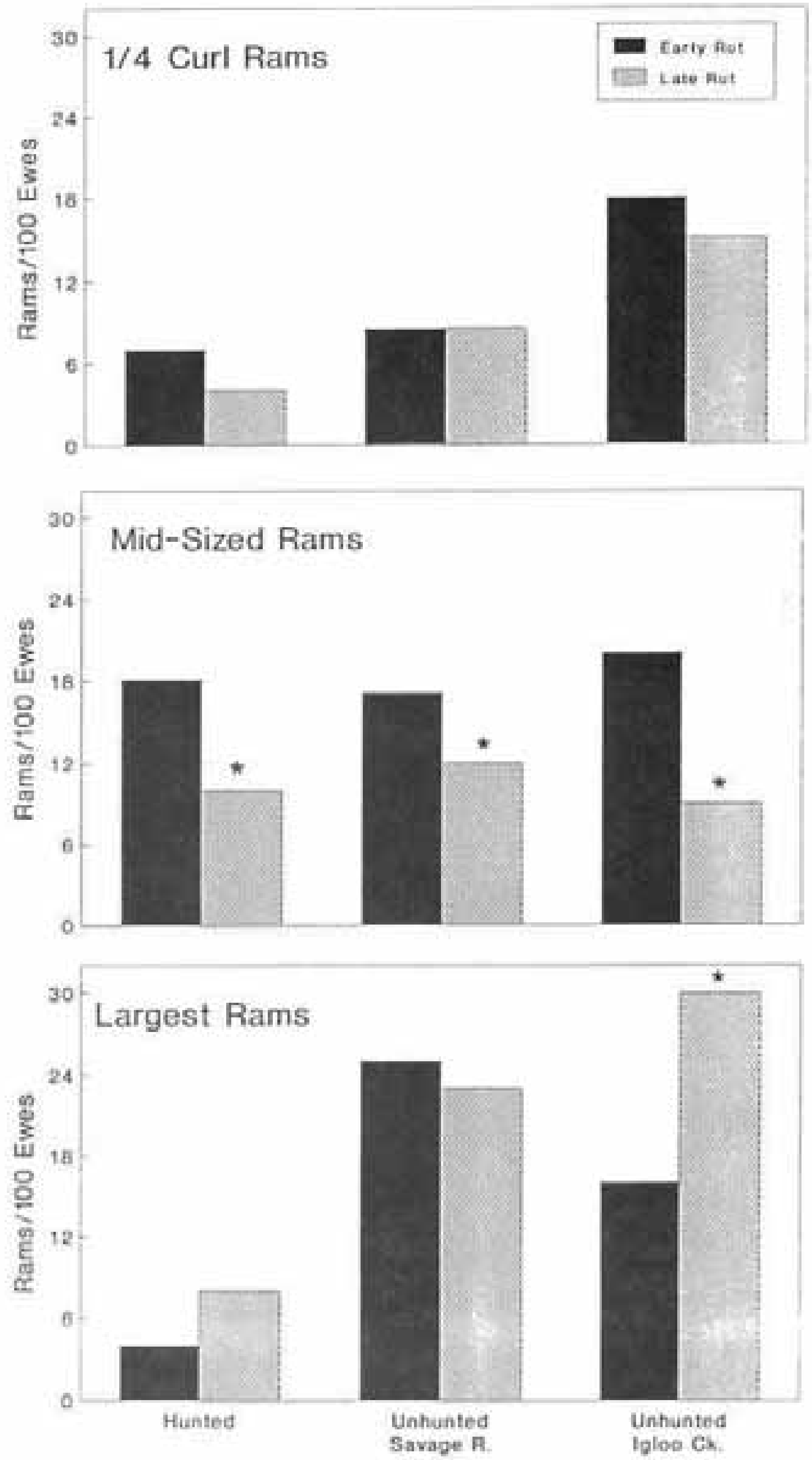


Fig. 2. Number of mount attempts by Dall sheep rams accepted by ewes per 100 ewe-hours of observation during early (15-30 Nov) and late (1-15 Dec) rut in the hunted and unhunted central Alaska study populations. (n = 51 mount attempts in the unhunted herd, n = 59 hunted herd). Observation times during early rut were n = 153 ewe-hours in the unhunted herd and 161 ewe-hours in the hunted, while late rut observation times were 58 ewe-hours in the unhunted herd and 121 hours in the hunted herd.



1/4 Curl Rams

Mid-Sized Rams

Largest Rams

Fig. 3. Change in ram:ewe ratios during the late rut in 1 hunted and 2 unhunted populations of Dall sheep in Alaska in 1983 and 1984. Asterisk denotes a significant difference between early and late rut periods, $\underline{P} < 0.05$.

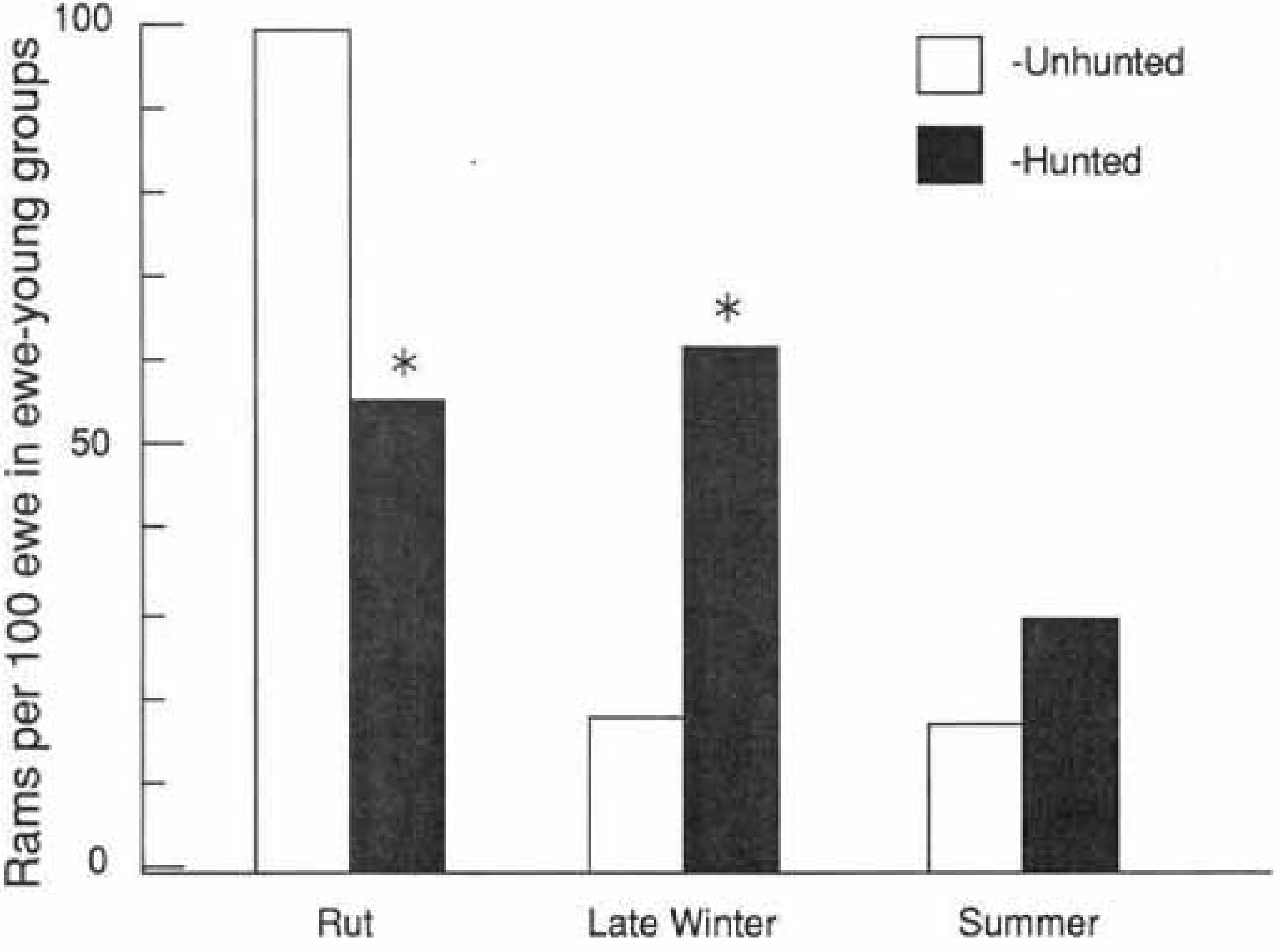


Fig. 4. Rams per 100 ewes in ewe-young groups in the rut, late winter (Mar-Apr), and summer (Jun) in the hunted (Usibelli) and 1 unhunted (Savage River) Dall sheep populations in central Alaska. Asterisk denotes significant difference, $\underline{P} < 0.05$.

observations and similar lambing chronology suggested breeding dates were more similar between the areas in 1970. A wider range of lambing dates, however, occurred in the hunted population in 1972. Later breeding dates were also observed in the central Alaska Range hunted population in 1983 and 1984 (Fig. 5).

Less guarding behavior and less gathering of rams about estrus ewes were observed in the hunted compared to the unhunted Kenai population. As a result, estrus condition was more difficult for the observers to detect in the hunted population. Mounts were attempted in the hunted population with less preliminary indication of the ewes receptivity (Nichols 1972). More twists were performed in the hunted central Alaska Range population by rams toward ewes (Table 1). Possibly as a consequence of these courting differences, a higher proportion of mount attempts were accepted by ewes in the unhunted area (no. mounts per ewe-hour of observation) than in the hunted area during late rut ($\underline{P} > 0.05$, Fig. 2), when most ewes were in estrous.

No evidence of depressed production or recruitment based on classification ratios was observed in either the Kenai (Nichols 1978, Murphy et al. 1990) or central Alaska study populations. Pregnancy rates were not available for the study populations and we do not know if they differed.

Depressed Survivorship of Young Rams

No evidence of depressed survivorship of young rams in the absence of large-horned rams was observed in either the Kenai, Lake Clark National Park, Gates of the Arctic National Park or other Alaska herd comparisons ($\underline{r}^2 = 0.133$, $\underline{P} > 0.05$, $\underline{n} = 25$ surveys, Murphy et al. 1990). No depressed survivorship of young rams was demonstrable by classification techniques in the central Alaska hunted areas 4 years after adoption of the more conservative 7/8-curl regulation; ratios of young rams (< 5/8-curl) in the hunted central Alaska herd (35 young rams per 100 ewes) did not differ from the unhunted central Alaska herd (38 young rams per 100 ewes, $\underline{P} > 0.05$) during helicopter classifications.

DISCUSSION

Social Disruption

Compared to mature males, young male ungulates court females in a less ritualized, more hurried, and more aggressive fashion (Geist 1971, Ozaga and Verme 1985, Valdez et al. 1991). Apparently as a result, adult ewes accepted a higher proportion of attempted mounts in the unhunted area. Although we observed differences in courtship behavior and accepted mounts between young rams in hunted compared to unhunted sheep herds in central Alaska, we observed no differences in production or recruitment of young in the Kenai or central Alaska. Despite differences in courtship behavior (as we observed for young rams), when

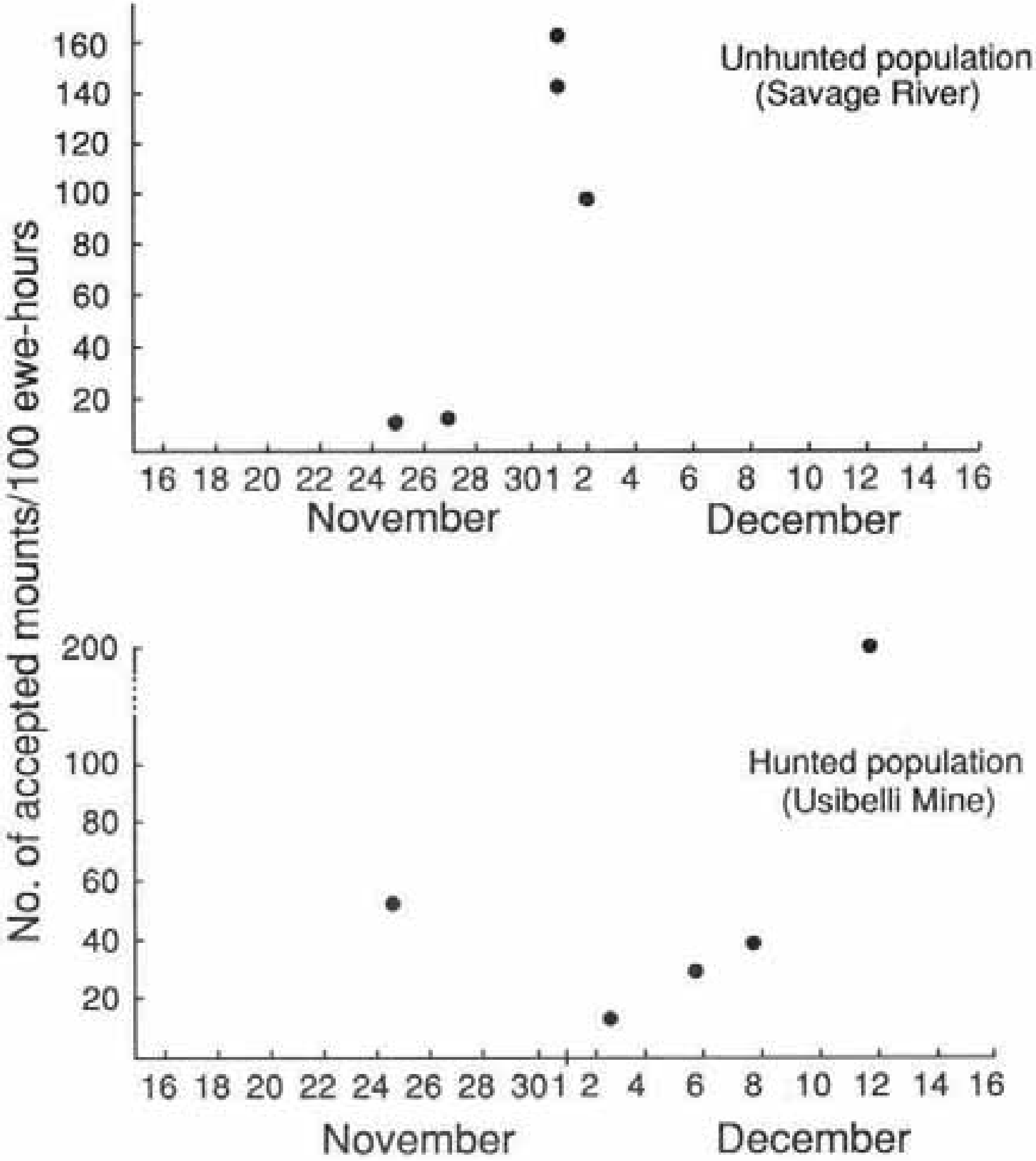


Fig. 5. Dates of copulations in hunted and unhunted Dall sheep populations in central Alaska in the breeding seasons of 1983 and 1984. (*n* = 59 mount attempts in the hunted herd, *n* = 51 in the unhunted herd). Copulations are expressed as no./100 ewe-hours of observation where ewe-hour = no. ewes x no. hours.

yearling white-tailed deer (Odocoileus virginianus) bucks assumed all breeding activity, there was no difference in breeding dates, pregnancy rate of does or any other evidence of lower sire quality (Ozaga and Verme 1985). The high level of synchrony of lamb ratios between the Kenai study areas suggested some other factors such as weather, and not hunting, was responsible for the variations between years in lamb success.

Ewes were potentially subjected to more stress in the hunted central Alaska area. Young rams in the hunted area were more aggressive in their courtship, and ewes were more likely to run away than to walk away from courting rams (Singer et al. 1991). The observation of more rams in ewe/young groups in late winter in the hunted versus unhunted area, raises the possibility of greater energetic costs to both adult ewes and young rams during a critical period.

Magnet Effect of Older Rams

Our data relative to the magnet hypothesis was equivocal; the magnet hypothesis was not supported by our observations during the late rut, but the hypothesis was supported by our observations during late winter.

Equivalent early departure of mid-sized rams from rut groups in the hunted central Alaska population did not support the magnet hypothesis. Breeding activity was more intense during late rut and we suspect the unsuccessful competition with large-horned rams for estrus ewes caused the mid-sized rams to leave. The remaining smallest rams (mostly 1/4-curl) do compete less with the largest rams; interactions are more frequent and intense between rams of most-nearly equal sizes (Geist 1971). Early departures of mid-sized rams in all 3 herds resulted in a loss of immediate breeding opportunity for them, but possibly their residual reproductive value and fitness may be enhanced. Geist (1986) reported some subadult male cervids opt out of rutting [the "dove" strategy of Barash (1982)], although these males were successful when the opportunity arose, and some became dominant breeders later in life. We speculate that the energy savings to mid-age classes of rams leaving rut groups during late rut contributes to their long-term survival and fitness. Since early departures of mid-sized rams was observed in both areas, no apparent effect of harvest removals on the energy saving strategy was observed.

Young rams, however, associated about 3 times more with ewe-young groups in the hunted central Alaska herd in late winter, thereby supporting the magnet hypothesis. Adult male and female mountain sheep typically segregate during all of the year except during the rut (Geist 1968, 1971, Shank 1982, Aschcroft 1986). The selective force for the segregation remains equivocal. Female ungulates occupy better ranges in many instances (Watson and Staines 1978, Shank 1985, Beier 1987), but Wehausen (1980) and Shank (1982) observed the opposite. Male bighorn sheep were found on better ranges than female-young groups. Male ungulates typically initiate the separation from female-young groups

(Charles et al. 1977, Geist and Petocz 1977, McCullough 1979, Shank 1982). Sexual segregation of ungulates outside of the rut period reduces energetically expensive sexual and agonistic behavior between males and females (Rand 1952, McCullough 1979). Avoidance of sexually agonistic stimuli outside of the rut by rams should maximize their individual fitness (Morgantini and Hudson 1981).

The magnet hypothesis predicts that older rams are required to lead young rams to segregated ranges. An alternate explanation for winter associations of young rams in ewe-young groups is that, in wolf-occupied habitat, young rams seek out the oldest and most experienced sheep to aid them in detecting and avoiding predators--in this case older ewes. Festa-Bianchet (1989) reported young rams (< 3 years old) were more vulnerable to predators and diseases than older rams. This hypothesis is consistent with our observations that rams in the hunted population associated most with ewe-young groups during the late winter, a period of more intense wolf predation (Murie 1944, Haber 1977), than during the summer. Successful departure of some young rams from ewe-young groups without old ram leadership during late rut, suggests the leadership is not required.

Immature Ram Incompetence

We observed no discernible, short-term deleterious effects of trophy hunting on reproduction or recruitment rates in Dall sheep. Our data were limited to aerial or ground classifications, and we did not compare pregnancy rates or early neonatal losses between the populations. We obtained preliminary evidence suggesting breeding occurred later and ewes accepted fewer mount attempts in the hunted populations. We suggest further more detailed work on the question of later breeding since visibility conditions were limited during late rut in the hunted Kenai population in 1971. Observátion conditions were excellent in the central Alaska population in 1983 and 1984. although we did not try to monitor nighttime breeding activity, we observed 1,291 rutting interactions between rams and ewes during 127 hours of daytime group observations. In his classic study of mountain sheep, Geist (1971) observed 596 interactions between Stone's sheep rams and ewes, and 205 for bighorns, or 62% of our total. A more definitive study than ours, with a great deal more replication, will require considerable time and personnel.

We conclude that guarding or tending occurs at a much lower rate in Dall sheep in Alaska than in other mountain sheep. Only 16% of estrus ewes in our central Alaska Dall sheep populations were observed in tending pairs under conditions of uninterrupted views of the tundra rutting ranges, versus 50% of estrus pairs of mountain sheep in Montana (Hogg 1984). A tradeoff in reproductive fitness may exist between remaining with and defending an estrus ewe and maximizing the probability of siring her offspring (Hogg 1988), versus attempting to breed other estrus ewes present in the area. The larger density of breeding sheep (and estrus ewes) present in Dall sheep study populations may explain the lower rate of guarding (Nichols 1972).

Depressed Survivorship of Young Rams

Our data, based primarily on aerial surveys, do not indicate that hunter-reduced numbers of older rams adversely affects the survival of young rams in Alaska. However, aerial surveys are essentially snapshots in time of population composition; variation due to cohort differences in size and survivorship (Murphy and Whitten 1976) could obscure harvest-related effects on survival of sublegal rams. Our most robust test of the hypothesis is the Surprise Mountain-Cooper Landing comparison, where no evidence of depressed survivorship was detected from aerial classification data even though virtually all 3/4-curl and larger rams were cropped over a 15-year period of study (Murphy et al. 1990). Stewart (1980) and Hoefs and Barichello (1984) also failed to find evidence of the depressed survivorship hypothesis.

Several other studies involving tagged males provide conflicting evidence. Festa-Bianchet (1989) reported higher than expected mortality rates in young mountain sheep rams from a herd subjected to hunting in Alberta, but he had no control study area. His control was skull remains from the unhunted Denali Park Dall sheep population (Murie 1944). Biases in skull collections may preclude their direct comparison of mortality studies involving the tagging of live animals (Murphy and Whitten 1976, Festa-Bianchet 1989). Festa-Bianchet (1989) reported high mortality of yearling rams, which he could not attribute to hunting effects. Yearling rams are not observed to participate in breeding even in trophy-hunted populations (this study, Singer et al. 1991, Shackleton 1991). Either 4-5 year-old rams or 5-6 year-old rams, not yearling rams, (depending on the size class of the hunting restriction) do most of the breeding, and therefore assume higher mortality rates (Geist 1971, Murphy et al. 1990).

Heimer et al. (1984) reported a high disappearance rate of young rams from a hunted population during a period of less restrictive (3/4-curl) harvest. The high disappearance, however, could have also been due to dispersal. No comparable data on disappearance rates were available for young rams from unhunted populations.

Evidence that more restrictive harvests increase survivorship of rams is reported from the eastern Alaska Range (Heimer and Watson 1990). Thirty-three percent more rams were harvested from this area following raising the size class restriction from 7/8-curl to full-curl (Heimer and Watson 1990). Ewe numbers were apparently stable during the period. Hunter participation increased 58% during the full-curl harvest, but Heimer and Watson (1990) rejected this as an explanation for the increased harvest of rams. There were no control populations for the study (i.e., a comparison population where the ram harvest remained at 7/8-curl), ewe fecundity and survival increased at Dry Creek during the study and weather and wolf numbers also varied (Heimer and Watson 1990). Festa-Bianchet (1989) stressed that behavior observations of rutting males, causes of death, and experimental manipulation of hunting regimes are necessary to determine if the depressed survivorship hypothesis applies.

RESEARCH RECOMMENDATIONS

We recommend further research into the possible effects of trophy hunting of male mountain and Dall sheep. Greater replication of study conditions, and use of control study areas, or use of the same areas for control and manipulations (crossover experiments) establish cause and effect relationships. Longer term studies are suggested (1-2 decades or more) especially if crossover experiments are conducted. In particular, we recommend further research into the possibility of later breeding dates, the behavioral and ecological implications of more rams associated with ewe/young groups during late winter, and the implications of decreased competition among males in hunted areas.

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MANAGING BIGHORN HABITAT FROM A LANDSCAPE PERSPECTIVE

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Abstract: Three levels of bighorn (*Ovis canadensis*) habitat management address (1) metapopulations, (2) herds that comprise metapopulations, and (3) local projects. Projects are implemented to enhance specific seasonal ranges, migration corridors, or inter-herd corridors. There has been an emphasis on projects in the management of sheep. Developing comprehensive long-range plans for maintaining or enhancing herds and metapopulations has been neglected. Three types of bighorn metapopulation structures are proposed. Management needs and constraints for each of the 3 levels of management are discussed. State wildlife departments are in the best positions to provide needed leadership in developing and coordinating management that will identify and achieve long-term goals for metapopulations and for local herds.

Conservation of bighorn sheep and their genetic resources requires strategies for maintaining local populations, and for maintaining their interconnections as metapopulations. Ideally, these strategies are implemented in a series of prioritized and coordinated management projects. There has been an emphasis on projects in bighorn sheep management. Meanwhile, developing comprehensive long-range plans for maintaining or enhancing local populations and metapopulations has been neglected. My objective is to emphasize the limitations of this situation, and to stimulate discussion and development of more comprehensive management.

MANAGEMENT OF METAPOPULATIONS

Metapopulations of bighorn sheep consist of local populations (herds) interconnected by movements of animals across inter-herd corridors. Movement between 2 herds may be totally, or mostly, one way; or may approach being equal in both directions. Movements may be frequent or occasional. Exchange of animals and their genes among herds:

(1) may be necessary to maintain small herds having poor demographic characteristics. Berger (1990) concluded that herds of <50 sheep were not viable, and herds <100 sheep probably were not viable, for >50-70 years. Persistence of such small herds would be enhanced by periodic immigrations from nearby herds.

(2) may be necessary to avoid serious inbreeding depression of reproduction and survival. Geist (1975:105) arbitrarily selected 125 sheep as the number necessary to avoid this level

of inbreeding. Franklin (1980) concluded that 50 "effective breeders" would be necessary to avoid an arbitrarily selected 1% level of inbreeding. Fitzsimmons (1992) calculated that a herd of about 150 sheep is needed to provide the equivalent of 50 effective breeders.

(3) allows the spread and persistence of genes, including genes that may be relatively rare, thereby maintaining the genetic diversity and adaptability of the species in the long term. Recommendations (Franklin 1980, Thomas 1990) are that >>1000 animals are needed for long-term maintenance of genetic diversity in large vertebrates.

These 3 benefits of metapopulations are important to the wise use, including preservation, of bighorn sheep and their genetic resources.

Metapopulation Structure

Identifying and managing metapopulations are needed to preserve genetic diversity within regional aggregations of bighorn sheep. It may also be desirable to preserve the genetic purity of sheep within a region. If this is assumed, each managed metapopulation should exist within only 1 major ecosystem, such as the Mojave Desert, or Central Rocky Mountains, to preserve 1 ecotype of bighorn.

A widely distributed metapopulation will require management coordination among many landowners and agencies. Too many landowners and agencies may confound and perhaps preclude coordination. Also, a widely distributed metapopulation may have multiple risks of exposure to disease, especially from domestic sheep (Desert Bighorn Council Technical Staff 1990). Thus, there are both practical and theoretical considerations in choosing the size of a metapopulation for management purposes. This topic needs further discussion. I arbitrarily propose that management plans should recognize bighorn metapopulations having at least 1000 sheep, or the potential for at least 1000 sheep.

Metapopulation structure may vary with 1) the mean and variance of local population sizes; 2) the proportion of local habitat patches occupied at one time; and 3) the amount and frequency of movement among local populations. At least 5 types of metapopulations have been proposed (Hanski 1991:27, Harrison 1991:78). It is not clear how many types apply to bighorn sheep because long-term studies of interherd movements have been rare, and because metapopulations of bighorns in pristine North America have been fragmented by herd extinctions and habitat loss - and have not been reestablished. Within a species, metapopulation structure will vary with the number and spacing of suitable habitat patches, barriers between patches, and the sizes and qualities of patches. For managing bighorn sheep, I propose 3 types of metapopulations be considered. This classification is arbitrary and intermediate combinations occur:

Megapopulations of bighorn sheep contain ≥1000 animals distributed rather continuously over a large area. Bighorn megapopulations are organized into herds that use different seasonal ranges, such as lambing areas and winter ranges; but barriers between herds are inconsequential and movements of sheep among herds occur annually. Bighorn in the Canadian Rocky Mountains and in the Black Mountains of Arizona are examples of megapopulations. If habitat is lost or degraded, megapopulations may decline into either core-satellite or patchy metapopulations.

Bighorn core-satellite metapopulations contain ≥1000 animals, distributed in ≥1 large, persistent core herd(s) and several smaller satellite herds that depend upon the core herd(s) and may be transitory. Core herds are expected to occupy relatively large, continuous areas of quality habitat, with populations of ≥150 sheep. Satellite herds occupy lesser and/or poorer areas. Consequently, satellite herds occasionally fluctuate to very low numbers of sheep, and may become extinct, especially in times of stress such as drought or severe winter. Animals may move both ways between core and satellite herds, but the preponderance of movement is to the satellite herds. Satellite herds depend upon this immigration for demographic persistence and genetic diversity. (However, relatively isolated satellite herds in unique environments may develop locally-adapted genotypes that, in time, could influence evolution of the metapopulation.) Megapopulations may also have satellite herds. If habitat is lost or degraded, core-satellite populations may decline into patchy metapopulations.

Patchy metapopulations of bighorn sheep contain ≥1000 animals distributed in interdependent herds of ≤100 sheep. Size and persistence of herds may vary, but several herds should approach 100 sheep and be persistent ("primary-patch" herds). In patchy metapopulations, each herd (and its inter-herd movements) plays an approximately equal role in maintaining the metapopulation and its genetic diversity. Many herds are "stepping-stone" populations, facilitating movement of animals between other pairs of herds. Bleich et al. (1990) described a bighorn patchy metapopulation. If habitat is improved or expanded, patchy metapopulations may increase and become core-satellite metapopulations.

Management Needs

Although a need for managing metapopulations of bighorn sheep has been noted (Bur. of Land Manage., n.d.; Bleich et al. 1990; Ramey 1991), there appear to be few, if any, metapopulation management plans. Meanwhile, plans and projects affecting local herds and ranges, and inter-herd corridors, are being developed and implemented without considering existing or potential metapopulation roles of the herds or lands. Among these are federal agency plans for multiple-use and wilderness areas, and state transplant projects.

Most metapopulations of bighorn sheep traverse lands managed by many owners and/or agencies. Consequently, metapopulation management requires interagency agreement and cooperation. Often, a state wildlife department will be the only agency with responsibility across an entire metapopulation. Occasionally 2 state departments will be involved. State departments should lead in convening interagency discussions of bighorn metapopulation goals and in developing interagency agreements for management plans. Plans should identify all local participating herds and establish goals for each herd and its range. Goals will relate to a metapopulation role designated for each herd and range (core, satellite, primary-patch, and/or stepping-stone herds). Goals should specify the desired number of sheep, the habitat conditions needed for immigration and emigration, and desired habitat conditions on herd ranges. Most goals should be measurable so that failure to achieve or maintain them will trigger a response from management agencies. Metapopulation management plans should (1) designate agencies responsible for monitoring all herds, seasonal ranges and movement corridors; (2) designate an agency that will maintain a complete record of the metapopulation; and (3) be updated periodically as knowledge and habitats change.

Particular attention should be paid to core herds and primary-patch herds because: 1) they comprise major proportions of metapopulations; 2) other herds are at least somewhat dependent upon them; and 3) political uncertainties and demands from other land uses will increasingly threaten herd ranges and corridors, while resources for managing bighorn sheep will always be limited, forcing difficult choices and a need for priorities.

Management Constraints

A state wildlife department with broad responsibility for a metapopulation usually manages little land. Rather, many landowners and agencies with diverse, perhaps conflicting, objectives manage local bighorn ranges and inter-herd corridors. Interagency coordination and compromise are most difficult at this level of bighorn management.

The benefits, and failures, of managing or neglecting metapopulations will accrue slowly, especially in relation to the tenures of biologists and administrators in their jobs. Also, the credit or blame for metapopulation conditions will be distributed among several agencies. The resulting lack of agency commitment to metapopulation management may provide little incentive or reward for participating in this management, and personal identification of individual wildlife biologists with metapopulation management may be limited.

COMPREHENSIVE MANAGEMENT FOR BIGHORN HERDS

The year-round range of a bighorn herd may include up to 6 seasonal ranges and connecting migration corridors (Geist 1971). However, many herds are sedentary because of limited habitat and/or because they are transplanted herds that have not established long movements. Movement across a diversity of seasonal ranges will benefit bighorn sheep in 2 ways. First, a diversity of habitats provides a herd with options for responding to variable weather conditions or to harassment, thereby maintaining security and access to quality forage. Second, altitudinal migration provides prolonged access to green forage, as the seasons change, thereby enhancing animal quality (Geist 1987). Maintaining or enhancing seasonal ranges and migration corridors, and maintaining or reestablishing migratory movements, may be necessary for achieving either optimization goals or wilderness goals (Bailey 1992) for a bighorn herd.

Management Needs

Bailey (1986) and Risenhoover et al. (1988) discussed management of bighorn herds. They recommended that existing and potential seasonal ranges and migration corridors be identified and managed. Despite their recommendations, there appear to be few such management plans established and approved in agency documents. Rather, documented goals are often vague (i. e. maintain at least 100 sheep) and usually specify nothing about maintaining movements of sheep, or maintaining the specific ranges and corridors that support these movements. Sometimes, comprehensive management plans exist in the heads of biologists, and are lost when they transfer among jobs.

Once the existing or potential seasonal ranges and migration corridors have been identified, habitat conditions on each range unit should be assessed. Several methods for evaluating bighorn habitats are now available (Hansen 1980, Armentrout and Brigham 1988, Smith et al. 1991) and are being tested and improved. Habitat evaluation will allow prioritization of habitat-improvement needs, so that the most critical needs are addressed first (and resources are not wasted treating habitat conditions that do not limit herd size or movement). Lastly, there should be a realistic assessment of the constraints and of the resources needed, in the long term, to achieve the plan's goals. If the goals are truly impossible, more realistic goals are needed, or agencies and publics should be advised that resources are not adequate for their expectations. We may have to abandon some seasonal ranges, or even some herds, in order to maintain other ranges, or herds, with the resources and constraints that are likely to prevail. Comprehensive planning for bighorn herds will produce confrontations with budgets and reality, and will demand difficult choices. However, without such plans, habitat management projects may be inefficient or even worthless, in the long run. (We may be just nibbling around the edge - even the wrong edge - of a problem with unknown and large dimensions).

Where bighorn herds migrate across administrative boundaries, coordination and compromise among landowners and agencies will be needed in developing comprehensive, long-range management goals and strategies. Usually a small number of landowners and/or agencies will be involved. Leadership should rest either with a state wildlife department, or with an agency responsible for the major portion of the herd's range. In either case, state involvement will be needed to coordinate herd management plans with regional metapopulation goals.

Management Constraints

There is limited tradition for the level of inter-agency coordination needed in comprehensive management. A common situation involves state management to optimize a bighorn herd, while much of the herd's range is in a wilderness where optimization is not a goal and wilderness management plans have not been done (Bailey 1992). In addition, conflicts with the desires of private landowners may be difficult to resolve. An interspersion of private land on a seasonal range may greatly limit options for habitat maintenance or management (for example, with prescribed ignition of fire).

Agency priorities and incentives for biologists may emphasize management projects at the expense of comprehensive planning. The result of planning is a document. The results of projects are <u>numbers</u>: numbers of animals moved or treated, numbers of acres burned or fertilized, etc. Numbers are needed for year-end reports. Projects also create positive, although sometimes naive, publicity; and attract funding from private foundations. The rewards and incentives favor implementing more projects, while delaying comprehensive, long-range planning.

HABITAT MANAGEMENT PROJECTS

Habitat management projects include vegetation manipulation, soil fertilization and artificial water developments. Projects are numerous in bighorn management. Agencies requested funding from the Foundation for North American Wild Sheep for 25 habitat improvement projects in 1992. Other foundations also support habitat projects, and other projects are funded entirely with agency monies. Habitat management may be used on seasonal ranges and migration corridors of bighorn herds, or on inter-herd movement corridors.

Management Needs

Factors limiting the achievement of goals for bighorn herds must be identified to assure effectiveness of management. Otherwise, habitat management may not treat limiting factors and may be either inefficient or worthless. Identification of limiting factors should be part of comprehensive planning for bighorn herds.

Few management projects for bighorn sheep are evaluated for their effectiveness in achieving goals (Bailey 1990). At least some projects should be conducted as management experiments with suitable experimental designs. Confounding of multiple projects on one herd should be avoided so that effects of individual projects may be evaluated.

Management Constraints

Developing comprehensive plans for bighorn sheep, and testing the effectiveness of management projects, requires a personal and public admission of 1) the limitations of agencies and resources in solving complex problems, and 2) some degree of ignorance of bighorn populations, their habitats, and limiting factors. The tradition in wildlife public relations is not to admit limitations or ignorance. Administrators, and the public, are more easily seduced by (unproven) claims of effective management. Career advancement for wildlife biologists should depend more upon producing bighorn sheep; and less upon merely attracting funding and completing projects. In this regard, wildlife professionalism and administrative leadership are lacking.

CONCLUSION

There is a need for coordination of habitat management for bighorn sheep across seasonal ranges and migration corridors of local herds, and across inter-herd corridors of metapopulations. Comprehensive planning is needed to deal with long- and short-term problems of local herds. Bureaucratic inertia, numerous constraints, funding mechanisms, and lack of incentives for individual biologists are delaying the management of bighorn sheep on such a landscape basis (Fig. 1). Biologists who will question current practices and provide a broader, more realistic, view of bighorn management are needed. Agency leadership in developing and coordinating management to achieve long-term goals is lacking. State wildlife departments are in the best position to provide this leadership.

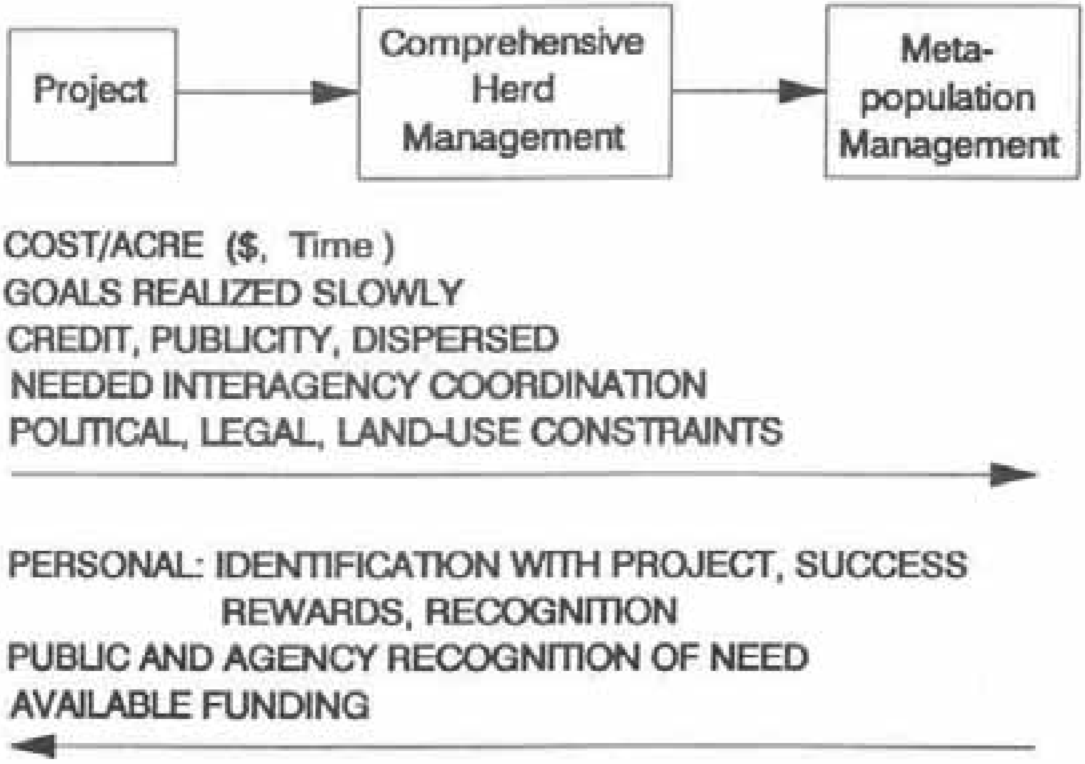

Fig. 1. Some fiscal and political factors differing among 3 levels of bighorn sheep management. They favor an emphasis on completing projects that are not prioritized or coordinated within comprehensive long-range plans for herds or metapopulations.

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MANAGEMENT IMPLICATIONS OF AN INTENSIVE STUDY OF WINTER FORAGING ECOLOGY OF BIGHORN SHEEP

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Abstract: Factors limiting nutrition of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) were investigated on 2 montane winter-spring ranges in north-central Colorado. Under snow-free conditions, we investigated effects of rapid increase in forage quality during green-up (Mar-Apr) on feeding behavior, diet quality, and nutrition of ewes. Bighorn switched to green forage when availability of fresh vegetation was limited. Consequently, bite size and dry-matter intake rates declined, and increases in nutrition often lagged a month behind increases in diet quality. Snow caused bighorn to nose or paw to reach forage resulting in lower bite rates. Although bite size of ewes increased on both ranges with snow; dry matter intake rates declined at 1 area. Diet quality declined in both areas because bighorn were unable to forage selectively. With snow, bighorn shifted from feeding in open sites to areas of shrub cover and cliffs which enhanced forage accessibility. Managers need to determine preferred habitats of bighorn under both snow-free and snow-covered conditions even on ranges where snow is usually shallow and transitory. If bighorn sheep have adequate habitat during snow-covered conditions, enhancing availability of green forage during green-up will likely benefit them. This objective can often be met by removing overstory of shrubs, trees, or dead herbs through prescribed fire, chemical, or mechanical treatment. In some cases, availability of snow habitat and/or green forage can be improved by extending ranges of bighorn to lower elevations or into different habitats through transplanting.

Factors limiting nutrition of free-ranging ungulates are difficult to determine. Observational studies can often identify important factors, however, without experimental control researchers are limited in determining their relative importance (Lauer and Peek 1976). Experimental studies using tame, supplementally fed animals can control variables more efficiently (Hobbs et al. 1983), however, results may not accurately represent natural conditions. We combined observational and experimental approaches in order to define limiting factors for nutrition of free-ranging bighorn ewes on 2 montane winter-spring ranges in north-central Colorado.

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Two major natural contrasts were used to identify factors limiting nutrition of bighorn ewes: the dramatic increase in availability of high quality forage from March to April; and the contrast between forage availability under snowfree conditions and with snow cover. Our objective was to document behavioral responses of free-ranging bighorn ewes to changes in forage availability and quality; and to determine the effects of changes in behavior and forage supply on nutrition. To accomplish this objective we estimated habitat selection, activity budgets, biting rates, bite sizes, and diet quality of ewes under different environmental conditions. Major guiding hypotheses were (1) that foraging behavior of ewes was sensitive to changes in foraging conditions, and (2) that changes in feeding behavior acted to enhance nutrition.

The Department of Fishery and Wildlife Biology and the College of Forestry and Natural Resources of Colorado State University, the Boettcher Foundation, the Colorado Mountain Club Foundation, the Foundation for North American Wild Sheep, the Rocky Mountain Bighorn Society, the National Park Service, the Colorado Division of Wildlife, and J. Goodson provided support for our study. We thank G. Bennett, R. Mumby, and the MacGregor Lodge for permission to observe bighorn on their properties.

STUDY AREAS AND BIGHORN POPULATIONS

The 2 study areas were similar in size (2 km^2) and located on predominantly south-facing slopes above the Fall River in north-central Colorado (Goodson et al. 1991_a_,_b_). The Fall River area was bisected by the east boundary of Rocky Mountain National Park and included private lands. The Endovalley area was within the Park.

Distinct subpopulations of female and juvenile bighorn sheep used the areas although adult rams moved between them (Stevens and Hanson 1986). Herds were estimated at 100 bighorn at Fall River; and 80-100 bighorn at Endovalley. On both areas, due to lack of hunting and abundant human activity, bighorn were habituated to people and easily observed.

Study areas were accessible parts of the total winter range of each subpopulation, and have been previously described (Goodson et al. 1991_a_,_b_). The Endovalley area was higher in elevation (2,590-2,900 m) than Fall River (2,400-2,650 m). Important foraging areas at Endovalley were aspen (_Populus tremuloides_)-Kentucky bluegrass (_Poa pratensis_) associations and grasslands dominated by bluegrass and cheatgrass (_Bromus tectorum_). These areas were interspersed with Douglas-fir (_Pseudotsuga menziesii_) stands with understories dominated by sedge (_Carex spp._ and mountain muhly (_Muhlenbergia montana_).

Mountain shrub with variable overstory of ponderosa pine (_Pinus ponderosa_) and Douglas-fir was the dominant vegetation type at Fall River. Dominant understory species were mountain muhly, blue grama (_Bouteloua gracilis_), and needle-and-thread (_Stipa comata_). Bluegrass lawns and sparsely vegetated disturbed sites were associated with residences and motels.

METHODS

Foraging Behavior, Diet Quality, and Nutrient Intake Rates

Bighorn were observed at Fall River from January through mid-May, 1985 and 1986; and at Endovalley from January to mid-May 1985 and 1987, and from March to May 1986. We located bighorn groups from roads or by traversing study areas on foot. The first group sighted that included adult ewes were approached for behavioral observations.

Methods were described in Goodson et al. (1991a,b). We observed foraging activity of individual adult ewes with 9 X 35 binoculars from distances of 6-76 m ($\bar{x}$ = 30 m). Bites of herbs and shrubs were recorded orally on tape. An experimental unit was a foraging sequence ($\geq$3 min long) of 1 ewe. We recorded 141 sequences at Fall River, and 166 sequences at Endovalley.

For each foraging sequence, the path of the ewe was described using landmarks. After the bighorn left the area, we retraced the ewe's path and located freshly bitten vegetation. To estimate diet composition we mimicked individual bites by clipping nearby vegetation. At least 20 bites of herbs ($\bar{x}$ = 32) and 10 of each species of shrub consumed were collected per sequence. For each sequence simulated herb bites were combined and separated into dead material, green grass, and green forbs. We oven-dried and weighed samples to estimate mean bite sizes and diet composition. To estimate dry-matter intake we multiplied biting rates by mean bite size (dry weight) for each sequence.

Diet components (green grass, green forbs, dead herbs, browse) comprising $\geq$5% of monthly diets were analyzed for protein concentration (Kjeldahl nitrogen X 6.25), in vitro dry matter digestibility, and neutral detergent fiber. Nutrient intake rates were estimated by multiplying nutrient concentrations by dry matter intake rates.

Activity Budgets

We estimated activity budgets of ewes during dawn-dusk observations under snow-free conditions and snow-covered conditions at Fall River (n = 6, with snow; n = 6, without snow) and Endovalley (n = 2, with snow; n = 10, without snow). We classified activities of all ewes in the group at 5-minute intervals as resting, resting-ruminating, standing, traveling, socializing, or foraging.

Statistical Analyses

We used linear regression to analyze relationships between proportions of green forage in ewe diets and diet concentrations of neutral detergent fiber, protein, and digestible dry matter. We used t-tests with separate estimates of variances if needed (Steel and Torrie 1980:106-107) to test differences in bite size, bite rate, dry-matter intake rate, and foraging time (as a percent of daylight time) between pre green-up and green-up conditions and between snow-free and snow-covered conditions within each study area.

RESULTS

Diet Composition

Diets of ewes in both study areas were dominated (85%, Fall River; and 96%, Endovalley) by graminoids (grasses and sedges) (Goodson et al. 1991b). During mid-winter (Jan-Feb), there was some green material available at the bases of graminoids, and ewes typically selected foraging areas where they could obtain a mixture of green and dead forage. Because percent green material in the diet was positively correlated with percent diet protein ($r^2 = 0.88$) and percent diet in-vitro digestibility ($r^2 = 0.80$) and negatively correlated with percent diet fiber ($r^2 = 0.62$), we used percent green material to indicate diet quality.

Snow-free Conditions

The major impact of foraging behavior and nutrition of bighorn ewes under snow-free conditions was the dramatic increase in diet quality that occurred during green-up (Mar-Apr) each year. Ewes began switching to new green grasses as soon as green growth began in March. Because new grasses were short, bite size declined (Table 1). Bite rates increased during green-up but only partially compensated for declines in bite size and dry-matter intake rates declined in both study areas (Table 1).

The limiting effect of availability of green forage on ewe nutrition was further demonstrated by the inverse relationship between bite size and diet quality during green-up ($r^2 = 0.55$, $P < 0.0001$, Fall River; $r^2 = 0.44$, $P < 0.0001$, Endovalley, Goodson et al. 1991b). Despite increases in bite rates dry-matter intake rates were also inversely related to diet quality during green up ($r^2 = 0.27$, $P < 0.0001$, Goodson et al. 1991b).

Bighorn shifted to green forage during green up although its limited availability caused intake rates to decline. Effects on nutrition were mixed. Intake rates of protein generally but not always increased during green-up (Goodson et al. 1991b, Table 1). However, intake of digestible dry matter which provides energy did not increase significantly (Fall River) or declined (Endovalley) (Table 1). Levels of energy intake finally increased in May as green grass became more abundant, and new growth of shrubs and forbs increased in availability (Goodson et al. 1991b).

During green-up, Fall River bighorn preferred open mountain shrub-mountain grass areas, disturbed areas and blue-grass lawns. Ewes favored previously grazed areas of mountain grass that began growth early due to removal of dead material through previous grazing. At Endovalley, bighorn preferred open areas dominated by bluegrass and/or cheatgrass. These areas were heavily grazed and formed grazing lawns (McNaughton 1984) characterized by dense, continuous short grasses. In both areas, selected types offered low total biomass but a high percentage of new growth.

Table 1. Changes between pre green-up (Jan-Mar) and green-up (Apr) in average diet quality (estimated by percent green material in diet), bite size, bite rate, and intake rates of dry-matter, protein, and energy (estimated by in-vitro digestible dry-matter (DDM)) of bighorn ewes at Fall River and Endovalley, north-central Colorado, 1985-87.

	Fall River			Endovalley		
	Pre Green-up	Green-up	_P_	Pre Green-up	Green-up	_P_
Diet quality	0.26	0.75	0.001	0.37	0.74	0.001
Bite size (g)	0.12	0.08	0.001	0.08	0.05	0.001
Bites/min	36.7	50.5	0.001	47.06	61.32	0.001
Intake rates (g/min)						
Dry-matter	4.45	3.79	0.038	3.76	2.70	0.001
Protein	0.35	0.63	0.001	0.41	0.54	0.001
DDM	2.16	2.58	0.06	2.13	1.81	0.006

Snow-covered Conditions

With snow cover, foraging conditions for bighorn ewes changed dramatically. Bighorn had to nose or paw through the snow layer to reach forage. As a result, biting rates declined in both study areas (Table 2). Ewes shifted foraging from open areas with short forage and low biomass to areas which shed snow (cliffs) or vegetation types providing snow shielding (shrub types) (Fig. 1). In these areas, ewes were able to obtain larger bites. Despite the increase in bite size, dry-matter intake rates declined with snow at Fall River. At Endovalley, the increase in bite size offset the decline in bite rate and intake rates increased (Table 2).

At both areas, diet quality declined steeply (Table 2). Bighorn were unable to forage selectively with snow. New green forage was short and buried under the snow and provided such small bite sizes that with reduced bite rates intake rates would have been inadequate. At Fall River, bighorn ewes shifted to areas with dense shrubs and rock outcrops that were lightly grazed and had higher biomass of forage with a low proportion of green material (Fig. 1). Ewes fed around the bases of shrubs where the shrub canopy intercepted snow and made forage more accessible. At Endovalley, ewes shifted to areas with shrub overstories and also to cliffs (Fig. 1). The south-facing cliffs shed snow and ewes fed at rock edges where snowmelt was most rapid.

The inability of ewes to maintain intake rates and/or diet quality influenced their activity budgets. Without snow, Fall River bighorn ewes foraged 63%, and Endovalley ewes foraged 79% of total daylight time (Table 2). With snow, ewes at Fall River increased their foraging time to 75% of daylight time. In contrast, foraging time at Endovalley fell to 58% (Table 2). Ewes at Fall River were able to compensate for

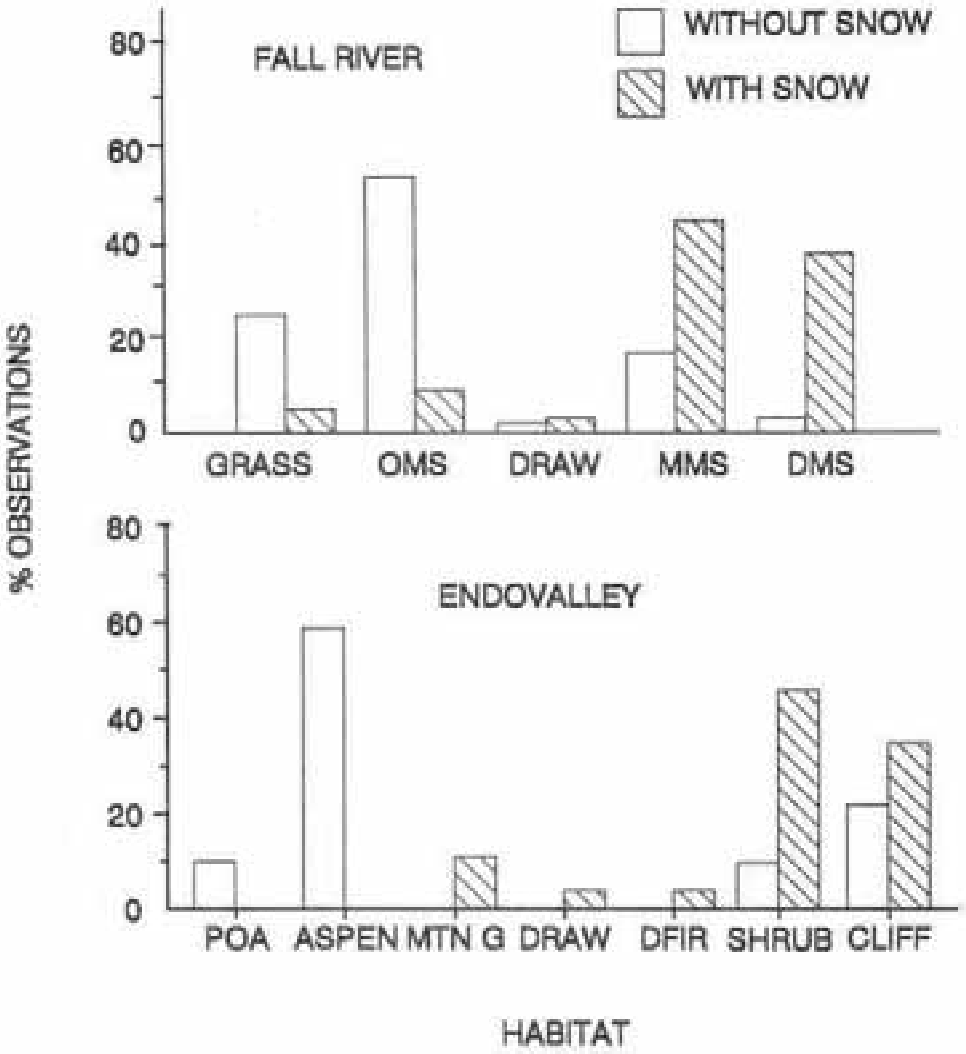

Fig. 1. Changes in habitat use between snow-free and snow-covered (5-12 cm) conditions for bighorn ewes on 2 montane study areas in north-central Colorado, 1985-87. Habitat types were GRASS (open grassland), OMS (open mountain shrub), DRAW (riparian), MMS (moderately dense mountain shrub), DMS (dense mountain shrub), POA (bluegrass-dominated grassland), ASPEN (open aspen stand with bluegrass-dominated understory), MTN G (bunchgrass-dominated grassland), DFIR (Douglas-fir stand with sedge-dominated understory), SHRUB (alder and/or gooseberry dominated habitats), and CLIFF (cliffs).

Table 2. Changes between snow-free and snow-covered (1-12 cm) conditions in average bite size, bite rate, dry-matter intake rate (DM intake), diet quality (estimated by percent green material in diet), and foraging time (expressed as a percent of total daylight hours) of bighorn ewes at Fall River and Endovalley, north-central Colorado, 1985-87.

	Fall River			Endovalley		
	No Snow	With Snow	P	No Snow	With Snow	P
Bite size (g)	0.12	0.18	0.001	0.07	0.13	0.001
Bites/min	45.07	27.19	0.001	50.07	35.04	0.001
DM intake (g/min)	4.99	4.75	0.001	3.44	4.26	0.025
Diet quality	0.60	0.12	0.001	0.50	0.17	0.001
Foraging time	0.63	0.75	0.001	0.79	0.58	0.001

declines in dry-matter intake rates and diet quality by increasing foraging time during the day. At Endovalley, foraging time was already near maximum during snowfree conditions. With snow, ewes at Endovalley decreased foraging time, presumably because foraging was unproductive.

Changes in ewe distribution during periods of persistent snow cover also indicated that snow prevented Endovalley ewes from foraging efficiently. In 1986, snow was unusually heavy during early winter. The Endovalley area was blanketed with over 20 cm of snow when fieldwork began in January and no bighorn were present. Periodic snowfalls maintained snow cover through most of February and bighorn did not return to stay in the study area until early March.

Endovalley is the only low elevation winter range used by this subpopulation. The remainder of the winter range lies at higher elevations, primarily above treeline. Even during heavy snow periods there are some alpine areas blown free of snow by the strong winds typical above treeline. Our observations indicated that during periods of persistent snow, Endovalley bighorn were forced to leave the study area and move up to windswept alpine ridges to find foraging areas free of snow.

DISCUSSION

Factors limiting nutrition of ewes differed with snow conditions. Without snow, bighorn selected open areas providing opportunity for selective foraging. These areas were the first to green-up in spring and provided high quality forage. Without snow, our observations indicated nutrition of ewes was limited by the area and productivity of habitats providing early green-up.

With snow, ewes selected areas for snow shedding or shielding characteristics. These areas provided greater availability of forage with lower quality, and enabled ewes to enhance total intake. Nutrition of ewes during snow-covered conditions was limited by the extent and productivity of habitats providing accessible forage.

With snow, bighorn shifted foraging from open areas with low biomass and a high proportion of green growth which permitted selective feeding to areas providing more accessible forage of lower quality. Their foraging strategy changed from optimization of diet quality to maximization of bite size and total intake. Despite this change in foraging strategy, intake rates declined at Fall River and diet quality declined in both areas.

MANAGEMENT IMPLICATIONS

Managers need to determine habitat selection of bighorn sheep under snow-free and snow-covered conditions even if snow is normally shallow and transitory. Limiting habitats should be determined, then management strategies to extend or enhance these habitats can be planned.

If habitat preferences differ with snow conditions as in our areas, managers need to insure that sufficient areas of snow-shedding or shielding habitat are available to provide adequate forage even in severe winters. Information on frequency, and duration of snow cover during average and severe winters is necessary to estimate bighorn sheep requirements for snow habitat. If preferred habitat during snow-covered conditions is adequate or abundant, managers should consider increasing the area and/or productivity of vegetation types providing early green-up.

Two basic approaches are available to enhance limiting habitats. the more common way is to treat current ranges to change habitat composition or enhance productivity of limiting habitats. The second approach is to extend ranges of the population to increase the area of limiting habitat.

If areas providing early green-up are lacking habitat improvement will generally increase exposure to the sun through setting back succession. Options include converting tree stands to shrub-grass or grassland; converting dense-shrub to open-shrub or grassland; and enhancing grassland by removing dead material. Methods to accomplish these objectives include mechanical methods such as logging, chaining, and chopping; chemical treatment; and burning.

Methods which provide longterm habitat enhancement are to be preferred over methods such as fertilization, which provide only shortterm benefits. Natural or prescribed fire that maintains grasslands or converts tree stands to grasslands can provide lasting benefits on bighorn ranges. The aspen-dominated slopes which provide most of the foraging areas on the Endovalley range were created by fires about 100 years ago. These areas are still providing habitat for bighorn and will continue to do so for the indefinite future. Wakelyn (1987) documented the negative effects of advancing forest succession (permitted by fire suppression) on bighorn ranges in Colorado.

Range extension can effectively improve habitat for bighorn sheep. Our 2 study areas provide an example. The Endovalley areas is a small low-elevation range used by a bighorn population whose primary winter range is above treeline in the Mummy Mountains of Rocky Mountain National Park. The Mummy Range bighorns are a native herd which lost most of their lower elevation range through human interference (Goodson 1980). Our results indicate that the remaining low elevation winter range at Endovalley is inadequate to support bighorn during winters of above average snowfall.

The Fall River bighorn population is the result of a 1977 transplant in which Rocky Mountain National Park and the Colorado Division of Wildlife cooperated (Stevens and Hanson 1986). The objective of the transplant was to restore bighorn sheep to low elevation winter range near the east boundary of Rocky Mountain National Park. The transplant reestablished use of low elevation winter range in the ponderosa pine zone which provides a complete winter range capable of supporting bighorn sheep through the normal range in winter snow conditions.

Although the Endovalley and Fall River ewes share summer range above treeline in the Mummy Range, the female-juvenile segments of these 2 herds remain distinct. Adult males, however, move between the areas. The transplant has succeeded in doubling the bighorn population in the area, and the Fall River herd has provided over 100 bighorn for transplants.

This example suggests the magnitude of benefits which successful range expansion can provide. Managers need to be open to opportunities to improve bighorn habitat through extending ranges into new areas capable of providing limiting resources.

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STATUS OF MOUNTAIN SHEEP IN MORGAN CREEK, EAST-CENTRAL IDAHO

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Abstract: Habitat relationships of the Morgan Creek mountain sheep (*Ovis canadensis*) population were observed in 1989 and 1990. The population increased from approximately 100 in 1970 to at least 278 in 1988, the highest level recorded. Rams used areas further from water and frequently-used roads than did ewes. Comparisons of areas subject to grazing by cattle along with a 1417 ha area excluded from livestock grazing show improved grass cover since 1973, with no differences between the excluded area and adjacent grazed areas. Blood chemistry data indicated this population to be in relatively poor condition in late winter. Live-trapping individuals for restoration to vacant habitat could be intensified as a means of recovering the vigor of this population.

Mountain sheep populations and the habitat in Morgan Creek, a tributary to the Salmon River in east-central Idaho, were the subject of a major controversy in the late 1960's between livestock and wildlife interests. Populations of sheep had declined from over 250 in 1963 to approximately 70 in 1970 (Morgan 1970). The resulting management activities included establishment of a rest-rotation grazing system for cattle using the area, closure of hunting, and a continuing population monitoring program by Idaho Department of Fish and Game. Subsequently, sheep populations increased and distributions were probably altered by the changed grazing pattern (Bodie and Hickey 1980). Objectives of this study were to determine sheep population size, distributions, and condition, and to assess vegetative composition and trend.

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STUDY AREA

The Morgan Creek sheep winter range lies approximately 21 km north of Challis, Idaho (Fig. 1). Elevations range from 1450 m at the mouth of Morgan Creek to 2700 m at the top of Red Butte. Soils are granitic and basaltic in origin, shallow and very rocky (Morgan 1970). Annual precipitation at Challis, Idaho, 40 km southeast of the winter range averaged 24 cm from 1968-90, mostly as snow, and averaged 17.5 cm for years 1988-89 (N.O.O.A. 1969-1990).

Sheep habitat is dominated by sagebrush communities. Wyoming big sagebrush (Artemesia tridentata wyomingensis) - bluebunch wheatgrass (Agropyron spicatum) (Arwy-Agsp)occurs on shallow soils at lower southerly aspects. A Wyoming big sagebrush-bluebunch wheatgrass-bluegrass (Poa sandbergii and P. fendleriana) (Arwy-Agsp-Poa) community occurs on more mesic sites on lower slopes and other aspects. A threetip sagebrush (A. tripartita) - Idaho fescue (Festuca idahoensis) (Artr2-Feid) community occurs on higher elevations on deeper soils. A threetip sagebrush-bluebunch wheatgrass (Artr2-Agsp) community occurs on slightly drier sites, and is found with big sagebrush and low sagebrush (A. arbuscula). A low sagebrush community is present on dry flat ridges with poorly developed soils. Cliffs were separated as a unique community and were comprised of mixtures of the above communities and plants representative of more mesic microsites where moisture and shade allowed their development.

In 1973, a 3 pasture rest-rotation grazing system was established in Morgan Creek. Additionally, approximately 1147 ha of primary sheep winter range were fenced to exclude livestock. Most of the Morgan Creek winter range is administered by the U.S. Bureau of Land Management with small portions of private land along creek bottoms, a few sections of state-owned land, and some in the Challis National Forest.

METHODS

Sheep were captured using a helicopter and a net-gun (Jessup et al. 1988). Seasonal distributions of radio-collared sheep were determined from 11 rams and 9 ewes in 1988 and 1989 using ground and aerial search. Each sheep relocation was recorded by Universal Transverse Mercator (UTM), slope, aspect, elevation, group size, and sex/age class throughout winter, spring, and summer of 1989 and 1990. In March 1988 and April 1990, aerial censuses of the winter range made with a Hiller 12E helicopter. Sheep were classified according to sex and age class following Geist (1968). Mean ram:ewe and lamb:ewe ratios and variances were estimated using each group as an observation. Relocations of radio-marked sheep were plotted on a USGS topographic map and distances to water sources and roads were recorded.

Vehicle use of roads on the winter range was monitored daily from January through April, after which roads became too dry and hard for vehicle tracks to be observed. Vehicle traffic was classified as high (>1 time per day) or low (<5 times during Jan through Apr). Fifty random locations were also plotted to determine random distances from roads and water.

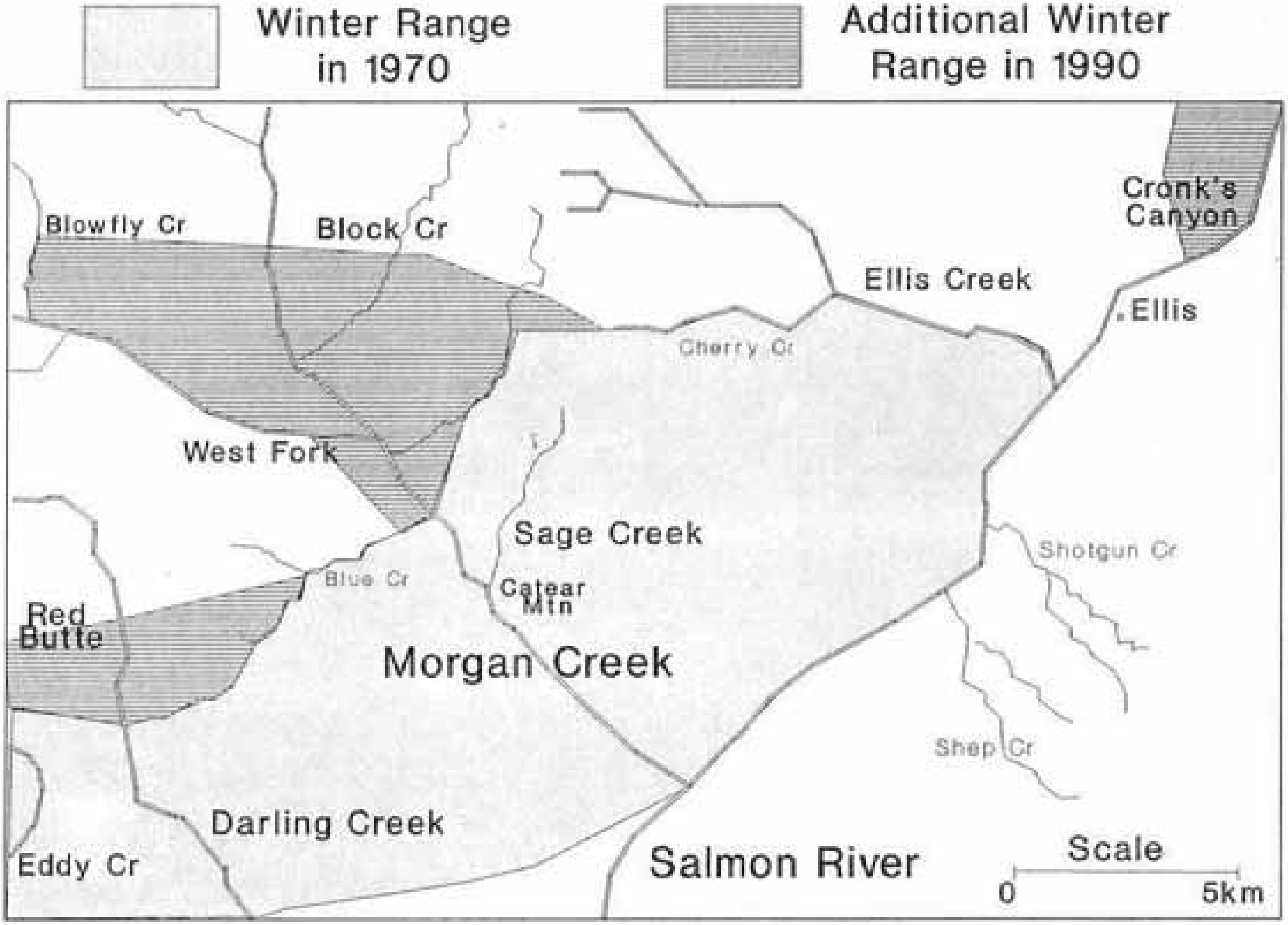

Fig. 1. Morgan Creek bighorn sheep winter range, showing the expansion of area occupied from 1970 to 1989-1990.

Multivariate analysis of variance (MANOVA) was used to test for differences between sheep relocation distances and random distances to water and roads, and least squares means were used to determine where differences existed. A chi-square test was used to test for differences in use of cover types between males and females. Cover types used less than 5 times were dropped from the analysis. After the chi-square indicated overall significance, 90% confidence intervals were constructed to determine where differences existed (Marcum and Loftsgaarden 1980).

Clusters of permanent vegetation transects established by Morgan (1970) were reanalyzed using his techniques. Three transects per cluster were laid in a straight line following the contour of the slope. Three clusters of 3 transects each were analyzed. The cluster sites were Catear Mountain (Cluster 5), Mud Springs Gulch (Cluster 7), and Spring Gulch (Cluster 9). Each transect consisted of 20, 2X5dm plots to determine canopy coverage of all plant species, and percent of bare soil, rock, litter, and moss and lichen at ground level. In addition, the 4 corners of each plot (leg point hits) were recorded as hitting bare soil, rock, litter, moss and lichen, or vegetation. For 1977, cluster 7 data and leg point hit data for all clusters were missing. For 1986 only 19 plots per transect were recorded. MANOVAS tested the null hypothesis that winter range plant species composition was similar among 1968, 1977, 1986, and 1990.

Ten to 40 ml of blood were taken from each sheep trapped in the winter of 1989, centrifuged, and protected from freezing and extreme heat. Levels of blood urea nitrogen (BUN), calcium, phosphorous, and magnesium were determined at the Washington State University Clinical Diagnostic Laboratory in Pullman, Washington. BUN, magnesium, phosphorus, and calcium levels were compared with those from bighorn sheep in the Poudre River area in Colorado (Davies 1976) and to values established as normal in winter for bighorn sheep from Canada, Montana, Wyoming, and Washington by Franzmann (1971a). T-tests were used to compare the data (Sokal and Rohlf 1973).

RESULTS

Numbers

Two hundred and seventy eight sheep were counted in March 1988, including 36 class IV rams, 23 class III rams, 27 class II rams, 5 class I rams, 156 ewes, and 31 lambs. Overall ram:ewe ratio was 58:100 (variance = 0.056) and overall lamb:ewe ratio was 20:100 (variance = 0.003). In April 1990, flights over the winter range recorded 130 sheep, including 13 class IV rams, 12 class III rams, 18 class II rams, 9 class I rams, 66 ewes and 12 lambs. Overall ram:ewe ratio was 82:100 (variance = 0.135) and overall lamb:ewe ratio was 15:100 (variance = 0.004). No significant differences occurred in the ram:ewe ratio or the lamb:ewe ratio from 1988 to 1990 ($\underline{P}$ = .2236 and $\underline{P}$ = .2004, respectively).

Distribution

Relocations totalled 222 in 1989 and 364 in 1990. Most collared ewes wintered in lower Morgan Creek, primarily in the Catear Mountain and Mud Springs Gulch area; a few wintered in Darling Creek (Fig. 1). Rams generally used higher elevations and different areas than ewes.

The mean distance between winter and summer ranges was 37.03 km (SD = 81.02, n = 90). Ewes averaged 24.2 km (SD = 12.6, n = 51) to summer range, while rams averaged 53.8 km (SD = 120.2, n = 39). Movements to summer range began in mid-May each year and continued through June. Some ewes returned to winter range in early August.

Habitat use

Cover type use was significantly different ($P < 0.0005$) between rams and ewes. The ARWY-AGSP and CONIFER cover types were used more frequently by rams, whereas the ARWY-AGSP-POA and ARAR cover types were used more frequently by ewes ($P < 0.01$). Both sexes used CLIFF and ARTR2-FEID types similarly.

Rams stayed further from water and high-use roads than ewes. Distance to water and high-use roads was significantly greater for random sites than for sheep relocations ($P < 0.05$) (Table 1), but there was no significant difference in distance to low-use roads between random sites and sheep relocations. Ewe relocation distances were significantly less than random location distances from both water and high-use roads, but ram relocation distances were significantly less than random distances from high-use roads only.

Vegetation trend

Significant changes in canopy coverage of 9 common species occurred on the permanent transects (Table 2). Wyoming big sagebrush cover remained stable over the 22 year period on both Catear Mountain and Mud Springs Gulch. Low sagebrush increased on Catear Mountain (P = 0.0001), and shadscale did not change on Spring Gulch. Bluebunch wheatgrass increased on Catear Mountain (P = 0.0001), and increased from 1968 to 1986 then declined in 1990 on Mud Springs Gulch (P = 0.0001). Wildrye showed an increasing trend through 1986 and declined from 1986 to 1990 at Spring Gulch, but the changes were not significant. Indian ricegrass slowly increased at Spring Gulch (P = 0.0093). The bluegrasses remained stable on Mud Springs Gulch, and showed an initial decrease in 1977 (P = 0.0033), then increased to 1986 at Catear Mountain (P = 0.0405). Forbs, including lava aster (*Aster scopulorum*), phlox (*Phlox* spp.), rock cress (*Arabis hoelbelli*), and stonecrop (*Sedum lanceolatum*), generally increased from 1968 to 1986 and declined from 1986 to 1990, reflecting the drought. Additionally, mean canopy coverage on all 3 sites of 13 common species is shown for each year of the long term study. Canopy cover of vegetation appeared to increase with increasing precipitation, and decrease with drought. However, because only 4 estimates of canopy cover were made, no statistical analysis was done. Litter generally increased on all three sites over the 22 year period. Mosses and lichens fluctuated, while vegetation increased at Mud Springs Gulch and Spring Gulch, and was stable at Catear Mountain.

Table 1. Proportion of relocations of radio-collared mountain sheep within cover types and proportional availability of these cover types on the Morgan Creek winter range. Least squares means of distances to water and roads for both sheep locations and random sites.

Cover Type	Availability	Rams	Ewes	All Sheep
ARWY-AGSP	0.10a[a]	0.11a	0.06b	0.07a
ARWY-AGSP-POA	0.27a	0.21a	0.28a	0.26a
ARTR2-FEID	0.15a	0.09a	0.06b	0.07b
ARTR2-AGSP	0.01a	0.02a	0.00a	<0.01a
ARTRTR	0.01a	0.00a	<0.01a	<0.01a
CLIFF	0.19a	0.46b	0.45b	0.46b
CONIFER	0.11a	0.09a	0.02b	0.04b
ARAR	0.03a	0.00a	0.11b	0.08b
SHADSCALE	0.06a	0.02b	0.01b	0.01b
RIPARIAN	0.06a	0.01b	0.01b	0.01b
n	-	126	320	446
Distances(meters):				
Water:				
LSMean	728.17a	658.41a	469.41b	525.36b
SD	402.63	398.65	398.64	406.58
High use roads:				
LSMean	3041.39a	2165.48b	852.67b	1241.33b
SD	1431.75	1417.40	1417.37	1526.61
Low use roads:				
LSMean	952.47a	853.71a	849.38a	850.66a
SD	532.52	527.15	527.10	526.59
n	50	135	321	456

[a] Same letter denotes no significant difference from availability at $P < 0.05$; Comparisons were made between availability and ram locations, availability and ewe locations, and availability and total sheep locations.

Table 2. Mean and standard deviation (SD) of vegetal canopy cover from permanent transects (Morgan 1970) on the Morgan Creek mountain sheep winter range, east-central Idaho.

	1968[a]			1977		1986			1990		
	Catear Mtn	Mud Springs	Spring Gulch	Catear Mtn	Spring Gulch	Catear Mtn	Mud Springs	Spring Gulch	Catear Mtn	Mud Springs	Spring Gulch
<u>Agropyron spicatum</u>											
Mean	1.92	6.27	0.00	8.83	0.00	15.92	15.35	0.00	15.79	9.08	0.00
SD	4.13	7.53	-	8.93	-	13.70	14.57	-	12.58	12.59	-
<u>Poa</u> spp.											
Mean	5.71	0.17	0.00	2.75	0.00	4.96	0.18	0.00	4.75	0.54	0.00
SD	5.68	0.63	-	2.38	-	5.27	0.64	-	5.22	2.06	-
<u>Artemisia tridentata wyomingensis</u>											
Mean	4.38	14.19	0.00	3.42	0.00	5.18	16.93	0.00	4.25	16.08	0.00
SD	11.74	24.82	-	14.19	-	15.00	27.83	-	13.99	26.69	-
<u>Artemisia arbuscula</u>											
Mean	0.00	0.00	0.00	6.62	0.00	10.48	0.00	0.00	8.88	0.00	0.00
SD	-	-	-	11.72	-	17.64	-	-	14.25	-	-
<u>Atriplex</u> spp.											
Mean	0.00	0.00	1.67	0.00	2.75	0.00	0.00	5.00	0.00	0.00	3.88
SD	-	-	5.76	-	7.73	-	-	15.48	-	-	11.03

(Table 2 continued)

	1968ᵃ			1977		1986			1990		
	Catear Mtn	Mud Springs	Spring Gulch	Catear Mtn	Spring Gulch	Catear Mtn	Mud Springs	Spring Gulch	Catear Mtn	Mud Springs	Spring Gulch
Phlox longifolia											
Mean	1.88	0.00	0.00	3.12	0.00	4.74	0.00	0.00	0.75	0.00	0.00
SD	1.09	-	-	5.76	-	7.73	-	-	15.48	-	-
Phlox muscoides											
Mean	3.29	0.00	0.00	9.96	0.00	6.58	0.00	0.00	4.00	0.00	0.00
SD	4.05	-	-	12.38	-	7.94	-	-	5.66	-	-
Penstemon spp.											
Mean	0.04	0.00	0.04	0.33	0.12	0.39	0.00	0.75	0.38	0.00	0.04
SD	0.32	-	0.32	0.86	0.55	0.92	-	2.16	0.90	-	0.32
Sedum spp.											
Mean	0.67	0.00	0.00	0.54	0.00	1.01	0.00	0.00	0.17	0.00	0.00
SD	1.11	-	-	1.04	-	1.24	-	-	0.63	-	-
Aster scopulorum											
Mean	0.00	0.00	0.00	0.62	0.00	0.92	0.00	0.00	0.38	0.00	0.00
SD	-	-	-	1.09	-	2.20	-	-	0.90	-	-

(Table 2 continued)

	1968[a]			1977		1986			1990		
	Catear Mtn	Mud Springs	Spring Gulch	Catear Mtn	Spring Gulch	Catear Mtn	Mud Springs	Spring Gulch	Catear Mtn	Mud Springs	Spring Gulch
Arabis spp.											
Mean	0.00	0.38	0.08	0.00	0.00	0.00	1.93	0.13	0.17	0.04	0.00
SD	-	0.91	0.45	-	-	-	2.11	0.56	0.63	0.32	-
Elymus ambiguus											
Mean	0.00	0.00	5.50	0.00	8.17	0.00	0.00	6.49	0.33	0.29	6.75
SD	-	-	10.95	-	13.60	-	-	10.53	0.86	1.96	10.37
Oryzopsis hymenoides											
Mean	0.00	0.00	0.25	0.00	1.42	0.00	0.70	3.33	0.00	0.33	3.58
SD	-	-	0.76	-	5.49	-	4.97	8.01	-	1.98	10.81
Bare soil											
Mean	9.29	7.63	32.46	-	-	17.72	21.18	25.66	23.71	14.88	18.79
SD	10.81	9.29	34.36	-	-	15.25	21.80	26.07	16.96	12.62	16.05
Rock											
Mean	6.42	27.08	0.00	-	-	14.12	45.79	55.83	16.88	44.42	19.42
SD	7.34	23.24	-	-	-	11.29	27.48	27.47	11.88	24.14	17.94

(Table 2 continued)

	1968[a]			1977		1986			1990		
	Catear Mtn	Mud Springs	Spring Gulch	Catear Mtn	Spring Gulch	Catear Mtn	Mud Springs	Spring Gulch	Catear Mtn	Mud Springs	Spring Gulch
Litter											
Mean	0.58	4.07	2.92	-	-	18.64	16.23	4.30	41.21	25.38	13.71
SD	2.08	6.73	7.27	-	-	16.01	13.90	5.38	21.43	18.80	13.56
Moss & lichen											
Mean	0.54	0.00	0.00	-	-	0.39	0.00	0.00	2.46	3.88	0.08
SD	1.04	-	-	-	-	2.05	-	-	3.10	6.25	0.45

[a] 1968: clusters 5 and 9 *n* = 60, cluster 7 *n* = 59; 1977: clusters 5 and 9 *n* = 60, cluster 7 data missing; 1986: clusters 5, 7, and 9 *n* = 57; 1990: clusters 5, 7 and 9 *n* = 60.

BUN and calcium levels for Morgan Creek sheep were significantly lower than for Poudre River sheep, but phosphorous was not (Table 3). Normal BUN levels (Franzmann 1971a) were greater than levels for Morgan Creek sheep, while levels of calcium, phosphorus, and magnesium in Morgan Creek sheep were greater.

DISCUSSION

The area used as winter range by sheep has increased since 1970 (Morgan 1970) (Fig. 1) probably reflecting a doubling of population size. Movements to and use of summer range were similar to those reported by Morgan (1970), as was mean distance between winter and summer ranges.

The population survey in 1988 was more reliable than in 1990. Deep snows in 1988 concentrated animals on windswept slopes, and no sign was noted in timber. In 1990, very little snow cover occurred, sheep were widely dispersed, and often seen in timber. Signals from several radio-collared animals were heard, but the sheep were not seen in 1990, suggesting that significant numbers of sheep were not counted. Assuming that no sheep were counted more than once, the 1988 total count of 278 sheep is the highest population number ever recorded on the Morgan Creek winter range.

Rams appeared to select only cliff habitats, while ewes selected lower elevation, cliff areas. Geist and Petocz (1977) found that rams preferred open slopes and ewes preferred cliffs.

The main water sources, Morgan Creek and Salmon River, occur adjacent to high-use roads and major cliff areas, so the corresponding use of areas closer to high-use roads may reflect this. MacArthur et al. (1982) found that reactions by sheep to road traffic were minimal. However, the sheep population studied was partially habituated to humans due to recreational activities in the area, and the authors predicted a greater reaction by sheep in less habituated populations such as the Morgan Creek population.

The differences in distance to high-use roads and water sources and in use of cover types between the sexes were not necessarily due to differences in habitat selection. Geist and Petocz (1977) and Shank (1982) found that although both sexes occupy contiguous range, they were concentrated in different areas on that range. Reasons for these differences in spatial use of the range are poorly understood. Geist and Petocz (1977) theorized that rams minimize competition with females and their prospective offspring by segregating spatially and by using different habitat, thereby maximizing their own reproductive fitness. Shannon et al. (1975) found that mountain sheep distribution was only loosely coupled to environmental cues with most of the variation related either to random search or to "occupational" patterns that were strongly shaped by tradition. Environmental variables not yet identified may be important to sheep in determining habitat use.

The greater amount of total canopy cover for cluster 5 in 1986 than all other years may reflect the continuing improvement of the

Table 3. Mean, standard deviation (SD), and sample size (n) of blood chemistry values (mg/100ml) of mountain sheep in Morgan Creek, east-central Idaho and comparisons of these values to other studies.

	Morgan Creek[a]			Poudre River			Franzmann			T-test P values	
	mean	SD	n	mean	SD	n	mean	SD	n	89-PR[c]	89-F
BUN[b]	10.49	3.21	43	13.98	2.89	24	23.50	8.30	65	<0.001	<0.001
Ca	9.80	0.87	21	11.49	1.22	24	8.80	1.69	65	<0.001	0.013
P	6.22	1.28	21	5.85	1.47	24	4.00	1.29	65	0.398	<0.001
Mg	3.12	0.37	21	-	-	-	1.70	1.21	65	-	<0.001

[a] Morgan Creek data collected Dec. 1988-Feb. 1989; Poudre River, Wyoming data collected January, 1975 (Davies 1976); Franzmann data compiled from herds in Wyoming, Montana, and Canada in winter, 1969-1970 (Franzmann 1971a)

[b] BUN = blood urea nitrogen; Ca = calcium; P = phosphorus; Mg = magnesium

[c] 89-PR = comparison between Morgan Creek sheep in 1989 and Poudre River herd in 1975; 89-F = between Morgan Creek sheep in 1989 and Franzmann (1971a)

Morgan Creek winter range through the years. The fact that Catear Mountain had less overall canopy cover in 1990 than in 1986 may be attributable to the severe drought that has occurred for the past several years in this area. Generally, there was greater canopy cover and leg point hits of litter in 1990 than other years. Although there were no differences in leg point hits on vegetation between years, the greater amount of litter in 1990 may reflect the greater vegetation availability due to increasing quality of the range, but earlier seasonal senescence of plants due to several years of drought.

Relative changes in canopy cover over the 22-year period were compared for the permanent transects. Cover of Wyoming big sagebrush, the dominant shrub on Catear Mountain (within the exclosure) and at Mud Springs Gulch (grazed), remained stable over the 22-year period. Cover of shadscale, the dominant shrub at Spring Gulch (grazed), also did not change. It appears that the rest-rotation grazing system in this area generally did not affect shrub cover. Bluebunch wheatgrass, the dominant grass species at Catear Mountain and Mud Springs Gulch, increased through time at both places, but decreased with drought only in the grazing system. This may reflect an interaction between drought and grazing effects on this species. It must be noted that these transects were located in different cover types and differences between the sites themselves may explain differences in relative changes over the years. Canopy coverage of bluegrasses remained relatively stable over the 22-year period through both wet and dry years.

