SPATIAL RELATIONSHIPS AND BEHAVIOR OF BIGHORN SHEEP SHARING A WINTER RANGE WITH MULE DEER AND ELK IN CENTRAL IDAHO

By

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1992

SPATIAL RELATIONSHIPS AND BEHAVIOR OF BIGHORN SHEEP SHARING A WINTER RANGE WITH MULE DEER AND ELK IN CENTRAL IDAHO

A Thesis

Presented in Partial Fulfillment of the Requirements for the

DEGREE OF MASTER OF SCIENCE

with a

Major in Wildlife Resources

in the

GRADUATE SCHOOL

UNIVERSITY OF IDAHO

by

Holly Anne Akenson

December 1992

AUTHORIZATION TO SUBMIT

THESIS

This THESIS of HOLLY AKENSON, submitted for the degree of MASTER OF SCIENCE with a major in WILDLIFE RESOURCES and titled "SPATIAL RELATIONSHIPS AND BEHAVIOR OF BIGHORN SHEEP SHARING A WINTER RANGE WITH MULE DEER AND ELK IN CENTRAL IDAHO", has been reviewed in final form and approved, as indicated by the signatures and dates given below. Permission is now granted to submit final copies to the Graduate School for approval.

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ABSTRACT

The effects of behavioral interactions on bighorn sheep by mule deer and elk were assessed on a shared winter range. Bighorn sheep, mule deer, and elk were observed on the Cliff Creek study area in central Idaho. Behavior, locations, and proximity to the closest herd of another species were determined through scan sampling. Seasonal habitat use was similar among bighorn sheep, mule deer, and elk during winter and spring. Bighorn sheep and mule deer showed a positive association, especially in spring when both species fed together in grasslands. This tendency to be in close proximity to each other probably reflects the lack of competition between these species and may reflect an antipredator advantage of mixed species grouping. Bighorn sheep and elk herds were further from each other than bighorn sheep and mule deer, and were rarely observed in mixed groups. Elk used higher elevations than sheep. Elk and sheep generally had a neutral to negative association. The low use of the study area by elk and infrequent contact between sheep and elk prevented a thorough assessment of this relationship. The one situation in which sheep and elk were consistently observed in mixed groups was when coyotes were present on the study area. Interspecific relationships, both positive associations and competition, appear to explain behaviors and distribution of bighorn sheep, mule deer, and elk on the Cliff Creek study area, but other explanations could not be statistically eliminated. Recent changes in bighorn sheep and

elk numbers now provide an opportunity to compare interspecific relationships at 2 population levels to evaluate changes in these ungulate relationships on the Cliff Creek study area.

ACKNOWLEDGMENTS

I express my appreciation to Ernie Ables, my major professor, who allowed me to develop a research topic from my own interests. He guided me in formulating the study objectives, and always provided encouragement and found time to discuss and review my project. I am indebted to John Byers, one of my committee members, who provided significant technical advice in the study plan development and data analysis, and who forced me to focus my analysis and critically evaluate the significance of my findings. I really appreciate the contributions of Ed Krumpe, a committee member and a supervisor when I was the Manager of the Taylor Ranch Research Station, who helped me edit and refine my thesis and provided support and encouragement for my research activities at Taylor Ranch. I am indebted to Mike Scott for his insightful review of my thesis and his timely offer to serve on my committee. The University of Idaho Statistical Consulting Center and the Computer User Services provided valuable technical assistance on computer data entry and statistical analysis. I thank my husband Jim Akenson for assisting in data collection and providing moral support.

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INTRODUCTION

Spatial relationships among animals influence an individual's fitness and how it interacts with its environment. Gregarious ungulates choose whether to join a group of conspecifics or to live alone. A herd of one species may respond to a nearby herd of another species in a positive, negative, or neutral manner.

Many factors influence whether an individual will benefit from joining a group. The risk of predation and the need to forage efficiently are among the most important forces responsible for the formation of groups (Rubenstein 1978). Competition is the primary constraint of group living.

Ungulates living in open habitats decrease their predation risk by forming groups. Groups of animals are more likely than solitary animals to detect a predator before it attacks. The probability of a group of animals detecting a predator increases with group size, even though the chance of each individual detecting a predator decreases (Caraco 1979, Lipetz and Bekoff 1982). The likelihood of an individual being selected and killed by a predator is lower when living in a group (Hamilton 1971, Leuthold 1977). Only social species can utilize communal defenses such as harassment, mobbing, and attack against predators (Berger 1979, Lipetz and Bekoff 1982).

Foraging efficiency of individuals increases when feeding in a group, because individuals spend less time scanning the environment (Alderman et al. 1989, Berger 1978, Dale and

Bailey 1982, Lipetz and Bekoff 1982, Pfister et al. 1989, Risenhoover and Bailey 1980, Risenhoover and Bailey 1985, Rubenstein 1978, Underwood 1982) or have an increased probability of finding food (Mangel 1990). Berger (1978) determined that the foraging efficiency of individual bighorn sheep in groups of 1 to 5 animals is significantly lower than those in larger groups of sheep, but individuals in groups larger than 5 do not gain additional efficiency as group size increased. Risenhoover and Bailey (1985) found that foraging efficiency of bighorns in groups of more than 10 animals is less influenced by habitat visibility and distance to escape terrain than that of sheep in small groups. When food is abundant animals are more likely to be in groups, because competition is less significant than the antipredator benefits of group living. Furthermore, grazing by herds of animals encourages regrowth of plants and keeps vegetation in a highly nutritious early growth stage better than dispersed animals (Bell 1971, Leuthold 1977, Senft et al. 1987).

The potential for intraspecific competition is greater when animals live in groups, because they are directly competing for the same resources. Competition increases as food becomes limited, causing groups to disband. Increased conspicuousness of groups in open terrain makes animals more readily detectable by predators, therefore group living in visible habitat is only advantageous if the animals can flee from predators. Dominant individuals derive greater benefits from living in groups than subordinates (Caraco 1979, Rubenstein 1978). In a model for predicting advantages of group living, Rubenstein (1978) contends that while the dominant individual always has higher fitness when living in a group, for a subordinate animal the relative advantages to living in a group or alone, depend on whether interference of a dominant animal offsets the benefits of reduced predation risk. Mortality from the effects of diseases and parasites is greater when animals are in close contact.

Those species that form large intraspecific herds are more likely to participate in mixed groups (Leuthold 1977). Joining or forming a mixed species group may be beneficial to an individual. Interspecific competition for food resources is less severe than intraspecific competition. Two sympatric ungulate species rarely have identical foods habits. They may eat different plant species, plant parts, or feed in different areas. Physiological needs of ruminants differ by body weight (Bell 1971); larger ruminants require large quantities of food that can be less digestible and contain less protein than that required for the smaller more selective ungulates which require high protein digestibility and lower cell wall constituents. Hobbs et al. (1983) found this relationship to hold for elk, mule deer, and bighorn sheep, with elk being least selective and sheep most selective. Bell (1971) predicted that when food quality is low, the larger species will displace the smaller species, but when food is scarce the smaller species will displace the larger species.
Facilitation occurs for some African grazers when one species

improves the vegetation structure for feeding by another species through grazing succession (Bell 1971): larger ungulates feed on the coarser upper layer of grasses which exposes the lower layer of forbs and new shoots for grazing by smaller ungulates.

Predator detection can improve for one or both species when the two species have different means of detection (visual, hearing, olfactory). Communication occurs between species in a mixed group. Thomson's gazelles respond to Grant's gazelles alarm postures and alarm snorts when in mixed species groups (Fitzgibbon 1990). Alarm postures of mountain sheep, mule deer, and elk are almost identical (Geist 1971).

A disadvantage of mixed species grouping occurs for one species when it is disproportionately selected by predators or when it is the only species preyed on by a predator (Fitzgibbon 1990, Rubenstein 1978). Fitzgibbon (1990) found that a Thomson's gazelle was more likely to be preyed upon in a large mixed species group with the larger Grant's gazelle and few conspecifics than when in a smaller single species group with more conspecifics. In African ungulates interference competition, the overt aggression between two species in an interspecific group is rare, although threat behaviors are sometimes used; usually individuals of one species attempt to avoid direct encounters by yielding the right-of-way to the other species (Leuthold 1977). Hediger (1940a, 1942/50 as cited in Leuthold 1977) designated this relationship a "biological hierarchy" in which two or more species with similar physical characteristics and ecological requirements are in competition for the same resource. The position of a species in the biological hierarchy of a mixed species group will influence the relative advantage of mixed grouping. The "biologically dominant" species is most often the larger one and generally obtains resources without being challenged.

Sinclair (1985) postulated that the forces of interspecific competition, intraspecific competition, and predation affect nearest neighbor distances between ungulate herds of two species in different ways. Herd distances between two species would be greater than randomly expected for interspecific competition, random for intraspecific competition, and closer than expected if predation was the primary influence on these animals.

Many mixed species ungulate associations have been reported for African species: zebra, wildebeest, and Thomson's gazelle (Bell 1971); gerenuk, lesser kudu, giraffe, and black rhinoceros (Leuthold 1978); Walia ibex, klipspringer, and Gelada baboon (Nievergelt 1981); wildebeest, zebra, Thomson's gazelle, Grant's gazelle, topi, kongoni, impala, waterbuck, warthog (Sinclair 1985); Thomson's and Grant's gazelles (Fitzgibbon 1990). Interspecific relations of red, roe, and fallow deer in Scotland have been investigated (Batcheler 1960), as well as foraging relationships of llamas, alpacas, and domestic sheep in Peru (Pfister et al. 1989).

In North America mule deer and elk sometimes occupy the same or overlapping ranges as bighorn sheep, creating the potential for competition (Buechner 1960, Capp 1868, Collins and Urness 1983, Constan 1972, Cowan 1947, Haas 1979, Lauer and Peek 1976, Mackie 1981, Ratcliff and Sumner 1945, Smith 1952, Spowart and Hobbs 1985, Trefethan 1975). Direct competition through exploitation occurs when two species utilize a limited food supply and one species causes a degradation of the habitat or decrease in food supply for both species. Investigations of relationships of these ungulates and the potential for competition have primarily focused on comparative food habits of mule deer and elk (Collins and Urness 1983); mule deer and bighorn sheep (Spowart and Hobbs 1985); elk, mule deer, and bighorn sheep (Cowan 1947, Constan 1972, Haas 1979, Hobbs et al. 1983); and bighorn sheep and cattle (McCollough et al. 1980) as well as habitat relations of bighorn sheep, elk, and mule deer (Capp 1968, McCullough and Schneegas 1966), and mule deer and elk (Severson and Medina 1983) occupying the same ranges.

Studies of winter diet overlap and habitat use have shown that the potential for competition between bighorn sheep and elk is usually greater than for bighorns and mule deer or elk and mule deer (Cowan 1947, Capp 1968, Constan 1972, Haas 1979, Nelson 1982). Food habits studies indicate that elk and bighorn sheep winter diets are more similar than either are to deer diets (Cowan 1947, Capp 1968, Constan 1972, Hobbs et al. 1983) and that elk and sheep are in direct competition when using the same range. Constan (1972), Oldemeyer et al. (1974), and McCullough and Schneegas (1966) determined that although sheep and elk diets are very similar, the respective feeding areas overlap little.

Many populations of bighorn sheep share their winter range with mule deer. Winter diets of mule deer and bighorn can be similar, but often differ in dominant food type. Mule deer consume mostly browse and forbs while sheep primarily eat grasses and forbs (Capp 1968, Constan 1972, Cooperrider et al. 1980, Cowan 1947, Hobbs et al. 1983, Keating et al. 1985, Smith 1954, Spowart and Hobbs 1985, Tilton and Willard 1981), although diet composition can vary greatly among populations and seasons. Lauer and Peek (1976) suggested that competition between sheep and deer may be greatest in late winter at the initiation of spring greenup of grasses on low elevation slopes, while Hobbs and Spowart (1984) felt that the limited quantity and quality of food in winter results in more potential for competition than in spring when diet overlap is greater.

Potential for competition is greatest in severe winters when deep snows and harsh weather conditions force animals to concentrate in the same area (Constan 1972, Geist and Petocz 1977, Oldemeyer et al. 1971). McCullough and Schneegas (1966) observed that in winter, ranges of deer, elk, and cattle barely overlap with ranges of bighorn sheep in California and that forage competition is absent. On the contrary, intense competition between bighorns and elk was noted by Capp (1966), Murie (1941), and Ratcliff and Sumner (1945), particularly when elk populations are increasing or encroaching on bighorn sheep range. Constan (1972), Haas (1979), and Oldemeyer et al. (1971) found that only during severe winters do elk overlap areas where bighorn sheep concentrated. When elk and sheep utilize the same limited food resource in the same area elk are considered the more successful competitor (Buechner 1960, Cowan 1947, Capp 1968, Constan 1972, Nelson 1982). Capp (1968) cited several examples of circumstantial evidence that bighorn sheep are displaced from historic ranges by elk.