These general increases in canopy cover of forage species, especially bluebunch wheatgrass, over the last 22 years provided more forage for sheep. Dissipation of the drought would improve production and possibly foster a continuation of the observed trends in plant composition, until some equilibrium is again reached. Similar changes following establishment of a rest-rotation grazing system in a nearby drainage were documented by Yeo et al. (1990), suggesting that these systems are an appropriate means to improve grass cover on mountain rangeland in east-central Idaho.

Franzmann (1971b) found that differences in quality of forage intake most affected BUN levels, while magnesium, calcium, and phosphorus did not seem to change with either forage quality or excitability. Protein intake is significantly related to BUN levels (Seal et al. 1978, Lewis 1957). However, since protein anabolism may change to protein catabolism during mid-winter to early spring (Hebert 1978), BUN samples taken during this period may or may not be a reflection of forage quality at this time. The relationship between time of year and protein metabolism is highly variable.

Although calcium, phosphorus, and magnesium levels for the Morgan Creek sheep in 1989 are within normal limits (M. R. Dunbar, Cascade, Id., pers. commun.), this could be due to elevated serum levels from depletion of bone reserves. Hebert (1978) stated that previous superior nutrition can maintain a sheep's nutritional status while it is feeding on low-quality winter forage. However, the prolonged drought may indicate the greater amount of calcium, phosphorus, and magnesium, but lower BUN levels in Morgan Creek sheep in 1989 than in sheep sampled by

Franzmann in 1971 is due to body protein catabolism and bone reserve depletions by the sheep because of low quality forage rather than to previous superior nutrition on the fall range. This may explain the overall poor body condition of the herd and the likelihood of poor quality forage at that time period.

No estimation of body condition was given for the Poudre River herd, so we don't know if this herd was catabolizing body protein or depleting bone reserves of calcium and phosphorus. Perhaps they were in better condition than the Morgan Creek sheep in 1989, however, because of high hemoglobin and packed cell volume values of the Poudre River herd (Coles 1967, Franzmann 1971b) in addition to its higher levels of BUN and calcium than the Morgan Creek herd (Davies 1976).

Fecal nitrogen can be used to indicate whether an animal is above or below the protein maintenance level (Hebert 1978). The Morgan Creek herd in 1989 had only 1.26% fecal dry matter nitrogen and body condition was poor in January-February, so it was likely catabolizing body protein. We recommend future studies of nutritional status of sheep determine both blood urea nitrogen and fecal nitrogen levels to better understand herd condition.

The count of 278 sheep in 1988 is the highest number ever recorded on the Morgan Creek winter range. However, the sheep are also in poor body condition and incidence of lungworms is higher than normal (Ballard 1991). Adequate protein appears to be lacking in the diet. It is unlikely that these sheep are limited by the available forage because forage utilizations does not appear to be high. Poor forage quality and early senescence of grasses due to extended drought may be a factor. Signs of pneumonia were evident in this population during the trapping in January and February. This was not surprising due to the very high lungworm loads, and the stress on these animals from poor winter forage quality (due to extended drought), and from being chased by a helicopter during this stressful time period. Overall, the Morgan Creek sheep appear to be in relatively poor body condition in mid to late winter.

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POPULATION DYNAMICS, SEASONAL DISTRIBUTION AND MOVEMENT PATTERNS OF THE LARAMIE PEAK BIGHORN SHEEP HERD

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Abstract: Radio-collared adult bighorn sheep ewes and associates were relocated from fall 1989 to spring 1992. The Laramie Peak bighorn sheep herd appears to be stable to declining based on herd unit numbers and sex ratios. Annual adult ewe morality was 10.8%. Mortality of three radio-instrumented ewes was caused from a fall, from Pasteurella sp., and from coyotes. Lambing rates were as high as 75%, but lamb survival was 33% or less. Lungworm infection levels were higher than levels found in other sheep herds in Wyoming. Ewes exhibited movements greater than 51 km from wintering areas to lambing areas. Bighorn ewes exhibited a social intolerance of domestic livestock when cattle were grazing in riparian areas.

Rocky Mountain bighorn sheep (Ovis canadensis canadensis) were reintroduced into the Laramie Peak area of east central Wyoming in 1964 from the Whiskey Mountain herd near Dubois, Wyoming (Bohne 1989). By 30 June 1989, 186 bighorn sheep had been released in the Laramie Peak Data Analysis Unit (DAU). In spite of the transplants, the Laramie Peak bighorn sheep herd appeared to be declining (Bohne 1989). Quantitative data on the Laramie Peak sheep herd are inadequate. Seasonal ranges, lambing areas and diet quality were poorly documented or unknown. Considerable effort has been expended to document sex and age ratios of the herd. However, due to the rugged and remote terrain, insufficient data have been collected.

The Wyoming Game and Fish Department has set the objective for the Laramie Peak bighorn sheep herd at 500 animals and the harvest objective at 24 rams annually. However, since the first hunting season in 1969, no single year harvest has exceeded 7 rams (Bohne 1989). The postseason 1991 population was estimated at 218 sheep, including 20 sheep released in January 1989 near Marshall.

In this paper we: (1) Evaluate herd composition and productivity, (2) examine mortality factors, and (3) estimate overlap for forage and space with domestic livestock.

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STUDY AREA

The Laramie Peak bighorn sheep herd was composed of subherds that inhabited: the Laramie Peak Wildlife Habitat Management Area and the Laramie River (DUC), the Sheep Creek drainage near Marshall (MAR), the LaBonte Canyon and Horseshoe Creek drainages (LAB), the Black Mountain-Albany Peak area (B-B), and the North Laramie River (NLR) canyon (Fig. 1).

Sheep were primarily found on steep slopes composed of big sagebrush (*Artemisia tridentata*)/and mixed grass and mixed shrub/mixed grass. Grass-dominated communities on windblown ridges were heavily used during winter months while ponderosa pine (*Pinus ponderosa*) and lodgepole pine/Douglas fir (*Pinus contorta*/*Pseudotsuga menziesii*) forests were used occasionally. Elevation ranged from 1,585 m to 3,131 m. Predominant soil types were very stony sandy loam and very cobbly sandy loam (Malcolm Edwards, Medicine Bow National Forest Soil Scientist, pers. comm.). Temperatures ranged from 33 C in summer to -40 C in winter. Precipitation averaged 35 cm at lower elevations. Wind speed exceeded 100 km/h in January and February during each year of the study.

METHODS

Fifteen adult bighorn sheep ewes were captured using a CODA netgun from a helicopter or immobilized with a dart containing a ketamine/xylazine mixture. Ewes were affixed with Telonics radio collars, aged by tooth replacement and horn annuli, ear tagged and blood samples were drawn by jugular venipuncture. Radio-instrumented sheep were relocated at least twice a week at MAR and DUC.

Herd composition was determined by relocating radio-collared ewes and their associates. Individuals were categorized into: adult ewes, yearling ewes, lambs, yearling rams, Class II, Class III, and Class IV adult rams (Geist 1971). All groups of sheep encountered were classified. Wyoming Game and Fish Department herd composition data collected between 1977 and 1989 were used to supplement population data from this study. These classifications were also used to assess herd productivity and population dynamics.

Mortality factors and lamb survival were assessed from classifications of radio-collared ewes and their associates. Dead sheep

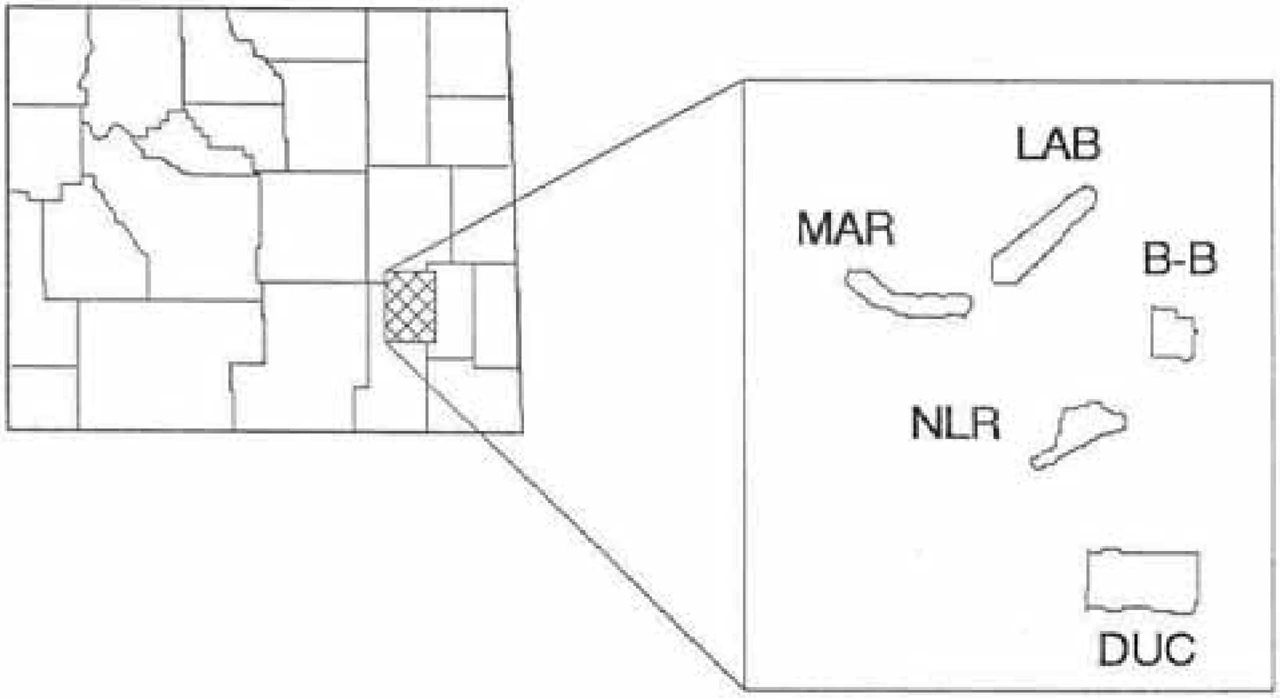

Fig.1. Study area and subherd locations of the Laramie Peak Bighorn Sheep Herd, Wyoming. (Laramie Peak Wildlife Habitat Management Area and the Laramie River (DUC), Sheep Creek Drainage near Marshall (MAR), LaBonte Canyon and Horseshoe Creek drainages (LAB), Black Mountain-Albany Peak Area (B-B), and North Laramie River (NLR)).

encountered were necropsied in the field or taken to the Wyoming State Veterinary Lab in Laramie for diagnosis.

Levels of lungworm infection in sheep were estimated by counting lungworm larvae per gram of dried fecal material using the Baermann technique (Beane and Hobbs 1983). Fecal samples were collected whenever found fresh in the field. They were grouped together for each area. Comparisons were made on a monthly basis. Fecal samples were divided into adult or lamb based on size of pellet. We were not able to collect in all winter months. Density of larvae in bighorn fecal material generally reflects severity of lungworm infection in lungs (Forrester 1971, Uhazy et al. 1973).

Relocations of radio-collared sheep were plotted on USGS 1:24,000 topographic maps. Spatial and temporal overlap of habitats by domestic cattle (Bos taurus) and bighorn sheep in the Duck Creek subherd were estimated by recording location, date, time, number, habitat type, and activity of the 2 species when encountered. Relocation points of cattle and radio-instrumented bighorn sheep ewes were plotted on USGS 1:24,000 topographic maps. Movement maps were constructed to compare seasonal ranges for cattle and bighorn sheep.

To monitor cattle grazing on the Duck Creek allotment, 5 square exclosure cages (1.2 m x 1.2 m x 1.2 m [4 ft. x 4 ft. x 4 ft.]) and 2 cone-shaped exclosure cages (0.9 m x 0.9 m at the base [3 ft. x 3 ft.]) were placed along Duck Creek in the riparian zone. Five cone-shaped exclosure cages of the same size as above were placed from 45 m (ca. 50 yds.) to 90 m (ca. 100 yds.) up the slope from the riparian zone. Vegetation inside and adjacent to the cages was clipped in May 1991 and 1992 prior to turnout of cattle on the allotment. Vegetation was clipped in and adjacent to the cages in September or October 1990 and 1991 after cattle were removed from the allotment. Three 0.089-m^2 (0.96-ft^2) random circular plots were clipped inside the exclosure cages and 5 were clipped outside the cages.

RESULTS

Herd Composition

Herd composition consisted of a minimum of 29 adult ewes at DUC, 22 at MAR, 24 at NLR, and 3 at B-B (Table 1). Number of adult males included a minimum of 14 at DUC, 9 at MAR, 8 at NLR, and 3 at B-B. The single day non-repetitive high count of Class III rams was 5 at DUC, 4 at MAR, and 1 each a NLR and B-B. Single day non-repetitive high counts for lambs were 12 at DUC, 11 at MAR, 16 at NLR, and 2 at B-B.

Yearling male and female ratios per 100 adult ewes declined from 27.5 in 1989 to 12 in 1991 apparently at DUC. Similar declines were observed at the other subherds. Lamb ratios at DUC were variable between years and declined within the year (Table 1). Similar results were observed at other subherds (Table 1).

A group of 5 ewes wintering south of the main herd at MAR during 1990 and 1991 apparently was not bred and did not produce lambs for 2

Table 1. Minimum, non-repetitive estimates of sheep at Duck Creek, and the North Laramie River, Wyoming.

Year	Adult ewes	Yearling ewes	Yearling rams	Summer lambs	Winter lambs
			Duck Creek		
1989	29	4	4	4	2
1990	27	5	1	8	3
1991	25	2	1	12	4
			Marshall		
1989	19	4	4	7	6
1990	21	4	2	7	2
1991	22	4	1	11	4
			North Laramie River		
1989	10	3	3	5	3
1990	18	1	2	9	3
1991	24	2	1	16	12

Table 2. Seasonal lungworm infection levels for the Laramie Peak bighorn sheep herd and from other studies.

	L. Peak		N. Platte[a]		Encampment[a]		Whiskey Mtn.[b]		Alberta[c]		Alberta[d]		Montana[e]	
	mean	n	mean	n	mean	n	mean	n	mean	n	mean	n	mean	n
Winter	492	28	306	366	112	95	385	152	185	153	520	80	337	146
Spring	413	68	144	152	-	-	-	-	218	231	535	96	554	142
Summer	88	118	92	433	55	116	32	98	23	5	135	52	337	158
Fall	128	73	87	405	40	100	35	120	80	80	472	32	327	137

[a] Cook et al. 1989

[b] Thorne et al. 1979

[c] Gates 1975

[d] Uhazy et al. 1973

[e] Forrester and Senger 1964

consecutive years. One radio-instrumented ewe, after spending the majority of the winter with these non-breeding ewes in 1991, rejoined the main group of sheep at MAR during April 1991. This ewe made a substantial movement to LaBonte Creek (LAB) during July-August 1991. The ewe subsequently died apparently from a fall on 19 August 1991. When necropsied, the ewe was pregnant with a near term ewe lamb.

Mortality

Three radio-collared ewes died during the study. Two died at LAB, 1 from a fall (the pregnant ewe) and the other from Pasteurella- induced pneumonia. Coyotes killed a radio-collared ewe at DUC. Fifteen adult ewes were monitored for an average of 1.84 years, yielding an average annual adult ewe mortality of 10.8%.

Parasites

Mean monthly lungworm larvae per gram dried fecal material for adults ranged from 279 in February 1992 to 24 in July 1991 at DUC. Lungworm levels were higher at MAR ranging from 1,811 in November 1991 to 60 in August 1990. Lungworm larvae in lambs at MAR ranged from 0 in October 1991 to 571 in August 1991. Lungworm infestation rates at NLR were 1,166 larvae per gram in April 1991 and 26 in August 1990. Lungworm larvae in lamb feces from NLR ranged from 0 in August 1991 to 294 in January 1990. Seasonal lungworm infection rates for the Laramie Peak sheep herd were higher than levels reported from herds in other parts of Wyoming (Table 2).

Spatial and Temporal Overlap

Bighorn sheep ewes used the Duck Creek riparian zone and adjacent canyon walls extensively during April-June (Fig. 2). Bighorn sheep ewes were not found in or near the Duck Creek riparian area during July (Fig. 3). From August to September, bighorn sheep ewes again used the riparian zone and canyon walls extensively (Fig. 4). Bighorn sheep seasonal diet composition shifted from grasses and forbs in April-June to bitterbrush (Purshia tridentata) browse in July and back to grasses and forbs in August-September. Cattle used the Duck Creek and Ashley Creek riparian zones exclusively while on the allotment in July. Cattle were not observed grazing up the slopes of the canyon walls.

Forage utilization by cattle in the Duck Creek riparian zone indicated moderate to heavy grazing. Forage removal was 66% in 1989, 52% in 1990, and 57% in 1991. Pre-turnout utilization was 51% in May 1992 compared to 15% in May 1991.

Small bands of 15 to 75 domestic sheep (Ovis aries), occurred within 1.0 km of most of the subherds of the Laramie Peak bighorn sheep herd. At MAR, a flock of domestic sheep occupied range frequented by bighorn sheep.

Radio-collared ewes at DUC used the Duck Creek riparian area extensively during April-May, June, and August-September. These ewes were not observed in that riparian zone during July, 1991. Winter distribution of sheep at DUC was more dispersed than at any other time of year.

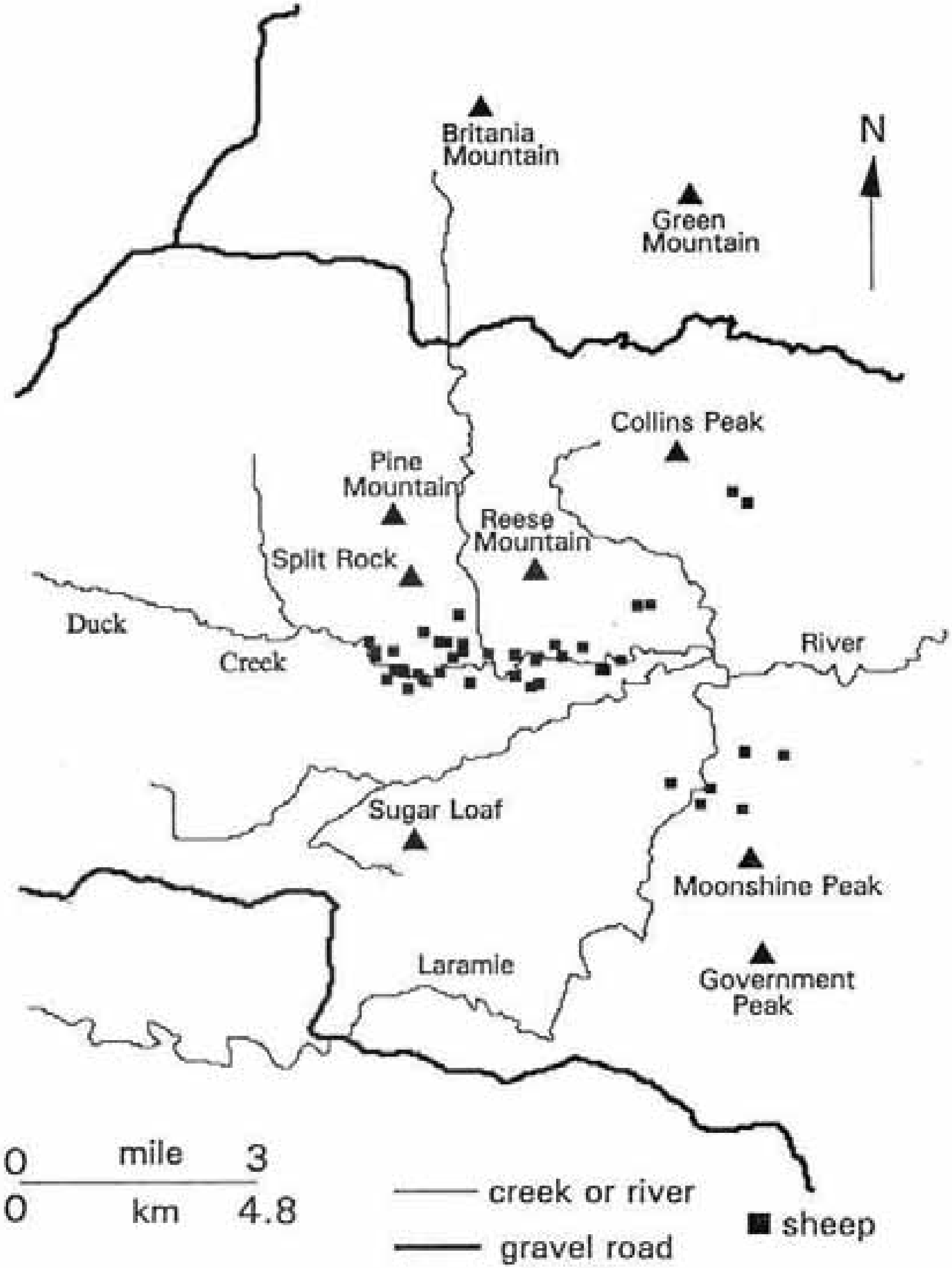

Fig. 2. Distribution of radio-collared sheep ewes and associates in the Duck Creek subherd near Laramie Peak, Wyoming, April-June 1990-92.

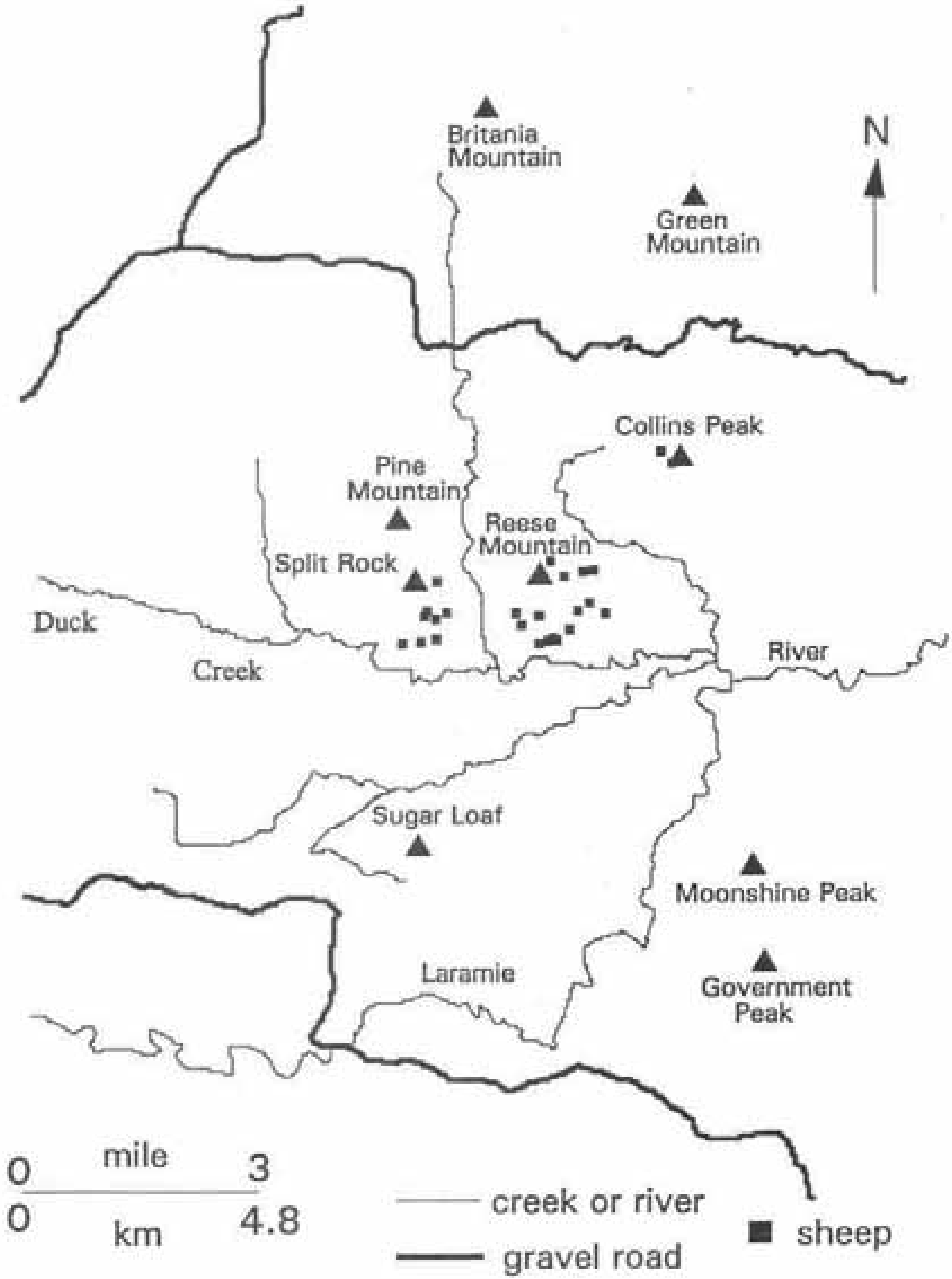

Fig. 3. Distribution of radio-collared bighorn sheep ewes and associates in the Duck Creek subherd near Laramie Peak, Wyoming, July 1989-91.

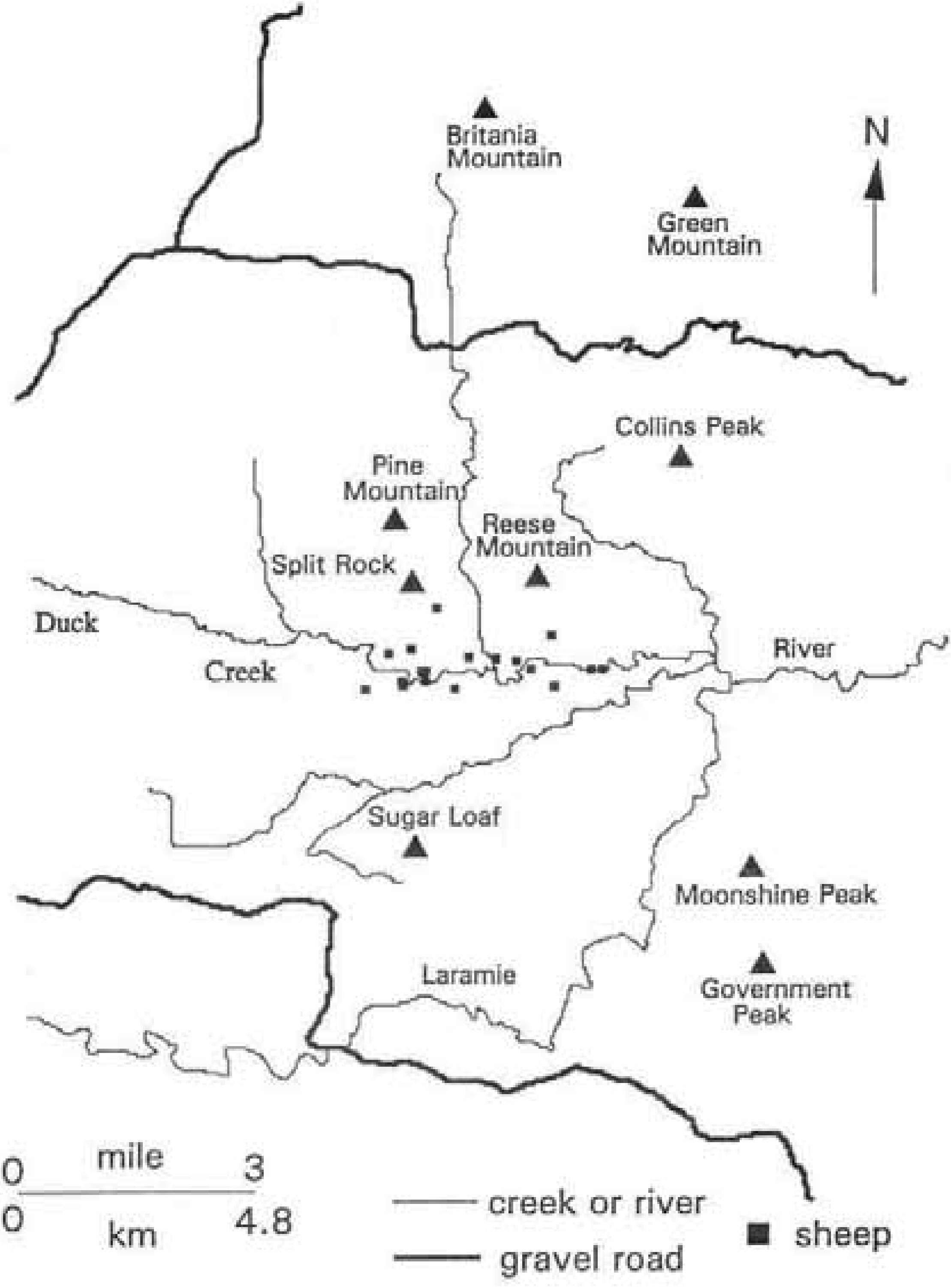

Fig. 4. Distribution of radio-collared bighorn sheep ewes and associates in the Duck Creek subherd near Laramie Peak, Wyoming, August-September 1989-91.

DISCUSSION

Variation in productivity among the subherds could have been due to available forage. For example, bighorn sheep in the MAR subherd had access to irrigated meadows. These meadows provided lush forage during hot summer months. Sheep in the NLR subherd had access to large alfalfa fields, while sheep at DUC did not have access to irrigated meadows or alfalfa fields, but had access to riparian vegetation. Sheep at DUC used springs and seeps on the higher slopes of Reese Mountain and Split Rock if other forage was not available.

Ewes at NLR had higher lambing rates and higher lamb survival than ewes in the Marshall or Duck Creek subherds perhaps due to the higher quality alfalfa diet. Lambing rates and survival were higher in 1991 than the previous 2 years due to increased forage from heavy summer rains. Over 20.3 cm (8 in.) of rain fell in the Duck Creek area from 15 May to 15 June 1991. Another 6.9 cm (2.7 in.) fell on 24 July 1991. Increased forage production due to above average rainfall could have been responsible for the increased lamb recruitment in winter 1991. High lamb:ewe ratios in 1989 at MAR were probably due to release of 9 adult ewes and 5 lambs from the Whiskey Mountain herd in January 1989. The ewes were likely pregnant prior to release. High yearling:ewe ratios at MAR during winter 1989 could also be attributed to the transplant.

Bighorn sheep ewes avoided the riparian zone of Duck Creek during July 1991 when cattle were present. Other studies indicate conflicts between bighorn and cattle for forage in Idaho (Anderson 1976) and British Columbia (Demarchi 1970). In Utah, desert bighorn sheep did not move into an area after it had been grazed by cattle (King and Workman 1984). When cattle grazed areas year-round, bighorn sheep avoided the areas (Bodie and Hickey 1980). Other studies concluded little overlap in distribution by desert bighorn (O. c. mexicana) and cattle or a social intolerance of cattle by bighorn sheep (Wehausen and Hansen 1986, Dodd and Smith 1988). Cook et al. (1989) found little impact on bighorn sheep grazing from livestock at Douglas Creek, Wyoming. Bighorn sheep that used Duck Creek when cattle were not present, avoided the area when cattle were present, and returned to the area after cattle were removed indicate a social intolerance to cattle. Our results show sheep were displaced to higher slopes that the cattle did not utilize. Because of displacement, lactating bighorn ewes were deprived of high quality forage found in the riparian zone. Cook et al. (1989) inferred that milk production by lactating ewes declines when forage quality decreases. Lamb survival was also reported to decline when ewes produce low levels of milk during July and August (Cook et al. 1989). Lamb survival declined during September at DUC.

Four trespass horses were confined to approximately 1.25 km (0.78 mi.) of the Duck creek riparian zone for 4 weeks in early 1992. This stretch of the Duck Creek riparian area was severely grazed when checked in May 1992.

A combination of factors appeared to control the Laramie Peak bighorn sheep herd. Lamb survival and recruitment could drop to levels that cannot maintain the herd if lactating ewes are unable to find high quality forage from riparian areas, alfalfa fields or irrigated meadows.

Although lamb productivity and yearling recruitment were variable among subherds, data for 1989-1991 suggest sufficient recruitment for the herd to maintain itself most years (Table 1). If adult mortality of radio-collared ewes is representative of this segment of the sheep population, then adult ewe mortality may offset recruitment.

Small isolated bands of ewes that were not bred indicated rams were few or could not locate ewes during the normal breeding season. Differences in available forage could explain variation in juvenile:adult ewe ratios between subherds. Alfalfa fields at NLR provided high quality forage for lactating ewes during late summer, when lamb:ewe ratios were 67:100 in 1991 (Table 1).

More important than high quality forage, small bands of domestic sheep occurred within 1.0 km of most of the subherds of the Laramie Peak bighorn sheep herd. Transmission of pathogens from domestic sheep to bighorn sheep has been implicated (Foreyt 1990, Foreyt 1992). Exposure of domestic sheep to bighorn sheep, permitting nose to nose contact has caused 100% mortality of bighorn sheep (Foreyt 1992). No amount of high quality forage will compensate for exposure to lethal pathogens. Bighorn sheep and domestic sheep are not compatible on the same range according to Foreyt (1992).

MANAGEMENT IMPLICATIONS

Disease and inadequate forage are major problems facing biologists attempting to manage the Laramie Peak bighorn sheep herd.

If habitat for bighorn sheep is the primary goal, and forage is a limiting component of the habitat, domestic livestock and horse grazing must be curtailed. A major problem for bighorn sheep in the Duck Creek subherd was displacement from an area containing high quality and quantity of forage at a time when lactating ewes were under nutritional stress. Appropriate fences or removal of livestock grazing are needed to resolve the problem.

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DECLINE AND HABITAT ABANDONMENT BY BIGHORN SHEEP ON BATTLEMENT MESA, COLORADO, 1906-1990

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Abstract: Bighorn sheep (Ovis canadensis) on Battlement Mesa, Colorado, numbered up to 250 animals in the early 1900's and declined to about 50 animals by 1970. Minimum herd sizes during 1989 and 1990 were 23 and 26, respectively, including 4 lambs each year. Since 1961, the herd has abandoned about 56 km^2 of historic range. The decline corresponded with probable vegetation changes on Battlement Mesa, intensive livestock grazing through the 1950's, reports of poaching and an increasing elk (Cervus elaphus) herd. Bighorn sheep remained on the western portion of the range during winter and spring, 1989. During dry months (Jul 89, Aug 89, Jun 90), sheep concentrated in Anderson and Durant Gulches near a free-flowing spring and seep. Bighorns on Battlement Mesa appear limited by dense mountain shrub stands that separate productive meadows from escape terrain and cover historic migration routes. In 1989-90, sheep remained mostly on shale slopes. Without intensive and long-term habitat management this small unique herd will remain static or decline.

In 1915 Colorado supported about 7,320 Rocky Mountain bighorns but by 1970, only about 2,200 remained (Bear and Jones 1973). Today there are approximately 6,100 sheep in 67 herds, including about 2,400 in transplanted populations (Bailey 1990). Many of these sheep are in small remnant herds intermittent throughout historic range. Herds that were not extirpated persisted in isolated or highly productive portions of their range. The bighorns of Battlement Mesa are a classic example of a remnant, isolated population. The Battlement Mesa bighorn sheep are 1 of 4 indigenous, low-elevation, herds remaining in Colorado (J. A. Bailey, Colo. State Univ., pers. commun.). Battlement Mesa is within the geographic range of desert bighorn (Ovis canadensis nelsoni) as reported by Manville (1985). It is not clear if Battlement Mesa bighorns should be considered O. c. canadensis or O. c. nelsoni. In 1988, information on the herd was limited to scattered Colorado Division of Wildlife (CDOW) aerial counts and hunter surveys, scattered United States Forest Service (USFS) reports, local newspaper clippings and knowledge held by local residents. A Colorado State University (CSU) internship project in 1976 (McGowan and Van Sant 1976) and an Environmental Assessment developed for the herd in 1986 (White River Wildlife Team 1986) provided the most current herd data. CDOW classified the herd as declining or static. Seasonal ranges and factors limiting the herd were uncertain. We initiated a research-descriptive study to gather data necessary to effectively manage thisunique herd. Pre-treatment data on numbers of sheep and areas of use were needed to measure post-treatment effects for any herd or habitat management that might be implemented.

Study objectives were to (1) develop an historic perspective of bighorn sheep on Battlement Mesa, (2) determine herd size and sex-age composition, (3) determine seasonal distributions, including lambing area(s), water sources, migration corridors, timing of major activities and movements including rutting (1989) and lambing (1989, 1990), (4) evaluate potential limiting factors, and (5) suggest management options.

This study resulted from cooperation among the White River National Forest (WRNF), Grand Mesa National Forest (GMNF), CDOW and the Rocky Mountain Bighorn Society (RMBS). J. Ellenberger, J. Frothingham, J. Broderick and A. Trujillo from the CDOW are thanked for their assistance. J. Grode, WRNF, is acknowledged for coordinating the USFS support. Numerous volunteers assisted with field data collection.

STUDY AREA

Battlement Mesa is located in northwest Colorado, approximately 80 km east of Grand Junction, and encompasses 96 km^2 on National Forest, Bureau of Land Management (BLM) and private lands (Fig. 1). The range crests northeast to southwest, with lands of the GMNF and BLM on the south slopes and WRNF on the north slopes. Elevations range from 1830 m at the west to 3337 m on North Mamm Peak. Bighorn sheep remain within about 40 km^2 on the west end of Battlement Mesa at elevations of 2040-2700 m (lower Battlement Mesa). There are 2 private inholdings within the range. Topography is characterized by steep south-facing cliffs with scattered shrubs, forbs, and grasses and steep north-facing slopes with forest and shrub communities.

Arid to sub-arid conditions exist at low elevations, especially on south-facing slopes. The highest elevations on upper Battlement Mesa are more moist. Lower Battlement Mesa receives 38.1-63.5 cm annual precipitation while upper Battlement Mesa receives 50.8-76.2 cm.

Lower Battlement Mesa has 5 major habitats: 1) pinyon pine (<u>Pinus edulis</u>)-juniper (<u>Juniperus osteosperma</u>) at lower elevations, 2) Douglas-fir (<u>Psuedotsuga menziesii</u>) on north-facing slopes at higher elevations and in draws, 3) mountain shrub, predominantly gambel oak (<u>Quercus gambelii</u>) and serviceberry (<u>Amelanchier alnifolia</u>) at middle to higher elevations, in draws and on dry sidehills, 4) aspen (<u>Populus tremuloides</u>) on north-facing slopes at higher elevations, and 5) fescue meadow (<u>Festuca thurberi</u>-<u>Festuca idahoensis</u>) at higher elevations on north facing slopes (White River Wildlife Team 1986). Shale slopes were considered a sixth habitat for analysis during this study. Upper Battlement Mesa has 3 major habitats: (1) fescue meadow interspersed with (2) aspen and (3) Douglas-fir.

Historically, rangelands on Battlement Mesa were overgrazed by both domestic sheep and cattle based on historic Forest Service reports (U.S. For. Serv. 1914-1990). Lower Battlement Mesa is presently divided among 3 allotments of which 1 is utilized by cattle on a 3-pasture

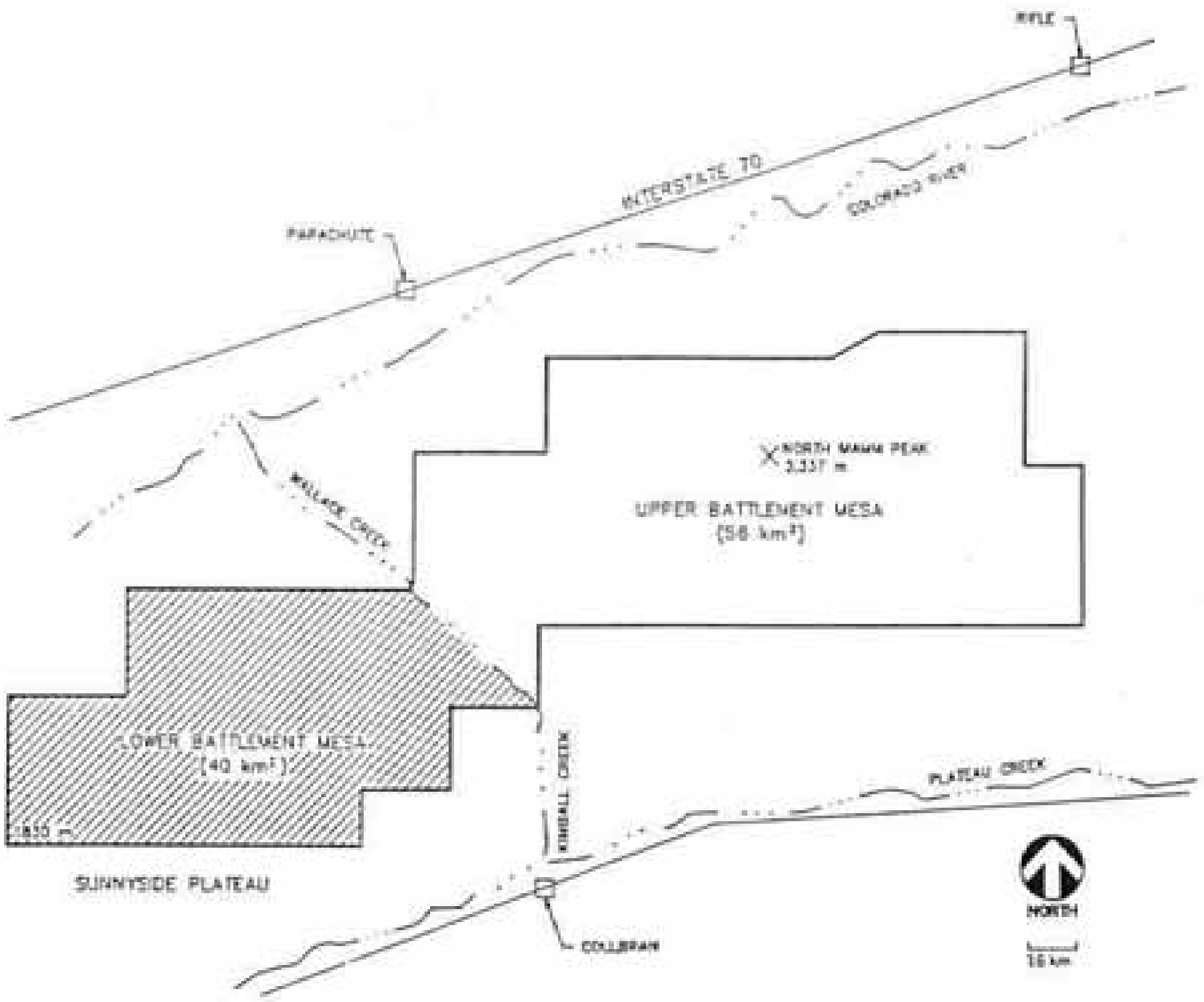

Fig. 1. Schematic diagram of Battlement Mesa, Colorado, depicting nearby towns, roads and important land features.

rotation system for 117 days from mid-June through mid-October. No livestock grazing occurs on the other allotments.

METHODS

Determining Current and Historic Bighorn Ranges

We determined present bighorn sheep range on Battlement Mesa from observations (1988-90) and by mapping reported sheep locations (1980-90). Seasonal range boundaries followed the lowest elevation contour recorded for locations during summer and winter, respectively. We searched CDOW, WRNF, GMNF files and local newspapers for information on historic bighorn sheep sightings and distribution to gain an historic perspective on the herd. We interviewed 13 local residents, including ranchers and outfitter-guides familiar with the area, for knowledge of past herd numbers and areas of use.

Historic migration routes were estimated from historic observations and the locations of potential sheep escape terrain. We estimated historic bighorn sheep summer range (upper Battlement Mesa) from past CDOW surveys, documents and from interviews. We searched these areas on 15 occasions in 1988-90, using fixed-wing aircraft and horses, to validate range abandonment.

Determining Herd Size and Sex-age Composition

We attempted to capture bighorn sheep for radio-collaring from 1988-90 (Cunningham 1991). Clover traps (Clover 1956) baited with alfalfa hay, apple pulp and salt were unsuccessful. One ewe, a 36 kg 2.5 year-old, was captured using a dart gun and fitted with a radio collar on 15 March 1989.

Intermittent observations of sheep began 5 December 1988, with intensive data collection occurring 3 January 1989 through 12 January 1990 and 5 June 1990 through 11 July 1990. We divided the suspected present range into 16 units to effectively search for sheep (Cochran 1977). We based unit boundaries on topographic features and the ability of field personnel to completely search a unit in 1-2 days. Sheep were located by (1) tracking 1 radio-collared ewe from the ground to obtain visual observations, (2) systematically searching the 16 units between 13 July 1989 and 27 October 1989 (4 complete searches) when all units were accessible, (3) fixed-wing and helicopter flights along predetermined routes, and (4) ground reconnaissance of the range. Located sheep were classified by sex and age (Geist 1971). When possible we determined percent slope with a clinometer. We tested the null hypothesis that there was no difference in use of slope categories between uncollared and radio-collared groups of sheep with the Chi-square test for association (Steel and Torrie 1980). Maximum unduplicated counts of sheep in each sex-age class determined a known minimum population for 1989 and for summer, 1990.

Seasonal Ranges

We determined seasonal ranges by locating sheep in the 4 seasons based on forage phenology: (1) spring (16 Feb-30 May), (2) summer (1 Jun-30 Sep), (3) fall (1 Oct-15 Nov), and (4) winter (16 Nov-15 Feb) (Dale

1987). We monitored movements by the radio-collared ewe and by other identifiable sheep and inferred migration corridors within the present sheep range. We located potential lambing areas based on the lambing-area requirements of desert bighorn sheep because of the similarities between the present sheep range and desert environments (Bear and Jones 1973, Hansen 1985). We located ewes with lambs <2 months old to define and map present lambing areas. We determined rutting periods and rutting range by observing sheep behavior, changes in group composition, and locations during the fall.

Determining Potential Limiting Factors

We investigated factors affecting the Battlement Mesa bighorn sheep for the past 75 years and analyzed data from 1988-90, to identify potential limiting factors. Literature revealed factors limiting or adversely affecting other Rocky Mountain and desert bighorn sheep herds: (1) habitat, (2) diseases and parasites, (3) predation, (4) conflicts with elk, deer and livestock, (5) hunting and poaching, (6) exotic free-ranging ungulates, and (7) limited summer water supply. "Potential" is the key work in this summary of limiting factors. Unless a factor postulated as limiting to a herd of sheep is manipulated and a treatment and control group of animals defined, we cannot demonstrate the factor is indeed limiting. Each of the above factors were evaluated for their potential in limiting the Battlement Mesa bighorns.

Habitat.--We measured the area available to sheep for each of the 6 habitat types within the present range from USFS Resource Information System maps (U.S. For. Serv. 1986). Randomly selected sites were ground-truthed to confirm habitat types. We tested the null hypothesis that bighorn sheep use the available habitat on Battlement Mesa in proportion to the availability of each habitat type with the Chi-square goodness-of-fit test (Neu et al. 1974, Steel and Torrie 1980). We developed a preference index for each habitat type by dividing the proportion of observations within a habitat type by the proportion of that habitat type within the available study area. Preference and avoidance refer to the likelihood that a habitat will be selected more or less frequently than predicted based on availability (Petrides 1975, Thomas and Taylor 1990).

Other potential limiting factors.--We collected 9 fresh bighorn sheep fecal samples between January 1989 and April 1989. Samples were analyzed for lungworm larvae (Protostrongylus sp.) at the CDOW Research Laboratory, Fort Collins. Nasal swabs and skin scrapings from the captured ewe were analyzed for incidence of the Psoroptes mite or other external parasites. We recorded any clinical signs of pneumonia in observed sheep and recorded observations and sign for predators, elk, mule deer (Odocoileus hemionus) and cattle on lower Battlement Mesa. We summarized CDOW bighorn sheep harvest records for the herd between 1960 and 1982, interviewed long-time residents of the area and investigated reports of poaching incidents. We documented all reports of exotic, free ranging ungulates in the area, all water developments, and permanent water sources for sheep on the present range.

RESULTS

Systematic Searching and Opportunistic Observations

Between 5 December 1989 and 28 June 1990, we observed uncollared groups of sheep on 84 occasions and groups of sheep with the radio-collared ewe on 21 occasions. We observed sheep 14 times during 4 systematic searches of study area units between 12 July and 16 November 1989 (included in 105 total).

Bighorn Range

Current range.--The current range of bighorn sheep on Battlement Mesa is approximately 40 km^2, including summer and winter ranges. Observations during 1988-90 revealed 2 overlapping seasonal ranges and 1 migration corridor (Fig. 2). Mature rams were scattered over a larger area than were ewe-juvenile groups, which remained concentrated during lambing seasons and for most of the summers in Anderson and Durant Gulches.

Sheep remained on the west end of the range from December 1988 to May 1989 at elevations of 2073-2400 m. From April to July 1989, sheep migrated to summer range at 2340-2700 m. Observations between January and July 1990 revealed seasonal ranges similar to those recorded in 1989. Migration to lambing and summer range during 1990 occurred from 15 May to 28 June.

Historic range and herd size.--We observed no sheep or sheep sign during 8 searches of historic summer range on upper Battlement Mesa. We estimated historic range (including present range) at 96 km^2. On the upper Mesa, talus slopes, rock piles and cliffs occur in many areas adjacent to open meadows (potential and perhaps historic areas of sheep use) and there are numerous permanent water sources. All evidence suggests that bighorn sheep have abandoned this summer range, with no sheep observed since a sighting on Mamm Peak in 1961. Snow depth on upper Battlement Mesa may eliminate the possibility of sheep using the area in winter.

According to records and recollections of local residents, the herd numbered up to 250 animals in the early 1900's and declined to an estimated 50 animals by 1970. CDOW aerial and ground counts of sheep on Battlement Mesa from 1969-88 fluctuated widely with a general downward trend beginning in 1970. Search effort was not consistent over years and methods varied between helicopter counts and more intensive, though less extensive, ground counts. Agency records, newspaper articles and interviews also documented (1) 4 historic low-elevation bighorn herds within 19-74 km of Battlement Mesa, (2) alleged poaching and predation incidents, and (3) changing vegetation on Battlement Mesa, from 1906-88 (Cunningham 1991).

Habitat Use

Sheep used 3 of the 6 habitat types on lower Battlement Mesa in 73 observations of uncollared sheep and 21 observations of the radio-collared ewe and her group (Tables 1, 2). They used shale slopes with scattered

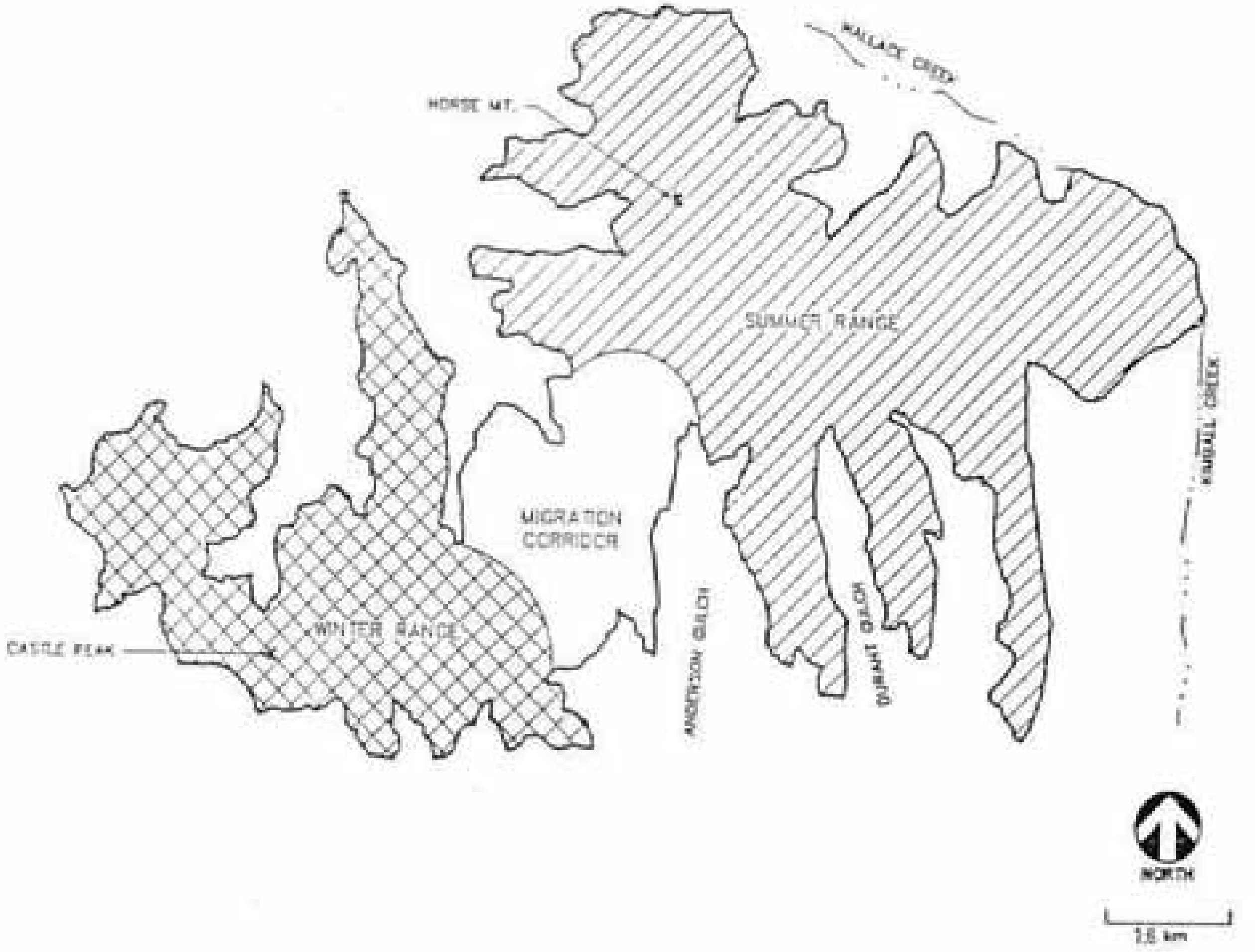

Fig. 2. Seasonal home ranges and migration corridor used by bighorn sheep on lower Battlement Mesa, Colorado, 1989-90.

grasses, forbs, and shrubs most of the time. We never observed sheep in nearby meadows that were separated from shale slopes by stands of mountain shrubs or aspen. Sheep were found in open Douglas-fir stands (<20% canopy cover) on south slopes on 2 occasions. These stands were adjacent to a shale slope and the sheep never ventured more than 30 m from escape terrain. Pinyon-juniper habitat was used by uncollared sheep during winter and spring when sheep were at lower elevations where this habitat was more available.

Table 1. Use of habitat types by uncollared bighorn sheep in 73 observations on Battlement Mesa, Colorado, 1989-90.

Habitat type	Hectares available		Bighorn observations[a]
	Hectares	(%)	(% of 73)
Pinyon-juniper	2320	38	12.3
Mountain shrub	1366	22	0.0
Douglas fir	1335	22	1.4
Shale slope	713	12	86.3
Aspen	303	5	0.0
Meadow	49	1	0.0

[a] $\chi^2 = 381.1$, $P \leq 0.001$; based on observed numbers of observations in each habitat type vs. expected numbers calculated from habitat composition.

Table 2. Use of habitat types by collared bighorn ewe in 21 observations on Battlement Mesa, Colorado, 1989-90.

Habitat type	Hectares available		Bighorn observations[a]
	Hectares	(%)	(% of 21)
Pinyon-juniper	2320	38	0.0
Mountain shrub	1366	22	14.3
Douglas fir	1335	22	4.8
Shale slope	713	12	81.0
Aspen	303	5	0.0
Meadow	49	1	0.0

[a] $\chi^2 = 96.6$, $P \leq 0.001$; based on observed numbers of observations in each habitat type vs. expected numbers calculated from habitat composition.

The observations (73) of uncollared sheep emphasized slopes >200% while observations of the radio-collared ewe (19 with slope category recorded) were more often on slopes 51-100% (Table 3). Use of slope categories was not significantly different between the 2 groups. When sheep were not observed on slopes >200%, distance to escape terrain averaged 6.1 m for uncollared sheep and 35.6 m for the radio-collared ewe.

Table 3. Steepness of terrain used by bighorn sheep in 73 observations of uncollared sheep and in 19 observations of a radio-collared ewe, Battlement Mesa, Colorado, 1989-90.

Slope category (%)	Observations (% of total)[a]	
	Uncollared (73)	Radio collared ewe (19)
0-50	4	5
51-100	23	37
101-150	21	32
151-200	4	5
>200	48	21

[a] $x^2 = 4.59$; $\underline{P} \geq 0.05$

Rutting, Lambing, and Population Size

Rutting behavior was observed during November-January on both summer and winter ranges. Lambing occurred on summer range with estimated dates of birth from 15 April through 25 June during both 1989 and 1990 (Cunningham 1991).

The known minimum population of sheep during 1989 was 23 individuals including 4 1989 lambs, 3 yearlings, 7 adult ewes and 9 adult rams. Less search time and a restricted search area during 1990 leaves no doubt sheep were missed. The known minimum population of sheep during summer 1990 was 18, although 26 is a more likely number assuming no loss in any age classes between December 1989 and June 1990, except for 1 lamb not observed after August 1989. Four lambs were observed in 1990. Based on known minimum numbers of ewes, lamb:ewe ratios were 57:100 and 50:100 in 1989 and 1990, respectively.

Potential Limiting Factors

Habitat.--Bighorn sheep did not use habitats in proportion to their availabilities on Battlement Mesa and emphasized use of shale slope habitat (Tables 1, 2). This suggests they were selecting the most secure habitat on or near escape terrain, and avoiding less secure, but more productive, foraging areas. Preference-avoidance indices for both uncollared and radio-collared sheep support these results (Table 4).

Table 4. Preference indices for 6 habitat types available to bighorn sheep on Battlement Mesa, Colorado, 1989-90.

Habitat Type	Preference Index[a]	
	Uncollared sheep (N = 73)	Radio-collared (N = 21)
Pinyon-juniper	0.3	0.0
Mountain shrub	0.0	0.6
Douglas fir	0.1	0.2
Shale slope-cliff	7.2	6.8
Aspen	0.0	0.0
Meadow	0.0	0.0

[a] Proportion of observations within a habitat type divided by proportion of that habitat type within the available study area.

Other potential limiting factors.--Three of 9 bighorn sheep fecal samples had low incidences of *Protostrongylus* larvae (0.4-8.6/g). The remaining samples were negative. No die-offs or clinical signs of pneumonia were recorded. No parasites were recovered from swabs or scrapings from the radio-collared ewe. Contact between bighorn and domestic sheep probably occurred in the early 1900's when up to 40,000 domestic sheep grazed in the area. Chances for disease transmission were presumably high, but no records of die-offs were discovered.

Evidence of predation was limited to finding 3 decayed lamb skulls. One skull had punctures on the cranium, indicating mountain lion (*Felis concolor*) predation. Reports of alleged lion predation on the sheep have occurred since 1927.

On Battlement Mesa, elk, mule deer and bighorn ranges overlap throughout the year, but especially in winter on the western portion of the bighorn range. CDOW trend counts indicate elk numbers increased substantially on Battlement Mesa from 1973-89. There was no range overlap between bighorn and cattle during 1989-90. Exotic ungulates occurred in 3 areas, 3.2-19.3 km from the present bighorn range.

Hunting for bighorn sheep occurred from 1960-82 when 121 licenses were issued and 17 rams harvested. The area was closed in 1982 due to suspected low numbers of sheep and hunter complaints of seeing few or no sheep. Five of the 13 residents interviewed knew of sheep poaching incidents.

We found 12 springs and seeps on lower Battlement Mesa. One guzzler and 3 redwood tanks were installed on or near the sheep range in the early 1980's, but 3 sites were outside of the present range. The tanks were either destroyed, not holding water, or required maintenance. We observed no sheep sign at 3 of the water development sites. The destroyed site, which contained a natural pool, had sheep sign.

DISCUSSION

Historic Perspective on the Herd

All evidence indicates that the Battlement Mesa bighorn sheep herd once was larger and occupied a larger range. The herd migrated farther to summer range and wintered at lower elevations adjacent to the present winter range. Local residents reported changing vegetation on Battlement Mesa, indicating that more oakbrush and heavy timber are present in the area today. Battlement Mesa bighorns abandoned historic summer range about 30 years ago and today occupy about 42% of the historic 96 km^2 yearlong range. The present summer and winter ranges have similar vegetation, but no water sources occur on present winter range.

Wallace Creek and Dry Kimball Creek, north and east, respectively, of present sheep range, are likely historic migration routes based on historic sheep observations and topography. These drainages are dominated by dense shrubs, a habitat avoided by Battlement Mesa sheep. Beyond these migration routes, historic summer range still has escape terrain adjacent to permanent water and productive foraging areas with little visual obstruction. Abandonment of this summer range was verified during 1989-90. Range abandonment, decline of sheep numbers and the general decline of herd quality on this isolated range, have coincided with habitat change. Expansion of dense shrub vegetation was presumably due to historic overgrazing by livestock and curtailment of wildfire for over 60 years. Other factors that may have contributed to herd decline are considered less important in limiting the herd today (Cunningham 1991).

Present Condition of Battlement Mesa Bighorn Sheep

Lamb:ewe ratios on Battlement Mesa (0.57 and 0.50 in 1989 and 1990, respectively) were not unusual for bighorn herds. Ratios vary greatly among and within herds (Goodson 1978, Turner and Hansen 1985). This variation has been attributed to population density, forage quality (Geist 1971) and possibly to degree of inbreeding (Skiba and Schmidt 1982). Goodson (1978) concluded that yearling:ewe ratios, not lamb:ewe ratios, have been correlated with herd trends. The yearling:ewe ratios at Battlement Mesa (0.41 and 0.38 in 1989 and 1990, respectively) were similar to those reported for "slowly increasing" herds (Goodson 1978). However, given the small number of sheep at Battlement Mesa, herd increase cannot be predicted as loss of one yearling (or ewe) would alter the ratio greatly.

The Battlement sheep exhibited 2 characteristics that Geist (1971) considered common in low quality bighorn herds with static or declining population size. These are (1) small body size, and (2) tightly curled horns. The 36 kg ewe captured on Battlement Mesa appeared similar in size to her associates. In contrast, Hansen (1985) estimated the average desert bighorn ewe at 47 kg. Risenhoover and Bailey (1988) reported an average weight of 66.4 kg for ewes at Waterton Canyon, Colorado and Blood et al. (1970) estimated the average Rocky Mountain bighorn ewe at 72 kg.

Rams harvested from the Battlement herd also exhibited small body size and small horns (John Ellenberger, Colo. Div. of Wildl., pers. commun.).

Geist's "dispersal theory" (1987) links herd quality to the duration of available green forage, which is enhanced when animals migrate altitudinally. On Battlement Mesa, loss of migration and consequent loss of summer ranges, has reduced the duration of access to green forage. On habitats preferred by Battlement sheep (shale slopes), green forage is scarce, sparsely distributed, and available only briefly each year. On present summer range, forage options are limited to true mountainmahogany (Cercocarpus montanus), bitterbrush (Purshia tridentata), Indian ricegrass (Oryzopsis hymenoides) and scarce forbs and other grasses near permanent water sources. A few small meadows occur on summer range but are separated from sheep escape terrain by barriers of dense shrubs. On historic summer range, shrub types are absent and meadows are dominated by Idaho and Thurber fescue, Kentucky bluegrass (Poa pratensis), other grasses, and several species of forbs.

Battlement sheep must have been primarily grazers during summer on historic summer range. Today their summer diet is dominated by shrubs. The loss of grasses from the diet may have caused natural selection to favor the smaller-bodied animals; or the current small size of Battlement sheep may be a phenotypic response to limited forage resources. Productivity of the herd may also be limited by quantity and quality of forage.

CONCLUSION

Currently, the Battlement Mesa bighorn herd is limited in distribution, herd size, and perhaps in animal quality. The strongest evidence indicates that habitat change, especially the expansion of dense shrub vegetation, has influenced the decline of Battlement Mesa bighorn, and that habitat conditions limit the herd today. This evidence includes coinciding changes in habitat and herd decline with range abandonment, the current non-use of excellent foraging areas surrounded by barriers of dense shrubs, and the use restricted primarily to secure habitats with good visibility. As a case study, the Battlement herd illustrates trends that Wakelyn (1987) concluded have been common in Colorado. Habitat improvement, including reduction of shrubs, will be necessary to restore this unique herd (Risenhoover and Bailey 1988, Cunningham 1991). A 4-phase management plan for the Battlement Mesa herd is proposed by Cunningham (1991).

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CRITIQUE OF CARRYING CAPACITY CONCEPTS CONCERNING DALL SHEEP

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Abstract: The classic concept of nutritional carrying capacity tends to complicate management of Dall sheep (*Ovis dalli dalli*) populations because they often exist at relatively constant population sizes over extended periods. The fundamental axiom taught in the wildlife management curriculum is that population growth will follow the logistic curve until it reaches or exceeds carrying capacity where further growth is limited by nutritional constraints. A common extension of this is concept is that any numerically static population has reached nutritional carrying capacity. Obviously, Dall sheep populations grew to present-day levels by overcoming environmental resistance until the equilibrium we typically observe in continental climates was established. Hence, managers reason that lowering population density will result in compensatory increases in productivity, recruitment, and individual growth as the population tries to reach carrying capacity again. However, in northern ecosystems with abundant predators, environmental resistance resulting from non-nutritional causes is highly dynamic, and probably more influential than density-dependent nutritional constraints in limiting population growth. This calls the fundamental axiom and its commonly assumed postulate into question. It is important for managers to recognize this confusion because managed cropping mortality of a population limited by density-dependent nutritional constraints may result in compensatory increases in productivity or growth as the axiom predicts. However, managed cropping mortality in a population limited by non-nutritional environmental resistance will be additive. The former cropping scheme will not lower population size or productivity; the later will.

When articulating the working hypothesis of Dall sheep management (Heimer 1988), I stated that Dall sheep should not be expected to show explosive population growth, and that we should anticipate relative stability in population size over time. This hypothesis was based on the conclusion that Dall sheep are adapted to continuous use of climax vegetative systems. Adaptation to a stable food source (in contrast to the cyclically transient forage bonanzas which occur in successional habitats) should confer no selective advantage for nutrition-mediated increases in reproduction such as the multiple births or accelerated sexual development seen in seral-adapted species such as moose (*Alces alces*) and deer (*Odocoileus* spp.) under ideal conditions.

Dall sheep populations which exhibit relatively consistent sizes, particularly where sheep densities are high, have often been assumed to be at nutritional carrying capacity. This conclusion has typically resulted from the assumptions which underlie the carrying capacity theory. Population reduction, the classic management action suggested by this conclusion, is risky. If the assumptions and conclusions are correct, managers succeed; if not, they fail. Hence, understanding our general thinking and its relevance to specific situations has significant management implications.

Review of Dall sheep adaptations to their environment, as well as awareness of their specific ecological relationships, will show that assuming populations of Dall sheep are at carrying capacity because they exist at relatively static population sizes is not dependable. The purposes of this paper are to identify general adaptations of Dall sheep, to discuss specific biological findings about Dall sheep, and to highlight the likelihood of incorrect reliance on classic population "symptoms" to diagnose nutritional limitation. Clearly, management actions are recommended as results of diagnosis by managers. Hence, incorrect diagnosis may lead to inappropriate management actions. An alternate approach to management will be offered.

METHODS

The common, operational understanding of carrying capacity theory and its underlying assumptions were assessed by interviewing wildlife managers and hunters over the last 15 years. Literature relevant to Dall sheep population adaptations as well as their autecological relationships to classically defined symptoms of nutritional carrying capacity constraint were also reviewed. Findings were related to the prevailing interpretations of the carrying capacity model as assessed by the interviews.

RESULTS

The Carrying Capacity Model

About 15 years ago, I began to question the relevance of carrying capacity theory to management of Dall sheep in intact ecosystems (ecosystems where natural predators still exist). At that time, I began to raise the question with working wildlife managers and hunters. I interviewed managers because most approach management from this perspective. I interviewed hunters because they are commonly taught to use carrying capacity in their justifications for hunting. Whatever the original and true intent of the carrying capacity model may have been, the common understanding among those I interviewed was as follows.

The carrying capacity model is commonly expressed as a plot of population size over time (Fig. 1). It is based on several assumptions. These include:

1. Range resources are fixed and finite while ungulate populations are dynamic and capable of outgrowing their food supply.
2. When ungulate populations reach a certain size or density, access to nutritional resources becomes an inverse function of the number of animals present in the population, i.e. the higher the number of animals, the lower the per capita food.

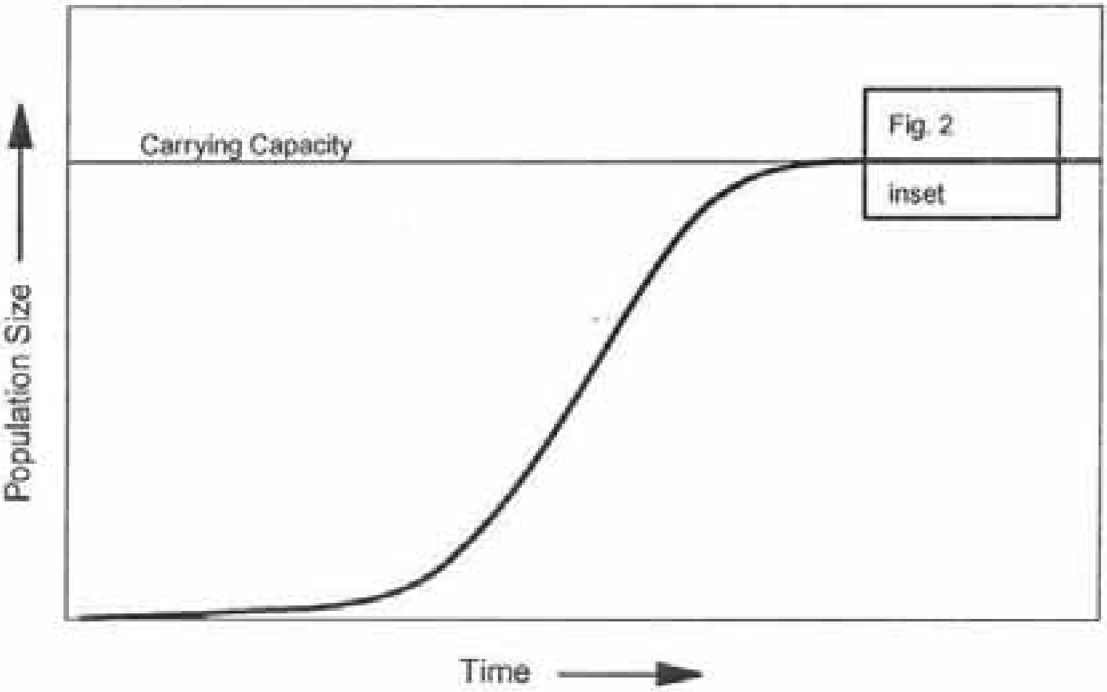

Fig. 1. Classic logistic growth curve.

3. A result of this inverse function is a symmetrical second degree polynomial we call the logistic growth curve. It predicts that population size in a "new" population will increase geometrically until food becomes limiting. Then the rate of increase will slow, initially to linearity, and eventually approach a "zero growth" asymptote when food resources can no longer support higher population numbers.

4. The asymptotic population size defines nutritional carrying capacity.

5. Populations always strive to reach carrying capacity.

Alternately, in temperate or sub-tropical climates where predators are absent, environmental resistance may be so low that introduced populations reach a level greatly above carrying capacity. This overpopulation may then result in a nutrition-mediated population crash. As a result of overgrazing which occurred when the population was above carrying capacity, habitat is presumably damaged; and the post-crash population size is projected to stabilize at a lower nutritional carrying capacity (Caughley 1970).

Dall Sheep Adaptations and Autecology

Dall sheep exhibit relatively slow population increases compared with seral-adapted ungulate species. In spite of observations of aloemothering (Hoefs 1978), multiple births are unknown in Dall sheep.

With respect to their relatively small body size, onset of reproductive activity among Dall ewes is typically delayed--to 3 or 4 years of age. However, this delay is not a result of delayed ovulation resulting from poor nutrition but of delayed breeding (Heimer and Watson 1986a,b).. Available data show Dall ewes uniformly ovulate at 18 months in the wild (Heimer and Watson 1986a, b, Nichols 1972) and in captivity (R. Bullerman, Milwaukee County Zoo, P. Smith, Denver's Zoo pers commun.). In captivity ewes typically breed at 18 months and have their first lamb at 24 months of age (Heimer and Watson 1986a). However, in the wild Dall ewes normally don't deliver their first lambs until age 3 or 4 years (Bunnell and Olsen 1981, Heimer and Watson 1986a). In unusual circumstances associated with a scarcity of mature rams (which is frequently the case in zoos), a significant percentage of ewes breed at 18 months and have their first lamb in the wild at 2 years of age (Heimer and Watson 1986a).

In addition, mortality during the first year is typically high for Dall lambs, averaging about 40% in measured herds, (Murie 1944, Deevey 1947, Heimer and Watson 1986a). Dall sheep live in hazardous ecosystems where unfavorable weather, snowslides, falling rocks, and falling sheep combine with full compliments of predators to produce formidable environmental resistance to population growth. This environmental resistance is variable, but when coupled with comparatively low, climax-adapted fecundity it appears to have resulted in populations which tend toward slow growth or maintenance.

I previously suggested (Heimer 1988) nutritional limitations are more probably produced by a "bottleneck" in winter food quality than by chronically insufficient forage quantity or compromised food quality resulting from overgrazed ranges. Summer food quality and abundance are very high (Whitten 1975, Winters 1980). Conversely, winter food is of such uniformly poor quality (Heimer 1983) that slow passage rates through the digestive tract probably limit the ability of Dall sheep to gather energy. Hence, Dall sheep lose weight during winter (Heimer 1983). I think it follows that these circumstances result in a relative abundance of low quality food being available under normal winter foraging conditions. If so, the number of individuals on winter range is not critical as long as there is enough low quality food to keep each rumen filled and functioning.

Still, sheep show greater mortality during (Watson and Heimer 1984), and lower productivity after (Heimer and Watson 1986b) winters with deep snow accumulation than they do when winters are less severe. This is probably because lighter snow interferes less with access to the higher quality food plants which occur on the lower fringes of their ranges (Heimer 1983). Severe winters preclude access to these more nutritious plants by confining sheep to windblown ridges throughout winter and delaying their access to high quality forage at lower elevations during late winter and early spring. Hence, at observed population levels, winter severity should be expected to influence population productivity and survival more than does sheep density. Even crowded populations (where the quantity of forage is most likely to be limiting) produce spectacularly high lamb:ewe ratios when environmental conditions are favorable (Heimer and Watson 1986b, F. Mauer, USFWS, pers. commun.). That is, when environmental resistance is transiently lowered, populations which otherwise appear to be at carrying capacity produce lambs at the rate of 70 to 85:100 ewes instead of their usual 30-40.

Further confounding the definition of carrying capacity for Dall sheep is the demonstration that several classic indicators of nutritional insufficiency in other species are mimicked by unusually low ram abundance and the accompanying distortions of ram age and social structures (Heimer and Watson 1986a). These symptoms appear in populations where ram age structure is radically skewed toward young rams. In 1980, I raised the question of whether population quality (Geist 1971), then considered a function of food quality, was a result of nutrition or other factors (Heimer 1980). Subsequently, Sarah Watson and I (Heimer and Watson 1986a,b) demonstrated that several classic indicators of nutritional carrying capacity were more rationally attributable to behavioral than nutritional factors. These indicators included low lamb production (Heimer and Watson 1986b), low ovulation rates (Heimer and Watson 1986a), and low ram survival (Heimer et al. 1984). We now have data that suggest even ram horn growth may be compromised by these conditions (Heimer unpubl. data).

DISCUSSION

Reviewing the suite of evolutionary adaptations and the specific autecology of Dall sheep reveals an almost bewildering array of circumstances which may conspire to produce relatively unchanging population sizes. Still, high Dall sheep densities, and relatively static population sizes, have led many managers to suppose Dall sheep populations typically exist at or above nutritional carrying capacity. Extending the density-dependent assumptions of nutritional limitation, which derive from the carrying capacity model, typically leads managers to 1 of 2 conclusions.

The first is that sheep populations are "too high" for their food resource, and that any decrease in population performance is an indicator of insufficient nutrition. Based on these assumptions, managers frequently suggest reducing the number of sheep will increase the amount of food available to each remaining sheep. Hence, as a result of increased food availability, each survivor will eat better. The cumulative result of better _per capita_ nutrition will be a collective increase in population productivity and growth.

The second conclusion is that because Dall sheep populations are at or above carrying capacity, and because the carrying capacity model stipulates populations will always grow until constrained by density-dependent nutrition, any reduction (below carrying capacity) will result in sustainable production of a harvestable surplus as the population tries to return to carrying capacity. It is assumed that this surplus will be produced annually, and that the population will be stabilized below carrying capacity by annual removal of this surplus. In this scenario, it is assumed that reducing the population to generate the surplus and then removing it annually will become stable and manageable, limiting components of environmental resistance.

However, if Dall sheep populations, or populations of other ungulates, are already being held below carrying capacity by cumulative environmental resistance, density dependent nutrition should not be a factor. When this is so, managers should not expect downward adjustment of population size by managed cropping to produce the theoretically expected increases in productivity and growth. Instead, cropping should be expected to lower population size because the increased mortality (which would be expected to stimulate productivity in a population limited by density dependent factors) will be additive, not compensatory. Continued cropping will, in all likelihood, result in continued population declines.

Kuck (1980) reported carefully managed cropping of female mountain goats (_Oreamnos_ _americanus_) in Idaho produced this exact result. This experience, and the arguments presented here suggest managers should critically evaluate their assumptions with awareness of adaptations common to K-selected species before applying carrying capacity theory to climax-adapted species. Similarly, managers should be careful when assigning causes to changes in population performance and status.

Even climax-adapted species selected for population stability or maintainence, like Dall sheep, exhibit population fluctuations about the stable level or "asymptote" (Figs. 1 and 2). Consequently, it may be productive for Dall sheep managers, or managers of other ungulates which do not exhibit radical, density-dependent "boom and bust," cycles, to

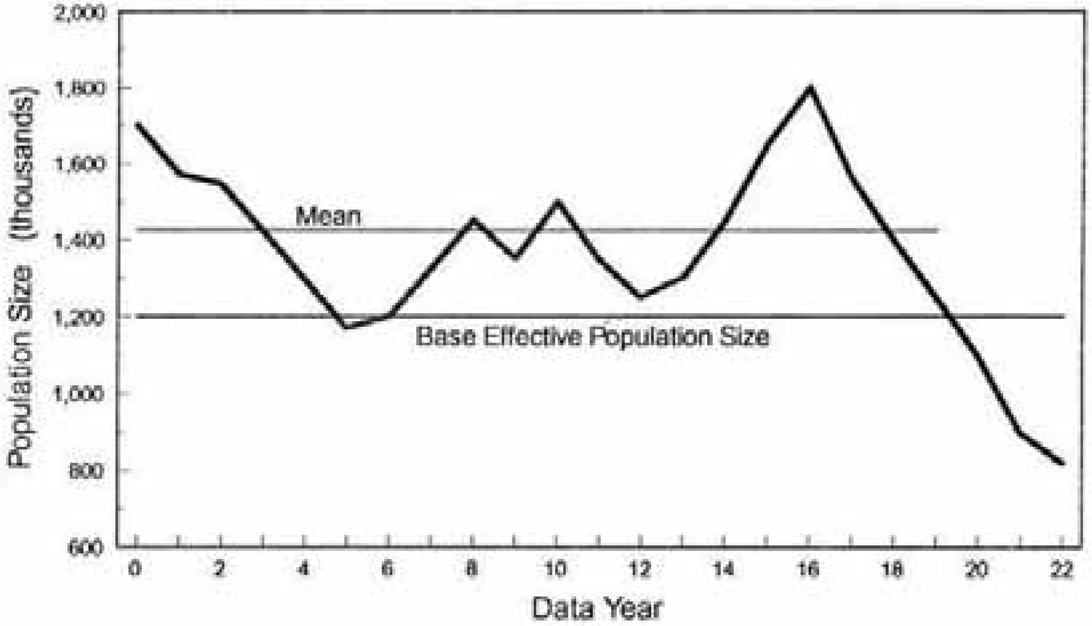

Fig. 2. Stylized population size modeled from Dry Creek, Alaska Range.
(Greatly magnified from Fig. 1.)

reconsider the causes and biological significance of population size fluctuations. I suggest that we consider the notion of "base effective population size" as the relevant population statistic rather than mean population size (Fig. 2).

Variations in environmental resistance produce the observed variations in population size through a variety of mechanisms. Given a data set with fluctuations over time, our natural inclination is to draw a line through the middle with positive and negative fluctuations about the mean (Fig. 2). However, if we consider the typical lower level reached by population size fluctuations as the base effective population, and any fluctuations above this line as results of transient decreases in environmental resistance, management is simplified.

Setting population objectives at the base effective population offers practical advantages not available when the mean population size is used to define the population size objective. If a manager selects the mean, the population objective will not be met about half of the time. That is, the population objective will not be obtained whenever population size is below the mean. Hence, the manager will face uncertainty about whether corrective management actions are appropriate. This will not be a problem if the population objective is set at base effective size.

When populations are above base effective population size, managers must monitor; but need not take corrective action for every observed downward fluctuation. Only those dips which fall below the population size objective, which was set at base effective population size (Fig. 2), will require corrective management actions. The appropriate management responses in these cases are actions to reduce environmental resistance. Further lowering of population density in hopes of increasing _per capita_ nutritional benefits to survivors is unlikely to succeed in increasing production or survival.

For example, Dall sheep populations in Interior Alaska experienced population declines which approached 25% during winter 1981-82 (Watson and Heimer 1984). These changes were results of variations in cohort size precipitated by changes in environmental resistance (Watson and Heimer 1984). The declines were alarming, but actually of little management import because mild weather (transient, low environmental resistance) had produced transiently high population sizes by allowing several strong cohorts of sheep (which were earlier results of transient decreases in environmental resistance) to survive longer than normal. Hence, these decreases from "high" populations did not require corrective management actions. I do not recommend ignoring longer-term downward population trends, particularly if their cause and nature are not understood.

Here it should be emphasized, that base effective population need not represent the lowest level reached by naturally regulated, unmanaged populations. Base effective population size should be set by the manager to produce a level of human benefits sustainable by practical management actions. For example, in the Eastern Alaska Range 25 years of experience have shown that satisfactory ram harvests by humans are associated with a trend-indicator population size of 1,200 sheep in the Dry Creek study area (Heimer and Watson 1986a, b, 1990). Recorded high population sizes in this trend-indicating population have approached 1,800 sheep, and the Eastern Alaska Range has yielded increased ram harvests resulting from periods with higher population levels. Unregulated lows have not been observed because past management practices, including predator reduction programs (Heimer and Stephenson 1982), have maintained population size in the indicator area above 1,170 sheep. Experience suggests the base effective population required to produce acceptable ram harvests from the Eastern Alaska Range is indicated by a minimum population of about 1,200 sheep in the Dry Creek study area.

Obviously, determining the base effective population size requires a fairly long-term data base including population size, the magnitudes of documented fluctuations, and the level of human benefits desired. However, we should remember management has always, and will always, require application of specific information about the managed population.

As a manager, I think this approach has merit because I consider carrying capacity theory secondary to specific observation. That is, as a sheep manager, I am willing to rely more on the specific autecology of Dall sheep than on the synecology of ungulates in general. While reliance on the observed specifics of Dall sheep biology has produced management benefits (Heimer and Watson 1990), my past failure to directly address the carrying capacity question, which is fundamental to the thinking of most traditionally trained wildlifers, has interfered with their ability to consider and understand my arguments. I hope this discussion results in creative interchange among biologists regarding components of environmental resistance in addition to density-dependent nutrition. I also hope it results in greater direct application of what we know specifically instead of what we postulate in general.

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DETERMINING THE FUTURE OF BIGHORN HERDS IN WILDERNESS AREAS

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Abstract: Outside wilderness, managers usually seek to optimize some characteristics of bighorn sheep (*Ovis canadensis*) herds for abundant consumptive and non-consumptive use. In contrast, the Wilderness Act of 1964 and subsequent wilderness regulations emphasize protecting natural processes in wilderness. Agency manuals appear naive regarding the dynamics of natural populations and offer inconsistent directions for maintaining these wilderness values. Processes expected in natural bighorn populations are proposed as goals for management of wilderness bighorns. Strict interpretation of the Forest Service manual could jeopardize many herds, especially in small wilderness areas. In 11 western states, there are >287 wilderness areas and 63 % are <20,250 ha (50,000 acres). Over 100 areas contain bighorn sheep. Few wilderness management plans have been completed. Consequently, policies for managing wilderness vary greatly among administrative units, especially in the Forest Service. Recommendations for managing bighorn sheep in wilderness areas include revising the Forest Service manual, designating bighorns as primary components of much wilderness, and management intervention to simulate natural processes in order to achieve the highest possible degree of naturalness in most wilderness bighorn herds. Plans should specify goals for bighorns, including reintroduction to historic range, participation in regional bighorn metapopulations, minimum acceptable levels for herd sizes and movements, and elimination of contact with domestic sheep.

In 11 western states, more than 100 designated wilderness areas contain bighorn sheep populations. In addition, there are numerous wilderness study areas with bighorn herds. Several wilderness management plans are now being developed by the U. S. Forest Service and Bureau of Land Management, and many plans will be written in the next 5-10 years. These plans will set precedents and will determine the future of many of the nation's bighorn sheep. Consequently, policies and practices for managing bighorn sheep in wilderness areas deserve abundant discussion and careful consideration.