Spatial relationships of bighorn sheep, mule deer, and elk have not been quantitatively evaluated. Evidence suggests that attraction and avoidance can occur between these species. Disturbance competition results in the avoidance of other species or areas, and may prevent bighorn sheep from optimally utilizing their range. Horejsi (1975) and Wilson (1975) both observed that bighorn sheep avoid cattle on desert bighorn sheep range and avoid those parts of the range where cattle were frequently found. Bighorns return to these sites when cattle were removed. Trefethen (1975) suggested that the avoidance of cattle by bighorn sheep is an expression of competition for space. Kramer (1973) analyzed interspecific spatial relationships of mule deer, white-tailed deer, cattle, and coyotes and found both mixed species aggregations and avoidance patterns. Reports of mixed species groups of bighorn sheep, mule deer, and elk occur in the literature, but are often anecdotal. Smith (1954) observed bighorns and mule deer grazing or using mineral licks together on 16 occasions during spring in central Idaho. He observed bighorns with elk on 2 occasions, but noted that deer also occurred in the same group. Smith characterized the relationship between sheep and deer in a mixed group as "an attitude of complete indifference". Simmons (1962) observed mule deer feeding and bedded near bighorn sheep. He noted that usually both species ignore each other. Haas (1979) described an attitude of mutual indifference by sheep and deer in close proximity, except when one group is alarmed it often causes a reaction in the other species. From 5 observations of close deer and sheep and 3 observations of close elk and sheep, she felt that deer attempt to avoid very close contact with sheep while elk and sheep were indifferent. During artificial feeding, Hunter and Pillmore (1954) watched bighorns chase deer from a feeding station.

JUSTIFICATION

Interspecific competition is always a potential force within a biological community that contains several ungulate species. In stable communities, where the number of each species does not vary much over time, competition is not overtly expressed, because each species has already altered its behavior to avoid interspecific competition. Food habits and habitat preferences have diverged; spatial relationships and the timing of activities have been established to avoid competition.

In an area where ungulate distribution or numbers are changing, an adjustment in interspecific relationships and actions of one species toward another may occur. Shifts in distribution or population size can be the result of natural causes like fire altering the habitat, or disease; or man induced causes such as animal transplants, changes in hunting pressure, or habitat changes due to logging or grazing.

In order to understand, manage for, and predict changes in the distribution and relative abundance of bighorn sheep, mule deer, and elk, more must be learned about the dynamics of these ungulate relationships under a variety of population levels, range conditions, climatic conditions, and habitats. In Idaho, bighorn sheep have been designated "management priority" status on most of their ranges by the Idaho Department of Fish and Game in its management plan for trophy species (Idaho Department of Fish and Game 1981). This means that all potential threats to a bighorn sheep population should be evaluated, including the impact of the rapidly increasing elk population on Big Creek.

This study provides information about the distribution and activities of bighorn sheep, mule deer, and elk sharing a central Idaho winter range under the specific environmental conditions documented in this report. The results have local significance for managing the Big Creek bighorn population and also provide one sample of interspecific relationships among bighorn sheep, mule deer and elk, which can be incorporated with other studies to better predict one species' response to changes in the distribution or population size of another species. This study provides statistical analyses and speculation about the relationship between observed distribution and activities of bighorn sheep, mule deer, and elk and the forces of competition.

The Big Creek winter range in central Idaho provides an excellent opportunity to analyze behavior and spatial relationships of bighorn sheep with mule deer and elk. The study area is used simultaneously by all three species. The area supports a significant proportion of the bighorn population, while only a small proportion of deer and elk on the Big Creek winter range rely on this site for their winter survival. The limited size of bighorn winter range relative to deer and elk winter ranges makes this site particularly important for the survival of the Big Creek bighorn sheep population.

Past research in central Idaho which has addressed winter range conditions and whether competition occurs between bighorn sheep and deer or elk has yielded a variety of conclusions. Range condition and trend studies conducted in the 1950's indicate that most winter ranges along the Middle Fork of the Salmon River adjacent to Big Creek were static or exhibiting a downward trend and that many browse species had been severely hedged in the past (Smith 1954). Although, Smith (1952, 1953) determined that in the Salmon River Mountains serious competition for forage did not occur between bighorns and other ungulates, since sheep winter diets containe a greater proportion of grasses and forbs. He did recommend that in limited areas where game use was depleting the range, deer or elk harvest should be increased to eliminate severe competition with sheep. Later censuses and range studies on the Middle Fork of the Salmon River and Big Creek (Kindel, et al. 1949-1970) indicated there was no serious competition for forage. Claar (1973) determined that despite high forage utilization on the Big Creek winter range, ungulate use is not detrimental to the range; mule deer, elk, and bighorn sheep populations were healthy; and palatable forage was abundant in winter. The discrepancies among these results may be due to actual differences in severity of competition at different time periods or in different areas or may reflect different methods to assess competition. This study provides another perspective on interspecific competition, by comparing behavior and distribution of bighorn sheep, mule deer, and elk when near other species and when alone.

OBJECTIVES

A. To determine bighorn sheep, deer, and elk behavior and daily activity patterns during winter and spring on a portion of the Big Creek winter range.

B. To record seasonal occurrence, distribution, and habitat use of bighorn sheep, deer, and elk during winter and spring on a portion of the Big Creek winter range.

C. To identify differences in bighorn sheep, deer, and elk behavior, activity patterns, and habitat use.

D. To compare bighorn sheep, deer, and elk behavior when in close and distant proximity to a herd of another species.

E. To assess spatial relationships among bighorn sheep, deer, and elk herds.

STUDY AREA

General Area

Research was conducted in the Frank Church River of No Return Wilderness in central Idaho. The 2.3 million acre Frank Church River of No Return Wilderness is administered by the U. S. Forest Service. Idaho Department of Fish and Game manages the big game hunting seasons in this area. Research was conducted from the Taylor Ranch Wilderness Field Station, operated by the University of Idaho Wilderness Research Center. The study area was located on Big Creek, a tributary of the Middle Fork of the Salmon River.

The Big Creek drainage ranges in elevation from 1050 to 2850 m. It is an eastward flowing stream. Topography is steep and dissected in the more arid lower canyon; the upper reaches vary from gently rolling forest and meadows to alpine basins and mountain peaks. Lower elevations support bluebunch wheatgrass (Agropyron spicatum) and Idaho fescue (Festuca idahoensis) grassland plant communities (Tisdale 1979) and Douglas fir (Pseudotsuga menzesii) forested communities (Steele 1981) as well as mountain mahogany (Cercocarpus ledifolius), big sagebrush (Artemesia tridentata), and riparian shrub communities. Higher elevations are dominated by lodgepole pine (Pinus contorta), Douglas fir, subalpine fir (Abies lasiocarpus), and white bark pine (Pinus albicaulis) forested communities, and also contain wet meadows, alpine meadows, and rocky ridges.

Fauna

A variety of native ungulates live in the Big Creek area. Mule deer (Odocoileus hemionus), Rocky Mountain elk (Cervus elaphus), and Rocky Mountain bighorn sheep (Ovis canadensis) share the "Big Creek winter range", while small populations of white-tailed deer (Odocoileus virginianus), Shiras moose (Alces alces), and mountain goats (Oreamnos americanus) winter in isolated pockets.

Predators on the winter range include coyotes (Canis latrans), mountain lions (Felis concolor), and bobcats (Felis rufus). Black bears (Ursus americanus) are common on Big Creek from spring through fall. Hornocker (1970) found that mountain lions primarily prey on elk and mule deer on Big Creek. From observations of coyotes and examinations of kills in the study area, I found that coyotes primarily preyed on deer, although a pair of coyotes learned to hunt bighorn sheep in the study area and were successful during the years of this study. Bobcats and black bears are not significant predators of ungulates on the study area during winter and spring.

Absolute population numbers as well as relative population sizes of bighorn sheep, deer, and elk have varied throughout the last century in the Big Creek drainage. See Appendix A for the history of ungulate populations on the Big Creek winter range. Deer numbers have fluctuated dramatically and have recently appeared to be lower than the peak numbers in the 1940's and 1950's. Bighorn sheep have experienced several declines, but the population increased to record high

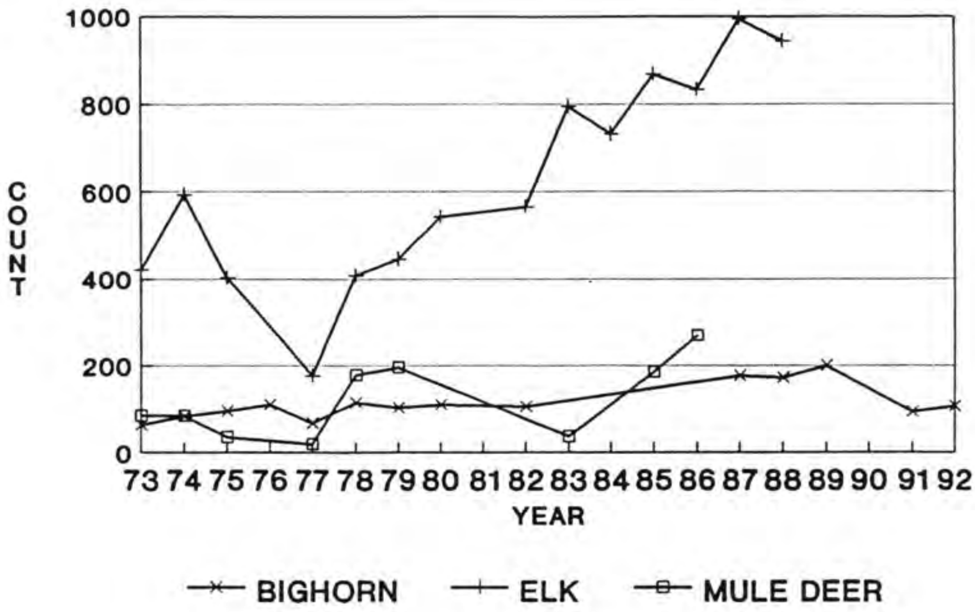


Fig. 1. Spring aerial surveys for bighorn sheep, mule deer and elk on Big Creek (Unit 26) by Idaho Fish and Game.

numbers in the late 1980's. Elk were absent or rare on the Big Creek winter range until the 1940's. Since 1940 the elk population has expanded rapidly.

Idaho Department of Fish and Game spring aerial counts from 1973 to 1989 show that the number of elk on the Big Creek winter range has increased dramatically (Fig. 1). The elk population was at an historical high on Big Creek during the years of this study and has continued to increase. Deer have not been monitored as regularly as elk and bighorn sheep, but the number of deer appears to be down in the last ten years (personal communication with Mike Schlegel, Idaho Fish and Game, McCall, ID). During this study sheep numbers were at the highest level since aerial counts were initiated in 1973

(Fig. 1). The Big Creek bighorn population reached a peak in 1989 and declined sharply by the 1991 spring aerial count. In late 1986 winter lamb:ewe ratios declined from values of 35-45 lambs per 100 ewes to 16 lambs per 100 ewes and remained at this level or below until 1991 (Akenson and Akenson 1992).

Winter Range

The Big Creek winter range extends for 45 km along the lower portion of Big Creek. Most big game use is concentrated on the north side of Big Creek within 2-3 km of the stream. Southern aspects provide maximum thermal benefits and earlier green-up of vegetation in spring than adjacent areas. Cliffs, talus, and outcrops are characteristic of the lower Big Creek canyon where the study area is located. Rocky south facing slopes are interspersed with occasional grassy hillsides and forested areas and are dissected by narrow stream canyons. Elevations range from 1050 to 1900 m. Precipitation in lower Big Creek averages 30 to 38 cm per year. The lowest temperatures, around -30½C, usually occur in late December. Snow depths are low, and southern aspects in the lower canyon may remain snow free for much of the winter. Snow is deepest in late January and February. Maximum snow depth on the study area was 38 cm. Fog inversions during winter often held cold air along the canyon bottom, while snows melted from the upper slopes above 1500 m elevation.