The objectives of this paper are to (1) compare goals for optimizing bighorn sheep to goals for maximizing wilderness values of bighorn sheep; (2) illustrate some inconsistencies, confusion, and naivete in the manuals guiding wilderness management, as they apply to bighorn sheep; (3) document the current status of wilderness management, as it applies to bighorns; and (4) recommend policies and practices that may maximize wilderness values of bighorns, yet reduce conflicts between optimization management and wilderness management of bighorn herds, especially those herds that migrate across wilderness boundaries.

We thank the following for responding to our survey of management policies and practices in wilderness areas: Ariz. BLM, S. Richardson; U.S. Forest Service, R1, A. Christensen; R3, B. Rickel, M. Ross, B. Wagenfehr, T. Skinner, D. Garcia; R4, P. Shields; R5, S. Loe, P. Rich, E. Rodriguez, K. Noland, and 2 anonymous respondents; R6, G. Silovsky. V. Bleich, G. Byrne, J. Emmerich, A. Fisher, M. Hess, G. Jense, R. Johnson, R. Lee, M. McCarthy, L. Oldenburg, J. Olterman, and W. Van Dyke identified wilderness areas containing bighorn sheep.

OPTIMIZATION MANAGEMENT OF BIGHORN SHEEP

Many, perhaps most, management plans for bighorn herds and habitats do not contain detailed statements of management goals. However, there is usually an intent to optimize one or several characteristics of the managed herd and habitat. These optimal characteristics may include:

(1) a large herd, perhaps controlled at some level believed to be the range carrying capacity, with the herd well above the minimum viable level, allowing abundant consumptive and/or non-consumptive use.

(2) a fairly stable herd size, without periodic declines or local extinctions of herd segments.

(3) high and stable levels of animal condition, reproduction, and resistance to disease.

(4) abundant, high-quality, diverse and fairly stable habitat resources, including a diversity of seasonal ranges and migration corridors accessed by periodic movements of animals.

(5) local forage resources in good condition; "excessive" use of forage does not occur, except perhaps locally in exceptional years.

(6) no contact with domestic sheep.

(7) genetic diversity is maintained by the large herd size, by immigration from nearby herds, or by occasional transplants into the herd.

WILDERNESS MANAGEMENT

The goals for wilderness areas are not consistent with all of these goals of optimization management for bighorn sheep. (While the Forest Service manual, FSM2323.35, and the Bureau of Land Management manual, BLMM8560.34.C.1, state similarly, "Objectives for the management of wildlife and fish habitat are normally compatible with the objectives for maintaining wilderness values", it is abundantly clear that optimization of a wildlife species is not a wilderness goal. For example see FSM2323.35a, 2324.22.7, BLMM8560.34.C.3.)

The Wilderness Act of 1964 defines wilderness as "an area where the earth and its community of life are untrammeled by man ...undeveloped ... without permanent improvements ... and managed so as to preserve its natural conditions." A wilderness "generally *appears* to have been affected primarily by the forces of nature, with the imprint of man's work substantially *unnoticeable*". Italics have been added to emphasize that this wording does not preclude man's works; it allows works that are not apparent. In fact, the Wilderness Act allows certain "grandfathered" uses of wilderness areas to continue, in the pre-existing manner and degree, after wilderness designation. These uses are mining and grazing, and the use of aircraft and motorboats (Keiter 1988). Also, wild horses or burros may be considered part of the natural wilderness system, although their numbers will be controlled by human intervention (BLMM8560.37.C).

The Wilderness Act and subsequent legislation (National Forest Management Act of 1976, Federal Land Policy and Management Act of 1976) emphasize the preservation of natural features, including species, and natural forces or processes in wilderness areas. Consequently, the Bureau of Land Management Manual, BLMM8560.11A, states, " BLM must foster a natural distribution of native species ... by ensuring that natural ecosystems and ecological processes continue to function." Likewise, the Forest Service seeks to "maintain wilderness in such a manner ... that plants and animals develop and respond to natural forces." (FSM2320.2.2) and to "provide an environment where the forces of natural selection and survival ... determine what numbers of wildlife species will exist." (FSM2323.31.1).

However, there is inconsistent and confusing direction for the management and maintenance of natural processes in Forest Service wilderness areas. For examples:

(1) While natural selection and survival are to determine numbers of wildlife (FSM2323.31.1), predators may be controlled to protect livestock (2323.33c), domestic sheep may be allowed to transmit serious diseases to bighorn herds (if "grandfathered in" during wilderness designation), and wildlife shall be held in balance with their habitat through public hunting or trapping (2323.35).

(2) While an objective of wilderness is to permit lightning caused fires to play, as nearly as possible, their natural ecological role in wilderness (FSM2324.21.1), prescribed ignitions may be used only to reduce unnatural buildups of fuels (2324.22.6). This may preclude use of prescribed ignitions to maintain the natural ecological roles of fire. Fortunately, the BLM Manual recognizes these other roles of fire (BLMM8560.35.3a) and allows prescribed ignitions for maintaining fire-dependent ecosystems, for sustaining a primary wilderness value, or for promoting endangered species (BLMM8560.34.C.4).

Furthermore, it is becoming clear that the idealistic goal of allowing all ecological processes to function naturally in wilderness areas will be impossible, especially in the small areas that predominate in our wilderness system. The Forest Service admits that "absolute wilderness" is impossible and that activities including mining, grazing, visitor-use, and control of fire and pests will constrain achievement of absolute wilderness (FSM2320.6). (A neglect of the constraints imposed by small wilderness size and by boundary conflicts in this section of the Manual suggests naivete regarding natural processes in mobile wildlife populations and metapopulations.) Recognizing these limitations, the Forest Service and BLM Manuals require that human activities deviating from absolute wilderness be minimized. The manuals also allow human activities that might replace and simulate natural processes in wilderness areas. Manipulation of vegetation or wildlife habitat may be used to enhance or perpetuate the wilderness resource where natural processes have been unsuccessful, or to correct abnormal conditions resulting from human influence (BLMM8560.34.C.2-4, FSM2323.35a). However, strict interpretation of FSM2324.22.6 would indicate that prescribed ignition of fire may not be used to manipulate vegetation for these purposes. Manipulation of habitats within wilderness areas has also been delayed by the lack of completed wilderness management plans; and may be limited by a low federal priority and budget for wilderness, and by the relatively high costs and risks associated with management, especially prescribed fire, in wilderness.

It is implied that all natural processes in wildlife populations contribute to wilderness value. However, the Forest Service and BLM manuals offer few and very general examples of these processes. Fire, biotic succession, and evolution are mentioned. But the Forest Service manual provides directions that conflict with maintaining these processes, as noted above. Directions for maintaining natural ecological processes in wilderness areas are probably unclear because these processes are very diverse and complex. For example, Christensen (1988) described the great range and complexity of natural processes in plant populations.

NATURAL PROCESSES IN BIGHORN POPULATIONS

If bighorn sheep populations are to contribute as much as possible to wilderness values, then wilderness management plans must recognize and provide for the natural processes expected in natural bighorn populations. These include:

(1) variation of herd size and sex-age composition; variation of animal condition, reproduction and survival; some herds may fluctuate a great deal, others may never be large.

(2) emigration and immigration.

(3) natural selection: coevolution with dynamic populations of diseases, predators, and forage plants; adaptation to a variable physical and biotic environment through selection from a large and diverse gene pool; however, herd bottlenecks, local inbreeding incidents, re-foundering, and outbreeding from immigration may also occur in some populations.

(4) variation in range use: occasional habitat abandonment and pioneering of new ranges; some herds relatively sedentary, others migrate annually over varying distances; local impacts on forage resources vary widely among areas and years, with persistent and sometimes obvious forage impacts in zootic climax (Cayot et al. 1979) areas, such as near water sources or mineral licks, and in snow-free or thermally-attractive sites.

(5) metapopulation dynamics: some herds are core populations supporting the persistence and/or genetic diversities of other herds; some are dependant, perhaps ephemeral, satellite populations; some herds are interdependent in a patchy distribution (Bailey 1992).

(6) no contact with domestic sheep.

In pristine North America, some of this natural variation of bighorn herds has been caused by fires and biotic successions that periodically improved and degraded habitats; by occasional severe winters and periodic droughts; and possibly by epizootics that occurred because of the bighorn's marginal immune capacity (Desert Bighorn Council Technical Staff 1990). Optimization management addresses these factors. Prescribed fire is used to maintain habitats (Risenhoover et al. 1988); winter ranges are often emphasized; water supplies are maintained artificially in deserts; some diseases are treated (Miller et al. 1987); and disease-carrying domestic sheep are avoided.

Natural processes in bighorn herds are not all congruent with goals for optimizing bighorn sheep, listed above. Many bighorn herds migrate across wilderness boundaries, so herds are often managed by agencies with conflicting goals. Conflicts between state and federal agencies have resulted (Sizer and Carr 1989, Bleich et al. 1991). However, federal regulations leave little, if any, room for compromising wilderness objectives. Where there are conflicting decisions or choices, "the wilderness resource is the overriding value" and this value "shall dominate over other considerations" (FSM2320.6, 2320.3.1). Where objectives for managing wildlife habitat are incompatible with wilderness character or values, the requirements for maintaining wilderness values take precedence (FSM2320.35, BLMM8560.34.C.1).

Smaller wilderness areas will experience a lower frequency of lightning caused fires that may be necessary to maintain bighorn ranges and migration corridors. Small and narrow wilderness areas also have a large ratio of boundary to area. As a result, most natural fires will be suppressed in these wildernesses due to the high risks of fire leaving the areas (FSM2324.21.2 and .22.6d, BLMM8560.35.A1). In addition, fire suppression outside wilderness will reduce the frequency of natural fires entering wilderness. The resulting lack of fire could gradually diminish the amount of early-successional habitats beneficial to bighorns (and other early-successional species). It could also allow fuels to accumulate, producing very infrequent, but very large, fires. For bighorns, a long period with few fires would cause gradual population decline and increasing sedentariness. Such a population may decline to the size of non-viability and disappear. If the population survives, it may expand rapidly in response to an infrequent, very large, fire. These possibilities of sedentariness, extirpation, or boom-and-bust fluctuations, are probably not natural in most wilderness areas.

A small wilderness may not contain the diversity of habitat resources that a pristine, mobile bighorn herd once used. Some of the once-used habitat diversity (including water sources or mineral licks) may, or may not, persist outside the small wilderness. Habitat diversity provides a wildlife population with options for responding to, and compensating for, adverse environmental variation, particularly adverse weather such as drought or severe winter. A bighorn herd unable to use a diversity of habitat resources would fluctuate more widely in response to environmental variation. For small herds, these fluctuations may result in loss of genetic diversity or extirpation. Both the excess fluctuations and the possible extirpation may be unnatural.

The natural processes listed above occurred in pristine North America when bighorn sheep were much more abundant and more continuously distributed than today. Bighorn herds and ranges have contracted for several reasons, including fire suppression in the Rocky Mountains (Wakelyn 1987, Cunningham 1991), and other human-caused impacts upon desert environments, especially upon water sources (McCutchen 1981:174-176). Many natural processes of bighorn populations will not occur, or will be limited in degree, within small, isolated wilderness areas. This may lead to extirpation of bighorn herds from these areas, unless limited unnatural human intervention is used to compensate for the small size and restricted habitat diversity of many wildernesses. If wilderness managers fail to recognize this dilemma, and pursue a purist non-intervention policy, many bighorn herds may slowly decline, become unnaturally sedentary, and may disappear from the smaller wilderness areas. The irony is that some intervention will be necessary to provide the highest possible degree of naturalness in many wilderness bighorn herds.

STATUS OF WILDERNESS MANAGEMENT RELATING TO BIGHORN SHEEP

The Forest Service and BLM administer 287 wilderness areas in 11 western states, excluding Alaska (U.S. For. Serv. 1990, Bur. of Land Manage. 1991). Many of these areas contain both BLM and Forest Service lands; 7 wilderness areas overlap state boundaries. (Additional wilderness areas administered by the U. S. Fish and Wildlife Service and the Park Service are not included here.) Bighorn sheep occur in 106 of these wilderness areas, according to a survey of state biologists. Additional wilderness areas contain historic range from which bighorns have been extirpated.

Sixty-three percent of these 287 wilderness areas are <20,250 ha (50,000 acres, Table 1) and 40 of these smaller wilderness areas currently have bighorn sheep. Arizona added 39 BLM wilderness areas in 1990; 33 of these were <20,250 ha. Consequently, Arizona has the largest number of small wilderness areas among the western states

(Table 1). The preponderance of small wilderness areas may increase similarly in other states when more BLM study areas are designated as wilderness. Small wilderness areas are not likely to include the entire annual ranges of bighorn herds. A survey of 18 bighorn herds in Colorado (Wakelyn 1984:55) suggests that a herd of 150 sheep will range over about 16,000 ha (40,000 acres). While many wilderness areas exceed this area, some proportion of each wilderness area is not suitable bighorn habitat.

Table 1. Characteristics of Forest Service and Bureau of Land Management wilderness areas in 11 western states.

Size (10^3 acres)	Number of wilderness areas[a]											
	AZ	CA	CO	ID	MT	NM	NV	OR	UT	WA	WY	Total
<10	18	4	3	0	1	2	0	7	1	4	0	40
10-50	48	24	4	0	3	13	7	16	10	11	5	141
50-100	9	6	7	0	2	2	4	4	1	1	0	36
100-150	4	3	6	0	0	0	2	3	0	3	2	23
150-200	1	4	3	0	1	0	0	2	0	3	2	16
200-250	0	2	1	2	2	2	0	0	0	0	0	9
>250	1	3	1	2	3	1	0	2	1	3	5	22
Total	81	46	25	4	12	20	13	34	13	25	14	287
Ave. size (10^3 acres)	34	86	103	1031	262	76	61	62	60	104	219	96
% <50,000 acres	81	61	28	0	33	75	54	68	85	60	36	63
No. with bighorn	32	7	19	4	8	6	10	3	3	3	11	106

[a] Seven wilderness areas occurring in 2 states are listed in the states having the largest portions of the areas. This "diminishes" the number of wilderness areas in Idaho, Montana and Wyoming by 1 area each, and in Oregon and Utah by 2 areas each.

Not only are many wilderness areas small in relation to the ranges of bighorn sheep, they are often narrow in width. The average width across 25 wilderness areas in Colorado is about 9.7 km (6 miles, S = 4.8 km or 3 miles); the average width across 81 wildernesses in Arizona is about 5.6 km (3.5 miles, S = 3.2 km or 2 miles). In contrast to these dimensions, many bighorn herds once migrated annually over longer distances, and some still do. For example, Smith (1954) noted that Idaho bighorns commonly migrated 16-32 km (10-20 miles), and 1 herd migrated 64 km (40 miles), each year. Maintaining or reestablishing such migrations, often across wilderness boundaries, would enhance the naturalness, and therefore wilderness value, of bighorn herds.

We surveyed the status of wilderness management in 6 western regions of the Forest Service and the Arizona BLM. Our survey emphasized practices and policies related to prescribed natural fires, prescribed ignitions of fire, development and maintenance of wildlife water sources, and use of aircraft for wildlife census, reintroduction of native species, and capture of animals. Responses were obtained from the BLM, from 4 Forest Service regional offices, from 4 of 11 Forest offices in the Southwest Region, and from 5 of 17 Forest offices in the California Region of the Forest Service. These responses related to 226 wilderness areas.

We found only 14 wilderness areas (7 FS, 7 BLM) with approved wilderness management plans, or wilderness fire management plans. Another 41 plans (20 FS, 21 BLM) were reported as currently being developed or scheduled before 1995. Without such plans, almost all natural fires must be suppressed in wilderness. (In 1 Forest Service region, respondents from 3 Forests indicated that their Forest plans authorized letting some natural fires burn in some wilderness.) We found evidence that some natural fires had been allowed to burn in 21 Forest Service wilderness areas since 1980. Apparently, all fires have been suppressed in more than 200 wilderness areas in the West.

Respondents identified 30 wilderness areas that are, or are expected to be, managed under a policy allowing some natural fires to burn. Twelve of these areas are >81,000 ha (200,000 acres). Ten are <20,250 ha (50,000 acres), 1 in California and 9 in Arizona. Respondents from the heavily forested Rocky Mountains believed that natural fires could not be allowed to burn in "small" wilderness areas because the risk of fire leaving the area would be unacceptable.

Respondents were asked if prescribed ignitions of fire might be used in wilderness to allow fire to play its natural ecological role, or to correct unnatural vegetative conditions resulting from human influence. Results were highly variable. For 2 Forest Service regions, respondents quoted the agency manual (2324) to claim that prescribed ignitions were not authorized for these purposes. In another region, the respondent believed that prescribed ignitions were authorized, but would not be approved. In 3 regions of the Forest Service, prescribed ignitions of fire to maintain natural vegetation in wilderness is authorized, at least on some Forests. We found only 1 instance of prescribed ignition having been used in wilderness to restore fire to its natural role in the ecosystem. (It was also noted that bighorn sheep were a significant wilderness value that would be sustained by this fire.) The Arizona BLM is allowed to consider using prescribed ignition of fire to maintain natural vegetation under the guidelines of 7 completed wilderness fire plans.

We found water developments for bighorn sheep in 18 wilderness areas in Arizona (16 BLM, 2 FS) and 1 wilderness in California (FS). There was complete agreement among respondents that maintenance of these structures must be by primitive means and with the minimum equipment needed - to minimize disruption of wilderness conditions. We found no evidence that proposals to construct water developments for bighorn had been denied; although the Arizona BLM policy is to defer such proposals until the appropriate wilderness management plans are done.

The Arizona BLM responded that aircraft may be used in wilderness areas for wildlife census, for capture of animals, and for reintroduction of native species. However, responses varied greatly among units of the Forest Service. Use of aircraft for census is not allowed on 1 Forest; it requires a special decision on 2 Forests and throughout 2 Regions; it is allowed on 1 Forest and throughout 2 Regions. (These 4 Forests with different policies are in 1 Region.) Use of aircraft for capture of animals is not allowed on 1 Forest and throughout 1 Region; requires a special decision on 2 Forests and throughout 3 Regions; is allowed on 1 Forest and throughout 1 Region. (Again, the Forests are in 1 Region.) Use of aircraft for reintroducing native species requires a special decision on 3 Forests and throughout 4 Regions; is allowed on 1 Forest and throughout 1 Region. (The Forests are in 1 Region.)

The status of wilderness planning and the interpretation of wilderness regulations in the manual vary greatly among Forests and Regions of the Forest Service. At an extreme, 1 Region has no wilderness management plans completed or being developed, suppresses all natural fires in wilderness, responded that prescribed ignition of fire is not authorized in wilderness, and would not allow use of aircraft for capture of animals in wilderness. In another Region, there is an emphasis on developing wilderness management plans, natural fires may burn in several wildernesses - even relatively small ones, and a prescribed ignition of fire has been approved to enhance wilderness value. In our survey, several state biologists complained that wilderness management policies also varied when supervisors changed within BLM or Forest Service units. We believe some of this variation is due to lack of clear direction in the Forest Service manual.

RECOMMENDATIONS

Although the wilderness act emphasizes preservation of natural processes as a goal of wilderness management, the Forest Service manual provides limited and inconsistent directions for achieving naturalness in wilderness. A Forest Service workshop, with experts in ecology and the dynamics of ecosystems, should be convened to revise at least those portions of the manual dealing with wildlife, habitat management, and fire. Until revisions are done, wilderness plans should be based upon interpretations of the entire wordings of the manual, and not upon strict interpretations of isolated sections.

Each wilderness area is unique and offers original opportunities and challenges for maintaining - to the extent possible and practical - a natural ecosystem. Small wilderness size and abundant interactions across boundaries characterize most wilderness areas. These problems should be addressed for each wilderness area by convening representatives of agencies and publics affected by each wilderness management plan, including state fish and wildlife agencies that manage animals migrating across wilderness boundaries (FSM 2323.32, BLMM 8560.34.A.2). Joint understanding of specific wilderness goals, and joint determination of the extent to which these goals may be achieved, should reduce conflicts between optimization management and wilderness management; and may eliminate conflicting and inefficient management activities.

In desert areas, development and care of bighorn water sources can maintain both optimization and wilderness values of the animals. Water sources are often funded by agencies and/or foundations primarily interested in optimization values; while costs for development and care are often increased by requiring primitive methods that will preserve wilderness values. In these cases, financial support of bighorn water sources from federal agencies or from wilderness foundations is justified.

The western states need almost 300 wilderness management plans. All these plans will not be completed quickly. Until plans for wilderness bighorn sheep are developed, management should maintain options for maximizing wilderness values of bighorn herds. Interim goals should be to maintain existing populations and their genetic diversities, and to maintain existing traditionally-used seasonal ranges and migration corridors. (This may require some of the management strategies suggested below.) In wilderness areas where bighorns have been extirpated, and it is clear that reestablishing bighorns is possible and will contribute to the wilderness area's natural biodiversity, transplanting sheep need not be delayed until detailed wilderness management plans are done.

In summarizing the results of a workshop on ecosystem management for parks and wilderness areas, Johnson and Agee (1988:11-12) suggest that planners (1) identify primary components of wilderness systems; (2) define ecosystem boundaries, perhaps going beyond wilderness boundaries, for these components; (3) adopt goals and management strategies for primary components; and (4) develop monitoring systems to assess goal achievement for each component. (The concept of identifying "primary values" of wilderness areas is introduced in FSM 2323.35a.) In most, if not all, wilderness areas containing bighorn sheep, they should be designated as primary components for many of the following reasons:

(1) Most wilderness bighorn herds have exceptional recreational and esthetic values.

(2) Some herds have locally important economic value. Congress has recognized economic values of other wilderness resources by allowing grazing and mining to be "grandfathered in".

(3) Most bighorn herds should have large home ranges. Maintaining their habitats may protect smaller species having similar habitat needs and may stimulate coordination of management across wilderness boundaries. Thus, bighorn sheep qualify as an indicator species (Salwasser 1988:95).

(4) Bighorn sheep are far below their pristine abundance and distribution (Buechner 1960). Only a few other large western mammals have been reduced as much (or more) as bighorns. Bighorns are listed as "threatened" in California.

(5) Dispersed, relatively small bighorn herds must be managed as metapopulations in order to preserve the genetic resources of the species (Bleich et al. 1990, Bailey 1992), and these resources contribute to wilderness value. Some metapopulations will include herds in wilderness areas.

Wilderness plans should not be vague in defining goals for bighorn sheep. The "complete naturalness" goal and "let it be" strategy can result from indolent disregard of the diversity and dynamics of natural processes and of the real constraints for achieving naturalness in wilderness. Indolence may be fostered by the slow rates at which herds decline and become sedentary, in relation to the rates at which government employees transfer among jobs.

Goals for wilderness bighorn sheep should be developed according to local opportunities and constraints. They should include reintroduction of sheep into historic ranges, participation in regional bighorn metapopulations, minimum acceptable levels for herd sizes and movements, and the elimination of contact with domestic sheep.

Bighorn sheep should be reintroduced onto historic ranges within wilderness (BLMM 8560.34.D.1, FSM 2323.33a). Goals for reintroduced herds should include reestablishing historic movement patterns.

Each wilderness plan for bighorn sheep should address the potential contribution of the wilderness herd and habitat to a larger metapopulation that will conserve genetic variation of the species. This mandate is implied in many sections of the BLM and FS manuals that emphasize the preservation of natural resources and processes - in this case, genetic resources and evolution. Metapopulations should be recognized in management plans of all agencies responsible for the metapopulations' herd-components and their habitats. Ideally, contacts between herds would involve natural movements. However, some wilderness bighorn herds surrounded by unsuitable habitat should be augmented genetically by occasional transport of sheep from other herds.

Herd sizes and movements should be allowed to fluctuate, without human interference, above threshold levels. These thresholds should be selected to reduce to acceptable levels, the threats of herd extinction, and of long-term loss of migratory habits and genetic resources. When bighorn herds or their movements decline to threshold levels, human intervention is warranted. This may include prescribed ignition of fire, simulating a natural fire regime (BLMM8560.35.A.3, FSM 2323.35A); providing artificial water sources to replace waters that have been depleted inside or out of wilderness by human activities (BLMM 8560.34.C.6, FSM 2323.35A); and transplanting sheep to provide "artificial immigration" and augment genetic diversity. Such intervention may be necessary to maintain a herd in as natural a state as possible.

Selecting a minimum population threshold for a wilderness bighorn herd will be somewhat subjective and arbitrary. Small herd size fosters inbreeding, but acceptable rates of inbreeding are unclear. The risks of stochastic fadeouts due to small herd sizes are also uncertain, and will be greater in wilderness areas with more variable physical environments and less diverse habitat resources. These risks must be weighed against the amount of human intervention, and compromise of other wilderness values, necessary to maintain a larger, less threatened, herd.

In reviewing the historic record, Berger (1990) concluded that populations of <50 bighorns are not viable, and that long-term persistence of herds <100 is questionable. Soule' (1980) suggested that vertebrate populations equivalent to <50 "effective breeders" will exceed an (arbitrarily selected) unacceptable rate of inbreeding. In bighorn sheep, having the equivalence of 50 effective breeders will require a herd of about 150 animals (Fitzsimmons 1992), depending upon sex-age structure and other factors. Even with 150 bighorns, genetic variation and adaptability will gradually be lost through random selection (drift). Maintaining genetic variation in large mammals will require ≥1000 animals (Franklin 1980). These animals may exist in a metapopulation of several herds connected, genetically, by occasional movements of individuals.

Given the scientific uncertainty, we suggest that wilderness planners select ≥150 bighorn sheep as a minimum threshold for herds proposed as core populations (Bailey 1992) of recognized metapopulations. Selecting a threshold of <150 sheep may be appropriate for 1) small wilderness areas incapable of supporting many sheep, for which herds are designated interdependent components of patchy metapopulations; and 2) wilderness bighorn ranges for which occasional extirpation and refoundering are considered natural processes in satellite populations. Most often the metapopulation will include herds outside wilderness boundaries. We encourage abundant critique and discussion of these suggestions (cf. Geist 1975:105, Thomas 1990). However, 2 recent surveys (Thorne et al. 1985; Bur. of Land Management, n.d.) indicate that >60% of bighorn herds in the United States contain <100 sheep. Achieving 150 bighorn would improve the security of many wilderness bighorn herds, and goals may be revised as new information may dictate. We believe many wilderness bighorn herds are now isolated and <150 animals. For these herds, human intervention is already warranted and should be considered in developing wilderness plans and in interim management of areas without completed plans.

We suggest that wilderness planners establish goals to maintain at least 1 migration corridor between each pair of seasonal bighorn ranges within a wilderness, and to maintain suitable corridors between some wilderness herds and nearby herds outside the wilderness. A common threat to these corridors will be biotic succession, a consequence of lack of fire. We believe many wilderness bighorn herds are now unnaturally sedentary, warranting timely human intervention (Risenhoover et al. 1988).

A wilderness goal for bighorns should be to eliminate contact with domestic sheep (Desert Bighorn Counc. Tech. Staff 1990). Options are to vacate existing allotments, or convert them to cattle, perhaps through exchange of use with areas away from bighorns. Other options are to stringently control the distribution of domestic sheep, and to encourage and maintain dense forests as barriers to discourage movements of wild sheep toward domestic sheep.

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BIGHORN DISEASES

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EFFECT OF PNEUMONIA ON POPULATION SIZE AND LAMB RECRUITMENT IN WHISKEY MOUNTAIN BIGHORN SHEEP

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Abstract: During the winter of 1990-91, a major die-off of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) occurred in the Whiskey Mountain area near Dubois, Wyoming. Onset of the die-off was attributed to increased physiological stress resulting from several weeks of -40 C temperatures and 80 km/hr winds during peak rutting activities and human visitation. Three carcasses and various tissues from 8 additional sheep were collected from affected winter ranges and examined at necropsy. All lungs were grossly pneumonic and microscopically characterized as suppurative to fibrinopurulent bronchopneumonia. *Pasteurella haemolytica* was isolated from all tonsils cultured, but from only 1 lung. No bacterial pathogens were isolated from 4 lungs, *Moraxella* sp. was isolated from 2 lungs and *Chlamydia psittaci* was isolated from 1 lung. Viral respiratory pathogens, lungworms and other parasites did not appear to be significant in causing mortality. The deaths of 124 bighorn sheep were directly attributed to pneumonia, although computer simulations suggested actual mortality probably exceeded 450 sheep. Animals died in approximately the same sex and age categories as existed prior to the die-off, based on examination of carcasses in the field. Lamb:ewe ratios declined from 44:100 in December 1990 to 16:100 in May 1991, but the percentage of yearling sheep observed in December 1991 indicated lamb mortality during the die-off did not exceed normal levels. Hunting licenses issued in 1991 for 3/4 curl rams were reduced by 22% from previous years. This reduction tended to mask effects of the die-off as success and average age of harvested rams remained similar to previous years. By December 1991, surviving sheep recovered from acute effects of pneumonia. Reduced lamb recruitment during 1991 (6 lambs:100 ewes in December) and predicted sub-normal production in 1992 will pose future management challenges as these age classes carry through the population. However, in spite of losing an estimated 30-40% of the population in 1991, the long-term prognosis is favorable.

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[1] Deceased

Pneumonia is a well documented and significant mortality factor in bighorn sheep populations throughout their North American distribution (Spraker 1979, Feuertein et al. 1980, Wishart et al. 1980, Spraker and Hibler 1982, Festa-Bianchet and Samson 1984). Although not completely understood, outbreaks of pneumonia generally occur when animals are stressed above levels which they are accustomed to and/or contact domestic sheep. Further, extant viral and bacterial respiratory pathogens and parasites can affect the severity of a given pneumonia related die-off.

The Whiskey Mountain area in west-central Wyoming supports one of the world's largest wintering concentrations of Rocky Mountain bighorn sheep. Sheep from this area have been utilized to re-establish or supplement populations throughout Wyoming and 5 other western states. They are also becoming more important locally as a source of economic revenue from nonconsumptive wildlife users. One of the reasons this population has been attractive as transplant stock is because it has not undergone a major disease-related die-off in recent history. This paper documents the effects of the first large-scale pneumonia outbreak in Whiskey Mountain sheep.

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STUDY AREA

The majority of winter habitats utilized by bighorn sheep in the Whiskey Mountain herd lie immediately south of Dubois, Wyoming. Geology, climate, and vegetation of these habitats were summarized by Butler (1977). Within the general wintering area, sheep have historically congregated on 3 "key" sites. These sites include Sheep Ridge, BLM Ridge, and Torrey Rim. The combined number of animals utilizing these sites varies between 600-900 annually.

Livestock grazing has been greatly reduced over the past 20 years as habitats were acquired for management as sheep winter range. Currently, 20-40 domestic horses (Equus caballus) graze portions of the winter range and only 2 forest allotments have active cattle (Bos taurus) preference within the Fitzpatrick Wilderness. There are no domestic sheep (Ovis spp.) grazing permits in the area. Winter and summer ranges of bighorn sheep are also used extensively by backpackers, photographers, fisherman, hunters, and other wildlife enthusiasts.

METHODS

Clinical evidence of pneumonia was first documented in Whiskey Mountain sheep on 13 December 1990. By 6 January 1991, pneumonia was so prevalent that annual trapping operations were cancelled in order to prevent stress and avoid possible introduction by translocation of disease to other bighorn sheep herds. To determine the cause of the pneumonia outbreak, 2 animals shot while exhibiting clinical signs of pneumonia, 1 complete carcass of an animal found dead, and various tissues from 8 additional bighorn sheep were examined at the Wyoming State Veterinary Laboratory, Department of Veterinary Sciences, University of Wyoming.

Carcasses and tissues were examined grossly and body condition assessed subjectively based on the amount of visceral and bone marrow fat. Representative tissues were fixed in 10% buffered formalin. These were processed routinely for paraffin embedment, stained with hematoxylin and eosin and examined by light microscopy. Special stains included PAS and Gram's.

Tissues collected at necropsy were cultured at 37 C on Columbia agar base with 5% sheep blood and MacConkey agar incubated aerobically in 5% CO2. Isolates were identified using accepted methods (Lennette et al. 1985, Carter and Cole 1990). Lung and/or spleen samples were tested by fluorescent antibody tests for bovine respiratory syncytial virus (BRSV) antigen, bovine virus diarrhea virus (BVDV) antigen, parainfluenza 3 (PI3) virus antigen, infectious bovine rhinotracheitis virus (IBRV) antigen (Carbrey et al. 1971), and Chlamydia psittaci antigen (Riggs 1979). Virus isolation was attempted on ovine embryonic testicle cells using the techniques of Carbrey et al. (1971). Chlamydial isolation was attempted on McCoy cells (Haven et al. 1992). Feces were examined for intestinal parasites by sugar flotation and for lungworm larvae by the Baermann technique (Soulsby 1982).

In addition, to assess what potential respiratory pathogens might have been present in the herds prior to the epizootic and in the subsequent year, sera collected in January 1990 and 1992 were tested by virus neutralization for antibodies against BVDV, IBRV, PI3 virus, and BRSV (Carbrey et al. 1971), by complement fixation for Chlamydia spp. (Texas Veterinary Medical Diagnostic Laboratory, College Station, Texas), and by enzyme-linked immunosorbent assay (ELISA) for Pasteurella haemolytica specific antibody (K. W. Mills, unpubl. data). Sera were not collected during the epizootic in 1991 because trapping operations were cancelled.

From 11 January through 16 May 1991, sheep were surveyed approximately every 12 days. All animals observed were classified as to sex, age (Geist 1968), and whether or not they exhibited signs of pneumonia (i.e., coughing and/or nasal discharge). Percentages of the population infected with pneumonia were estimated using these data. All dead animals found were recorded as to location, sex, age, and, if suitable, submitted for necropsy.

Classification data were compiled and analyzed using Version 6.10 of the computer model POP-II (Barthelow 1990). Simulations were directed at data alignment from 1986-91 using harvest mortality, post-hunting season sex and age ratios, and trapping/transplanting removals. To determine total mortality associated with the pneumonia outbreak, winter Mortality Severity Indices (MSI) in the model were increased to simulate the observed decline in lamb:ewe ratios from December 1990 (i.e., post-season) to May 1991 (i.e., end-of-biological year). Following these analyses, license quotas were set for 1991. Harvest data for 1991 were collected and analyzed, and sheep were classified again in December 1991. The simulation model was updated in spring 1992 using all 1991 data. Vegetation data presented in this paper were collected using methods outlined in Butler (1977).

RESULTS

Winter, 1990-91

From 1985-89, western Wyoming experienced above normal daily temperatures and below normal precipitation patterns (U.S. Department of Commerce 1992). Drought conditions peaked during 1988 and contributed to the massive Yellowstone wildfires. In the Wind River Mountains, drought appeared to moderate during the summer of 1990. As a result, lamb survival through the 1990 post-hunt period was slightly higher than the previous 3-yr average (44 lambs:100 ewes versus 39 lambs:100 ewes). Late-winter snows and heavy rains just prior to the birth of lambs apparently resulted in good post-partum foraging conditions. Better than average forage production on summer range was reflected in data collected on key winter use sites (Table 1). Herbaceous forage production improved dramatically above long-term average levels for sampling sites on BLM and Sheep Ridge. However, production was well below the long-term average for sampling sites on Torrey Rim.

Table 1. Comparison of herbaceous forage production (kg/ha) among Whiskey Mountain bighorn sheep winter use sites.

Site	1990	1991	5 yr. avg.
Torrey Rim West	302	537	417
Torrey Rim East	373	837	540
Sheep Ridge East	563	567	451
Sheep Ridge West	484	359	312
BLM Ridge East	998	639	573
BLM Ridge West	499	476	404
Averages	537	569	450

The winter of 1990-91 was generally mild except for a 2-week interval in December 1990. Temperatures during this time dropped as low as -40 C. Under these conditions, winds are usually negligible. However, during the December cold period, winds in excess of 80 km/hr were common. Thus, wind chill factors of -85 C occurred during the rut when animal energy expenditures were high and human visitation was at a peak. The combination of high animal energy expenditures, increased human disturbance, extremely cold temperatures, and below normal forage production on Torrey Rim corresponded to the appearance of clinical pneumonia within that segment of the herd. By mid-February, the disease appeared in animals on BLM Ridge and Sheep Ridge.

Since pneumonia was not diagnosed in sheep on BLM or Sheep Ridges until mid-February, those areas were not surveyed as intensively until that time (Table 2). Several trends are evident when comparing classification data collected from 13 December 1990 to 16 May 1991. First, rams left wintering areas in large numbers following cessation of the rut. Total ram:ewe ratios declined significantly in late-January, February, and April and those rams observed were primarily yearlings and Class I animals. Second, on Torrey Rim where the disease was first diagnosed, the 1990 lamb crop was essentially eliminated by May. Lamb mortality was not as significant on BLM and Sheep Ridges. Finally, numbers of sheep observed in the area declined steadily until May. Declines were probably caused by a combination of increasing sheep mortality and movement of some animals off primary wintering sites. Increased numbers of sheep observed in May were thought to be the result of early plant green-up at lower elevations. Lush, succulent vegetation probably attracted animals which had previously left these areas.

A total of 124 dead bighorn sheep were found, mostly by horn hunters during and after the die-off. Thirty-six percent of all rams observed during 1990 post-season classifications were yearlings. Only 11% of documented ram mortalities were yearlings. Thus, yearlings died at a lower rate than they existed in the population prior to onset of pneumonia, while older, breeding-age rams succumbed at a higher rate.

Class I rams comprised 35% of all rams aged 2+ and older. Yet, only 19% of adult ram mortalities occurred in this age category. Conversely, Class II rams made up 30% of the classification sample, but 51% of the documented adult ram mortalities. Class III and Class IV rams died at rates similar to percentages of the population observed in December (24% observed versus 22% of mortalities and 11% observed versus 8% of mortalities, respectively). Total ewe mortality was not determined through data collection efforts, but is thought to have occurred in proportion to this sex class's occurrence in the herd.

Late, heavy snow accumulations in April 1991, coupled with heavy rains and more high elevation snow in May, forced sheep to remain on winter habitats much later than in most years. By 31 May, snow depths exceeded 1 m at elevations above approximately 2,900 m and many animals remained at low elevations. As a result, early lambs were being born on traditional wintering sites.

Using a POP-II computer model, post-season lamb:ewe ratios from 1986-90 were aligned to within 1 lamb:100 ewes of observed values. Simulated post-season ram:ewe ratios were left to track approximately 11 rams:100 ewes above observed values because some ram bands winter at high elevations and were missed during ground surveys.

After aligning the model with observed data by adjusting winter Mortality Severity Indices, it calculated a total mortality of 467 animals. Estimated ewe and lamb losses appeared feasible when compared with changes in observed age ratios from December 1990 to May 1991 and documented mortalities. However, the model could not accurately simulate documented ram mortality with its existing initial age

Table 2. Bighorn sheep classifications conducted on Whiskey Mountain winter use sites during the pneumonia outbreak of 1990-91.

Location and date	Rams	Ewes	Lambs	Rams:100 ewes: lambs	Total counted (% sick)
Torrey Rim:					
12/13/90	71	195	86	36:100:44	352 (0%)
1/11/91	37	125	64	30:100:51	226 (9%)
1/18/91	50	151	47	33:100:31	248 (8%)
1/24/91	52	162	42	32:100:26	256 (5%)
1/30/91	31	124	40	25:100:32	195 (4%)
2/08/91	55	188	52	29:100:27	295 (4%)
2/15/91	21	164	42	13:100:26	227 (4%)
2/22/91	11	82	23	13:100:28	116 (3%)
4/15/91	29	139	12	21:100:9	180 (2%)
5/16/91	29	115	8	25:100:7	152 (0%)
BLM Ridge/Sheep Ridge:					
12/15/90	82	221	94	37:100:43	397 (0%)
1/11/91[a]	42	59	12	105:100:20	113 (0%)
1/18/91[a]	46	97	33	47:100:34	176 (0%)
1/24/91[a]	28	91	35	31:100:38	154 (0%)
1/30/91[b]					130 (0%)
2/08/91[b]					156 (10%)
2/15/91[c]	27	233	95	12:100:41	355 (1%)
2/22/91[d]	26	207	77	13:100:37	310 (2%)
4/15/91[d]	21	138	32	15:100:23	191 (3%)
5/16/91[d]	60	210	52	29:100:24	322 (2%)
Area-wide Surveys:					
12/15/90	153	419	180	37:100:43	749 (0%)
2/15/91	48	397	137	12:100:35	582 (2%)
2/22/91	37	289	100	12:100:35	426 (3%)
4/15/91	50	277	44	16:100:16	371 (2%)
5/16/91	89	320	60	27:100:18	474 (1%)

[a] BLM Ridge surveyed only.

[b] BLM Ridge surveyed only, none classified because no sick sheep observed.

[c] BLM & Sheep Ridge surveyed, no sick sheep observed on Sheep Ridge.

[d] BLM & Sheep Ridge surveyed, sick sheep observed on both.

structure. Thus, total estimated mortality was considered conservative.

All carcasses and tissues examined at necropsy were collected on the Torrey Rim portion of the winter range from 4 January to 5 February 1991. Three carcasses and scavenged remains from 8 bighorn sheep were examined. Eight samples were from ewes, 1 was from a ram, and the sex of 2 were unidentified. Four of these samples were from lambs, 1 was from a yearling, 5 were from adults, and age of 1 specimen was not determined. Body condition was determined to be excellent in 2 cases, good in 4 cases, poor in 1 case, and 1 animal was judged to be emaciated. Two adult ewes were pregnant. Other documented carcasses were discovered, but were not suitable and/or not submitted for examination.

No bacteria were isolated from 4 of 7 lungs cultured. Moraxella-like bacteria were isolated from 2 lungs, and P. haemolytica was isolated from 1. Tonsils from 3 bighorn were cultured and all were positive for P. haemolytica, including the animal that had this bacteria in the lung. Actinomyces pyogenes was also isolated from the lung of this affected animal. All P. haemolytica isolates were nonhemolytic and typical of T types. The Moraxella-like organism was identified based on the following biochemical and other criteria: Gram negative, oxidase positive, catalase negative, vancomycin resistent, TSI K/K, urea negative, motility negative, nitrate negative, and no growth on MacConkey agar (R. Ellis, Colorado State Univ., pers. commun.).

All fluorescent antibody tests on lung tissues for respiratory viruses and Chlamydia were negative as were attempts at virus isolation. However, C. psittaci was isolated from the lung of 1 animal. Parasite burdens were considered low to moderate; 10, 80, and 150 larvae of Protostrongylus sp. per gram of feces were found in 3 animals. Eggs and oocysts of Nematodirus sp., Trichuris sp., and Eimeria sp. were detected in fecal samples, but numbers were low. Sarcocysts were identified in skeletal and/or cardiac muscle of 4 animals by microscopic examination.

Bronchopneumonia was grossly apparent in all lungs examined. Some were autolytic and many had been frozen and thawed prior to examination. The anteroventral regions were involved in all animals for which distribution could be determined. In those animals, grossly recognizable lungworm nodules were in the dorsal diaphragmatic lobes. Microscopically, the lesions in lung were characterized by vascular congestion and exudation of edema, neutrophils and macrophages into bronchi and alveoli. Fibrin within alveoli and on the pleura was observed in some animals. Areas of necrosis occurred in 2 animals, including the animal from which P. haemolytica was isolated from the lung. Mild bronchial epithelial hyperplasia was recognized in 1 animal. Bacteria were observed within pulmonary parenchyma, but large colonies were not common. Mild multifocal granulomatous to pyogranulomatous inflammation was associated with eggs, larvae, and adult lungworms in alveoli.

Results of virus neutralization tests indicated that BVDV was not present in the Whiskey Mountain herd (0 of 12 seropositive in 1990 and 0 of 27 seropositive in 1992). However, serologic evidence indicates other potential respiratory pathogens are very common. Eleven (92%) of 12 bighorns were seropositive for antibodies against PI3 in 1990 (reciprocal geometric mean titer [GMT] = 106, range 1:16 - 1:256) and 27 (100%) of 27 were seropositive in 1992 (GMT = 131, range 1:16 - 1:1024). Similarly, 11 (92%) of 12 bighorns were seropositive (GMT = 60, range 1:16 - 1:512) for respiratory syncytial virus antibodies in 1991 and 27 (100%) of 27 were seropositive (GMT = 69, range 1:16 - 1:2048) in 1992. Twelve (100%) of 12 bighorn were seropositive (GMT = 30, range 1:16 - 1:64) in 1990 and 25 (93%) of 27 were seropositive (GMT = 59, 1:16 - 1:64) for antibodies against _Chlamydia_ spp. in 1992. In 1990, 9 (69%) of 13 bighorns were positive for _P. haemolytica_ antibodies by ELISA and in 1992, 25 (93%) of 27 animals were seropositive. Seropositive animals for respiratory pathogens in 1992 included 1 lamb, indicating that transmission occurred between the time of it's birth in June 1991 to January 1992.

Winter, 1991-92

Because preliminary data analyses from 1990 suggested a substantial die-off had occurred, the number of hunting licenses for fall 1991 was reduced from 82 to 64. Reducing total licenses by 22% was successful in lowering the harvest of 3/4 curl or larger rams by 17% from the previous 3-yr average (39 versus 47, respectively). However, hunter success increased from 57% to 61%, the average age of harvested rams remained at 6.5 yrs, and the percent of Class III and IV rams in the harvest increased from 33% to 46%. Thus, reduced license numbers effectively masked any detectable influence of the die-off on harvest statistics.

On 17 December 1991, bighorns were again classified on low-elevation winter ranges. A total of 608 sheep was observed during these classifications. An additional 354 animals were observed during aerial surveys. Only 1 animal exhibited signs of pneumonia and it was shot; necropsy revealed chronic resolving pneumonia. Lamb production declined to 6 lambs:100 ewes, the lowest level ever documented for this sheep population. Ram:ewe ratios were similar to those observed in 1990 (i.e., 39 rams:100 ewes each year).

DISCUSSION

Acute to subacute, suppurative to fibrinopurulent bronchopneumonia was responsible for the mortality observed in the Whiskey Mountain herd in 1991. No known respiratory pathogen was consistently isolated from lungs and in 4 cases no bacteria were isolated. Microscopic lesions were most consistent with _P. multocida_ or other bacterial induced bronchopneumonia and were not typical of lesions usually observed with _P. haemolytica_ lung infection (Dungworth 1985). There was no evidence to suggest that viral respiratory pathogens were involved in this epizootic, even though the serologic data indicate that these viruses are ubiquitous in this herd. The role of _Chlamydia_ spp. is not clear. It may act synergistically with bacteria to produce pneumonia and may have been important in at least 1 animal.

P. haemolytica was isolated from the tonsils of 3 bighorns, but it was only present in the lung of 1 animal. Apparently, even though this bacteria is carried in the oropharynx, it may not be important in initiating bronchopneumonia even in the face of considerable environmental stress. The bighorn that had P. haemolytica in the lung was in poor body condition, also had A. pyogenes and Chlamydia in the lung, and the course of clinical disease was more prolonged than observed in the other animals. Perhaps, multiple factors allowed P. haemolytica to colonize the lung.

Moraxella and Pasteurella are taxonomically similar bacteria, though Moraxella is not considered a primary respiratory pathogen in domestic ruminants (Timoney et al. 1988). Moraxella liquifaciens was isolated from healthy bighorns from Whiskey Basin in 1976 and 1977 (Thorne et al. 1979) suggesting that it is probably not a primary pathogen. Similarly, PI3 virus appears to have been present in the Whiskey Mountain herd for a long period of time without causing appreciable clinical disease. Thorne et al. (1982) reported 23 (77%) of 30 bighorns seropositive by virus neutralization in 1976 and 1977. Long-term data are not available on the other potential respiratory pathogens, but there was little difference in seroprevalence to BRSV, Chlamydia, and P. haemolytica between 1990 and 1992. This, along with no evidence these were active in animals necropsied, suggests they were unimportant in the epizootiology of this pneumonia outbreak.

The epizootic occurred following a period of severe environmental stress. Animals varied in body condition. Two animals shot because of pneumonia were judged to be in excellent body condition. Thus, body condition alone was not a predisposing factor. However, a comparison of 1990 post-season ram classifications with the age structure of ram mortalities suggest that males may have been the first animals to become sick during the December cold period. Since Class II, III, and IV rams perform most of the breeding, these age classes would be expected to be in poorer physical condition than yearling and Class I rams. Thus, they should be more susceptible to a stress-related disease outbreak and would theoretically be more likely to succumb at higher rates than other ram age classes.

Originally, lambs were thought to have died at a much higher rate than they occurred in the population. However, the percentage of yearling sheep observed in December 1991 surveys was not significantly lower than average. Thus, lamb mortality during the die-off may have been compensatory to normal natural mortality in this segment of the herd. Although relatively few lamb mortalities were documented, avian scavengers and other predators rapidly removed all evidence of a carcass soon after death. During several sheep surveys, lambs which were discovered within hours of death were almost completely consumed.

During the pneumonia outbreak, wintering animals foraged in large, compact herds. This herding behavior probably facilitated spread of the disease among animals. Because several dead rams were found in Dry Whiskey Creek between Torrey Rim and BLM Ridge, males traveling between ewe-lamb groups in these areas during the rut may have carried the disease to western portions of the area.

Despite death of an estimated 30-40% of the population, the long-term prognosis for this herd is favorable. Since approximately 1,000 animals were observed 1 yr after the die-off, adequate numbers of sheep remain to retain learned migratory behavior. We feel this behavior is essential to reduce forage use on winter ranges and maintain high physiological and genetic fitness. In addition, winter habitats at Whiskey Mountain continue to be intensively managed to increase forage production and expand sheep distribution into suitable, but currently unused areas. Reduced lamb recruitment during 1991 and predicted sub-normal production in 1992, however, will pose future management challenges as these age classes carry through the population.

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LAMB SURVIVAL AND HERD STATUS OF THE LOSTINE BIGHORN HERD FOLLOWING A *PASTEURELLA* DIE-OFF

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Abstract: Two-thirds of the Lostine bighorn sheep herd (Northeast Oregon) died during a *Pasteurella* epizootic in winter 1986-87. Circumstantial evidence indicated the disease was transmitted from domestic sheep. Lamb survival was poor the first 2 years following the die-off, but gradually improved thereafter. The current herd status, productivity, and management implications are summarized.

Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) (Bailey 1936) were native to Northeast Oregon, but disappeared by the mid 1940's. Recent archaeological evidence indicates bighorns were abundant in what is now Wallowa County. Faunal remains from archaeological digs in Hells Canyon indicate bighorns were the most important ungulate food item for pre-settlement Indians.

Restoration efforts in Oregon began in 1971 when 15 ewes and 5 rams from Jasper National Park, Alberta, Canada were released in the Lostine River drainage of the Wallowa Mountains (Coggins 1988). The herd was migratory, wintering on open grass slopes on the north end of the Wallowa Mountains (Lostine Wildlife Area) and summering 8 to 16 km (5 to 10 miles) south in high-elevation alpine basins along the Hurricane Divide. The Lostine bighorns did well and limited ram hunting started in 1978. Trapping and transplanting was initiated in 1977 and 152 bighorns were moved to 9 different sites by 1986. Winter population levels were kept at relatively stable numbers of about 80 sheep by hunting and live trapping.

An all-age die-off from *Pasteurella* pneumonia was diagnosed in November, 1986 and reduced bighorns from an estimated 100 to 34 animals (Table 1). Circumstantial evidence linked the die-off to contact with domestic sheep (Coggins 1988), as has been reported by Onderka and Wishart (1988), Foreyt and Jessup (1982), and others.

The assistance of many Oregon Department of Fish and Wildlife personnel, numerous volunteers, and others that aided with this project is greatly appreciated. Special thanks are due to Dr. Bill Foreyt, Washington State University (WSU), for his assistance and advice on disease monitoring. Also special thanks are due Rosemary Peterson, who typed and retyped the manuscript.

Table 1. Lostine bighorn sheep herd composition and population surveys, 1972-92.

Year	Ewes	Lambs	Rams	Total classified	Lambs per 100 ewes	Rams per 100 ewes	Highest winter count[a]	Population estimate
1972[b]	14	3	3	20	21	21	19	22
1973	13	3	3	19	23	23	19	25
1974	17	8	5	30	47	29	30	40
1975[b]	25	12	10	47	48	40	47	55
1976[b]	26	19	8	53	73	31	53	60
1977[b]	24	19	17	70	79	71	63	70
1978		No data					78	85
1979	33	23	22	78	70	67	85	95
1980	37	19	30	86	51	81	86	95
1981	55	11	26	92	20	47	92	100
1982	42	16	25	83	38	59	83	95
1983	38	27	28	93	71	74	96	110
1984	46	25	24	95	54	52	96	110
1985	58	19	20	97	33	34	97	110
1986	46	15	26	87	33	57	87	100
1987[c]	19	2	11	33	11	58	33	34
1988[c]	21	2	13	36	10	62	36	36
1989[c]	21	2	9	32	10	43	32	33
1990[c]	19	7	8	34	37	42	34	36
1991[c]	21	9	10	40	43	48	40	45
1992[c]	23	10	15	48	43	65	48	55

[a] Jan through Apr counts unless otherwise noted. Highest count by ground or supercub aircraft. Includes bighorns transplanted.

[b] Jun through Aug counts on summer range.

[c] Winter range counts involving tagged animals.

METHODS

Surviving Lostine bighorns were captured in a corral trap and ear tagged with alflex numbered tags. All known surviving bighorns except 1 ram were eventually ear tagged.

Individual records were kept on animal movements, body condition, treatments received, blood and nasal test results through January 1992. Herd composition counts were conducted in June-July on the summer range and again in December-February on the winter range. Trapping was conducted during mid-winter to tag surviving lambs and collect blood samples and nasal smears. Cotton tipped swabs were used to rub the nares. Nasal swabs were placed in Amies transport medium and submitted within 48 hours after collection to the Washington Animal Disease Diagnostic Laboratory, Pullman, Washington, for bacteria analysis. Bacterial isolates were confirmed by biochemical testing (Carter 1984). Biotyping and serotyping methods for P. haemolytica were completed using established formats (Biberstein 1978, Frank and Wessman 1978). Replicate ground counts were made from December through February on the winter range until observers were satisfied that the census was complete. Ear tag numbers were recorded on individual record cards that aided in the accuracy of the surveys. Marked animals that were not located for 2 years were considered dead.

RESULTS AND DISCUSSION

Lamb Survival Since Die-Off

June-July lamb production counts indicate lamb:ewe ratios varying from a low of 43:100 in 1988 to 71:100 in 1990 (Table 2). December-February herd composition counts (Table 2) indicated lamb survival was poor the first 2 years following the die-off with lamb ratios of 11 and 10:100 ewes in 1987 and 1988, respectively. Survival increased from a low of 22% the first lambing period after the disease outbreak to 66% in 1991.

Table 2. Bighorn lamb:ewe ratios from surveys conducted during June-July and December-February, and percent lamb survival between July and December counts, 1987-91.

Year	June-July Lambs/ 100 ewes	(n)	December-February Lambs/ 100 ewes	(n)	Percent Survival
1987	50	(21)	11	(21)	22%
1988	43	(30)	10	(23)	23%
1989	No data		37	(36)	
1990	71	(36)	43	(30)	61%
1991	65	(28)	43	(33)	66%

Poor lamb survival following Pasteurella die-offs has been reported by Onderka and Wishart (1984), Festa-Bianchet (1988), and Foreyt (1988). Foreyt (1988) reported lambs born to captive ewes shedding P. haemolytica in nasal secretions were healthy until 6 to 11 weeks of age when they developed pneumonia and died. In his study, all lambs died for 3 years after the pneumonia outbreak. Festa-Bianchet (1988) also reported low recruitment following a pneumonia epizootic. In the Alberta study, only 13% of the lambs born the year of the die-off (1985) survived to 1 year of age. Lamb survival 2 years later was 41% (1986) and 36% (1987), respectively. Onderka and Wishart (1984) also reported low lamb production and survival the 2 years following a die-off in southern Alberta. Lamb:ewe ratios were 23 and 18:100 in 1983 and 1984, respectively, following the disease outbreak.

Time of Lamb Losses

The timing of lamb losses appeared to be similar to that reported by Foreyt (1988). Most Lostine lambs were born between 15 May and 1 June. July herd composition lamb counts were conducted on the summer range when lambs were 6 to 8 weeks old. Random counts conducted between September and November indicate lamb losses had occurred by this date. A few sick lambs (generally smaller in size than normal) were observed during this time period, but by December when winter surveys began, lambs generally looked healthy. Visual observations of lambs pre- and post-disease, suggest a greater proportion of poor quality lambs (smaller body size) since the die-off; however, information on body weights were not obtained.

Lambs less than 11 weeks of age born to ewes surviving a Pasteurella die-off may be protected by colostral immunity as reported by Foreyt (1988). Our observations indicate lamb mortality began shortly after birth; however, most lamb mortality occurred after 15 July at a time when consumption of milk appears to be dropping as grasses and forbs make up an increasing proportion of their diet.

Lambs born in 1987 and 1988, that survived until winter, also suffered a 50% mortality through winter 1991-92. Both 1987 lambs have survived to date, but the 2 1988 lambs (1 male, 1 female) were last seen in spring 1989 and are presumed dead. Survival of lambs beyond winter counts was difficult to assess in 1989-91 since fewer survivors were ear-tagged.

Adult Survival Since "Die-Off"

Twenty ewes (1 year or older), 2 lambs, and 12 rams (1 to 4 years of age) survived this die-off. Six of these adult ewes, have since been found dead or disappeared and are presumed dead, for a 70% post die-off survival rate. Two ewes died or disappeared in 1988, 1 in 1989, and 3 in 1990. Four ewes were seen with injuries, in poor condition, or appeared lethargic prior to their disappearance. Predation could have been a factor in at least 1 case judging from injuries on the animal. Of the 2 lambs, a female and male, only the female appeared to have survived. The ram was last seen in 1990 as a 4 year old, 16 km north of the winter range in flat agricultural land.

Six of the 12 surviving rams (50%) have disappeared and one 7 1/2 year old was taken by a hunter in 1991 (the first year sheep season reopened). Four rams were last seen in 1988 and they were 3 and 4 years of age at that time. Two 4 year old rams were last seen in 1989 and 1990. Why post die-off ram survival was lower than for ewes is unknown. It is possible that some emigration occurred, but no tagged Lostine rams have been observed in other herds. None of the rams unaccounted for appeared in poor condition or were noted with injuries as was the case with ewes. Poaching or cougar predation are other possibilities, but known illegal kills have rarely occurred in the area. The cougar population is moderate to high in this unit (Minam Wildlife Management Unit) and a few rams killed by cougars were found in past years when sheep population densities were higher. Harrison and Hebert (1988) found that cougars were selective in preying on rams in British Columbia and that kills were seldom located without intensive searches of gully bottoms and thickets. They also found the heaviest mortality in November and December after the rut. Older Lostine rams generally moved away from lamb-ewe groups, following the rut, to winter range that had more cover. Presumably this could make them more vulnerable to cougar predation. However, no dead rams were found or reported since the die-off, but brushy bottoms and thickets were not searched.

Herd Recovery

Bighorn losses from the Lostine die-off took 2 forms. The direct losses from the disease reduced the herd by 66% and poor lamb survival kept the herd at static levels for 3 years following pneumonia episodes (Fig. 1).

Herd size began a slow increase as lamb survival improved (Table 1) and 40 animals were counted the winter of 1990-91. This past winter (1991-92), 48 bighorns were counted and the herd size was estimated at 55 animals. Lamb survival appears to be approaching normal levels with 43:100 ewes classified on the winter range.

Ram numbers are also increasing with 15 rams located this past winter or 65:100 ewes. Most rams are 1 to 3 years old, the result of improved recruitment since 1989. Only 6 rams between 7 and 9 years of age are known to be in the herd.

Disease Testing

Nasal swabs and blood samples have been collected from bighorns captured on the winter range. It is beyond the scope of this paper to report on these results. However, test results from nasal swabs appear to indicate a drop in Pasteurella spp. shedding by adults.

MANAGEMENT IMPLICATIONS

The Lostine Pasteurella die-off has had a devastating impact on Oregon's Rocky Mountain bighorn recovery program. This herd was used as a source of transplant stock as well as providing the bulk of hunting

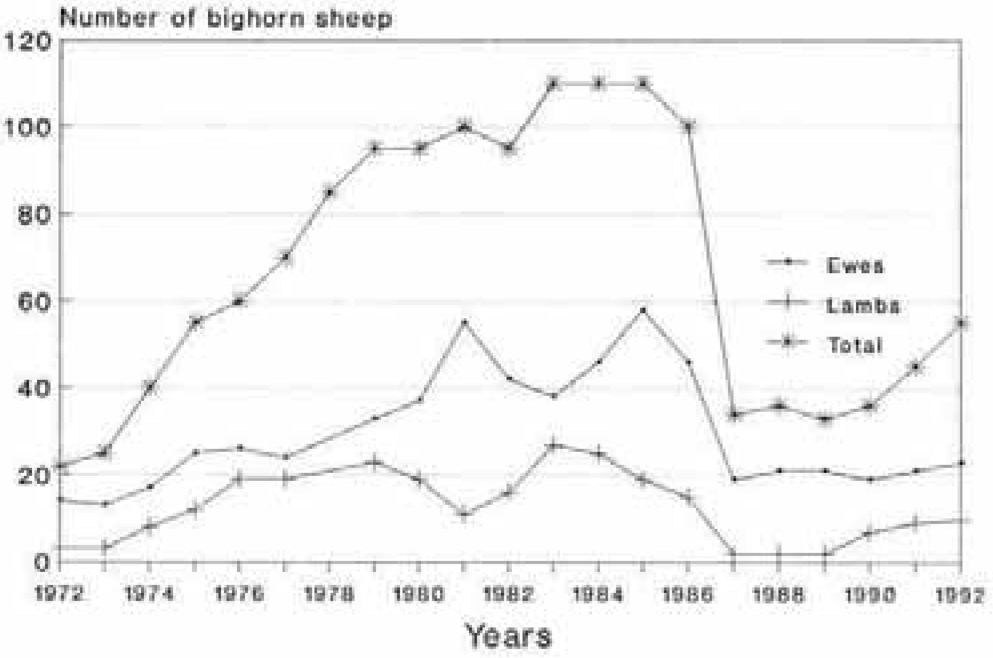

Fig. 1 Lostine bighorn sheep herd composition and population status based on surveys conducted during winters 1972-92. Excludes 1978 when no data were collected.

opportunity. Bighorns have not been transplanted from this herd since 1986. Ram hunting opportunity dropped from 6 tags authorized annually from 1979 to 1986, to no hunts authorized from 1977-90. One tag was offered in 1991 and future tag numbers will be increased if the herd size and ram numbers continue to grow. There is a gap in the age structure of the ram segment of the herd with no known surviving rams between the ages of 4 to 6 and 10 to 12+ years. Hunting opportunity for trophy quality rams will be very limited until the age structure becomes more evenly distributed.

The disease problem also had other implications to Oregon's Rocky Mountain bighorn (RMB) programs. Only 1 RMB transplant in an adjacent wildlife district has been completed since the 1986-87 die-off. Disagreement between Oregon Department of Fish and Wildlife (ODFW), and the Wallowa-Whitman National forest over domestic sheep grazing on sites occupied by bighorns led to a cancellation of all bighorn transplants on the forest. Considerable controversy occurred when hunting and conservation groups, several Indian tribes and livestock interests entered the dispute. Agreement between ODFW and Wallowa-Whitman National Forest was finally reached this past winter and several transplant sites on the forest will be available in the future to continue restoration efforts. Attitudes are changing. ODFW completed several controlled burns on bighorn ranges during Spring 1992. These habitat projects were partially financed by the Foundation for North American Wild Sheep in cooperation with the Wallowa-Whitman National Forest. Hopefully, restoring Oregon's Rocky Mountain bighorns to suitable former range will proceed in a more timely manner with multi-agency support.

There are several other management questions regarding bighorn herds surviving _Pasteurella_ die-offs that need to be answered:

1. At what point (if ever) should supplemental transplants be considered?
2. Should bighorn herds that have recovered from a _Pasteurella_ outbreak be used for transplant stock? If so, at what point should trapping and transplanting begin?
3. What are the risks (if any) of contact between bighorns from a "recovered" herd and adjacent "healthy" animals.

MANAGEMENT RECOMMENDATIONS

The main lesson learned from the Lostine disease problem is to keep domestic sheep and bighorns separated. When contact occurs, serious long-term disease problems and drastic reductions in bighorn numbers and lamb survival can be expected.

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FAILURE OF AN EXPERIMENTAL PASTEURELLA HAEMOLYTICA VACCINE TO PREVENT RESPIRATORY DISEASE AND DEATH IN BIGHORN SHEEP AFTER EXPOSURE TO DOMESTIC SHEEP

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Abstract: An experimental bacterin-toxoid vaccine of *Pasteurella haemolytica* A2, T3, and T10 was evaluated in bighorn sheep (*Ovis canadensis canadensis*). Three bighorn sheep were vaccinated twice, 14 days apart, and 3 bighorn sheep were not vaccinated. Challenge infection was accomplished by introducing 4 clinically healthy domestic sheep that had detectable *P. haemolytica* in nasal sinuses onto the 2.4 ha pasture with the bighorns. Five of 6 bighorn sheep, including the 3 vaccinates died within 40 days after exposure to domestic sheep. *Pasteurella* sp., *P. haemolytica* T3,4,10,11, an untypeable *P. haemolytica*, and *P. multocida* were isolated from dead bighorn sheep, and *P. haemolytica* A1, A2, and *P. multocida* were isolated from the domestic sheep. Vaccine efficacy could not be determined, as *Pasteurella* spp. in dead bighorns differed from those in the vaccine. However, the vaccine did not protect the vaccinated sheep from clinical pneumonia and death. The experiment reinforced the premise that domestic sheep and bighorn sheep should be separated or bighorns may die from pneumonia.

Respiratory disease is a major mortality factor in bighorn sheep populations in North America (Buechner 1960, Spraker and Hibler 1982). Predisposing factors, such as lungworms (*Protostrongylus* spp.), respiratory viruses and bacteria, and various stressors, are often associated with bighorn sheep pneumonia (Post 1962, Forrester 1971, Spraker and Hibler 1982, Onderka and Wishart 1984, Spraker et al. 1984), however, the major organism isolated from pneumonic bighorns is *P. haemolytica*, a gram negative pneumophylic bacterium (Coggins 1988, Onderka and Wishart 1984, 1988, Foreyt 1989). Two major biovars, A and T, serovars 1 through 15, and several untypeable serovars are part of the *P. haemolytica* complex. The T biotype, which is often nonhemolytic on blood agar, is isolated commonly from pneumonic and clinically healthy bighorn sheep (Onderka et al. 1988, Wild and Miller 1991).

Contact with domestic sheep is an important predisposing factor for some pneumonia episodes in bighorn sheep. Under experimental and field conditions, high mortality rates have occurred for bighorn sheep after such contacts (Coggins 1988, Onderka and Wishart 1988, Onderka et al. 1988, Foreyt 1989, 1990). Serotypes of *P. haemolytica* that are usually nonpathogenic in domestic sheep are likely transferred to bighorn sheep, resulting in fatal pneumonia in bighorn populations (Foreyt and Jessup 1982, Onderka and Wishert 1988, Foreyt 1989, 1990). It is also probable that recruitment in residual bighorn sheep populations surviving *P. haemolytica* pneumonia after domestic sheep association or from indigenously acquired pneumonia will be low for several years (Bailey

1986, Coggins 1988, Foreyt 1990). Lambs likely acquire P. haemolytica from oral and nasal secretions from their dams, and die from pneumonia at 6-11 weeks of age when colostral immunity wanes (Foreyt 1990). Although the exact mechanism which is responsible for pneumonia in bighorn sheep following association with domestic sheep is not known, experimental and field data indicate that bighorn sheep and domestic sheep are not compatible species on the same range. Physiologically, bighorn sheep alveolar macrophage function and arachidonic acid metabolism differ significantly from domestic sheep and may be factors in the increased sensitivity of bighorn sheep to respiratory disease compared to domestic sheep (Silflow et al. 1991).

This study evaluated the efficacy of an experimental P. haemolytica bacterin-toxoid vaccine against respiratory disease in bighorn sheep by placing domestic sheep on the same pasture with vaccinated and unvaccinated bighorn sheep. Clinical pneumonia and mortality were the major parameters used to determine effectiveness of the vaccine.

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MATERIALS AND METHODS

Six Rocky Mountain bighorn sheep (Ovis canadensis canadensis), 3 males and 3 females, ranging in age from 1 to 5 years, were used. Five of the sheep were born and raised in captivity at Washington State University, Pullman, Washington, and 1 sheep (No. 5) was captured in the wild and held for 6 months with the other 5 sheep before the experiment began. Fresh water and a shelter were available at all times, but supplemental feed was not provided because pasture forage conditions on the 2.4 ha pasture were excellent.

Nasal swabs were collected from each bighorn 5 months prior to initiation of the experiment, and at the time of the first vaccination. Sheep were sampled for bacteria by inserting cotton tipped swabs into the nares of each sheep, and immediately placing them in Stuart's transport medium without agar. Swabs were submitted within 2 hours after collection to the Washington Animal Disease Diagnostic Laboratory (WADDL), Pullman, Washington 99164, for bacteriologic analysis. Bacterial isolates were confirmed as P. haemolytica by routine biochemical testing (Carter 1984). Biotyping and rapid plate serotyping methods were done according to established formats (Biberstein 1978, Frank and Wessman 1978).

Three bighorn sheep, a 3 yr-old and a 5 yr-old female, and a 1 yr-old male, were not vaccinated, and 3 bighorn sheep, 2 3-yr-old males, and a 3 yr-old female were vaccinated intramuscularly with 2 mls of an experimental P. haemolytica vaccine (NOBL Laboratories, Sioux Center, Iowa 51250) on 10 and 24 April 1990. The formalinized vaccine was a bacterin-toxoid prepared from leucotoxoid and outer membrane proteins of P. haemolytica, types A2, T3, and T10. The original strains of P.

haemolytica were isolated from bighorn sheep that died from pneumonia after exposure to domestic sheep (Foreyt 1990). Types A2, T3, and T10 antigen components were prepared in identical fashion until batching into the vaccine. Each component was grown in RPMI-1640 containing L-glutamine. Bovine serum albumin was supplemented at 0.1%. Final bulk harvest was 6 passages beyond the original isolate. Growth was at 37 C in a glass bottle, and cultures were stirred at a moderate speed. Cultures were harvested during log phase at 6 hours and found to be well encapsulated. Fluids were centrifuged and the cells separated from the supernatent. Fluids were concentrated approximately 10 times using an Amicon unit equipped with a Y-10 filter. Formalin was added to a concentration of 0.5% (v/v) and the mixture stirred at 4 C for 48 hr. This leukotoxoid was adsorbed to 10% aluminum hydroxide (v/v). The cell fraction was resuspended in normal saline and sonicated until capsules were no longer evident by microscopic examination. The sonicate was centrifuged and the supernate retained. The leukotoxoid and the crude outer membrane proteins were combined with an oil adjuvant for administration.

On 10 April 1990, 28 domestic sheep at the University of Idaho Sheep Center, Moscow, Idaho, were sampled for bacteria using nasal swabs as described previously for bighorn sheep. Duplicate swabs were collected and submitted for viral isolation. Routine laboratory isolation techniques were used for isolation of aerobic bacteria and viruses. Isolation of Chlamydia spp. and Mycoplasma spp. was not specifically attempted. Four domestic sheep, identified as carriers of P. haemolytica, were purchased and introduced into the bighorn sheep pen on 8 May 1990, 2 weeks after the second bighorn vaccination. A second nasal swab was collected 30 days after the first.

Fecal samples were collected from the rectum of all animals at the initiation of the experiment, and from dead animals that were necropsied. A Baermann apparatus was used to isolate larvae from feces, and the sediment was examined microscopically for lungworm larvae. All sheep were observed twice daily for clinical signs of disease. Sheep were to be euthanized if they became clinically affected. A complete necropsy, with emphasis on isolation of respiratory pathogens, was done on each dead sheep. Standard necropsy, histolopathogic, parasitologic, and microbiologic techniques were used by WADDL personnel.

RESULTS

Pasteurella haemolytica was not isolated from nasal swabs from any of the bighorn sheep before or at the time of vaccination. From the 4 domestic sheep, P. haemolytica A1 was isolated from 2, P. haemolytica A2 from 3, and P. multocida from 3 (Table 1). Some coliform bacteria, Streptococcus sp., Bacillus sp. and Pseudomonas sp., were isolated from 1 or more of the bighorn sheep, but were not considered important.

Five of the 6 bighorn sheep, including the 3 vaccinates, died between 26 and 40 ($\overline{X}$ = 34) days after exposure to the domestic sheep. All 5 bighorn sheep that died developed a clinical syndrome of tachypnea, dyspnea, incoordination, and weakness prior to death. Sheep developed clinical signs within 24 hr of death. All bighorn sheep died during the

Table 1. Summary of *Pasteurella* spp. isolated from domestic sheep and bighorn sheep during a vaccine trial.

Sheep number	Age	Sex	Day of death	Nasal swab isolations Experimental day 0	 Experimental day 30	Lung isolations at death
Vaccinated bighorns						
1	3	F	26	None Isolated	NA[a]	*Pasteurella* sp.[b]
2	3	M	33	None Isolated	ND[c]	*P. haemolytica*[d] (untypeable) *P. multocida*
3	3	M	34	None Isolated	ND	*P. multocida*
Unvaccinated bighorns						
4	5	F	35	None Isolated	ND	*P. multocida*
5	1	M	40	None Isolated	ND	*P. haemolytica* T3,4,10,11
6	3	F	NA	None Isolated	ND	NA
Domestic sheep						
7	Adult	F	NA	*P. haemolytica* (untypeable)	*P. haemolytica* A2 *P. multocida*	NA
8	Adult	F	NA	*P. haemolytica* A1 *P. multocida*	*P. haemolytica* A1 *P. haemolytica* (untypeable)	NA
9	Adult	F	NA	*P. haemolytica* A1	*P. multocida* A2	NA
10	Adult	F	NA	*P. haemolytica* A2	*P. haemolytica* A2	NA

[a] NA = Not applicable.
[b] Also *Pasteurella* sp. from tracheobranchial lymph nodes.
[c] ND = Not done.
[d] Also *P.* multocida and *P. haemolytica* T3,4,10,11 from tracheobronchial lymph nodes.

night and were found in the morning. At necropsy, all bighorns had adequate body fat and had lesions which were typical of severe hemorrhagic, necrotizing bacterial pneumonia. Grossly, lung lobes were dark red, firm, friable, and consolidated, and were often covered with fibrin tags. Up to 90% of lung parenchyma was involved with fibrous adhesions between lung lobes, pericardium, and parietal pleura. Histopathologic pulmonary lesions were consistent with bacterial pneumonia and included marked accumulation of neutrophils, macrophages, cellular debris, and proteinaceous fluid. The pleura was thickened and disrupted by infiltrates of histiocytes, lymphocytes, and neutrophils. Fibrin and necrotic debris replaced much of the pulmonary tissue.

Bacterial isolates from the vaccinated bighorns included Pasteurella sp. (species could not be identified) from lung and tracheobronchial lymph node of bighorn No. 1, an untypeable P. haemolytica and P. multocida from lung, and P. multocida and P. haemolytica (cross reacted with T3,4,10, and 11) from tracheobronchial lymph node of bighorn No. 2, and P. multocida from lung of bighorn No. 3 (Table 1). The 2 unvaccinated bighorn sheep that died yielded P. multocida and P. haemolytica (cross reacted with T3, T4, T10, and T11) from lung of No. 4, and P. multocida from lung of No. 5 (Table 1). Viruses were not isolated, lungworms were not detected in lungs, and lungworm larvae were not detected in feces or histologically in any bighorn sheep. The last bighorn survived the experiment and remained healthy for 12 months after the termination of the experiment.

All 4 domestic sheep remained clinically healthy during the 60 days they were on the pasture with the bighorn sheep. Viruses, lungworms, or lungworm larvae were not isolated from them.

DISCUSSION

Five of 6 bighorn sheep developed clinical pneumonia and died 26-40 days after exposure to domestic sheep, supporting previous reports that association with domestic sheep may predispose bighorn sheep to fatal pneumonia (Foreyt and Jessup 1982, Coggins 1988, Onderka and Wishart 1988, Foreyt 1989, 1990). In previous reports, P. haemolytica has been incriminated as the major pathogen transmitted from domestic sheep. In this experiment, P. multocida was the only pathogen isolated from lungs of 2 of the bighorn sheep (1 vaccinate and 1 nonvaccinate), and was also isolated with P. haemolytica in 2 others, supporting the results of Callan et al.(1991), who isolated P. multocida from 5 of 6 dead pneumonic bighorns after exposure to a flock of exotic wild and domestic sheep. Based on all published reports, it is likely that some strains of P. haemolytica and P. multocida are pathogenic to bighorns after transfer from domestics.

Vaccinated and unvaccinated sheep died within the same time period, 26 to 40 days after exposure to domestic sheep, and lesions in all dead sheep were similar. This indicated that the vaccine did not exacerbate clinical disease. Wilke et al. (1980) reported that calves vaccinated with a P. haemolytica bacterin and then challenged with P. haemolytica, were more severely affected by clinical disease and lesions than were unvaccinated calves.

The only P. haemolytica isolated from vaccinated bighorn sheep lungs was untypeable. A second vaccinated bighorn sheep had a Pasteurella sp. that could not be identified to species. These results involving P. multocida, untypeable P. haemolytica, and uncharacterized Pasteurella sp. further complicate knowledge regarding the epizootiology of the bighorn sheep pneumonia complex and the association with domestic sheep. It is likely that a variety of Pasteurella spp. organisms may be lethal to bighorn sheep, and more reliable diagnostics are needed for bacterial isolation and identification. Bacteria may have similar morphologic characteristics in culture, yet their identities may differ, suggesting that many colonies per agar plate must be identified. Several serotypes of P. haemolytica have been isolated from single morphologic colony types (Onderka et al. 1988), and several DNA types and ribotypes may be present within serovars (Snipes et al. 1992). DNA analysis, ribotype analysis, and cytotoxicity studies may clarify the identification and pathogenicity of organisms important in the bighorn sheep pneumonia complex.

Culture of tonsillar biopsies and pharyngeal swabs from bighorn and domestic sheep has indicated that many bighorn and domestic sheep are carriers of P. haemolytica, even though bacteria cannot be isolated from nasal swabs (Shreeve and Thompson 1970, Gilmour et al. 1974, Al-Sultan and Aitken 1985, Onderka and Wishart 1988, Dunbar et al. 1990, Wild and Miller 1991). Only nasal swabs were used in this experiment; therefore, it is possible the bighorns were carriers of P. haemolytica and/or P. multocida sequestered in pharyngeal tissue, without shedding bacteria in nasal secretions. However, no Pasteurella spp. were isolated from bighorn sheep nasal swabs 5 months before the experiment and on the day of vaccination, indicating that if Pasteurella spp. were present, shedding rate was low.

Possible important factors in the epizootiology of the pneumonia complex include stress from the presence of domestic sheep in close proximity to bighorns, and bacteria from domestic sheep suppressing bighorn immune function, allowing indigenous bacteria to colonize and initiate pathogenic responses. However, based on available data, bacteria transferred from domestic sheep to bighorn sheep likely resulted in bighorn deaths. Unusual human activity, noise, inclement weather, nutritional deficiencies, adverse social encounters, population density factors, or other stressors could not be identified specifically before or during the experiment, but stress in various forms could have occurred. Stress parameters were not eliminated. The bighorn sheep usually segregated from the domestic sheep on the pasture, but occasionally shared common resting and feeding areas, and interacted socially with the domestic sheep. Effects of inapparent stressors that could be important in the epizootiology of bacterial pneumonias in bighorn sheep remain to be evaluated. Although adequate nutrition, minimal population density, and other management factors reduce the probability of disease related die-offs, association with domestic sheep appears to function independently in predisposing fatal pneumonia.

Only 1 bighorn sheep survived the experiment, and remained clinically normal 1 year later. This sheep was born in captivity, and to my knowledge did not experience respiratory disease before, during, or after the experiment. Inherent genetic resistance or acquired immunity are possible explanations for survival. Acquired immunity or inherent genetic resistance could protect sheep from pneumonia, and could explain bighorn ewes surviving a die-off related to domestic sheep exposure and producing lambs that for several successive years succumb to fatal pneumonia (Coggins 1988, Foreyt 1990).

The vaccine used in this experiment did not protect bighorn sheep against clinical pneumonia and death. However, Pasteurella spp. strains isolated from dead bighorns may not have been in the vaccine, specifically, P. multocida, untypeable P. haemolytica and Pasteurella sp. Therefore, vaccine efficacy could not be evaluated from this experiment, but the vaccine was a failure in terms of preventing sickness and death. Newer vaccines are likely to include many serovars important in the Pasteurella spp. complex. Vaccines incorporating serovars types that have cross protective characteristics would be most effective. An effective vaccine against P. haemolytica and P. multocida in free-ranging bighorn sheep, and possibly domestic sheep, would represent a significant and needed advance in wildlife management by protecting herds from massive die-offs caused by Pasteurella spp., and the deleterious effects of low recruitment following the initial mortality (Bailey 1986, Coggins 1988, Foreyt 1990).

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NATURALLY OCCURRING PNEUMONIA IN CAESARIAN-DERIVED ROCKY MOUNTAIN BIGHORN SHEEP LAMBS

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Abstract: Survival of bighorn lambs beyond 10 weeks of age was reported to be as low as 4% in some regions of central Idaho in 1988-89. Observations of lambs during the first weeks of life in 1990 confirmed early death losses but did not establish the causes. Pregnant ewes were captured in April of 1991 from 2 herds in which low lamb recruitment had been reported. Single male lambs were taken by caesarian-section from 2 of the ewes and a third ewe gave natural birth to a single ewe lamb. The caesarian-derived lambs were bottle fed in isolation for the first 3 weeks of life and remained free of *Pasteurella* spp. until they were exposed to their mothers. At 8 and 10 weeks of age the 2 lambs developed evidence of inner ear irritation and pneumonia. The infections were allowed to progress until it was concluded that the lambs would die due to the pneumonia complex if left untreated. Transtracheal wash samples were collected from the lungs of each lamb. Lungworms (*Protostrongylus stilesi*), transmitted from the dams by the placenta, and biotype T *P. haemolytica* were recovered from transtracheal wash samples of both lambs. Both lambs recovered fully after treatment with antibiotics and an antihelmintic.

Idaho Department of Fish and Game officials, backpackers and hunters reported hearing harsh coughing from the majority of bighorn sheep (*Ovis canadensis canadensis*) observed on the Salmon River drainage of central Idaho in fall and winter 1988-89. Survival of lambs was subsequently reported to be low in herds of that area in 1989 and 1990. Respiratory disease has been reported to be a primary factor associated with poor lamb survival (Spraker et al. 1984). Potential causes of respiratory disease are multiple and may vary between herds, climatic conditions, and other contributing factors. Viruses, bacteria, and lungworms have been identified as causes of pneumonia associated with lamb mortality (Parks and England 1974, Spraker et al. 1986). University of Idaho, Department of Fish and Game, and Idaho Department of Agriculture personnel joined in efforts to identify causes of respiratory disease and poor lamb survival in Idaho herds.

During spring and summer 1990, 10 radio-collared ewes were monitored to determine the health status of their lambs (J. and H. Akenson, pers. commun.). Each of the 10 ewes delivered live lambs, all of which died within 8 weeks of birth. Three lamb carcasses were found and examined for causes of death. However, scavenger activity and the small number of carcasses found limited the amount of information that could be applied to determination of causes of death of the 10 lambs. Therefore, the following study was conducted to evaluate the health of lambs in a controlled environment.

METHODS

Two 4-year-old ewes were captured on 11 April 1991 by helicopter net-gunning techniques from free-ranging herds near Challis, Idaho on the Morgan Creek drainage. They were hobbled, blind-folded, and transported by helicopter in sheep-bags from the capture site to a processing location. Blood, feces, tonsillar, and nasal samples were collected from the ewes while physical and pregnancy examinations were made. Body temperatures of the ewes were closely monitored to avoid hyperthermia. The ewes were loaded into a 1.3 X 2.5 m darkened wood box and transported approximately 358 km (222 mi) to a 30.3 X 30.3 m pen near the University of Idaho Caine Veterinary Teaching and Research Center (CVTRC) south of Caldwell, Idaho. A third ewe was captured on 8 April 1991 on the Big Creek drainage east of McCall, Idaho by immobilization with 3 mg carfentanil citrate injected with a dart gun. This ewe was hobbled, blind-folded, and injected with 300 mg naloxone. Half of the naloxone was injected intramuscularly and the remainder subcutaneously into the ewe prior to her transport by airplane to the Caldwell airport. She was then taken by truck to the Caldwell facilities and placed in a pen 15 m from the pen for the ewes from Morgan Creek. The pens were constructed of wood poles 20-30 cm in diameter, 1.85 m high New Zealand fencing and topped with 3 strands of high tensile wire which was connected to an electrical fence unit. Black depredation netting was attached to the inside of the New Zealand fencing to make it more visible for the sheep. The ground level on the eastern side of the pen was approximately 3 m higher than on the west side thus providing an area where the sheep could seek higher elevation and reduce stress associated with the presence of people presenting feed at a lower gate. Mixed grass and alfalfa hay was placed in the lower portion of the pen once a day and water was provided in an automatic waterer. The animals were watched with field glasses from a distance of approximately 100 m to monitor mammary development signalling approaching parturition.

On 16 May when it was judged that the ewes were close to lambing, they were captured by use of linear drive nets, blind-folded, hobbled, and transported to the CVTRC surgical section. The ewes were prepared for abdominal ultra-sonogram (Aloka 210 instrument; Corometrics, Wallingford, Connecticut 06492 USA) and checked for colostral secretions. Both of the Morgan Creek ewes were producing colostrum and ultra-sonograms indicated well developed lambs. The udder of the Big Creek ewe contained minimal secretions and the ultra-sonogram of the lamb indicated a less developed lamb. Therefore, the decision was made to take the lambs by caesarian-section from the highly excitable Morgan Creek ewes, but not from the more docile Big Creek ewe. Anesthesia of the ewes was induced and maintained with halothane. Caesarian-sections were performed through a ventral midline surgical approach. Both lambs (BR91-017 and BR91-018) were males and judged to be near term. Colostral secretions were collected from the ewes and given to their respective lambs, both of which nursed vigorously from bottles. Surgical sites were closed and the ewes were returned to their enclosure. Antibiotics were not administered postoperatively. Recovery of the ewes was complete and unremarkable. The third ewe gave birth to a ewe lamb (BR01-019) 1 week after caesarian-sections were performed on the 2 other ewes.

The caesarian-derived lambs were isolated from other animals and fed non-sweetened canned evaporated milk every 4-6 hrs for the first 2 weeks of life. At 15 days postdelivery (PD) feeding of pasteurized milk from domestic ewes was initiated. A lamb milk replacer (Land O'Lake, Inc., Fort Dodge, Iowa 50501 USA) was used to supplement ewe milk as needed through the 7th week. Milk replacer was the only source of milk fed during weeks 8-18. Rectal body temperatures were taken at each feeding time. Free access to mixed grass and alfalfa hay and water was provided following the 2nd week. The lambs were placed in pens with their mothers for 1-4 hrs/day on PD days 20, 22, 28, 29, 34, 35, 37 and 44 to allow them to acquire microbial flora from their dams.

Culturette swabs (Marion Laboratories, Inc., Kansas City, Missouri 64114 USA) were used to collect nasal and tonsillar samples from the ewes and lambs. These samples and transtracheal wash samples were cultured for bacteria at CVTRC. Viral transport swabs (Becton Dickinson Microbiology Systems, Cockeysville, Maryland 21030 USA) were used to collect samples from ewes and lambs. The latter swabs were submitted to the Washington State Animal Disease Diagnostic Laboratory (WADDL) for virus isolation procedures. Fecal samples were collected from ewes at the time of capture and monthly for 2 months, from the caesarian derived lambs at 12 days, and from all lambs at approximately 1 month of age. All fecal samples were examined for parasites at CVTRC. In addition, sera were submitted to the Idaho State Animal Industries Laboratory for testing to detect antibodies against viruses and bacteria (Table 1).

Three media; Columbia blood agar with 5% ovine blood (CBA), Columbia blood agar with bovine blood plus antibiotics to provide selectivity for Pasteurella (Ward et al. 1986), and Hayflick's agar selective for Mycoplasma (Stalheim 1990) were inoculated for isolation of bacteria. Culture media were incubated at 35C in an atmosphere with 5% added CO_2. All bacterial isolates were evaluated. Pasteurella identification and biotype differentiation were conducted by established procedures (Carter 1990, Kilian and Frederiksen 1981). Serotyping of the Pasteurella haemolytica isolates was conducted by slide agglutination tests with specific antisera (Frank and Wessman 1978).

RESULTS

All ewes were clinically normal prior to and following delivery of their lambs. The naturally delivered ewe lamb BR91-019, was vigorous and did not demonstrate clinical illness during the 5-month observation

Table 1. Antibody titers in sera of adult bighorn ewes to bacterial and viral pathogens, Caldwell, Idaho.

Disease agents (tests)[a]	Antibody titers/animal BR91-003	 BR91-008	 BR91-012
Bacterial:			
Anaplasma marginale (CF)	10[b]	NEG	NEG
Brucella ovis (ELISA)	NEG	NEG	NEG
Campylobacter fetus venerealis (MA)	NEG	NEG	NEG
Haemophilus somnus (MA)	NEG	NEG	NEG
Leptospira interrogans (MicroA)	50	NEG	50
Viral:			
Bluetongue virus (AGID)	NEG	NEG	NEG
Bovine viral diarrhea virus (SN)	8	NEG	NEG
Epizootic hemorrhagic virus (AGID)	NEG	NEG	NEG
Infectious bovine rhinotracheititis virus (SN)	8	8	NEG
Ovine progressive pneumonia virus	NEG	NEG	NEG
Parainfluenza-3 virus (SN)	NEG	NEG	NEG
Respiratory syncytial virus (SN)	NEG	8	8

[a] Antibody titers were quantitated by: CF, complement fixation procedure; ELISA, Enzyme-linked immunosorbent assay; MA, macroscopic agglutination; MicroA, microscopic agglutination; AGID, agar gel immunodiffusion; SN, serum neutralization.

[b] A titer of 10 to *Anaplasma marginale* antigen is considered significant. All other listed titers are too low to be considered diagnostic.

period. At 50 days PD, lamb BR91-018 developed ear irritation as demonstrated by tilting of the head to the right, drooping of the right ear, scratching of the ear with his rear leg, and head shaking. Otoscopy revealed a reddened ear-drum but no evidence of external irritants. On day 52 the lamb coughed frequently and the rectal temperature was elevated to 40.2C. The temperature continued to increase to 41.5C by day 54. The lamb reduced his milk intake, had signs of dehydration, depression, dyspnea, and was reluctant to move on day 55 when the decision was made to collect a transtracheal wash sample and initiate antibiotic treatment. An initial injection of Durapen™ (VEDCO, Inc., Overland Park, Kansas 66204 USA) was given followed by 6 daily injections of ampicillin. Both lambs coughed easily when pressure was applied to their chests. However, Lamb BR91-017 did not demonstrate clinical illness until day 65 when a head tilt and drooping of both ears became evident. The latter lamb was febrile (39.8C) on PD day 70 and was reluctant to nurse a bottle. The lamb was depressed by the following day when the rectal temperature was 40.6C. Therefore, a transtracheal wash sample was collected for examination. Two days later it appeared the lamb was becoming progressively worse and death appeared imminent. Lamb BR91-018 also continued to cough and appear slightly depressed. Therefore, both lambs were given daily injections of Naxcel™ (The Upjohn Company, Kalamazoo, Michigan 49001 USA) for 2 days followed by amoxicillin for 5 days. Ivermectin (MSD AGVET, Division of Merck & Co. Inc., Rahway, New Jersey 07065 USA) was given to both lambs on day 76 for elimination of Protostrongylus spp.

Pasteurella spp. were not isolated from nasal and tonsillar swab samples taken from the caesarian-derived lambs until they were 40 days old and had been placed in the pens with their mothers on repeated occasions (Table 2). Biotype A isolates were recovered from tonsillar samples of both caesarian-derived lambs when they were sampled at 40 days PD. At day 53, the predominant organisms in samples from these animals was P. haemolytica biotype T which agglutinated in antisera for types 3, 4, and 10. Biotype T P. haemolytica was isolated in pure culture and high numbers from the transtracheal wash samples. Pasteurella haemolytica biotypes A and/or 3 were isolated from all samples collected from lamb BR91-019 beginning at 10 days after birth. Biotype T P. haemolytica was not isolated from any samples collected from either this lamb or her dam.

Pasteurella haemolytica biotypes T and 3, and P. multocida were isolated from samples collected from the ewes (Table 3). The majority of P. haemolytica biotype T isolates agglutinated in antisera 3, 4, and 10. However, 1 biotype T isolate agglutinated only in antiserum for serotype 10.

No parasites or ova were detected in any of the first fecal samples from the lambs. However, P. stilesi was detected in the transtracheal wash samples from the 2 caesarian-derived lambs but not from the other lamb. Lungworm larvae were detected in the feces of the ewes from both Morgan Creek and Big Creek areas. In addition coccidia, Trichuris and Nematodirus were detected in feces of the ewes.

Table 2. *Pasteurella* cultured from samples collected from bighorn lambs at indicated ages, Caldwell, Idaho.

Lamb age (days)	Lamb ID No.	Type of sample[a]	*Pasteurella* isolated
10	BR91-019	N	none
		T	*P. haem* A[b] (UT)[c]
			P. haem 3
12	BR91-017	N, T	none
	BR91-018	N, T	none
29	BR91-019	N	*P. haem* A (1,2)
		T	*P. haem* A (UT)
			P. haem 3
34	BR91-017	N, T	none
	BR91-018	N, T	none
38	BR91-019	N	none
		T	*P. haem* 3
40	BR91-017	N	none
		T	*P. haem* A (5)
	BR91-018	N	none
		T	*P. haem* A (UT)
53	BR91-017	N	*P. haem* T (3,4,10)
		T	*Proteus* overgrowth
	BR91-018	N	*P. haem* T (3,4,10)
		T	*P. haem* T (3,4,10)
55	BR91-018	TTW	*P. haem* T (3,4,10)
64	BR91-018	N	*P. haem* A (UT)
		T	*P. haem* A (UT)
			P. haem T (3,4,10)
72	BR91-017	N	*P. haem* A (5)
			P. haem T (3,4,10)
		T	*P. haem* A (5)
			P. haem T (3,4,10)
	BR91-018	N	*P. haem* A (5)
		T	*P. haem* T (3,4,10)
73	BR91-017	TTW	*P. haem* T (3,4,10)
143	BR91-019	N	*P. haem* 3
		T	*P. haem* 3
		TTW	none

[a] Samples: N = nasal, T = tonsillar, TTW = transtracheal wash.

[b] *Pasteurella haemolytica* biotypes A, T, and 3.

[c] *Pasteurella* serotypes in (), UT = untypable.

Table 3. *Pasteurella* spp. cultured from samples of bighorn ewes at time of capture and following caesarian-section delivery of lambs from 2 ewes and natural delivery by the third ewe, Caldwell, Idaho.

Sampling time	Ewe ID no.	Type of sample[a]	*Pasteurella* spp. and Serotypes isolated
At capture	BR91-003	N	None
		T	*P. haem* 3[b] *P. haem* T (3,4,10)
	BR91-008	N	None
		T	*P. haem* 3 *P. haem* T (3,4,10)
	BR91-012	N	*P. haem* 3
		T	*P. haem* 3 *P. haem* T (3,4,10)
2 days post caesarian	BR91-008	N	None
		T	*P. haem* 3 *P. haem* T (3,4,10)
	BR91-012	N	None
		T	*P. haem* 3 *P. haem* T (3,4,10) *P. haem* T (10)
		TTW	*P. haem* T (3,4,10) *P. multocida*
32 days post caesarian	BR91-008	N	None
		T	*P. haem* 3 *P. haem* T (3,4,10)
	BR91-012	N	None
		T	*P. haem* T (3,4,10)
27 days post delivery	BR91-003	N	*P. haem* 3
		T	*P. haem* 3 *P. haem* T (3,4,10)

[a] Samples: N = nasal, T = tonsillar, TTW = transtracheal wash.

[b] *P. haem* - *Pasteurella haemolytica* biotypes: T and 3; serotypes in (). *P. multocida* - *Pasteurella multocida*: serotyping not conducted.

All nasal, tonsil, and transtracheal samples cultured negative for viruses. Low serum antibody titers were detected against several potential infectious agents (Table 1). However, the only titer considered significant was that against Anaplasma marginale.

DISCUSSION

Disease development in animals is dependent upon a number of factors including; the presence of infectious organisms in the environment, age and immunity of the host, genetic predisposition of an animal to specific diseases, nutrition, and stress (Biberstein 1981, Wiseman et al. 1978, Yates 1982). Most of our knowledge of respiratory disease in ruminants comes from studies of disease in cattle and domestic sheep. In these animals, virus infections of the respiratory tract are commonly associated with development of diseases caused, in part, by opportunistic bacterial pathogens (Carter 1973, Yates 1982). Pasteurella spp. are among the opportunistic bacterial pathogens which are commonly associated with viral infections which predispose their hosts to pneumonia. Infections with viruses or Mycoplasma spp. (Corstvet et al. 1973, Jensen et al. 1976) or infestations with parasites (Spraker 1979) which reduce the defense mechanisms of the lungs may contribute to respiratory pasteurellosis. Protostrongylus stilesi is a common parasite of bighorn sheep which is known to compromise the ability of the lungs to resist infection with opportunistic bacterial pathogens. These parasites may cross the placenta during the third trimester and infest the liver of lambs in utero. They subsequently migrate to the lungs after birth of the lambs and develop to sexual maturity at about 20 days. Larvae then develop and migrate up the bronchial tree causing granulomas in the lung. These events result in reduced resistance to infection with opportunistic bacterial pathogens (Spraker 1979).

Viruses were not isolated from samples collected from the caesarian-derived lambs prior to or at the onset of clinical pneumonia. However, P. haemolytica biotype T and P. stilesi were both present in lung lavage samples collected transtracheally. Both organisms appeared to have played a role in the pneumonic condition of the lambs. Antibiotic therapy improved the general appearance and responsiveness of the lambs but did not eliminate the persistent cough. However, following treatment with ivermectin, the cough response decreased, the lambs became more active, and antibiotic therapy was discontinued without subsequent recurrence of pneumonia.

Protostrongylus stilesi larvae were present in the lungs of the 2 caesarian-derived lambs monitored in this study. Due to age of the lambs at onset of disease and the mode of transmission of these parasites, it is evident that they would have been present in the lambs prior to birth. Thus, the lungworms were present prior to transmission of P. haemolytica from the ewes to their lambs initiating tissue damage resulting in increased susceptibility of the lambs to pneumonic pasteurellosis. Transplacental transmission of P. stilesi to lambs is common in free-ranging herds and may predispose lambs to pneumonia associated with particular strains of P. haemolytica to cause the "summer lamb mortality" syndrome. Isolates of P. haemolytica are being evaluated to identify strains which are associated with this syndrome.

Pasteurella haemolytica is a diverse group of bacteria which appears to be ubiquitous in ruminants (Timoney et al. 1988). These opportunistic pathogens rarely initiate disease but are generally associated with disease only if other factors, such as viruses or lungworms, reduce the resistance of the host. Differentiation between P. haemolytica strains can be achieved by identification of genetic differences revealing "ribotypes" (Snipes et al. 1992) and DNA "fingerprints". The DNA fingerprinting procedure which provides highly discriminatory and reproducible information was subsequently conducted on P. haemolytica isolates from the lambs and their mothers to determine the source of the organisms associated with disease in the lambs (to be published).

Summer lamb mortality causing low recruitment rates in bighorn populations for 4-5 years following a pneumonic outbreak is devastating to the affected herds. Monitoring will continue in bighorn populations to identify additional factors which contribute to this syndrome in efforts to alter or remove those factors which result in disease.

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THEORETICAL CONCEPTS OF DISEASE VERSUS NUTRITION AS PRIMARY FACTORS IN POPULATION REGULATION OF WILD SHEEP

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Abstract: Concepts concerning population regulation, including carrying capacity as it relates to nutrition as the primary population regulating mechanism in wild sheep, are discussed. Literature is reviewed and theoretical concepts are postulated that implicate evolution of the immune system as an important intrinsic factor in population regulation. Population density, as an environmental stressor additive with other environmental stressors, acting upon animal's immune system may be a major population regulatory factor in wild sheep. The concept of immune system dependence versus independence of pathogens, especially regarding *Pasteurella haemolytica*, is proposed by the author. Management implications and recommendations are discussed.

Numerous studies have been conducted to understand complex interactions among animals and environmental factors thought involved in regulation of wildlife populations. As a result, basic concepts have been developed to explain fluctuations or stability, in wildlife numbers and density. These include concepts such as carrying capacity, density dependency, environmental stressors, limiting factors and others, which have helped shape our understanding of population regulation. Without an understanding of concepts and mechanisms that regulate wildlife populations, many management strategies will be ineffective. Although controversy exists and neither scientific nor empirical data adequately justify the relative importance of these concepts, they form the basis of current management strategy. Other, more recent, concepts used to explain population regulation in large ungulates, such as stress and disease as primary factors, have, until recently, been mostly ignored. And, because wild sheep appear more susceptible to adverse affects of epizootic disease than other wild ungulates in North America, they may have evolved with different population regulatory mechanisms making disease more important.

Among biologists, there appear a wide array of opinions concerning cause of sudden declines in wild sheep populations that are similar in nature and circumstance. Most investigators support the concept of carrying capacity and suggest nutritional deficiencies cause or act as triggering mechanisms for these declines. Management strategies, based on this concept, are then used in attempts to reverse or prevent further declines.

However, current management of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) and their habitats does not appear effective despite genuine efforts (Risenhoover et al. 1988, Smith et al. 1991). Without more effective management, bighorn sheep numbers could be expected to further decline over the next 25 years (Jahn and Trefethen 1978). Therefore, if we are to more effectively manage wild sheep populations, we must critically analyze not only management techniques, but concepts on which current management is based. Although the concept of animal population regulation has not been proven, I support the hypothesis and believe that wild sheep are regulated at least partially by intrinsic factors such as the influence of chronic stress upon immune systems.

This report reviews past studies on population dynamics of wild sheep and proposes concepts that may allow better understanding of proposed population regulation, therefore contributing to more effective management.

NUTRITION VERSUS DISEASE

In 1798, Rev. T. R. Malthus pointed out that animal populations always increase up to the limit of their food resources. And, that lack of food through starvation and disease, then acts to prevent further increase (Sinclair 1989). The Malthusian hypothesis has been at the center of all subsequent debate on what regulates populations. However, others have proposed that animal populations may be regulated at a level below that imposed by food supply (Chitty 1960, Stelfox 1976).

Carrying capacity is a concept developed to explain the relationship between habitat and ungulate population size or density. It is defined as, an equilibrium between animals and vegetation (Caughley 1979). This or some similar concepts are used by wildlife managers to justify various strategies and techniques to alter habitat or population size to achieve desired goals. These strategies are premised on the idea that animal numbers and recruitment are based primarily on nutrition and intraspecific competition. Disease, as a population regulator, is often relegated to a proximate mechanism based on nutrition (Davidson 1981, Cook 1990, Cook et al. 1990).

Many investigators of wild sheep in North America have concluded nutrition is the primary factor involved in population regulation. Allen (1962: 59) in discussing the decline of bighorn sheep, stated, "There are numerous factors involved, it seems, in actual control of herd size; but a great deal of it appears traceable to range." Johnson (1983: 149) stated, "diseases have probably been responsible for large scale mortalities in many bighorn populations in North America." He believes that the impact of parasites and disease on population dynamics of bighorn sheep is not well understood, and concludes, "The most important factor in management of bighorn sheep is habitat" (Johnson 1983: 174).

Buechner (1960: 107), stated, "as a population regulation mechanism, the parasite-disease complex,...operates almost independently of the condition of range vegetation." However, in concluding remarks, he considered poor nutrition as the "triggering" mechanism predisposing bighorn sheep to the parasite-disease complex. Streeter (1970a) believed Buechner's final conclusion was unfounded because nutrition range-analysis studies before, during and after die-offs were not made. This was often the case with studies of wild sheep die-offs or annual variations in natality where poor nutrition was considered an important factor (Marsh 1938, Buechner 1960, Woodward et al. 1972, Stelfox 1974, Whitten 1975, Long 1980, Schuerholz 1984, Whitfield and Keller 1984, Festa-Bianchet 1988, Cook 1990). And, when correlation of range conditions and mortality or low recruitment was made, physiological assessment of nutrition was not (Marsh 1938, Buechner 1960, Streeter 1970b, Horejsi 1972, Stelfox 1974, Whitten 1975, Hoefs and Brink 1978, Long 1980, Hoefs and Bayer 1983, Schuerholz 1984, Festa-Bianchet 1988, Cook 1990), casting suspicion on conclusions that vegetation had a primary effect on the population. Complex forces such as nutritional, behavioral, environmental and genetics that act upon a population, have been traditionally assessed by secondary indicators such as habitat, food habits, and population characteristics. Theoretically, assessment of primary indicators obtained directly from animals representing a population would minimize many sources of variation and provide greater precision for studies. Primary indicators reflect the health of the animal, and by proper sampling, the health of a population (Franzmann 1972, Fowler 1986). Consequently, there has been a gradual shift from assessment of carrying capacity by vegetation utilization studies and change in population characteristics to that of establishment of nutritional status of wild populations (Franzmann 1971a, Franzmann 1971b, Hebert 1978). It should no longer be sufficient to simply monitor animal numbers or habitat conditions. One should view with suspicion previous studies conducted on wild sheep population dynamics that suggested nutrition as a cause for population declines, when assessment of health or physiological status was not conducted. Investigators that document a positive correlation between recruitment and range vegetation or precipitation often fail to acknowledge decreased forage production may serve to decrease area of available habitat, thereby increasing population densities. Increase in population density could account for decreased natality without regard for decreased forage quantity or quality.

Some investigators found that preceding a disease induced die-off, bighorn sheep were in fact in good body condition, suggesting little correlation between nutrition and the die-off. Festa-Bianchet (1988: 70) in his study of a pneumonia epizootic in bighorn sheep in Alberta, found "dead sheep in good body condition, with no obvious evidence of malnutrition." Post (1962:4) investigated an outbreak of pasteurellosis in a captive sheep population in Wyoming and found the dead animals to be in "excellent body condition, as denoted by amount of body fat." Other studies involving captive sheep found similar results (Foreyt 1988, Miller et al. 1991). Ryder et al. (1992) in investigating a bighorn sheep die-off in 1991 near Whiskey Mountain, Wyoming, concluded there were good range conditions prior to the die-off of approximately 40% of the herd.

Bailey (1986:333) studied a bighorn sheep herd in Waterton Canyon, Colorado, and after investigating an all-age die-off, concluded "Waterton sheep were in excellent physical condition, indicating no shortage of forage." Other investigators (Fisher 1927, Spraker 1974, McQuivey 1978, Wishart et al. 1980, Spraker and Hibler 1982, Onderka and Wishart 1984, Spraker et al. 1984, Andryk and Irby 1986) found similar results. Cook (1990:215) studied two bighorn sheep herds in Wyoming and, even though he concluded poor nutrition was the cause of death, found nearly all mortalities to be lambs dying from disease and stated "Chlamydia infection likely originated from outside sources and caused substantial mortality even in lambs considered to be in good condition." Heimer (1988:42) in discussing Dall sheep (Ovis dalli dalli) management in Alaska, stated "Nutritional stress may occur in unusual circumstances, but normal circumstances do not lead to this problem. Comparisons of nutrient quality of winter range plants selected by sheep, the summer nutrient quality of these food plants, and the body condition of ewes during rut and in late winter revealed no caloric advantage for a low density population when compared with a high density population." He concluded "Still, population performance was strikingly different between the two; the low density population had better performance."

If nutrition is not a predisposing factor in many die-offs or population regulation of bighorn sheep, what is? Some investigators (Forrester 1971, Hudson 1972, Thorne et al. 1982, Hoefs and Bayer 1983, Spraker et al. 1984, Bailey 1986) believed stress was an important factor in disease caused die-offs in bighorn sheep. And, some (Post 1976, Feuerstein et al. 1980, Spraker and Hibler 1982, Stevens 1982) suggest stress without regard for nutrition, may play a role in bighorn sheep die-offs.

Stress is defined as the need for an individual to make abnormal or extreme adjustments in physiology or behavior to cope with adverse aspects of its environment (Fraser et al. 1975). Stress operates by inducing elevated circulating glucocorticoids and possibly other hormones, which may inhibit immune or reproductive systems, predisposing an animal or population to reduced natality or infectious disease (Christian and Davis 1964, Hunninghake and Fauci 1977, Spraker 1977, Kelley 1988, Griffin 1989, Anderson 1991). Although stress has been shown to affect reproductive function by lowering natality in some animal species (Christian and Davis 1964, Christian 1971), evidence is not available to suggest it operates in this manner in wild sheep populations and will not be discussed. Cohen (1987) proposed that acute stress does not exert a significant effect on immunocompetence, and it is only chronic stress which causes an impairment of immunity compatible with the development of disease. Therefore experiments designed to acutely reduce immune system function by administration of glucocorticoids to mimic stress, may lead to erroneous conclusions. Chronic stress factors, or environmental stressors occur in a variety of forms. Nutrition may be a stressor, acting upon an animal's immune system, predisposing to disease (Chandra and Newberne 1977). Other stressors include population density, inclement weather, chronic diseases, parasitism and harassment.

Several investigators have discussed concepts of stressors that reduce immune system functions and the role stress plays in reducing a populations' resistance to disease. Spraker et al. (1984) discussed stress and the pathogenesis of stress upon bighorn sheep in a die-off in Colorado resulting in the death of 75% to 85% of the population. They concluded stress, mostly from human disturbance caused increased levels of cortisol resulting in inhibition of the inflammatory process and increased susceptibility to bacterial pathogens.

Schwantji (1986:247) studied 3 herds of bighorn sheep in southeastern British Columbia and concluded, "...at a certain population density, additional or increased levels of pre-existing stressors appear to overwhelm the functional immune system and precipitate the occurrence of epidemic disease." Streeter (1970_b_: 50), in comparing demography of 2 bighorn sheep herds in Colorado stated "Based on these statistics, mean breeding population mortality varied directly with mean population density. Mean survival of lambs and mean breeding population growth varied inversely with mean population density." He concluded, "The mechanism could be social stress induced by intraspecific interaction or a nutritional stress induced by a decrease in available forage." He did not find a definitive correlation between mortality and specific forage limitations.

Wehausen et al. (1987) reviewed data from a desert bighorn sheep herd in southern California during 1953 through 1982. During the periods 1953-61 and 1977-82, the population experienced low recruitment rates and suspected disease epizootics. Concerning the population decline beginning in 1977, they stated (p. 95): "Given that average recruitment ratios suggest that this population essentially had been stable since 1977, it would be tempting to interpret its recent dynamics as nothing more than a usual attainment of an ecological carrying capacity set by the interaction of vegetation and the sheep population density alone. Under this interpretation disease would act only as secondary factors precipitated by nutrition. Two factors do not support this interpretation: (1) the substantial discontinuity in recruitment rate that occurred in 1977 and (2) the increased precipitation in critical months during the 1977-82 period, the effect of which should have been a raised carrying capacity and subsequent population increase rather than stabilization." They further concluded, "Our analysis indicate that 3 independent precipitation factors, 1 disease factor and 1 probable population density factor all exhibited measurable effects on the dynamics of lamb recruitment in the Santa Rosa Mountains between 1962 and 1982."

Hudson (1972:33) investigated the functional activities of lymphocytes in sheep that were subjected to capture, transport, and confinement fed medium quality hay and demonstrated alterations of _in vitro_ characteristics of peripheral lymphocytes during stress associated with introduction to captivity. He concluded, "Since bighorn sheep are particularly susceptible to disease when brought into captivity, it is possible that depressed _in vitro_ lymphocyte reactivity reflected impaired immunity." Other investigators have also suggested stress is a factor that reduces the ability of the immune system and increases susceptibility to disease.

Belden et al. (1990) found, in their study of captive bighorns, fluctuations in B cell responses occurred around time of lambing and concluded that this would not be beneficial to the population. This suggests that stress factors are operating upon the immune system at a critical time, during lambing. Time of lambing and especially 6-8 weeks thereafter, when colostral antibodies begin to wane, are certainly a time of high susceptibility in bighorn sheep. At this time densities of sheep can attain highest levels on nursery areas and cause social stress and increased disease transmission, predisposing to disease. Spraker et al. (1984) suggested that stress-related summer lamb mortality was a result of 1 of 2 factors; stressed ewes producing less colostral antibody resulting in lamb deaths due to lack of maternal protection or secondly, surviving ewes carry high levels of Pasteurella spp. which they may transfer to lambs, overwhelming their immune system and causing fatal pneumonia. I suggest both factors could be a result of stress caused by high population density.

Population density historically was viewed as a factor upon which environmental variables depended; increasing their effect as density increased and functioning to reduce density to an equilibrium. These density dependent variables were thought to be an integral part of population regulation. In fact, environmental factors that were not density dependent were not part of the regulation mechanism (Sinclair 1989).

However, I propose population density, or overcrowding, acts as another environmental stressor, intrinsic in nature and may at times act independent of nutrition. It acts upon an animal's immune system via complex interactions of hormones, including mainly glucocorticoids, predisposing to disease. And, other environmental stressors, as previously mentioned, are additive forces serving to suppress population numbers in the same manner as stress resulting from population density.

Marsh (1938) pointed out that crowding was an important factor in pneumonia in bighorn sheep in his studies in Glacier National Park. Hobbs et al. (1990) reported that disease-induced die-offs in bighorn sheep were repeated at approximately 20 year intervals when populations attained peak densities.

Onderka and Wishart (1984) found that the timing of pneumonia outbreaks corresponded to the breeding season of bighorns, when animals are concentrated. Dunbar (Wildl. Dis. Res. Inst., unpubl. data) found high summer lamb mortality in a bighorn sheep herd in central Idaho, when population density was at or near a recorded all time high (Idaho Fish and Game files), and physiological assessment of ewes just prior to lambing revealed they were in good physical condition.

Murphy and Whitten (1976) found ewe:lamb ratios of Dall sheep in McKinley Park, Alaska, was significantly lower in the area of highest density. Investigations into all-age die-offs of bighorn sheep in the East Kootenay region of British Columbia in the 1960's and 1980's determined these die-offs were preceded by high population density (Schwantji 1986). Burles et al. (1984) in their study of Dall sheep in Yukon Territory, Canada, found population density to be a significant contributor to variations in productivity among populations. These studies found little or no correlation with mortality and any specific forage limiting factor.

Based on these and other investigations, I believe information exists that supports a concept that nutrition does not necessarily serve as a predisposing agent to either catastrophic die-offs or reduced natality due to disease. While much remains to be discovered about proximate causes, predisposing agents, and etiology of disease, circumstantial evidence suggests that bighorn pneumonia is induced by multiple stress factors (Potts 1938, Spraker 1977, Feuerstein et al. 1980, Spraker and Hibler 1982, Spraker et al. 1984, Onderka and Wishart 1984, Bailey 1986).

This interaction of stressors can be visualized if a stress index factor of 1.0 is required to suppress a population to the point of stabilization. The effect of population density could have a stress factor range of 0.3-1.0, inclement weather 0-1.0, harassment 0-0.4, chronic parasitism 0-0.2, nutrition 0.1-0.6 (unless the regulatory system is overridden, then 1.0). One could then understand how these factors become additive. However, population density or weather alone could account for a population decline, or with no inclement weather and a lowered density, a combination of other factors could achieve a population decline. But a lowered population density, hence reduced stress, would allow a population to increase again to an equilibrium once the other stressors returned to lower levels. The effect of all environmental stressors acting upon a population would be in a dynamic equilibrium with the population.

The concepts of carrying capacity, density dependency and intra-specific competition for forage are not discounted here. Stelfox (1976) hypothesized that bighorn populations that increase in density will suffer die-offs before they reach a balance with their environment. Chitty (1960) proposed that intrinsic factors, those characteristics of an individual such as behavior, physiology and genes, could act to regulate the population at a level below that imposed by the food supply. I believe that forage is the ultimate factor that will limit population size, but that food serves in many cases, not as a regulatory but a limiting mechanism. Concepts of population limitation and regulation should not be confused. For example, the amount of space, food, or water (limiting factors) may limit the size of a population but competition (stress) for space, food, or water may serve to regulate a population and is a function of population density. Extrinsic and intrinsic factors may function to regulate populations. For example, an intrinsic factor such as chronic stress resulting from high population density may influence physiologic functions such as immune systems and cause disease (extrinsic factor). Populations that are regulated may attain optimum size or density that would be beneficial for long term survival of the species. Populations that are not regulated but limited may at times reach peak population numbers but may not be beneficial for long term survival.

Bailey (1986:332) states, "...if we become satisfied with, or promote "stress" as an explanation [for die-offs], we may impede development of understanding of the causes of stress in bighorn sheep." I agree; however, many biologists have accepted the simplistic concept of carrying capacity which has impeded our understanding of population regulation in bighorn sheep. I believe the acceptance of the concept of stress, its effect on the immune system and its role in population regulation would be a major step towards understanding this complex issue.

IMMUNE SYSTEM DEPENDENT VERSUS INDEPENDENT

To combat an array of pathogens, animals, including wild sheep, have developed various sophisticated immunological defense mechanisms. The pathogenicity of potential disease causing organisms is usually dependent upon the functional level of the animal's immune system. I will call those pathogens that rely upon the functional level of the immune system to cause disease as "immune system dependent". Those pathogens that, because of their high virulence, the high susceptibility of sheep, or their ability to overwhelm an uncompromised immune system and cause disease, I will term "immune system independent". These immune system independent pathogens are those that usually are not enzootic in sheep populations but increase in virulence or number due to factors independent of sheep populations. These factors may include numbers of secondary or intermediate hosts, or vector populations. An example of an immune system independent pathogen would be Bluetongue virus. Its affect on bighorn sheep populations is related to the size of the vector population _Culicoides_ spp., and not to the functional level of the bighorn sheep's immune system. Some pathogens may serve as both immune system dependent and independent, depending on their nature or virulence such as _P. haemolytica_. However, most pathogens are immune system dependent and are enzootic to wild sheep populations. It is my belief that immune system dependent pathogens serve to regulate populations versus independent ones that do not.

It is my belief if _Pasteurella haemolytica_, regardless of source, operated only in an immune system dependent manner, epizootics would be a major factor in regulating populations. However, in my opinion, _P. haemolytica_, originally dependent on the functional level of the animal's immune system to cause disease, gains in virulence (Spraker 1977, Feuerstein et al. 1980, Ellis 1984, Wilkie and Shewen 1988, Callan et al. 1991) as it passes through many animals weakened by its effects and thereby begins operating in an immune system independent manner. The effects of _P. haemolytica_ would then not be regulating populations, but serve as a catastrophe.

A more virulent _P. haemolytica_ would then be transferred, usually by young rams (Onderka and Wishart 1984), to adjacent sheep and to other populations, overwhelming the immune system without need for stressors. It would then lose its increased virulence over time due to intrinsic factors operating within the bacterial population and again become immune system dependent. A mechanism similar to this may have been proposed by Festa-Bianchet (1988:73) when he stated, "Population dynamics after the [bighorn sheep] epizootic, particularly lamb survival may reflect lingering effects of the disease and therefore not show the expected density dependent relationships."

In an attempt to model population dynamics of bighorn sheep, Hobbs and Miller (1993) postulated that epizootics due to Pasteurella spp. regulated bighorn numbers and that external forces such as habitat changes, environmental stress, parasitism and contact with domestic animals, do not appear necessary to produce periodic pasteurellosis epizootics in bighorn herds. In my opinion, I believe their model points out that bighorn numbers are reduced by epizootics caused by Pasteurella spp. but these epizootics do not function to regulate bighorn populations because they are apparently operating in an immune system independent fashion.

In this postulated system of population regulation, it seems logical that wild sheep have evolved to "fine tune" their immune system to regulate population density and compensate for other environmental stressors to their benefit in long term survival. However, this system has evolved in close association with the environment. Therefore, man's manipulation of the environment may be disrupting this system.

DISEASE VERSUS DIE-OFF

Disease is defined as a specific state of malfunctioning in an animal (Dorland 1963). It is the culmination of various defects, abnormalities, excesses, deficiencies and injuries as they occur at the cell and tissue level which ultimately result in clinically apparent dysfunction (Slauson and Cooper 1982). Disease may sometimes go undetected at the clinical level even though the lesions underlying the disease have been present in the tissues for a long time. In this discussion, disease will be limited to a dysfunction caused by living organisms (bacteria, viruses and parasites, etc.).

Traditional investigations on causes of mortality where disease was believed involved were aimed at identifying single cause (a pathogen) and effect (morbidity and mortality). These studies, in effect, equate disease with die-off or population crash. Investigators (Stelfox 1976, Hobbs et al. 1990, Hobbs and Miller 1993) therefore, attempted to model population dynamics of sheep based on this concept and suggest disease is a population regulator. However, one should realize that disease causing organisms are numerous in bighorn sheep populations (Adrian 1981, Dieterich 1981, Goodson 1982, Thorne et al. 1982, Fowler 1986), and to ignore their significance to long term regulation is missing the point. Die-offs in sheep populations are mostly a result of a respiratory pathogen which is usually P. haemolytica. To study only the mechanics of a population die-off due to Pasteurella spp. will lead only to understanding pathogenesis of die-offs, not of mechanisms of population regulation due to disease factors that constantly affect and regulate sheep populations. To understand population regulation, more emphasis should be placed on understanding bighorn sheep populations that are apparently stable, or where numbers fluctuate little. To understand the regulatory nature of environmental variables and intrinsic factors that are constantly at work, we should not place emphasis on studying populations that may temporarily have lost control due to a catastrophic event, disease or otherwise.

Stelfox (1974) was probably correct in concluding that bighorn sheep in the Canadian National Park did not exhibit any density dependent self-regulating mechanism. He was considering population die-offs, or disease pathogens that are not dependent upon functional level of the immune system, rather than long term effects of pathogens that are dependent upon the animal's immune system to cause disease.

Hudson and Stelfox (1976:110) pointed out in their attempt to model, "disease interfered with a more finely tuned mechanism of population regulation." They equate disease with die-off in their model and would have been justified in their conclusions if they had stated that die-offs interfered with a fine-tuned mechanism for population regulation. The finely tuned mechanism of population regulation they elude to, may in fact be disease other than Pasteurella spp. at least, it may be Pasteurella spp. that operates in an immune system dependent rather than independent manner to which die-offs may be attributed.

The term disease must include pathogenic or potentially pathogenic organisms operating in a population. One should not single out a pathogen, in most cases Pasteurella spp., and model their effect under the guise of disease. Consequently, one must understand the pathogenesis of combined diseases and realize the difference between disease factors that regulate by their immune system dependence and those that effect but do not regulate, by their immune system independence. Many pathogens, combined with or without Pasteurella spp. may serve to regulate bighorn sheep populations by operating on newborn lambs, where mortality due to disease is often high but often ignored by investigators, especially when populations appear stable.

DENSITY VERSUS MOBILITY

Nicholson (1933) revolutionized thinking about population regulation when he introduced the concept of density dependent factors. Because population density appears to be so important, I wish to give some definitions of density and propose a concept which should be considered when disease factors are involved. Animal density is defined as, "individuals per unit of area" (Dasmann 1964:90). He also points out densities should be related to occupied habitat rather than mere geographic area and must always be measured at a particular point in time. I believe density must also be considered when disease is the object of study as a stressor acting upon the animal's immune system. Population density is also a factor as it relates to disease transmission among individuals within a population. The greater the density, the higher the rate of disease transmission. And, in regards to density and disease transmission, another factor to be considered is mobility of a population. Mobility refers to the distance traveled per day. Optimum mobility would include a large mean distance traveled per day with a low standard deviation value.

As individuals become weakened due to disease, number and virulence of pathogens may increase, making transfer of pathogens to others easier. Larger distances traveled would tend to increase the likelihood of weakened individuals lagging behind and being excluded from the group, thereby reducing disease transmission.

The greater the mobility of a population, the greater the effect of this natural quarantine, which allows populations to achieve greater densities. This would have a dramatic effect at lambing and nursery areas, where ewes concentrate and reach high densities. Lambs in nursery areas that are on discreet limited habitats would suffer greater losses to disease than those on expanded habitats where density is less and mobility greater. Hoefs and Bayer (1983), in their study of Dall sheep in Canada, found sheep densities more than doubled on nursery areas as compared to year-round ranges. Lenarz (1979) reported most lamb mortalities in his study in New Mexico occurred during movements between ewe ranges (those lagging behind).

However, as population size may diminish, lamb nursery areas may diminish in size due to an attempt by ewes to concentrate onto key habitats as determined by physiographic features. Densities may vary little until population size is reduced to a certain point. This concept of sheep maintaining high densities by concentrating themselves into more highly preferred areas in the face of population declines has been observed by Spraker (1974).

It should also be mentioned that mobility may have negative effects on a population. Onderka and Wishart (1984:360) in their study of a sheep die-off in Canada state, "The highly mobile component of rutting rams was probably responsible for spreading the disease [pasteurellosis] over such a large area."

MANAGEMENT IMPLICATIONS

As stated, despite genuine efforts current management of Rocky Mountain bighorn sheep populations and their habitats does not appear to be effective (Risenhoover et al. 1988). Transplanting of bighorn sheep onto historic ranges may, in some instances, be an effective management tool today. Transplants involving California bighorn sheep (Ovis canadensis californiana) into southwestern Idaho ranges is an example of the success of this type of management (Bodie et al. 1990). However, historic ranges suitable for transplanting are limited. And Risenhoover et al. (1988) suggests that many transplanted bighorn sheep populations are not expected to survive. Smith et al. (1991) also believe that transplanting bighorn sheep as a management tool to increase numbers has failed in the western United States.

Protection of existing habitats from degradation and protection of sheep from illegal harvest are also management strategies where success is in question. Habitat manipulation and range improvements on existing key bighorn sheep ranges has shown little success. Bighorn sheep populations continue to decline. Jahn and Trefethen (1978) warned that without more effective management, an additional loss of 8% of bighorn sheep could be expected over the next 25 years.

If disease is a major factor contributing to population declines, and if it is based on population density rather than nutrition, then management strategies based on reducing densities should take priority. However, does reduction of sheep numbers through increased hunter harvest of ewes or transplanting from a population decrease density to the degree required? Possibly not. Decreasing number of ewes on lamb nursery areas should be of greatest benefit if it results in decreasing ewe densities. But in many cases, even if harvest strategies allow such a reduction, they may have to be substantial because ewes in bordering marginal nursery areas may concentrate on key nursery areas, maintaining high densities. It would therefore seem more beneficial to increase the size of nursery areas through habitat manipulation. These habitat manipulations would probably consist of creating optimum physiographic characteristics, i.e., increasing visibility in steep rocky areas overgrown with small trees and shrubs or creating or improving movement corridors between nursery areas, rather than increasing vegetation quality.

This same concept applies to manipulation of winter range habitat. In other words, one should create more area of sheep habitat, rather than creating better quality habitat in the same key areas, as is the present management strategy. Management strategies based on creating more and larger areas of sheep habitat not only would reduce sheep densities but would increase mobility.

A similar management strategy of increasing area was postulated by Risenhoover et al. (1988). They believe bighorn sheep have abandoned migration corridors to less favorable ranges due to forest succession reducing visibility. And, "The resulting phenomenon of mostly small, isolated, and sedentary sheep herds perpetuates population declines and habitat loss through loss of traditional movements", (Risenhoover et al. 1988:348). They also concluded that burning existing winter range will not expand a herd's area and will not encourage a herd to re-establish abandoned movement patterns. They stated, "For many herds, we believe that population size, distribution, and movement must be increased if they are to remain viable", (Risenhoover et al. 1988:348). Increasing access to escape terrain and improving visibility within habitats are generally believed to be the primary determinants of distribution and habitat use (Cook 1990). These management strategies are similar to those that consider immune system dependent disease factors as primarily regulating sheep populations through population density and mobility.

Other factors found important in sheep management such as reducing harassment should be considered. Chronic stress from harassment on sheep populations at high densities, low mobility, and low planes of nutrition may produce catastrophic die-offs. These additive stress factors may lead to respiratory, or other pathogens, reverting from a regulating immune system dependent effect to an immune system independent associated die-off.

SUMMARY

Current management of bighorn sheep does not appear effective. Bighorn sheep numbers continue to decline. If we are to more

Management strategies based on reducing population density and increasing mobility, rather than increasing forage quantity or quality should produce more effective results. Increasing area of habitat rather than increasing forage values in existing sheep habitats should be considered if increasing and stabilizing numbers of bighorn sheep is the desired goal. However, research on the role disease and parasites play in the population dynamics of wild sheep is also needed. The effect of disease on bighorn sheep populations cannot be determined until its interrelationship with population density and nutrition are measured and understood.

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PHARYNGEAL MICROFLORA OF DALL AND DOMESTIC SHEEP IN ALASKA: MANAGEMENT IMPLICATIONS?

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Abstract: Anticipating the occurrence of disease-related, all-age die-offs is a common component of contemporary bighorn management strategies. Domestic sheep have often been implicated in these bighorn die-offs. In Alaska, documented exposure of Dall sheep to domestic sheep has been limited to 2 3-to 6-week periods during late-winter when domestic sheep were run on a Dall sheep winter range near Palmer. The results of this exposure are not yet known, but a disease-related die-off in Dall sheep has never been documented. As the exposure of Dall sheep to domestic sheep near Palmer demonstrates, wildlife managers in Alaska were unable to exclude domestic sheep from Dall sheep ranges. Because data demonstrating effects of domestic sheep diseases on Dall sheep are not available, we began to investigate a possible causative relationship between domestic sheep and disease in Dall sheep. We started with a bacteriologic survey of tonsils from 16 domestic ewes produced in the Tanana Valley near Fairbanks. These ewes carried pharyngeal microflora typical of those reported for domestic sheep elsewhere, including the Pasteurella haemolytica strains and serotypes which have been implicated in bighorn die-offs. Next, 43 wild Dall sheep of both sexes from a remote area of the Brooks Range were also assayed for pharyngeal flora using tonsil biopsies and nasal swabs. These Dall sheep carried numerous species of bacteria, including the P. haemolytica strains and biotypes implicated in bighorn sheep die-offs. Relevance of these findings to the domestic-bighorn sheep connection and future research possibilities are discussed.

Anticipating occurrence of disease-related die-offs of bighorn sheep is a common component of bighorn sheep management strategies in North America (Heimer 1990). The literature which necessitates this management position is extensive. After description of the lungworm (Protostrogylus stilesi) life cycle came the demonstration of alternate-host "hot spots" (Lange 1974), and the demonstration of transplacental transmission of lungworm larvae (Schmidt et al. 1979). These findings led most bighorn managers to conclude that the lungworm-pneumonia complex was a classic density-dependent factor limiting bighorn populations. With the development and administration of anthelmintic drugs (Schmidt et al. 1979, Foreyt and Johnson 1980), it became possible to mitigate some of these effects; and many managers thought the disease problem had been solved.

These findings had scarcely been presented when a major, well documented die-off of bighorn sheep began in the Kootenay region of British Columbia. This die-off was the best-studied large disease event in the history of bighorn sheep. The results implicated P. haemolytica varieties as etiologic agents (Onderka and Wishart 1984, Schjwantje 1984).

In classically simple experiments, Onderka and Wishart (1988) demonstrated that this fatal pneumonia could be produced in healthy bighorn sheep by P. haemolytica nonhemolytic biotype T cultured from the tonsils of bighorns that died during the epizootic. Onderka also demonstrated this bacterium, cultured from healthy domestic sheep, caused fatal pneumonia in captive bighorns. Additionally, Onderka (1986) produced fatal pneumonia among captive bighorns with biotype A of this Pasteurella spp., which had been modified for use as a cattle vaccine. These experiments also demonstrated a predisposing viral infection was unnecessary for development of fatal bacterial pneumonia in captive bighorns. Domestic sheep were consistently and uniformly refractory to the organisms which killed bighorns.

Domestic sheep were further implicated as carriers of pathogens for bighorns by the work of Foreyt (1988, 1990). In replicate trials, he showed that apparently healthy bighorn sheep soon perished when apparently healthy domestic sheep were introduced into their pens. Callan et al. (1991) also demonstrated fatal pneumonia among desert bighorns penned with domestic sheep. Again, Pasteurella spp. was implicated. These findings clearly suggest that allowing domestic sheep on wild bighorn ranges carries some risk.

In Alaska, exposure of Dall sheep to domestic sheep was undocumented until domestic sheep were found on Dall sheep winter ranges between the Knik and Matanuska Rivers near Palmer, Alaska in spring 1990. These domestic sheep mingled with Dall sheep on grazing leases let by the Chickaloon Native Association (CNA). CNA had received the land as part of the settlement of their aboriginal land claims (Heimer 1980), and leased grazing on it to generate income. These unfenced grazing leases were adjacent to late-winter ranges used by Dall sheep. Immediately after snow at lower elevations melted in spring of 1990, domestic sheep were introduced to the unfenced grazing leases by the lease holder. There, they mingled with Dall sheep on their late-winter ranges for several weeks before the Dall sheep moved to summer ranges. The domestic sheep remained alone on the Dall sheep winter ranges until fall 1990 when they were moved to wintering grounds away from Dall sheep ranges. In early spring 1991, the domestic sheep were again returned to Dall sheep ranges where they once again mingled with Dall sheep until the Dall sheep again left for their summer ranges. After the domestic sheep were removed in fall 1991, they were sold, and not returned to the lease.

Although we were surprised by this specific introduction of domestic sheep to Dall sheep range, Alaskan Dall sheep and wildlife disease researchers had already identified potential problems with introduction of diseases by domestic livestock (Heimer et al. 1982). As a result of our earlier concern, we continued to document the disease histories of Dall sheep throughout Alaska. Our previous work centered on viral serology (Zarnke et al. 1983; Zarnke 1987, 1991; Zarnke and Rosendal 1989).

As a response to demonstration that fatal bacterial pneumonia could occur in bighorn sheep independent of lungworm or viral infection, we expanded our program to include bacterial pathogens. Bacterial diseases, particularly pneumonia involving Pasteurella spp., were of greatest interest because of the findings listed above. Bacterial investigations of both domestic and Dall sheep in Alaska became practical when it was reported bacteria could be isolated from the tonsils of wild and domestic sheep under Alaskan field conditions (D. Onderka, Univ. Alberta, pers. commun.; Dunbar et al. 1990).

METHODS

We slaughtered 16 adult mixed-breed domestic ewes which had been produced and maintained in the Tanana Valley in Interior Alaska. Prior to slaughter, nostrils were swabbed with rayon-tipped swabs. Swabs were introduced into Amies modified medium with charcoal. Specimens were stored for 36 hours at 25 C, then packaged in insulated cool containers, and shipped by same-day mail to Al Ward of the Caine Veterinary Center, Caldwell, Idaho where they were immediately plated and subsequently identified (Queen et al. 1992).

At slaughter, the soft palates of these domestic ewes, including the tonsilar crypts, were removed and packaged in plastic bags. Samples were then air-expressed to Dr. Ward where he inoculated cultures within 48 hours. See Queen et al. (1992) for details.

Dall sheep from the south slope of the eastern Brooks Range were captured by helicopter using a skid-mounted projectile net (Heimer and Mauer 1990). Nasal swabs and tonsil biopsies (Dunbar et al. 1990) were collected from 19 sheep in October 1990. An additional 9 swab and biopsy samples were collected from Dall sheep in the same area in 1991. Fifteen sample sets were also collected from the north side of the Brooks Range in the Hula Hula River drainage at this time. All samples were flown to Arctic Village and air-expressed to bacterial laboratories identification and typing.

RESULTS

Domestic sheep produced in Alaska harbored pharyngeal microflora typical of domestic sheep in the lower 48 states and Canada. This included the Pasteurella spp. organisms which have been implicated in wild sheep die-offs. Details of the bacterial species found in the tonsils of domestic sheep in Interior Alaska were reported by Queen et al. (1992). Six gram-negative bacteria were present in notable percentages (Table 1).

Table 1. Gram-negative bacteria present in 16 adult domestic ewes from the Tanana Valley, Alaska in summer, 1990.

Bacteria	Occurrence (%)	
	Nasal	Tonsil
Enterobacter agglomerans	64	45
Enterobacter cloaca	45	0
Neisseria denitrificans	0	64
Moraxella ovis	0	18
Pasteurella haemolytica T	0	91
Pasteurella haemolytica A	0	27

Dall sheep from the remote portions of the Brooks Range, had pharyngeal microflora which included P. haemolytica biotypes A 5, A-untypable, T 3, T 4, T 10, and T-untypable (Table 2). Pasteurella spp. organisms were not isolated from material collected in 1991. Delay in getting the material to the laboratory was the probable cause of these negative results.

DISCUSSION

There are currently 3 schools of thought regarding the origin of Pasteurella spp. pneumonia in bighorn sheep. One school, led by Foreyt, suggests contact with domestic sheep infects bighorns with a fatal Pasteurella spp., which is foreign to them, but is carried by domestic sheep without effects. Once bighorns are infected, high mortality results (Foreyt 1990). Prevention of exposure by keeping domestics and bighorns apart is seen as unlikely for political and economic reasons, so treatment by development of a vaccine and vaccinating bighorns has been recommended by this school.

The second school suggests bighorn sheep typically carry the pathogenic Pasteurella spp. strains and biotypes, and that stress compromises the bighorn immune system resulting in fatal pneumonia (T. Spraker, Colo. State Univ., pers. commun.; Belden et al. 1990) . We infer that the management recommendation of this school is to limit stresses to benefit bighorn populations.

The third school suggests there are both bighorn and domestic varieties of Pasteurella spp.. Should bighorns become infected with the domestic strain, they will develop pneumonia and die, but domestic sheep are not affected by the bighorn strain (Onderka and Wishart 1988). We infer the recommendation of this school is to prevent contact between domestic sheep and bighorns. If separation of bighorns from domestics is not maintainable, bighorns should be managed as wild sheep to minimize losses to disease, but not vaccinated or treated (W. Wishart, Alberta Wildlife Branch, pers. commun.).

Table 2. Bacteria isolated from nasal swab and tonsil biopsies of 19 Dall sheep from the Brooks Range, Alaska in 1990.

	Positive isolates	
Bacteria	Nasal	Tonsil
Pseudomonas flourescens	2	3
P. solanacearum	1	0
P. syringae PV aptata	0	1
P. sp.	1	0
Flavobacterium meningosepticum	1	0
Moraxella bovis	2	0
Moraxella osloensis	1	1
Moraxella sp.	0	1
Actinobacillus actinomycetem comitans	2	0
Actinobacillus sp.	1	0
Pasteurella haemolytica T 3, T 4, T 10	0	6
Pasteurella haemolytica T-untypable	0	1
Pasteurella haemolytica A 5	0	1
Pasteurella haemolytica A-untypable	1	1
Pasteurella-like	4	3
Eschericia coli	1	8
Acinetobacter calcoaceticus	1	0
Enterobacter agglomerans	0	1
Micrococcus sp.	1	0
Staphylococcus aureus	1	2
S. epidermidis	0	3
S. haemolyticus	1	0
S. homins 2	0	1
S. saprophyticus	1	0
S. sciuri	1	0
S. typhi A	0	1
S. warneri	2	3
S. xylosus	3	1
Streptococcus bovis 1	1	2
S. bovis 2	3	2
S. bovis 1 or 2	1	3
S. equisimilis	1	0
S. mitis	0	1
S. moribillorum	0	1
S. mutans	2	1
S. salivarius	0	1
S. sanguis 1	0	2
S. sanguis 3	1	0
S. suis 1	2	0
S. spp.	1	2
Bacillus spp.	2	2

Dall sheep in the remote parts of the Brooks Range have, in all probability, never been in contact with domestic sheep. Still, these Dall sheep carry P. haemolytica biotypes A 5, T 3, T 4, and T 10, as well as untypable varieties of A and T. These are presumably the same Pasteurella spp. biotypes which produce fatal pneumonia in bighorns, yet no disease-related die-offs have been documented in Dall sheep. These findings, along with the commonly accepted origin of North American wild sheep, a common ancestor which migrated from Asia via Beringia (Cowan 1940, Geist 1971), suggest Pasteurella spp. bacteria are enzootic to wild North American, and perhaps Asian, mountain sheep. If this is so, it is probable that North American wild sheep have "always" had these bacteria. Hence, it is unnecessary to postulate domestic sheep as the source of all Pasteurella spp. bacteria which have been implicated in bighorn pneumonia. Furthermore, apparently healthy bighorns, both in pens and in the wild, carry Pasteurella spp. bacteria (T. Spraker, Colo. State Univ., pers. commun.). Our conclusion, that the pneumonia pathogens need not come entirely from domestic sheep, is based on these data and the assumption that conventional laboratory techniques (Ward et al. 1990) characterize these bacteria adequately.

Still, we question whether conventional laboratory techniques adequately characterize these bacteria. Pasteurella spp. is one of several gram-negative, pleomorphic bacteria (Ward et al. 1990). Pleomorphic bacteria change their form, or morphology, depending on culture media. If the morphology of these bacteria is variable, we suggest it is possible that ability to use specific metabolites, which is the basis of conventional taxonomy, may change also. Should changes in metabolic capability be associated with morphological changes, they would produce differing results in biotyping and perhaps even species identification. If this were the case, conventional classification on the basis of Gram-staining and metabolite use in culture would result in differing designations for a single organism which is more adaptable than we presently appreciate. Techniques beyond metabolic capability in culture may be required to address these questions.

The finding that Dall sheep have pharyngeal microflora which are quite similar to those of domestic sheep does not contradict the stress or species-specific schools of thought. However, it is difficult to imagine that Dall sheep exist with less stress than commonly defined for bighorn sheep. Most Dall sheep have lungworms. Those which have been studied appear to have moderate larval fecal outputs of 200 larvae per gram of feces. Additionally, Dall sheep endure at least 8 months of winter each year, are subject to natural predation, human harvest, intense non-consumptive use, and industrial development. Finally, Dall sheep frequently exist at densities which are greater than bighorn populations which have suffered die-offs in the past. Still, we do not see all age die-offs among Dall sheep.

Through the process of elimination, the Onderka and Wishart hypothesis seems most acceptable for describing the origin and pathogenicity of P. hemolytica. Without better identification of these bacterial varieties, we are unable to offer a better explanation. Several laboratories are working on the nuclide sequences from the

Pasteurella spp. organisms isolated from Dall and domestic sheep from Alaska as well as from bighorn and domestic sheep from other regions. We are currently unaware of their findings.

The possibility that Dall sheep are immunologically more competent than bighorn sheep also exists. If specialization, which Geist (1971) postulated for bighorn races, resulted in a narrower spectrum of immune responses, it would be reasonable to anticipate more robust immunocompetence in the less specialized thinhorn races.

These possibilities could be addressed experimentally by inoculating Dall sheep with various Pasteurella spp. organisms from domestic and bighorn sheep under well-controlled laboratory conditions. Alternately, comparative studies of Pasteurella spp. cytotoxins on Dall and bighorn sheep white blood cells may be useful. We plan such experiments in the future. We will cooperate by supplying Dall sheep or Pasteurella spp. organisms from Dall sheep to investigators who present well designed experiments to test these possibilities. In any case, we suggest that Dall sheep with no history of involvement with domestic sheep present good experimental opportunities to further investigate the development of Pasteurella spp. pneumonia pending the outcome of DNA sequence analysis.

Whatever the cause of Pasteurella spp.-related die-offs, history shows that prevention of disease is more effective than treating it. Consequently, our recommendations are:

1. Wherever possible, prevent domestic and wild sheep mixing.

   In Alaska, the Alaska Department of Fish and Game (ADF&G) will continue to oppose introduction of domestic livestock, especially domestic sheep, to Dall sheep ranges.

   Close cooperation between ADF&G and the Foundation for North American Wild Sheep recently resulted in removal of domestic sheep from Dall sheep range near Palmer, Alaska. Sampling of sheep from the domestic and wild sheep herds involved in this transient exposure is a high priority. Management actions appropriate to the findings will be recommended.

2. Wherever possible, minimize stresses on mountain sheep populations.

   Dall sheep appear, by our standards, to be highly stressed. Still, most of the stresses we can identify are stresses to which they have become adapted over time. Introduction of new stressors should be carefully weighed and mitigated to the extent possible.

3. Accelerate work on DNA sequencing of Pasteurella spp. and other Gram-negative pleomorphic bacteria.

4. Address the question of differing levels of immunocompetence among bighorn and thinhorn races of wild sheep.

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GASTROINTESTINAL PARASITES OF BIGHORN SHEEP IN WESTERN MONTANA AND THEIR RELATIONSHIP TO HERD HEALTH.

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Abstract: Gastrointestinal parasites of bighorn sheep (Ovis canadensis canadensis) from 11 western Montana herds were investigated by postmortem examination of 68 animals over an 18-year period. Necropsy findings were supplemented by fecal examination data from additional sheep for which postmortem material was not available. Sixteen helminth and coccidian species were found, of which 64% also parasitize domestic sheep. Major enteric parasites included nematodes (10 species), cestodes (2 species) and coccidia (4 species). The abomasal nematode Marshallagia marshalli was the most prevalent species overall, occurring in all herds and in 62% of the sheep examined statewide. The thread-necked strongyle Nematodirus was next in order of frequency, occurring in 9 herds with a composite prevalence of 40%. The whipworm Trichuris was found in 7 herds, in which 26% of the sheep were infected. Low prevalence nematodes, characterized by restricted geographic distribution and usually by low numbers, included the pinworm Skrjabinema, 3 herds; the intestinal threadworm Trichostrongylus, 2 herds; and the stomach worm Ostertagia, 2 herds. Genera limited to 1 herd were the small intestinal roundworm Cooperia, the large-mouthed bowel worm Chabertia and the nodular worm Oesophagostomum. Cestodes were present in 6 of the herds examined: the bighorn tapeworm Wyominia tetoni was found in 5 herds, and the double-pored tapeworm Moniezia was recovered from 2 herds, 1 in which Wyominia also occurred. Four species of coccidia were identified in sheep from 4 herds. Eimeria crandallis was the most common type and occasionally occurred in association with Eimeria ahsata. Oocyst counts suggestive of clinical coccidiosis were seen infrequently but in several instances were superimposed on mixed intestinal helminth populations. Management implications of these findings suggest that enteric parasites as a group may constitute a recognizable stress factor in Montana sheep, particularly the Wildhorse Island, National Bison Range and Sun River herds.

Among the variety of disease agents having a recognized impact on bighorn sheep populations, protostrongylid lungworms have received extensive attention (Pillmore 1957, Forrester 1971, Spraker 1979). Other parasite-related problems such as psoroptic scabies (Lange et al. 1980, Boyce et al. 1990, Foreyt et al. 1990) have been identified as factors responsible for periodic declines of wild sheep in western United States. In some instances recognition of parasites as etiologic agents associated with field outbreaks of disease has stimulated the development of control programs which have demonstrated management value (e.g., Schmidt et al. 1979).

On the other hand, limited information is available on the prevalence in wild sheep of parasites other than lungworms, and their potential role as disease agents in free-ranging bighorn populations is virtually unknown. Available data indicate that many worm parasites and coccidia reported from Ovis canadensis are recognized pathogens of domestic sheep (Honess and Winter 1956, Becklund and Senger 1967, Nielsen and Neiland 1974). However, their impact on the health of bighorn sheep exposed to a variety of environmental stresses is unclear. The purpose of this report is to present retrospective data on the occurrence of enteric parasites in 11 western Montana bighorn herds. The ultimate goal is to help clarify existing uncertainties about the management implications of this type of parasitism, particularly in view of its frequent association with acute and/or chronic disease problems in domestic sheep.

METHODS

Animals for postmortem examination were obtained from a variety of sources including road-killed specimens, field mortality cases, hunter-killed rams, and sheep provided by the Montana Department of Fish, Wildlife and Parks. At necropsy, the gastrointestinal tract from the abomasum to the lower colon was removed intact. Most animals were processed within 48 hrs, although in some instances viscera were frozen for later examination. Fecal analysis was used to supplement postmortem data in a limited number of sheep for which necropsy material was not available. Of the 11 herds represented in the study, 7 were located west of the Continental Divide in extreme western Montana and 4 herds were situated east of the Divide in or around Yellowstone or Glacier National Parks. Population estimates and the number of sheep examined from each herd at postmortem are listed in Table 1.

At necropsy the gastrointestinal tract was opened and the contents of each area were washed separately onto 20-, 40-,80- or 100-mesh screens to separate worms from ingesta. The entire gut mucosa was scraped and washed to remove attached parasites. Washed ingesta and mucosal scrapings were examined in illuminated trays and with a dissecting microscope to facilitate recovery of worms. Fecal samples were collected routinely during postmortem processing of sheep viscera. In some instances, random pellet collections were also made in the field to obtain additional data on parasite prevalence in specific herds for which limited postmortem data were available. A modified version of the Wisconsin centrifugal flotation technique was used to estimate the prevalence and intensity of helminth ova and coccidian oocysts (Lane 1928). Nematodes were fixed in a mixture of 95 parts 70% ethanol and 5 parts glycerin for microscopic examination. Tapeworms were fixed in 10% buffered formalin. Total worm counts were estimated from the number of parasites present in aliquots of washed gut contents. Intensity of coccidial infections was ranked from + to + + + according to the relative number of oocysts observed in fecal flotations.

RESULTS

Gastrointestinal helminths were noted in 10 of the 11 herds surveyed between 1973 and 1991 (Table 2.) Ten species of nematodes were found in 68 sheep examined. The most common parasite was the abomasal nematode Marshallagia marshalli, which occurred in all herds and in 62% of the sheep examined overall. The thread-necked strongyle Nematodirus was found in 9 herds in which 40% of the animals sampled were infected. Third in order of frequency was the whipworm,

TABLE 1. Demographic summary of 11 western Montana bighorn herds examined for gastrointestinal parasites (1973-91)*

Herd	Total no. sheep	Present status*	No. sheep examined
Sun River	1,100	Decreasing?	27
Thompson River	481	Growing	4
Ural - Tweed	100	Growing	7
Kootenai Falls	175	Stable	2
Lost Creek	180	Decreasing	5
Spanish Peaks	150	Stable	1
Bitterroot (East Fork)	100	Stable	4
Yellowstone	300 - 350	Decreasing	4
Stillwater	33 - 38	Stable/ Decreasing	4
Wildhorse Island	50	Stable	7
National Bison Range	60	Stable	2

*(Thorne et al, 1985:78-79)

Table 2. Prevalence and distribution of gastrointestinal parasites in 11 bighorn sheep herds from western Montana, with an estimate of their clinical significance.

Parasite	Prevalence %	Herds infected	Clinical signs/ pathogenesis
Marshallagia	62	Lost Creek, Kootenai Falls, Sun River, Wildhorse Island, National Bison Range, Ural-Tweed, Thompson River, Spanish Peaks, Bitterroot (E. Fork), Yellowstone Park, Stillwater	Damage abomasal mucosa; destroy gastric glands; reduce feed efficiency
Nematodirus	40	Kootenai Falls, Sun River, Wildhorse Island, National Bison Range, Ural-Tweed, Thompson River, Spanish Peaks, Yellowstone Park, Stillwater	Diarrhea and weakness resulting from destruction and necrosis of intestinal mucosa
Trichuris	26	Sun River, Wildhorse Island, National Bison Range, Ural-Tweed, Thompson River, Yellowstone Park, Stillwater	Probably insignificant
Skrjabinema	5.8	Sun River, Ural-Tweed, Stillwater	Probably nonpathogenic
Trichostrongylus	7.3	Wildhorse Island, National Bison Range	Loss of appetite with profuse watery diarrhea
Ostertagia	4.4	Wildhorse Island, National Bison Range	Nodule formation and destruction of gastric glands in abomasum
Cooperia	1.4	National Bison Range	Necrotic inflammation of duodenum
Chabertia	2.9	Wildhorse Island	Mucoid diarrhea; edema and ulceration of colon
Oesophagostomum	2.9	National Bison Range	Nodular lesions in bowel lining

Table 2. Continued.

Parasite	Prevalence %	Herds infected	Clinical signs/ pathogenesis
Capillaria	1.4	Sun River	Probably nonpathogenic
Wyominia	23.5	Lost Creek, Sun River, Ural-Tweed, Thompson River, Bitterroot (E. Fork)	Unknown
Moniezia	5.8	Sun River, Stillwater	Mechanical blockage of intestine; may interfere with digestion and absorption
Eimeria	33.8	Sun River, Wildhorse Island, Spanish Peaks, Yellowstone Park	Diarrhea and electrolyte imbalances, damage intestinal lining

Trichuris, which occurred in the cecum and upper colon of 40% of the sheep examined in 7 herds.

Other nematode infections encountered included 6 genera of stomach and intestinal roundworms which were limited geographically and typically were present in low numbers. The intestinal threadworm Trichostrongylus and the medium stomach worm Ostertagia occurred in 2 and 3 herds, respectively, in limited numbers. The pinworm Skrjabinema parasitized the lower colon of sheep from 3 herds. Intensity of individual infections ranged from less than 10 to more than 2,000 worms per animal. The intestinal nematodes Cooperia, Oesophagostomum, and Chabertia had the most limited geographic distribution of the roundworms identified in the study. Two animals were infected with the nodular worm Oesophagostomum and the large-mouthed bowel worm Chabertia; the intestinal roundworm Cooperia was limited to a single individual.

Cestode infections of 2 types were found. The bighorn tapeworm, Wyominia tetoni, occurred in 5 herds. It was particularly prevalent in the Sun River herd, where 12 of 27 sheep were infected. Infection intensity varied from 1 to 25 tapeworms/animal, with adult worms located in the gall bladder and bile ducts. The double-pored tapeworm, Moniezia, was present in the Sun River and Stillwater herds, where 3 positive sheep were found.

Four species of coccidia were identified in a total of 40 sheep originating from the Wildhorse Island, Sun River, Yellowstone, and Spanish Peaks herds. Prevalence was highest in Sun River sheep, where approximately 52% of the animals sampled were infected, and on Wildhorse Island, where 43% were positive. The predominant species in all instances was Eimeria crandallis, which was originally described from bighorn sheep in Wyoming (Honess 1942). Other coccidian species that occurred sporadically in 1 or more of the infected herds were E. ahsata, E. granulosa and E. ovina.

Frequency of infections with 2 or more parasite species existing concurrently in the same animal is shown in Table 3. Multiple infections were most frequent in the Wildhorse Island and Ural-Tweed herds, but occurred at all locations except the Bitterroot East Fork herd. All 7 Wildhorse sheep examined were concurrently infected with Marshallagia and Nematodirus. Three of 7 animals from this herd had 3 gastrointestinal nematode infections concurrently. One sheep from this herd had mixed populations of 5 nematode species and in another instance, 6 different roundworm species were found.

A comparison of the prevalence of gastrointestinal parasites in native vs. introduced bighorn herds in western Montana indicated that, in general, native sheep had fewer parasites than transplanted animals (Table 4). An average of 6 species of helminths were found in sheep grazing ancestral ranges, whereas 9 species were recovered from introduced herds. Coccidian infections were acquired by sheep on both types of range.

DISCUSSION

Aside from providing basic information on the nature and extent of parasitism of the gastrointestinal tract in wild sheep, data derived from the present study have several potential applications for bighorn management. For example, it is possible to

Table 3. Prevalence of gastrointestinal parasites in 10 Montana bighorn herds.[a]

Herd	Gastrointestinal Helminths[b]			Parasite Prevalence		Coccidia	Total species	Frequency of multiple infections
	Mar.	Nem.	Trich.					
Wildhorse Island	100%	100%	43%	Ostertagia	28%	+	7	100%
				Trichostr.	43%			
				Chabertia	28%			
Sun River	52%	37%	26%	Skrjabin.	04%	+	7	44%
				Wyominia	37%			
				Capillar.	1.4%			
National Bison Range	14%	100%	50%	Ostertagia	50%	-	6	50%
				Trichostr.	50%			
				Cooperia	50%			
				Oesophag.	100%			
Lost Creek	40%	0	0	Wyominia	20%	-	2	20%
Kootenai Falls	50%	50%	0	----------		-	2	50%
Ural-Tweed	86%	14%	43%	Wyominia	29%	-	4	71%
Thompson River	75%	25%	25%	Wyominia	50%	-	4	50%
Bitterroot (E. Fork)	75%	0	0	Wyominia	25%	-	2	0
Yellowstone	75%	75%	25%			+	4	50%
Stillwater	25%	25%	25%	Skrjabin.	25%	-	5	50%
				Moniezia	25%			

[a] Spanish Peaks herd omitted because of insufficient postmortem data

[b] Mar. = Marshallagia; Nem. = Nematodirus; Trich. = Trichuris

Table 4. Comparative prevalence of gastrointestinal parasites in native and introduced bighorn sheep herds in western Montana.*

Herd	Abomasum		Small Intestine				
Status	Marshallagia	Ostertagia	Nematodirus	Trichostrongylus	Cooperia	Wyominia+	Moniezia
Native	+	-	+	-	-	+	+
Introduced	+	+	+	+	+	+	-

	Large Intestine					Total
	Trichuris	Chabertia	Oesophag.	Skrjabinema	Eimeria	Species
Native	+	-	-	+	+	7
Introduced	+	+	+	-	+	10

*After Stewart's 1985 classification of native and introduced herds in Montana.

+Technically a liver parasite

rank the relative severity of parasite burdens encountered in the survey area and to estimate their impact on the health of a specific herd. Two parameters that appear to be most useful for this purpose are (1) the total number of parasite species in a particular herd, and (2) the relative frequency of multiple infections. Using these criteria, Wildhorse Island sheep ranked as the most heavily parasitized herd studied, followed by the Bison Range and Sun River herds. Depending on the relative weight attached to total parasite inventory vs. frequency of multiple infections, Ural-Tweed, Thompson River and Stillwater herds ranked next in terms of severity of enteric parasitism. Sheep from the Kootenai Falls, Lost Creek, Bitterroot East Fork and Yellowstone herds showed the lowest levels of infection.

Attempts to estimate the relative pathogenicity of the helminths and coccidia identified in western Montana bighorns require extensive extrapolation from the veterinary literature. In most instances, relevant information on their disease-producing potential in wild sheep is lacking and must be inferred from studies with domestic sheep. Based on these sources and other supporting data on parasite prevalence and intensity, Marshallagia and Nematodirus appear to be the 2 most important enteric parasites (Table 2). Both genera are known to destroy intestinal epithelial tissue and interfere with digestion and absorption of nutrients (Soulsby 1965, Thorne et al. 1982). Four other nematode genera that occurred infrequently and in limited numbers--Trichostrongylus, Ostertagia, Chabertia and Oesophagostomum--are regarded as serious pathogens in domestic sheep. However, their absence in major herds such as the Sun River and Thompson River sheep suggests that they are not a current threat to the health of sheep in the region. The other nematodes (Cooperia and Capillaria) were recovered rarely and appear to be accidental in bighorn sheep in the study area. Neither of the tapeworms found during the survey is known to cause clinical illness in wild sheep, although Moniezia is thought to be a possible cause of retarded growth and decreased wool production in domestic sheep (Spasskii 1951).

The role of coccidian infections in producing disease in bighorn sheep has not been documented, although several species of Eimeria recovered during the present study are recognized pathogens in domestic sheep (Honess 1942). Eimeria ahsata is considered to be the most pathogenic species of domestic sheep, where it produces fatal infections in lambs (Smith et al. 1960). It occurred only in Wildhorse Island sheep in this study. Eimeria granulosa and E. ovina occurred sporadically in the Sun River and Spanish Peaks herds. Neither species is regarded as highly pathogenic in domestic sheep (Levine and Ivens 1970). Overall, the possibility that coccidiosis presently exists as a clinical problem in western Montana sheep seems remote. Nonetheless, the presence of moderate to high level coccidian infections in approximately half of the Sun River and Wildhorse Island bighorns examined indicates that the potential exists for symptomatic coccidiosis to occur where heavy range use occurs on a regular basis. Routine diagnostic testing involving periodic fecal analysis supplemented by necropsy data when available appear to be the best procedures for monitoring parasite levels and detecting significant accumulations of gastrointestinal parasites requiring management intervention.

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EXPERIMENTAL CONTACT ASSOCIATION BETWEEN BIGHORN SHEEP, ELK, AND DEER WITH KNOWN PASTEURELLA HAEMOLYTICA INFECTIONS.

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Abstract: Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*), were placed with elk (*Cervus elaphus*), and deer (*Odocoileus* spp.) at Washington State University to determine susceptibility of bighorn sheep to pneumonia caused by *Pasteurella* spp. carried by these animals. Four elk, 2 white-tailed deer (*Odocoileus virginianus*), and 1 mule deer (*Odocoileus hemionus hemionus*) were introduced into a 0.72 ha pen which contained 10 resident bighorn sheep. Another group of 4 elk was placed in a 0.4 ha pen with 3 additional bighorn sheep. *Pasteurella haemolytica* was isolated from the pharyngeal swab samples of all elk and deer and 11 of 13 bighorn sheep cultured at the time of elk and deer introduction. An isolate of *P. haemolytica* which reacted in antisera to serotypes T3, 4 and 10 was the most prevalent serotype detected, and was isolated from 5 of 8 elk, 3 of 3 deer, and 6 of 13 bighorn sheep. *Pasteurella multocida* was isolated from elk and bighorn sheep, but not from deer. All animals remained clinically healthy during the 6 months of close association. Therefore, no disease was associated with *Pasteurella* spp. carried by any of the animals included in this study.

The bighorn sheep pneumonia complex is a major mortality factor in bighorn sheep populations, and large scale mortality can result. Viruses, lungworms, stress factors, and bacteria can be important as multifactorial predisposing factors in the disease, and are often isolated or identified during episodes of pneumonia. Bighorn sheep in wild populations (Foreyt and Jessup 1982, Coggins 1988,) and in captive herds (Onderka and Wishart 1988, Foreyt 1989, Foreyt 1990, Callan et al. 1991) have developed bacterial pneumonia and died following exposure to domestic sheep. Domestic and exotic sheep were circumstantially incriminated as the source of bacteria, primarily *P. haemolytica*, that caused pneumonia in bighorns in the reports cited above. However, the potential role of elk and deer to serve as reservoirs of bacteria which may cause pneumonia in bighorn sheep has not been investigated.

Therefore the objective of this experiment was to determine the effects of close association of elk and deer known to be carriers of *P. haemolytica* on the health of captive bighorn sheep.

I thank the Washington Department of Wildlife, the Oregon Department of Fish and Game, and the Idaho Department of Fish and Game for assistance in obtaining the elk calves. The assistance of John Lagerquist and a number of enthusiastic veterinary students who participated in capturing the elk and obtaining samples from the animals is appreciated. Cooperation of personnel in the Washington Animal Disease Diagnostic Laboratory who isolated and evaluated the bacteria isolates is gratefully acknowledged.

METHODS

Animals.--Eight elk, 2 white-tailed deer, 1 mule deer, and 13 Rocky Mountain bighorn sheep were used in this experiment. The elk calves, 7 males and 1 female, were captured in the wild as free ranging calves before they were 7 days of age, and raised on unpasteurized goat milk until they were weaned at approximately 10 weeks of age. Calves were originally obtained from southeastern Washington (*n* = 4), northeastern Oregon (*n* = 3), or central Idaho (*n* = 1). The Washington and Idaho calves were captured by searching the elk calving areas on foot and physically catching the calves when found. The Idaho calf was captured after it fell off a cliff and fractured the dorsal spinal process of 3 lumbar vertebrae. It recovered with supportive care, but walked with a limp. The other calves were normal and healthy. The deer fawns were orphans from southeastern Washington, and were raised in the same manner as the elk. All elk and deer were raised on a private facility with no contact with other ungulates. The bighorn sheep were 2 captive herds at Washington State University, Pullman, Washington. All bighorn sheep had been born in captivity or had been in captivity for a minimum of 2 years, and were well acclimatized to captivity and their respective pens.

On 16 August 1991 (experimental day 0), all deer and elk were transported to Washington State University and placed in 2 pens with the bighorn sheep. Four elk calves (3 males and 1 female), and the 3 deer were released into pen 1 which was 0.72 ha and contained 10 resident bighorn sheep (7 adult females, 1 adult male, 2 lambs). Four male elk calves were released into pen 2 which was 0.4 ha and contained 3 bighorn sheep (a 2-yr-old castrated male, a 2-yr-old ewe, and a ewe lamb). Both pens had abundant natural grasses, a shelter, feeder, and water. Supplemental feed consisting of alfalfa and barley, and mineralized salt were available at all times. Animals were observed daily for abnormal behavior or signs of disease.

Bacteria sampling procedures.--On experimental day 0, pharyngeal swabs were obtained from each animal. A mouth speculum was used to hold the mouth open while a sterile cotton-tipped swab was used to briskly rub the tonsillar area. Swabs were placed in Amies transport medium (Spectrum Diagnostics, Inc., Houston, Texas 77032, USA) and submitted within 1 hour after collection to the Washington Animal Disease Diagnostic Laboratory (WADDL), Pullman, Washington, for bactera isolations and analysis. Bacterial isolates were confirmed by routine biochemical testing (Carter 1984). Biotyping and rapid plate serotyping methods for *P. haemolytica* were done according to established formats (Biberstein 1978, Frank and Wessman 1978). All animals were sampled a minimum of 2 additional times between 1 and 6 months after initiation of the experiment (Table 1). Not all animals were sampled at each sampling period (Table 1).

RESULTS

All animals remained healthy throughout the 6 month experimental period. Signs of respiratory disease were not observed, and all animals survived.

On day 0, P. haemolytica was isolated from 11 of 13 bighorns, and all deer and elk. An isolate of P. haemolytica that reacted in antisera to serotypes T3, 4 and 10 was the most common, and was detected in 6 of 13 bighorns, 5 of 8 elk, and 3 of 3 deer. Other serotypes in bighorns included A7 (n = 1), and serotypes that were untypeable because they did not agglutinate with known antisera (n = 8); in elk: untypeable serotypes (n = 5); in deer: T3 (n = 1 white-tailed deer), T3, 4 and 10 (n = 1 mule deer), and an untypeable serotype (n = 1 white-tailed deer). P. multocida was isolated from 1 of 13 bighorn sheep and 2 of 8 elk, but not from the deer (Table 1).

For the remainder of the 6 month experiment, P. haemolytica was isolated at least once from every animal. An isolate of P. haemolytica that reacted in antisera to serotypes T3, 4 and 10 was the most common in all 3 animal species. Other isolates of P. haemolytica reacted in antisera to serotypes T3 and 4; T3, 4 and 10; and untypeable isolates in bighorn sheep; T3; T3 and 4; T3, 4 and 10; and untypeable in elk; and T3, T3, 4 and 10; and untypeable in deer. P. multocida was isolated from bighorns and elk, but not from deer (Table 1). Other bacteria of potential importance that were isolated included Moraxella sp. from 2 elk, and Hemophilus sp. from 2 elk.

DISCUSSION

Close association between bighorn sheep, elk, and deer in this experiment did not result in pneumonia or death of any animal. Throughout the experiment, P. haemolytica and P. multocida were isolated commonly, but attempts to track transmission of the isolates between species was not attempted. However, future studies using DNA analysis techniques may indicate which bacteria were cross-transmitted between species, but without evidence of disease.

Previous research involving close association between bighorn sheep and domestic sheep has clearly indicated that bighorn sheep often die after association, most likely due to transmission of specific types of P. haemolytica from domestic sheep to bighorn sheep. When T strains of P. haemolytica from domestic sheep were given intratracheally to 2 bighorns at a concentration of $2x10^{12}$ organisms, both bighorns developed respiratory disease and died within 42 h postinoculation (Onderka et al. 1988). Recent results from my laboratory indicated that a strain of P. haemolytica A2 from healthy domestic sheep is usually lethal to bighorn sheep within 48 h when administered intratracheally at a concentration of less tha $2x10^{10}$ organisms. The same strain did not affect domestic sheep at the same inoculum level (Foreyt, Wash. State Univ., unpubl. data). Based on

Table 1. Isolations of Pasteurella haemolytica and P. multocida from captive bighorn sheep, elk, and deer.

Days post inoculation	Bighorn Sheep (n =13)		Elk (n = 8)		White-tailed Deer (n = 2)		Mule Deer (n = 1)	
	P. haem	P. mult	P. haem	P. mult	P. haem	P. mult	P. haem	P. mult
Day 0	11/13[a]	1/13	8/8	2/8	2/2	0/2	1/1	0/1
Day 27	9/13	3/13	NS[b]	NS	NS	NS	NS	NS
Day 55	NS	NS	2/2	1/2	2/2	0/2	1/1	0/1
Day 87	NS	NS	7/8	3/8	NS	NS	NS	NS
Day 123	NS	NS	NS	NS	NS	NS	NS	NS
Day 146	3/3	0/3	6/8	3/8	NS	NS	NS	NS
Day 172	10/13	2/13	8/8	3/8	2/2	0/2	1/1	0/1

[a] Number of animals positive for Pasteurella sp. / Number of animals sampled
[b] NS = No sample

experimental data and data collected from dieoffs of bighorn sheep in the field after exposure to domestic sheep, it has become a widely accepted tenet to prevent contact between domestic sheep and bighorn sheep in order to minimize domestic sheep induced mortality in bighorn populations. Similar recommendations could not be made regarding elk or deer and bighorn sheep based on the results of this experiment because all animals remained clinically healthy.

Information regarding Pasteurella spp. in wild ruminants is less extensive than for domestic animals (Rosen 1970, Thorne 1982, Biberstein 1990), but based on unpublished data from our ongoing investigations, it is likely that most wild ruminants carry a variety of strains of Pasteurella spp., and if samples are collected and processed according to established recommendations (Wild and Miller 1991), the probability of isolating P. haemolytica is high. It has been my experience that the most reliable method of isolation of P. haemolytica from bighorn sheep and other wild ungulates is to collect pharyngeal swabs and streak them directly on blood agar for bacterial isolation. This has resulted in significantly more isolations from live animals and a greater percentage of positive animals.

Based on the limited results from the current experiment, the strains of P. haemolytica and P. multocida that were identified in the elk and deer did not result in clinical disease in the bighorn sheep. Because the elk and deer in these studies were reared in captivity, it is not known if the bacterial isolates identified in the experiment are representative of the isolates found in wild populations of elk and deer. Future studies that compare isolates from wild populations and the isolates from animals in these studies will clarify that question. Further research is necessary to evaluate the association between bighorn sheep, elk , deer and other ungulates.

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MANAGEMENT AND RESEARCH TECHNIQUES

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SEASONAL CHANGES IN LAMB:EWE RATIOS

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Abstract: Lamb:ewe ratios were calculated seasonally (birth, Jun, Sep, and late winter) over a 16 year period for marked individuals in a bighorn sheep population which experienced a phase of population growth (1981-91) and a period of stability (1975-80) during which adult ewes were experimentally removed. Despite fecundity rates that averaged 92% (range 82-100) over the 16 years, lamb mortality by September had reduced lamb:ewe ratios (ewes $\geq$ 2 yrs) to 63 lambs:100 ewes (range 36-82). Post-hunt and late winter ratios calculated during ewe removal years failed to accurately reflect additional lamb mortality since ratios actually increased because of a reduction in the number of ewes. June ratios were weakly correlated with yearling recruitment the following year. Post-hunt and late winter ratios were also correlated with yearling recruitment but only during non-removal years. None of the ratios were correlated with the percent change in population size the following year. Significant correlations were found, however, if lambs were excluded from the following year's population total. June ratios combined over 2 consecutive years (non-ewe removal years only) were significantly ($P <$ 0.01) correlated with the percent change in the population between those years. Consecutive winter ratios were also found to be significantly (P $<$ 0.05) correlated with changes in winter population size but again, only during years with no ewe removals.