Bighorn sheep, elk, and mule deer each use certain areas of the Big Creek winter range. Wintering bighorns only occupy the north side of the lowest 20 km of Big Creek. They primarily inhabit nonforested areas including cliffs and outcrops as well as grasslands. Deer and elk are found throughout the 45 km length of the Big Creek winter range, mostly on the north side of Big Creek. Elk congregate near large grassy areas or open forest and usually frequent less rocky areas. Most elk use of the winter range occurs in the upper segment of Big Creek. Deer are found in small groups scattered throughout the winter range. They favor the rough terrain in early winter, then congregate near grasslands in spring.

Study Area

The study area was selected because of its proximity to Taylor Ranch Field Station and because this area is a significant winter range for all three species. This site is located at the confluence of Cliff Creek with Big Creek. Elevations range from 1150 to 1750 m with southern aspects.

Four habitat associations were differentiated in the study area: grassland, mountain mahogany-outcrop, open Douglas fir forest, and talus. The study area encompassed 230 hectares which included 44% grassland, 32% mahogany-outcrop, 20% forest, and 4% talus. The study area is representative of the Big Creek bighorn sheep winter range, except the proportion of grassland is much greater on the study area than on the rest of the lower Big Creek winter range. The grasslands are located in the center of the study area and encompass the grassy benches and swales in the mid to lower elevations. Although slopes range from gentle to steep (>65% slope), the ground surface is smooth, without rocky outcrops. Soils are moderately well developed, particularly in the grassy swales. Dominant vegetation in the grasslands include bluebunch wheatgrass, Idaho fescue, balsamroot (Balsamorhiza sagitatta), Sandburg bluegrass, and cheatgrass. A more detailed list of plants of the grasslands is in Appendix B. Much of the mountain mahogany-outcrop habitat occurs in the western portion of the study area. The mahogany-outcrop habitat association contains steep, broken terrain with loose gravelly soils and many outcrops, cliffs, talus slopes and draws. Snows melts quickly from these slopes. Vegetation is sparse. Mountain mahogany, sagebrush, bitterbrush (Purshia tridentata), Gooding's gooseberry (Ribes velutinum) and wax currant (Ribes cereum) shrubs grow on the cliffs and rock outcrops with wheatgrass, cheatgrass (Bromus tectorum), Sandburg bluegrass (Poa secunda) and cymopteris (Cymopterus terebinthinus). Talus habitat associations are small rock slides that do not have any vegetation, except for scattered syringa (Philadelphus lewisii) or chokecherry (Prunus virginianus) along the edges. Forested areas occur on the upper elevation northern and eastern sides of the study area and are primarily open Douglas fir/wheatgrass or Douglas fir/pinegrass (Calamagrostis rubescens) habitat types (Steele 1981). Little understory vegetation covers the very steep slopes, rock outcrops, and gravelly soils.

Bighorn Sheep, Mule Deer, and Elk Use

Bighorn sheep are the first animals to migrate to the study area to winter. Ewes and lambs return from summer ranges in September and October; rams in November. Bighorns rut on the area in late November and early December. Deer return in early November and rut on the area in mid November. Elk use the study site irregularly through the fall, but do not stay. They use the area more frequently after November. Elk use lower elevations, including the study area, much more in years when snow accumulations are deep, than when there is little snow cover. In spring bighorns, deer, and elk migrate to other ranges before grass production peaks. All three species feed intensely on plants in the early stages of phenology in spring.

METHODS

I conducted field work from January 10, 1985 through May 25, 1985 and from December 5, 1985 through May 25, 1986. I collected data during 193 2-hour observation periods; 99 observations in the first winter and 94 observations in the second winter. Observations were made during daylight hours between 7:00 a.m. and 7:00 p.m., with starting times randomly determined using a random numbers table.

Data from each observed group of animals were recorded on a scan sample field form (Appendix C., Scan Sample). Information collected for each herd included date, species, time, herd size, age and sex composition, location, habitat type, nearest neighbor distance, distance to the nearest herd of another species, and environmental conditions such as temperature, precipitation, cloud cover, snow depth, percent snow cover, snow texture, and plant phenology. Physiographic class, physical features, elevation, percent slope, and aspect were also recorded from maps or ground measurements. Locations of each herd were recorded on a map of the study area (Appendix C., Cliff Creek Study Area).

Sheep herd composition was classified according to Geist (1971): lamb, yearling ewe, yearling ram, adult ewe, class I ram, class II ram, class III ram, class IV ram, unknown ewe or yearling, or unknown. Deer and elk were classed: fawn/calf, yearling doe/cow, yearling buck/bull, adult doe/cow, buck/bull, unknown antlerless, or unknown. Habitat type was determined from plant formation-associations (Steele et al.

1981). A "group" or "herd" was defined as a single species aggregation in which each animal was less than 45 meters from its nearest neighbor. When a group split into two groups or two groups of conspecifics merged during a 2 hour observation, the smaller groups were designated "subgroups" and data were recorded for each subgroup, but combined for analyses not related to group size.

The study area was searched for bighorn sheep, mule deer, and elk herds with 10X binoculars and a 20-60X spotting scope during each observation period. I observed herds on the study area from Taylor Ranch Field Station on the opposite hillside at distances of 200 to 1800 meters.

There was some bias in observability of animals when vegetation or topography interfered with observability, but this bias was the same among the 3 species. Poor observability primarily occurred in the forested areas and data likely under represented use of forest habitats. I felt that all 3 species were similarly detectable under most conditions. Some exceptions were: deer were less easily detected on grasslands than elk and bighorns, while bighorn sheep and deer were more difficult to detect than elk in the broken terrain of the mahogany outcrop habitat. Bedded animals and smaller herds were more difficult to detect. The problems of detectability were minimized by the use of 2-hour observation periods in which the study area was repeatedly searched 9-14 times.

Plant phenology was evaluated every 2 weeks to assess temporal changes in plant growth and foliage availability. Four grassland units were selected as phenology sites representative of the grassland habitat. Growth of new vegetation, was measured on 4 agropyron, 4 fescue, and 4 poa plants in each unit, including grass height, grass leaf blade length, and number of leaf blades. Forb height was measured and bud or seedhead development was rated at each site.

Herd Sizes and Population Parameters

Data were summarized from observation periods. Mean group sizes, numbers of groups, and numbers of animals per observation period were calculated. Most analyses were calculated using SAS program statistics (SAS Institute 1988) on a mainframe computer. Alpha level of significance is 0.05 unless otherwise stated. F-tests were used to determine differences in use of the study area by each species by season and year. Differences in seasonal habitat use among bighorn, deer, and elk were determined from the Cochran-Mantel-Haenszel chi-square statistic. Kruskal-Wallace and Wilcoxon's rank sums tests were used to test for significant differences in elevations and slopes used by bighorns, deer, and elk.

Activity Patterns

Several behavioral sampling methods were used to determine the time spent in various activities and the frequency of specific behaviors. These techniques included instantaneous scan sampling, nearest neighbor sampling, and event sampling.

Instantaneous scan sampling involves the observation of behaviors of all animals at the same time or of each animal at a specific time (Altmann 1974). It is a technique best used on behavioral states for interpreting activity budgets. Scan sampling was used in this study to determine diurnal activity budgets of sheep, deer, and elk. During each observation period all herds were scanned at 10 or 15 minute intervals and the behavior of every animal in each herd was recorded. Activity categories were feed, bed, stand, travel, comfort movements, paw, intraspecific interactions, interspecific interactions, other, and undefined or unknown behaviors. The frequency of each behavior category was summed for an observation period. Percent of time spent in each activity was calculated from frequency data. Scan sampling data were entered on the mainframe computer at the University of Idaho. Kruskal-Wallace and Wilcoxon's rank sum nonparametric tests were performed to test for differences in the proportion of time a herd spent feeding when mixed with another species or alone. Differences in feeding time as herds got closer or further away from each other were analyzed with Wilcoxon's signed rank tests.

Spatial Relationships of Two Species when in Close and Distant Association with Each Other

To evaluate the spatial relationships between species, categories were designated to denote the proximity to another species. For each herd, the nearest herd of another species within 300 meters was identified and designated the "nearest neighbor herd". If no other species was observed within 300 meters, that herd was considered to be "alone". When herds of two species were 45 meters or less from each other, these herds were termed a "mixed species" group; each referred to as being "with" the other herd. Two groups of different species that were more than 45 and less than 300 meters from each other were labeled "near" each other. Distances between herds less than 45 meters apart were estimated in animal body lengths (the distance from the base of the animal's neck to the base of the tail) using the conversion of one deer or sheep body length approximately equalling one meter. Further distances were ocularly estimated from known distance within the study area or from study area and USGS quadrangle maps.

Frequency distributions of the distances to nearest neighbors within 300 m of each other were plotted in 30 meter increments for each species-neighbor combination. Expected proportions for each of the 10 categories were determined from the formula (Ðr$_{X}$» - Ðr$_{X-30}$») - ð(Ðr$_{X}$» - Ðr$_{X-30}$») where x was the 30 meter increment between 0 and 300 meters. Chi-square goodness-of-fit tests were used to determine whether the observed distances to nearest neighbors differed from a random distribution. Wilcoxon's rank sum tests were used to compare the observed and expected distances to nearest neighbors for sheep with elk neighbors and elk with sheep neighbors, since sample sizes were too small for Chi-square analyses, with more than 20% of X" expected values less than 5 (Ott 1984). Random nearest neighbor distances were generated for the expected distances using the formula r=«(random number - Đ).

Chi-square goodness-of-fit tests were done to compare the occurrence of nearest neighbor pairs with their expected probability of being neighbors. Expected probability was determined from the relative frequency of occurrence of each of the 2 possible neighbor species during all observations. The null hypothesis was that neighbor pairs occurred in the same proportion as the 2 neighbor species occurred in all observations. Goodness-of-fit tests were also used to compare the proportions of both nearest neighbor species (μ300 meters away) and the relative occurrence of those two species during the study. A second chi-square goodness-of-fit analysis was done with data from spring and grassland habitat to compare the proportion of each species within 60 meters and the proportion of herds of each species observed during this time. Chi-square goodness-of-fit tests were done to compare the proportion of sheep herds mixed with elk and the expected proportion for all sheep herds.

Chi-square analyses of variance were used to test the relationships between 1.) proximity to nearest neighbor and species of nearest neighbor, 2.) presence of coyotes and mixed groups of bighorn sheep and elk, 3.) time of day and mixed grouping.

Median group sizes of each species were calculated when near each nearest neighbor species and when alone. The relationship between group size and the distance to nearest neighbor herd was analyzed using chi-square analysis of groups less than or equal to 5 or greater than 5, and nearest neighbor distances less than or equal to 45 meters or greater than 45 meters. The Wilcoxon's rank sum test was used for sheep and elk analyses to determine the relationship between group size and whether neighbors were mixed or near.

Chi-square analysis was used to evaluate the relationship between the proportion of mixed herds and season and time of day.

The Effect of Proximity to Another Species on Activity Patterns

Z-tests were done to determine whether activity patterns differed when a nearest neighbor herd was close and when a single species was alone, alpha level was set at 0.01 to decrease experimentwise error rate. Kruskal-Wallace nonparametric tests were used to determine whether a herd of one species spent a different proportion of time feeding or bedding when either of the other two species was within 300 meters (close) or neither of the other two species was within 300 meters (far or not present in the area). Wilcoxon's rank sum two sample nonparametric tests determined whether there was a difference in the proportion of time a herd of one species spent feeding or bedding when a herd of a second species was within 300 meters or when there were no herds of a different species within 300 meters. Data included in these analyses were from herds observed in grassland habitats during

Julian dates 61 through 140. Wilcoxon's signed rank one tailed test was used to compare the proportion of time each herd spent feeding when closer to another species and further.

RESULTS

Herd Sizes and Population Parameters

The Cliff Creek segment of the Big Creek winter range, the study area, was used primarily by bighorn sheep (Table 1). This area is of much greater importance to the population of bighorn sheep wintering on Big Creek than to deer or elk, because sheep only utilize a third of the range deer and elk use for wintering. Sheep and deer herds were observed in similar numbers, but since bighorn herd size was twice as large as deer, observations were made on almost twice as many sheep. Fewer elk herds were observed than either deer or sheep.

Table 1. Summary of herd observations from 1985 and 1986, Cliff Creek winter range.