Lamb:ewe ratios are commonly used as indicators of the health of bighorn sheep (*Ovis canadensis*) herds (Leslie and Douglas 1980, Wehausen et al. 1987, Hebert and Harrison 1988). High ratios are assumed to imply healthy, expanding herds of high quality while the reverse is applied to herds with low ratios (Geist 1971). Smith (1988) found that declining populations of mountain goats (*Oreamnos americanus*) in Alberta were associated with low kid:adult ratios. There have, however, been no studies where actual ratios have been used to correlate with known changes in population size. There have also been no attempts to document seasonal changes in lamb:ewe ratios. Most studies use winter ratios obtained from either ground or aerial surveys. Such ratios, however, do not accurately reflect fecundity because of unknown levels of lamb mortality which occurred between birth and whenever the ratio was calculated.

Further compounding the accuracy and interpretation of lamb:ewe ratios, are how animals are classified during surveys. It is usually difficult to distinguish yearlings (ewes and rams) and 2-year-old ewes from older reproductively mature ewes. These animals end up included in the "ewe" component of the lamb:ewe ratio. How this factor affects actual ratios has not been determined.

The purpose of this paper is to examine how lamb:ewe ratios change seasonally and are affected by the inclusion of non-reproducing individuals. Ratios are also examined for their usefulness as indicators of population change and recruitment. Funding support is gratefully acknowledged from the Alberta Fish and Wildlife Division, the Alberta Recreation, Parks and Wildlife Foundation, the Craighead Wildlands Wildlife Institute, and the University of Sherbrooke.

STUDY AREA AND METHODS

Ram Mountain is an isolated outcrop of sheep habitat in west-central Alberta. The study area ranges in elevation from 1082 to 2173 m, with treeline at about 1830 m, and includes approximately 38 km^2 of alpine and subalpine habitat used by sheep. It is surrounded on 3 sides by conifer covered foothills. On the fourth side, the North Saskatchewan River separates Ram Mountain from Shunda Mountain, a similar outcrop that supports a small population of sheep.

Sheep have been trapped since 1971 in a corral trap baited with salt. All sheep are trapped annually and marked with either individually identifiable ear tags or collars. Any unmarked animals were lambs which, if not captured in the year of their birth, were captured and tagged as yearlings the following year. The population has ranged in size from a low of 94 in 1977 to a high of 232 in 1991.

Lactation was determined each year 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 parturition. This type of mortality was classified as neonatal mortality. Lambs were paired with ewes on the basis of suckling. The disappearance of marked lambs and the subsequent cessation of lactation in the respective mother was considered summer mortality.

Between 1972 and 1980, 12-24% of the total number of ewes one year of age and older, were removed from the population in September. Ewes were either shot or transplanted.

Ratios were calculated by dividing the number of lambs alive at a particular time by the number of ewes alive at that same time. All ratios and population sizes were based on actual numbers of marked animals which represented the entire population. Post-hunt ratios were ratios calculated after the annual ewe removals. Since field work was completed by October, mid-winter ratios were unknown, however, late winter ratios were calculated based on animals surviving to the following spring. Mid winter ratios would, therefore, fall somewhere between post-hunt ratios and late winter ratios. Linear regression was used to look for correlations between ratios and various population parameters.

RESULTS

Seasonal Lamb:ewe Ratios

At birth.--Bighorns normally do not produce their first lamb until 3 years of age. Considering only ewes 3 years and older, lamb:ewe ratios at birth on Ram Mountain averaged 0.99 (range 0.82-1.36) between 1975 and 1991 (Table 1). Values greater than 1.00 were years when some 2-year-old ewes produced lambs. Most ewes of reproductive age therefore gave birth to a lamb each year. Including 2-year-old ewes, the average ratio was only 0.78 (range 0.65-0.91).

June.--The average ratio (ewes ≥ 2yrs) at birth declined from 0.78 to 0.67 (range 0.48-0.82) (Table 1). There was considerable annual variation in the level of neonatal lamb mortality. Neonatal mortality ranged from 4% in 1976 to 33% in 1977.

September.--By the end of summer, ratios (ewes ≥ 2yrs) had declined further to average 0.63 (range 0.36-0.82) (Table 1). This represented a drop from June of only 0.04, indicating that lamb mortality during the summer was very low. With the inclusion of yearlings in the ewe component of the ratio, the average ratio was 0.43 (range 0.25-0.54).

Post-hunt.--Following the hunting season for trophy rams and the removal of any ewes (only during 1972 to 1980), the ratio (ewes ≥ 2yrs) averaged 0.71 (range 0.36-1.13) (Table 1). This ratio was higher than the September average ratio of 0.63.

Late-winter.--At the end of winter, the ratio (ewes ≥ 2yrs) averaged 0.61 (range 0.24-1.00) (Table 1). By including yearlings in the ewe component of the ratio, the average dropped to 0.40 (range 0.17-0.59).

Table 1. Seasonal lamb:ewe ratios from Ram Mountain, 1975 to 1991.

	Lamb:Ewe Ratio			
Season	Mean	Range	N*	Ewe Component
At Birth	0.99	0.82-1.36	17	Ewes ≥ 3 yrs
	0.78	0.65-0.91	17	Ewes ≥ 2 yrs
Jun	0.67	0.48-0.82	17	Ewes ≥ 2 yrs
	0.45	0.34-0.56	17	Ewes and yrlgs
Sep	0.63	0.36-0.82	17	Ewes ≥ 2 yrs
	0.43	0.25-0.54	17	Ewes and yrlgs
Post-hunt	0.71	0.36-1.13	16	Ewes ≥ 2 yrs
Late winter	0.61	0.24-1.00	16	Ewes ≥ 2 yrs
	0.40	0.17-0.59	16	Ewes and yrlgs

* No. of years

Ratios as Predictors of Recruitment and Population Change

June and September ratios (ewes ≥ 2yrs) were positively correlated with the number of yearlings recruited to the population the following year (Table 2). Post-hunt and late winter ratios, however, were not correlated.

When all years (1975 to 1991) were combined, ratios (ewes ≥ 2yrs) calculated during any season were poor predictors of percent population change to the next year (Table 3).

However, if the following year's lamb crop was excluded from the calculation of percent population change, then June and September ratios were strongly correlated ($\underline{P} < 0.01$) with percent population change (Table 4). Post-hunt ratios were correlated as well but only during those years when no ewe removals occurred.

Table 2. Pearson correlations between seasonal lamb:ewe ratios[a] and yearling recruitment, 1975 to 1991.

			N[b]	r	P
Jun ratio	vs	No. of yrlgs. the following May	16	0.54	<0.05
Sep ratio	vs	No. of yrlgs. the following May	16	0.54	<0.05
Post-hunt	vs	No. of yrlgs. the following May	16	0.09	NS
Late winter	vs	No. of yrlgs. the following May	15	0.16	NS

[a] Ewes ≥ 2 yrs [b] No. of yrs

Table 3. Pearson correlations between seasonal lamb:ewe ratios[a] and percent population change from one summer to the next summer, 1975 to 1991.

			N[b]	r	P
Jun ratio	vs	% Pop. change (summer)	16	0.14	NS
Sep ratio	vs	% Pop. change (summer)	16	0.09	NS
Post-hunt (includes removal years)	vs	% Pop. change (summer)	16	0.28	NS

[a] Ewes ≥ 2 yrs [b] No. of yrs.

June and September ratios were also correlated ($P < 0.05$) with percent population changes from the previous year (Table 5). Post-hunt ratios were not correlated ($r = 0.05$, $P > 0.05$) except during non-removal years ($r = 0.88$, $P < 0.01$).

Table 4. Pearson correlations between seasonal lamb: ewe ratios[a] and percent population change, excluding lambs, 1975 to 1991.

			N[b]	r	P
Jun ratio	vs	% Pop. change (excludes lambs)	16	0.85	<0.01
Sep ratio	vs	% Pop. change (excludes lambs)	16	0.78	<0.01
Post-hunt (includes removal years)	vs	% Pop. change (excludes lambs)	16	0.31	NS
Post-hunt (post removal yrs only)	vs	% Pop. change (excludes lambs)	9	0.92	<0.01

[a] Ewes ≥ 2 yrs.
[b] No. of yrs.

Table 5. Pearson correlations between seasonal lamb: ewe ratios[a] and percent population change from the previous year, 1975 to 1991.

			N[b]	r	P
Jun ratio	vs	% Pop. change (summer)	17	0.56	<0.05
Sep ratio	vs	% Pop. change (summer)	17	0.46	<0.05
Post-hunt (post removal)	vs	% Pop. change from previous yr.	9	0.88	<0.01
Post-hunt (removal yrs.)	vs	% Pop. change from previous yr.	8	0.31	NS

[a] Ewes ≥ 2 yrs.
[b] No. of yrs.

Because the 2 apparent largest factors affecting change in population size from one year to the next, appeared to be a combination of recruitment and lamb production, lamb:ewe ratios (ewes $\geq$ 2yrs) from 2 consecutive seasons were combined and regressed with population changes between the 2 years. Consecutive year June ratios were significantly ($r = 0.58$, $N = 16$, $P < 0.05$) correlated with changes in percent population change. That correlation was stronger during post-removal years ($r = 0.87$, $n = 9$, $P < 0.01$) (Fig. 1). Two consecutive winter ratios were also significantly correlated ($r = 0.73$, $N = 8$, $P < 0.05$) with a change in the winter population but during post-removal years only (Fig. 2).

DISCUSSION

Lamb:ewe ratios varied considerably between seasons and between years on Ram Mountain. This variability was due to differences in lamb mortality and not to differences in adult mortality except during years when ewes were experimentally removed from the population. During these removal years, calculated post-hunt and late winter ratios were actually greater than the corresponding June or September ratios. Additional lamb mortality could, therefore, no longer be estimated from changes in the lamb:ewe ratio.

Ratios were not good indicators of fecundity. Most ewes 3 years or older produced a lamb each year but varying levels of lamb mortality reduced ratios such that by late winter ratios as low as 0.24 were seen. Obtaining true ratios was further compounded by the inability to correctly classify younger animals such as 2-year-olds or yearlings. Including these non-producers into the ewe component of the ratio, resulted in a further lowering of the calculated ratio.

It is important, therefore, to try and classify yearlings during any survey and to specify what age class of individuals were included in any age ratio calculations. This is important if comparisons are to be made with ratios reported in other studies.

At Ram Mountain, June and September lamb:ewe ratios were good predictors of recruitment to the next year. Such predictive value was lost, however, if ratios were determined following the hunting season in years of ewe removals. Despite the correlation of summer ratios with recruitment, there was no correlation with percent population change the next year.

While not useful in predicting population changes between consecutive years, ratios were, however, useful in predicting population changes between one year and the previous year. This was due to the large influence the number of lambs born the following year had on population change. There was also a good correlation between summer ratios and population change the following year but only if the followings year's lamb crop was not included in the population total.

Post-hunt and late winter ratios could be used to predict similar changes in population size but only during years when there were no ewe removals. The additional ewe "mortality" in those years altered the ratios enough to negate the correlation.

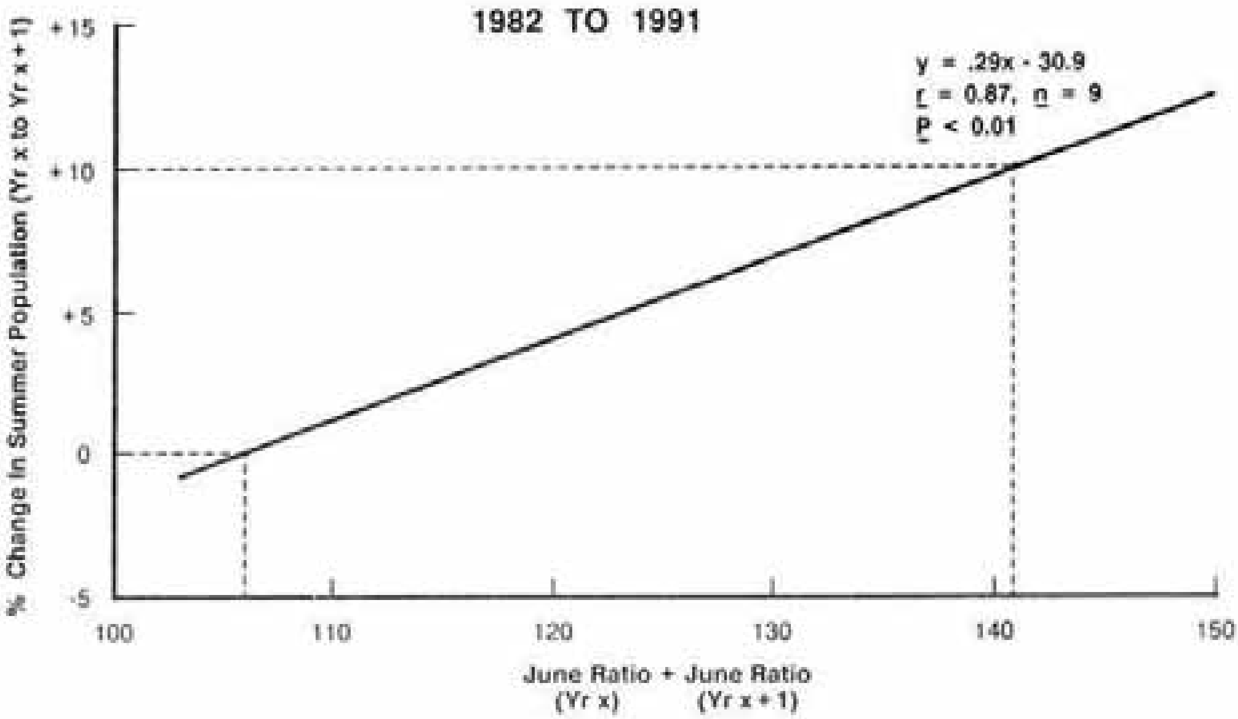

Fig. 1. The relationship between population change and consecutive year June lamb:ewe ratios.

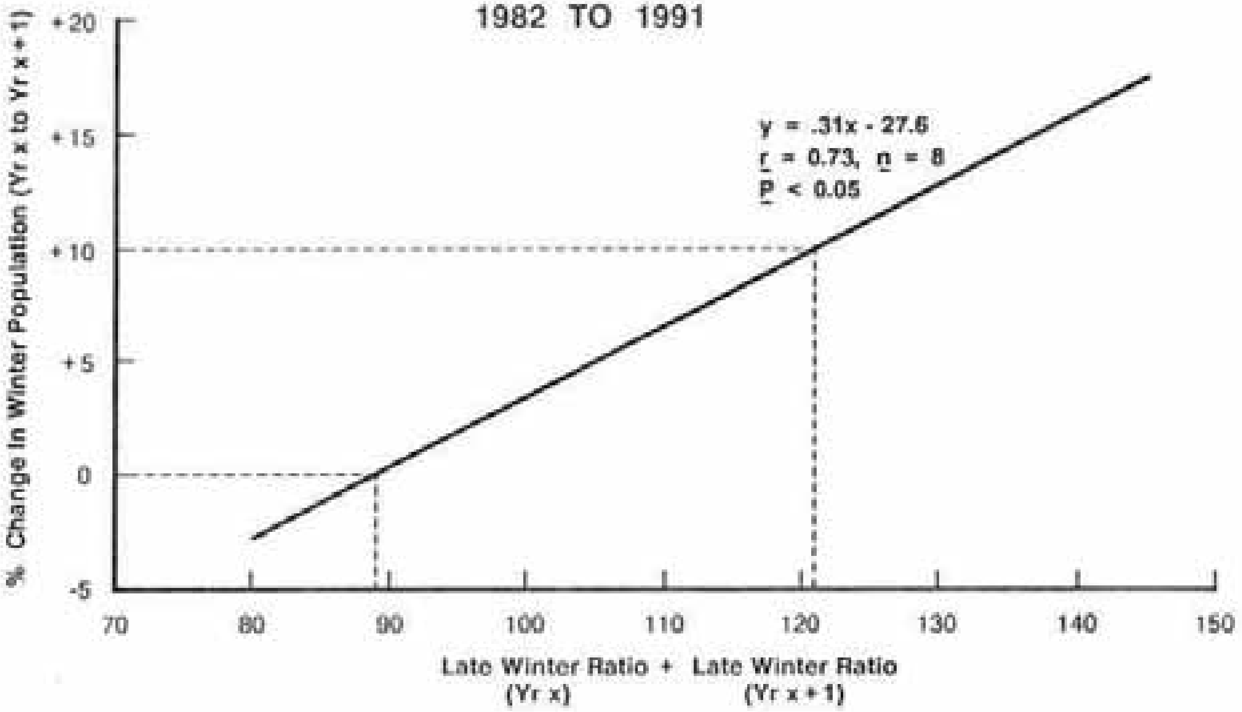

Fig. 2. The relationship between winter population change and consecutive year late winter lamb:ewe ratios.

Those factors contributing most to a change in population size from one year to the next would be recruitment from the previous year, lamb production during that year, and mortality over the previous winter. Since summer ratios were good predictors of both recruitment and population change (from the previous year), it would follow that a combination of ratios taken over 2 consecutive years would be good predictors of population change between those years. This was the case at Ram Mountain, but was applicable only to years of no ewe removals. Similarly, consecutive winter ratios could be used to predict changes in winter population size.

Overwinter mortality could also be expected to have a significant influence on population change. In order for there to be a correlation between ratios and population change, adult mortality rates would have to be consistent on an annual basis. Such was the case at Ram Mountain where annual survival rates averaged 83% with a range of only 80-86% over 10 years. Most of the predictive value of lamb:ewe ratios would thus be lost for populations experiencing large fluctuations in annual adult mortality.

The relationships found in this study were developed based on actual ratios and not from estimates of lamb:ewe ratios based on a sample of the population. Such detailed information is not usually available for most bighorn populations and managers must rely on data gathered during ground or aerial sampling. Such surveys vary in their ability to accurately sample the population. If only a small proportion of any herd is actually sampled, the bias of the subsequent age ratio will likely increase, further weakening the value of such ratios as indicators of population change.

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USE OF AGE RATIOS TO PREDICT BIGHORN SHEEP POPULATION DYNAMICS

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Abstract: Age ratios are used as an index of the well-being of wild sheep populations under the assumption that high ratios indicate a growing and healthy population. I tested whether age ratios in June and in January predicted recruitment (number of yearlings) to the population or changes in total and nursery herd size. Lamb:ewe ratios in June did not predict either recruitment or population changes. Lamb:ewe ratios in January were good predictors of yearling recruitment only if yearlings were not classified as ewes. Lamb:ewe ratios, however, were not good predictors of population changes, regardless of whether or not the year of a pneumonia epizootic was included in the analysis. Lamb survival from June to January, calculated by the change in lamb:ewe ratio, was not correlated with change in population size. Yearling:ewe ratios in January were a poor predictor of changes in population size. These results suggest that age ratios in June are not useful for predicting population changes, and age ratios in January have limited usefulness. The inability to distinguish adult ewes from yearlings of both sexes during aerial surveys further limits the usefulness of age ratios. The results question the relevance of yearly variations in lamb survival with respect to changes in population density.

Wildlife managers are often interested in predicting changes in population size of wild animals. For bighorn sheep (Ovis canadensis), population size is usually estimated from winter counts. Bighorns inhabit open habitat, are gregarious, very traditional in their use of winter ranges, and easier to see than most other ungulates, particularly if surveys are flown after fresh snowfalls. Similar techniques are used for Dall sheep (Ovis dalli), except tha summer counts are preferred (Nichols 1978), because a white sheep is easier to spot against a brown-green background than on snow. There are few published estimates of potential errors in aerial or ground censuses of bighorn sheep (Irby et al. 1988), and there is little information on potential biases. For example, lambs may not be distributed randomly among nursery groups; moreover, that differences in snow condition, weather, sheep distribution and observer experience can bias the probability of finding and correctly classifying sheep.

Aerial mountain sheep censuses are expensive and can cause harassment (Bleich et al. 1990). Therefore, replicate censuses are rarely undertaken and managers have to rely on single surveys to estimate population size and trends in population dynamics. As an alternative to accurate complete counts, age ratios are often used to attempt to predict changes in population size, or to assess the "health" of a sheep population (Leslie and Douglas 1980, Burles and Hoefs 1984, Douglas and Leslie 1986, Wehausen et al. 1987, Coggins 1988, Jorgenson 1988, Hebert and Harrison 1988). The use of age ratios relies upon the assumption that high lamb:ewe or yearling:ewe ratios are indicative of a healthy, growing sheep population. There have been, however, no attempts to actually compare age ratios to changes in recruitment or in population size, nor is there any information on how any usefulness of these ratios may change according to the time of year when censuses are undertaken. For example, Hoefs and Bayer (1983) reported wide fluctuations in lamb:ewe ratios (0.10 - 0.64) during a 12-year study of Dall sheep characterized by only 10% variation between the minimum and the maximum number of ewes observed. On the other hand, Smith (1988) found that a decline in kid:adult ratios in mountain goats (Oreamnos americanus) accompanied a decline in overall population size over a wide area in west-central Alberta.

Here I compare several types of age ratios with changes in recruitment and population size in a marked bighorn population monitored for 11 years. I test the null hypothesis that age ratios are not correlated with either recruitment (number of yearlings present the following May) or changes in population size.

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STUDY AREA AND METHODS

The study population in southwestern Alberta overwinters in the Sheep River Wildlife Sanctuary and areas to the east (Festa-Bianchet 1986a,b). The study began in March 1981 and since 1982 over 85% ($\bar{x}$ = 94%) of the ewes present each year have been individually marked with colored ear tags. The high proportion of marked ewes and the ease of finding them in the winter range (an average of 97% were seen during each census in winter) allowed exact counts of nursery herds (ewes, lambs, and yearlings of both sexes). The proportion of rams marked was smaller (51 - 74%, $\bar{x}$ = 61%). Estimate of ram numbers were made more difficult by the seasonal presence of non-resident rams, and by their use of areas east of the

Sanctuary in winter, where they were difficult to find (Festa-Bianchet 1986b).

Rams in this population are hunted outside the Wildlife Sanctuary (Festa-Bianchet 1986c). Ewe permits are also issued, but ewe harvest averages less than 1 ewe/year. A minimum of 6 rams, 3 ewes and 1 lamb were poached during the study.

The number of lambs produced each year was estimated by the number of ewes that had extended udders or were seen nursing a lamb. Lamb:ewe ratios in June were obtained by dividing the total number of lambs seen (therefore not including those that presumably died at or soon after birth) by the number of ewes alive in June. Lamb:ewe ratios in January were obtained by dividing the number of lambs alive in January by the number of ewes alive in January. An average of 69% of the lambs were marked by January. January yearling:ewe ratios were obtained from total counts of yearlings and ewes. Beginning in 1982, an average of 83% of yearling females and 65% of yearling males were ear-tagged each year. To approximate aerial surveys, some of the lamb:ewe ratios were recalculated including yearlings of both sexes as "ewes".

Lamb survival was calculated in two ways: actual survival (the number of lambs that survived to May 1 divided by the number born the previous year) and survival calculated dividing the January lamb:ewe ratio by the June lamb:ewe ratio. The data are complete counts, not estimates based upon a sample. Although it is likely that some small errors were involved (not all sheep were marked, especially in the first few years of the study), the data are more accurate than censuses of unmarked populations.

RESULTS

Population Changes

Table 1 summarizes the changes in population size and in age ratios during the study. The drop in numbers after 1985 was caused by pneumonia (Festa-Bianchet 1988a). Because of the die-off, the number of sheep in March varied considerably during the study, from a low of 99 to a high of 153 (55% difference). The nursery herd varied from 65 to 106 animals, a difference of 63%. Age ratios also varied during the study; in most cases the highest ratio was twice or more the lowest ratio.

Relationships of Age Ratios to Recruitment

Most attempts to find correlations between age ratios and recruitment failed (Table 2). The only exception was the significant correlation between the January lamb:ewe ratio and the number of yearlings recruited the following May. The June lamb:ewe ratio had no relationship to the number of yearlings recruited the following May, and when yearlings of both sexes were included as "ewes" I even obtained a near-significant negative correlation.

Table 1. March population size and age ratios for the Sheep River bighorn sheep herd, southwestern Alberta, between 1982 and 1991. Ratios in June refer to the same year, while January ratios refer to the following year. The category "ewe" includes yearlings of both sexes.

	Year									
	82	83	84	85	86	87	88	89	90	91
Numbers										
Adult females	49	48	50	53	49	46	44	48	50	54
Yearling females	6	15	12	18	8	3	7	5	9	5
Yearling males	6	11	9	8	7	3	3	8	7	8
Total Nursery herd	97	103	100	106	71	65	68	80	88	89
Adult males	43	41	47	47	36	34	31	29	30	29
Total population	140	144	147	153	107	99	99	109	118	118
Ratios										
Lamb:ewe (Jun)	0.88	0.76	0.85	0.81	0.69	0.87	0.80	0.67	0.77	0.68
Lamb:"ewe" (Jun)	n/a	0.52	0.58	0.59	0.62	0.70	0.62	0.50	0.56	0.50
Lamb:ewe (Jan)	0.54	0.64	0.54	0.31	0.42	0.35	0.41	0.53	0.43	
Lamb:"ewe" (Jan)	0.33	0.46	0.35	0.24	0.36	0.29	0.32	0.40	0.35	
Yearling:ewe (Jan)	n/a	0.47	0.37	0.13	0.21	0.28	0.33	0.34	0.36	

Relationships of Age Ratios to Population Changes

Lamb:ewe ratios in either June or January were very poor predictors of population changes. The January yearling:ewe ratio was correlated with change in total herd size only because of the inclusion of data from 1985-86, a year of very poor yearling survival followed by a drastic decline in herd size caused by pneumonia. When 1985-86 was excluded, the correlation was no longer significant (Fig. 1). A similar situation was found for the correlation between January lamb:ewe or yearling:ewe ratio and the change in nursery herd size excluding lambs, the most variable component of the population (Hoefs and Bayer 1983) (Table 3).

Lamb survival from birth to 1 year was correlated with changes in population size (Table 3), but only because of the pneumonia die-off. The correlation disappeared when that year was eliminated, suggesting that the significance was spurious and due mostly to point-cluster correlations like the one illustrated in Fig. 1. Lamb survival from June to January, calculated by the change in lamb:ewe ratio, was not correlated with changes in population size (Table 3), particularly if the die-off year was excluded from the analysis.

Table 2. Pearson correlation coefficients (r) between recruitment of yearlings (number of yearlings the following May) and age ratios or population characteristics for the Sheep River herd, 1981 to 1991. The category "ewe" includes yearlings of both sexes. P values: NS, not significant; * <0.05, **<0.01. For each comparaison, the first line indicates the results from all years, the second line indicates the results of the same analysis excluding 1985, the year of a pneumonia die-off.

Age ratio or population character	N	r	P
Jun lamb:ewe	8	0.03	NS
	7	0.18	NS
Jun lamb:"ewe"	8	-0.54	NS
	7	-0.65	NS
Jan lamb:ewe	8	0.89	**
	7	0.85	*
Jan lamb:"ewe"	8	0.75	*
	7	0.60	NS
% lactation	8	0.64	NS
	7	0.72	NS
% lactation, 2-3-yr-olds	8	0.16	NS
	7	0.41	NS

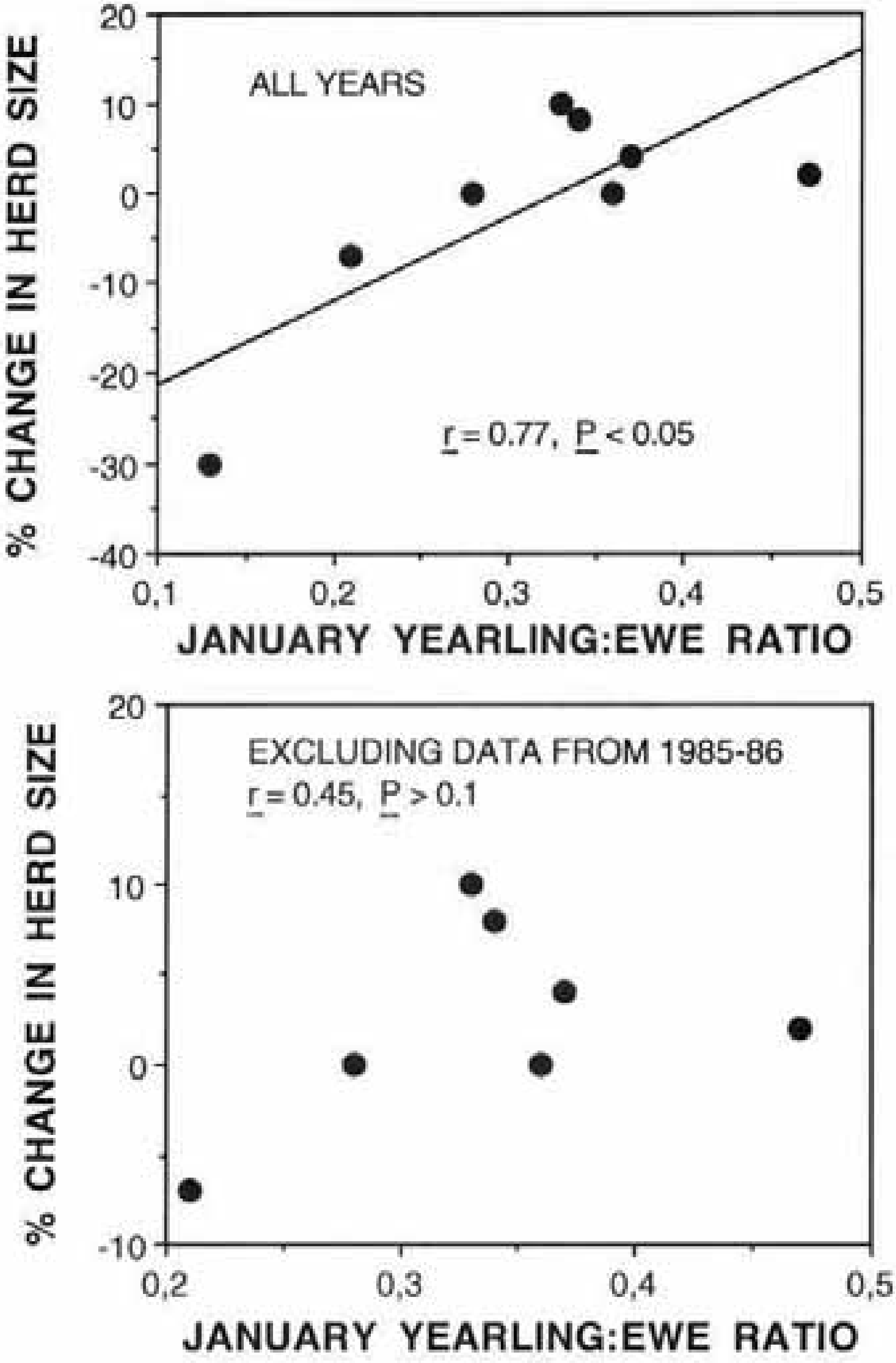

Fig. 1. Correlation between January yearling:ewe ratio and percent change in total herd size for bighorn sheep at Sheep River, Alberta, 1982 - 91.

Table 3. Pearson correlations between age ratios, population characteristics and relative change in population size for the Sheep River herd, 1981 - 91. The category "ewe" includes yearlings of both sexes. The Jan:Jun lamb:ewe ratio is the survival of lambs from June to January according to the change in lamb:ewe ratio. *P* values: NS, not significant; * <0.05, **<0.01. For each comparison, the first line indicates the results from all years, the second line indicates the results of the same analysis excluding 1985, the year of a pneumonia die-off.

Correlation				
between	and	N	*r*	*P*
Jun lamb:ewe	Jun lamb:"ewe"	9	0.67	*
		8	0.68	NS
Jun lamb:ewe	% total change	9	0.06	NS
		8	0.09	NS
Jun lamb:ewe	% nursery herd change	9	0.06	NS
		8	0.29	NS
Jan lamb:ewe	% total change	9	0.57	NS
		8	0.22	NS
Jan lamb:ewe	% nursery herd change	9	0.40	NS
		8	0.16	NS
Jan lamb:ewe	% nursery herd change[a]	9	0.66	*
		8	0.46	NS
Jan yearling:ewe	% total change	9	0.77	*
		8	0.45	NS
Jan yearling:ewe	% nursery herd change	9	0.64	NS
		8	0.11	NS
Jan yearling:ewe	% nursery herd change[a]	9	0.84	**
		8	0.68	NS
Lamb survival from birth to 1 year	% nursery herd change	9	0.71	*
		8	0.18	NS
Lamb survival from birth to 1 year	% total change	9	0.78	*
		8	0.35	NS
Jan:Jun lamb:ewe	% total change	9	0.52	NS
		8	0.16	NS
Jan:Jun lamb:ewe	% nursery herd change	9	0.33	NS
		8	0.24	NS

[a] Nursery herd excluding lambs

Data from the die-off year strongly affected most correlations between age ratios and changes in population (Table 3), but had little effect upon the correlations between age ratios and recruitment of yearlings (Table 2).

DISCUSSION

Age ratios appear to be poor predictors of either recruitment or changes in population size in bighorn sheep. The only age ratio that may have some use is the winter yearling:ewe ratio, that is almost impossible to obtain from aerial surveys. By their second winter, "yearlings" are almost 2 years old and difficult to distinguish from adult ewes. An experienced observer, however, could classify most yearlings correctly in a ground count. Overall, it seems that information on the number of yearlings is more useful than information on the number of lambs.

Lamb:ewe ratios (or, even worse, lamb:"ewe" ratios) in June appear to be useless to predict either recruitment or population changes. This result is not surprising in view of the very high fecundity rates of northern populations of bighorn sheep (Festa-Bianchet 1988b, Jorgenson and Wishart 1986). It appears that since almost all adult ewes produce lambs, year-to-year fluctuations in yearling recruitment or in population size are due mostly to variations in survival, not in production. The number of lambs produced, either in absolute terms or in relation to the number of ewes, is not by itself a useful parameter to predict population changes. The survival of lambs and older sheep is likely to be of greater interest, although my analysis suggests that lamb survival calculated simply by the change in lamb:ewe ratio is not very useful to predict recruitment or population changes.

Lamb:ewe ratios in January (when most aerial censuses are done) were a slightly more useful indicator of recruitment than lamb:ewe ratios in June, but were not a reliable predictor of population changes. Nevertheless, the number of yearlings that may recruit in a bighorn population remains a parameter of interest to managers, especially in populations where ewes are harvested. Therefore, it would appear that lamb:ewe ratios in January could be used to forecast changes in recruitment, but any such forecast would likely include a wide margin of error.

In conclusion, it appears that there is no substitute for complete counts to assess changes in bighorn population size. Age ratios cannot reliably forecast such changes. Nevertheless, drastic changes in age ratios (Wehausen et al. 1987, Festa-Bianchet 1988a), could be detected by aerial counts. These changes would provide clues to the possible occurrence of disease or to changes in other factors, such as predation, that may affect lamb survival (Wehausen et al. 1987). It remains to be seen, however, whether changes in lamb survival affect population size in bighorn sheep. The data presented here and in other studies (Hoefs and Bayer 1983, Jorgenson 1992) suggest that yearly variations in lamb survival may not have very strong effects upon bighorn sheep populations. Lamb production varies little between years, and changes in survival of yearlings and adults may play a key role in determining population size. That pattern is to be expected in populations of long-lived animals.

It would be interesting to compare these data with other long-term studies. In my study, the population suffered a pneumonia epizootic. It is possible that results obtained from populations not affected by disease would be different. It remains to be seen whether age ratios are a more reliable predictor of changes in population size in populations whose density changes over a wider range than that available during my study. Results from the Ram Mountain study (Jorgenson 1992) suggest that the usefulness of age ratios may indeed be universally limited.

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ESTIMATION OF DALL SHEEP NUMBERS IN THE WRANGELL-ST. ELIAS NATIONAL PARK AND PRESERVE

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Abstract: Aerial sample surveys of Dall (*Ovis dalli dalli*) sheep were conducted in Wrangell-St. Elias National Park, Alaska, in July 1990 and 1991. The sample surveys included a 2-stage stratified random sampling procedure combined with double sampling. Observers in a fixed-wing aircraft completed an aerial survey on a random sample of count units in high, medium, and low density sheep regions in the entire survey area (fixed-wing survey). The double sampling consisted of a more intensive survey by observers in a helicopter on a subsample of these units (helicopter survey). The helicopter survey provided groups of sheep known to exist in the count units which were either detected or missed during the fixed-wing survey. The probability of detection of a given size group during the fixed-wing survey was then estimated using logistic regression. The 2-stage sample combined with double sampling allowed extrapolation of sheep counts, corrected for visibility bias, to the entire survey area. The 2 years of survey allowed a comparison of independent estimates of Dall sheep density using nearly identical methodology.

Aerial surveys designed to count all the animals present in an area generally lack information necessary to estimate the accuracy and precision of the counts. Unfortunately these surveys often underestimate animal abundance (Caughley 1977). A major reason for inaccuracies in aerial surveys is the lack of an estimate of the number of animals not counted due to visibility bias (Caughley 1974, 1977). In an evaluation of the effects of several factors on the accuracy of aerial surveys, Caughley et al. (1976) found that speed, height above ground, width of survey strips, and observers had significant effects on survey results. Samuel et al. (1987) found that visibility of elk in northcentral Idaho was significantly influenced by group size and vegetation cover. Other studies of visibility bias in aerial surveys have reported affects from species (Broome 1985), season (Gasaway et al. 1985), sex, terrain, past experience with aircraft (Singer and Mullen 1981), and age-specific behavior (Miller and Gunn 1977).

Several methods of adjusting aerial survey data for visibility bias have been described. Samuel et al. (1987) described sightability models for predicting the probability of observing elk groups during winter aerial counts. Eberhardt and Simmons (1987) suggested "double sampling" as a way to calibrate aerial observations. McDonald et al. (1990) estimated visibility bias associated with aerial surveys of Dall sheep in the Arctic National Wildlife Refuge (ANWR), Alaska, using logistic regression to estimate visibility as a function of measurable explanatory variables.

Because of the size of the parks in Alaska, conventional surveys can cover only a small portion of sheep range. Wrangell-St. Elias National Park and Preserve (WRST) was last surveyed by the National Park Service (NPS) and the Alaska Department of Fish and Game (ADF&G) during a 4-year period from 1981 through 1984. These and previous sample surveys of WRST were an attempt to count all the sheep in the areas surveyed using a variety of aircraft and personnel. Past surveys provided valuable information necessary for the management of sheep in the Park and Preserve. However, the survey design, potential visibility bias, and extended survey period made interpretation of sample survey data difficult. In addition, the extensive flying necessary for a total count, much of the time in fixed-winged aircraft, made surveys expensive and dangerous.

An aerial sample survey of Dall sheep was conducted in late June - early July of 1990 and 1991 in WRST. WRST is a 53,418 square kilometer (20,625 mi^2) national park in southcentral Alaska. The sample surveys were conducted in the Wrangell Mountains and the adjacent portion of the Chugach Mountains in the park. The surveys used a stratified random sample with double sampling for correction of visibility bias. Sheep abundance was estimated by counting sheep from a fixed-wing aircraft in a random sample of count units stratified by sheep density. Counts made during the fixed-wing flight were corrected for visibility bias by comparison with a double sample from a helicopter on a subset of units, and used in a 2-stage sampling plan to estimate the abundance of sheep in the entire WRST.

This project is part of a regional effort to improve sample surveys of Dall sheep in National Parks of Alaska. The specific objectives of the sample surveys were:

1. to estimate abundance of Dall sheep in the Wrangell and Chugach mountains within WRST with known accuracy and precision;
2. to develop and test a sampling design that is more cost effective than those used in past surveys and can be completed easily in 1 season; and
3. to develop and test a sampling design that is safer than those used in past surveys.

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METHODS

Surveys were conducted during the last week in June and first week in July both years. The surveys utilized a 2-stage random sampling procedure with stratification combined with double sampling. The double sampling method involved conducting a comparatively extensive survey of Dall sheep from a fixed-wing aircraft in a stratified random sample of survey units, followed immediately by a comparatively intensive survey from a helicopter on a subsample of these units. We assumed that the intensive helicopter survey detected a random sample of sheep groups present, "marked" their location, and gave an exact count of sheep numbers present in detected groups. The fixed-wing survey either detected or did not detect the marked groups. Double sampling with helicopter and fixed-wing surveys allowed the use of logistic regression for estimation of visibility bias inherent in the extensive fixed-wing survey (Eberhardt and Simmons 1987, Samuel et al. 1987). We used the results of the relatively large sample size of the fixed-wing survey, corrected for visibility bias, to extrapolate a density estimate to all units in the stratum.

WRST, was divided into 31 primary sampling units (Fig. 1) grouped into high, medium, and low-density strata according to procedures described in Taylor et al. (1989). Previous surveys (Singer 1982, Mullen and Cella 1984) established the primary sampling units, that ranged in size from 96 to 2002 km^2 (37 to 773 mi^2) (Table 1). We selected a random sample of primary units from each density stratum for conducting fixed-wing surveys. The number of units selected in each stratum was proportional to expected sheep density. Each of these primary sampling units was further divided into subunits ranging in size from 132 to 471 km^2 (49 to 182 mi^2) (Table 2). The subunits were small enough that they could be sampled in 1 flight by the helicopter in the same amount of time required to fly the entire primary unit in the fixed-wing and large enough so that movement between subunits was minimized. The large size of some primary sampling units presented logistical problems for counting sheep from a fixed-wing aircraft within the time frame of the survey. Therefore, in larger primary units, a random sample of subunits was counted in the fixed-wing survey rather than the entire primary unit. In those cases, the helicopter survey counted sheep in a random sample of the subunits included in the fixed-wing survey.

Table 1. Area in square kilometers of the primary units in the Dall sheep survey at Wrangell-St.Elias National Park and Preserve, July 1990 and 1991.

High density strata:		Medium density strata:		Low density strata:	
Unit	Area km^2	Unit	Area km^2	Unit	Area km^2
1	1185.76	10	1199.83	25	1258.54
2	1361.36	13	535.76	26	1158.41
3	2002.15	15	507.90	27	469.17
4	1037.93	16	513.33	28	901.63
5	652.65	17	363.04	29	748.26
6	793.39	18	894.65	30	1323.90
7	999.99	19	1161.15	31	1199.82
8	733.47	20	550.54		
9	734.63	22	916.50		
11	337.54	23	716.14		
12	610.33	24	475.49		
14	96.00				
21	213.32				
Total	10758.52		7834.01		7059.74

While the same basic sampling procedures were used in both years, survey methodology was changed slightly in 1991 as a result of experience gained in 1990. To the extent possible, the same sample units randomly selected for the 1990 survey were also sampled in 1991 to permit comparisons between years. Counting procedures from the fixed-wing aircraft were modified slightly in 1991 so comparisons with 1990 counts (unadjusted for visibility bias) were limited to counts from the helicopter survey. Additional primary units and subunits were randomly selected from the low, medium, and high density strata in 1991 to provide additional units and subunits for both the fixed-wing and helicopter surveys in the event that larger sample sizes were possible.

Experienced pilots and observers conducted both the fixed-wing and helicopter surveys. Data collected during surveys included the number of groups of sheep detected, number of sheep counted in each group, and habitat characteristics at the location of the group. All observed sheep were classified to the extent possible as lambs, rams (>1 year old), and ewe-like (ewes plus

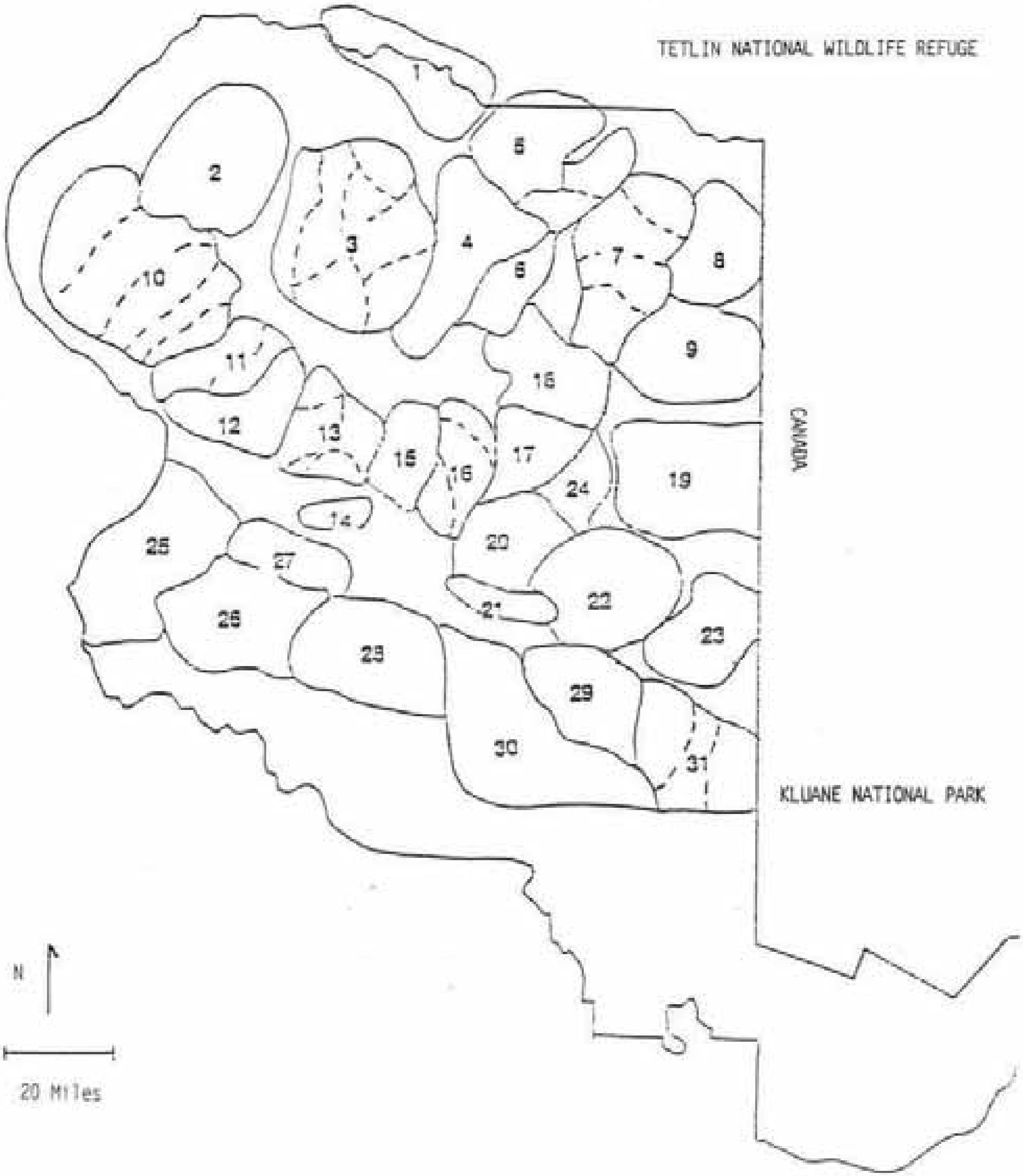

Fig. 1. Map of the Wrangell-St. Elias National Park and Preserve showing 31 primary sampling units. Dashed lines divide units into subunits.

subadult rams). Observers recorded habitat variables including substrate (vegetation or rock color), terrain, and percent slope. Locations of groups were marked on U.S.G.S. 1:250,000 scale quadrangle maps with a contour interval of 61 m (200 feet). Groups were considered distinct if they appeared to consist of a unique group of individuals based on location and sex and age composition.

Table 2. Actual survey time spent by the fixed-wing aircraft and the helicopter during the survey of Dall sheep at Wrangell-St.Elias National Park and Preserve, July 1990, 1991.

	1990			1991		
Unit	Time min.	Area km^2	Min. per km^2	Time min.	Area km^2	Min. per km^2
Fixed-wing flights:						
3A	N.S.[a]	N.S.	N.S.	70	277.81	0.29
3B	N.S.	N.S.	N.S.	78	343.15	0.23
3D	50	131.91	0.38	36	131.91	0.27
3G	70	313.78	0.22	58	313.77	0.18
6AB	N.S.	N.S.	N.S.	83	397.59	0.21
7A	179	471.72	0.38	N.S.	N.S.	N.S.
7B	N.S.	N.S.	N.S.	101	278.64	0.36
7C	N.S.	N.S.	N.S.	49	236.00	0.21
11AB	66	337.53	0.20	76	337.54	0.23
14	22	95.99	0.23	26	95.99	0.27
10A	45	353.79	0.33	N.S.	N.S.	N.S.
10DE	76	291.17	0.26	60	291.17	0.21
13ABCD	117	535.77	0.22	76	535.77	0.15
16ABC	93	513.34	0.18	118	513.34	0.23
27ABC	85	469.18	0.18	98	469.18	0.21
31ABC	109	1199.8	0.09	83	1199.7	0.07
Helicopter flights:						
3A	N.S.	N.S.	N.S.	89	277.81	0.32
3D	66	131.91	0.50	91	131.91	0.69
6B	76	205.72	0.37	N.S.	N.S.	N.S.
7A	106	471.72	0.22	N.S.	N.S.	N.S.
7B	N.S.	N.S.	N.S.	155	278.63	0.56
11A	55	164.13	0.24	36	153.15	0.24
14	30	95.99	0.31	43	95.99	0.45
10E	40	164.13	0.24	72	164.13	0.44
13D	39	152.89	0.26	58	152.89	0.38
16A	N.S.	N.S.	N.S.	40	116.99	0.34
27BC	N.S.	N.S.	N.S.	66	473.97	0.14
31C	N.S.	N.S.	N.S.	43	473.02	0.09

[a] N.S. = No survey conducted.

Fixed-wing flights were made in a Piper PA-18 Super Cub or an Arctic Tern over the entire primary unit or subunit. Fixed-wing flights used the same aerial survey procedures as the helicopter flights, but at a greater distance from the sheep, with less circling, and with less time used. The fixed-wing flights in both years were conducted at a speed of approximately 0.19 min/km^2 (0.3 min/mi^2); but the 1991 survey flew farther from the mountain slopes and with less circling than the 1990 survey. Helicopter surveys were conducted from a Bell Jet Ranger

II in 1990 and a Hughes 500D in 1991. Helicopter flights occurred at the rate of approximately 0.3 min/km^2 (0.48 min/mi^2).

In 1990 either the fixed-wing or the helicopter survey may have been conducted first in a subunit. However, in 1991 the fixed-wing flight was conducted first to minimize disturbance potentially caused by the helicopter survey. For safety, the helicopter survey usually began when informed the fixed-wing aircraft was leaving a count unit. Generally only 1-3 hours elapsed between surveys and never more than 6 hours. Data were not used if more than 6 hours passed between the 2 surveys flights. Both surveys were conducted so that there was a minimum of disturbance to sheep (ie. minimal circling and avoiding flying directly toward sheep).

Each day, immediately following survey flights, helicopter and fixed-wing crews compared mapped locations and descriptions of sheep groups. Criteria used to decide if groups were observed by both survey crews included proximity of recorded locations and age and sex composition of observed groups. Reconciled groups were used to show which groups "marked" by the helicopter survey were missed by the fixed-wing survey and which were sighted. Often, groups recorded and marked in close proximity were pooled to account for movement, aggregation, and segregation between surveys based on deductive judgement of the survey crews. Crews used a conservative approach so that it was unlikely that incidental movement of sheep between surveys resulted in sheep recorded as seen by the helicopter and not the fixed-wing surveys. This approach yielded a conservative estimate of the population size because it tended to overestimate the probability that a given group will be detected during the fixed-wing survey.

We estimated visibility bias with logistic regression (Samuel et al. 1987) and standard errors and sampling distributions of sheep density using the Jackknifing procedure (Manly 1991). The visibility bias of a sheep group during the fixed-wing survey within a given density stratum was estimated using a logistic regression model that was a function of the explanatory

variables group size and habitat. We also examined helicopter and fixed-wing survey counts of sheep in groups sighted by both surveys to decide if the helicopter survey but detected by the fixed-wing survey did not enter the calculation of visibility bias in any way.

<u>The jackknife method</u>.--The jackknife method (Manly 1991), is a repeated sampling procedure which allows the calculation of confidence intervals when no better methods are available. In our case, the method was used to estimate a mean and standard error of population density.

We first fit 1 logistic model using data from all primary units, calculated the visibility bias, adjusted all fixed-wing surveys and estimated the density of sheep using the appropriate formula for 2-stage stratified random sampling. These calculations were then repeated n times dropping each primary unit from the logistic regression one-at-a-time. These n+1 estimates of density were then used in the Jackknife procedure to compute n pseudo-estimates of density:

$$D_{pk} = n^*D_t-(n-1)^*D_{tk},$$

where D_{pk} was the pseudo-estimate of density with 1 primary unit dropped, n was the number of primary units in the sample, D_t was the estimated density with all units present, and D_{tk} was the estimate of density with the k<u>th</u> primary unit dropped.

Finally, the jackknife procedure was completed by averaging these n pseudo-estimates to arrive at a single estimate of density. The standard error of estimated density was computed from the variation in the n pseudo-estimates. The total number of sheep in WRST was computed by multiplying the jackknifed estimate of density by the total area of all primary units. The stratified random sampling formula and Jackknife procedures are described in more detail in McDonald et al. (1990). Confidence intervals based on the jackknife procedure were computed as if the n pseudo-values represented a simple random sample of size n using the standard t-distribution.

We examined the initial stratification of primary units based on the number of sheep seen by the 1990 and 1991 surveys. A primary unit was placed into a different density stratum if the analysis suggested the unit was misclassified. Following post-stratification we repeated the estimation procedures described above and obtained additional estimates of sheep density for the purpose of evaluating the effectiveness of the initial stratification.

Logistic regressions were run on PC-SAS (SAS Institute, Inc. 1985) using the CATMOD procedure, VMS SAS (SAS Institute, Inc. 1986) using the LOGIST procedure, and SOLO (BMDP Statistical Software, Inc. 1988) using logistic regression. All programs gave comparable results.

RESULTS

The 1991 fixed-wing and helicopter surveys covered more area (8191 km^2; 3124 mi^2) than the 1990 surveys (6089 km^2; 2351 mi^2) and resulted in a larger sample of sheep groups. The 1990 helicopter survey covered all or a portion of 7 primary units including 6 subunits, an area of 1357 km^2 (531 mi^2). The 1990 fixed-wing survey covered all or a portion of 9 primary units including 21 subunits, an area of 4713 km^2 (1820 mi^2) (Table 2). In 1991 the helicopter survey covered all or a portion of 9 primary units including 10 subunits, an area of 2318 km^2 (895 mi^2), while the fixed-wing survey covered 10 units including 25 subunits, an area of 5773 km^2 (2229 mi^2) (Table 2). The fixed-wing survey took less time in both years (0.19 min/km^2; 0.5 min/mi^2) than the helicopter survey (0.30 min/km^2; 0.78 min/mi^2).

A total of 2,486 individual sheep were seen in 1990 and 3,518 individual sheep in 1991. The 1990 survey detected 348 separate groups and the 1991 survey detected 624 separate groups (Tables 3 and 4). The helicopter crew saw 15 more groups than the fixed-wing survey in double sampled units in 1990, and 89 more groups in 1991. However, the helicopter survey missed 21 groups seen by the fixed-wing survey in 1990 and 30 groups in 1991 indicating both surveys are subject to visibility bias. The logistic regression model used only the groups of sheep seen by the helicopter survey as the test set of groups of sheep known to be present in the survey area (75 in 1990 and 218 in 1991).

The relationship of sightability, group size, and substrate was evaluated by logistic regression (Fig. 2). Only group size had a significant affect on sightability in 1990 ($\underline{P}$ = 0.0009) and 1991 ($\underline{P}$ = 0.0039). The fixed-wing survey detected approximately 1 out of every 3 solitary sheep both years (35 % in 1990 and 38 % in 1991). As group size increased to 40 the probability of detection increased to approximately 90%.

The estimate for the average density of sheep for the study area in 1990, when counts are expanded without correction for visibility bias, was 0.64/km^2 (1.65/mi^2) (Table 5). This resulted in an estimate of 16,313 sheep. The jackknifed estimate, corrected for visibility bias in the fixed-wing survey, was 1.01/km^2 (2.62/mi^2). The jackknifed standard error of density was 0.12 with a CV = 11.8%. The approximate 95% confidence interval on the total number of sheep

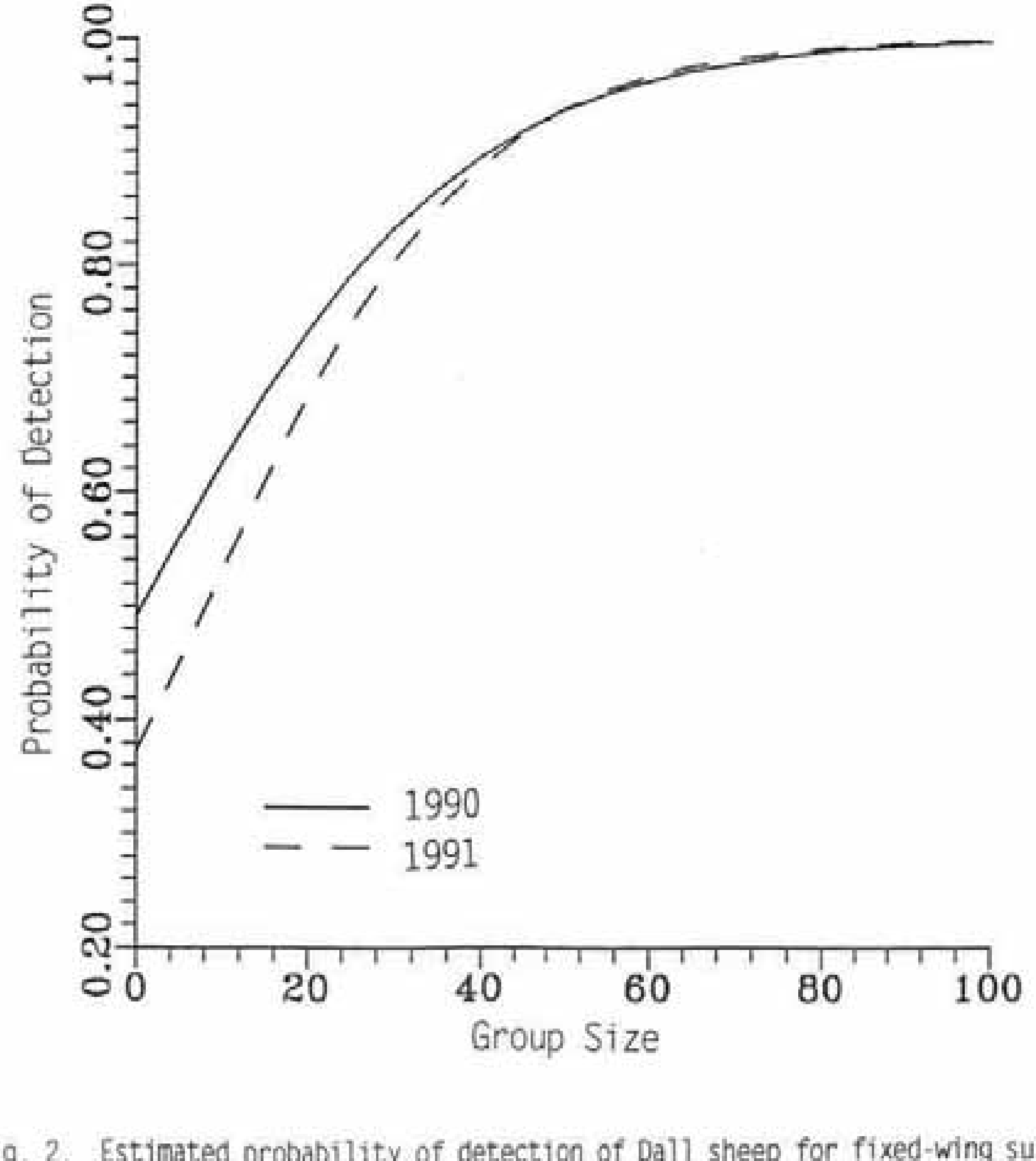

Fig. 2. Estimated probability of detection of Dall sheep for fixed-wing survey as a function of group size in Wrangell-St. Elias National Park and Preserve, 1990 and 1991.

Table 3. Number of Dall sheep counted by unit or subunit during fixed-wing and helicopter surveys at Wrangell-St.Elias National Park and Preserve, 1990.

Double sampling survey

Unit	Fixed-wing survey		Helicopter survey		Groups helicopter missed	Groups fixed-wing missed
	Sheep	Groups	Sheep	Groups		
3D	220	24	276	33	6	15
7A	57	9	104	16	3	10
10E	11	2	26	1	2	1
11A	60	4	79	7	1	4
13D	167	8	127	7	3	2
14	134	13	124	11	6	4
Total	649	60	736	75	21	36

Complete fixed-wing survey

Unit	No. sheep 1990	No. groups 1990
3	571	76
7	523	66
10	147	15
11	219	12
13	355	28
14	149	19
16	185	18
27	75	14
31	16	3
Total	2240	251

was 25,972 ± 6,233 sheep (Table 6). The estimated density of sheep for the study area in 1991, when counts were expanded without correction for visibility bias, was 0.52/km^2 (1.347/mi^2) (Table 7). This resulted in an uncorrected estimate of 13,341 sheep. The jackknifed estimate of density, corrected for visibility bias in the fixed-wing survey, was 0.978/km^2 (2.533/mi^2) (SE = 0.46, CV = 18%). The approximate 95% confidence interval on the total number of sheep was 25,088 ± 10,598 sheep (Table 6).

A total of 10 subunits in 8 primary units and 1 entire primary unit was surveyed from a helicopter in 1991 compared to 5 subunits in 5 primary units and 1 entire unit in 1990 (Table 8). The 4 subunits and 1 primary unit surveyed both years provided some comparative data. Counts in 1991 exceeded 1990 counts in 2 subunits and the primary unit, but are lower than 1990 counts in 2 subunits. Both surveys provided complete coverage of the subunits and primary unit using similar techniques.

The range of estimated density of sheep in individual primary units in the high density stratum overlapped with estimates for units in the medium density stratum. Likewise, estimated density of sheep in individual primary units in the medium density stratum overlapped with estimates for units in the low density stratum (Table 9). During both years the density estimate for unit 11 in the high density stratum fell within the range of densities estimated for the medium density stratum. Units 11 and 12 in the high density stratum and 13, 15, and 16 in the medium density stratum are similar in vegetation and terrain. Additionally, the density estimated in 1991 for unit 10 in the medium density stratum was less than the estimated density in unit 27 within the low density stratum. Density estimates for units 10 and 27 were almost identical in 1990.

Table 4. Number of Dall sheep counted by unit or subunit during fixed-wing and helicopter surveys at Wrangell-St.Elias National Park and Preserve, 1991.

Double sampling survey

	Fixed-wing survey		Helicopter survey			
Unit	Sheep	Groups	Sheep	Groups	Groups helicopter missed	Groups fixed-wing missed
3A	185	20	235	37	6	23
3D	140	30	234	50	4	24
7B	105	33	237	75	10	52
10E	19	5	34	6	0	1
11A	24	5	35	5	1	1
13D	151	13	162	17	2	6
16A	2	1	2	1	0	0
14	137	11	172	16	1	6
27BC	10	3	54	8	0	5
31C	27	8	16	3	6	1
Total	800	129	1181	218	30	119

Complete fixed-wing survey

Unit	No. sheep 1991	No. groups 1991
3	1354	213
6	352	83
7	437	93
10	47	18
11	130	18
13	277	29
14	137	12
16	161	19
27	73	12
31	27	8
Total	2995	505

This overlap in density of the 3 strata prompted us to investigate the potential effects of re-stratification of primary units (with a new stratified random sample in future years). Unit 10 was post-stratified into the low density stratum and units 11 and 12 were placed in the medium density stratum. Following post-stratification, the jackknifed estimate of density for 1991, corrected for visibility bias in the fixed-wing survey, was $1.08/km^2$ ($2.8/mi^2$) (SE = 0.28, CV = 10%). The approximate 95% confidence interval on the total number of sheep was 27,796± 6,448 (Table 10). Using the same post-stratification, the revised estimate of sheep using 1990 data was slightly higher (Table 10), but with a smaller variance (CV = 7%) than the original 1990 estimate (CV = 11.8%).

We examined the difference in counts of sheep within groups detected by both surveys in 1991 to find if a correction should be made for counting errors in the fixed-wing survey (Table 11). The fixed-wing survey counted 97% of the sheep counted by the helicopter survey suggesting counts by the fixed-wing survey slightly underestimated the number of sheep in a group (assuming counts from the helicopter were correct). However, we chose to be conservative and made no under-count correction to fixed-wing counts and raw data were used to correct for visibility bias.

Table 5. Estimated total number of Dall sheep by unit (uncorrected for visibility bias), estimated density by strata, and estimated stratified density in the Wrangell-St. Elias National Park and Preserve, July 1990.

Unit	% Area surveyed	Total km^2	No. sheep observed	Estimated total sheep	Density sheep/km^2
High density strata:					
3	21.11	202.15	571	2705	
7	47.17	999.99	523	1109	
11	100.00	337.54	219	219	
14	100.00	96.00	149	149	
Total		3435.68	1462	4182	1.22
Medium density strata:					
10	53.77	1199.53	147	273	
13	100.00	535.76	355	355	
16	100.00	513.33	185	185	
Total		2248.62	687	813	0.36
Low density strata:					
27	100.00	469.17	75	75	
31	100.00	1199.82	16	16	
Total		1668.99	91	91	0.05

Table 6. The estimated number of Dall sheep and density, corrected for visibility bias, by stratum in Wrangell-St.Elias National Park and Preserve, July 1990 and 1991

		1990		1991	
Density of strata	Area[b] km^2	Density[b] per km^2	No. sheep	Density[b] per km^2	No. sheep
High[a]	10758.52	2.03	21849	1.811	19484
Medium[a]	7834.01	0.52	4083	0.398	3117
Low[a]	7059.74	0.11	763	0.116	819
Total	25652.27	1.04	26695[b]	0.913	23420[b]
Jackknifed estimates		1.01	25972[c]	0.978	25088[c]
SE		0.119	3060	0.179	4596

[a] Standard errors are not available because the sample size in each stratum is too small to use the jackknife procedure.
[b] Corrected for visibility bias but not jackknifed.
[c] Corrected for visibility bias and mathematical bias by the jackknife procedure.

Sheep observed during the helicopter surveys were classified by sex and age as completely as possible in 1991 (Table 12). These data were not corrected for differences in visibility. Ewe groups likely contained yearling and 2-year-old rams that were not easily classified. Thus, we categorized sheep as either mature ram, ewe-like, or lamb (Table 12). The ratio of lambs to ewe-like was

.17, the ratio of young to all adults was .12, and the ratio of rams to ewe-like was .42.

Table 7. Estimated total number of Dall sheep by unit (uncorrected for visibility bias), estimated density by strata, and estimated stratified density in the Wrangell-St. Elias National Park and Preserve, July 1991.

Unit	% Area surveyed	Total km^2	No. sheep observed	Estimated total sheep	Density[a] sheep/km^2
High density strata:					
3	53.27	2002.15	1354	2542	
6	50.11	793.40	352	702	
7	51.46	999.99	437	849	
11	100.00	337.54	130	130	
14	100.00	96.00	137	137	
Total		4229.08	2410	4360	1.03
Medium density strata:					
10	53.77	1199.53	47	87	
13	100.00	535.76	277	277	
16	100.00	513.33	161	161	
Total		2248.62	485	525	0.23
Low density strata:					
27	100.00	469.17	73	73	
31	100.00	1199.82	27	27	
Total		1668.99	100	100	0.06

[a] Stratified average density: 0.52 sheep per km^2

Table 8. Comparison of the number of sheep observed by helicopter surveys in 1990 and 1991 at Wrangell-St. Elias National Park and Preserve.

Unit	No. sheep 1990	No. sheep 1991
3A	N.S.[a]	235
3D	276	234
7A	104	N.S.
7B	N.S.	237
10E	26	34
11A	79	35
13D	153	162
16A	N.S.	2
14	124	172
27BC	N.S.	54
31C	N.S.	16
TOTAL	762	1181

[a] N.S. = No survey conducted.

Table 9. Stratification analysis by unit for the 1990 and 1991 surveys at Wrangell-St. Elias National Park and Preserve.

Strata	Unit	No. sheep 1990	Corrected density per km^2	No. sheep 1991	Corrected density per km^2
High	3	571	1.93	1354	2.27
High	6	N.S.	N.S.	352	1.81
High	7	523	1.65	437	1.69
High	11	219	0.76	130	0.68
High	14	149	2.34	137	2.30
Medium	10	147	0.34	47	0.17
Medium	13	355	0.86	277	0.85
Medium	16	185	0.45	161	0.47
Low	27	75	0.26	73	0.14
Low	31	16	0.022	27	0.05

[a] N.S. = No survey conducted.

Table 10. Post stratified estimated number of Dall sheep and density, corrected for visibility bias, by stratum in Wrangell-St. Elias National Park and Preserve, July 1991.

Density of strata	Area[b] km^2	1990		1991	
		Density[b] per km^2	No. sheep	Density[b] per km^2	No. sheep
High[a]	9810.65	1.858	18216	2.033	19950
Medium[a]	7582.35	0.687	5211	0.667	5047
Low[a]	8259.27	0.193	1598	0.138	1141
Total	25652.27	0.976	25025[b]	1.019	26138[b]
Jackknifed estimate		1.025	26286[c]	1.083	27792[c]
SE		0.0678	1740	0.1090	2796

[a] Standard errors are not available because the sample size in each stratum is too small to use the jackknife procedure.
[b] Corrected for visibility bias but not jackknifed.
[c] Corrected for visibility bias and mathematical bias by the jackknife procedure.

DISCUSSION

The most recent attempt at sample survey of sheep in the WRST was during the period 1981-1984. Singer and Mullen (1981) reported covering 17 1/2 (73%) of the count units in a helicopter survey in 1981, Singer (1982) reported the results of the 1981 surveys as well as surveys of additional areas in 1982, and Mullen and Cella (1984) reported surveys of 5 additional count units in 1983 and 1984. No estimate of survey time was provided for the first 2 survey years. The 1983 and 1984 surveys took slightly over 16 hours of survey time. The 1981 and 1982 surveys covered a much larger area than the 1983 and 1984 surveys and probably required more than twice the time. It appears our surveys in both years were more cost effective. Also, our surveys were safer than previous surveys if it is accepted that more flight time with an objective of counting all sheep increases risk.

Table 11. Analysis of possible bias by group size during the survey of Dall sheep at Wrangell-St. Elias National Park and Preserve, July 1991.

Group size	No. sheep fixed-wing	No. sheep helicopter	Ratio fixed to helicopter	No. groups
1 to 5	134	146	0.92	60
6 to 10	131	131	1.00	18
11 to 15	157	184	0.85	14
16 to 20	18	16	1.13	1
21 to 25	41	46	0.89	2
26 to 30	23	30	0.77	1
31 to 35	57	34	1.68	1
36 to 40	44	38	1.16	1
41 to 45	0	0	0	0
46 to 50	0	0	0	0
51 to 55	53	52	1.02	1
Total	658	677	0.97[a]	

[a] Ratio of totals.

Table 12. Herd composition data for Dall sheep from helicopter flights at Wrangell-St. Elias National Park and Preserve, July 1991.

Unit	Rams	Ewe-like	Lambs	Unclas-sified	Ram: ewe-like	Lamb: ewe-like
3	105	310	55	15	0.339	0.177
7	69	106	20	42	0.651	0.189
11	2	33	0	0	0.610	0
14	38	48	5	81	0.792	0.104
10	8	26	0	0	0.308	0
13	41	102	19	0	0.402	0.186
16	0	2	0	0	0	0
27	10	12	6	26	0.833	0.50
Total	276	650	107	147	0.425	0.165

It can be argued that cost effectiveness is a function both of cost and accuracy of results. Our results provide an estimate of sheep abundance with a measure of accuracy and precision. Sample surveys during the 1981-1984 period were an effort to count all sheep present. Over this 4 year period, 10,496 sheep were counted in 25 of the 29 primary count units in the WRST. Singer (1982) estimated sheep numbers in uncounted units in the Wrangell's portion of the area and corrected the total using a factor of 1.25 to account for missed sheep. Singer's "corrected" estimate was 15,723 sheep. This estimate is only slightly below our estimates of sheep without correction for visibility bias. No measure of accuracy or precision was provided by Singer.

Both the 1990 and 1991 surveys resulted in substantially higher estimates of sheep in the WRST than the previous surveys. However, the densities reported by Singer (1982) in some high density units exceeded our overall estimate of density in this stratum. Singer (Undated) reported densities of 1.08/km^2 (2.8/mi^2) in the Preserve portion of WRST and 0.656/km^2 (1.7/mi^2) in the Park portion. In a survey of Dall sheep at the northwestern limit of their range in the Brooks Range of Alaska, Singer, et al. (1983) reported densities as high as 0.71/km^2 (1.85/mi^2) with an average of 0.162/km^2 (0.42/mi^2). Densities in other Alaska populations as reported by Singer (Undated) ranged from a low of 0.154/km^2 (0.4/mi^2) in Noatak to 0.81/km^2 (2.1/mi^2) in the Gates of the Arctic National Park. Densities from both the 1990 and 1991 surveys of WRST after correction for visibility were well within this range.

The estimate of 25,088 total sheep in 1991 based on the original stratification is very close to the estimate of 25,972 sheep obtained in 1990. But, the precision of the 1991 estimate is less than the 1990 estimate. The precision of the estimates made in our survey was a product of the jackknifing procedure and was sensitive to the variation in estimates of sheep density among individual units in each stratum included in the survey sample. The Jackknife procedure calculated pseudo-values for sheep density by dropping 1 surveyed unit at a time and then estimating total sheep for WRST. Dropping a misclassified unit from the calculation of density for a particular stratum effected the density estimate for that stratum far more than dropping a properly classified unit.

The original stratification used in this study was based on an extensive aerial reconnaissance of WRST (Taylor et al. 1989). However, the existing grouping of units resulted in overlap in densities between high and medium density strata and medium and low density strata. This greatly contributed to the width of confidence intervals in 1990 and 1991. While the overlap was greater in 1991 the relationship was consistent for both the 1990 and 1991 surveys suggesting a problem in the initial stratification. Following post-stratification, the estimate of sheep in WRST increased for both areas and the precision improved. It is possible that estimates of sheep numbers with the smaller standard errors following post-stratification were a better representation of sheep numbers in WRST at the time of the surveys. However, it is likely that a new stratified random sample from the re-stratified units for future survey will yield more precise results than the 1990 or 1991 surveys.

The logistic regression indicated that group size was the only significant explanatory variable in determining sightability from the fixed-wing. The logistic regression with substrate variables indicated that tundra, dark rock, light rock, and mixed substrate lacked significant influence on sightability. McDonald et al. (1990) also found that group size was the only significant variable affecting the probability of detecting Dall sheep in ANWR. When the roles of the fixed-wing and helicopter aircraft were reversed in the analysis of our data, this same relationship existed, although the helicopter was better able to detect single sheep and small groups. This suggests the helicopter is a better vehicle for observing sheep and confirms the important influence of group size on detection probabilities. Each variable recorded during aerial surveys increases the difficulty of the survey. Future surveys of Dall sheep in similar habitat could ignore substrate as a potential influence on sightability.

During both years of survey the fixed-wing and helicopter crews counted approximately the same number of sheep in groups seen by both. While a slight upward adjustment of less than 3% could have been made to the fixed-wing counts, in the interest of a conservative estimate, no correction was made. In future surveys, this relationship should continue to be monitored since different observers, and changes in habitat and counting conditions may affect fixed-wing counts.

This study was not designed to evaluate the difference in sheep response to helicopter versus fixed-wing surveys. Nevertheless, no extraordinary avoidance behavior was noted during either survey in 1990 or in 1991. On 2 occasions during the 1990 helicopter survey, a large group of sheep seen in open flat terrain responded to the helicopter by grouping tightly together and running. However, these groups did not seek rough terrain or escape cover. There was some concern voiced by reviewers of the 1990 survey that the helicopter may disturb sheep and bias subsequent counts by the fixed-wing crew. To address this concern, 1991 helicopter flights occurred after fixed-wing flights in all double sample surveys. Disturbance of sheep was kept to a minimum in our surveys as neither survey flew close enough to obtain a complete classification of sex or age and repeated circling was avoided.

The design of our surveys did not provide accurate composition counts. But, the helicopter survey in 1991 attempted to classify all sheep as lamb, ewe-like, or ram. Identification of lambs in small groups of sheep was relatively easy while differentiating between yearling rams and ewes and classification of individuals in the larger groups of sheep was more difficult. Young rams and lambs were likely misclassified in the larger groups and some yearling rams were likely misclassified in all groups.

The ratio of rams to ewe-like in our study may be biased since classification of large ewe-lamb groups contained few yearling rams. The rams classified in the ewe-lamb groups contained some young rams, but we made no estimate of the bias associated with misclassifying rams in large groups. Nonetheless, our estimate of the ratio of rams to ewe-like was within the range of similar ratios recently reported for Dall sheep throughout Alaska (Singer et al. 1981, Singer et al. 1983, Ayres 1986, Heimer and Watson 1986, Ayres 1987, Taylor et al. 1987, Singer Undated). The 42 rams per 100 ewe-like in our study was identical with the ram:ewe ratio reported for WRST by Singer and Mullen (1981).

Singer (Undated) reported the proportion of lambs in the 1970's and 1980's within National Parks and Preserves in Alaska. Proportions ranged from 18% to 32% with WRST reported as 18% in the 1970's and 19% in the 1980's. Kellyhouse (Undated) surveyed a portion of WRST in 1981 and 1984 and reported 19% and 16% lambs, respectively. This is slightly higher than our estimate of 10% in 1991. The ratio of lambs to ewe-like in our sample was similar to the ratio reported by Garrett (1987) for Dall sheep in the Hulahula River and adjacent drainages of the ANWR, Alaska. However, the ratio in our study was lower than other lamb:ewe ratios recently reported for Dall sheep in Alaska (Singer et al. 1981, Singer et al. 1983, Ayres 1986, Heimer and Watson 1986, Ayres 1987, Taylor et al. 1987, Singer Undated). The ratio was much lower than the most recent lamb:ewe ratio reported for WRST (Singer and Mullen 1981). While likely an underestimate, the low ratio of lambs to ewe-like in our study and the declining lamb proportions reported by Kellyhouse (Undated) suggest the need for a survey designed to more accurately find the sex and age composition of Dall sheep in WRST.

RECOMMENDATIONS

1. Estimates of Dall sheep in the WRST from the 1990 and 1991 surveys are substantially higher than previous surveys and contain estimates of precision. Future surveys using the same methods would provide managers with a better measure of the trend in sheep numbers.

2. Future surveys using the double sampling strategy should attempt to increase the speed of the fixed-wing survey. This would allow more primary units to be surveyed and thus increase the confidence in expansions of density data to the entire area. Or, surveys of a fixed set of primary units could be done with less flying and thus result in a less costly and safer survey.

3. The 1991 survey attempted to classify sheep as to sex and age. Lamb:ewe ratios are minimum estimates due to the inclusion of young males as ewes. Future surveys combining helicopters with fixed-wing aircraft should include sex and age composition counts in the data collected by helicopter surveys. Classification of animals into age and sex categories should be done by a combination of observations from the helicopter and a sample of herds classified from the ground. Ground counts can be used to correct helicopter counts of young males and ewes. Observations from a fixed-wing aircraft should be used to expand estimates of abundance and age and sex ratios to the entire population based on double sampling procedures. A random survey would result in a less biased estimate of the ratios than provided by the more haphazard approach used in 1991.

4. Sex and age composition data are characteristics of populations. WRST is a large area containing several management units. If more than 1 population exists in WRST then classifications and population estimates should be made so they are relevant to individual populations.

5. Because the fixed-wing survey crew saw groups not seen by the helicopter crew, an alternative approach is suggested to population estimation when composition counts are considered unnecessary. A sample survey could employ 2 fixed-wing crews which could calibrate each other (i.e., develop sightability correction factors) by flying the same units prior to flying additional separate units. This method should be evaluated in the WRST or a similar area.

6. Planning for future surveys should attempt to reduce time lost in ferrying between fueling locations, the base of operations, and survey units.

7. The survey depends on the accurate location of sheep groups by fixed-wing and helicopter survey crews. Global Positioning System technology should be investigated for use in locating sheep groups by both surveys.

8. Some subunits in our surveys were too large for the helicopter survey and some boundaries were difficult to follow. Boundaries of all subunits should be evaluated before future surveys. Past sheep observations should be used to evaluate existing boundaries.

9. The 2-staged sampling plan used in 1990 and 1991 was necessitated by the NPS's desire to survey sheep within the existing sampling units. The variance of the jackknifed estimate of sheep density should decrease if more smaller units are used. An alternative to the present sampling strategy is to subdivide all primary units so that subunits are approximately the same size. A stratified random or systematic sample could then be taken of the subunits, treating them as primary units.

10. WRST should be re-stratified using the existing or smaller survey units. A few units appear misclassified in the original stratification based on both 1990 and 1991 survey results. Most of the subunits should be placed in the same stratum as the original primary unit. However, there may be enough variability in some of the larger units to warrant a change in the stratum for some smaller units. The original stratification was based on

an aerial stratification survey. Ideally, stratification surveys should be completed immediately prior to sample surveys. However, logistics and cost constraints may prevent stratification surveys prior to each sample survey. An alternative approach is to use the data from the 1990 and 1991 surveys along with data on habitat, precipitation, harvest, etc., and restratify without stratification surveys.

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PRELIMINARY TESTS OF A MOUNTAIN SHEEP HABITAT MODEL USING A GEOGRAPHIC INFORMATION SYSTEM

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Abstract: Since 1850, 45 populations of mountain sheep (*Ovis canadensis* ssp.) have become locally extinct in California. Conservation efforts for this species emphasize restoration of these extirpated populations. Although models that assess potential relocation sites exist for mountain sheep, none have been adequately tested. We used the overlay capabilities and proximity functions of a vector-based geographic information system, and aerial telemetry data from a reintroduced population of desert-dwelling mountain sheep, to test the significance of vegetation, topography, and availability of water as predictors of mountain sheep presence. Statistical results indicate that, while these variables are important, their use in the model evaluated was not predictive. For instance, while slope was a significant variable, and the steepest slope categories were selected by mountain sheep, all other categories of slope were avoided, even though the model suggested moderate use in some categories.

In the decades following the California gold rush, a rapid loss of mountain sheep populations occurred (Wehausen et al. 1987). Unregulated market hunting and grazing of domestic livestock are implicated in this decline, as are certain diseases that are associated with livestock, particularly with domestic sheep (Buechner 1960). Despite legal protection of the species by the California legislature in 1873, populations failed to increase in size, or to recolonize vacant habitats. Moreover, the extirpation of mountain sheep populations continued; 45 of 104 mountain sheep populations thought to exist prior to 1850 are extinct in California (Wehausen et al. 1987). Although management efforts may have resulted in some population increases, little natural recolonization has occurred. Mountain sheep conservation strategies currently emphasize

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3 approaches: (1) isolation from domestic sheep (Desert Bighorn Council 1990); (2) habitat improvement, primarily through the construction of artificial watering devices (Bleich and Pauli 1990); and (3) the establishment of this species on formerly occupied ranges (Bleich et al. 1990b).

Several habitat evaluation procedures have been developed for desert-dwelling mountain sheep (Ferrier and Bradley 1970, Merritt 1974, Hansen 1980, Wilson et al. 1980, Holl 1982, Armentrout and Brigham 1988, Cunningham 1989, Wakeling and Miller 1990), but they have not been adequately tested. Of those currently available, the model developed by Hansen (1980) is the most widely-used. However, given the expense and complexity of mountain sheep translocation projects (Bleich 1990, Bleich et al. 1991), it seems prudent to evaluate that model further, in an effort to enhance the success of future translocations (Smith et al. 1991).

Hansen's (1980) procedure rates the suitability of mountain sheep habitat on 7 factors: natural vegetation, topography, precipitation, evaporation, water availability, existing mountain sheep use, and human impacts. Individual sections (1 mi^2) of habitat are rated, using a point system, based on these factors, and a total score is calculated. Sections having the highest numerical scores are deemed the most important, or most suitable, for mountain sheep. Sections with moderate, or low, scores are considered to be of lesser value to mountain sheep.

A geographic information system (GIS) is a computer tool that can be used to rapidly analyze and model the types of spatial data necessary for informed decisions on wildlife management options (Johnson 1990, Nicholson and Bowyer In Press). Indeed, several authors have used the overlay capabilities and spatial analysis functions of a GIS to evaluate habitat, and wildlife use of habitat (Donovan et al. 1987, Broschart et al. 1989, Pereira and Itami 1991, and others). Several parameters in the Hansen Model lend themselves well to GIS analyses; therefore, we used a vector-based GIS to test predictions of the model with respect to topography, vegetation, and water availability.

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STUDY AREA

The Sheephole Mountains are a relatively precipitous, low elevation mountain range located in the southern Mojave Desert, San Bernardino County, California. The mountain chain follows a northwest - southeast orientation and reaches a maximum elevation of 1,406 m (Pauli and Bleich 1991). Soils predominantly are of granitic origin (Weaver and Mensch 1971). Daytime maxima frequently exceed 38 C during the summer, but temperatures $\leq$ 0 C are not uncommon in winter (Freiwald 1984). Precipitation averages 7 cm annually, and occurs mostly during winter from Pacific weather fronts; summer storms are infrequent, unpredictable and highly localized (Weaver and Mensch 1971). Vegetation in the study area is predominantly creosote bush (_Larrea tridentata_) scrub, with higher elevation slopes supporting _Ephedra_ spp. and _Yucca_ spp.

The study area was defined by the extreme southwest and northeast distribution of mountain sheep in the Sheephole Mountains, as determined from aerial telemetry data. The study area is 12.4 km from east to west, 10.5 km from north to south, and is 132 km^2 in size. Historically, mountain sheep occurred in the Sheephole Mountains, but they were nearly extirpated during the recent past. Mountain sheep were translocated to the range during 1984 (_n_ = 11) and 1985 (_n_ = 16) (Bleich et al. 1990_a_).

SOURCES OF DATA

From 1984-86, 401 aerial telemetry fixes were obtained from 11 adult, female, mountain sheep. Bimonthly flights were conducted as described by Krausman et al. (1984), and the estimated locations of mountain sheep were plotted on 15' United States Geological Survey (USGS) topographic maps during each flight. These locations were digitized, and projected into Universal Transverse Mercator coordinates (Monmonier and Schnell 1988).

We extracted vegetation data from an Integrated Terrain Unit Map (Dangermond et al. 1982) supplied by SCE. Categories of vegetation were then reclassified as either "low desert shrub" or "middle desert shrub" (Hansen 1980:326, Table 1).

We used the ARC/INFO TIN Module (ESRI, Redlands, Calif.) to derive a slope map from commercially available USGS 3-arc-second Digital Elevation Models (Carter 1988). Because Hansen (1980) described slope in relative terms, such as flat or steep, we adapted the criteria of Armentrout and Brigham (1988) to quantify 5 of Hansen's slope descriptors: level (0% slope), undulating (>0-8% slope), rolling hills (>8-100% slope), and steep (>100% slope) (Table 2). For some analyses of slope selections, we also separated rolling hills into two categories (>8-30% and >30-100%).

Using the criteria of Hansen (1980:325), the slope map adapted from Armentrout and Brigham (1988), and a map of dry stream courses, we created a terrain model that incorporated 3 topographic parameters. This model considers slope, as well as the juxtaposition of steep terrain to slope classes, and the brokenness of terrain. Thus, we were able to simulate six terrain categories that Hansen included in his model.

Table 1. Mountain sheep use of Hansen's (1980) vegetation types in the Sheephole Mountains, San Bernardino County, California, 1984-1986. Sheep use of vegetation was significantly different from availability ($\underline{X}^2 = 20.2$, $\underline{P} < 0.001$, 1 df).

Vegetation type	Available hectares	Sheep locations
Low Desert Shrub	2,108	31
Middle Desert Shrub	11,110	370

No naturally-occurring permanent water sources occur in the Sheephole Mountains (Weaver and Mensch 1971, Pauli and Bleich 1991). The location of the only artificial water source was plotted on a 15' USGS topographic map, and digitized into the GIS.

ANALYTICAL METHODS

All spatial data mentioned above were inventoried and analyzed with ARC/INFO. We evaluated whether mountain sheep used habitat in a manner consistent with predictions based on Hansen's (1980) model. We used the method of Neu et al. (1974) to calculate whether use of vegetation and terrain differed statistically from expected values, based on availability.

The Hansen Model effectively is raster-based, and the cells are 1 mi^2. In the Model, the value of each cell is rated, in part, on the presence or absence of water; however, if we simply examined the study area for presence of water, our results would be of little value. Because we used a vector-based GIS, we were able to calculate the distance of each sheep location to the point source of water in the Sheephole Mountains.

We tested the hypothesis that mountain sheep distribute themselves randomly with respect to the availability of water by comparing the distribution of sheep locations in 11 classes of distance to water (each 1 km in width) with the distribution of an equal number of randomly generated points. Because the water source was located in steep terrain, we corrected for possible interactions between slope class and distance to water by eliminating "flat" areas from analyses. Frequencies were compared using the Bonferroni procedure (Neter et al. 1985).

RESULTS AND DISCUSSION

Mountain sheep in the Sheephole Mountains selected middle desert vegetation (Table 1). This was consistent with the prediction of Hansen (1980). Although the Hansen Model includes a total of 8 vegetation types, only two were present in the study area. The predictive power of the Model remains to be tested with respect to the six other vegetation types recognized by Hansen (1980).

Table 2. Mountain sheep use of five slope classes in the Sheephole Mountains, San Bernardino County, California, 1984-1986. Mountain sheep were not distributed in proportion to the availability of slope classes ($\underline{X}^2 = 542$, $\underline{P} < 0.001$, 4 df).

Slope class(%)	Available hectares	Sheep locations
0	336	5
0.01-8.00	6,599	21
8.01-30.0	3,237	97
30.01-100.0	3,040	276
>100.0	9	2

Mountain sheep selected steep terrain and avoided flat areas; this is consistent with the expectations of the Model (Table 2). However, sheep also avoided moderate slopes (>8-30%), and this is contrary to the Hansen Model. We suggest additional tests, in a number of mountain ranges, before conclusions can be reached regarding the predictive power of terrain classes in the Hansen Model.

Table 3. Mountain sheep use of 6 terrain classes (Hansen 1980) in the Sheephole Mountains, San Bernardino County, California, 1984-1986. Mountain sheep were not distributed in proportion to the availability of terrain classes ($\underline{X}^2 = 622$, $\underline{P} < 0.001$, 5 df).

Terrain class	Available hectares	Sheep locations
Level, >1.6 km from rocky or steep terrain	6,366	11
Level, <1.6 km from rocky or steep terrain	569	15
Rolling hills >1.6 km from rocky or steep terrain	1,963	13
Rolling hills <1.6 km from rocky or steep terrain	4,313	361
Rocky and steep, w/o washes, slopes >100%	5	1
Rocky and steep, cut by washes, slopes >100%	4	0

When we quantified Hansen's (1980) slope categories by adapting the criteria of Armentrout and Brigham (1988), we discovered an apparent typographical error in their paper that eliminated a major slope category (>30-60%). We call this to the attention of the reader because this slope class was strongly selected by the animals in our study, and is of clear importance to mountain sheep (Table 3).

Mountain sheep distributed themselves significantly closer to water than would be expected if they behaved randomly with respect to proximity to water ($\underline{X}^2 = 765$, $\underline{P} < 0.001$, 10 df). This result was unchanged when slope interactions were eliminated ($\underline{X}^2 = 302$, $\underline{P} < 0.001$, 10 df).

These results, although preliminary in nature, indicate that the Hansen Model has value in evaluating sites that are being considered for the reintroduction of desert-dwelling mountain sheep. However, further multivariate GIS analyses are necessary before firm conclusions can be reached.

GIS technology was used to test this model in an effort to bring the potential value of this analytical tool to the attention of wild sheep managers. This is the first application of a GIS to the management of mountain sheep, and it proved to be extremely valuable. However, managers are cautioned that the accuracy of the results of their analyses will be a function of the quality of the original data that they use to develop their application (August In Press, Lunetta et al. 1991).

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HABITAT RELATIONS

Bienn. Symp. North. Wild Sheep
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FORAGING BEHAVIOR AND VEGETATION RESPONSES TO PRESCRIBED BURNING ON BIGHORN SHEEP WINTER RANGE

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Abstract: Prescribed burning has been used as a habitat management tool on the South Fork of the Shoshone River, near Cody, Wyoming for over 15 years. The primary emphasis has been to improve foraging conditions for wintering Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*). In 1986 a study was initiated to determine the effect of prescribed fire on winter range vegetation, sheep diet quality, and foraging behavior. Burning increased herbaceous plant production and removed shrubs that obstructed visibility. Diet quality and foraging efficiency of wintering sheep were greater on burned vegetation types when compared to sagebrush and juniper dominated sites. Radio-collared sheep selected burned areas as foraging habitats in spring. Prescribed burning may increase nutrient density, allowing sheep to obtain higher quality diets and higher nutrient intake rates. Implications of these findings to bighorn sheep habitat ecology management are discussed.

Bighorn sheep populations in the western United States have declined markedly in both distribution and density since the early part of this century (Buechner 1960). Transplants of sheep into their former ranges and supplements to stagnated populations are often attempted to reverse the decline. In Wyoming, such efforts have been relatively unsuccessful (Smith and Butler 1988). Failure of reintroductions and attempts to rejuvenate herds can be attributed primarily to altered habitat conditions. Loss of open foraging areas and traditional migration routes to conifer and shrub encroachment has been suggested as being responsible for the loss of many sheep populations (Wakelyn 1987).

Fire suppression and lack of habitat management have been

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identified as major factors responsible for the degradation and loss of suitable bighorn sheep habitat (Wakelyn 1987). Many bighorn sheep winter ranges exist within shrub-grass vegetation communities, where fire plays an important role in the maintenance of ecological processes (Wright and Bailey 1982). Fire increases herbaceous plant production, eliminates competing shrubs and trees, facilitates nutrient recycling, and encourages use by herbivores. Following settlement of the west, fires were suppressed and livestock grazing increased. These changes altered the structure and productivity of big game habitats (Houston 1973, Gruell 1980, Gruell 1986).

We examined the effect of prescribed fire upon winter range vegetation and determined the effect of vegetation changes upon bighorn sheep foraging behavior. Specific objectives were to determine:

1. Herbaceous forage production responses to prescribed fire.
2. Shrub and tree response to fire.
3. Diet quality of wintering sheep on burned and unburned vegetation types.
4. Foraging efficiency of wintering sheep in burned and unburned vegetation types.

Bighorn sheep on the South Fork of the Shoshone River are habituated to humans and can be approached closely without interrupting normal feeding behavior. Such habituation allowed us to collect detailed diet quality and foraging behavior data.

This project was supported by several agencies and individuals. Financial support was provided by the Foundation for North American Wild Sheep, Marathon Oil Co., Amerada-Hess Corp., National Rifle Association, Safari Club International, U.S. Forest Service (USFS), and the Wyoming Game and Fish Department (WGFD). Specific individuals deserving recognition include Terry Killough, Gary Brown, Jim Yorgason, Tim Fagan (WGFD), Jay Carlson, Martin Mufich, and Barb Franklin (USFS). Also many thanks to the residents of the upper South Fork, especially Mike and Jackie Strain, Harvey and Reta Collins, and Jerry and Kim Capron.

STUDY AREA

The South Fork study area is located approximately 64 km (40 mi) southwest of Cody, Wyoming (Fig. 1), and lies within the Shoshone National Forest. Within this geographical area, we sampled a narrow strip of sheep winter range that rarely exceeded 1.6 km (1 mi) in width and covered approximately 1,066 ha (2,618 ac). The boundaries of the study area included Ishawooa Creek, Cabin Creek, the South Fork of the Shoshone River, and Ishawooa Mesa. Although the winter range is primarily on Forest Service lands, several parcels of private land intermixed with the federal holdings are used extensively by sheep. Although quite variable, sheep numbers on the winter range averaged 275 to 300 animals.

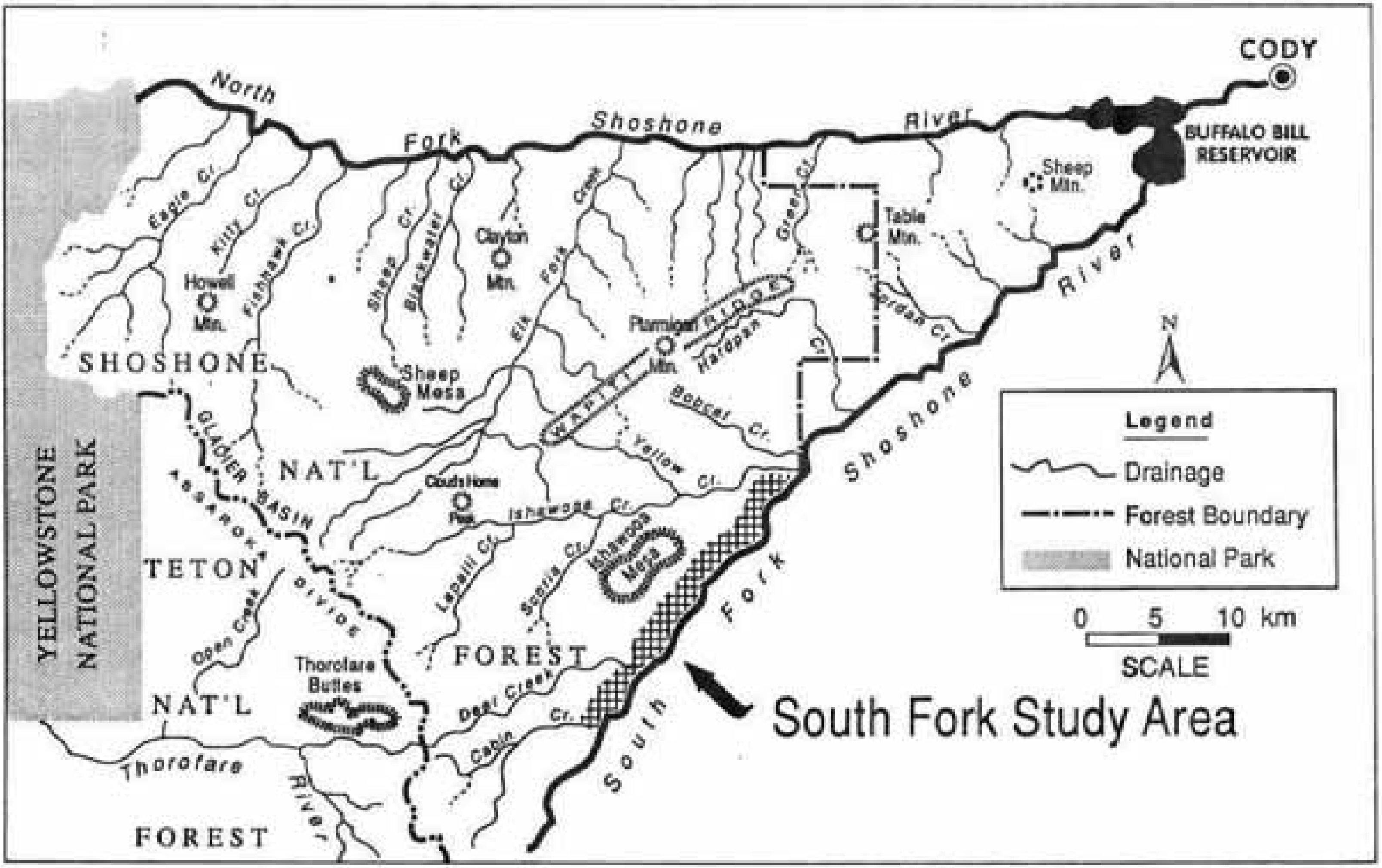

Fig. 1. Location of South Fork Study Area, northwestern Wyoming.

Topography within the study area consists of massive cliffs, steep hillsides, and gently sloping sagebrush grasslands with little or no transitional areas. The majority of the winter range is composed of southeast-facing, sagebrush-covered slopes that vary in elevation from 1,891 m (6,200 ft) to approximately 2,135 m (7,000 ft). These sagebrush grasslands are characterized by foothills and alluvial fans with moderate to deep soils varying in texture from cobbly sand loam or loamy sand to gravelly sand or clay loam (U.S. Dep. Agric. 1986).

Although a variety of vegetation communities exist on the South Fork of the Shoshone River, for purposes of this study 3 general vegetation types were delineated based on structural and compositional characteristics: sagebrush-grassland (SG), sagebrush-grass-juniper (SGJ), and burn (BURN).

The SG type consists primarily of Wyoming big sagebrush (Artemisia tridentata wyomingensis) and basin big sagebrush (Artemisia tridentata tridentata) with an understory of various grasses including bluebunch wheatgrass (Agropyron spicatum), needle-and-thread (Stipa comata), prairie junegrass (Koeleria cristata), and Sandberg bluegrass (Poa secunda). Most forbs that occur on the study area are essentially unavailable to wintering sheep due to desiccation and senescence.

The SGJ type is similar to the SG type, except for the addition of Rocky Mountain juniper (Juniperus scopulorum), creeping juniper (Juniperus horizontalis), and an occasional limber pine (Pinus flexilis). Herbaceous vegetation production in SGJ types is scant due to competition for light and nutrients from the juniper and dense sagebrush components.

Four prescribed burns (BURN) were sampled, ranging from 3 to 14 years in age and varying in size from 2.4 ha (6 ac) to 8.1 ha (20 ac). They encompassed both spring and fall burns, and occurred in both SG and SGJ vegetation types. Species composition of the burned areas included many of the same species as unburned areas, except for the addition of kingspike fescue (Leucopoa kingii), green needlegrass (Stipa viridula), rubber rabbitbrush (Chrysothamnus nauseosus), and Douglas rabbitbrush (C. viscidiflorus). The most noticeable feature within the BURN vegetation type, however, was the significant reduction in shrubs and trees.

METHODS

Vegetation Sampling

Permanent transects were established to monitor vegetation responses. The four burned sites were sampled using four 25-m transects each. An unburned control area of similar elevation, slope, and aspect was sampled in the same manner at each BURN site. Fifteen 0.1 m^2 quadrats were sampled along each transect for percent canopy cover and frequency of herbaceous species (Daubenmire 1959). Herbaceous production was estimated using a double-sampling technique (Wilm et al. 1944).

Shrub cover was sampled along each transect with a point-intercept technique (Mueller-Dombois and Ellenberg 1974). Presence or absence of shrubs was recorded at each of 50 points along the transect. Maximum height of each shrub was also measured.

Diet Quality

Simulated diets of bighorn sheep were collected by following randomly selected adult ewes and hand-plucking a 50-100 g sample that mimicked plants and plant parts that were observed to be eaten. Samples were collected every 2 weeks in each of the 3 vegetation types.

Simulated diets were oven dried at 65 C for 24 hrs, ground in a Wiley mill to pass through a 1mm mesh screen, and analyzed for crude protein. Crude protein content (Kjeldahl nitrogen X 6.25) was determined using methods described by the Association of Official Agricultural Chemists (1965). Data were averaged for winter (Nov-Feb) and spring (Mar-May) periods.

Foraging Habitat Selection

Selection of foraging habitats was determined by comparing use with availability of the various vegetation types. Use of vegetation types was obtained from weekly visual relocations of 13 radio-collared sheep. Availability was estimated from aerial photos and ground-truthed vegetation maps.

Foraging Behavior

Information collected on foraging behavior included bite rates and foraging time. Bite rates were obtained by recording the time required for an individual ewe to obtain 100 bites. The stopwatch was running only while the animal's head was down biting or searching for forage. When the animal's head was lifted, the clock was stopped. A bite was defined as a distinctive jerking motion of the head while the animal was feeding. Time required per 100 bites was converted to the number of bites/minute. Bite rate estimates were obtained monthly in each vegetation type ($\underline{n}$ = 594). This sampling technique was designed to be an index to the time required to search for and ingest forage.

Foraging time was determined from 10-minute activity profiles conducted in each vegetation type ($\underline{n}$ = 581). The behavior of an adult ewe was recorded each minute (instantaneous sample). Behaviors recognized were feeding, walking, alert, resting, running, and courtship. Data were summarized by vegetation type to arrive at an estimate of minutes spent feeding/10 minutes. Information gathered concurrently with activity profiles included date, time, location, aspect, slope, elevation, snow depth, group size, distance from escape terrain, and distance travelled during the 10-minute sample. Foraging behavior data were also averaged over winter and spring periods.

Data Analysis

One-way analysis of variance (ANOVA) was used to test for differences in vegetation between burned areas and their respective controls (Zar 1984). One-way ANOVA was also used to examine differences in diet quality and foraging behavior among vegetation types. If the ANOVA was significant ($\underline{P} < 0.05$), least significant difference (LSD) multiple range tests were performed to determine the significant differences among the various vegetation types.

Foraging habitat selection was determined using Chi-square analyses, which tests the hypothesis that all vegetation types are used in proportion to their availability (Neu et al. 1974). Application of Bonferroni confidence intervals to situations where the null hypothesis has been rejected allows identification of selected habitats, avoided habitats, and those used in relation to their availability (Byers et al. 1984). Selection behavior of sheep was analyzed for winter and spring periods separately.

Data reported are from the 1988-1989 winter. This winter followed a drought period responsible for extensive fires in the Greater Yellowstone Ecosystem (Romme and Despain 1989).

RESULTS

Vegetation Response

Herbaceous production was consistently greater on burned areas compared to controls (Fig. 2). However, significant differences were found on only 2 sites. Shrub cover was significantly less on burned areas compared to controls for all sites. (Fig 3). Shrub height on burned areas was less than that of nearby unburned control areas (Fig. 4). Significant differences were detected on 2 of the 4 sites.

Diet Quality

Crude protein content of simulated sheep diets from BURN vegetation types was consistently greater than diets obtained from SG and SGJ types. However, this relationship was significant only in spring (Fig. 5).

Foraging Behavior

Bite rates of sheep feeding in BURN vegetation types were significantly greater than rates obtained by sheep feeding in SG and SGJ communities with one exception. Although greater, bite rates in the BURN did not differ significantly from those in the SG type in winter (Fig. 6). Time spent feeding was significantly greater for sheep feeding in BURN vegetation types compared to those feeding in SG and SGJ types in both winter and spring (Fig. 7).

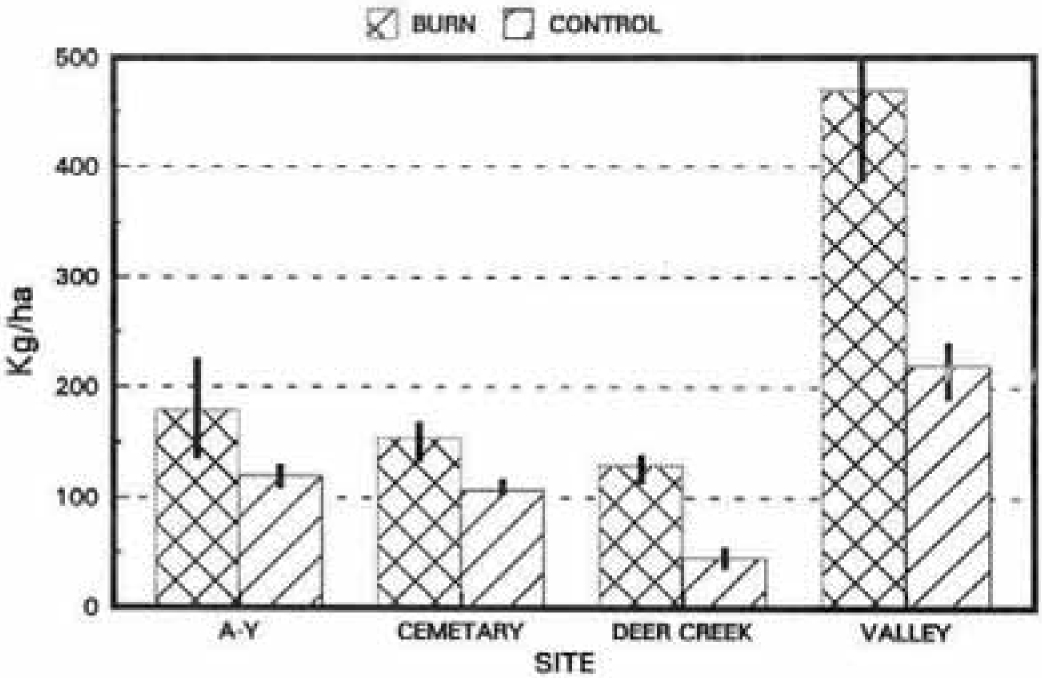

Fig. 2. Herbaceous forage production (± S.E.) on burned and unburned vegetation types, South Fork Shoshone River, 1988.

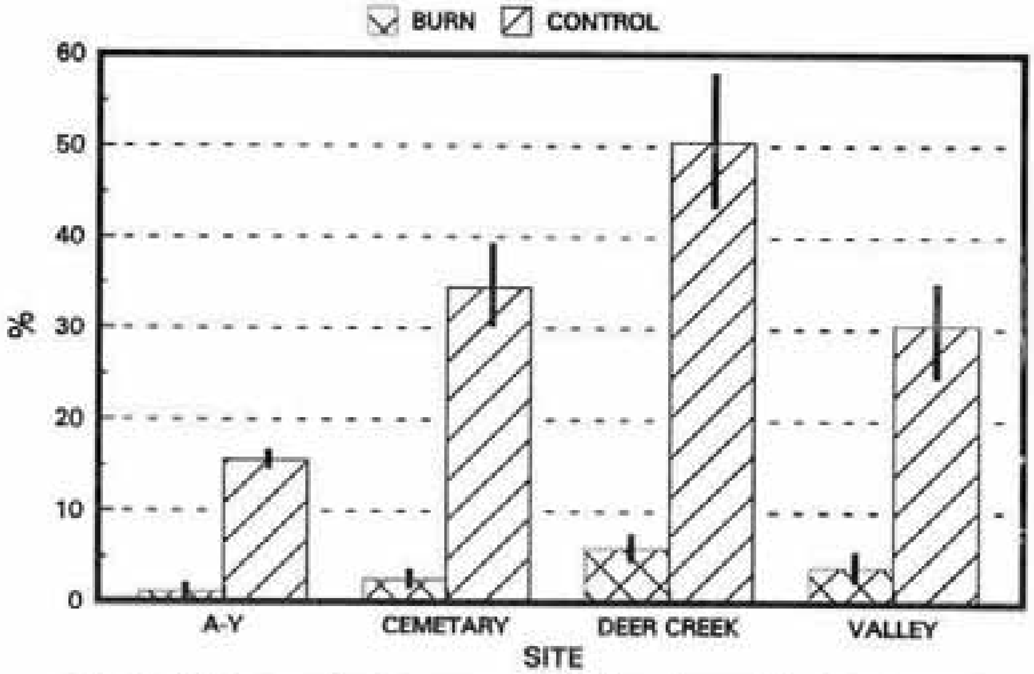

Fig. 3. Average shrub cover (± S.E.) on burned and unburned vegetation types, South Fork Shoshone River, 1988.

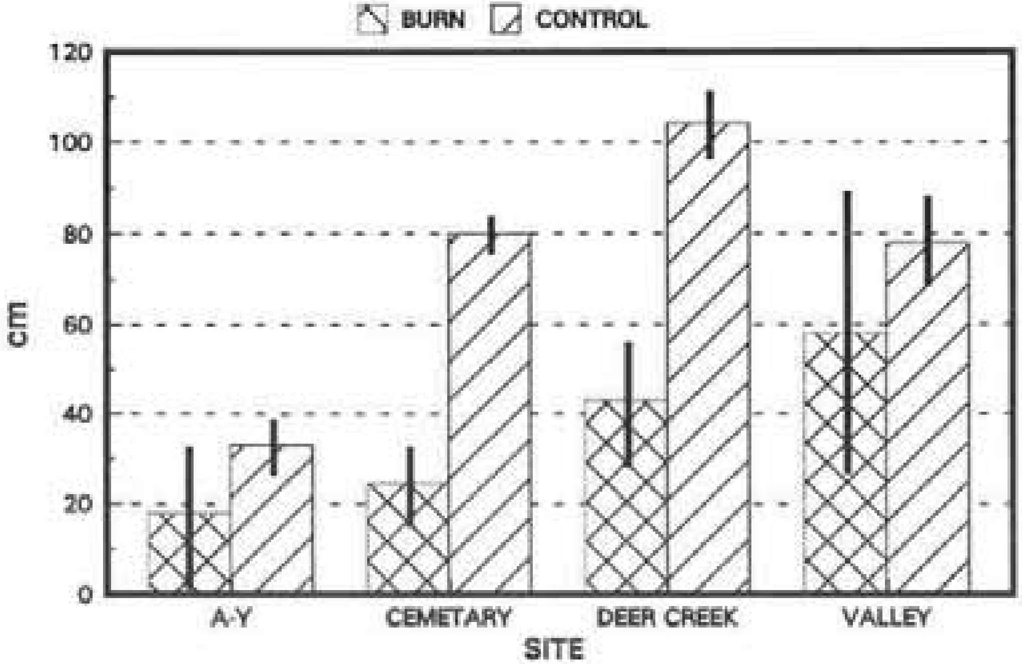

Fig. 4. Average shrub height (± S.E.) on burned and unburned vegetation types, South Fork Shoshone River, 1988.

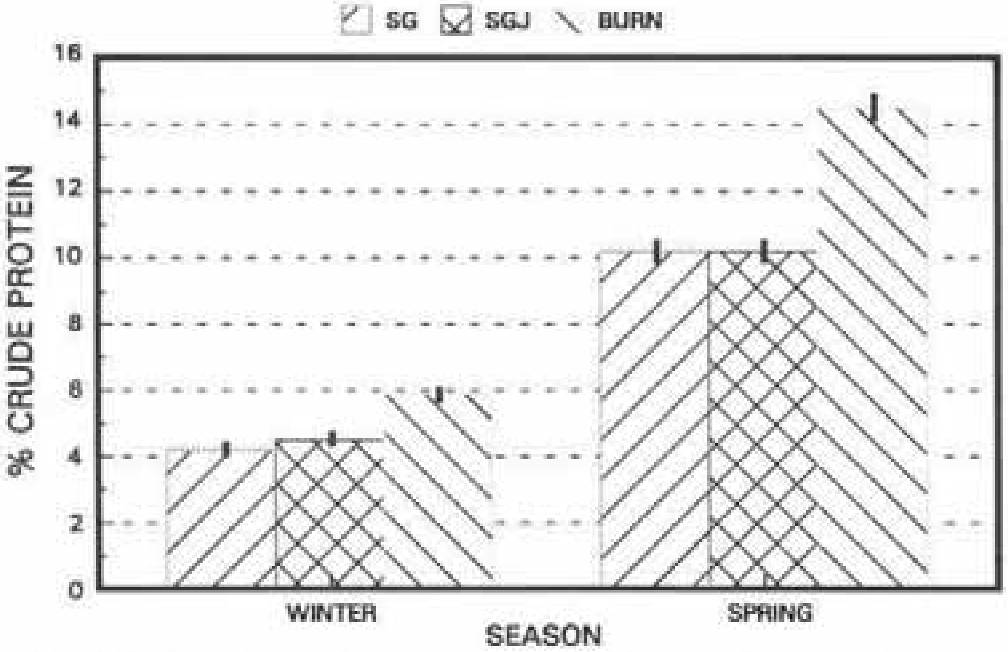

Fig. 5. Crude protein content (± S.E.) of simulated bighorn sheep diets, South Fork Shoshone River, 1988-89. SG = Sagebrush/Grass, SGJ = Sagebrush/Grass/Juniper.

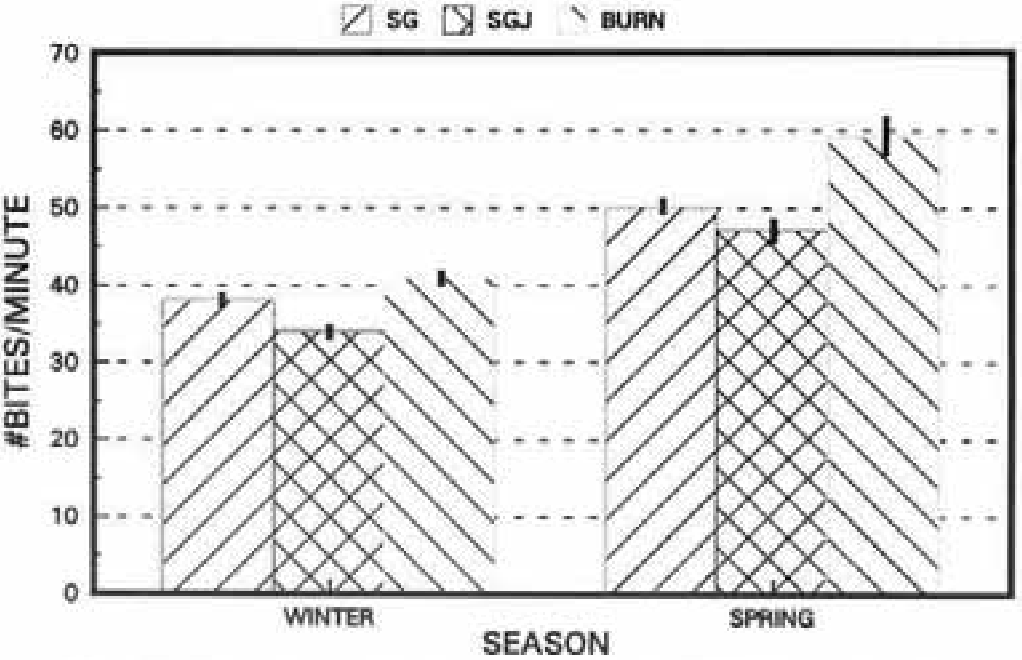

Fig. 6. Bite rates of bighorn sheep (± S.E.) in burned and unburned vegetation types, South Fork Shoshone River, 1988-89. SG = Sagebrush/Grass, SGJ = Sagebrush/Grass/Juniper

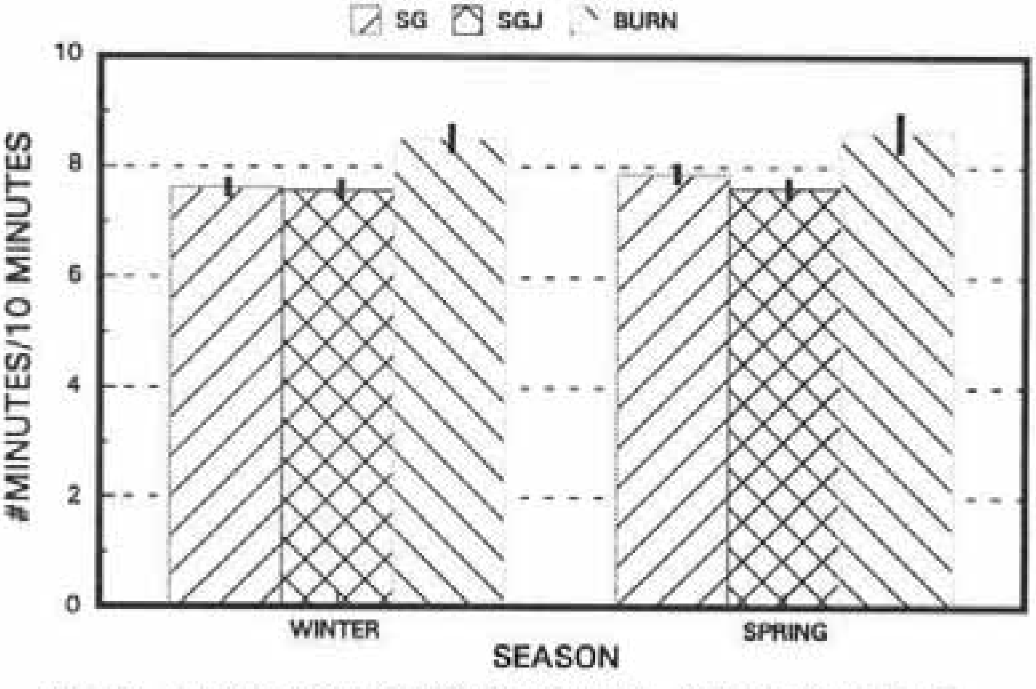

Fig. 7. Foraging time of bighorn sheep (± S.E.) in burned and unburned vegetation types, South Fork Shoshone River, 1988-89. SG = Sagebrush/Grass, SGJ = Sagebrush/Grass/Juniper

Foraging Habitat Selection

Winter habitat selection analysis revealed that SG vegetation types were used less than would be expected based on availability. Although selection for BURN types approached significance, both BURN and SGJ types were used in relation to their availability (Table 1). Selection of foraging habitats in spring revealed a preference for BURN vegetation types, while use of the SG was less than expected and SGJ types were used in proportion to availability.

DISCUSSION

Observed vegetation responses to burning have a profound effect upon the foraging ecology of bighorn sheep. Subtle increases in nutrient content of forages in burned areas have been documented (Willmset al. 1981, Harris and Covington 1983, Cook et al. 1990).

Table 1. Foraging habitat selection by bighorn sheep, South Fork Shoshone River, Wyoming, 1988-89.

Vegetation type	Proportion expected	Proportion observed	95% C.I.	Selection behavior
WINTER (*n* = 103)				
SG[a]	0.694	0.417	0.296 - 0.539	-[d]
SGJ[b]	0.195	0.262	0.154 - 0.370	NS[e]
BURN[c]	0.024	0.087	0.018 - 0.157	NS
SPRING (*n* = 121)				
SG	0.694	0.322	0.216 - 0.428	-
SGJ	0.195	0.281	0.179 - 0.383	NS
BURN	0.024	0.174	0.088 - 0.260	+[f]

[a] Sagebrush-grass vegetation type
[b] Sagebrush-grass-juniper vegetation type
[c] Burn vegetation type
[d] Use of vegetation type less than expected
[e] Use of vegetation type in relation to availability
[f] Use of vegetation type greater than expected

Although such increases may appear to be slight, when coupled with increased forage production, nutrient density is increased. Increased nutrient density should allow an animal to obtain a higher quality diet. Our data support this contention, as sheep diet quality was greatest in BURN vegetation types. The combination of increased forage quality and quantity may allow an animal to be more selective,thus optimizing diet quality.

Observed vegetative responses to prescribed fire also had a large effect on the foraging behavior of wintering sheep. Higher bite rates were observed from sheep feeding during foraging bouts in burned areas and sheep spent more time actually feeding in burned areas compared to unburned communities. This can be explained by the reduction in shrub cover and shrub height as a result of burning. The removal of the shrub canopy allows sheep to forage more efficiently. Less time is spent in search of potential bites as a result of increased forage densities, and time spent feeding increases as a result of the increased visibility resulting from shrub removal. In addition, sheep preferred these open areas as foraging habitats.

Many researchers have examined total daily feeding time in response to vegetation characteristics, pasture conditions, and animal foraging behavior responses (Allden and Whittaker 1970, Seip and Bunnell 1985, Hudson and Frank 1987), but few have looked at the percentage of time spent feeding in various vegetation types on an instantaneous basis. Studies that have been conducted to address this question have found that visibility and group sizes are very important in determining the amount of time spent feeding in different habitats (Berger 1978, Alados 1985, Risenhoover and Bailey 1985, Warrick and Krausman 1987).

Visibility is a very important aspect of sheep foraging ecology. This is primarily due to the predator avoidance response of bighorn sheep. Sheep rely almost exclusively on eyesight to detect predators (McCann 1956, Geist 1971). When vision is occluded, the ability to detect predators is reduced. Therefore, when sheep feed in areas where visibility is limited, a substantial amount of time is spent watching for predators or watching for visual cues from cohorts (Risenhoover and Bailey 1985). Such time spent in alert behaviors can seriously reduce the amount of time actually spent ingesting forage. Data from the 10-minute activity profiles revealed that sheep did spend significantly more time in alert postures when feeding in SG and SGJ vegetation types when compared to BURN vegetation types. This is, as stated above, attributable to decreased visibility in SG and SGJ types. When feeding in BURN types, sheep could scan the environment for predators while their head was down. Thus, foraging time need not be spent surveying for predators.

With increased diet quality of sheep feeding in BURN vegetation types, and increased foraging efficiency (bite rates, time spent feeding), one would expect that nutrient intake rates could be enhanced by prescribed burning. Prescribed burning on the South Fork of the Shoshone River has been shown to increase forage production, visibility, diet quality, and foraging efficiency. Together, these factors represent the creation of high quality habitats for bighorn sheep.

MANAGEMENT RECOMMENDATIONS

By nature, bighorn sheep are very sensitive to habitat loss or alteration. Fire suppression and lack of habitat management have been identified as factors which have caused the degredation and loss of many suitable bighorn ranges (Wakelyn 1987). Efforts must be made to actively manage sheep habitat or risk further losses. Although these recommendations are specific for the South Fork of the Shoshone River, they may have broad application for burning on bighorn sheep winter ranges. Recommendations are:

1. Implement prescribed burns when and where applicable. Although dominated by low potential range sites, there are areas on the winter range that will respond favorably to fire. Even if herbaceous vegetation response is not optimal, the creation of open foraging areas without obstructing shrubs and trees, will benefit sheep through increased foraging efficiency. Areas that might not burn in average years may have sufficient fuels following high forage production years. Efforts should be made to treat pre-determined areas when these circumstances arise.

2. As stated by Smith (1988), prescribed burns should be large enough, to attract sheep. This would also reduce the potential for over utilization of recent burns. It appears from this work that the benefits of burning last a minimum of 15 years. A rotational treatment schedule in which 1/15 - 1/20 of the "burnable" winter range is treated each year might be optimal. This would create a diversity of seral types, providing high quality foraging areas for sheep while providing for habitat requirements for other wintering ungulates as well.

3. As emphasized in many prescribed burn plans, resting the burn from livestock grazing the first growing season after the fire is a must. One of the burns on the South Fork was grazed the season following treatment. This resulted in removal of preferred grass species and establishment of cheatgrass and other undesireable annuals. If fine fuel accumulations are necessary in order for a project to succeed, deferment of grazing prior to burning should be considered.

4. Treatments should be applied in a manner that creates a mosaic of vegetation types. Because large concentrations of other big game species exist on the South Fork, habitat improvements should not be directed solely at bighorn sheep. Consideration should be given to other species, especially mule deer (<u>Odocoileus</u> <u>hemionus</u>), when vegetation manipulation techniques involve the removal of shrubs. In addition, Goodson et al. (1991) has shown that sheep forage in dense shrub communities when snow precludes feeding in open vegetation types. This behavior was not observed on the South Fork of the Shoshone River, but could be explained by the very mild winters during which data were collected.

5. Although not applicable to most areas in the high security, alpine summer ranges of the Absaroka Mountains, prescribed burning may provide foraging efficiency benefits to other sheep herds where spring-summer-fall ranges are threatened by shrub-conifer encroachment. This would be particularly useful to the semi-low elevation sheep herds of south-central Wyoming.

6. Numbers of sheep utilizing the South Fork winter range seems to be increasing and may be approaching ecological carrying capacity. Due to heavy use of hay meadows, private landowners play a significant role in the determination of acceptable/allowable numbers of sheep. In addition to unacceptable levels of use in the private meadows, native vegetation types might be adversely affected. Repeated overuse could degrade native communities and increase dependence of sheep upon the meadows. This situation should be addressed promptly. Transplant options, as well as female harvest, should be investigated as potential methods of herd reduction. Harvest objectives for other big game species should be achieved as well in order to reduce the potential for direct and indirect competition for space and forage.

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THE ROLE OF PRECIPITATION AND TEMPERATURE IN THE WINTER RANGE DIET QUALITY OF MOUNTAIN SHEEP OF THE MOUNT BAXTER HERD, SIERRA NEVADA

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Abstract: The study of population ecology of wild ungulates often has emphasized the role of nutrition relative to demography, notably reproduction and survival. Consequently, diet quality is an important consideration in modeling such populations. An assessment of the principle environmental variables driving winter range diet quality of mountain sheep from the Mount Baxter population in the Sierra Nevada was made using 14 years of fecal crude protein data. Fecal crude protein, a measure of diet digestibility, should reflect the availability of growing plant tissues, which in turn should reflect the role of temperature and precipitation. The amount of winter precipitation proved to be a relatively unimportant influence, while the timing of the first major storm that initiated plant growth was very important. Second in importance was temperature. These results are discussed in the context of application to demographic models.

Diet quality has long been considered an important parameter in the population ecology of wild ungulates (Leopold 1933). Most studies have approached diet quality from the standpoint of the quantity of available forage and resultant resource competition when forage quantity is in short supply. This approach has been influenced strongly by work on winter ranges where forage quantity is obviously limiting to the ungulate population(s). Fundamental concepts and models of density-dependence, as a negative feedback loop regulating herbivore populations, have been derived from such environments (McCullough 1979). Such simple population models may adequately represent ungulates whose populations are limited by the availability of nutrients on a winter range, and whose winter range affords no opportunities for forage growth during the winter months due to low temperatures. However, such models will become increasingly less able to predict population parameters as more variables influence diet quality. Warm arid ecosystems of variable precipitation input, in which the quality of winter diets may be influenced by active plant growth, in addition to forage available from a previous growing season, are an example (Wehausen et al. 1987).

Because of the frequent warm winter daytime temperatures, the eastern base of the Sierra Nevada in Owens Valley may be such an ecosystem. On the basis of fecal crude protein (FCP) curves, Wehausen (1980) noted substantial differences for 1976-78 in both winter and summer range diet quality of the Mount Baxter mountain sheep (Ovis canadensis) population in the Sierra Nevada. Winter range diet quality was hypothesized to be influenced by the timing of the first winter storms. This paper reexamines the factors underlying the winter range diet quality of the Mount Baxter population based on FCP data from 14 different winters.

These analyses are made in the context of attempting to derive a predictive model of winter range diet quality that can be incorporated in a demographic model.

Wehausen (unpubl.) has shown that FCP measures apparent digestibility of the diet rather than other quality parameters, which are measured only to the extent that they are correlated with digestibility. For herbivores, forage digestibility is inversely related to the amount of plant structural components in the diet, especially lignin (Van Soest 1982). In general, the more rapidly plant tissues are growing, the lower their content of structural components, and the higher their digestibility. For a foraging sheep, the more growing plant tissue there is around them, the better they will be able to select a diet high in digestibility.

Of various factors potentially influencing plant growth, water and temperature were hypothesized to account for much of the variation in winter range plant growth and, hence, forage digestibility and FCP values. Precipitation was expected to be the major influence on FCP levels through both the timing and amount of winter rain; the latter should determine the length of the growing season through soil moisture reserves. No plant growth and, thus, no rise in FCP was expected prior to the first soaking winter rain. Temperature was expected to influence forage growth and sheep diet quality in 2 ways. First, there is a temporal sequence in the initiation of growth among the plant species present, beginning with the most cold tolerant (e.g., grasses) and ending with the most cold intolerant (various shrubs). As the growing season becomes progressively warmer, there will be more species growing and more from which sheep can choose; additionally, some of the species that initiate growth later produce higher quality forage (Wehausen 1980). Second, within any period of the growing season, year-to-year variation in temperature was expected to influence diet quality through the rate at which plants produced new growth.

The Los Angeles Department of Water and Power provided the precipitation and temperature data used. Support for this research has come from: The California Dept. of Fish & Game; The University of California, White Mountain Research Station; The National Park Service; The U. S. Forest Service; and The Foundation for North American Wild Sheep; and was conducted as part of the California Dept. of Fish & Game Bighorn Sheep Program. V. C. Bleich and S. G. Torres provided useful comments on the manuscript.

STUDY AREA

The winter range of the Mount Baxter population encompasses the base of the eastern escarpment of the Sierra Nevada from Thibaut Creek to Sawmill Canyon, northwest of Independence, California. Sheep occupied elevations as low as 1,450 m (4,800 ft) but rarely exceeded 2,075 m (6,800 ft) while on this winter range. Their alternate range encompasses alpine and subalpine habitats at considerably higher elevations. Winter range use by this population has varied considerably among years. Peak numbers of sheep have consistently occurred in March, coincident with ewes entering their third trimester of pregnancy and rapid increase in winter range diet quality. While most ewes have usually left the winter range in

April prior to the onset of lambing, in years of heavy snow, rams have remained there into the second half of May. Only in the the heaviest snow years has there been much winter range use prior to February, potentially beginning as early as late November. During the recent series of consecutive drought years beginning in 1987, winter range use, even in March, has dropped to almost nothing.

The vegetation on this winter range is a sagebrush scrub community dominated by shrubs, but includes a substantial cover of perennial grass, primarily *Stipa speciosa*. Young et al. (1977) classified this vegetation as a southern Great Basin community separate from the more northern sagebrush steppe, which begins north of Owens Valley; milder winters in the south were considered the important discriminating factor. More detailed description of this community, and of the food habits of the sheep occupying it, can be found in Wehausen (1980).

METHODS

Fresh fecal samples were collected from mountain sheep on the winter range every year from 1976 to 1990 except 1980. An attempt was made to obtain samples at least once every month while sheep were on the winter range. Because winter range use varied considerably among years, the number of samples collected in any year has varied from 2 to 6. The earliest samplings were in December, but typically began in late January or early February. Sampling occurred on a single day and represented that point in time, rather than the month as a whole. At each sampling, pellets were collected from numerous sheep, from which a composited sample was submitted for Kjeldahl crude protein analysis.

Temperature data were from the town of Independence at 1,200 m (3,925 ft). Precipitation data were from Independence, as well as from Onion Valley at 2,700 m (8,850 ft), which lies in the Sierra Nevada due west of Independence. Because the rain shadow on the east side of the Sierra Nevada causes a steep precipitation gradient with elevation, precipitation data from Independence substantially underestimated rainfall on the sheep winter range, while those from Onion Valley represented an overestimate. Consequently, an average of the precipitation from the 2 sites was used as an approximation of what occurred on the sheep winter range.

Sixteen variables were developed for use as independent variables in regression models (Table 1). Three were time variables: (1) the sampling date measured as the number of days after 30 November; (2) the sampling date measured as the number of days after the storm that initiated winter range forage growth; and (3) the date of the initiating storm, measured as the number of days after 31 October. To qualify as the initiating storm, it had to produce enough rain or snow to soak the soil deep enough to initiate perennial grass growth. This usually was based on direct observations of soil moisture and plant response on the winter range. In most cases, this date was obvious on the basis of such observations or precipitation data; in the few cases in which it was not, the first storm to exceed 13 mm (0.5 in.) of rain was chosen. There was considerable variation in the date of this initiating storm, ranging from 5 November to 13 February. For the 14 years of data, this storm occurred 5 times in November, 6 times in December, once in January, and twice in February.

Table 1. Independent variables and their abbreviations used to build regression models of winter range diet quality for mountain sheep from the Mount Baxter herd in the Sierra Nevada.

	Variable	Abbreviation
1.	DAYS AFTER NOV 30	DATE
2.	DAYS AFTER FIRST STORM	DAYS/STORM
3.	1ST STORM DATE (DAYS AFTER OCT 31)	STORMDATE
4.	PPT 7-30 DAYS PRIOR TO SAMPLING	PPT/7-30D
5.	PPT 7-60 DAYS PRIOR TO SAMPLING	PPT/7-60D
6.	PPT NOV 1 TO 7 DAYS PRIOR TO SAMPLING	PPT/7D-11/1
7.	PPT 31-60 DAYS PRIOR TO SAMPLING	PPT/31-60D
8.	PPT NOV 1 TO 61 DAYS PRIOR TO SAMPLING	PPT/61D-11/1
9.	PPT FIRST MONTH AFTER INITIATING STORM	PPT/1STMO
10.	AVERAGE HIGH TEMP. PREVIOUS 15 DAYS	TEMP/15D
11.	AVERAGE HIGH TEMP. PREVIOUS 30 DAYS	TEMP/30D
12.	AVERAGE HIGH TEMP. PREVIOUS 45 DAYS	TEMP/45D
13.	DEGREE-DAYS ABOVE 40 F	D-D>40
14.	DEGREE-DAYS ABOVE 48 F	D-D>48
15.	SQUARE ROOT OF DEGREE-DAYS ABOVE 40 F	SQRT D-D>40
16.	SQUARE ROOT OF DEGREE-DAYS ABOVE 48 F	SQRT D-D>48

Precipitation variables were defined by amounts occurring during different time periods prior to each FCP point. The 3 basic periods were: 7-30 days; 31-60 days; and >61 days, but not earlier than 1 November. Combinations of these variables were used to provided 2 more such precipitation time periods: 7-60 days prior; and 7 days to 1 November. A minimum of 7 days prior to the sampling time was chosen on the assumption that it would take at least a week after rain for vegetation to produce a response that might influence sheep diet quality. In the couple of cases where samples were obtained prior to the initiating storm, it took about 1 month for any FCP response to be measured. A sixth precipitation variable was the amount occurring in the first month of the growing season, beginning with the initiating storm.

Three temperature variables investigated were the average high temperatures 15, 30 and 45 days prior to each sampling point. Additionally, 2 composite variables were developed that combined temperature and days since the initiating storm into a single variable. This was done by integrating daily high temperatures in Independence between the initiating storm and the sampling date above 2 baseline temperatures: 4.4 and 8.9 C (40 and 48 F). These 2 baseline values were used to approximate 1.7 and 6.1 C (35 and 43 F) on the sheep winter range, based on elevation differences from Independence and the temperature lapse rate from further north in the Sierra Nevada (Major 1977). The latter temperature is considered the minimum for grass growth (Langvatn and Albon 1986). These composite variables were measured in degree-days, where 1 degree F above the baseline temperature for 1 day was 1 degree-day.

The relationship between digestibility and FCP is curvilinear (Wehausen unpubl.). A log transformation of FCP linearizes this relationship well; consequently, lnFCP was used in all analyses as the measure of diet quality. Analyses consisted of building simple and multiple regression models with an interactive stepwise regression program using lnFCP as the dependent variable. Automated stepwise regression was not used. A correlation matrix also was produced to investigate any possible lack of independence among variables that would cause multicollinearity (Neter and Wasserman 1974).

Subsequent to developing a variety of predictive models from the existing data set, 5 previously unused fecal samples from the years used to derive these models were discovered. FCP values were obtained for these, and they were used to test the predictive abilities of these models. These 5 samples included considerable variation in the variables most influential in the resulting models.

RESULTS

There was a significant ($\underline{P} < .001$) overall increasing seasonal trend in lnFCP values. However, points were widely scattered, with DATE (days after 30 November) accounting for only 56.6% of the variation in lnFCP. Examination of the residual variation by individual years points out the strong influence of the timing of the growth initiating storm (Fig.1). Changing the independent variable to days after this storm substantially tightened the cluster of points and accounted for 78.4% of the variation. Alternatively, adding the date of the first storm as a second independent variable with DATE increased this to 82.3% (Table 2). Again, examination of yearly patterns within the residual variation shows clear patterns. In this case, it can be explained by temperature differences among years. Figure 2 illustrates 3 of these. The 1985 growing season began with an early first storm; but it was followed shortly by a particularly cold early winter period that almost ceased gains in diet quality until warmer weather again prevailed. The 1983 season also had an early first storm; but instead, that year experienced a particularly cool late winter and spring. The result is a lnFCP curve that crosses from the upper side of the data points to the lower side during spring. In contrast, because the first storm did not occur until mid-February in 1987, it was followed immediately by warm weather, causing the diet quality curve to climb completely out of the rest of the data points (Fig. 2).

An attempt to account for these temperature differences with the composite degree-days variables was only partly successful. First, the variable with the lower baseline temperature (4.4 C/40 F) provided the better fit of the two (Table 2), but the relationship was somewhat curvilinear. A square-root transformation straightened this and improved the fit; but it still accounted for only an additional 3.7% of the variation in lnFCP compared with DAYS/STORM, and essentially nothing additional when compared with the multiple regression of DATE and STORMDATE (Table 2). Second, there remained yearly temperature differences apparent in the residuals (Fig. 3). The 1978 and 1983 growing seasons were particularly wet years (Fig. 4), the former of which was a warm winter, while the latter was cooler, especially in spring, as noted above. This temperature difference is very apparent in the parallel curves.

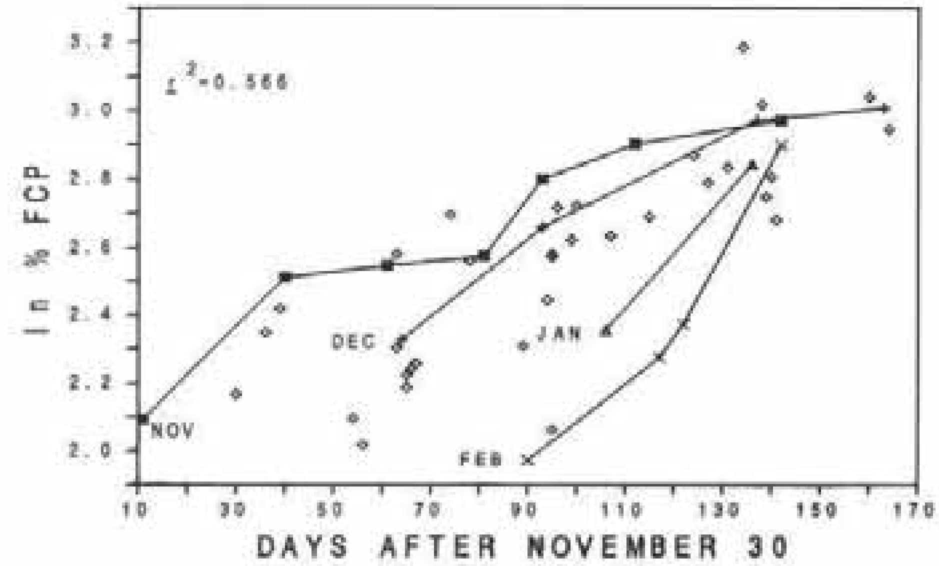

Fig. 1. Winter range fecal crude protein as a function of date for mountain sheep in the Mount Baxter herd, Sierra Nevada. Four years are plotted separately from the rest to illustrate the influence of the timing (by month) of the first major storm.

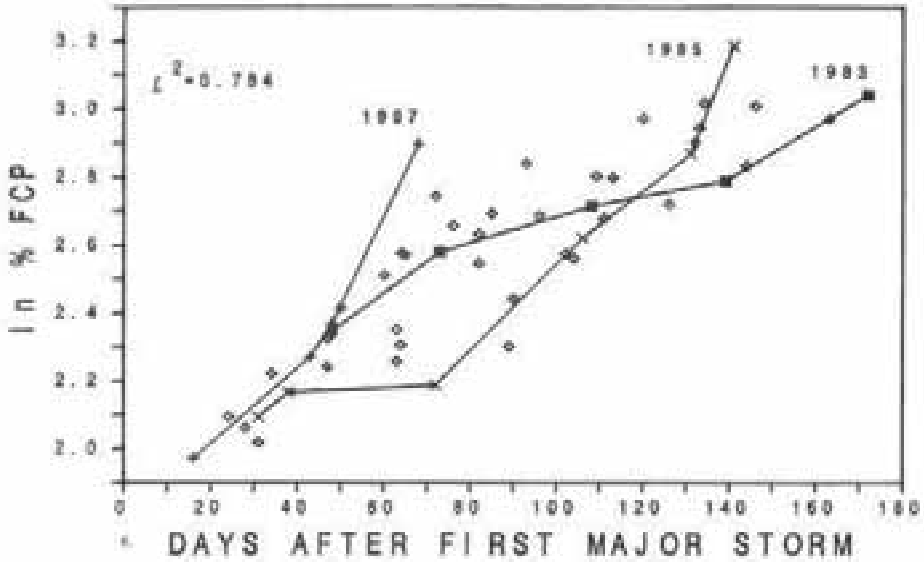

Fig. 2. Winter range fecal crude protein as a function of days since the first major storm for mountain sheep in the Mount Baxter herd, Sierra Nevada. The years 1983, 1985, and 1987 are labeled to illustrate the effects of temperature differences: a very cold period following growth initiation for 1985; very warm temperatures following very late growth initiation in 1987, and a cold late winter and spring in 1983.

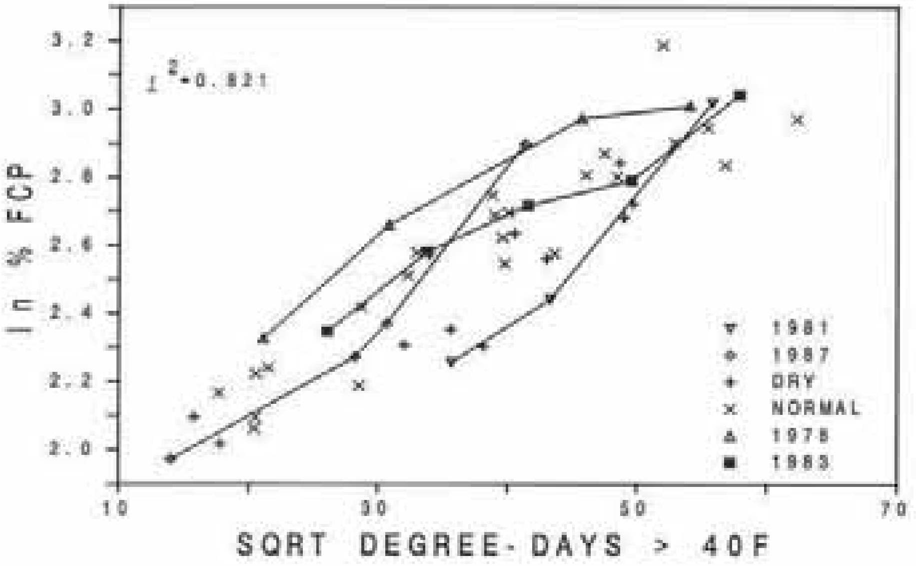

Fig. 3. Winter range fecal crude protein as a function of the square root of degree-days above 40 F since the first major storm for the Mount Baxter herd in the Sierra Nevada. 1981 and 1987 were both dry years, while 1978 and 1983 were particularly wet years, the former of which was notably warmer than the latter. 1981 experienced two months without rain following the growth initiating storm. This first storm did not occur until mid February in 1987.

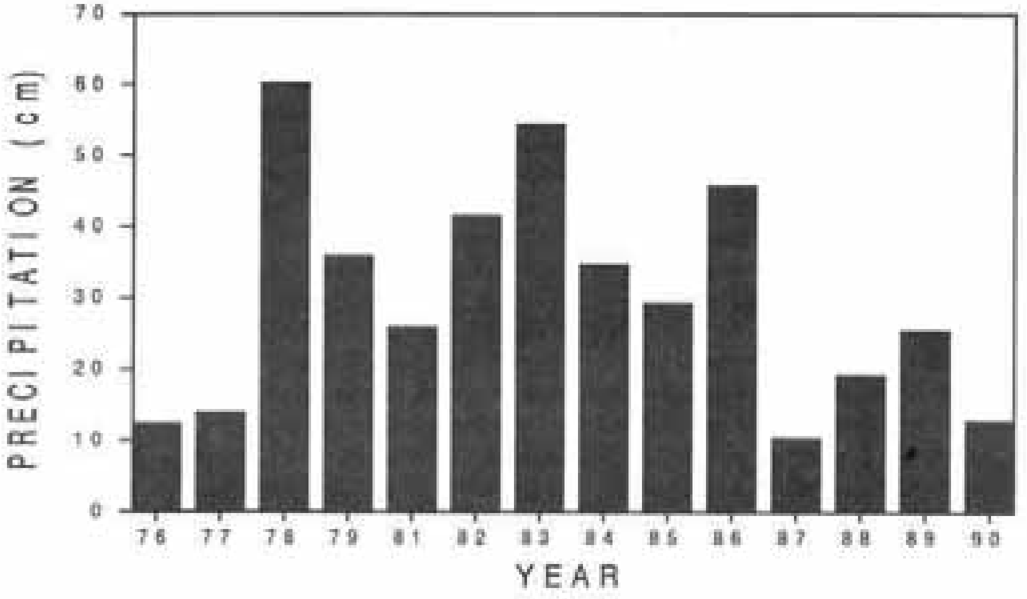

Fig. 4. November-March precipitation at Onion Valley (2700 m/8550 ft) in the Sierra Nevada for the years of study.

Table 2. Results of simple and multiple regression analyses of winter range diet quality (lnFCP) on time, temperature, and precipitation variables for mountain sheep from the Mount Baxter herd in the Sierra Nevada. Abbreviations are explained in Table 1.

X_1	X_2	X_3	X_4	S.E.(Y)	$\underline{R}^2$
DATE				.206	.566[1]
DAYS/STORM				.145	.784
DATE	STORMDATE			.133	.823
PPT/7-30D				.308	.027 (NS)
PPT/7-60D				.312	.000 (NS)
PPT/7D-11/1				.247	.376
PPT/31-60D				.310	.014 (NS)
PPT/61D-11/1				.219	.508
PPT/1STMO				.301	.068 (NS)
TEMP/15D				.204	.570
TEMP/30D				.170	.703
TEMP/45D				.170	.704
D-D>40				.144	.786
D-D>48				.153	.760
SQRTD-D>40				.132	.821
SQRTD-D>48				.140	.800
SQRTD-D>40	PPT/7D-11/1			.124	.845
SQRTD-D>40	PPT/1STMO			.120	.856
SQRTD-D>40	PPT/7D-11/1	TEMP/30D		.110	.882
SQRTD-D>40	PPT/1STMO	TEMP/30D		.110	.880
DAYS/STORM	TEMP/45D			.118	.861
DAYS/STORM	TEMP/30D			.117	.863
DAYS/STORM	TEMP/30D	PPT/7D-11/1		.108	.886
DAYS/STORM	TEMP/30D	PPT/7-60D		.108	.886
DAYS/STORM	TEMP/30D	PPT/1STMO		.107	.887
TEMP/45D	PPT/7D-11/1			.122	.850
TEMP/30D	PPT/7D-11/1			.122	.850
TEMP/30D	PPT/7D-11/1	DATE	STORMDATE	.108	.888

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[1] For simple regressions, all variables are significant ($P \leq .05$) except where noted otherwise; for multiple regressions, all variables are significant at $P \leq .01$.

Also, 1987, warm because of its late first storm, still exhibited a curve that increased upward through the other points, although no longer exceeding them.

Precipitation effects are also apparent in Figure 3. First, the 2 wettest years, 1978 and 1983, fall along the top of the points. Second, the drier years, which include 1981 and 1987, fall largely along the lower side. The 1981 season is illustrated because it was an extreme year due to a hiatus of 2 months with no precipitation that followed the storm which initiated growth. The effect on diet quality is clearly apparent (Fig 3).

The variance in total winter precipitation was great during the study period (Fig. 4). Using 25 and 50 cm (10 and 20 in.) of November-March precipitation in Onion Valley as separation points, years were partitioned into 3 categories: dry, normal, and wet. Covariance analysis of lnFCP for these categories, using SQRT D-D>40 as a covariate, produced a very significant precipitation effect (_P_ = .006), but this rainfall factor accounted for only 2.3% of the variation explained by the overall model.

When multiple regression models were built on SQRTD-D>40, precipitation and temperature variables could be entered significantly as second and third variables, respectively; however, these 2 added variables accounted for only an additional 6% of the variation in lnFCP. Further, using the same second and third variables with DAYS/STORM produced somewhat better models (Table 2). Clearly, the composite degree-day variables did not functioned as expected.

The ability to build statistically and biologically meaningful multiple regression models for lnFCP was somewhat limited by the lack of independence among some of the important variables. The greatest difficulties lay in correlations with time. Of the precipitation variables, only the long term ones that extended to the beginning of November correlated with time variables, especially with DAYS/STORM (Table 3). This pattern of correlations is to be expected, since later dates provide greater opportunities for increased cumulative precipitation. Because of the normal temperature rise from winter to spring, the temperature variables are strongly correlated with time variables (Table 3). Because of this lack of independence, when temperature variables were entered as second variables with DATE, the latter no longer contributed significantly to the overall regression. This result suggests that the time variables are significant by themselves largely because of this correlation with temperature. Of these 2 variable classes, temperature is biologically the more meaningful one. When temperature variables were used as the starting point of multiple regression models, total winter precipitation entered as the most significant second variable, and the total regression accounted for almost as much variation as 2-variable regressions beginning with time variables (Table 2). In these temperature-based models, the precipitation variable accounted for an additional 14.7% of the overall variation in lnFCP, and 17.3% of the variation accounted for. These were the only models in which the amount of precipitation accounted for more than a trivial portion of the variation. While it would be desirable to add STORMDATE alone to this model, it must be added along with DATE as a time reference to be meaningful. Both were

Table 3. Correlation matrix for the more important independent variables used in regression analyses of winter range diet quality for mountain sheep from the Mount Baxter herd in the Sierra Nevada. Abbreviations are explained in Table 1.

	DAYS/ STORM	STORM DATE	SQRT D-D>40	PPT/ 7-30D	PPT/ 7D-11/1	PPT/ 61D-11/1	PPT/ 1STMO	TEMP/ 30D
DATE	.70	.33	.74	.37	.38	.65	-.02	.80
DAYS/STORM	1	-.45	.96	.22	.66	.80	.21	.73
STORMDATE		1	-.33	-.17	-.40	-.25	-.31	.04
SQRTD-D>40			1	-.27	.53	.70	.08	.86
PPT/7-30D				1	.29	-.10	.37	.34
PPT/7D-11/1					1	.86	.64	.29
PPT/61D-11/1						1	.45	.50
PPT/1STMO							1	-.02

highly significant as added variables, but together accounted for only an additional 3.8% of the variation (Table 2), and the model again became fraught with the problem of the lack of independence between temperature and date.

In an attempt to quantify the relative importance of different classes of variables influencing diet quality, they were each investigated as second variables in multiple regressions with DATE by looking at their partial correlation coefficients and additional variance accounted for. The former measures the relative importance of these variables if date were held constant (Draper and Smith 1981). Storm date was clearly the most influential variable, precipitation variables the least influential, and temperature variables intermediate (Table 4).

Sixteen of the models in Table 2 were tested using the 5 additional past data points. The models with more independent variables that accounted for more of the variation in lnFCP did not generally yield smaller average deviations from predictions. In fact, the model with the smallest average deviation was the single-variable model using DAYS/STORM. However, this model also exhibited the highest variance among deviations from predictions (Table 5). With the exception of this model, all models tested overestimated lnFCP. It is possible that this bias reflected the length of time these samples had been stored before analysis. It will be necessary to make a prospective comparison using future samples to test this possibility and adequately test these equations. Because the average deviations from predictions are in units of lnFCP, their magnitudes are not easy to grasp and vary the FCP level. The smallest average deviation in Table 5 represents %FCP deviations of 0.1 and 0.3% for 8% and 20% FCP, respectively., while these values are 0.6 and 1.5% for the largest average deviation. These deviations are quite small compared with the natural seasonal variation.

Table 4. The relative importance of selected variables when entered as a second independent variable with DATE (days after Nov. 30) in regressions of winter range diet quality (dependent variable) for mountain sheep from the Mount Baxter herd in the Sierra Nevada. Abbreviations are explained in Table 1.

Variable	Additional variance accounted for (%)	Partial $\underline{R}$	Partial $\underline{R}^2$
STORMDATE	25.7	.769	.591
TEMP/45D	15.8	.604	.365
TEMP30D	15.5	.597	.356
TEMP15D	7.9	.425	.181
PPT/7-30D	1.5	.186	.034
PPT/31-60D	8.8	.450	.202
PPT/61D-11/1	8.6	.446	.199
PPT/7-60D	8.1	.431	.185
PPT/7D-11/1	12.7	.540	.291
PPT/1STMO	7.5	.414	.172

DISCUSSION

A number of the variables investigated can be discarded due to their relative lack of importance in the analyses. Among the temperature variables, TEMP/15D was consistently less important than the 2 longer periods. For the precipitation variables, PPT/7D-11/1 and PPT/1STMO were the 2 that consistently provided the best fit. PPT/61D-11/1 accounted for the most variation in lnFCP when considered alone (Table 2); however, it also was the precipitation variable most strongly correlated with DATE and DAYS/STORM (Table 3), which probably accounts for its strength alone, but not in conjunction with other variables.

The degree-day variables that integrated high temperatures after the first storm were the best single correlates with lnFCP; yet, they failed to improve the models when additional variables were included. This may be because the level of diet digestibility is not entirely a cumulative phenomenon, but is additionally influenced by forage quality differences among species with different temperature requirements for growth initiation. Sheep change their diet composition as these higher quality forages become available (Wehausen 1980). Consequently, temperature variables may be biologically the most meaningful representation of this process, as may be the multiple regression equations built on them.

Table 2 provides a welter of possible predictive models; which is best will be a function of the question being asked. If the goal is simply to predict winter range diet quality for specific dates using available temperature and precipitation data, the regression equation that

Table 5. Retrospective test using 5 data points from 1976 (2), 1978, 1979, and 1984 of selected regression models from Table 2 of winter range diet quality for mountain sheep from the Mount Baxter herd in the Sierra Nevada. Abbreviations are explained in Table 1.

X_1	X_2	X_3	X_4	Average Deviation[1]	SD
DAYS/STORM				-.014	.207
TEMP/45D				.071	.127
SQRTD-D>40				.018	.187
DATE	STORMDATE			.042	.158
DAYS/STORM	TEMP/45D			.043	.173
DAYS/STORM	TEMP/30D			.036	.181
SQRTD-D>40	PPT/7D-11/1			.016	.188
SQRTD-D>40	PPT/1STMO			.046	.189
TEMP/45D	PPT/7D-11/1			.073	.141
TEMP/30D	PPT/7D-11/1			.058	.147
SQRTD-D>40	PPT/7D-11/1	TEMP/30D		.046	.166
SQRTD-D>40	PPT/1STMO	TEMP/30D		.074	.169
DAYS/STORM	TEMP/30D	PPT/7D-11/1		.045	.174
DAYS/STORM	TEMP/30D	PPT/7-60D		.025	.178
DAYS/STORM	TEMP/30D	PPT/1STMO		.065	.176
TEMP/30D	PPT/7D-11/1	DATE	STORMDATE	.047	.170

[1] Deviations were measured as observed minus predicted.

best predicts future values will be the most useful. The ultimate measure of nutrient intake by sheep on this winter range is an integration of diet quality values over the period of occupation. The model that best predicts values by date could be used to produce such an integration; and the value of this integration then could be used as a variable in population models. Alternatively, a less rigorous modeling approach might look for a small set of variables that sufficiently represented the overall inter-annual variation in winter range diet quality. This would best be assessed by looking for correlations with values of the integrations discussed above. In the analyses above, the influence of timing of the first storm and temperature were each very strong and weak depending on how the analysis was built. This is probably because each accounts for different aspects of the overall variation. Temperature accounts for much of temporal variation within each year, and only a small amount of the inter-annual variation. In contrast, the strong influence of the timing of the first storm is entirely a function of inter-annual variation. As such, the date of the first major storm should be the single most important variable to represent inter-annual variation. Second in importance is likely to be a variable that indexes the relative winter-spring temperature regime. The amount of winter precipitation, while easier to obtain, appears least important.

Both integration and simple variable approaches to representing winter range diet quality in demographic models assume that the entire population uses this winter range for the time period in question. In reality, the population is commonly split between animals using the winter range and others wintering much higher, where diet quality is very different. Like the diet quality on the winter range, this split in use of the 2 ranges varies greatly, from years when the entire population uses the winter range to years of essentially no winter range use. Any attempt to model nutrient intake at the population level must take this split into account.

The elucidation of cause-and-effect relations of any ecological system requires observing dynamics in that system through natural or artificial perturbations (Sinclair 1979). The southern Sierra Nevada is clearly an ecosystem with considerable natural dynamics, but the years of this study have had the additional advantage of including a number of years of extreme conditions. Levins (1968) noted that of the attributes generality, precision, and reality, models in ecology and evolution can maximize only 2 at the expense of the third. If models are to represent reality, they will not be both general and precise. The approach taken here was to generate a precise model for a particular system. General models are classically simple, and include few parameters. These can only represent simple systems. The system investigated here clearly is complex, and not likely to be modeled adequately by simplistic models.

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WH

MOUNTAIN GOATS

Bienn. Symp. North. Wild Sheep
and Goat Counc. 8:293-304.

PRELIMINARY OBSERVATIONS OF TIMING AND CAUSES OF MOUNTAIN GOAT KID MORTALITY IN WEST-CENTRAL ALBERTA.

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ABSTRACT: The timing and causes of mortality of 11 of 26 radio-collared mountain goat (Oreamnos americanus) kids were monitored from June 1988 to April 1992 in west-central Alberta. The annual mortality rate of radioed kid to yearling age was 42%. Most mortalities (8/11) occurred by 30 November of each year and were caused by wolves (Canis lupus) (3/8), and grizzly bears (Ursus arctos) (2/8). A cougar (Felis concolor)-caused mortality, a fall, and a suspected grizzly bear-caused mortality accounted for the other 3 autumn deaths while the cause(s) of the 3 winter deaths were unconfirmed. We suggest that predation on kids is a major cause of poor recruitment into mountain goat herds in Alberta.

"Variation in age-specific mortality rates is the primary cause of different rates of increase for ungulates (Caughley 1970, 1976). Accordingly, managers charged with regulating harvests of ungulates should have knowledge of both the magnitude and agents of mortality.

Unfortunately, age-specific mortality rates of free-ranging ungulates are difficult to obtain. Indirect estimates, based on life tables derived from hunter-killed animals, are commonly used but are jeopardized by violation of several assumptions inherent in life table construction (Caughley 1977:90-96). Direct estimates of mortality based on marked animals are superior, particularly when animals are fitted with radio transmitters that provide certain knowledge of the fate of all animals in the sample (Heisey and Fuller 1985)" (Smith 1986:743).

Indirect estimates of mortality rates for kid and yearling mountain goats have been published (Hibbs 1966, Holroyd 1967, Rideout 1978, Stevens and Driver 1978, Youds et al. 1980, Adams and Bailey 1982). Moreover, Smith (1986) provided direct estimates of age-specific mortality rates and causes of death for mountain goats 1 year of age and older and concluded that predation and other natural causes of mortality primarily affected yearlings and goats older than 8 years. Prime-aged goats (age 2 - 8 years) were relatively invulnerable to natural mortality factors, but suffered considerable hunting mortality.

One factor which may limit population growth is the poor survival of mountain goat kids. On average, only half of the kids produced each year survive to yearling age (Chadwick 1983). Chadwick (1983) speculated on possible causes of high kid mortality and concluded that winter weather was the main limiting factor.

Annual mountain goat surveys in the Willmore Wilderness Area of west-central Alberta have been conducted since 1973. Results indicated a steady increase in mountain goat herds exposed to a a limited harvest of approximately 5 percent until 1980 (Smith 1988b). This increase appeared to be largely due to relatively good productivity and survival to 1 year. However,, between 1980 and 1983, populations began to decline coincident with poor kid:adult ratios and survival of kids. This decline occurred despite a reduction in harvest and very mild winter weather. Unhunted herds used as "controls" maintained themselves or increased slightly over the same time frame. However, they too experienced reduced kid:adult ratios and survival of kids although not at the same magnitude as hunted herds.

Direct assessment of mountain goat kid mortality has been limited to monitoring radio-collared or marked nannies with kids at heel (Joslin 1986, Foster and Rahs 1983). This technique has allowed the evaluation of timing and magnitude of kid mortality but not the causes.

Our study was designed to assess the timing and proximate causes of mountain goat kid mortality using radio-marked animals from June 1988 through April 1992.

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STUDY AREA

The Caw Ridge study area (54°N,119°W) is located approximately 30 km northwest of the town of Grande Cache, Alberta (Fig. 1). Caw Ridge is a front range of the eastern slopes of the Rocky Mountains and is separated from the main range by large tracts of coniferous forest. Areas used by mountain goats (approximately 21 km^2) range in elevation from 1750 to 2170 m. The weather is characterized by long, cold winters and cool, wet summers with annual precipitation averaging 540 mm. Above treeline (about 1950 m), the alpine meadows are comprised of grass and sedge species as well as lichens, mosses and a variety of herbaceous species. Vegetation below treeline is dominated

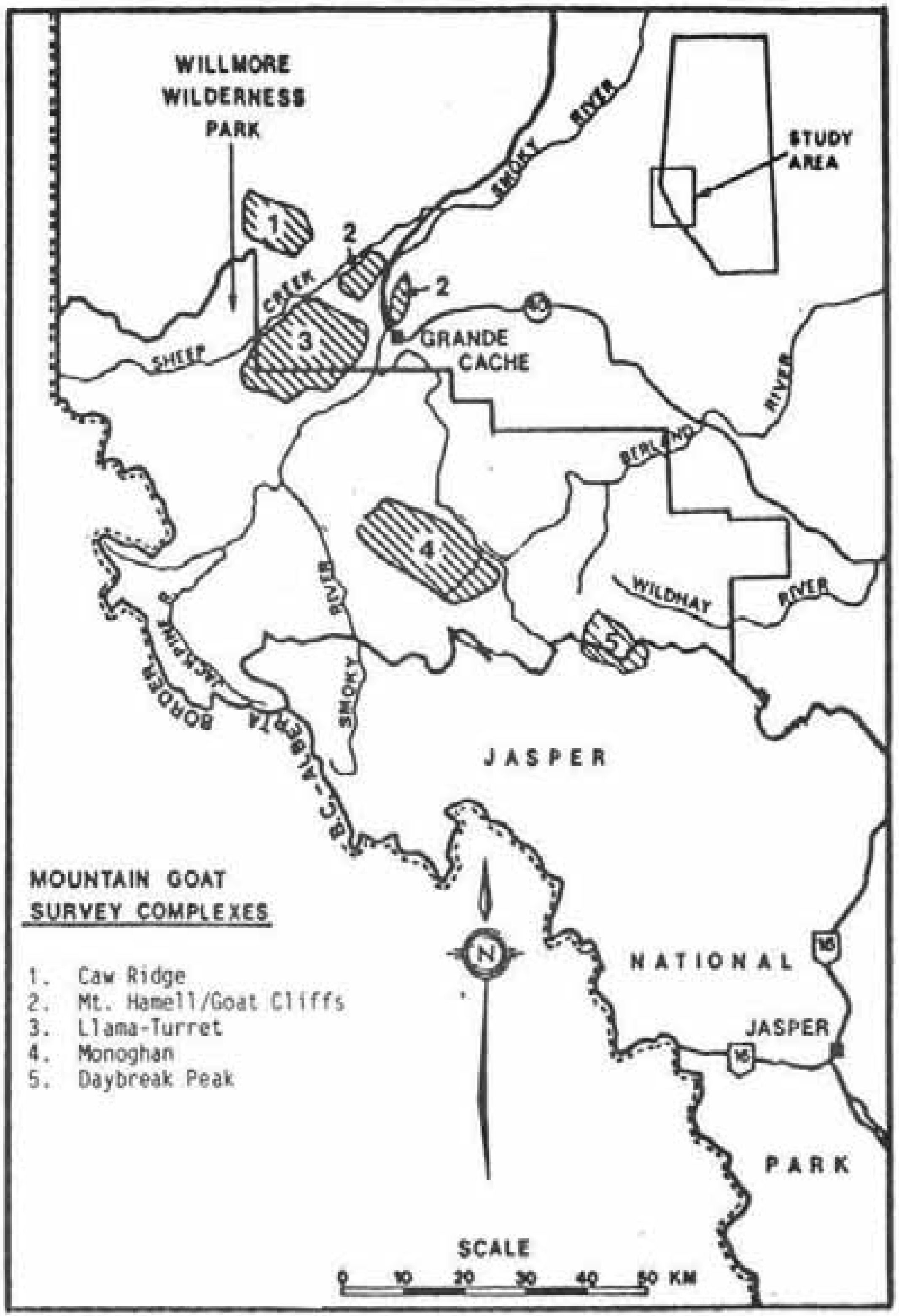

Fig. 1. Five mountain goat survey areas in west central Alberta including the location of the Caw Ridge study area.

by white spruce (Picea glauca) and alpine fir (Abies lasiocarpa) with lodgepole pine Pinus contorta) on fire-regenerated sites.

About 25-30 bighorn sheep (Ovis canadensis) inhabit the ridge, which is along a migration route and staging area for at least 250 woodland caribou (Rangifer tarandus). Elk (Cervus elaphus), mule deer Odocoileus heminous) and moose (Alces alces) are also present at low densities. Potential predators include wolves, coyotes (C. latrans), grizzly bears, black bears (U. americanus), wolverines (Gulo gulo), cougars and golden eagles Aquila chrysaetos). Further descriptions can be found in these proceedings (Fournier 1992) and Smith (1988b).

METHODS

Mountain goats were trapped in self-tripping clover traps and remotely-triggered Stevenson box traps baited with salt. Adults were immobilized by IM injection of xylazine. The effect was later reversed by IM injection of Idazoxan (Jorgenson et al. 1990). Adult females were fitted with color-coded radio collars or canvas collars and ear tags. Kids were handled without drugs and radio-collared with an expandable, break away elastic collar stitched with biodegradable thread. Each transmitter contained a 4-hour mortality switch (Telonics, Inc., Mesa, Ariz.). Standard measurements and weight were recorded and each kid was tagged with small Allflex ear tags. Collared kids were monitored daily from the ground for the period July 1989 to November 1991. Monthly helicopter relocations were conducted from December 1991 to April 1992.

Survival rates were estimated by dividing the number of mountain goat kids collared at time t and still alive at time t + 1 year by the number of collared kids at time t. We determined the cause of mortality by evidence at the mortality site including the presence of predators, hair, scats, tracks, the condition of the carcass (buried, covered or scattered) and presence of prey stomach contents. Scats were identified as bear, wolf or cougar based on size and shape characteristics (Larsen et al. 1989, Pall et al. 1988). The identity of predators could not be confirmed for the 3 mortalities which occurred during winter due to continued snow fall.

The study area was censused daily whenever weather permitted, if censusing did not affect trapping operations. Mountain goats were located visually or by following signals from radio collars. Groups were observed with binoculars and spotting scopes and location (UTM coordinates), group size and composition, identity and percent molt of marked goats were recorded.

Helicopter surveys of Caw Ridge and 4 other complexes were conducted in July 1991 and again between December 1991 and February 1992 in order to determine if the same pattern of autumn kid mortality that was being observed at Caw Ridge was also occurring in other herds in west-central Alberta. During the survey, mountain complexes were flown in a counter-clockwise pattern above timberline. The navigator-principal observer was to the left of the pilot, the second observer was in the left rear seat with the recorder in the right rear seat.

Mountain goats were classified as kids, yearlings and adults based on size (Smith 1988a). The July surveys were conducted between 0600-0900 and between 1700-2200 when goats were most active. The winter surveys were conducted throughout the day and tracks in the snow were utilized to locate herds.

RESULTS

A total of 26 mountain goat kids were radio-collared between June 1988 and August 1991. Kids were captured between 2 and 17 weeks of age ($\bar{x}$ = 9.7) assuming June 1 as date of birth. The annual mortality rate from kid to yearling age was 42% (Table 1). Most losses (8/11 = 73%) occurred by 30 November of each year. Wolves and grizzly bears accounted for 3 and 2 of the summer/fall deaths, respectively. A cougar, a fall and a suspected grizzly bear contributed to the other kid losses during that time of year (Table 2). Although the cause(s) of the 3 winter deaths could not be confirmed, wolves and a cougar were implicated by the presence of tracks and scats in 2 of the 3 cases.

Table 1. Mortality rates of radio-collared mountain goat kids at Caw Ridge, Alberta, 1988-1992.