	Total	Bighorn	Mule deer	Elk
Number of individuals (includes repeats)	5817	3430	1904	483
Number of herds	720	309	340	71
Mean number of groups per observation period	3.73	1.60	1.76	0.37
Mean number animals per observation period	30.2	17.8	9.9	2.5
Mean herd size		11.1	5.6	6.8
Herd size range		1-54	1-27	1-30

Seasonal Use of the Study Area

There was a significant difference in seasonal and annual numbers of bighorn sheep ($F=10.29$, $p<0.0001$) and mule deer ($F=10.15$, $p<0.0001$) in the study area, with season and year both being significant. Elk numbers in the study area also varied ($F=2.98$, $p<0.0055$), but only seasonal use was significantly different. Bighorns and mule deer each used the study area significantly more in spring than winter (Fig. 2). Although few elk used the study area, their use also increased in spring. Bighorn sheep and mule deer were observed in greater numbers in 1986 than in 1985. This was particularly apparent in late winter and early spring for deer and throughout the year for bighorn sheep (Fig. 2). Elk were observed in similar numbers in both years, except fewer elk used the study area in late spring 1986 than 1985 (Fig. 2).

Seasonal herd sizes varied between years. Herd sizes for all species increased from winter to spring and from each season in the first year to that season in the second year (Table 2). Proportional use of the study area by sheep, deer, and elk was similar for all season-year combinations, although in 1986 bighorns represented a slightly greater proportion of animals in both seasons. (Table 2).

Weather conditions during the two years of the study were similar. Maximum winter snow depths were 35-40 cm. Temperatures were normal to mild relative to the previous 3 years.

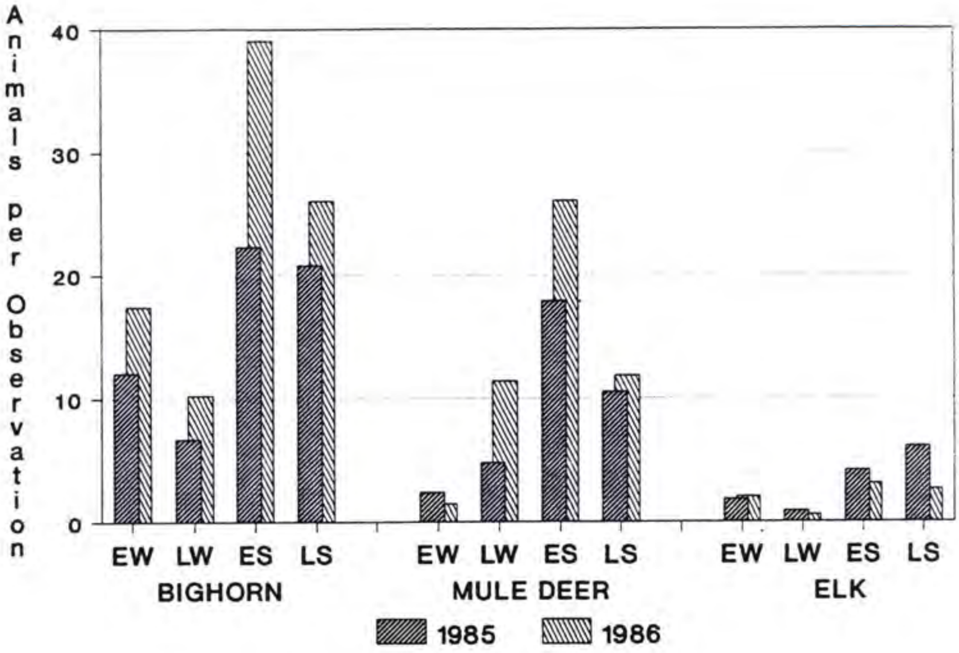
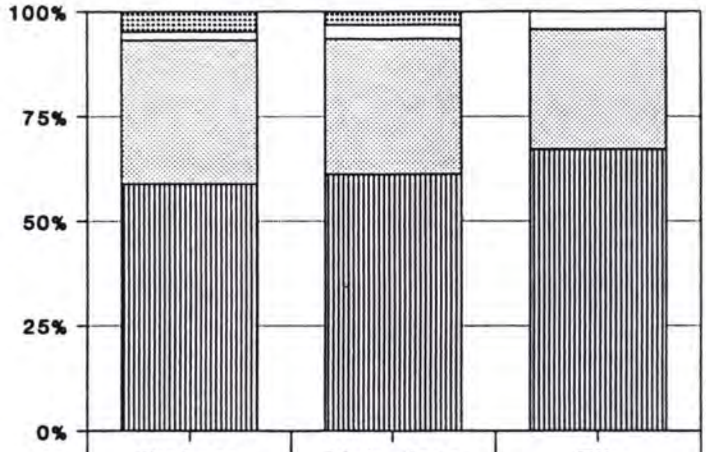


Fig. 2. Seasonal use of the Cliff Creek study area by bighorn sheep, mule deer and elk in 1985 and 1986. Seasons were early winter (EW): December 1 to January 30; late winter (LW): January 31 to March 11; early spring (ES): March 12 to April 10; late spring (LS): April 11 to May 30.

Table 2. Herd sizes, animals per observation, and proportions of bighorn sheep, mule deer, and elk by season and year.

	Winter		Spring	
Herd size	1985	1986	1985	1986
Sheep	8.43	11.04	10.28	13.10
Deer	4.17	4.95	5.54	6.59
Elk	2.84	6.73	9.23	7.47
Number of animals	1985	1986	1985	1986
Sheep	7.76	11.65	21.62	34.05
Deer	4.16	3.66	14.65	19.78
Elk	1.06	1.37	5.00	2.80
Proportion	1985	1986	1985	1986
Sheep	.60	.70	.52	.60
Deer	.32	.22	.36	.35
Elk	.08	.08	.12	.05



	Bighorn	Mule deer	Elk
Talus	15	11	0
Open Forest	6	11	3
Mahogany-Outcrop	104	108	20
Grassland	180	206	47

SPECIES

Fig. 3. Habitat use by bighorn sheep, mule deer, and elk herds. The table displays the number of herds observed in each habitat.

Habitat Use

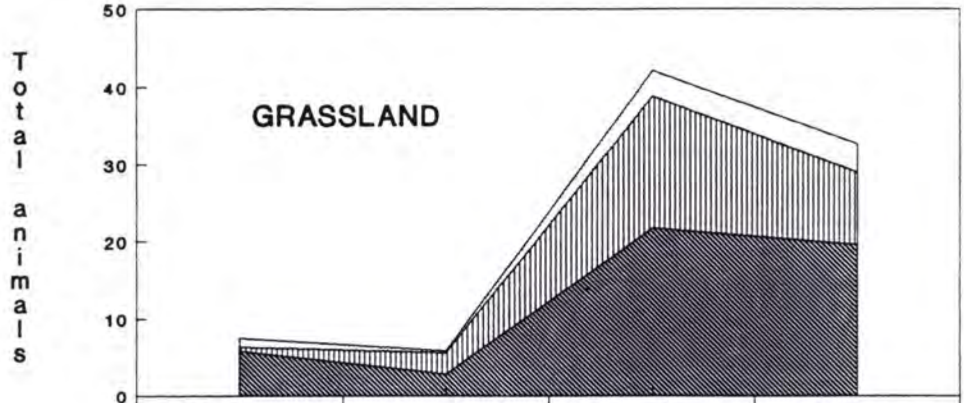
Bighorn sheep, deer, and elk used the four habitats in similar proportions (Fig. 3). There was no significant difference in habitat use among sheep, deer, and elk herds among 4 seasons (CMH X”=0.685, Á=0.05). Grassland was used most often. Mahogany-outcrop was also a frequently used habitat. Open forest and talus habitats were not common in the study area and had little use by any species.

Seasonal use of grassland habitats was low in early and late winter, then peaked in early spring and remained high until animals migrated from the study area (Fig. 4a). Mule deer left the study area after early spring, then elk departed in mid April, and several weeks later bighorn sheep began their migration to lambing and summer ranges.

Animal numbers in mahogany-outcrop habitats were similar in early winter, late winter, and early spring, then declined in late spring (Fig. 4b). Sheep use was highest in early winter, while more deer were observed in mahogany in late winter and early spring than in other seasons.

Bighorn sheep were more often in mahogany-outcrop in early and late winter, but were much more common in grassland in early and late spring (Fig. 5a). Seasonal deer habitat use was similar to sheep, except deer had a more gradual shift from mahogany to grassland (Fig. 5b). Elk spent more time in grassland habitats than mahogany in all seasons except late winter (Fig. 5c).

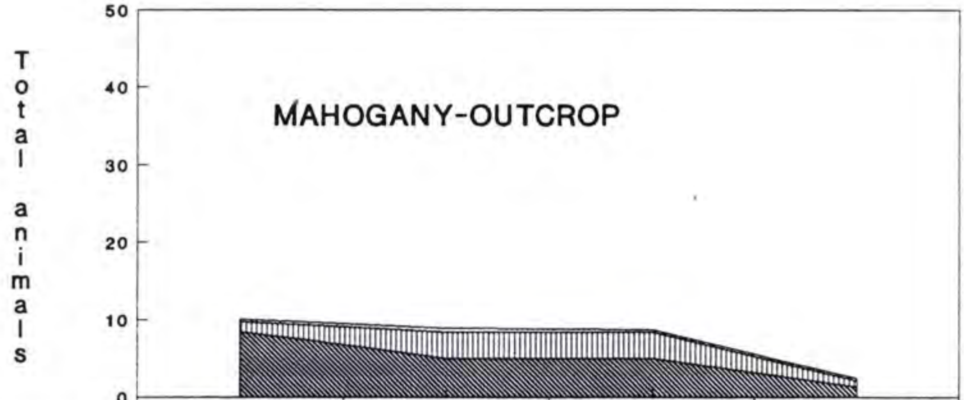
There was a significant difference in elevations used by bighorn sheep, deer, and elk herds in grasslands during spring (Kruskal-Wallis X”=19.70, p=0.0001). Elk were at higher elevations than both deer and sheep. There was no difference in the steepness of slopes used by bighorns, deer, or elk (Kruskal-Wallis X”=0.41, p<0.8129). Mean slopes for all species were 45-55% slope.



	Early Winter	Late Winter	Early Spring	Late Spring
Elk	1.2	0.2	3.3	3.7
Mule deer	0.5	2.8	17	9.4
Bighorn	5.8	2.8	21.8	19.6

SEASON

Bighorn Mule deer Elk



	Early Winter	Late Winter	Early Spring	Late Spring
Elk	0.4	0.5	0.3	0.3
Mule deer	1.2	3.4	3.4	0.8
Bighorn	8.5	5	5	1.3

SEASON

Bighorn Mule deer Elk

Fig. 4. Seasonal use of the grassland and mahogany-outcrop habitats by bighorn sheep, mule deer, and elk (mean number of animals per observation).

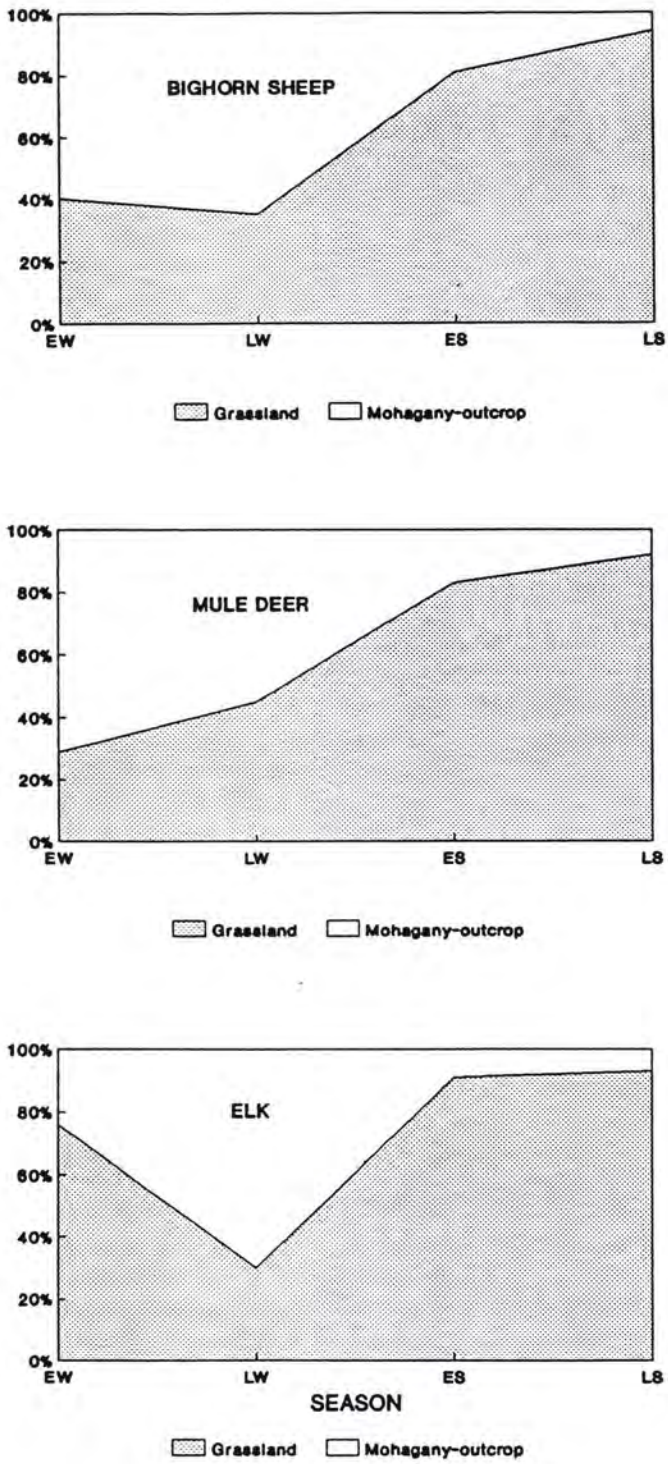


Fig. 5. Proportional use of grassland and mahogany-outcrop habitats by bighorn sheep, mule deer, and elk during 4 seasons: early winter (EW), late winter (LW), early spring (ES), late spring (LS).