Year	Mortality Rate (N)
1988-1989	0% (2)
1989-1990	40% (10)
1990-1991	46% (11)
1991-Apr 1992	67% (3)
TOTAL	42% (26)

Table 2. Timing and causes of mortality of 11 collared mountain goat kids, west-central Alberta, July 1989-April 1992.

Date	Cause	Sex of kid	Habitat[a]	Time between last live signal and discovery of carcass
16 Sep 1989	Wolves	Male	Subalpine	25 hr.
3 Oct 1989	Grizzly Bear	Female	Subalpine	6 hr.
28 Nov 1989	Wolves	Male	Krumholz	22 hr.
11 Feb 1990	?	Male	Subalpine	22 hr.
19 Aug 1990	Fall	Female	Krumholz	6 hr.
10 Sep 1990	Wolves	Male	Subalpine	20 hr.
21 Oct 1990	Grizzly Bear	Female	Subalpine	2 days
23-28 Oct 1990	?Grizzly Bear	Male	Krumholz	2 days
25-30 Jan 1991	?Cougar	Male	Subalpine	5 days
14 Sep 1991	Cougar	Female	Krumholz	3 days
14 Feb-31 Mar 1992	?Wolves	Female	Subalpine	45 days

[a] Subalpine = forested area below timberline, Krumholz = timberline

Aerial survey results indicated that the pattern of kid mortality observed on Caw Ridge in the fall of 1989 and 1990, did not occur on Caw Ridge in 1991 nor in any of 4 other mountain complexes (Fig. 2).

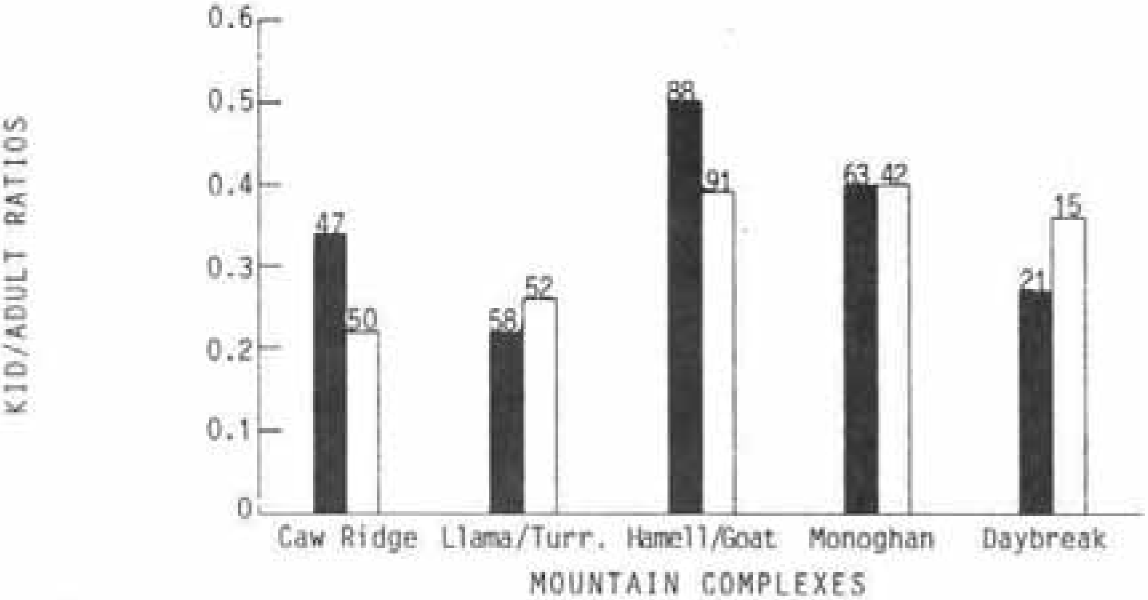

Fig. 2. Mountain goat aerial survey results for 5 mountain complexes in west central Alberta during July 1991 (solid bars) and December 1991, January and February, 1992 (open bars). (Numbers above bars are sample size).

DISCUSSION

Our original hypothesis was that the majority of mountain goat kid mortality at Caw Ridge would occur during winter (1 Dec-30 Apr) when deep snow and cold temperatures would reduce the availability of forage (that had already declined in food value) thereby placing the smallest members of the herd in a negative energy balance (Hobbs 1989). Moreover, snow would also restrict movements of mountain goats and increase the likelihood of predation. Because the majority of the kid mortality occurred by 30 November in 1989 and 1990 (when the sample size was 10 and 11, respectively) we reject this hypothesis.

In almost all instances, grizzly bear and wolf predation occurred at or below timberline. In 2 of the 3 years (1990 and 1991), mountain goats at Caw Ridge increased the amount of time spent foraging at timberline during the fall (Fig. 3). In the year when this habitat shift did not occur (1989), summer rainfall (Jun-Aug) was almost double that observed during the 2 subsequent years (Fig. 4). This might suggest that high precipitation during the summer months may have maintained green-up for a longer period which encouraged mountain goats to remain in alpine habitats later into the fall. Conversely, snow accumulation in the fall might be expected to drive mountain goats out

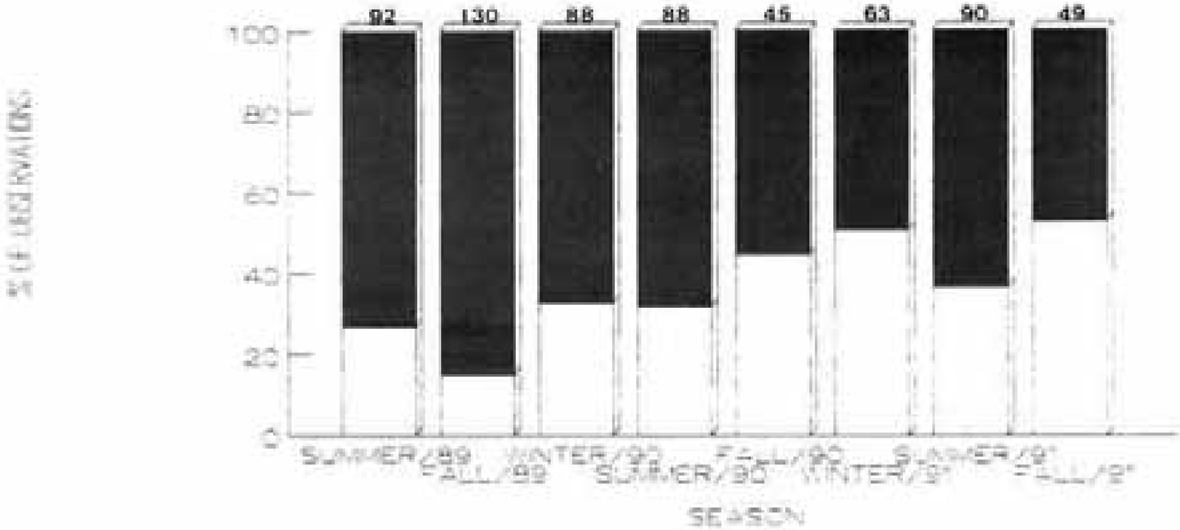

Fig. 3. Seasonal habitat use by mountain goats on Caw Ridge, Alberta, June 1989-November 1991. (Summer = Jun-Aug; Fall = Sep-Nov; Winter = Dec-May; solid bars = alpine habitat; open bars = treed habitat; numbers at top of bars are sample size).

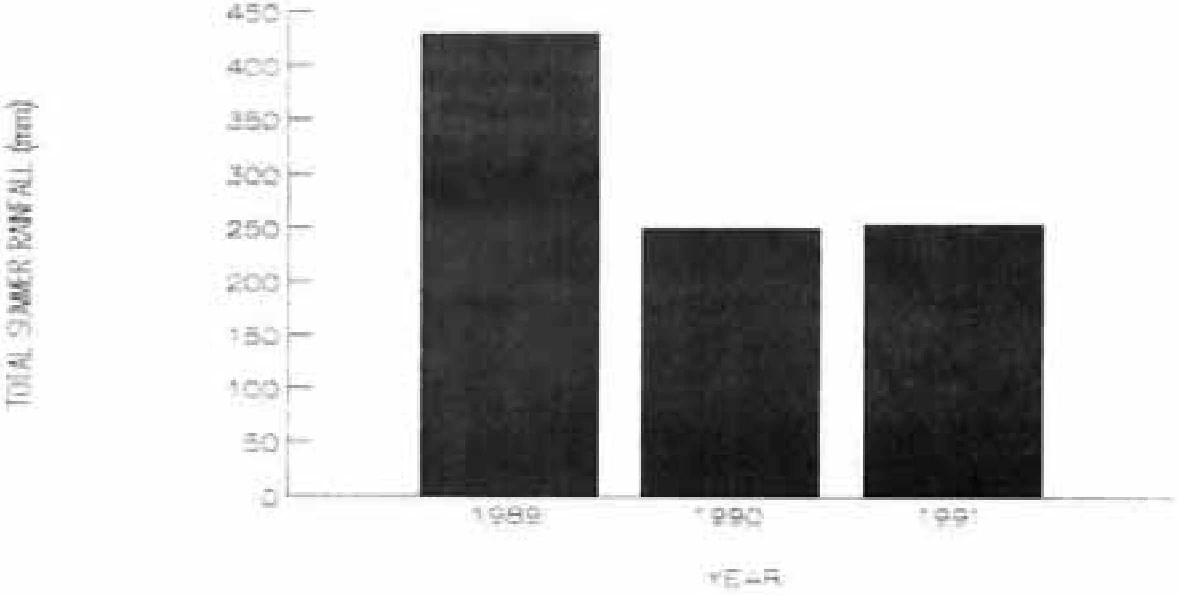

Fig. 4. Comparative summer rainfall (Jun-Aug) for 1989-91, Grande Cache, Alberta.

of the alpine. However, the snowfall accumulation in 1990 (Sep-Nov) was more than double that experienced in the year previous or the year following (Fig. 5) without any noticeable effect in habitat selection in the fall of 1990 (Fig. 3). Sample size is small and no conclusions can be made.

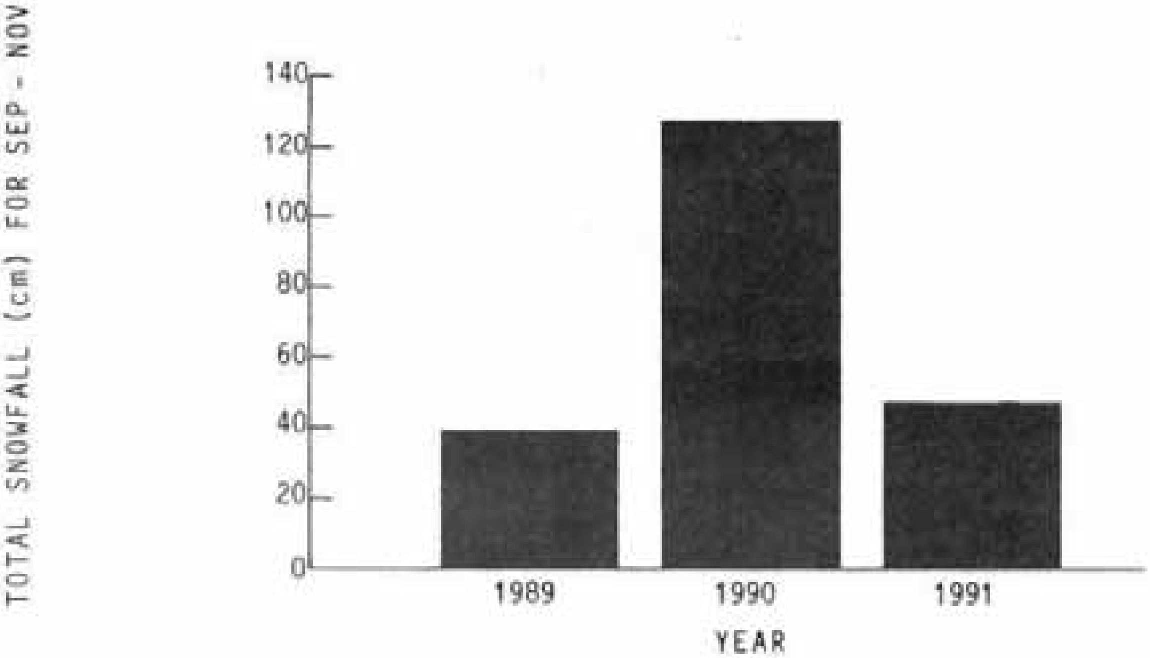

Fig. 5. Comparative autumn (Sep-Nov) snowfall for 1989-91, Grande Cache, Alberta.

If the search for green forage results in mountain goats shifting to timberline habitats in autumn it should reduce their ability to visually detect predators and might take them further from escape terrain. This coincides with the period when grizzly bears may also be feeding on mast crops in the same vegetation zone (Mundy and Flook 1973, Russell et al. 1979, Hamer and Herrero 1983). In addition, we suspect that the number of wolves on the study area may increase in the fall as they follow up to 250 woodland caribou which are migrating out of the mountains to winter in the boreal forest foothills. (Caw Ridge provides the major staging area for woodland caribou in west central Alberta and has also provided winter range for up to 50 woodland caribou in 1990/91). Cougar predation is a recent development and occurs throughout the year. Increased use of treed habitats might be expected to result in increased predator caused mortality of kids; however, there wasn't a detectable difference in the mortality rate of radio-collared kids between 1989 and 1990 despite a much greater use of treed habitat in the latter year (Fig. 3). (The 1989 and 1991 radio-collared samples were insufficient to detect a pattern).

Joslin (1986) monitored the reproductive histories of 11 marked female mountain goats from 1979-86 along Montana's Rocky Mountain

Front. In 4 cases, the earliest dates where the absence of a kid at heel was reported were 28 July, 31 July, 10 October and 13 October. In a fifth instance, the kid was missing sometime between 11 August and 25 February (G. Joslin, unpubl. data). The timing of mortality at Caw Ridge appears to be similar to that reported in Montana. Mortality of the radio-collared sample at Caw Ridge was not significantly different from the unmarked kids (Table 3; $\underline{x}^2 = 0.00$; 1 df; $\underline{P} < 0.0001$).

Table 3. Mortality of radio-collared vs unmarked mountain goat kids at Caw Ridge, Alberta, 1989-91[a]

Kid I.D.	Died	Survived	Total
Radio-collared	9	12	21
Unmarded	8	11	19

[a] Data are not available for unmarked kids in 1988 or 1992.

We are not able to provide a direct estimate of post-natal mortality since kids were not radio-collared immediately following birth. However, results from daily censusing efforts indicated that total kid numbers on 1 June of 1990 and 1991 did not decline any more by the end of the trapping season (mid Oct) than would have been expected based on the radio-collared sample.

We believe that predators and/or predator sign found at kid mortality sites within 72 hours indicate that predation was the cause of death. Ballard et al. (1981) suggests that large carnivores do not find moose calf carcasses until ≥ 30 hours after death. Similarly, Franzmann et al. (1980) found that moose calves were not scavenged by wolves and bears up to 8-10 days following death. Any of the Caw Ridge mortality sites that weren't visited by the observers within 72 hours were considered unconfirmed (Table 1).

In only 1 instance was the separation of the kid from the female thought to have contributed to the mortality of the radio-collared kid (the mortality resulting from a fall). In all 25 other cases, the female and kid were observed together following capture and abandonment was not considered a factor in subsequent mortality (see Livezey 1990).

We are not aware of any significant disease agents or parasites that have limited other mountain goat populations (Cooley 1976, Hebert et al. 1977, Kerr and Holmes 1966, Samuel et al. 1975). Forage availability appears to be exceptional at Caw Ridge and nutritional stress is not considered a limiting factor predisposing kids to predation; particularly during the period when the majority of mortality was detected. With the exception of the mortality caused by the fall, there was insufficient material at any of the mortality sites to provide samples for the determination of body condition.

Eight of the 9 known-age nannies whose kids died were 5 or 6 years of age. Although we have documented reproduction by nannies at Caw

Ridge at 4 years of age, the majority do not conceive until age 5. Therefore, it would appear that the majority of kids which died in their first year were offspring of first or, at most, second time mothers. In addition, none of the 4 members of the 2 sets of twins observed during the course of the study, survived to their first birthday.

The aerial survey data (Fig. 2) supports the rationale of being able to extrapolate kid mortality rates and timing from Caw Ridge to other herds in west-central Alberta. However, the pattern of mortality observed in 1989 and 1990 (73% by 30 Nov) was not detectable in either the radio-collared sample (only 3) or the aerial survey sample for 1991. It would be desirable to obtain aerial survey information in a year with a greater fall mortality of kids as documented in the 2 previous years.

In summary, preliminary evidence indicates that the majority of mountain goat kid mortality on Caw Ridge occurs before November 30 of each year and it is a result of predation by wolves, grizzly bears and cougar. Summer precipitation may influence mountain goat distribution; however, the increased seasonal density of large predators at or near timberline would appear to be the single, most important factor influencing the timing and amount of mortality. On a provincial basis, all of these predators would not influence all mountain goat herds (wolves decrease in density in a north-south gradient while cougars increase). However, kid mortality rates are comparable throughout the Province of Alberta and, in fact, may be similar to many herds in North America (Rideout 1978, Chadwick 1983). Management objectives for grizzly bears and cougars in Alberta are to increase the number of both of these species while only site-specific, temporary reductions in wolves have been targeted in exceptional circumstances (Alberta Fish and Wildlife 1990, 1991, 1992). Consequently, a predator reduction program to enhance mountain goat kid survival will not be implemented in Alberta and further work will be required before mortality rates can be accurately predicted.

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WINTER HABITAT SELECTION OF MOUNTAIN GOATS IN THE NORTH TOLT AND MINE CREEK DRAINAGES OF THE NORTH CENTRAL CASCADES

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Abstract: Aerial surveys were conducted during the winters of 1990, 1991, and 1992 to determine habitat use by mountain goats (Oreamnos americanus) in 2 drainages of the north-central Cascades. Mountain goat locations were evaluated for aspect, topography, stand age and structure, elevation, and snow accumulation levels. Forage production was estimated for clear-cut, partial-cut, and forested stands. Winter diet composition was determined through fecal pellet analysis. Snow accumulation data were used to detect elevational shifts in response to major snow events. Mountain goats in these drainages of the north-central Cascades have habitat selection characteristics that are intermediate between coastal and interior mountain goat ecotypes. The present Washington mountain goat habitat model is discussed, with specific regards to forest management activities.

Considerable research has been conducted on mountain goat habitat selection in coastal (Hebert and Turnbull 1977, Schoen 1978, 1979, Schoen et al. 1981, Fox and Taber 1981, Fox and Raedeke 1982, Schoen and Kirchoff 1982, Fox 1983, Smith 1986, Fox et al. 1989) and interior (Saunders 1955, Hjeljord 1973, Kuck 1977, Hebert and Turnbull 1977, Adams and Bailey 1980) regions. However, the habitat selection by mountain goats in the Cascade Mountains, where climatic characteristics are intermediate between these extremes, is poorly understood. With increasing logging activity occurring in mountain goat winter range, it is essential that we better understand the relationships between timber harvest and mountain goat habitat usage.

The 4 objectives of this study were: (1) to determine mountain goat winter habitat use with emphasis on areas of potential timber harvests; (2) to understand the role of goat diets, forage production, and snow accumulations in winter habitat selection; (3) to assess herd productivity and population status; and (4) to reevaluate the Washington Department of Wildlife's mountain goat habitat classification model.

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STUDY AREAS

North Tolt River Drainage

The North Tolt study site covers 41 km^2 on the Weyerhaeuser Company's Snoqualmie Tree Farm in west-central Washington state ($47^{O}45'$ N, $121^{O}36'$ W), approximately 50 km northeast of Seattle. The North Tolt River drains in a southwesterly direction to the Puget Sound lowlands. The Cascade range in this area varies in elevation from 488 to 1829 m.

The climate in this area of the Cascade mountains has both maritime and continental influences. Average annual precipitation in this area ranges from 120 cm to 300 cm. The average winter temperature (Dec - Mar) for the western Cascade mountains (213 to 1524 m) is 31.9 F, and ranges from 28.9 F (Jan) to 34.7 F (Mar).

This area is dominated by coniferous forest, with western hemlock (Tsuga heterophylla) and Douglas-fir (Pseudotsuga menziesii) at lower elevations, and mountain hemlock (Tsuga mertensiana) and true firs (Abies spp.) at mid to upper elevations. Extensive cliff systems, which are dispersed throughout the basin, are a composite of distinct cliffs and steep, rocky terrain, intermingled within forested and clear-cut habitats. The area is managed for timber production, and has undergone considerable recent harvest activity. Harvesting has progressed upslope from the valley floor and is currently occurring at elevations where mountain goats are found in the winter.

Mine Creek Drainage

The Mine Creek study site encompasses 3 km^2 35 km south of the North Tolt drainage ($47^{O}24'$ N, $121^{O}38'$ W). Mine Creek drains in a northerly direction into the Snoqualmie River. Elevation varies from 366 to 1500 m and vegetational associations, as well as climatic characteristics, are similar to the North Tolt site. This area has been intensively harvested, and the habitat consists primarily of recent clear cuts and residual patches of old-growth timber.

METHODS

Habitat Selection

Systematic helicopter surveys were conducted in the North Tolt drainage during the winter of 1989-90, and in both study areas during the winters of 1990-91 and 1991-92, to determine winter habitat use patterns by mountain goats. Preliminary surveys in the North Tolt drainage were conducted from 18 January to 19 March 1990 for a total of 4 surveys. Techniques and procedures were tested and areas of goat concentration were identified. Information from these surveys was not used in the analysis of habitat relationships.

Aerial surveys were conducted bimonthly from 6 December 1990 to 28 March 1991, for a total of 8 complete surveys (only 1 survey was completed in December and 3 surveys were completed in March). Monthly surveys were conducted in the North Tolt and Mine Creek drainages from 13 January to 12 March 1992 for a total of 3 surveys.

The geographic location of each goat observation was recorded by latitude, longitude and elevation, using a LORAN-C navigational system. Locations were also plotted on aerial photographs and/or topographic maps at the time of observation. A goat location was defined as any number of mountain goats observed in close proximity and appearing to interact. A track location was defined as any number of tracks in the snow observed in areas when no goats were visually observed.

Goat observations were recorded by habitat type and presence or absence of cliffs. Habitat type categories were clear cuts (including regeneration less than 15 years old), partial-cut old growth forests, open old growth forest (less than 50% canopy closure), and closed old-growth forest (greater than 50% canopy closure). Canopy closure was determined by visual estimation. "Forests" in the North Tolt drainage are predominantly remnant old growth stands. Cliffs were found in most classifications, so cliff designation was used only if no other habitat type was noted.

A cover type map for the entire North Fork Tolt basin was compiled using satellite imagery. The reflected electromagnetic wavelength signatures from the satellite image were grouped into cover types as follows: rocks, old forest (conifer >70 yrs old), mature (conifer 35-70 yrs old), young conifer (conifer 15-34 yrs old), old regen (conifer-hardwood 15-34 yrs old), new regen (replanted cuts <15 yrs old), and non-stocked (unplanted cuts). The conifer >70 yrs class represents the remaining uncut old growth of the area. The results of the satellite classifications were verified by cross checking with existing timber stand data. The resulting cover type map was incorporated into a GIS data base that could then determine percent coverage by plant cover types for different elevational bands or geographic areas within the basin.

Satellite imagery data and GIS procedures were used to compare habitat within goat concentration areas and the habitat within the North Tolt basin in general between 762 and 1524 m in elevation. These elevation limits coincide with the range of elevations where goats were observed during aerial surveys. Goat concentrations were defined by a minimum convex polygon from plotted goat locations. Relationships between the percentage of available forest and elevation were determined by separating the North Tolt drainage into 151 m elevational bands from 762 to 1524 m and then analyzing the available habitat within each band.

Forage Production

Percent plant cover was used as a measure of forage production in representative areas of recent clear cut, partial-cut old-growth, and closed forest old-growth stands. In each stand type, 20 5-m^2 circular plots were located 10 paces apart on transects running parallel to the slope from a randomly located starting point. For each plot, percent plant cover was recorded for 3 general vegetation categories (herbaceous plants, shrubs, and trees). Plant cover was recorded only for potential forage 0.15 to 1.83 m above ground. We did not quantify lichen and litterfall availability, which could be another source of forage in forested stands.

Food Habits

Winter mountain goat diet composition was determined through microhistological examination of fecal pellets. Pellets were collected in the early Spring of 1991 and 1992 in winter goat concentration areas. Five pellets from 20 different pellet groups were collected from 3 areas in North Tolt drainage. Pellets were taken from groups of varying depositional ages (fresh to old), to capture the variation in the diet over a greater portion of the winter.

For each sample, pellets were ground, mixed, and sub-sampled to determine diet composition. Analysis was conducted by the Wildlife Habitat Management Laboratory at Washington State University using analytical methodologies described by Davitt and Nelson (1980) and Nelson and Davitt (n.d.). Results are reported as percent diet composition, by forage classes and major plant species, using epidermal fragment cover as the sampling criterion. Correction factors for the differential digestibility of forage plants were not calculated.

Goat Distribution and Snow Patterns

General snow conditions were noted on each aerial survey, and recordings of snow conditions were made for each individual goat observation. Snowfall and snow accumulation records from nearby weather stations were used to analyze relationships between goat elevational patterns, snow patterns, and habitat use.

Herd Composition and Productivity

Goats observed during the helicopter surveys were classified by sex and age on the basis of body size (for kids and yearlings) and horn configuration. Most goats were observed from relatively close quarters (50-100 m) to more confidently classify goats into sex and age categories. In some cases goats were located in cover that did not allow classification, and were recorded as unknowns. No attempt was made to distinguish 2.5 year-old goats from adult goats.

RESULTS

Mountain Goat Observations

A total of 92 goat observations in 54 locations (42 in the North Tolt, 12 in Mine Creek) and 24 track locations (16 in the North Tolt, 8 in Mine Creek) were recorded during surveys conducted in the winter of 1990-91. A total of 38 goat observations in 19 locations (15 in the North Tolt and 4 in the Mine Creek drainage) were recorded during surveys in the winter of 1991-92. Only 1 track location was recorded in 1991-92, and this was in the Mine Creek Drainage. The low number of track locations may have been a result of the low snow levels throughout this winter.

Habitat Selection

Mountain goat habitat selection was closely tied to the presence of cliffs. Cliffs were noted in 77% and 65% of all goat locations in the North Tolt and Mine Creek drainages respectively.

With regards to habitat types selection, mountain goats were most often observed in open habitats (Fig. 1). Over the 2 year period, open forest and clear-cut habitats accounted for 53% and 26% respectively of the goat locations in the North Tolt drainage. In the Mine Creek drainage, goats showed a greater use of clear-cut habitats (67%) and less use of open forest habitats (28%).

Remnant old growth forests in the North Tolt area had relatively open canopies, with 57% of all stands older than 70 years of age classified as open forest (less than 50% canopy closure). Open and closed remnant forest where highly intermingled throughout the North Tolt drainage.

We found no significant differences (Chi-square, $\underline{P}$ = 0.253) between the composition of cover types in the goat concentration areas and in the basin in general (Fig. 2). A comparison of the goat locations with available cover types in the basins indicates a selection against closed forest stands.

Forage Production

Forage production was inversely related to forest canopy cover. Percent plant cover was consistently greatest in clear-cut habitats, lowest in forested habitats, and intermediate in partial-cut habitats (Fig. 3). An exception to this was the increase in tree browse production in partial cut units. The Mine Creek site lacked partial cuts. However, the same pattern of increased forage production in clear-cuts was found (Fig. 3).

Food Habits

Conifers were the dominant forage of mountain goats in the North Tolt drainage, making up an average of 45.1% of the winter diet (Table 1). Shrubs, forbs, and graminoids made up a considerable proportion of the remaining winter diet, with lichens and mosses accounting for only a small

Table 1. Diet composition of mountain goats in the North Tolt drainage based on fecal pellet analysis.

Forage Component	Percent of Composite diet		
	1990-91	1991-92	Average
Conifers	41.9	48.2	45.1
Shrubs	20.9	22.3	21.6
Forbs	11.5	0.8	6.2
Grasses	9.0	3.2	6.1
Sedge/rush	2.6	20.6	11.6
Ferns	8.4	4.3	6.4
Mosses	2.5	0.0	1.3
Lichens	1.3	0.7	1.0
Seed/nut	1.9	0.0	1.0
Insect	0.1	0.0	0.1

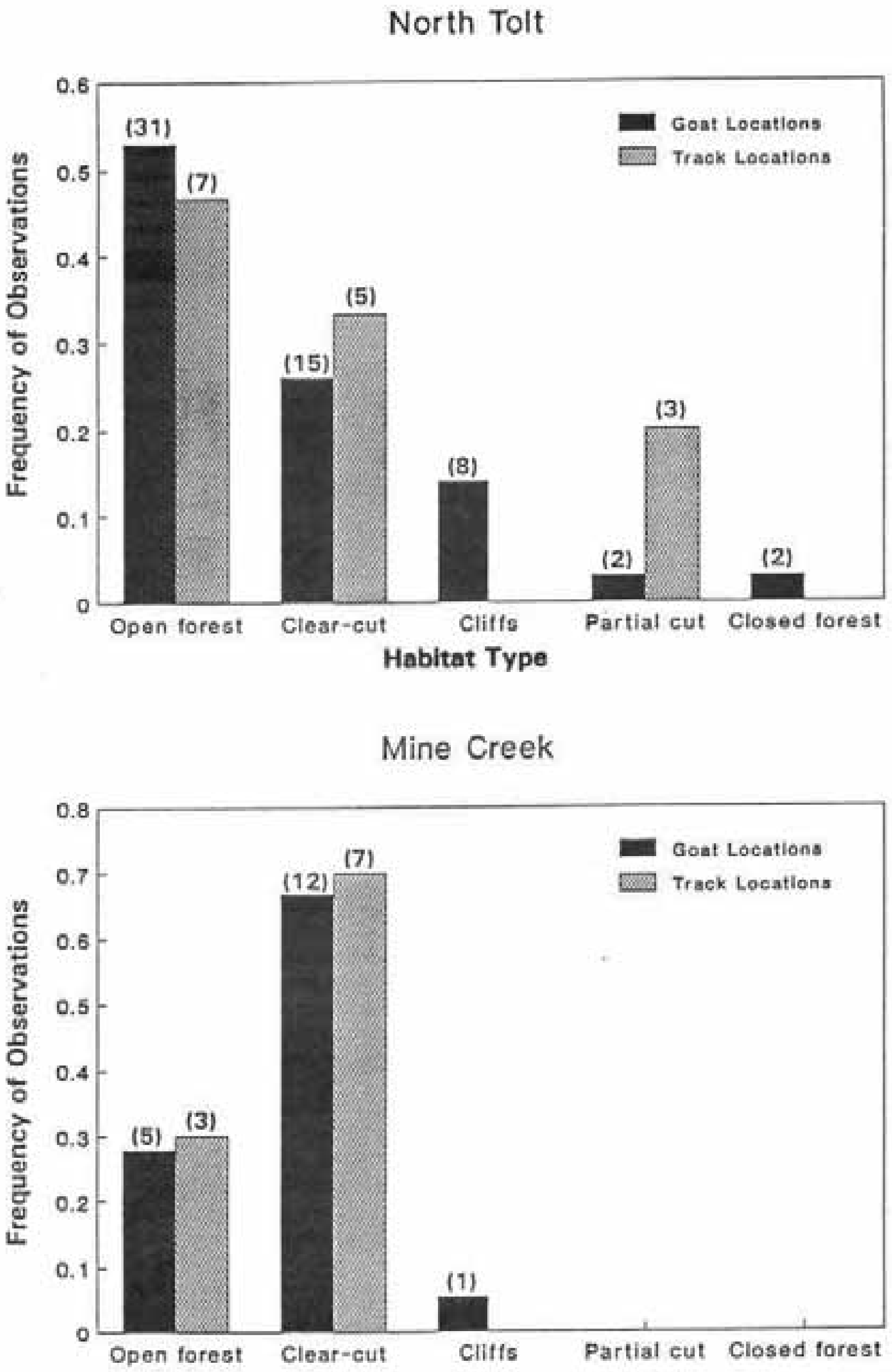


Fig. 1. Frequency of goat and track locations in specific habitat types recorded from aerial surveys conducted in the North Tolt and Mine Creek drainages, winters of 1990-91 and 1991-92. Number in parenthesis equals sample size.

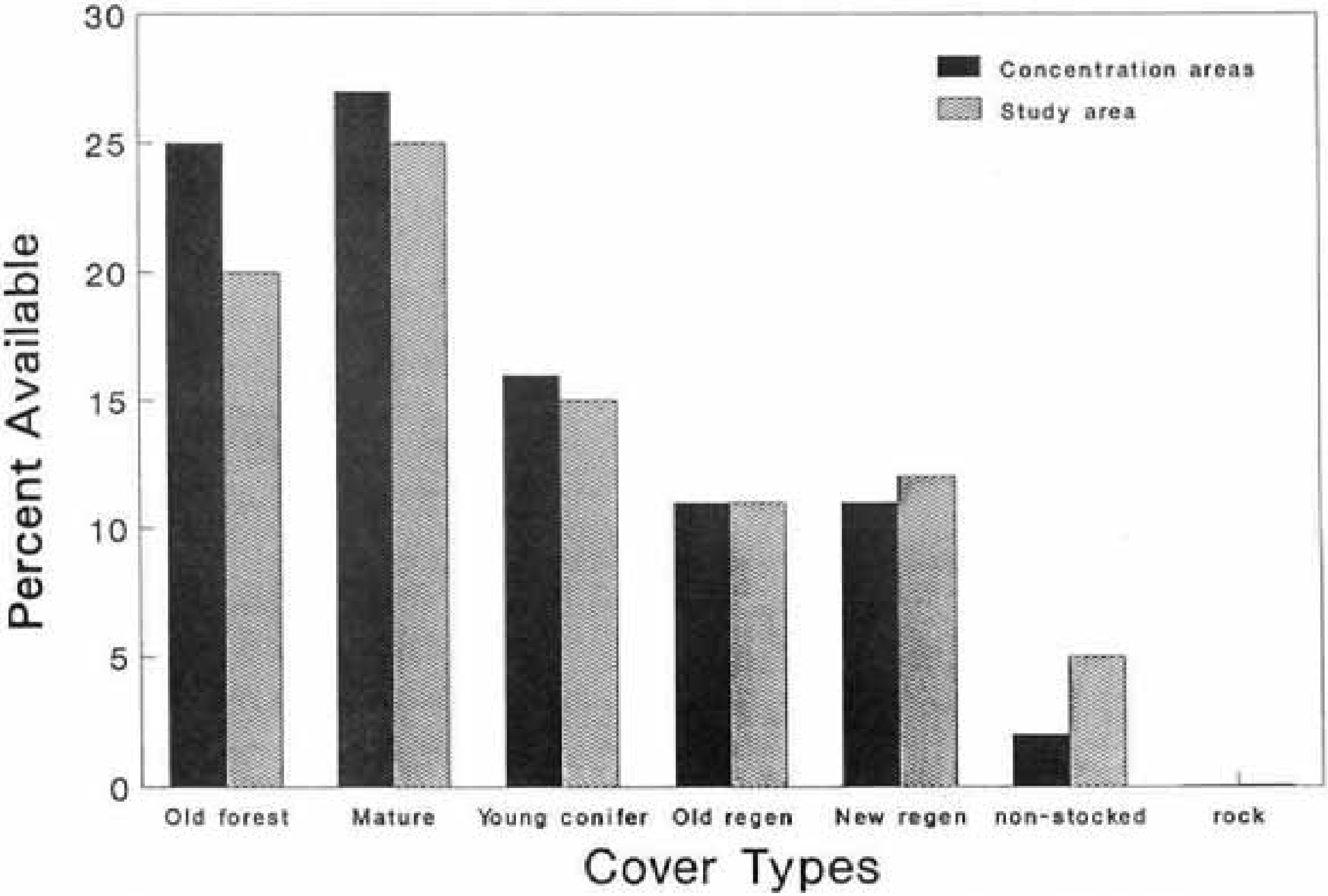


Fig. 2. Habitat available within goat concentration areas and the North Tolt study area between 762 and 1524 m. Categories are old forest (conifer > 70 yrs old), mature (conifer 35-69 yrs old), young conifer (conifer 15-34 yrs old), old regen (conifer-hardwood 15-34 yrs old), new regen (conifer < 15 yrs old), non-stocked (unplanted clear-cut), and rock.

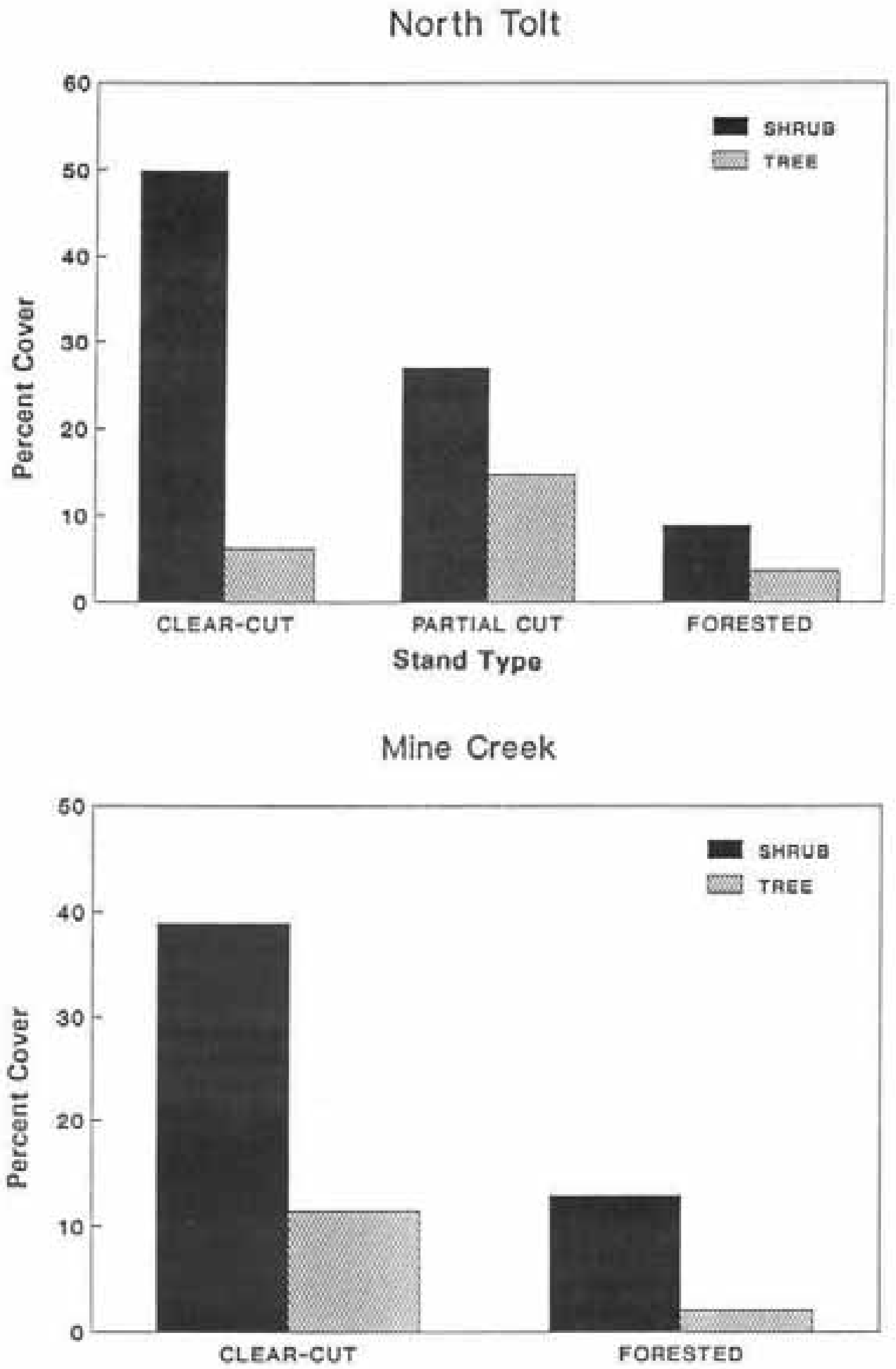


Fig. 3. Percent plant cover in 3 forest stand types in the North Tolt and Mine Creek drainagees, summer and fall of 1991.

percentage. Diet varied little between the 1990-91 and 1991-92 winters, with the exception of a decrease in forbs and an increase in the sedge-rush class.

Goat Distribution and Snow Patterns

Winter snow conditions, expressed as snowfall and snow accumulation levels, were considerably different in the winters of 1990-91 and 1991-92 (Fig. 4). The winter of 1991-92 had considerably less snowfall, and snow accumulations were well below annual averages.

Mountain goats were widely distributed in elevation over both winters (Fig. 5). The average elevation of goat locations for both winters combined was 1126 m in the North Tolt and 1055 m for the Mine Creek drainage. There was little difference in elevational distribution of goats between years (Table 2), even though snow patterns varied greatly. During the 1990-91 season, aerial surveys were conducted immediately following or within a week of 5 major snow events. The goat observations recorded during these flights showed no elevational shift.

Table 2. Average elevation (in meters) of mountain goats observations in the winters of 1990-91 and 1991-92.

	1990-91		1991-92	
Area	Avg. Elev	Std Error	Avg. Elev	Std Error
North Tolt	1116	140	1182	177
Mine Creek	1058	147	1164	144

When the elevation of goat observations in the North Tolt drainage was broken down by month, a pattern did appear (Fig. 6). We noted a significant change in average elevation from February to March during the winter of 1990-91 (*F* = 3.519, *P* = 0.004). However, multiple comparisons indicated that the difference in elevation of goat observations between flights was only significant for the last flight, when weather conditions restricted the survey to the lower elevations. In the winter of 1991-92, no decline in average elevation was noted, however lower snow levels during this winter may have confounded any comparisons between winters.

Herd Composition and Productivity

In 1990-91, 74 goats (with 20 unknowns) were classified in North Tolt, and 18 (with 6 unknowns) in Mine Creek. In 1991-92, 30 goats (with 8 unknowns) were classified in North Tolt and 8 goats (with 3 unknowns) in Mine Creek. Average group size varied from 1.8 for the North Tolt site and 1.5 for the Mine Creek site over the winter of 1990-91, to 2.0 in both the North Tolt and Mine Creek sites in 1991-92.

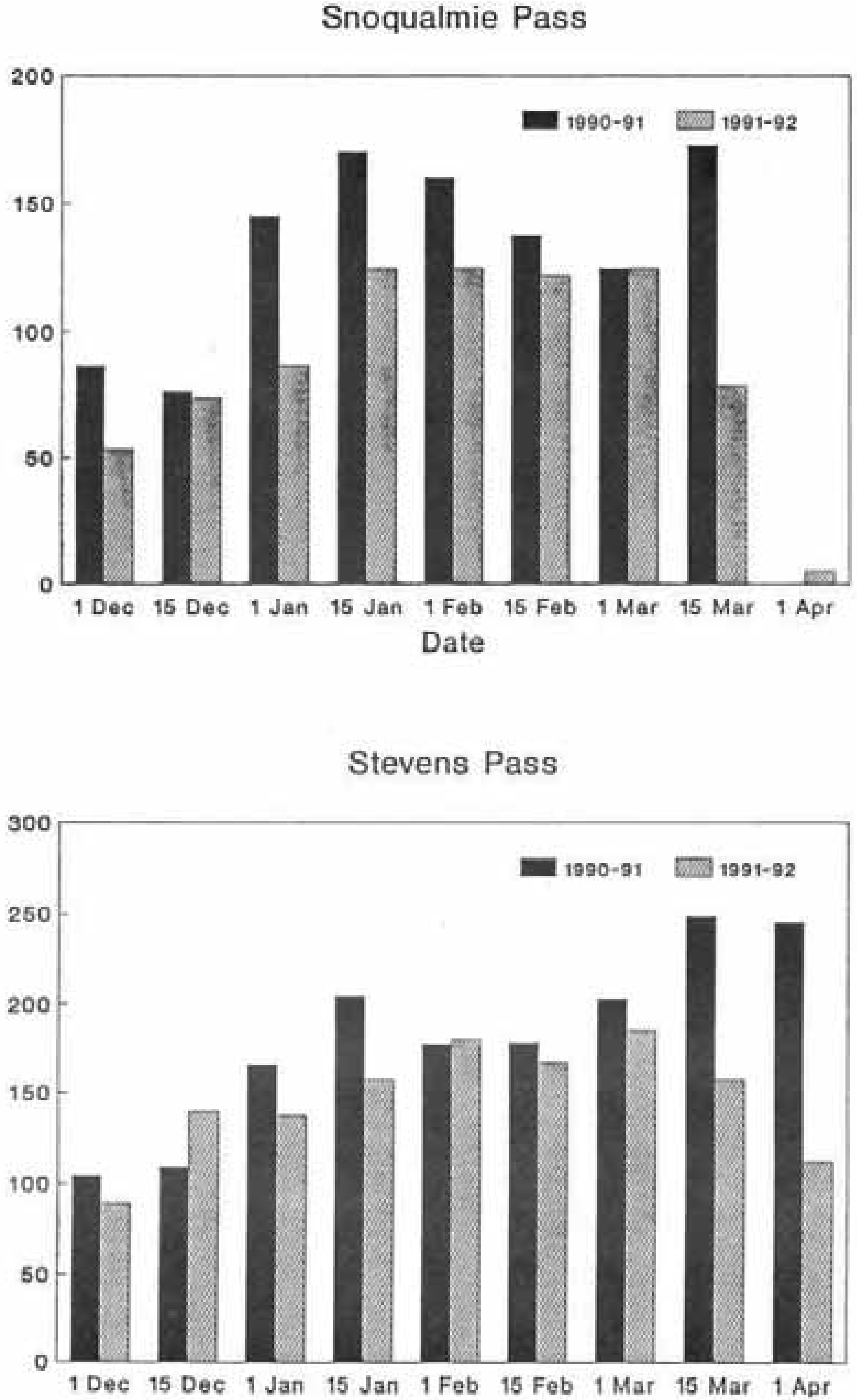
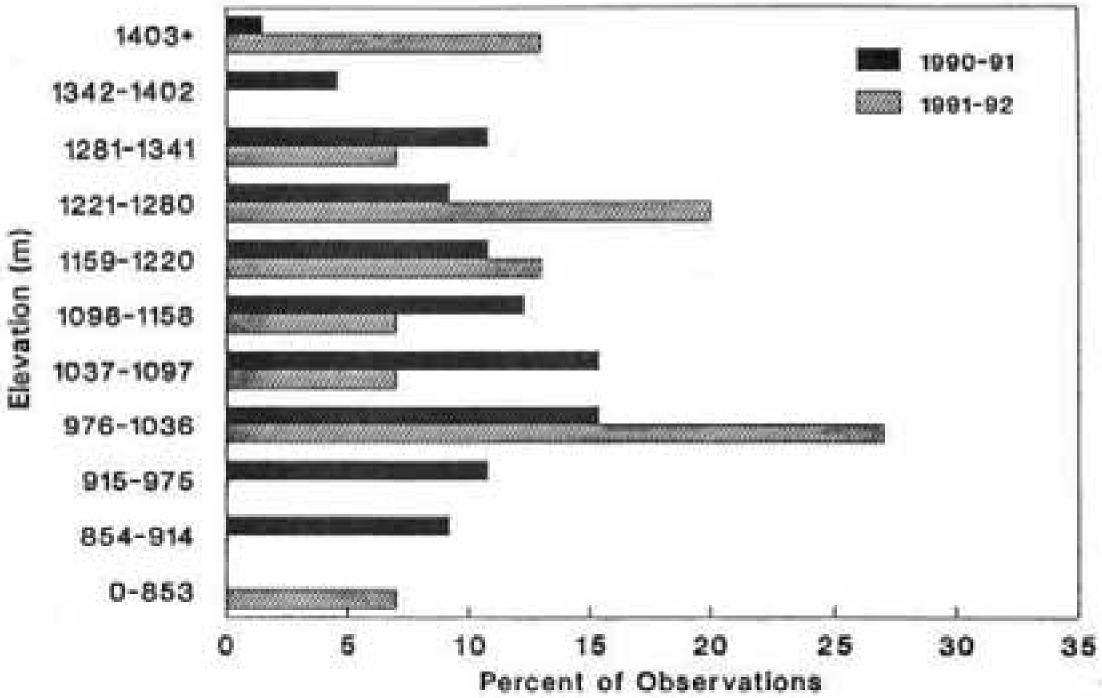
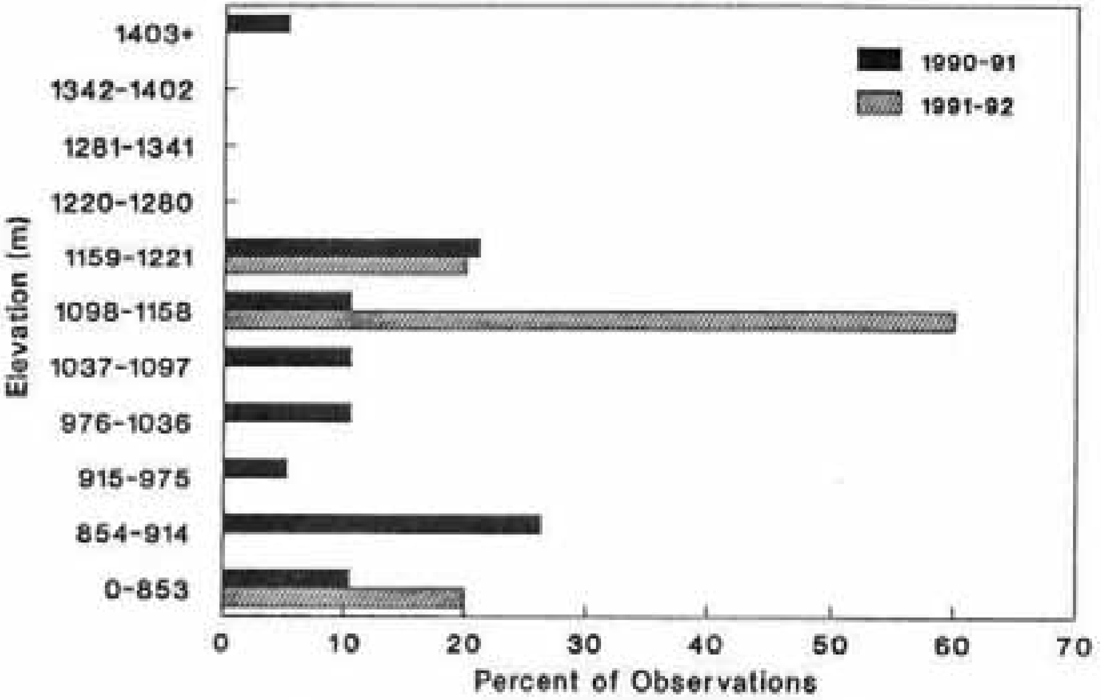


Fig. 4. Snow accumulation levels at Snoqualmie and Stevens Pass, winters of 1990-91 and 1991-92.



North Tolt



Mine Creek

Fig. 5. Elevational distribution of mountain goat observations from aerial surveys in the North Tolt and Mine Creek drainages, winters of 1990-91 and 1991-92.

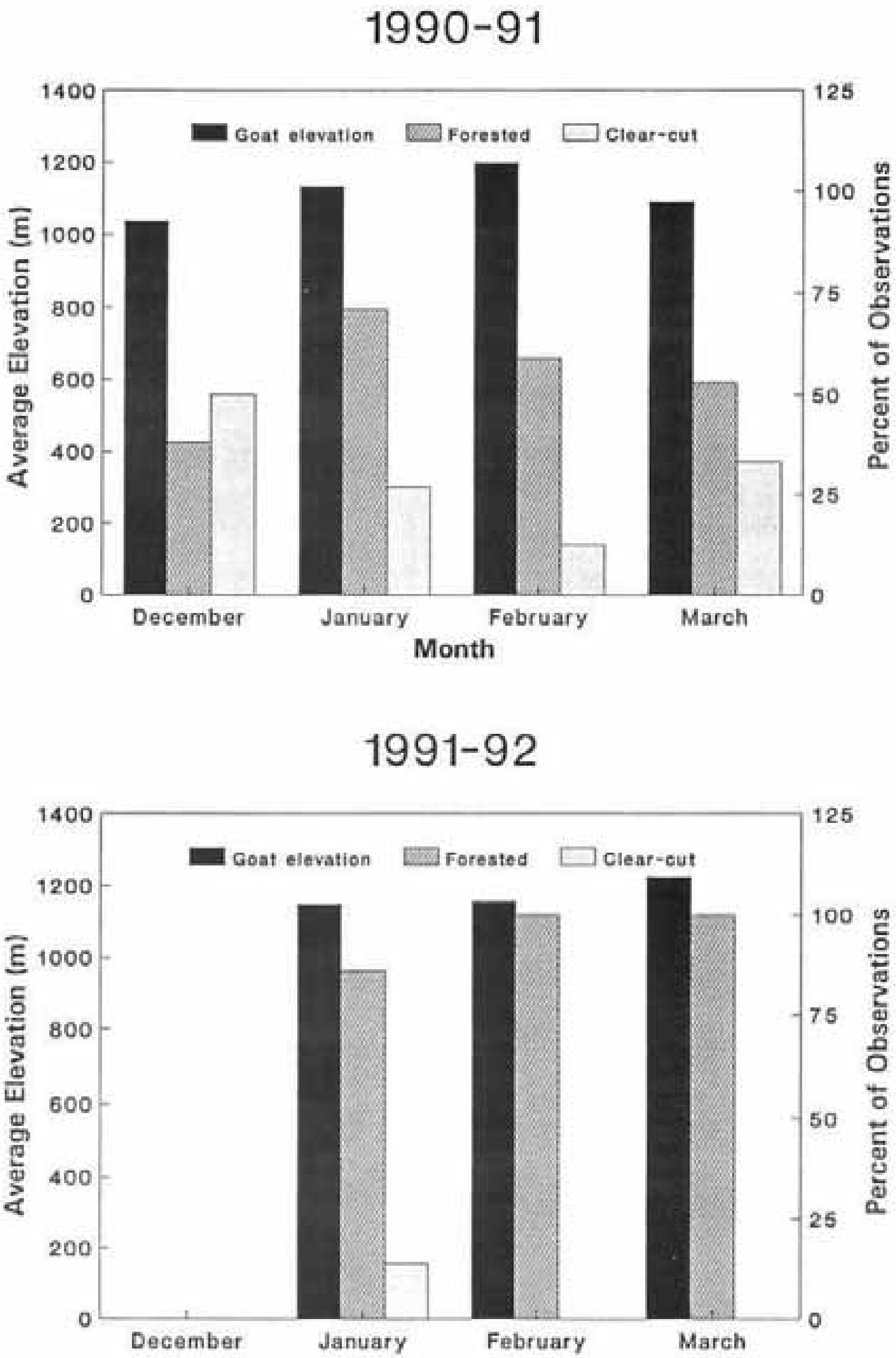


Fig. 6. Average elevation of goat locations and percentage of goat locations in forested and clear-cut habitats in the North Tolt drainage, winters of 1990-91 and 1991-92.

The average kid to nanny ratios for both winters combined were relatively high in the North Tolt (100:100), and slightly lower in Mine Creek (60:100) (Table 3). The proportion of billies in the classifications is relatively low (0.3 billies per nanny), approximating ratios from introduced herds in the Olympic mountains (Moorhead 1976).

In order to minimize the bias associated with our failure to identify some goats in the 1990-91 surveys, we classified unknown goats into sex and age categories based on herd composition records of billy to nanny ratios from Cascade mountain goat herds (Anderson 1940, Wright 1977, and Johnson 1983). We used average ratio of 0.81 billies per nanny to adjusted herd composition data for 1990-91.

Table 3. Herd composition from aerial surveys conducted in the North Tolt and Mine Creek drainages during the winters of 1990-91 and 1991-92. Composition is based on 100 nannies. Sample size (n) does not include unknowns.

		Goats per 100 Nannies			
Area	Year	Kids	Yearlings	Billies	*n*
North Tolt	90-91	83	17	30	54
	90-91[a]	70	15	85	74
	91-92	200	100	150	22
	90-92	100	33	52	76
Mine Creek	90-91	67	33	167	12
	91-92	50	100	0	5
	90-92	60	60	100	17

[a] Herd composition was adjusted to account for the unknowns

No billies were positively identified in the Mine Creek site during the winter of 1991-92. Unknowns accounted for 38% of the observations. Unlike the 1990-91 surveys, 75% of the unknown observations were in groups of 3 or more. This would indicate that a larger proportion of the unknowns were nanny groups and not single billies. The failure to classify these suspected nanny groups may explain the very high kid:nanny ratios and the elevated billy:nanny ratios.

DISCUSSION

Habitat Selection

Mountain goats wintering in this area of the north-central Cascades were closely associated with cliffs and rock outcroppings. The cliff systems were dominated by predominantly open canopied, old-growth forest stands, partial-cut, and clear cuts habitats. Open cliffs without trees were uncommon on goat winter range in this area.

Based on our mountain goat observations, closed forest stands were not heavily utilized by goats throughout the study period in both drainages. However, a comparison of the composition of the cover types in the goat concentration areas showed no selection for or against any cover type. In addition, an observational bias against detection of goats in closed forest must be considered. However, most cliff systems do not have extensive closed forest components. Unless goats are less dependent on cliffs than we have noted, or as has been reported elsewhere (Johnson 1983), closed forest detection bias would not have a significant effect on determining overall habitat selection.

There was a noted increase in goat observations in forest stands in mid-winter, coincident with the upward shift in elevational distribution (Fig. 6). This increase in use of forest stands may be an artifact of landscape patterns in this area. The percentage of available forest increased as elevation increased. Elevations at 762-1067 m were 56% forested while upper elevations at 1220-1372 m were 73% forested. Clear-cuts declined from 33% to 14.5% from the lower to the higher elevation band. This landscape pattern is a result of the historical logging activity, which proceeded sequentially upslope from the valley floor and is currently occurring in mountain goat winter range.

Forage Production

Although clear cuts produced the most forage, snow accumulations and logging slash must be considered when evaluating the availability of this forage to wintering mountain goats. It is energetically costly for goats to move in deep snow, or to maneuver through extensive slash accumulations. Heavy snow accumulations can bury forage. However, unlike southeast Alaska, where heavy snow accumulations restrict goat use to canopied habitats (Fox et al. 1989), the snow accumulations of the western Cascades are sporadic, lighter, and affected by rain on snow dynamics, especially at elevations from 915 to 1220 m. Use of open forest and partial-cut units may have been a response by the goats to increased forage availability and decreased snow accumulations under open canopies.

Food Habits

Analysis of diet composition over the two winters indicated that mountain goats in this area of the north-central Cascades have diet characteristics that are intermediate between coastal and interior ecotypes (Fig. 7). The high proportion of shrubs, forbs, and grasses indicates foraging activity in clear-cut or open forested stands. Lichens and mosses account for only 3.8% of the winter diet, which indicates very limited reliance on a canopied overstory for forage production. However, portions of the conifer component may have come from litterfall.

Coastal diets are characterized by forest related forage components such as conifers, lichens, and mosses, with small percentages of forbs, shrubs, and virtually no graminoids (Fox and Taber 1981, Fox and Smith 1988, Fox et al. 1989). Rocky mountain goat diets are characterized by high percentages of open space forage plants such as graminoids, shrubs, and forbs (Saunders 1955,

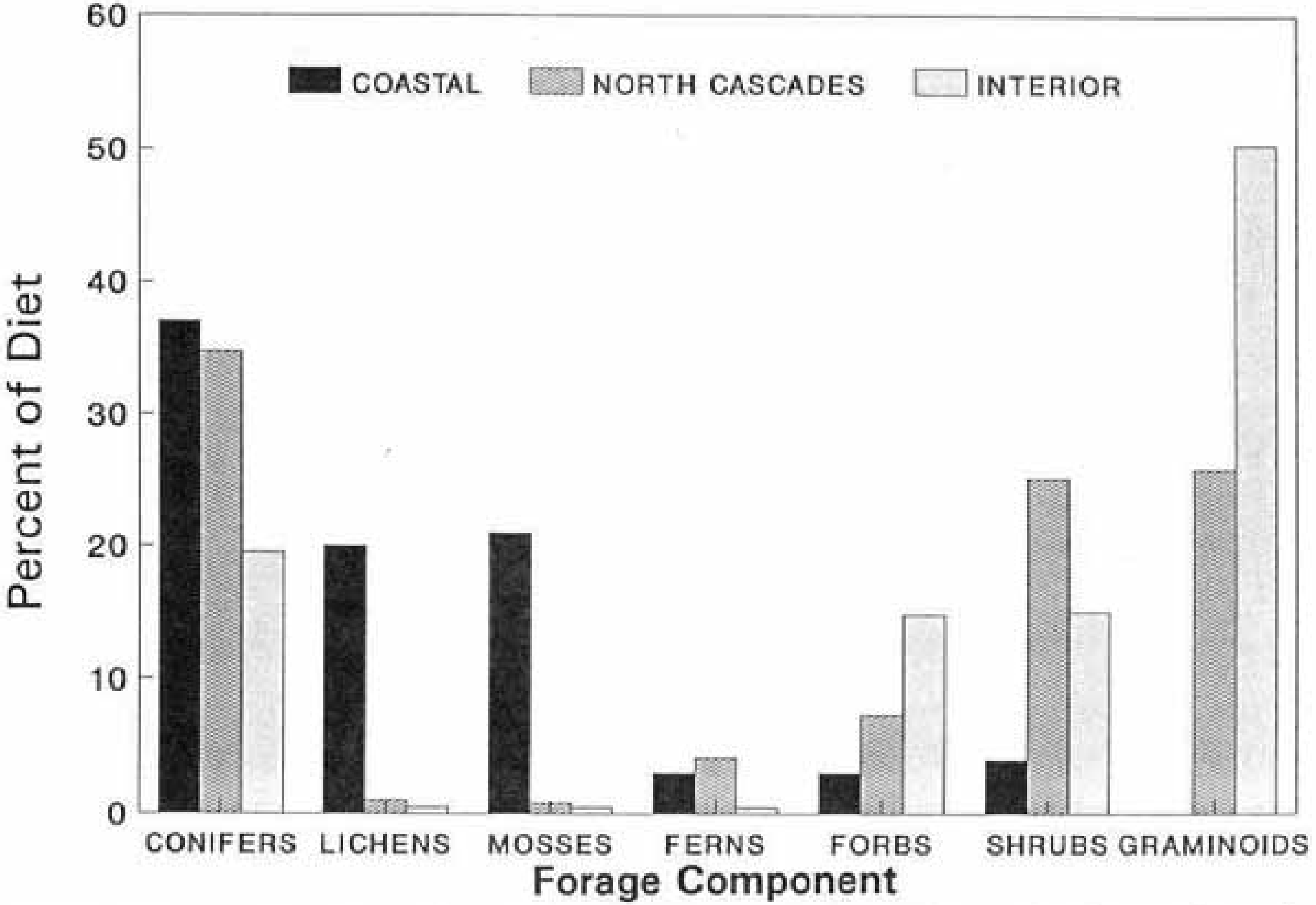


Fig. 7. Diet composition of mountain goats from coastal (Fox and Taber 1981, Fox and Smith 1988, Fox et al. 1989), Cascade (Johnson 1983, authors), and interior (Brandborg 1955, Saunders 1955, Adams and Bailey 1983) regions.

Brandborg 1955, Adams and Bailey 1983). There is a substantial component of conifer use in interior diets, however lichens and mosses are relatively unused.

Other studies have indicated great variance in diet composition over several winters (Johnson 1983). The diet of North Tolt mountain goats did not vary greatly between the winters of 1990-91 and 1991-92.

Goat Distribution and Snow Patterns

Major snow events did not cause noticeable shifts in mountain goat elevational distribution or habitat selection. The elevational distribution of goats was unchanged between two winters with great differences in snow accumulation levels. There was no increase in forest use during periods of higher snowfall or accumulations. In Mine Creek, goats used the forest stands only in 1992 when there was little or no snow on the winter range. Snowfall and goat habitat use patterns did not appear to be related in the North Tolt drainage.

Herd Productivity and Composition

Few studies have reported on the sex and age composition of mountain goats on winter range. The average fall kid:nanny ratio in an introduced and expanding herd on the Olympic peninsula of Washington state was 55:100 over a 6 year period from 1976 to 1981 (Stevens 1983). Brandborg (1955) reported an average ratio of 34:100 in the winter and early spring from 1949 to 1952 in the Salmon River range of Idaho. A kid to nanny ratio of 60:100 was reported for winter range in the Cascades of Washington from 1977 to 1980 (Johnson 1983).

The productivity of the mountain goats wintering in the North Tolt and Mine Creek drainages, interpreted from kid:nanny ratios and possible incidence of twinning, indicates high reproductive success. In the winter of 1992 in the North Tolt drainage, 29% of observed nannies had 2 kids at heel, which may indicate twinning. In addition, possible bias from classification of 2 yr-old females as adults would only increase kid:nanny ratios.

Possible bias due to classification of goats into an "unknown" category must be considered. During the winter of 1990-91, 60% of unknown goat classifications were singles. Due to the solitary nature of billies in winter (Johnson 1983), we feel that a majority of these unknown goats were males. Anderson (1940) found billy:nanny ratios of 77:100, 98:100, and 83:100 for various areas of the Cascades, and Johnson (1983) reported a ratio of 1:1 in the north Cascades. Our observed low proportion of adult males in this winter (0.3 billies per nanny) supports our conclusion that adult males are under-represented in our classifications.

During the winter of 1991-92, more of the unknown observations (75%) were in larger groups that included nannies. The bias from failing to classify all the nannies is reflected in the very high kid:nanny and nanny:billy ratios for this season.

MANAGEMENT IMPLICATIONS

As in other studies, cliffs were the primary factor determining mountain goat habitat selection in this area of the north-central Cascades. Creation or maintenance of a diversity of habitats, centered around commonly used cliff systems, would have beneficial effects on mountain goat productivity and conservation.

Timber harvesting in mountain goat habitat may have both beneficial and detrimental impacts. Primary among the negative effects is increased disturbance and vulnerability of mountain goats caused by road access to winter ranges (Johnson 1983). In our study sites, road access was strictly controlled by the Weyerhaeuser Company. The high productivity found in our study sites may indicate the positive results from increased forage production resulting from timber harvesting, coupled with effective control of road access.

The Washington Department of Wildlife describes mountain goat habitat by map cover types. This habitat mapping focuses on "thermal" and "transitional" cover types. The use of winter thermal cover by mountain goats has not been documented by previous studies. Fox and Taber (1981) indicated that thermoregulatory behavior was not an overriding determinate of goat habitat selection in Alaska goat populations. In the Department of Wildlife's description of mountain goat habitat types, both "winter thermal" cover and "transitional optimal" cover is associated with mature, old growth, and young forests with closed canopies.

In our study areas, non-forested habitats were selected by mountain goats. Although storm events are relatively short lived in the Cascades, goats may use closed forests more intensively during these periods. Future assessment is needed to determine if the increased use of forested habitats in mid-winter is an artifact of the distribution of the forest as a result of past logging activity, or if these upper elevation old growth forests are an important element of winter mountain goat habitat.

Mountain goats in our study areas exhibited habitat use patterns intermediate between coastal and interior ecotypes (Table 4). The study area goats occupied a wide range of elevations from 762 to 1524 m, while coastal goats generally range lower, and interior goats range higher.

Habitat selection by these mountain goats appeared to be a compromise between the dependence on forests by coastal ecotypes and the avoidance of forested areas by interior ecotypes. Unlike coastal ecotypes, the diet composition of Cascade goats indicates no dependence on forage from the forest canopy, although a portion of the conifer component may have come from litterfall under a canopy. The dominance of goat diets in the Cascades by conifers, graminoids, and shrubs indicates foraging in open habitats. However, graminoids do not dominate the diet as they do in interior regions.

Snow characteristics have been reported to play a dominant role in the winter site selection of mountain goats (Fox et al. 1989). Coastal regions receive wet, heavy snows that limit forage availability and goat mobility. Interior regions receive relatively light, dry snows that can be swept off by the wind. The North Cascades snow charac- teristics are influenced by both coastal and interior climes. Snow conditions change over the winter and heavy snowfall events are sporadic and short lived.

Whether mountain goat habitat selection in this area of the Cascades is representative of the Cascades in general is arguable. At this time there is very limited information available on habitat selection, population dynamics, and food habits of mountain goats in the Cascades Mountains. Although the North Tolt and Mine Creek information may not be applicable to undisturbed areas, it may be applicable to areas where intensive forest management has and is occurring. Our study areas are fairly representative of commercial forests in upper elevation river drainages of the north central Cascades. Issues of access and timber harvesting impacts in other areas of the north-central Cascades could be assisted by the information in this study.

Table 4. Summary of selected winter characteristics of coastal, interior and Cascade mountain goat ecotypes

Characteristic	Coastal	Cascades	Interior
Elevation	0-1494[a]	762-1524[b]	1524+[c]
Habitat types	Cliffs in dense forest[d]	Cliffs in clear-cut & open forest[e]	Cliffs,non -forested ridges[f]
Diet composition	1)Conifer 2)Moss 3)Lichen	1)Conifer 2)Graminoid 3)Shrub	1)Graminoid 2)Conifer 3)Shrub
Snow Characteristics	wet, heavy	intermittent, variable	dry, light windblown

[a] Fox et al. 1982, Schoen and Kirchoff 1982, Smith 1986, Fox et al. 1989
[b] Wright 1977, Authors
[c] Hebert and Turnbull 1977, Adams and Bailey 1980
[d] Hebert and Turnbull 1977, Fox and Taber 1981, Fox 1983, Fox et al. 1989
[e] Johnson 1983, Authors
[f] Hjeljord 1973, Hebert and Turnbull 1977, Adams and Bailey 1980

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MOUNTAIN GOAT HABITAT OF WYOMING'S BEARTOOTH PLATEAU: IMPLICATIONS FOR MANAGEMENT

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Abstract: From 1989 to 1991 characteristics of mountain goat (*Oreamnos americanus*) habitat were investigated on the Beartooth Plateau in northwestern Wyoming. Habitat information was gathered by observing non-radioed goats and by relocating 2 radio-collared goats. The potential bias of using observations versus radio telemetry are discussed. Habitat characteristics examined were cover type, slope, aspect, distance to cliff, elevation, and terrain. The data were analyzed using the use/availability technique. Just as in other areas, mountain goats on the Beartooth Plateau used cliffs and steep rocky slopes >75% as their primary habitat. They were usually within 402 m (1/4 mi) of cliffs and used the top half of slopes more than they were available. The goats did not exhibit a preference for aspect or elevation. Parturition areas, distribution, and movements are also discussed. Literature pertaining to mountain goat management and their sensitivity to human access and disturbance is reviewed. Finally, management recommendations are made for the major land uses: timber, minerals development, livestock operations, and recreation.

This study focused on habitat use and distribution of mountain goats on the Beartooth Plateau in northwestern Wyoming. Objectives were to: (1) supplement Hanna's (1989) information on goat distribution over the study area, (2) determine general mountain goat habitat selection patterns, (3) identify parturition (birthing) areas, (4) make a thorough literature review to compare results of this study to others, and (5) make management recommendations regarding livestock distribution, timber harvest, recreation, and petroleum exploration and development in relation to mountain goat habitat.

The study, conducted as part of a Masters thesis (Haynes 1991), was supported by the Shoshone National Forest and by Sigma Xi, the Scientific Research Society. I would like to acknowledge the assistance of the many Wyoming Game and Fish Department personnel who went out of their way to help with this study, as well as Brad Cicci, a local outfitter, and several volunteers. Finally, I would like to thank Dave Henry, of the Shoshone Forest, and Dave Patton, of Northern Arizona University. Both helped me immeasurably on this project.

STUDY AREA AND METHODS

The Beartooth Mountain range is located in southwestern Montana and northwestern Wyoming. The majority of the range is in Montana. Part of the range known as the Beartooth Plateau extends into Wyoming. The study area encompassed the Wyoming Beartooth Plateau south of Highway 212 and the eastern edge of the Line Creek Plateau in Montana (Fig. 1). The

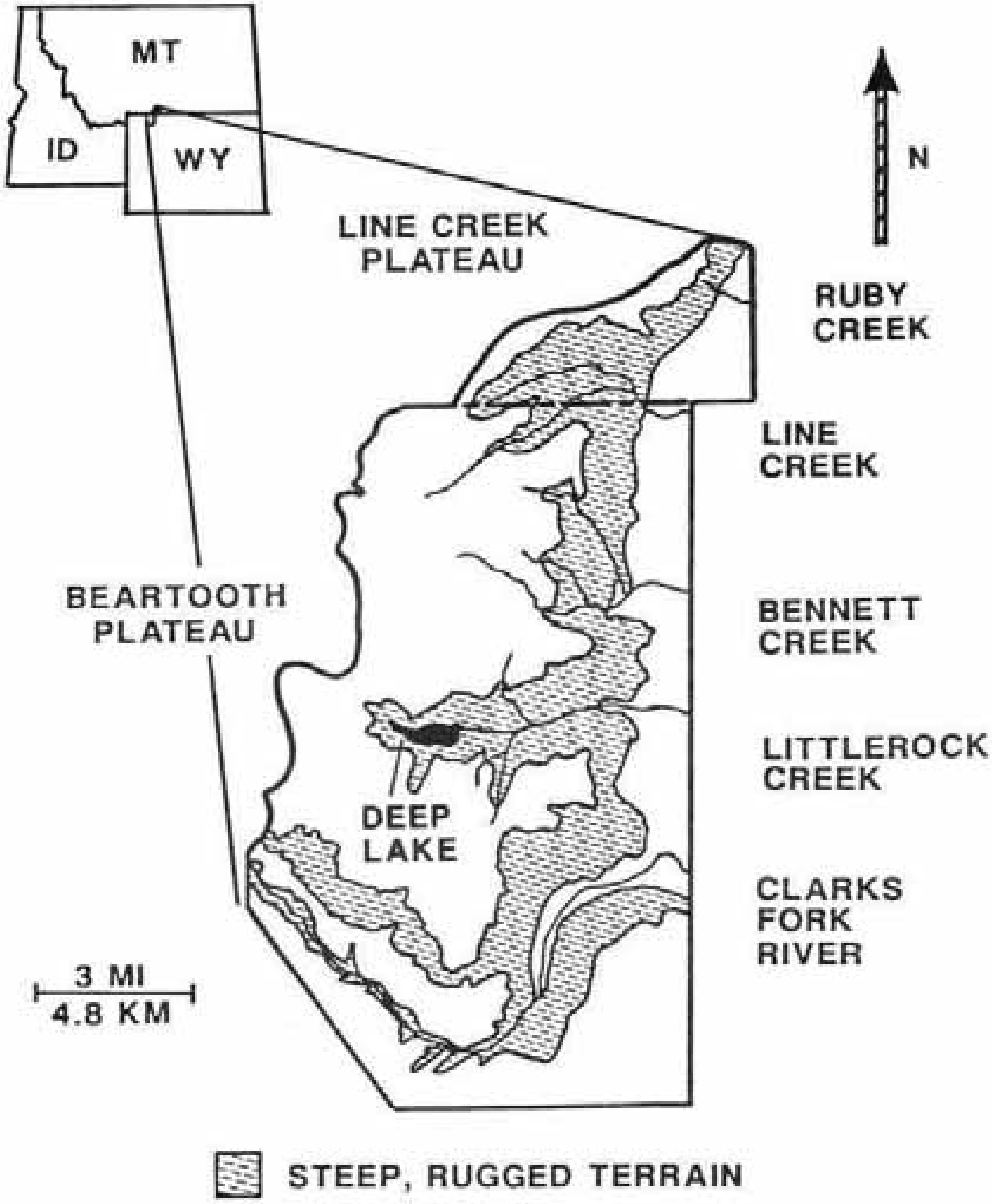

Fig. 1. Study area, Beartooth-Line Creek Plateau, Wyoming and Montana

southern boundary of the study area was the Clarks Fork of the Yellowstone River (hereafter referred to as the Clarks Fork). The western boundary was Thief Creek. There are four major drainages in the study area: the Clarks Fork River, and Little Rock, Bennett, and Line creeks. The study area is primarily used for sheep and cattle grazing and for dispersed recreation: hunting, fishing, backpacking, and horse-pack trips. It is open to lease for petroleum exploration and development.

The climate and vegetation on top of the Beartooth are alpine and are very similar to the Arctic (Billings 1988). Due to the wind, much of the study area, such as the lower part of the Clarks Fork Canyon, is often snow-free in winter. Vegetative composition is diverse ranging from alpine tundra near permanent snow fields on the top of the plateau to prickly pear (Opuntia spp.) and Yucca spp. at the bottom of Clarks Fork Canyon.

Two nannies were captured on Line Creek and radio collared in July 1989. They were stalked on the ground and darted with a Zoolu Arms Simmons rifle using a 3 cc Palmer Dart. In both cases 3.5 mg of Carfentanil were used and the antagonist was 25 mg of Xylazine. Seven more capture attempts were made in July 1989 and March 1990, all unsuccessful. Attracting goats to salt blocks was tried, but apparently these goats were not as attracted to salt as other populations. They were seen licking the salt (Jon Hanna, Wyo. Game and Fish Dep., pers. commun.), but not with any regularity or pattern. This may indicate there is adequate salt in their forage (Fox et al. 1989) or that it takes time for them to become habituated to artificial salt.

Goat number 3 was a 3-year-old and she had 1 kid of the year when she was collared. Number 0 was a 2-year-old and had no kids. They were relocated by air once or twice per month from August 1989 to September 1990 and once every several months thereafter by Western Air Research, Inc., a company specializing in wildlife telemetry flights. The flights were in a Maule M5-235C fixed-wing aircraft equipped with Yagi antennae on each wing strut, an on-board Loran navigation system, and a computer with which the pilot logs telemetry coordinates, date, weather, and other information.

In addition to the radioed goats, other goats were located during the course of the study. From August 1988 to August 1990, 29 trips were made to the study area, each trip varying from 1-5 days, and 329 goats were observed. Each group of goats seen was counted as 1 location, if they were together such that their location could be identified by 1 small dot or circle on a map. These goats were assumed statistically dependent. This was especially true with nannies with kids. Therefore, the 329 goats observed resulted in 120 locations. The same goat or group of goats was never counted twice in 1 day. If there was any doubt, the observation was not used.

There were days when few or no goats were located due to logistical problems and bad weather (fog, rain, hail, and snow, even in mid-summer). Most of the trips to locate goats were made in the spring, summer and fall, with an intensified effort made during spring and early summer 1990 to identify birthing areas. The entire study area was covered as much as possible to determine goat distribution and gather habitat-use data throughout the study area.

Goats were located using 8 X 35 binoculars and a 15-60 power spotting scope. Locations were photographed and plotted on 7.5-minute USGS topographic quadrangle maps. Date, time, weather, activity, goat age-sex classification (if possible), and cover type were recorded. Cover-type classifications were divided into 3 categories: cliff-rock-talus, grass-forb-shrub, and forest-krummholz. Categories were limited to these simple types, because this was the limit of detail that could be determined from aerial photographs for the comparative random points.

Several topographic characteristics were determined later from maps. These were slope, aspect, terrain, elevation, and distance to cliff. From a combination of slope values listed in the literature and from goat observations, cliff was defined as a rocky substrate with a slope $\geq$ 100%. Slope categories were 0-24%, 25-49%, 50-74%, 75-99%, and $\geq$100%. Aspect was divided into 8 categories: north, northeast, east, southeast, etc. Terrain categories were flat/ridgetop, top half of slope, and bottom half of slope/valley. Elevation was divided into 7 categories of 305 m (1000 ft) each between 1220 m (4000 ft) and 3355 m (10,999 ft). Distances to cliff were 0-402 m (0-0.25 mi), 402-805 m (0.25-0.50 mi), and >805 m (>0.50 mi). The "use/availability" technique, including Bonferroni Z analysis, was used to analyze habitat and topographic data (Neu et al. 1974, Marcum and Loftsgaarden 1980, Byers et al. 1984). The $\underline{P}$ level was 0.05 for all tests.

Regarding bias, there were 2 choices: (1) either use the 2 radioed goats and assume they represented the population or (2) use primarily the observed goats and have the potential of under-counting habitats in which they are not easily visible, such as forested areas. The latter route was chosen for 2 reasons: first, assuming that 2 radioed goats represented the population was a very weak assumption, and the small sample size would have further complicated analysis. Second, the radio locations, either from the ground or the air, were not accurate enough to determine detailed habitat-topography use. The Loran locations from the air were as much as 800 m (0.5 mi) from the actual location, if the goat was observed. On the ground, there was too much signal bounce off rocks to identify locations without visual verification. Smith (1976) had the same difficulty. Radio locations were not used unless a visual observation was made, because vegetation, slope, and aspect can change drastically within a few meters (i.e., extreme patchiness of habitat-topography). As a result, the radio locations were almost as vulnerable to observability bias as the general ground locations. In summary, the larger sample size associated with observed goats, even with the possibility of underestimating goats' use of forested habitats, was considered better than using the small sample size and potentially erroneous data from the radio-telemetered goats. If radioed goats were located visually from the ground or air, however, those locations were added to the data pool.

Johnson (1980) concluded that organisms select habitats in a hierarchical manner; what a researcher determines as available can greatly affect the outcome of use/availability analysis. He suggested that the order of selection varies from geographical range down to food items available at a feeding site. He contended that animals select habitat components only after they select a home range within a geographical range, because a home range contains all the habitat components an animal needs to survive and reproduce. Only then can a researcher look at the relative importance of habitat components. Unfortunately, home ranges of unmarked goats could not be determined and sample sizes were insufficient for radioed goats. Therefore, the availability of habitat variables over the entire study area were examined to at least determine general selection patterns on a study area-wide basis. The null hypothesis was:

> H_o: Mountain goats on the Beartooth Plateau utilize habitat characteristics in proportion to their availability (i.e., "no difference" in use) on the study area.

Since goats on the Beartooth live on a plateau incised by canyons rather than the more typical mountain-valley goat habitat, patterns of goat use of habitats in the Beartooth were compared to goat use of habitats in other areas. If patterns of use were similar, the available literature could be used to make management recommendations.

RESULTS AND DISCUSSION

Habitat Analysis

Chi-square.--Elevation was the only characteristic for which the null hypothesis was not rejected (Table 1). The null hypothesis of "no difference" between goat locations and random points was rejected for the other habitat attributes.

Table 1. Summary of Chi-Square analyses between goat locations (used) and random points (available) for 6 attributes of mountain goat habitat in northwestern Wyoming

Attributes	Chi-Square	DF	*P*	Reject H_o
Cover type	64.679	2	0.000	yes
Aspect	20.158	7	0.005	yes
Distance to cliff	83.418	2	0.000	yes
Terrain	35.001	2	0.000	yes
Elevation	10.852	6	0.193	no
Slope	88.357	4	0.000	yes

Use/availability analysis.--Of the 3 cover types, only cliff-rock was used by goats more than its availability (Table 2). Grass-forb-shrub was used less than its availability probably because large expanses of the study area are grass-forb-shrub. Goats use and require this type, both on alpine and grassland ranges, for forage (Fox 1983). However, its use is limited by distance from steep terrain. These results probably reflect the use of the entire study area instead of home ranges for the availability analysis. One cannot necessarily conclude that a component is of little value, just because it is used less than it is available (Johnson 1980).

Table 2. Use and availability of 3 cover types by mountain goats in northwestern Wyoming

Cover type	Proportion available (P_i)	Proportion used for P_i	Confidence interval	Selection[a]
Cliff-rock	0.125	0.625	$0.519 \leq P_1 \leq 0.731$	+
Grass-shrub	0.475	0.233	$0.141 \leq P_2 \leq 0.326$	-
Forest-krummholz	0.400	0.142	$0.065 \leq P_3 \leq 0.218$	-

[a] The + sign means that the proportion used is greater than the proportion available, the - sign means proportion used is less than available, and 0 refers to no difference.

Forest-krummholz was also used less than available, probably due to observation bias (Foster 1982). Goats probably use forest-krummholz as travel corridors between cliffs and for forage in the understory (Brandborg 1955, Chadwick 1973). However, in interior populations, research has shown they do not use forested areas nearly as much as cliff-rock-talus (Chadwick 1973, Thompson 1980).

Three categories of slope were used less than available: 0-24%, 25-49%, and 50-74% (Table 3). Goats used 75-99% and ≥100% slope categories more than available in their habitat. Goats were located on cliffs or within 402 m (0.25 mi) of cliffs much more than they were available (Table 4). Goats used distances to cliff 402-805 m (0.25-0.50 mi) and >805 m (0.50 mi) less than they were available. They used flat-ridge top and bottom half of slopes less than available, and used the top half of slopes more than available (Table 5).

Even though mountain goats on the Beartooth Plateau appeared to use various aspects in a manner other than random (Table 1), they did not show a preference for any one aspect (Table 6). This may be due to the physical nature of the study area. Drainages which form the cliffs flow in several directions. The Clarks Fork of the Yellowstone River, for example, enters the study area flowing southeast, makes a horseshoe bend, and then flows northeast. Little Rock Creek flows almost due east, but it has steep side canyons which flow north. Every canyon has steep cliffs on opposing sides, and goats seemed to utilize almost every available cliff regardless of aspect.

Table 3. Use and availability of 5 slope categories by mountain goats in northwestern Wyoming

Slope	Proportion available (P_i)	Proportion used for P_i	Confidence interval	Selection[a]
0 - 24%	0.467	0.142	$0.060 \leq P_1 \leq 0.224$	-
25 - 49%	0.250	0.092	$0.024 \leq P_2 \leq 0.160$	-
50 - 74%	0.192	0.100	$0.029 \leq P_3 \leq 0.170$	-
75 - 99%	0.058	0.167	$0.079 \leq P_4 \leq 0.254$	+
≥ 100%	0.033	0.500	$0.382 \leq P_5 \leq 0.618$	+

Table 4. Use and availability of 3 distances to cliff by mountain goats in northwestern Wyoming

Distance to cliff m (mi)	Proportion available (P_i)	Proportion used for P_i	Confidence interval	Selection[a]
0 - 402 (0 - 0.25)	0.383	0.933	$0.879 \leq P_1 \leq 0.988$	+
402 - 805 (0.25 - 0.50)	0.225	0.058	$0.007 \leq P_2 \leq 0.110$	-
> 805 (> 0.50)	0.392	0.008	$-0.012 \leq P_3 \leq 0.028$	-

[a] The + sign means that the proportion used is greater than the proportion available, the - sign means proportion used is less than available, and 0 refers to no difference.