Activity Patterns

A total of 30,287 scan data points were recorded, including 19,667 observations of sheep behavior, 8,258 of deer, and 2,362 of elk. Activity budgets of bighorn sheep, mule deer, and elk were very similar (Fig. 6), although the proportion of feeding and bedding varied throughout the winter-spring study period for each species. As the year progressed from winter to spring, bighorn sheep spent progressively less of their time feeding and more time bedding (Fig. 7a). Meanwhile, deer spent an increasing proportion of time feeding and less time bedding from winter to spring (Fig. 7b). Elk spent little time feeding on the study area in early winter, less in late winter, then dramatically increased their feeding time in spring (Fig. 7c).

Diurnal activity patterns were determined from activity budgets for each observation period hour. All three species had an early morning feeding peak, but the greatest proportion of feeding occurred at 4:00 pm (during the 3:00-5:00 pm observation period) for sheep and deer (Fig. 8a and 8b) and 6:00 pm for elk (Fig. 8c).

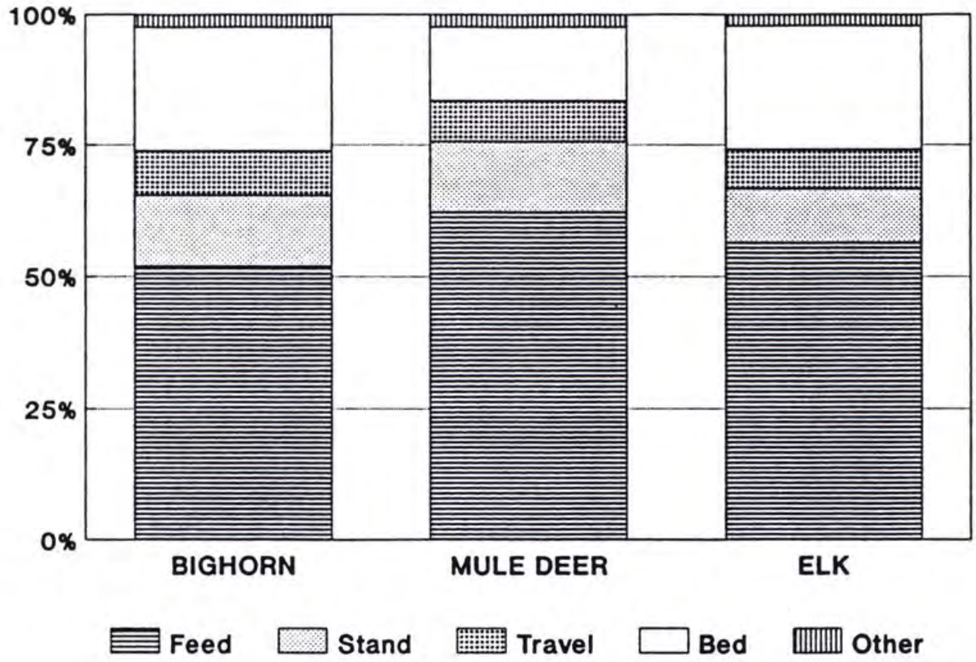


Fig. 6. Diurnal winter-spring activity budgets of bighorn sheep, mule deer, and elk on the Cliff Creek study area.

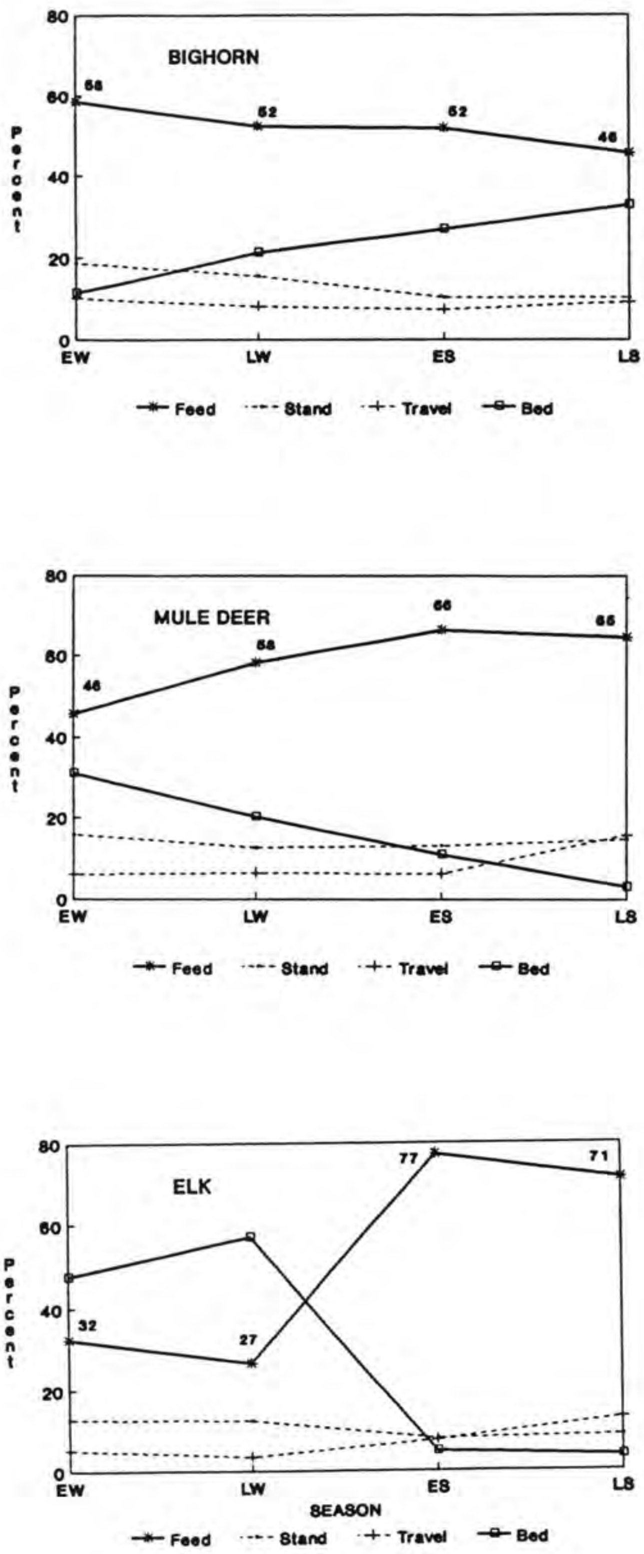


Fig. 7. Seasonal changes in activity of bighorn sheep, mule deer, and elk.

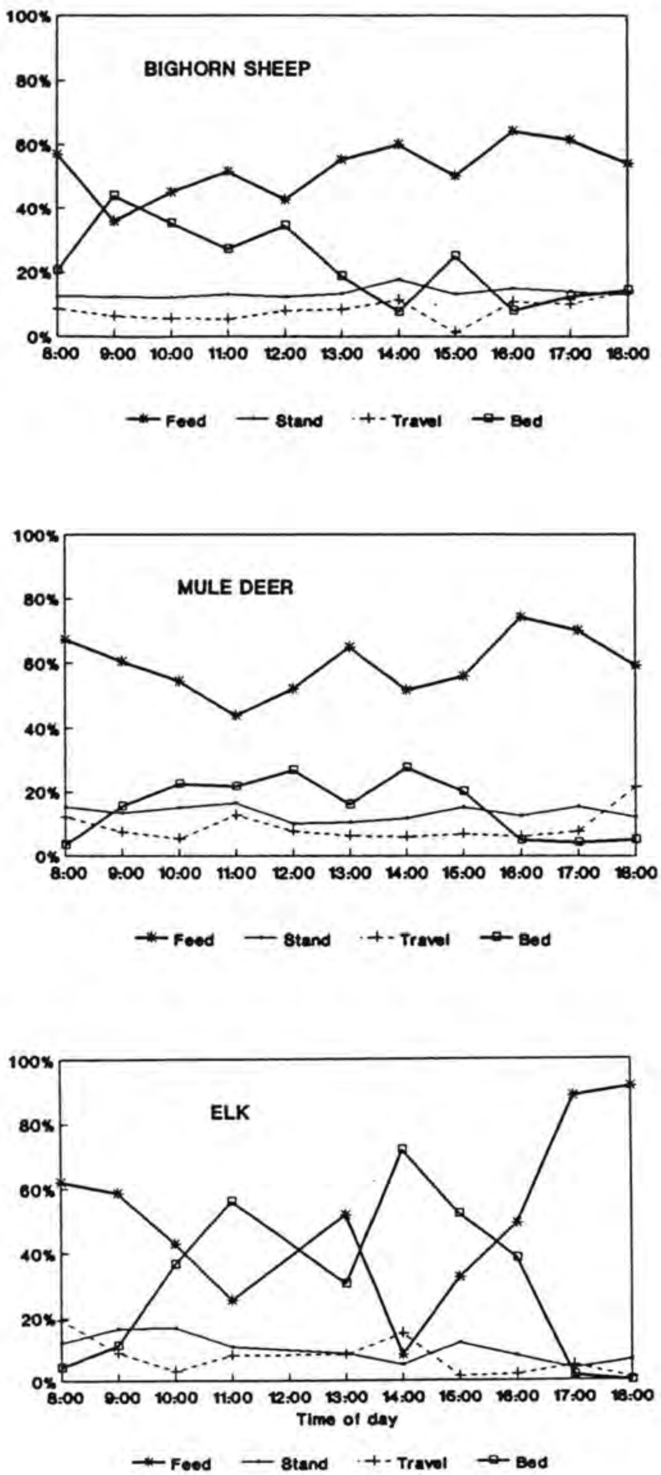
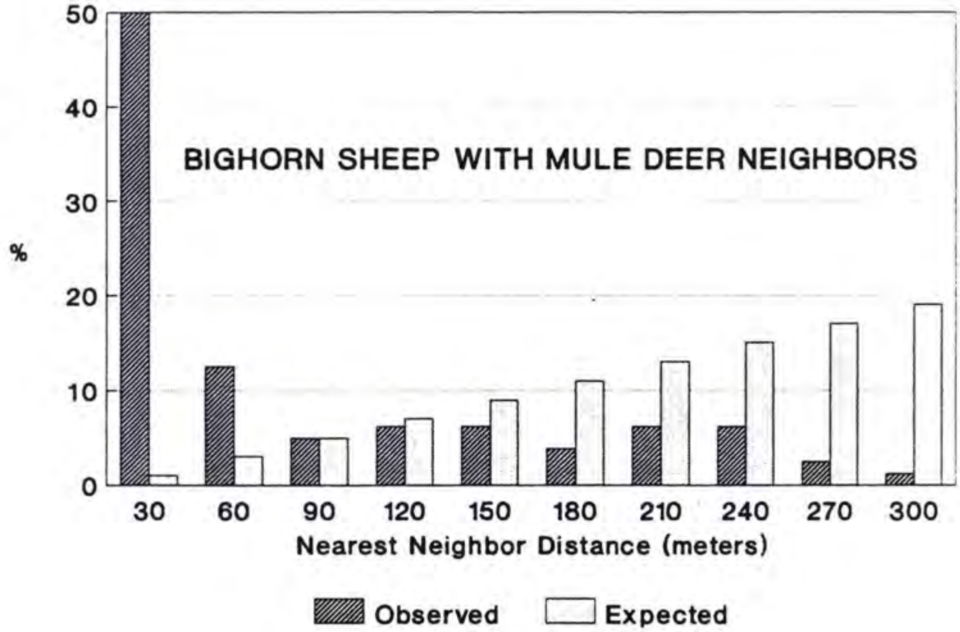


Fig. 8. Diurnal activity patterns of bighorn sheep, mule deer, and elk. Time of day is the median of observation time periods.

Spatial Relationships

Bighorn sheep, mule deer, and elk herds formed mixed species aggregations on the Big Creek winter range. Two herds were usually not intermingled, but were adjacent to each other with several individuals or one side of the group less than 45 meters from individuals of the other species. Sheep and deer were most commonly together and sheep and elk were least often together. When sheep and elk were together they were usually found in 3-way mixed species groups with deer.

Frequency distributions of nearest neighbor distance categories for sheep, deer, and elk showed that when another species is within 300 meters, all 3 species were often less than 30 meters from their nearest neighbor herd (Figs. 9 and 10). The high proportion of nearest neighbor distances within 30 meters indicates that the very close nearest neighbor distances may be advantageous to one or both species. The randomly expected proportions depicted a trend which was opposite of observed proportions. Sheep herds with deer as nearest neighbors, deer herds with sheep as nearest neighbors, deer herds with elk as nearest neighbors, and elk herds with deer as nearest neighbors all had nearest neighbor distributions that had significantly more close distances than expected from a random distribution pattern (Chi-square goodness-of-fit tests: $X^{2}_{8}=719.2$, $p<0.005$; $X^{2}_{8}=725.8$, $p<0.005$; $X^{2}_{2}=33.7$, $p<0.005$; $X^{2}_{2}=32.0$, $p<0.005$).



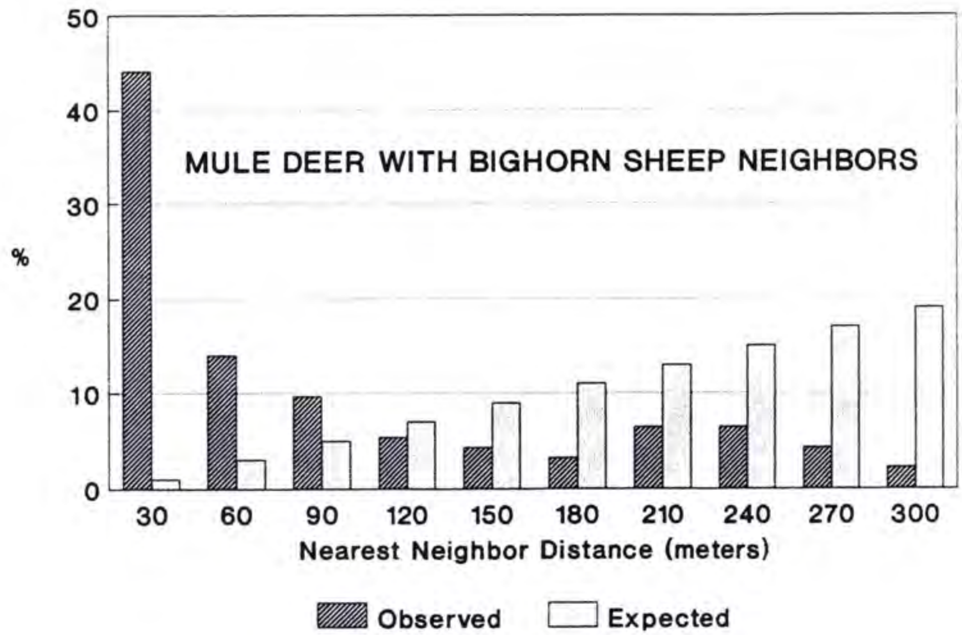
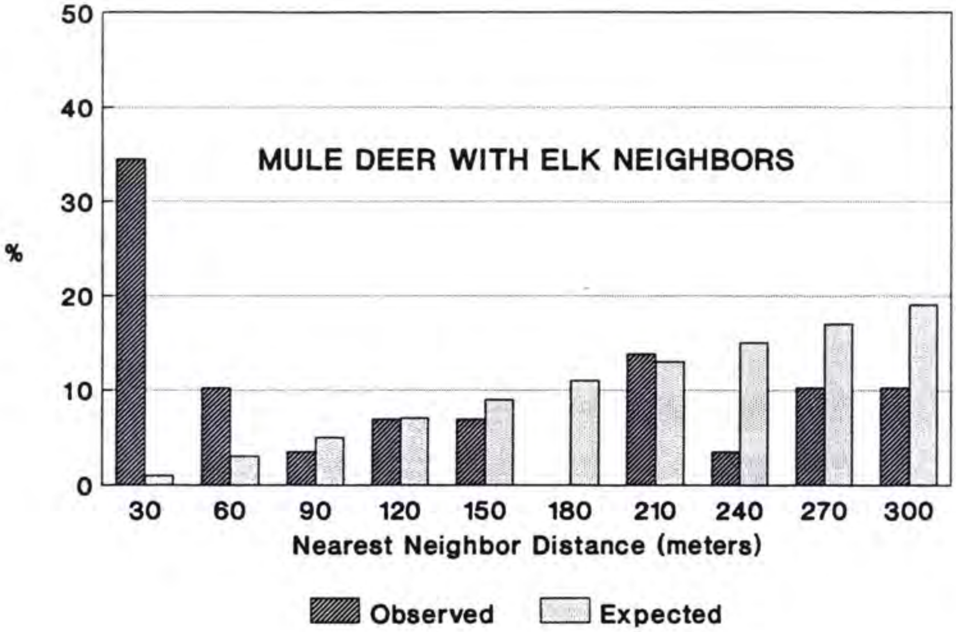


Fig. 9. Observed and expected frequencies of (a) bighorn sheep at varying distances from mule deer neighbors (n=80) and (b) mule deer at varying distance from bighorn sheep neighbors (n=93).



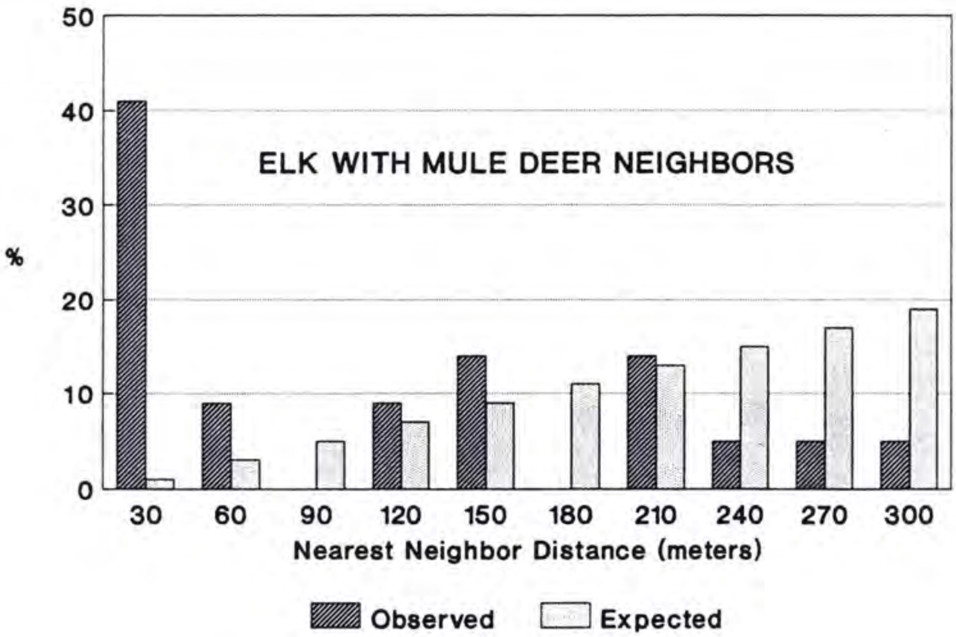


Fig.10. Observed and expected frequencies of (a) mule deer at varying distances from elk neighbors (n=29) and (b) elk at varying distances from mule deer neighbors (n=22).

Relationships of all pairs of neighbors when in mixed groups, near, and at distances greater than 300 meters were compared with expected frequencies based on the probability of that pair of species being nearest neighbors. Sheep and elk showed a negative association at close range and were in fewer mixed herds than expected (X^2=11.2, p<0.001), while deer and elk had a positive association and were more often "near" each other than expected (X^2=10.9, p<0.001). Sheep and deer occurred as expected from their probability (X^2=0.23, Á=0.05).

For each species, the relative proportions of both nearest neighbors were compared to their relative proportions throughout the study. Deer herds did not show any difference in their affinity to sheep or elk, since sheep herds were nearest neighbors and elk herds were nearest neighbors in the same proportion that sheep and elk herds were observed during the study (X”=2.54, Á=0.05). Sheep herds had significantly more deer herds and less elk herds as nearest neighbors (X”=6.13, p<0.025) than were predicted. Elk herds had significantly more deer herds and less sheep herds as nearest neighbors (X”=13.74, p<0.001). This analysis was repeated on the limited data set from grassland habitats during spring, comparing the relative frequency of each nearest neighbor species within 60 meters and the frequency of each species observed during spring in grassland. The results were the same as for data from all seasons and habitats: deer X”=0.04; sheep X”=5.94; elk X”=5.98. The net result of these tests was that sheep and elk were nearest neighbors and in mixed groups in spring less often than expected relative to the other neighbor pairs.

The proportion of sheep herds in mixed groups with elk as nearest neighbors was significantly less than expected for all observations of sheep ($X^2=5.58$, $p<0.025$ poisson distribution goodness-of-fit test) and elk were also less often in mixed groups with sheep neighbors ($X^2=5.87$, $p<0.025$ poisson distribution goodness-of-fit test).

The proportion of herds that were mixed with and near another species was determined for each species (Table 3). There was no relationship between nearest neighbor species and whether groups were mixed or near for sheep herds (X”=1.89, Á=0.05), deer herds (X”=0.74, Á=0.05), and elk herds (Z=1.05, Á=0.05).

Table 3. Proportion of mixed herds and near (but not mixed) herds.

	Sheep		Deer		Elk	
	NN=D	NN=E	NN=E	NN=S	NN=D	NN=S
% Mixed	55.0	35.7	48.8	56.3	48.6	30.0
% Near	45.0	64.3	51.2	43.7	51.4	70.0
Freq. Mixed	71	5	20	76	18	3
Freq. Near	58	9	21	59	19	7
Freq. Alone	160		149		23	

Sheep and elk were not often in mixed groups. They were nearest neighbors and in mixed groups in only 5 of 193 observation periods. When sheep and elk were together they were often in a 3 species aggregation of bighorn sheep, elk, and mule deer (Table 4). Coyotes were usually observed on the study area when sheep and elk were in mixed groups (Table 4). Although coyotes were seen in only 8 of 193 observation periods, they were observed 3 of 5 times that elk and sheep were mixed. The probability that on 3 occasions coyotes would be observed during the same observation when elk and sheep were in mixed groups was 0.00109, as determined from a poisson distribution. There was a strong positive relationship between the presence of coyotes on the study area and mixed groups of bighorn sheep and elk ($X^2=37.74$, $p<0.001$). The simultaneous occurrence of coyotes and mixed deer and elk herds was not significantly different than randomly expected ($X^2=1.65$, Á=0.05).

Table 4. Sheep and elk mixed group relationships.

Date	Herd Size		Other Species Present		Habitat
	Sheep	Elk	Deer	Coyote	
020 1985	20	3	no	no	mahogany
081 1985	5	18	mixed	no	grass
346 1985	12	5	mixed	mixed	grass
347 1985	26	5	near	near	grass
088 1986	16	7	mixed	far	grass

The proportion of sheep herds in mixed groups with deer and of sheep herds that were alone (nearest neighbor >300 meters away) were compared among seasons (winter and spring) and time of day (mid-day 10:00-16:00 vs morning and evening

7:00-10:00 am and 16:00-19:00). A greater proportion of mixed sheep and deer herds was observed in spring than winter (X”=15.28, $p<0.01$). During winter there was no relationship between the proportion of sheep herds mixed with deer herds and time of day (X”=3.0, Á=0.05), but during spring sheep were in mixed groups significantly more often in the early morning and late afternoon than mid-day (X”=12.39, $p<0.005$). There was no relationship between season and whether deer were alone or had elk as nearest neighbors ($X^2=3.76$, Á=0.05), and between season and whether elk were alone or had deer neighbors ($X^2=3.39$, Á=0.05).