The same is true for elevation. Line Creek carves the plateau at 3050 m (10,000 ft); the Clarks Fork carves a lower terrace at 1769 m (5800 ft). Therefore, the lack of a clear pattern suggested by the Chi-square analysis may be due to the propensity for goats to select cliffs wherever they occur. Other studies indicate a variety of aspect and elevational preferences (National Council of the Paper Industry for Air and Stream Improvement 1989), probably due to the unique topographic characteristics of each study area.

In summary, the 4 characteristics which seem to be "preferred" by goats in the use/availability analysis all pertain to steep, rocky slopes and cliffs. The characteristics are slopes ≥75%, top half of slope, cliff-rock-talus cover type, and 0-402 m (0-0.25 mi) distance from cliff. The use of cliffs by mountain goats on the Beartooth Plateau in Wyoming is

Table 5. Use and availability of 3 terrain categories by mountain goats in northwestern Wyoming

Terrain	Proportion available (P_i)	Proportion used for P_i	Confidence interval	Selection[a]
Flat/ridge top	0.308	0.175	$0.092 \leq P_1 \leq 0.258$	-
Top half of slope	0.225	0.600	$0.493 \leq P_2 \leq 0.707$	+
Bottom half of slope & valley	0.467	0.225	$0.134 \leq P_3 \leq 0.316$	-

Table 6. Use and availability of 8 aspect categories by mountain goats in northwestern Wyoming

Aspect	Proportion available (P_i)	Proportion used for P_i	Confidence interval	Selection[a]
North	0.042	0.117	$0.036 \leq P_1 \leq 0.197$	0
Northeast	0.067	0.100	$0.025 \leq P_2 \leq 0.175$	0
East	0.217	0.117	$0.036 \leq P_3 \leq 0.197$	-
Southeast	0.242	0.300	$0.185 \leq P_4 \leq 0.415$	0
South	0.125	0.192	$0.093 \leq P_5 \leq 0.290$	0
Southwest	0.183	0.067	$0.004 \leq P_5 \leq 0.129$	-
West	0.075	0.033	$-0.012 \leq P_6 \leq 0.078$	0
Northwest	0.050	0.075	$0.009 \leq P_7 \leq 0.141$	0

[a] The + sign means that the proportion used is greater than the proportion available, the - sign means proportion used is less than available, and 0 refers to no difference.

very similar to goat habitat selection in almost all other ranges that have been studied (National Council of the Paper Industry for Air and Stream Improvement 1989).

It is safe to conclude that, just as mountain goats in other ranges, goats in the Beartooth require cliffs and steep rocky terrain associated with alpine and subalpine vegetation. This is a general, macro, study-area wide conclusion, and there is still much to be learned about how mountain goats use micro areas within their home ranges on the Beartooth.

Distribution and Movements

Mountain goats were distributed in almost all available cliff habitats in the study area, with the exception of the southeast, south, and southwest slopes of Clarks Fork Canyon. Although the majority of observations were in the spring and summer, drastic changes in areas of goat use were not observed seasonally. Many of the aerial locations of goats were not used in the statistical analysis, especially in winter, due to the potential telemetry error mentioned previously. Therefore, sample sizes were too small to analyze the data seasonally. However, general observations on flights revealed that goats used some areas yearlong. Goats that wintered with radioed goat number 3 spent both winters at high elevations on Line Creek and "Middle" Line Creek, in the same places they used in the summer. Goat number 0 initially made a significant move from her capture site on Line Creek to Deep Lake, which may have been a response to capture stress. She spent the first winter, 1989-1990, in what was commonly thought to be summer range only, on the south side of Deep Lake. Although some goats do seem to shift to higher elevations in the summer, many remain low or travel occasionally to lower elevations, as number 3 did in early August when she moved to the base of Bennett Creek.

Some mountain goats that have been studied on other ranges make changes in areas of use, elevation, and/or aspect on a seasonal basis (Smith 1976, Nichols 1985). Other populations show little change between seasons (Chadwick 1973), and within populations both extremes can be exhibited. Nichols (1985) reported movements as far as 68 km (42 mi) between ranges (associated with billies) in Alaska, and yet had a female that spent 4 years on the same ridge, summer and winter. Nichols' (1985 p.11) comment sums it up: "Herd movements between winter and summer ranges may be generalized, but individual variations occur, and it is not always possible to predict where individual goats can be found or when they might be present in a particular area."

Parturition Areas

Although number 3 spent the majority of time near Line Creek and "Middle" Line Creek, she made movements to other drainages, such as North Bennett Creek and, unexpectedly, to Ruby Creek in Montana, approximately 8 km (5 mi) away. Previously, few sightings had been reported in Ruby Creek. In 1990 she had twin kids there. Nannies often select isolated cliffs away from other goats to have their young (Chadwick 1973). Ruby Creek and similar isolated rocky areas may be parturition areas. Number 3 was also relocated in Ruby Creek once each winter.

Nannies with newborn kids were located the first week in June on Line Creek and "Middle" Line Creek. It is not known whether parturition actually took place there or, like goat number 3, they moved back there shortly after delivering their kids in more isolated, secluded spots. The only parturition area identified with some degree of confidence is Ruby Creek.

Areas where there are concentrations of nannies and kids after parturition are sometimes called nursery areas. Such concentrations were noted on Line Creek, "Middle" Line Creek, the south side of Deep Lake, and the big cliff face on the north side of the mouth of Clarks Fork Canyon. However, since I was not able to survey all the areas in the early summer, there may be other nursery areas not yet identified.

Mountain Goat Management

Human Disturbance, Hunting, and Roads.--Many wildlife biologists believe goats are particularly sensitive to human disturbance (Smith 1976, Geist 1978, Chadwick 1983, Penner 1988). Goats do not survive well in captivity and are not common in zoos (Rideout 1978). In protected, unhunted populations, such as those in national parks, they seem to adapt to humans, especially when humans are a source of salt (Geist 1971). However, even without overt responses to human interaction, animals may have physiological effects, such as increased heart rates (McArthur et al. 1979).

Mountain goats have become increasingly desirable as trophy animals. In mountain goats it has been shown that hunting mortality may be more additive than compensatory, as with other ungulates (Kuck 1977, 1985). That is, goats do not increase productivity to offset mortality. Therefore, they must be hunted and managed very conservatively.

Roads, often built for development activities, increase the level of general human disturbance and are very much the key to illegal and legal hunter harvest levels. Several herds or populations have declined after increased access and disturbance following development (Brandborg 1955; Quaedvileig et al. 1973; Chadwick 1973, 1983; Foster 1977; Pendergast and Bindernagel 1977; Phelps et al. 1983; Joslin 1986). "Motorized access in or near mountain goat habitat is probably the single biggest threat to goat herds throughout North America" (Joslin 1980 p.3).

Land Management Recommendations.--For land management purposes, mountain goat "crucial range" was mapped on the Shoshone National Forest according to the following criteria: slopes >75%, foraging areas and travel corridors in between steep slopes, and foraging areas within 402 m (0.25 mi) of the tops of cliffs. "Crucial range" for mountain goats on the Beartooth is similar to "occupied yearlong mountain goat habitat" defined by Gorman et al. (1984).

Every season and every goat-use site is important on the Beartooth, because mountain goat habitat is limited, goats do not move or disperse to different areas seasonally, and conditions for survival and reproduction are severe. For many ungulates, summer is not a crucial time, because they are widely dispersed and summer range is not limited. The same is not true for goats. Summers are extremely short, and it "is the summer range...which sustains the population from year to year" (Joslin 1980 p.62), i.e., in 3 or 4 months goats must garner enough physiological resources to prepare and sustain them for the long winter, as well as reproduce. They must do so on the same ranges they occupy year around. Obviously, winter is a crucial time for goats, because it often lasts 8 to 9 months and is metabolically demanding. Therefore, the following management recommendations apply to "crucial range" year around:

1. Timber Harvest. Goats use forested areas as travel corridors between cliffs and for forage (Brandborg 1955, Chadwick 1973, Fox et al. 1989). Chadwick (1973) found that goats either used logged areas less frequently or abandoned them completely.

   Recommendations: (1) There should be a buffer zone of 402-805 m (0.25-0.50 mi) adjacent to goat habitat where no logging activity or road building takes place (Smith 1976, Fox et al. 1989). (2) Completely close and obliterate all logging roads within 1609 m (1 mi) of Crucial range. (3) No activity within 1609 m (1 mi) of goat habitat during birthing (1 May to 30 Jun) or breeding (1 Nov to 31 Dec) seasons (Joslin 1980). (4) Slash should be removed from potential travel corridors between goat habitats (National Council of the Paper Industry for Air and Stream Improvement 1989). (5) Leave vegetation and tree cover to screen activities from goat habitat (Joslin 1980). (6) Promote high-intensity, short duration activities rather than long drawn out activities (Joslin 1980). (7) Schedule operations in adjacent drainages so they are not concurrent (Joslin 1980). (8) A wildlife biologist familiar with mountain goat requirements should help lay out timber sales (Gorman et al. 1984).

2. Minerals Development. Oil, gas, and mineral developments are increasingly affecting mountain goat habitats. It is the one management activity that can increase human disturbance manyfold in the rugged back-country goat ranges. Roads and access are a significant impact as mentioned previously. In addition, many minerals activities include the impacts of helicopters, drilling, blasting, noisy machinery, and toxic chemicals. Mountain goat populations, kid production, and nanny survivorship have significantly declined following energy exploration and development (Pendergast and Bindernagel 1977, Joslin 1986).

   Recommendations: (1) Avoid constructing wells, pipelines, or roads within 1609 m (1 mi) of occupied yearlong habitat (Gorman et al. 1984). (2) Helicopter activity should be at least 500 m (1641 ft) above ground (Stockwell 1989) and over forested areas (Joslin 1980).

3. Livestock Operations. Since mountain goats forage on a wide variety of plants, any livestock grazing within 402 m (0.25 mi) of cliffs is potential competition. A lack of success in mountain goat introductions has been linked to prior heavy grazing by sheep (Rideout 1978). Finally, livestock operators often have dogs with them. MacArthur et al. (1979) found, with the exception of direct helicopter passes, that bighorn sheep (very similar to goats ecologically and behaviorally) had the highest heart-rate increases in response to dogs.

   Recommendations: (1) Livestock operators should be discouraged from grazing within 402 m (0.25 mi) of goat habitat. (2) Two crucial "peninsulas" (surrounded by cliffs on 3 sides) should not be grazed by domestic livestock: (a) Cyclone Mountain, between Little Rock Creek and Clarks Fork Canyon; (b) the Line Creek peninsula between Line Creek and "Middle" Line Creek. (3) Place salt for livestock at least 1207 m (0.75 mi) from goat habitat, preferably much further.

(4) Livestock operators should keep dogs at least 402 m (0.25 mi) from goat habitat. (5) Allotments should not be expanded to include more livestock (Joslin 1980). (6) Grazing should take place between 1 July and 15 Oct (Joslin 1980). (7) Joslin (1980) recommended that no sheep grazing be allowed in goat range, although that is not often possible, given land management multiple-use precedences. If the opportunity arises, however, the Beartooth sheep allotments should be converted to cattle or eliminated.

4. Recreation. "Although certain forms of recreational activity are legal and socially accepted, they may become detrimental to mountain goats and other wildlife if they are undertaken by increasing numbers of people or if recreation managers fail to identify conflict areas and thus do not take steps to avoid impacts to the wildlife" (Joslin 1980 p.76). Goats in a hunted population avoided suitable habitat in areas of intense hiker use (Benzon and Rice 1987). The key to managing recreation on or near goat habitat is to keep it primitive and low density.

   Recommendations: (1) All roads and trails on the Beartooth should stay very primitive, especially the Morrison Jeep Trail, including "the switchbacks" and the road in Clarks Fork Canyon. (2) No new permanent roads. (3) All developed recreation sites should be limited to the Beartooth Corridor (Highway), except between the East and West Summits, where it should be disallowed. (4) Snowmobiling should be prohibited within 1609 m (1 mi) of goat habitat and limited to the Beartooth Corridor, if possible.

The areas on the south side of the Clarks Fork River can be managed somewhat differently. This is "suitable low occupancy mountain goat habitat" (Gorman et al. 1984). Prior to initiation of a development activity, surveys should be made by a wildlife biologist to determine if goats are starting to use the area consistently. If so, then the area should be changed to "crucial range". If not, activities such as exploratory drilling, road construction and maintenance, timber harvest, off-road and trail vehicle travel, and any other mechanized activity which extends beyond 1 week in duration should have timing restrictions from 1 Nov to 31 Dec, for breeding, and from 1 May to 30 June, for parturition (Gorman et al. 1984).

SUMMARY

The evolutionary adaptations of mountain goats to their cliff habitat make them more vulnerable to management impacts than most other ungulates. Goats are restricted to cliffs which leaves them with few options when faced with disturbance other than to move to different, probably already occupied, cliffs. Geist (1978) noted that displacement into areas already occupied results in increased social contacts. Goats are aggressive to each other just for the purpose of avoiding aggregations in the face of limited habitat options. The other option they have is to acclimate to human disturbance (Smith 1982). It is clear from the evidence that hunted populations do not acclimate well. "Regardless of the mechanism of interaction, the ultimate result of a close association between humans and mountain goats seems to be the eventual reduction or elimination of goats"

(Joslin 1980 p.27).

Mountain goats seem especially sensitive to cumulative effects of human impacts (Joslin 1986, Penner 1988). Managers cannot have both the impacts of hunting and land development activities on the same herd of goats at the same time (Chadwick 1978). Goats can probably get by, conservatively, with 1 or the other, but not both. Since the Beartooth population is highly valued for hunting (and viewing), other potentially disturbing activities should be carefully managed if hunting is to continue, especially since the Beartooth population is essentially an "island" population. There are no opportunities for goats to immigrate from other areas.

The main key to goat habitat management was best expressed by Kuck (1985 p.6.). "Encourage the public land management agencies to avoid or limit use or access into, or adjacent to, goat habitat".

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POPULATION DYNAMICS AND BEHAVIOR OF MOUNTAIN GOATS USING ELLIOTT RIDGE, GORE RANGE, COLORADO

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Abstract: The Gore Range mountain goat (Oreamnos americanus) population started from 15 animals released between 1968 and 1972. Maximum population was estimated to be 120 in 1979. During the summers of 1990 and 1991, mountain goats were observed on Elliott Ridge, an area they began using in 1981. This alpine ridge lacks escape cover. Goats are attracted to 10 mineral licks on the ridge, regularly traveling at least 24 km, round-trip, to them. A radio collared nanny with kid moved >84 km from 2 July to 5 September 1991, primarily because of repeated visits to the licks. Group size averaged 26 animals for the 2 summers (Maximum = 69). Adult billies were absent from the ridge in late summer. During 1977-1991, the number of kids per 100 older animals ranged from 14 to 48, averaged 29.6, and negatively correlated to May snowfall and maximum snow depth. The population of 128 animals appears to be stable or increasing slightly. Hunter harvest averaged 6.9 adults since 1978 (range 1-12). Because of the large number of mountain goats congregating at licks, aggressive behaviors occurred at high rates. Large separations of >30 m between nanny and kid were often observed and the number of successful suckling attempts was low.

Between 1968 and 1972, 15 mountain goats were introduced into the Gore Range-Eagles' Nest Wilderness Area in Summit County, Colorado. The population was estimated at 120 animals in 1979 (Thompson 1981). Since then, there has been some concern over a possible population decline.

Thompson (1981) evaluated habitat use, food habits, distribution, and population dynamics of the Gore Range mountain goats. At that time, the Gore Range population exhibited one of the highest "r" (rate of growth) values reported for introduced mountain goats (Guenzel 1980).

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The population has been hunted since 1978. Hunting has varying impacts on mountain goat herds. Hebert and Turnbull (1977), Kuck (1977), Chadwick (1983), and K. Smith (1988) reported hunting being additive to mountain goat mortality in native populations. Adams and Bailey (1982), Stevens (1983), and Swenson (1985) observed density-dependent reproduction in introduced populations.

Since Thompson's (1981) study, Gore Range mountain goats began making extensive summer use of the relatively flat Elliott Ridge which has little of the typical steep goat habitat described by Hebert and Turnbull (1977), Kuck (1977), and Chadwick (1983). The area lacks significant escape cover, usually important to mountain goats (Brandborg 1955, Fox 1983, von Elsner-Schack 1986). However, Adams et al. (1982b) noted goats using habitat far from escape terrain in Colorado. The first report of goats using Elliott Ridge was 1981. Presumably they use this Ridge for its mineral licks.

We (1) review the status of Gore Range mountain goats and how different factors such as hunting and snow depth may affect kid production; (2) discuss mountain goat summer use of Elliott Ridge and goat behaviors at lick sites; and (3) document changes in summer range and habitat use by mountain goats in the Gore Range.

STUDY AREA

In north-central Colorado, the Eagles Nest Wilderness Area (542 km^2) encompasses most of the Gore Range. The range's highest peak is Mt. Powell (4125 m). The north end of the range forms an 8.6 km long, alpine ridge called Elliott Ridge. The Ridge descends northward from Meridian Peak (3787 m) to 3400 m at Blue Lake. Blue Lake is a major trailhead. Snow conditions preclude access until late June - early July. Elliott Ridge is relatively flat, averaging 0.6 km wide, with steep flanks east and west. The flanks have only a few rocky cliffs, potential escape cover. The Ridge supports alpine vegetation. Tufted hairgrass (Deschampia caespitosa), sheep fescue (Festuca ovina), sedges (Carex spp.) and clovers (Trifolium spp.) are dominant plants with some dense willow (Salix spp.) in wetter areas. More than 90% of Elliott Ridge is above treeline. Ten mineral licks occur along the ridge-top. The licks may be natural or could be areas where past herders have salted. About 800 domestic sheep annually grazed the Ridge from at least 1953 until 1989, primarily in the early fall.

METHODS

We used weather data from the National Oceanic and Atmospheric Administration station at Climax, CO (3460 m) which is 45 km southeast of the study area. Climax approximates the terrain and elevation at the study site.

Four mountain goats were captured and radio-collared during 1991. Collared goats were relocated from the ground and in monthly fixed-wing flights. Home ranges were calculated from the 3 most distant locations for each goat.

The field season lasted from 6 July to 2 September in 1990 and from 28 June to 5 September in 1991. On 54 days (1990:15; 1991:39), mountain goats were observed for a total of 242 hours. We made all observations at mineral licks using a 12x-36x spotting scope. On some days, randomly chosen nanny-kid diads were observed in 10-minute sessions. Activities and interactions were recorded during 22 separate sessions in July and August, 1991. Group size with each diad was recorded.

Mountain goats on Elliott Ridge were counted and classified, based on B. Smith (1988). Final ratios for each year were determined by averaging the daily counts. On most days, some goats were not classified and the final ratios do not include days when more than 50% of the total were unclassified. Kid:100 older animal (K:100 OA) ratios are considered most reliable when estimating production of goats classified while in large herds (Lentfer 1955; R.D. Schultz, unpubl. rep., Colo. Div. of Wildl., Fort Collins, 1973). The "older animal" classification lumps yearlings, subadults, and adults.

Data from past Colorado Division of Wildlife (CDOW) ground and flight observations were converted to K:100 OA ratios. Flights covered the entire Gore Range in some years (1976-79, 1982, 1985, 1989). During 1982 and 1986, there were coordinated ground counts by volunteers. The "minimum observed population" was the largest number of mountain goats seen on any day. "Minimum calculated population" size was computed by the cohort completion method (Smith 1976, Hayden 1984).

Soil samples were collected by hand from each of the mineral licks. Control samples from each of the different parent materials on Elliott Ridge were also collected. The Soils Laboratory at Colorado State University analysed soil samples from lick and non-lick (control) areas.

Spearmann and Pearson correlations were used to evaluate relationships between variables (Steel and Torrie 1980).

RESULTS

Movements

Mountain goats in the Gore Range often made 24 km round-trips to mineral licks on Elliott Ridge. Animals typically came from near Mt. Powell, travelled out the ridge to a lick, and often, after several hours moved back to the Mt. Powell area, completing a 24 km circuit.

In 1991, 4 radio-collared goats were relocated on 3 days from fixed-wing aircraft (18 Jul, 12 Aug, 27 Sep) and on 3 - 11 days from the ground. The collared adult nanny with kid travelled extensively, moving at least 84 km during 2 July - 5 September, including many trips out Elliott Ridge. On one occasion, she was relocated 16 km south of the Ridge, the furthest that any collared animal moved from the mineral licks. Her summer home range size was estimated at 48 km^2.

The adult collared billy moved a minimum of 32 km during the summer of 1991. Observations of the billy were few because he retired to steep terrain that prohibited location of his radio signal from Elliott Ridge. The billy's home range was estimated from flight and ground data to be 4.9 km^2 between 2 July and 27 September.

The 2 collared yearling billies spent the whole month of August and early September on Elliott Ridge or in the area nearby. Their home ranges were both estimated to be 5.3 km^2 between 2 August and 27 September.

Population Dynamics

Group size and composition.--On Elliott Ridge, group size averaged 26 animals (27.4 in 1990, 24.2 in 1991). Maximum observed group sizes were 53 in 1990 (12 July) and 69 in 1991 (29 July). The maximum number of goats seen on Elliott was 100 on 28 July 1991.

On some days (36% in 1990; 45% in 1991), at least 1 adult billy was observed on Elliott Ridge. However, adult billies were rarely seen on the Ridge after 17 July.

Group size on Elliott Ridge decreased as the summer progressed in both years (1991: Fig. 1; 1990: $r = -0.05$, $P = 0.08$, $n = 13$).

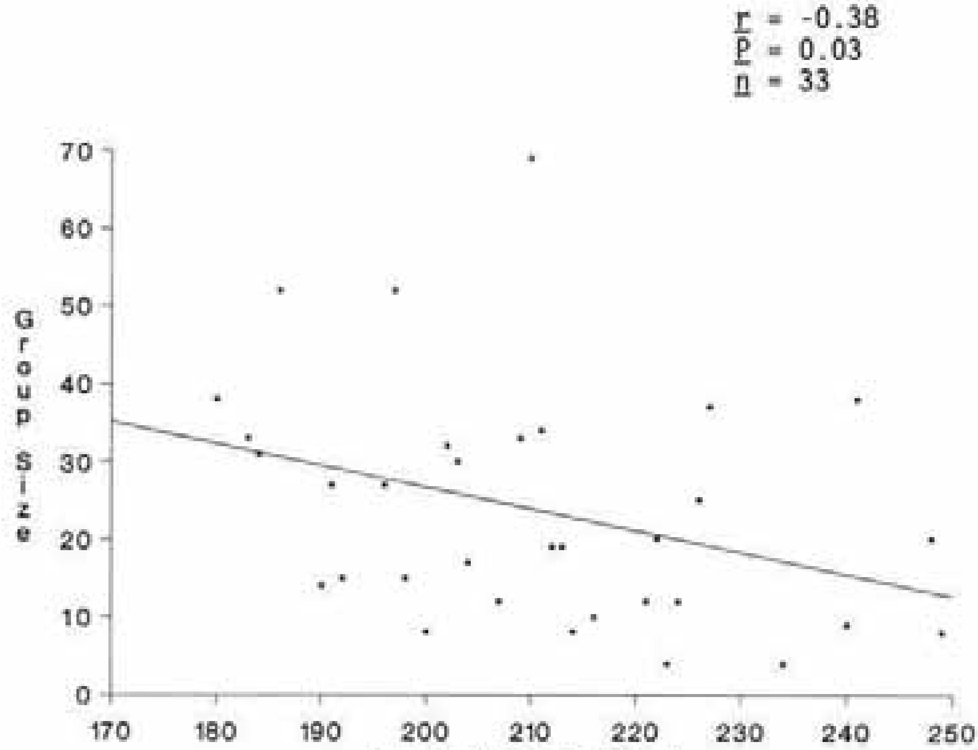

Fig. 1. Group sizes of mountain goats observed on Elliott Ridge, summer 1991. (11 Jul = day 192; 29 Aug = day 241).

Totals and ratios.-- Data from counts made in previous years for the entire Gore Range, including Elliott Ridge, are shown in Table 1. K:100 OA ratios from 1977 to 1991 ranged from 14 to 48 (avg. = 30). Minimum calculated population sizes for 1990 and 1991 were 76 and 128, respectively.

Table 1. Minimum observed population of mountain goats and calculated kid to 100 older animal (K:100 OA) ratios in the Gore Range, including Elliott Ridge, from 1977 to 1991. Minimum population size represents the largest number of mountain goats observed at one time.

Census Date	Minimum population	K:100 OA	Mode
Sep 1976	53	47[a]	Flight
Summer 1977	77	48	Flight
Summer 1978	92	20	Flight
Summer 1979	89	14	Flight
Aug 1981	49	34	Ground[b]
Aug 1982	57	30	Ground
Aug 1982	75	24	Flight
Jun 1984	60	20	Ground[b]
Jun 1984	49	26	Ground[b]
Aug 1985	75	44	Flight
Aug 1986	73	40	Ground
Jul 1987	53	33	Ground[b]
Aug 1989	65	18	Flight
Summer 1990	53	31	Ground[b]
Summer 1991	100	32	Ground[b]

[a] Yearlings were lumped with kids.
[b] Counts made only from Elliott Ridge.

Weather effects on kid production.--Increasing snowfall and snowdepth during winter and early spring (especially in May) had negative effects on K:100 OA ratios (Figs. 2, 3). Cumulative November thru May snowfall showed a close-to-significant negative relationship with K:100 OA ratios (r = -0.55; P = 0.06; n = 12).

Hunting.--During 1978-1991, hunters averaged 66% success in the Gore Range and nannies comprised an average of 52% of the harvest (Table 2). No gender data was available for 1986. Success has not changed significantly since 1978 (r = -0.26; P = 0.93; n = 14). Ages of the harvested mountain goats in 1989-1991 (CDOW) averaged 4.3 years (range 1-8). There was a negative, but not significant (r = -0.33; P = 0.35; n = 10) trend between the number of animals taken in the fall harvest and the K:100 OA ratio of the following spring.

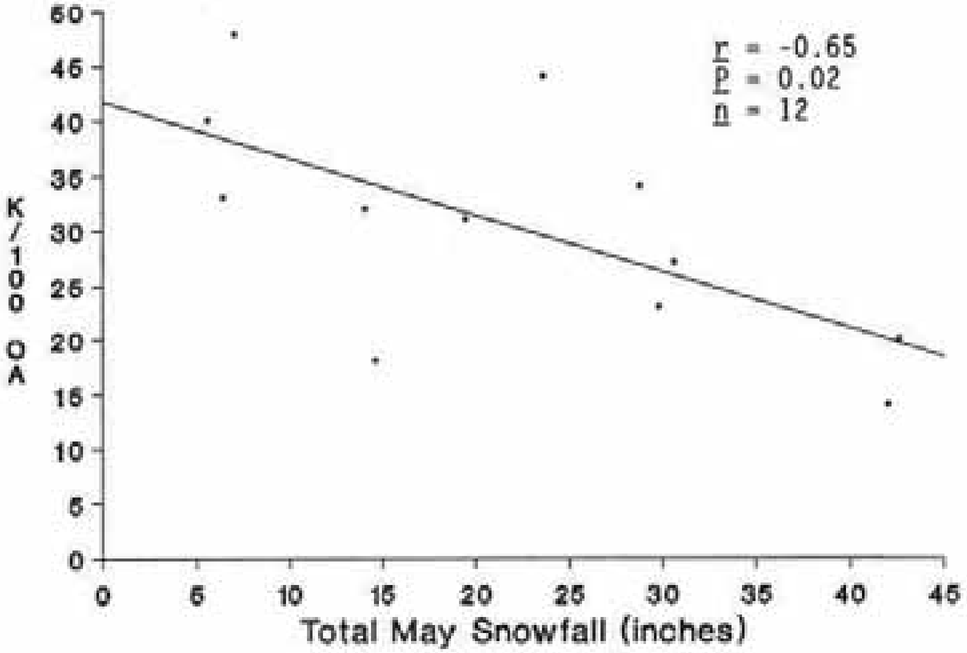

Fig. 2. The number of kids per 100 older animals in the Gore Range mountain goat herd in relation to total snowfall in May of the same year as the birth of the kids.

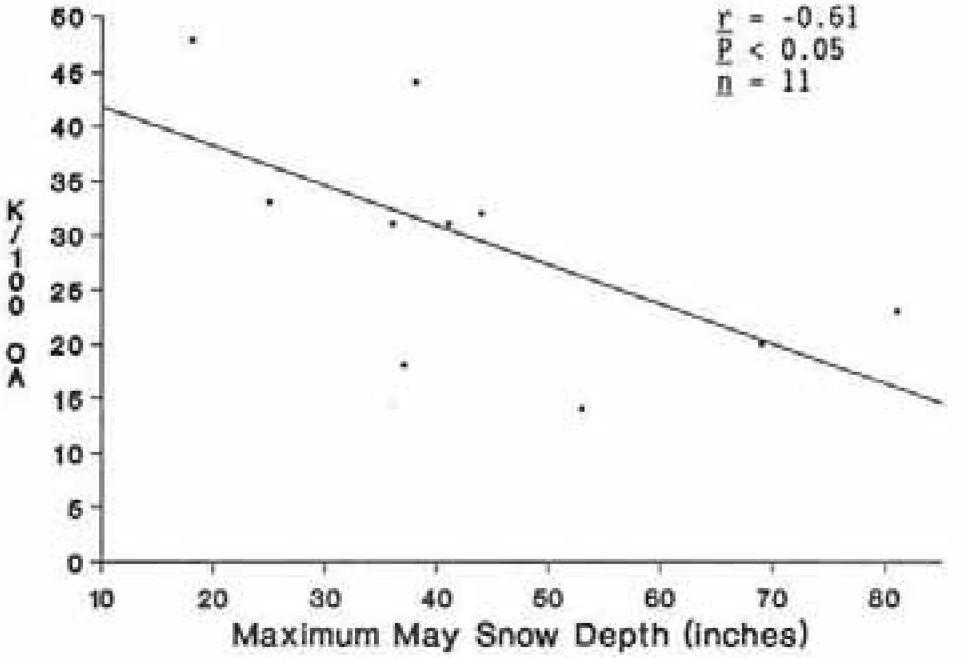

Fig. 3. The number of kids per 100 older animals in the Gore Range mountain goat herd in relation to maximum snow depth in May of the same year as the birth of the kids.

Table 2. Harvest statistics for mountain goats, Gore Range, 1978-1991 (CDOW). B = billy; N = nanny; Res = resident; Non-res = non-resident.

	Licenses Issued		Harvest		Total		% Nannies
Year	Res	Non-res	B	N	harvest	% Success	killed
1978	4	0	2	2	4	100	50
1979	8	0	4	1	5	63	20
1980	8	0	2	5	7	88	71
1981	8	0	3	4	7	88	57
1982	12	0	2	2	4	33	50
1983	10	0	4	3	7	70	43
1984	9	1	1	1	2	20	50
1985	9	1	1	0	1	10	0
1986	9	1	-	-	5	50	-
1987	11	1	5	7	12	100	58
1988	11	1	2	4	6	50	67
1989	11	1	4	5	9	75	56
1990	9	1	4	5	9	90	56
1991	9	1	5	3	8	80	38
Totals:	128	8	39	42	86	Averages: 66	52

For 1990 and 1991, kill locations for 13 of 17 harvested mountain goats are known. One (8%) was killed on Elliott Ridge, 9 (69%) within 2 km of Mt Powell, 2 (15%) near Slate Lake 8 km southeast of Mount Powell, and 1 (8%) near Deluge Lake 18 km southeast of Mount Powell. Ninety-two percent of the 13 known kill sites were in the northern-most portion of the Gore Range, within an area of approximately 14 square miles (36 square kilometers).

Behavior

Aggression.--While observing nannies and kids, 153 aggression events, as described by Geist (1964), DeBock (1970), and Chadwick (1977), were recorded (Table 3).

Aggression involving bodily contact between nannies and kids was recorded at least 20 times. In all but one of these interactions, the aggression was addressed towards the nanny's own kid. Nannies would butt and push their own kids out of the way when it interfered with the nanny's access to a lick.

Aggression occurred more frequently as summer progressed (Fig. 4) and as group size increased (Fig. 5). The rate of aggressive events at licks averaged 41.7 per hour or 0.7 per minute.

Suckling.--Twenty-four suckling attempts and 1 successful suckle were observed in 10 observation periods. This is a rate of 0.24 attempts per minute or 14.4 per hour. The overall success ratio (number of successful

Table 3. Aggressive threat behavior between mountain goats at mineral licks, Gore Range, Colorado, summer 1991. Data were recorded during 10-minute observation periods of nanny-kid diads. Nan = adult nanny; Bil = adult billy; Sa = subadult.

Threat Behavior	Percent of 153 Observed Threat Interactions					Total
	Nan-Bil	Nan-Nan	Nan-Sa	Nan-Kid	Sa-Kid	
Present	0.5	4	0	0	0	4.5
Weapon	0	0.5	0	5	0	5.5
Rush	1	3	7	5	2	18.0
Orientation	1	28	16	18	9	72.0
Totals	2.5	35.5	23	28	11	100.0

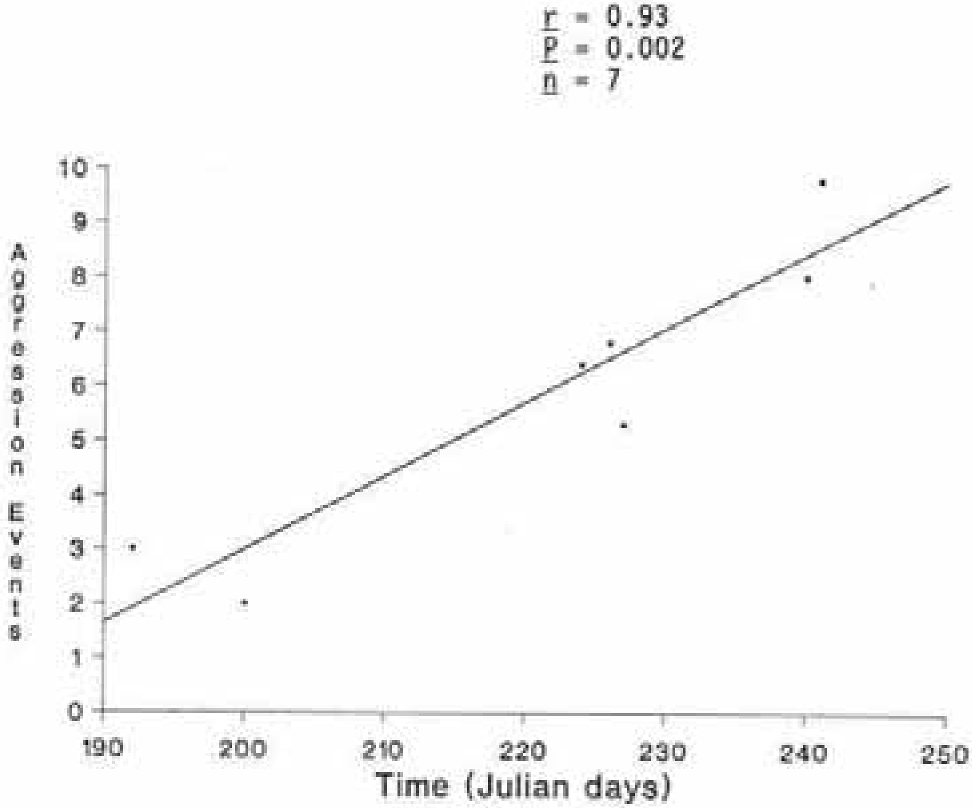

Fig. 4. The average number of aggressive events occurring between mountain goats at mineral licks during 22 10-minute observation periods on 7 days in the Gore Range, summer 1991. (11 Jul = day 192; 29 Aug = day 241).

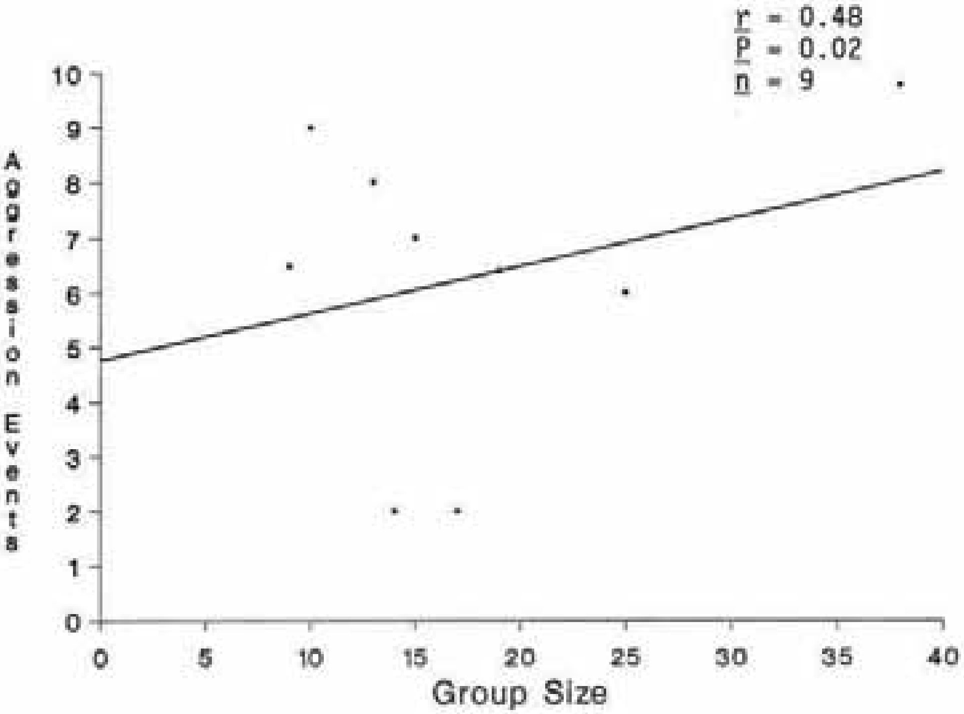

Fig. 5. The average number of aggressive events occurring between mountain goats at mineral licks during 22 10-minute observation periods in the Gore Range, summer 1991 in relation to the number of mountain goats in the group.

attempts/total number of attempts) is 0.04 for the observation periods. The average duration of a suckling event was 9.2 seconds (range 1-35).

Proximity.--Kids were often separated from their nannies. Kids were >30 m from their nannies at least 20 times. Once separated, the kid often vocalized. Upon reunion, the nanny and kid touched noses 10% of the time and the kid attempted to suckle 35% of the time. Maintenance of proximity is the kid's responsibility because a nanny will move off without looking at the kid (DeBock 1970, Hutchins 1984). Chadwick (1973) noted that kids maintained distances of <5 m from their nanny, but playing or exploring youngsters strayed 9-15 m and occasionally up to 30 m.

Mineral Lick Use and Soil Analysis

All age and sex classes used mineral licks. Relative use of the 10 licks differed between 1990 and 1991 (Table 4). All lick sites on Elliott Ridge, except number 10, contained much higher concentrations of Na and K than do the corresponding control areas (Table 5). In the Gore Range, Thompson (1981) noted a significant decline in Na and K concentrations on Dora Mountain. Analysis of soil from a Dora Mountain lick during my study showed lower mineral concentrations than he recorded and lower levels than most samples from Elliott Ridge.

Table 4. The number of days of use of 10 mineral licks on Elliott Ridge, Gore Range, by mountain goats, 1990 and 1991.

Lick	Days of use (%)	
	1990	1991
1	0	12 (34)
2	0	5 (14)
3	2 (15)	14 (40)
4	2 (15)	6 (17)
5	5 (39)	10 (29)
6	4 (31)	10 (29)
7	2 (15)	5 (14)
8	0	6 (17)
9	2 (15)	4 (11)
10	2 (15)	12 (34)

Table 5. Sodium (Na) and potassium (K) concentrations in licks 1-10 on Elliott Ridge, a lick on Dora Mountain, and Elliott Ridge control (non-lick) areas (C1-C4) in the Gore Range in 1991. Parent soil materials on Elliott Ridge: SS = sandstone; LS = limestone; B = basalt; G = gneiss.

Lick No.	Parent Material	Na (ppm)	K (ppm)
1	SS	352	184
2	SS	295	125
3	SS	229	1147
4	LS	561	92
5	SS	298	500
6	SS	324	482
7	LS	158	89
8	B	138	384
9	G	193	181
10	G	24	152
Dora Mt.	G	4	87
C1	SS	28	93
C2	LS	22	67
C3	G	31	129
C4	B	51	67

DISCUSSION

Movements

Mountain goats in the Gore Range move unusual distances in summer. Multiple trips to and from mineral licks on Elliott Ridge comprised much of the mileage (4-24 km round-trip). These represent greater distances and more frequent visits to mineral licks than in previous studies (Hebert and Cowan 1971; F. J. Singer, unpubl. rep., Natl. Park Serv., West Glacier, Mont., 1975; Bansner 1976). Hebert and Cowan (1971) reported goats travelling 3-24 km to mineral licks but only once per summer. In Colorado, Adams et al. (1982a) reported the average greatest linear distance between any 2 observations of a mountain goat was greater in summer (6.4 km) than in winter (1.7 km). In this study, the average greatest linear distance between any 2 observations for the 4 collared mountain goats in summer was 10.8 km.

The home-range sizes of the collared yearling (5.4 km^2) and adult (4.9 km^2) billies are similar to those of previous studies of mountain goats where yearly home range size was generally less than 25 km^2 (Wigal and Coggins 1982), but the collared nanny with kid's summer range (48 km^2) is much larger.

Habitat

Mountain goat behavior, in terms of use of Elliott Ridge, contradicts studies suggesting that goats' primary consideration in choosing habitat is proximity to escape terrain (Fox 1983, von Elsner-Shack 1986). Mountain goats in the Gore Range use open terrain on Elliott Ridge, up to 8 km from escape terrain, despite considerable human recreational use, which does disturb them according to our observations. The reasons for the frequent mineral lick visitation in the Gore Range are unclear. The abundant alpine vegetation on Elliott Ridge may play a role in attracting mountain goats. Together, vegetation and minerals, may serve as strong enough attractants to warrant the expenditure of energy and the risk of moving from escape cover to get to the Ridge. The absence of wolves in the Gore Range may reduce goat dependency on escape cover, although eagles and coyotes do frequent the area.

Population Dynamics

There does not seem to have been a great decline in kid production or change in the number of mountain goats in the Gore Range herd since the late 1970's (Thompson 1981). There were over 100 goats in the Gore Range in summer, 1991, with an estimated minimum calculated population size of 128 animals. This compares favorably with minimum estimated population of 89 and maximum of 116 in summer, 1979 (Thompson 1981).

The K:100 OA ratios for 1990 and 1991 (31:100 and 32:100, repectively) are near the average reported for native herds and herds established at least 16 years (28 kids:100 OA) (Bailey and Johnson 1977). The average ratio for 1977-1991 for the Gore Range herd is 30:100. Two populations in Colorado, 18-31 years after introduction, had higher averages. The Mt. Shavano average was 42:100 (R. F. Smith, unpubl. rep., Colo. Dep. Fish and Wildl., Fort Collins, 1979); at Sheep Mountain, the average was 41:100 (Adams and Bailey 1982).

Thompson (1981) and Adams and Bailey (1982) also reported spring snow depth negatively affecting reproductive success. Other studies have found lower kid production after severe winters (Brandborg 1955, Chadwick 1973, Hjeljord 1973, Rideout 1974, Smith 1984).

Although not significant, the trend that hunting negatively affects kid production is important. Others have reported that mountain goat populations are sensitive to over-harvest (Hebert and Turnbull 1977, Kuck 1977, Adams and Bailey 1982, Chadwick 1983, K. Smith 1988). Conservative harvesting of mountain goat herds seems justified.

Behavior

Behavior of mountain goats on Elliott Ridge is somewhat different from that reported by DeBock (1970), Chadwick (1977), Thompson (1981), and Hutchins (1984). Average group size is high compared to other areas, where it ranges from 2.5 - 6.4 (Brandborg 1955, Lentfer 1955, Smith 1976, Chadwick 1977, Smith and Raedeke 1982). On Elliott Ridge, average group size was 27.4 in 1990 and 24.2 in 1991. Adams et al. (1982b) found that Colorado goats tended to congregate in large groups, with a maximum summer group size of 83. Large group sizes on Elliott Ridge may provide numerical security from human disturbance or natural predators, such as eagles, as the goats travel far from escape terrain.

A behavioral cost of using Elliott Ridge licks in large groups is a high rate of aggression between animals. Pedevillano (1986) reported 3.2 aggression events/hour at a lick. We observed 41.7/hour. This difference is likely due to group size, as aggression increases with group size (this study, Chadwick 1977, Masteller and Bailey 1988). When groups were larger than 20, Singer (1977) and Dane (1977) found high rates of aggression (1 every 20 sec. or 180/hr.). Chadwick (1977) reported a rate of 6.1 agonistic encounters/goat/hour at salt licks with a group size of 8.

Kids on Elliott Ridge had a low overall suckling success ratio in comparison with a herd studied by Hutchins (1984) for several summers. This may be due to the sample size in this study, the higher number of aggressive interactions we observed, or the increase in nanny-kid separations in large groups.

Mineral Licks

Although Hebert and Cowan (1971) noted mountain goats using mineral licks only once in a summer, Singer and Doherty (1985) reported multiple trips to licks. At Elliott Ridge, the radio-collared mountain goats and other recognizable goats made several trips to licks. Most adult billies retired to remote areas after making visits to mineral licks during early summer.

Soil compaction may explain the variance between years in the use of licks on Elliott Ridge. Some licks which received high use in 1990 were so compacted in 1991 that we could barely obtain a soil sample. This might sometimes deter goats from intensely using a lick for 2 consecutive years. Compaction of the Dora Mt. licks, and their low levels of Na and K, may explain the onset of use of the licks on Elliott Ridge.

Management Recommendations

Using the calculated minimum population from this study (128 animals), current harvest levels in the Gore Range are 8% of the herd. However, if the average harvest for the last 14 years (6 animals) is used, harvest levels are at 5%, the recommended rate. Hebert and Turnbull (1977) suggested a harvest of 4% of the total population or 5% of the adults (2 year-olds and older) in native goat populations. Youds et al. (1980) and Smith (1986) stated that a 5% harvest of adults would be sustainable given moderate production (57 kids per 100 females). Bailey and Johnson (1977) and Guenzel (unpubl. rep., Univ. of Wyoming, Laramie, 1978) suggested similar management for goat populations that have been established for more than 15 years. In Colorado, Adams and Bailey (1982) suggested a harvest of 7% of the late summer population for the Sawatch Range herd.

As Thompson (1981) suggested, the survival of the previous year's kid crop and a reliable estimate of kid production should be 2 important management considerations. For the Gore Range population, present and historical census data shows an average K:100 OA ratio of 30:100 suggesting that present kid production is moderate and warrants a 5% harvest. Harvest levels should not be increased from current levels.

It is also important that, based on 1990 and 1991, most of the mountain goats in the Gore Range are being harvested in a 36 square kilometer area of the northern portion of the range, near easy access via Elliott Ridge. If numbers of permits remain at present levels it may be wise to allocate licenses on a drainage basis. Others have found that increased access into mountain goat range leads to over-harvesting in accessible areas (Chadwick 1973, Foster 1977, Hoefs et al. 1977, Johnson 1977, MacGregor 1977).

Yearly inventories are suggested to monitor the growth and sex-age composition of the Gore Range mountain goats. These censuses would be most effective if aerial surveys are combined with ground observations. As Risenhoover and Bailey (1982) suggested, the survey method must be standardized so biases are consistent and accurate trends in population changes may be determined.

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SOCIAL DOMINANCE AND ITS INFLUENCE ON THE FORAGING EFFICIENCY OF THE MOUNTAIN GOAT: A PRELIMINARY REPORT.

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Abstract: The social behavior of mountain goats (Oreamnos americanus) was studied as part of a study of reproductive success and population dynamics in an unhunted population in west-central Alberta, Canada. Social dominance relationships were examined, in a nursery herd, to assess the possibility that dominance influenced the foraging efficiency of adult nannies. Foraging efficiency was measured as the proportion of time spent feeding during the time the goats were active. It was hypothesized that dominant animals would forage more efficiently than subordinate goats. There was no significant difference between these 2 classes. Dominance hierarchies have been suggested for this species, but detailed quantitative measures are lacking. This study reveals a non-linear dominance hierarchy that is weakly age-related.

During the evolution and radiation of ungulates in the northern hemisphere, animals immigrated into unoccupied suitable habitats following glacial retreat (Geist 1971). This led solitary forest-dwelling animals to venture into open areas where the security of vegetative cover was absent. Mammals evolved social systems to benefit from group living (Wilson 1975), and since living in an open environment involved an increased predation pressure, ungulates benefited from groups in the form of anti-predator behaviors (Hamilton 1971).

There are disadvantages as well as benefits in sociality. Animals living in groups must compete with other group members for resources such as food or mates and individual space sometimes must be defended. Defense of resources produces intraspecific aggression and mechanisms to cope with competition. One such mechanism is social dominance.

Social dominance is defined as the relationship between 2 individuals, where one (the subordinate) yields to the second (the dominant) during aggressive interactions (Kaufmann 1983). Rowell (1974) suggested that when a group establishes a social dominance hierarchy, the outcome of subsequent aggressive interactions are predictable according to previous encounters. Dominance may serve 2 major functions. First, it may allow priority access to a limited resource which enhances the fitness of the individual (Kaufmann 1983). Second, it may reduce the level of aggression in a group (Rowell 1974, Bernstein 1981).

The benefits of dominance are the same for males and females, but the currency may be different. For most polygynous sexually dimorphic mammals, a dominant status is necessary for males in order to obtain access to estrous females during reproduction (Emlen and Oring 1977).

For females, on the other hand, dominance usually ensures priority access to a food resource. If dominance status does guarantee priority access to food, this advantage could translate into better growth and therefore may influence reproductive success. Such priority, and its benefits, have been described for other female ungulates such as red deer (Cervus elaphus, Clutton-Brock et al. 1982), woodland caribou (Rangifer tarandus, Barrette and Vandal 1986) and bison (Bison bison, Rutberg 1986).

The influence of dominance on feeding behavior may be evaluated by measuring foraging efficiency, defined as the amount of time that an individual spends foraging during its active time (Owen-Smith 1979). Individuals should benefit from increased foraging efficiency.

The mountain goat social system is based on dominance-subordination relationships. This system should favor a more predictable social environment, thus reducing the risk of injury and also lowering energy expenditures through diminished fighting. Reduction in aggression would be very profitable since these animals possess weapons than can inflict severe wounds to conspecifics (Geist 1964). If this social system does in fact provide a predictable environment, rates of aggression should be low. On the other hand, one may expect the rates of aggression to increase with group size since the distance between individuals may be reduced.

The objectives of this study were to characterize social dominance relationships between adult nannies, to determine whether social dominance affects the foraging efficiency of mountain goats, and to test if rates of aggression are a function of group size. Mountain goats are a good model for examining the possible advantages of social dominance because goats have a social system based on aggression, and they have a higher level of aggression compared to other gregarious female ungulates (Fig.1).

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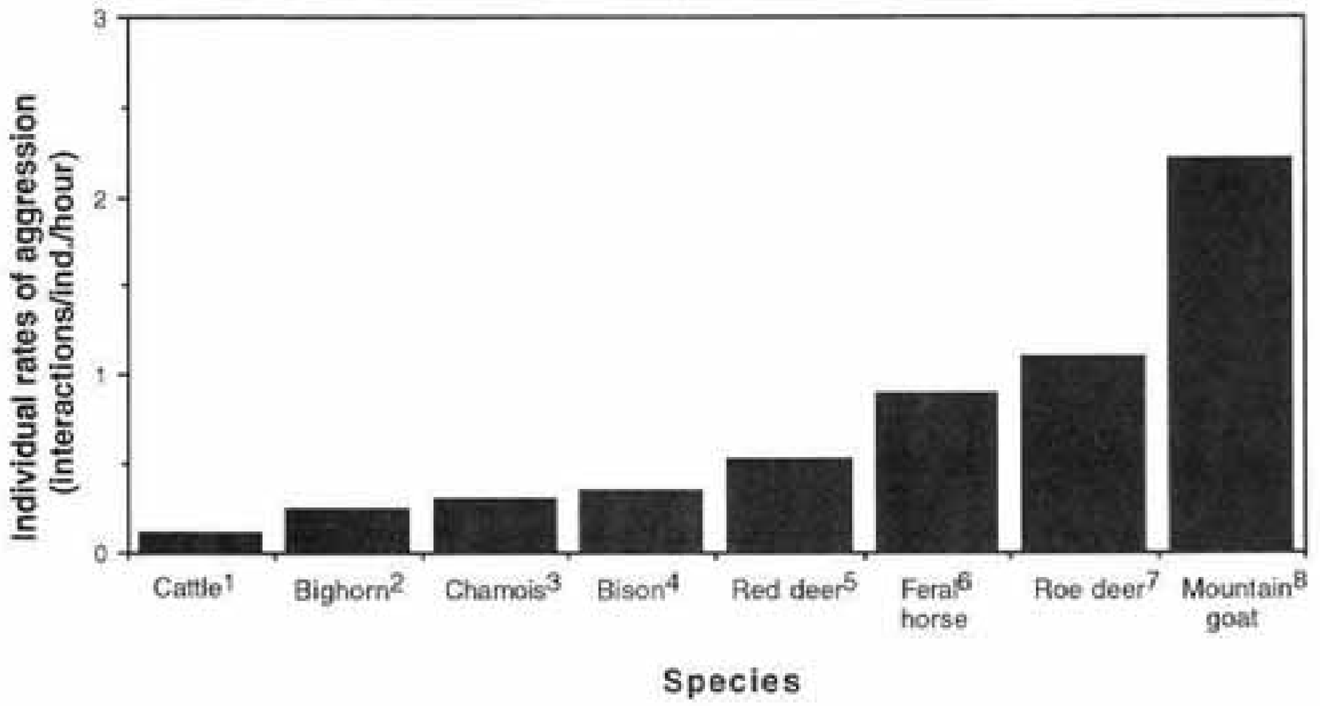

Fig. 1. Rates of aggression among female ungulates (1: Clutton-Brock et al. 1976, 2: Hass 1986, 3: Locati and Lovari 1990, 4: Rutberg 1986, 5: Thouless 1990, 6: Rutberg and Greenberg 1990, 7: Espmark 1974, 8: Caw Ridge, this study).

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METHODS

Study Area and Population

This study was conducted at Caw Ridge (54°N, 119°W), located approximately 30 km northwest of Grande Cache, Alberta. This site harbors the largest native population of mountain goats, in Alberta, outside of the National Parks. The area used by mountain goats (approximately 21 km^2) is a typical alpine habitat, characterized by forbs and grasses, between 1750-2150 m in elevation. The study area is a front range of the eastern slopes of the Rocky Mountains, and is separated from the main mountain range by 10-30 km of coniferous forest. Goat hunting on this site has been prohibited since 1969.

Goats were trapped with 2 remote-controlled Stevenson's box traps and 4 self-releasing clover traps. All traps were baited with salt blocks. Goats were drugged via intramuscular (IM) injection of xylazine and, once the handling of the animals was completed, the effects of the drug were reversed by IM injection of idazoxan (Jorgenson et al. 1990). Kids and most yearlings were not drugged. Captured goats were measured and weighed, then fitted with either plastic ear tags or canvas collars to permit easy identification. As of November 1991, about 62% of the 82 goats were individually marked and recognizable, including 23 adults fitted with radiocollars.

Goats were located visually and/or by radio telemetry on a daily basis between May and September 1991. Once located, the animals in the group were classified. Animals were separated into age-sex classes as follows: kids (male, female), yearlings (male, female), 2 year-olds (male, female) and adults (male, female). Nannies were also classified as with or without a kid.

Data Collection

Behaviors were observed with a 15x-45x spotting scope or 15X60 binoculars. Observations were centered on the nursery herd. Focal animal sampling (Altmann 1974) was used to measure time budgets and aggressive interactions. During aggressive interactions the following information was noted: initiator, receiver, winner, and approximate distance between the 2 goats at the start of the aggression. All aggressive interactions seen were noted using all-occurence sampling (Altmann 1974). Aggressive interactions were used to establish dominance relationships among adult nannies. Foraging efficiency was defined as the proportion of time that a goat spent feeding during its active time (Owen-Smith 1979). The remaining behaviors included in the time budget were alert, bedded, social and other.

Additionally, in order to evaluate the assumption that mountain goats defend a personal space (Chadwick 1977), I designated an arbitrary area of approximately 4 m around each focal animal. Whenever another goat entered this area it was noted as a possibility of aggression and the outcome of this meeting was noted. Ensuing aggression was noted, and lack of aggression was noted as no defense.

Dominance Relationships

Dominance ranks were determined by assembling a win-loss matrix (Schein and Fohrman 1955) based on outcomes of aggressive interactions between adult nannies ($\geq$ 3 years old). Individuals were ordered according to the ratio of wins versus losses, the highest ratios indicating superior ranks.

Since age was presumed to be a major determinant of dominance, a dominance index, which removes the effects of age, was calculated for each individual nanny. The index used was a modification of the one used by Clutton-Brock et al. (1986) which can be found in Festa-Bianchet (1991). First, the following ratio was calculated

$$OSD+OU+1/YSD+YU+1 ,$$

where OSD is the number of nannies of the same age or older dominated by the subject, OU is the number of older nannies with whom the subject interacted with no clear outcome, YSD is the number of nannies of the same age or younger that dominated the subject, YU is the number of younger nannies with whom the subject interacted with no clear outcome. The ratio was used to rank animals in each cohort, then the ranks were divided by the number of nannies in the cohort, resulting in dominance indices ranging from 0.25 to 1, in which higher indices represent higher ranks within the cohorts.

The linearity of the hierarchy was measured by Kendall's coefficient, K (Appleby 1983), using the win-loss matrix. Values of Kendall's coefficient range from 0 (complete absence of linearity) to 1 (complete linearity). For this study, a hierarchy is considered linear if $K \geq 0.9$. Arranging win-loss matrices into a specific order may create linear relationships were no such relationships exist, so the structure of the hierarchy was tested using the $\underline{x}^2$-test presented in Appleby (1983). This test measures the probability of the hierarchy occuring by chance.

RESULTS

In this population, rates of aggression of adult nannies were not a function of group size ($r^2 = 0.008$, $P = 0.5$, Fig. 2). Rates ranged in values from 0.01 to 13.5 interactions/individual/hour with an average of 2.18. The average group size sampled was larger than those examined in other studies ($\bar{x} = 58.9$, SD = 8.59, $n = 50$, range = 34-68).

Regarding the defense of a personal space, the relationship between the possibility of interaction and the resulting number of aggressive interactions was significant but weak ($r^2 = 0.283$, $P < 0.001$, Fig. 3). Removing the outermost datum produced a weaker correlation ($r^2 = 0.217$, $P = 0.0008$). Possibilities of interacting with another goat averaged 9.1 per hour of observation, and the actual number of resulting interactions was 2.02 ($n = 50$).

Dominance Hierarchy

A sample of 123 aggressive interactions between marked adult nannies was used to calculate the dominance hierarchy. Results of the win-loss matrix (Table 1) revealed a hierarchy among adult nannies that was not linear, but significantly non-random (K = 0.57, $x^2 = 105.9$, $P < 0.001$). Forty percent of possible dyads (nanny-nanny pair) were observed to interact.

The correlation between dominance rank and age was tested since 86% of the interactions were won by the older animal. The relationship between dominance and age for adult nannies was significant but weak ($r^2 = 0.443$, $P < 0.001$). Rank appears to increase with age until the animal reaches the age of 7, and then it may drop (Fig. 4).

In 50 hours of focal animal sampling the time budget of nannies did not vary significantly according to their dominance indices (Kruskall-Wallis ANOVA, $P > 0.05$). More specifically, there was no correlation between dominance index and the percent of time spent foraging ($r^2 = 0.004$, $P = 0.80$, Fig. 5), or the percent of time spent alert ($r^2 = 0.057$, $P = 0.32$, Fig. 6).

DISCUSSION

Previous studies of the effects of group size on the rates of aggression of mountain goats provide conflicting results. Chadwick (1977) found that rates of aggression increased with group size, whereas

Table 1. Win-loss matrix for adult female mountain goats, Caw Ridge, Alberta, 1991. Read across the table for number of interactions won by an individual; down for number of losses. Percentage of dyads observed interacting = 40. Number of interactions = 123.

Age	Individual	16	57	42	41	15	7	71	34	60	68	63	31	50	86	8	73	59	49	54	46	84
7	16			•	• •	• • •	• •		• • •	•			•	• •	•		• •			•		•
7	57	•						•	• •	•			•			•		•	• •	•	•	
9	42									• • •			• •			•	•	•			•	•
9	41							•		•						• •			• • • •	•		
8	15				• •				• •							•					•	
8	7								•							•		•	•			
6	71											•			•			•		•	•	•
9	34									•	•	•		• •		• •		•				
7	60										•	• •				•	• •		•	•	•	•
3	68												• •									•
5	63		•							•	•		•				•	•				
4	31							•											•			• • • •
4	50							•											• •			•
5	86																	•				
7	8																• •		• •		•	• •
6	73													•				•				•
5	59											• •							•			
6	49									•						•		•				•
6	54											•										
3	46																					
3	84																					

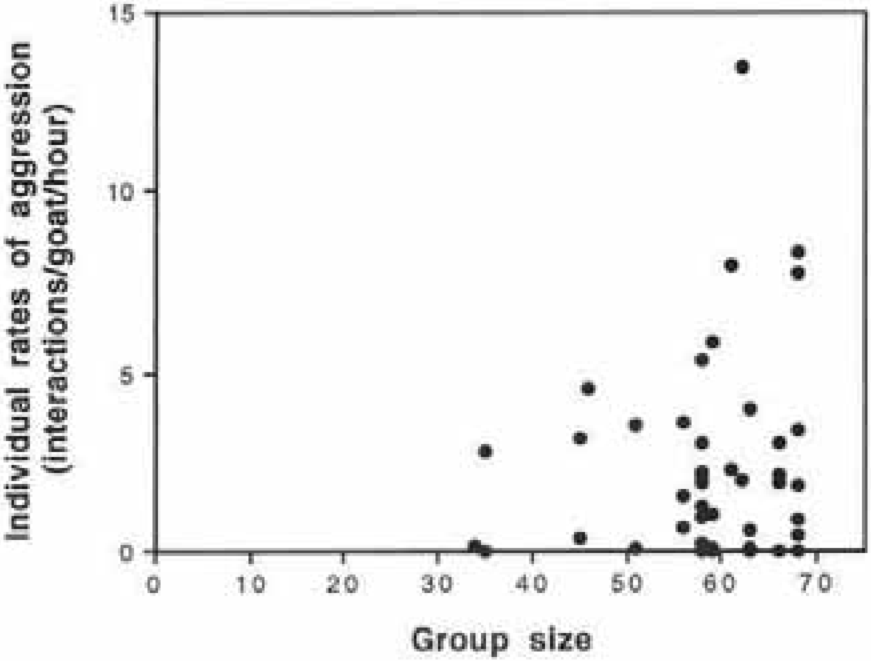

Fig. 2. Relationship between individual rates of aggression by adult female mountain goats and group size ($r^2 = 0.008$, $P = 0.6$, $n = 50$).

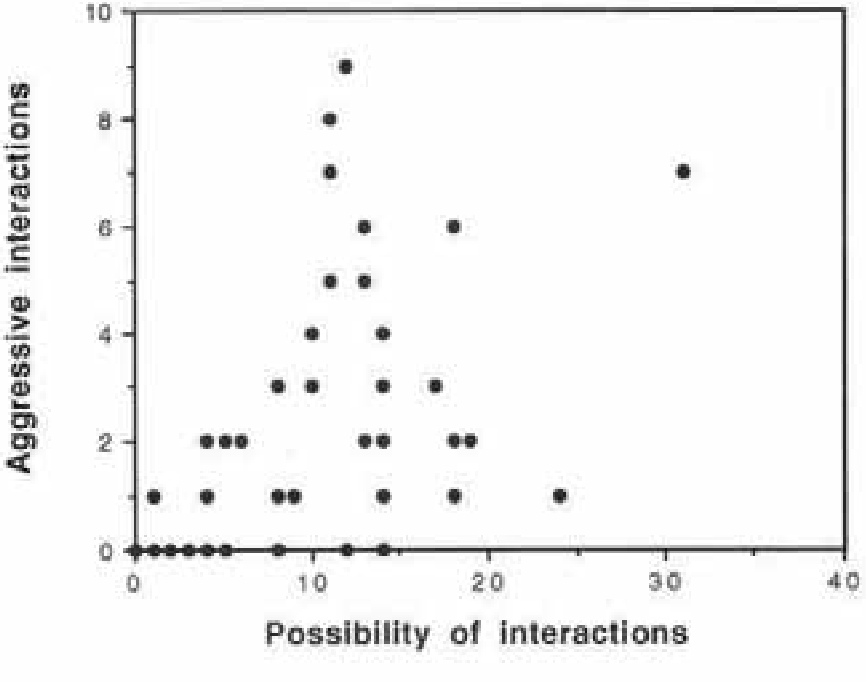

Fig. 3. Relationship between the possibility of interactions (goats within 4m) and the number of interactions according to 1-hour focal samples of mountain goat adult females ($r^2 = 0.283$, $P = 0.0001$, $n = 50$).

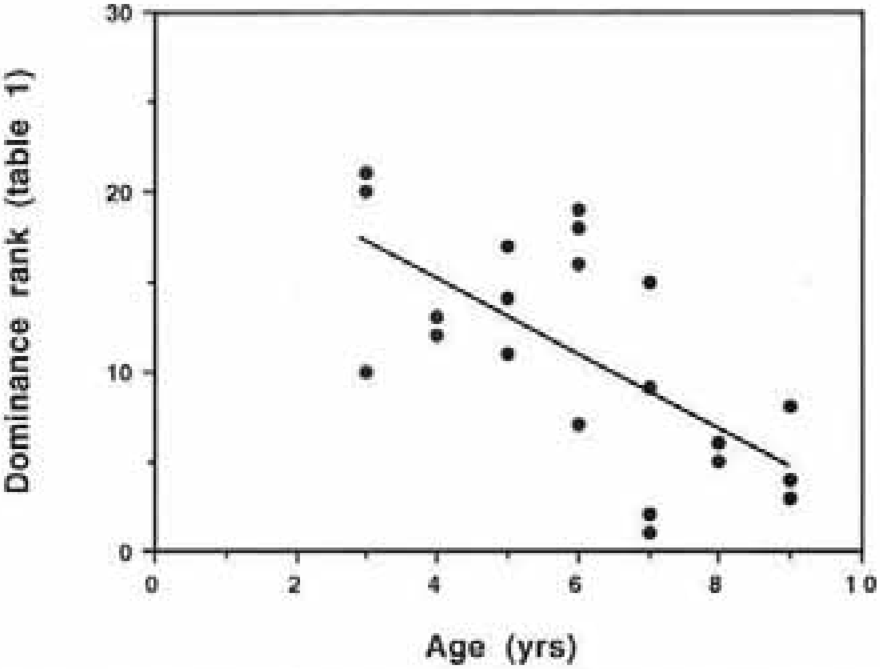

Fig. 4. Relationship between age and dominance rank of adult female mountain goats, Caw Ridge, Alberta, summer 1991 ($\underline{r}^2 = 0.44$, $\underline{P} = 0.001$, $\underline{n} = 21$).

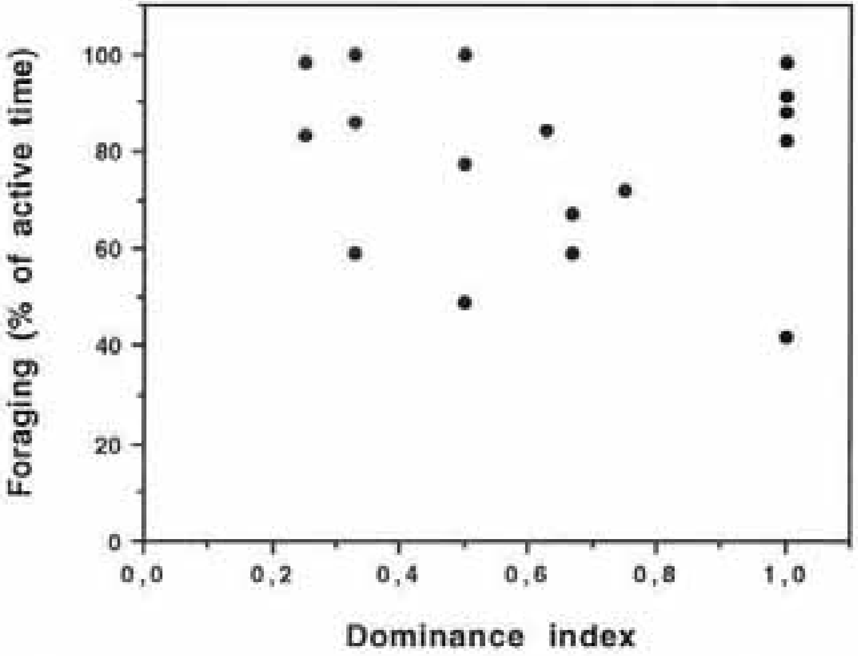

Fig. 5. Relationship between dominance index and the percent of active time spent foraging by adult female mountain goats, Caw Ridge, Alberta, summer 1991 ($\underline{r}^2 = 0.004$, $\underline{P} = 0.80$, $\underline{n} = 19$).

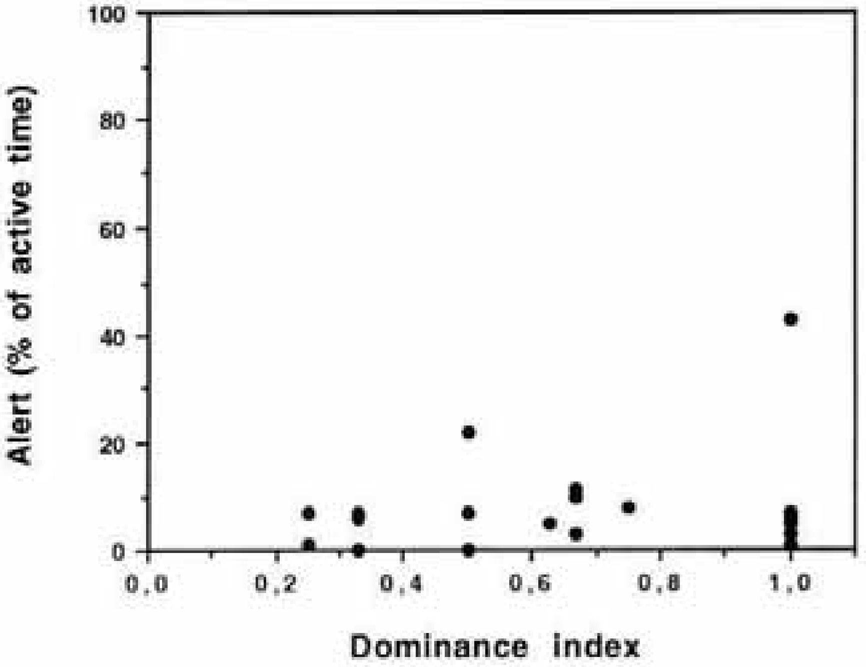

Fig. 6. Relationship between dominance index and the percent of active time spent in alert behavior by adult female mountain goats, Caw Ridge, Alberta, summer 1991 (r^2 = 0.057, P = 0.32, n = 19).

Risenhoover and Bailey (1985) reported that rates of aggression declined as group size increased to about ten animals. Their results differed from those of Chadwick because goats they observed in Colorado were introduced and their social structure might differ from native herds. Average group sizes recorded by Chadwick in Montana were small (2-3 goats), making it difficult to measure effects of group size. Furthermore, the goats used different habitats. In Montana (Chadwick 1977), the goats were on cliff outcrops where food was spatially limited, while Colorado's animals were in alpine tundra where food was more available (Risenhoover and Bailey, 1985). Although Caw Ridge might have offered me a chance to test the predictions that group sizes affect rates of aggression, it was found, however, that rates of aggression were not correlated with group size. In my study, the average group size was larger than those previously reported making a comparison with small groups difficult.

Chadwick (1977) suggested that the social organization of mountain goats was based on defense of a mobile personal space. A preliminary test of this assumption suggests that the goats do not always defend a personal space. The occurence of 2 adult females did not always result in an aggressive interaction. These results must be interpreted cautiously since they are preliminary, and this question will be addressed more thoroughly in the second summer of research.

Although the social organization of mountain goats has been classified as a dominance hierarchy (Chadwick 1977, Masteller and Bailey 1988), a detailed study of this organization is lacking. The goats have a dominance hierarchy, but this hierarchy is non-linear, indicating many reversals of rank. These conclusions have been drawn from studies on wild bighorn ewes (Hass 1991), captive ewes (Eccles and Shackleton 1986), bison (Rutberg 1986), and feral cattle (Hall 1986). Hass and Jenni (1991) found that for bighorn rams, the dominance hierarchy was linear and stable over many years. This suggests that a linear hierarchy is possible mainly when a contested resource (estrous females) may be defended. It is not clear if female mountain goats can defend a non-patchy food resource, and this might account for the lack of linearity in their hierarchy.

Dominance is correlated with age in bison (Rutberg 1986), red deer (Clutton-Brock et al. 1984, Thouless and Guinness 1986), white-tailed deer (*Odocoileus virginianus*, Townsend and Bailey 1981), bighorn sheep (*Ovis canadensis*, Festa-Bianchet 1991) and addax (*Addax nasomaculatus*, Reason and Laird 1988). Weight and age determined dominance in chamois (*Rupicapra pyrenaica*, Locati and Lovari 1991), whereas weight (Hirotani 1990) but not antler size (Barrette and Vandal 1986) correlated with dominance in caribou. Although most interactions were won by the older goat in each dyad (86%), dominance rank was only weakly corrrelated with age. This suggests a better clue for dominance in this population of goats may be weight or horn size; but available data are insufficient to permit me to explore these possibilities.

Other studies have shown that dominants differ in their time budget in comparison with subordinates (Appleby 1980, Deutsch and Lee 1991). Dominant animals had a priority to food resources in captive rhesus monkeys (*Macaca mulatta*, Deutsch and Lee 1991), in red deer stags (Appleby 1980), woodland caribou (Barrette and Vandal 1986) and wintering mountain goats at a localized bait (Masteller and Bailey 1988). Although I expected similar feeding competition in this population, no differential access to food, or foraging efficiency, was found. Thouless (1990) suggested that, for red deer hinds, feeding competition is a passive process whereby subordinates avoid conflict with a dominant by moving away from them during feeding bouts. He also found that dominant hinds had a better feeding efficiency than did subordinates (Thouless 1990). The data from Caw Ridge do not support this hypothesis for mountain goats. Lovari and Rosto (1985) found that, in a group of Apennine chamois, dominance affected foraging efficiency. Dominant females had a greater number of bites per minute and significantly fewer head-lifts per minute, a measure of alertness, than did subordinate females. These authors suggested that the stress encountered by subordinates was not from predation pressure but rather from the presence of potentially aggressive conspecifics (Lovari and Rosto 1985). This conclusion may be also valuable for mountain goats, but further work needs to be done in order to test this assumption.

According to Hamilton (1971) subordinate goats should be found more often on the periphery of the group and should therefore spend more time in alert behavior. These results were found for pronghorns (Antilocapra americana, Lipetz and Bekoff 1982). Although predation was a major mortality factor in this population (Smith et al. 1992), the goats often fed a fair distance away (> 400 m) from what appeared to be escape terrain and I found no difference between dominant and subordinate goats in the amount of time they were alert.

Although mountain goats demonstrate a high level of aggression, the reasons behind their aggression are poorly understood. This behavior must serve a purpose since valuable energy is spent on aggression. Further investigations into this aspect of mountain goat social behavior may enable us to better understand these animals.

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ABSTRACTS

Bienn. Symp. North. Wild Sheep
and Goat Counc.8:372.

MITOCHONDRIAL DNA VARIATION AND GENETIC POPULATION STRUCTURE IN ROCKY MOUNTAIN BIGHORN SHEEP

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<u>Abstract:</u> Maintaining fitness and high adaptive potential in a species requires the maintenance of genetic variation both within and between populations. Transplanting individuals between genetically differentiated groups may cause outbreeding depression. On the other hand, if herds are not genetically differentiated, supplemental transplanting can prevent loss of genetic variation and concomitant inbreeding effects within small herds. Understanding the genetic population structure (i.e., distribution of genetic variation within and among populations) of bighorn sheep would help in making transplanting decisions that do not compromise the species genetic resources. The amount and distribution pattern (i.e., genetic population structure) of mitochondrial DNA (mtDNA) variation in Rocky Mountain bighorn sheep was assessed to determine relationships among populations and the usefulness of mtDNA analysis as a tool for conserving genetic variation in bighorn sheep. Restriction enzyme analysis was conducted on mtDNA from 292 individuals from 22 indigenous herds located throughout the entire geographic range of the Rocky Mountain subspecies of bighorn sheep. Eleven different mtDNA genotypes were identified. A phylogeographic analysis revealed relatively divergent mtDNA genotypes within herds, and several geographically widespread genotypes. This suggested that gene flow has occurred on a regional scale at some time in the past (perhaps during colonization of the Rocky Mountains) and that populations have not been subdivided by long-term barriers to gene flow. Significant differentiation in mtDNA genotype frequencies among local herds and among herds from 6 regions (Canada, central Montana, southern Montana, Idaho, Wyoming, and Colorado) suggests that little mitochondrial gene flow exists among current populations. The differentiation may be due to population fragmentation and bottlenecks during the last 200 years. Alternatively, because significant mtDNA frequency differentiation occurs on a microgeographic scale (i.e., among herds separated by only 4 to 15 miles) much of the observed mtDNA differentiation could be due to philopatric behavior. Female philopatry and population substructure may have existed for thousands of years. Although population differentiation is extensive for mtDNA variation, we cannot determine how extensive differentiation is for the nuclear genes which make up most of an organism's total genome. This study and the population fragmentation and die-offs of recent years, suggest a need for an assessment of population differentiation for nuclear genes in Rocky Mountain bighorn sheep. Thus, our lab (under F. Allendorf) in collaboration with J. Hogg are currently developing nuclear DNA analysis techniques (i.e. polymerase chain reaction and DNA sequencing) which will allow for a thorough assessment of genetic differentiation.

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MODELLING DALL SHEEP HABITAT IN THE NORTHERN YUKON

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Abstract: The identification of important wildlife habitats in the Yukon Territory has been limited by the vastness of the land, the inaccessibility, and the associated costs of conducting field work in remote locations. Demands on the land in terms of land use development, utilization of renewable and non-renewable resources, and native land claims are increasing. Land planners and wildlife managers urgently need quality base-level data at various scales to incorporate into the decision making process. This pilot project was designed to demonstrate the capabilities of GIS (Geographic Information Systems) to quantify and map habitat parameters to better protect and manage wildlife.

This project was limited to Dall sheep lambing habitats where spring lamb locations were related to slope, aspect, and distance from escape terrain and winter range. The study area was extracted from a 1:250,000 digital topographic map and the contour lines used to generate a digital elevation model defining both slope and aspect. Escape terrain was mapped and hand digitized from stereoscopic aerial photographs; point locations of sheep seen during a winter helicopter survey were used to define winter range.

With the modelling capabilities of the GIS we then predicted potential lambing habitats for a test region, using the relationships identified in the first phase. While the model needs further refinement, this project clearly demonstrated the utility and cost-effectiveness of using GIS technology to predict the occurrence of a key habitat type and thus allow managers to recommend an appropriate level of protection.

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and Goat Counc. 8:374.

POPULATION DYNAMICS OF BIGHORN SHEEP USING RECLAIMED HABITAT IN OPEN PIT COAL MINES IN WEST-CENTRAL ALBERTA

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Abstract: The population dynamics of bighorn sheep (*Ovis canadensis*) using a reclaimed landscape between the years 1985 and 1991 are discussed. Maximum pre-rut counts have increased from 198 in 1985 to 314 in 1991. Alberta Fish and Wildlife have captured sheep from this site since 1984 for various transplant purposes. A non-trophy hunt has been conducted on the Cardinal River Coals Ltd. mine site for 6 out of the past 8 years. Ewe removal rates have averaged 15%. Ewe numbers showed an initial increase over the first 2 years but have remained stable since then. Individual sheep exhibit characteristics of a healthy, expanding population. The total amount of revegetation area on Cardinal River Coals Ltd. has increased by 96% between 1985 and 1991. Bighorn sheep have responded by quickly moving into new areas once a grass-legume mixture has been seeded, and incorporating these new areas into their seasonal occupation of range. Seventy-five percent of all sheep observations during a year period between September 1985 and September 1986 were within 300 m of escape terrain. Similar range expansions onto newly cleared or newly seeded reclamation have been documented at the neighboring Gregg River Resources Ltd. mine site.

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SPINSTER BIGHORN EWE GROUPS IN THE ARKANSAS RIVER CANYON, CANON CITY, COLORADO

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Abstract: A bighorn sheep (*Ovis canadensis canadensis*) habitat study using GIS (Geographical Information System) technologies has been conducted on a sheep range about 13 km long north of the Arkansas River between Parkdale and Echo Canyon in Colorado. Counts and observations indicated approximately 50-60 ewes in 2-7 subgroups with no signs of parturiency, nor any lambs, during spring, summer, and fall of 1991. No yearling or older rams have been observed in the area north of the river since the 1990 hunting season when two 1/2 curl rams were harvested. This contrasts markedly with the situation south of the river (across a narrow corridor of the Denver and Rio Grande Western railroad, Arkansas River, and U.S. Highway 50) where a more "normal" sex-age class has been consistently observed during the same period: the area south of the river had a lamb:ewe ratio of about 90:100 excluding females younger than 3. The difference in lamb:ewe ratios in these adjacent areas has led us to question the hypothesis that the river does not act as a barrier to sheep movement (ewes on the north consistently cross the railroad tracks for forage and water, and some cross the highway from the south as indicated by 2 road-kills during the summer of 1991). Failure to breed, however, represents the most plausible explanation for the absence of lambs. Other hypotheses, such as those involving habitat "sinks" and the role of reproductive disease, merit examination. A proximate solution to the problem has been tried by transplanting three 2-year old rams into the area north of the Arkansas River. Two of the 3 rams initially socialized with ewe groups north of the river and some late breeding (later than 21 Jan 92) may have occurred. By 28 and 38 days post-release, however, these 2 rams had left the ewes north of the river, crossed the river and highway, and joined other ewes south of the river. Whether they will rejoin ewe groups on the north remains equivocal. Long-term management should include assessing roles of hunting and non-hunting mortality on rams in this population.

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GUIDELINES OF THE NORTHERN WILD SHEEP AND GOAT COUNCIL

The purpose of the Northern Wild Sheep and Goat Council is to foster wise management and conservation of northern wild sheep and goat populations and their habitats.

This purpose will be achieved by:

1) providing for timely exchange of research and management information;

2) promoting high standards in research and management; and

3) providing professional advice on issues involving wild sheep and goat conservation and management.

I The membership shall include professional research and management biologists and others active in the conservation of wild sheep and goats. Membership in the Council will be achieved either by registering at, or purchasing proceedings of, the biennial conference. Only members may vote at the biennial meeting.

II The affairs of the Council will be conducted by an Executive Committee consisting of: three elected members from Canada; three elected members from the United States; one ad hoc member from the state, province, or territory hosting the biennial meeting; and the past chairperson of the Executive Committee. The Executive Committee elects it's chairperson.

III Members of the Council will be nominated and elected to the executive committee at the biennial meeting. Executive Committee members, excluding the ad hoc member, will serve for four years, with alternating election of two persons and one person of each country, respectively. The ad hoc member will only serve for two years.

The biennial meeting of members of the Council shall include a symposium and business meeting. The location of the biennial meeting shall rotate among the members' provinces, territories and states. Members in the host state, province or territory will plan, publicize and conduct the symposium and meeting; will handle its financial matters; and will prepare and distribute the proceedings of the symposium.

The symposium may include presentations, panel discussions, poster sessions, and field trips related to research and management of wild sheep, mountain goats, and related species. Should any member's proposal for presenting a paper at the symposium be rejected by members of the host province, territory or state, the rejected member may appeal to the Council's executive committee. Subsequently, the committee will make its recommendations to the members of the host state, territory or province for a final decision.

The symposium proceedings shall be numbered with 1978 being No. 1, 1980 being No. 2, etc. The members in the province, territory or state hosting the biennial meeting shall select the editor(s) of the proceedings. Responsibility for quality of the proceedings shall rest with the editor(s). The editors shall strive for uniformity of manuscript style and printing, both within and among proceedings.

The proceedings shall include edited papers from presentations, panel discussions or posters given at the symposium. Full papers will be emphasized in the proceedings. The editor will set a deadline for submission of manuscripts.

Members of the host province, territory or state shall distribute copies of the proceedings to members and other purchasers. In addition, funds will be solicited for distributing a copy to each major wildlife library within the Council's states, provinces and territories.

IV Resolutions on issues involving conservation and management of wild sheep and goats will be received by the chairperson of the Executive Committee before the biennial meeting. The Executive Committee will review all resolutions, and present them with recommendations at the business meeting. Resolutions will be adopted by a plurality vote. The Executive Committee may also adopt resolutions on behalf of the Council between biennial meetings.

V Changes in these guidelines may be accomplished by plurality vote at the biennial meeting.