In grassland habitats during spring deer were significantly closer to sheep than to elk (K-W $X^2=4.49$, $p=0.0342$). No differences were detected in the distances between sheep and their deer or elk neighbors (KW $X^2=1.04$, $p=0.3085$) and between elk and their sheep or deer neighbors (KW $X^2=0.27$, $p=0.6030$). Sample sizes of sheep-elk neighbors (n=4) were too small to detect a difference in distances. Mean nearest neighbor distances are listed in Table 5 for each nearest neighbor species.

Table 5. Mean nearest neighbor distance of bighorn sheep, mule deer, and elk herds by nearest species (when another species was <300 meters).

	Sheep		Deer		Elk	
NN Species	Deer	Elk	Sheep	Elk	Deer	Sheep
Distance (m)	81.3	124.6	76.2	99.3	88.7	133.7

The relationship between group size and the distance to nearest neighbor herd was analyzed to determine whether small groups were more likely to form mixed species herds, since smaller herds can gain greater antipredator benefits when they join another herd. In most cases group size did not differ among mixed groups and near groups (sheep with elk neighbors Wilcoxon rank sum Z=1.00, Á=0.05, deer with sheep neighbors X”=0.80, Á=0.05, and deer with elk neighbors X”=0.25, Á=0.05). There was a relationship between sheep group size and whether sheep were in mixed herds with deer or near deer (X”=7.23, p<0.001). When sheep were in mixed herds with deer they were more likely to be in larger groups of sheep (·6); when not mixed they were more often in smaller herds of 5 or fewer animals (Table 6).

In the grassland habitats during spring a linear regression analysis indicated there was an inverse relationship between sheep group size and distance to deer nearest neighbors (F=4.63, p<0.0348). No relationships were found between deer group size and distance to sheep neighbors (F=0.48, p<0.492) and sheep group size and distance to elk neighbors (F=0.03, p<0.8723).

Table 6. Mean group sizes when associated with each nearest neighbor, for all observations and only spring-grassland observations.

BIGHORN SHEEP		All seasons/habitats		Spring-grassland	
NN	Distance	Group size	S.E.	Group size	S.E.
Deer	mixed	12.59	1.28	14.76	1.75
Deer	near	8.50	1.03	9.94	1.57
Elk	mixed	15.80	3.56	10.50	5.50
Elk	near	12.22	3.85	11.33	6.74
None	alone	10.21	0.58	13.29	1.07
MULE DEER		**All seasons/habitats**		**Spring-grassland**	
NN	Distance	Group size	S.E.	Group size	S.E.
Sheep	mixed	5.95	0.60	6.78	0.87
Sheep	near	5.03	0.60	5.73	0.76
Elk	mixed	7.50	1.14	8.54	1.05
Elk	near	7.24	1.11	7.75	1.34
None	alone	5.21	0.32	6.57	0.58
ELK		**All seasons/habitats**		**Spring-grassland**	
NN	Distance	Group size	S.E.	Group size	S.E.
Deer	mixed	6.89	1.04	7.40	1.54
Deer	near	6.26	1.14	7.25	1.56
Sheep	mixed	5.00	1.15	7.00	
Sheep	near	5.43	1.71	6.00	1.53
None	alone	7.61	1.64	12.30	3.10

Effect of Proximity to Another Species on Activity Patterns

Statistical analyses of the effect of another species on activity patterns of bighorn sheep, deer, and elk were restricted to the spring-grassland period which included observations from Julian dates >60 to μ140 and within the grassland habitat. Sample sizes at this time and location were adequate, while season, weather, and habitat influences on activity patterns were minimized.

There was a relationship between nearest neighbor species and the proportion of time bighorn sheep herds spent feeding (Kruskal-Wallis p=0.044). Analysis of paired comparisons revealed that bighorn sheep herds spent significantly more time feeding when deer herds were close (µ300 m) than when sheep were alone (Wilcoxon rank sum test p=0.012). There were no significant differences in the proportion of time sheep herds spent feeding when elk were close or absent (Wilcoxon rank sum test p=0.512) and when deer or elk were close (Wilcoxon rank sum test p=0.978).

Kruskal-Wallis analysis of deer feeding behavior indicated that there was a weak relationship (p=0.067) between the proportion of time deer herds spent feeding and the identity of the nearest neighbor herd. Deer herds fed significantly more when they had elk neighbors than when deer were alone (Wilcoxon rank sum test p=0.015). There was no significant difference in the proportion of time deer herds spent feeding when they had bighorn sheep neighbors or when deer were alone (Wilcoxon rank sum test p=0.671); nor was there a difference when deer had sheep neighbors or elk neighbors (Wilcoxon rank sum test p=0.060, Bonferoni Á=0.017).

Differences in the proportion of time elk spent feeding when deer or sheep or neither species was close were not significant (Kruskal-Wallis test p=0.254). No further pairwise analyses were done on elk feeding time since the Kruskal-Wallace test did not show significance.

Bighorn sheep spent a different proportion of time bedded when associated with each nearest neighbor species (Kruskal-Wallis test $p=0.009$). Sheep herds spent significantly less time bedded when a deer herd was within 300 meters, than when deer were not close (Wilcoxon rank sum test $p=0.012$). There was no significant difference in the proportion of time sheep spent bedded when elk were close than when sheep were alone (Wilcoxon rank sum test $p=0.034$ Bonferoni Á=0.017). The proportion of time deer herds and elk herds spend bedded when other species were close or absent was not significantly different for either species (Kruskal-Wallis tests $p=0.701$ for deer and $p=0.676$ for elk).

Wilcoxon signed rank tests were used to evaluate the hypothesis that during a 2-hour observation period the proportion of time a herd spends feeding will be greater when it is closer to the nearest herd of another species and less when the herd is further from another species. No difference was detected in the proportion of time a deer herd spent feeding when that herd was closer or further from a herd of bighorn sheep ($p>0.05$, $n=15$). There was no difference in the proportion of time a bighorn sheep herd spent feeding when that sheep herd was closer or further from a herd of deer ($p>0.05$, $n=14$).

DISCUSSION

Ungulates make choices to optimize foraging and survival. This dynamic process includes responding to the presence of other species. Interspecific relationships reflect the benefits and costs of associating with another species. Bighorn sheep, mule deer, and elk using the Cliff Creek study area in winter influence the other species' distribution. Deer and sheep herds intermingled with each other often and likely benefitted from this relationship, while sheep and elk herds had little association.

Spatial Relationships

Bighorn sheep-mule deer and mule deer-elk neighbors were in closer association with each other than if they were randomly distributed. Sinclair (1985) postulated that the effect of interspecific competition, intraspecific competition, and predation would result in different trends in nearest neighbor distances between herds of different species. Herd distances between two species would be greater than randomly expected for interspecific competition, random for intraspecific competition, and closer than expected for predation.

Animal stocking levels and range quality can influence the benefits of mixed species aggregations. Mixed species groups should be preferred when stocking levels are low and range quality is high, since competition would be less intense and food habits should be more similar. Annual changes in the amount of mixed species grouping on a given range may reflect changes in quality of that range. One exception to the relationship between mixed species grouping and stocking level and range condition is when deep snow forces animals to be concentrated.

Bighorn - Elk Relationships

Bighorn sheep and elk generally responded to each other on the Cliff Creek study area by impartiality or avoidance. Elk spent little time on the study area. When elk were present they were usually far from bighorn sheep herds. Sample sizes were sometimes too small for detailed analyses of the relationship between sheep and elk.

In normal winters, like those which occurred during this study, Cliff Creek is not a significant elk winter range, but when snow is deep in the higher elevations, elk move into the more snow-free cliffs and outcrops favored by bighorns. Elk can impact sheep in several ways. They can directly compete for mountain mahogany during late winter when food is least available. They can also cause long term degradation to mountain mahogany winter ranges by excessive cropping.

Bighorn sheep and elk herds were less often nearest neighbors than expected. The reason they were not usually nearest neighbors may be the effect of competition or may be the result of differences in habitat preferences or spatial distribution unrelated to proximity of the other species. When sheep and elk were nearest neighbors they were statistically as likely to be in a mixed species group as were sheep and deer or deer and elk herds. The sample size of sheep and elk neighbors was small and may have prevented a difference from being statistically detected.

There was an attraction between sheep and elk herds when coyotes were observed on the study area. A pair of coyotes killed several bighorns on Cliff Creek during this study (pers. obs.). Elk were rarely preyed on by coyotes. Bighorn sheep may gain antipredator benefits from forming mixed species herds with elk. The statistically significant relationship between mixed sheep and elk herds and the presence of coyotes on the study area suggests that when predators are present, the benefits resulting from reduced predation risk outweigh the cost of increased competition. I believe that only after a predator is detected do groups of bighorn sheep and elk form mixed species herds. Since mixed herds of sheep and elk occur less often than expected, it appears that interspecific competition is usually a stronger force acting on sheep and elk than is predation.

In summary, at the present population level, elk use of the Cliff Creek study area does not appear to be harmful to bighorn sheep sharing this range. Although there is usually little contact between the two ungulates, sheep may gain a slight advantage against coyote predation by mixing with elk herds.

Bighorn - Deer Relationships

Bighorn sheep and mule deer had a positive association. They were more likely to be nearest neighbors and were closer to each other than sheep-elk or deer-elk herds. Sheep and deer were most likely to be observed in mixed groups during spring. At this time sheep and deer appeared to have similar diets, feeding in the grasslands on grasses and forbs between decadent bunches of wheatgrass. The frequent occurrence of mixed groups of bighorn sheep and mule deer on the Cliff Creek winter and spring ranges suggests that forage was not in short supply. Coyotes, the most common predator on the study area prey on sheep and deer. Both species should have a decreased risk of predation when in mixed groups, because of more rapid predator detection in a larger herd. Mule deer primarily use olfactory and auditory cues, while bighorns usually rely on their vision to detect predators. The use of multiple senses of deer and sheep in mixed groups should increase predator detection rates over a single species herd of the same size. Bighorn sheep and mule deer can mutually benefit from mixed species aggregations. Under Sinclair's hypothesis (1985) it appears that predation may influence the spatial relationship between bighorn sheep and mule deer more than interspecific or intraspecific competition, since sheep and deer herds were closer to each other than if they were randomly distributed. An alternative interpretation of the cause of the close association between bighorn sheep and mule deer is that the two species aggregate at mutually preferred feeding sites.

This hypothesis was not tested, but the observed grouping of sheep and deer herds was not likely to be caused by an attraction to a specific food source, because mixed herds occurred in many areas and food on the bunchgrass range in spring was abundant with a uniform or patchy distribution rather than localized distribution.

Sheep herds fed significantly more when with deer, but a herd did not alter the amount of time spent feeding as it approached or diverged from deer herds. The greater proportion of time sheep herds spent feeding when mixed with deer probably reflects factors such as concurrent feeding cycles and not an increase in feeding by sheep because of the presence of deer. I expected group size of each species in a mixed herd to be smaller than when in single species herds, if individual animals and small groups joined a group to obtain the greater antipredator benefits and foraging efficiency which occurs in larger groups. Berger (1978) found that individuals in groups of more than 5 bighorn sheep spend less time scanning their environment and more time feeding, but the benefits of larger group size do not increase as herd size increases beyond 5. Under this premise, only groups of 5 or fewer bighorns should receive additional predator detection benefits from forming mixed herds with deer or elk. On the contrary, I found that herd sizes of bighorn sheep were smaller when in herds of conspecifics than in mixed herds with deer as a nearest neighbor. Risenhoover and Bailey (1985) found that large groups of more than 10 bighorn sheep foraged

>100 meters from escape terrain significantly more than small groups. They suggested that foraging in large groups is a behavioral adaptation which allows sheep to use less secure habitats. The larger herd sizes I observed for bighorns with mule deer may reflect an increase in security for bighorns in a vulnerable situation. It is unclear whether the larger sheep group sizes observed when sheep were with deer is a correlation related to deer locations and distance to escape terrain, other factors, or whether sheep group size may reflect an insecurity by bighorn sheep about mixing with other species. Just as predation is a "perceived risk", sheep may perceive interspecific grouping as risky to the individual. An increase in conspecific group size may decrease the likelihood of an individual encountering interspecific aggression.

CONCLUSION

Observations were made of bighorn sheep, mule deer, and elk on the Cliff Creek study area during winter-spring 1985 and 1986. Weather conditions during these 2 winters and springs were within the normal range. The study area was primarily used by bighorn sheep and mule deer, and little used by elk.

Several statistical tests indicated that bighorn sheep behavior and distribution differed when another species was present then when it was absent. Interspecific competition or interspecific associations were the most plausible explanations for these differences, but other possible causes could not be statistically ruled out. As a result, my observations do not definitively show that bighorn sheep behavior and distribution was affected by interspecific relationships.

At population levels of bighorn sheep and elk in 1985 and 1986, there was little interaction between sheep herds and elk herds. If the Big Creek elk population continues to increase and uses the Cliff Creek bighorn sheep range more, then heavy elk browsing on mountain mahogany may decrease winter range habitat quality for bighorn sheep resulting in a decrease in sheep numbers or alternatively bighorn sheep may move from their traditional wintering area to avoid interspecific competition with elk.

Bighorn sheep and mule deer numbers were low enough to avoid interspecific competition. The common practice of bighorn sheep and mule deer herds feeding adjacent each other, particularly in the open grasslands during spring, likely reflected the lack of competition between these 2 species at this time of year. They might have even gained antipredator benefits by associating with each other.

Interspecific relationships, including interspecific competition, are dynamic processes. They can not be adequately investigated from observations at one point in time. Habitat selection and behavior of these ungulates may be expressions of the result of interspecific competition, as well as other environmental pressures. In order to separate the effects of interspecific competition from habitat and environmental influences, the interspecific relationships at a given site must be studied over time at various population levels, with other factors such as weather and habitat remaining fairly constant.

Since this study, the bighorn sheep population has declined more than 50% due to a disease related die off, while the elk population has continued to increase on Big Creek. There is an opportunity now, or in the near future to compare current habitat use, specifically site selection by bighorn sheep, elk, and mule deer with observations from this study to determine whether relationships between these species have changed since their numbers and relative abundance have changed.

RECOMMENDATIONS

This study of the spatial relationships of bighorn sheep revealed some interesting results about the relative relationships between bighorn sheep and deer and between bighorn sheep and elk. The possible costs and benefits of mixed species group formation were addressed in the discussion, but hypotheses related to antipredator advantages and interspecific competition were not tested. There is a relationship between group size and vigilance (Berger 1978, Caraco 1979, Lipetz and Beckoff 1982, Mangel 1990, Risenhoover and Bailey 1985, Rubenstein 1978). Individuals in larger groups spend less time in vigilant behaviors or (bighorns) feed further from escape terrain than solitary individuals or those in small groups. Studies of African ungulates have assessed the relationship between mixed species groups and risk of predation (Fitzgibbon 1990, Nievergelt 1981, Sinclair 1985).

I have several recommendations for additional research on the spatial relationships of bighorn sheep. Since relative and absolute numbers of bighorn sheep, elk, and mule deer on the Big Creek winter range have changed since this study, some of the recommendations are timely.

A. Examine the significance of the observed mixed species association between bighorn sheep and mule deer. Focal animal sampling can be used to see if there are relationships between: 1. foraging efficiency, 2. time spent in vigilance behavior, and 3. bighorn sheep distance to escape terrain when a herd is mixed with the other species or alone. Limiting observations to those which occur in spring and in grassland habitats will decrease variances within categories.

B. Determine whether changes have occurred in locations and habitats used by bighorn sheep and elk now that populations have changed. Changes can be assessed by mapping locations and determining habitat use by these species and comparing with the data collected during 1985 and 1986.

C. Assess the dynamics of the very large mixed groups. When do they form, why? Document occurrences, species composition, location, presence of predators and evaluate using multivariate analysis.

D. If there is a possibility that wolves will be introduced in central Idaho and may become established on the Big Creek winter range, there is a need to design a study to determine bighorn (and deer) foraging efficiency, distance to escape terrain, and frequency and characteristics of mixed groups. Data should be collected before and after establishment of a new predator to assess changes in behavior and foraging efficiency.

APPENDIX A

HISTORIC UNGULATE POPULATIONS OF THE BIG CREEK WINTER RANGE

Information about population sizes and relationships of bighorns, deer and elk on Big Creek was obtained from a variety of sources including game counts, diaries, letters, personal communications and oral histories, archaeological excavations and circumstantial evidence. Excavations of prehistoric Sheepeater Indian sites (120 to 2000 years ago) adjacent my study area, on lower Big Creek revealed that 90 percent of bone fragments found in Indian houses were from bighorn sheep and the remaining 10 percent were from deer (Thomas 1985). This may reflect the presence of a high number of bighorn sheep relative to deer and elk numbers at that time. Gold mining prospectors moved into the Big Creek canyon in the late nineteenth century and probably hunted whatever was available for meat and hides. A diary written by the Caswell brothers, miners living on lower Big Creek during 1895 to 1900 indicated that deer were killed frequently and sheep occasionally in lower Big Creek, while elk were taken infrequently, and only at higher elevations (Caswell 1900). From 1915 to 1934 Dave Lewis lived at Taylor Ranch in lower Big Creek and guided hunters in the area. Dave's hunters primarily hunted mule deer, black bear, and mountain goats (Lewis n.d., Loveland 1971). In 1940 the Forest Service made a spring game count on Big Creek (U. S. Forest Service 1940).

This census indicated that mule deer were abundant throughout the Big Creek winter range, bighorn sheep were locally common on the lowest section of Big Creek, and elk were uncommon, but occurred in several isolated sites in the middle section of winter range. Jess Taylor operated the Taylor Ranch as a hunting and fishing lodge from 1950 to 1970. He specialized in trophy bighorn sheep and mule deer, and steelhead, but also hunted mountain goats until the population declined and the season closed in the 1960s; Taylor began guiding elk hunters in the late 1960s (Loveland 1971, personal communication with Cliff Johnson, Boise, ID, a client and friend of Jess Taylor who hunted lower Big Creek from 1955 to 1986). Jess Taylor noted a decline in the deer population on lower Big Creek in the 1950s and a period of low bighorn lamb survival in the 1960s (Loveland 1971). Numbers of wintering elk have increased from 1940 to the present. One possible cause for the occurrence of large numbers of elk on the Big Creek winter range since the 1940s is that elk which traditionally spent the summer in the Chamberlain Basin area between Big Creek and the Salmon River may have been prevented from moving to their normal winter range on the Salmon River by a combination of hunter pressure and heavy snows in late fall (personal communication with Maurice Hornocker, Sun Valley, ID). The elk became established on this new range. It is unclear why elk were not common inhabitants of the Big Creek winter range before 1940. Idaho Fish and Game fixed wing spring greenup counts on Big Creek from 1960s to 1989 show an upward trend in elk numbers (Idaho Fish and Game n.d.). Aerial counts of mule deer and bighorn sheep have been conducted in many years since 1973 (Idaho Fish and Game n.d.). The results are graphed in Fig. 1.

APPENDIX B

FORBS OF THE STUDY AREA GRASSLANDS LISTED IN ORDER OF THEIR PHENOLOGICAL DEVELOPMENT

Hieracium albiflorum
Gilia aggregata
Lithophragma bulbifera
Lithophragma parviflora
Eriogonum heracleoides
Achillea millefolium
Ranunculus glaberrimus
Cymopterus terebinthinus
Cirsium utahense
Taraxacum officinale
Fritillaria pudica
Phlox longifolia
Collinsia parviflora
Draba verna
Draba spp.
Balsamorhiza sagittata
Astragalus arrectus
Astragalus purshii
Lomatium spp.
Lupinus sericeus
Viola purpurea
Brodiaea douglasii
Castilleja spp.
Phacelia linearis

APPENDIX C

FIELD DATA FORMS

SCAN SAMPLE

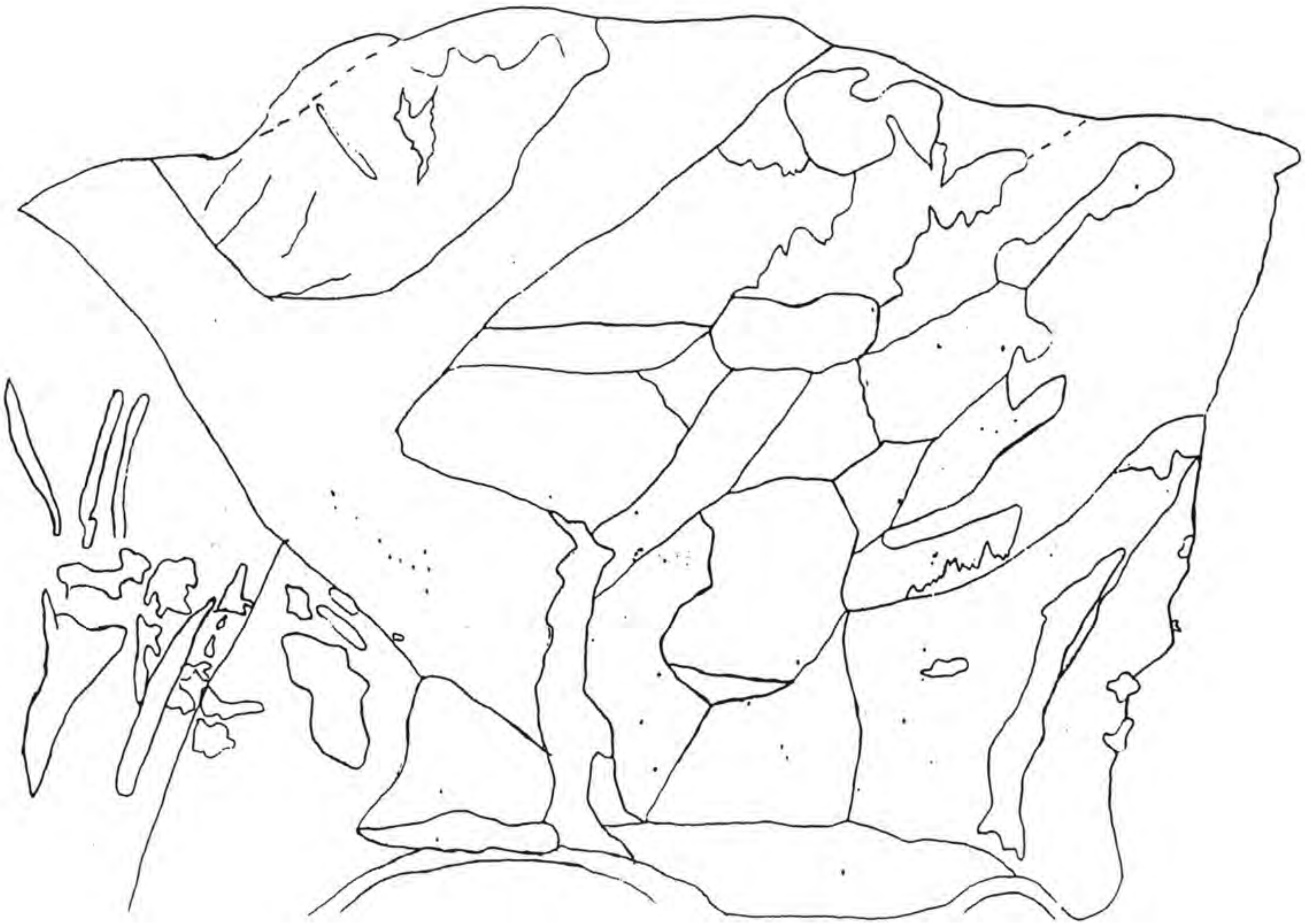
Date ☐☐☐☐☐ Obs. ☐ Species ☐☐ Time ☐☐☐☐

Snow Depth ☐☐ condition ☐ percent ☐☐☐ Temp. ☐☐☐

Cloud ☐☐☐ precip ☐ Herd Size ☐☐ Sex/Age ♂ ☐☐☐☐☐☐☐ ♀ ☐☐☐☐☐☐☐

Time	F S T B U	TOTAL	UA	NearestNeighbor	Dist. to other Species

CLIFF CREEK STUDY AREA



LITERATURE CITED

Akenson, J. J. and H. A. Akenson. 1992. Bighorn sheep herd composition and movements to lambing areas and summer ranges on Big Creek in central Idaho. Bienn. Symp. North. Wild Sheep and Goat Counc. 8.

Alderman, J. A., P. R. Krausman, and B. D. Leopold. 1989. Diel activity of female desert bighorn sheep in western Arizona. J. Wildl. Manage. 53:264-271.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227-267.

Batcheler, C. L. 1960. A study of the relations between roe, red and fallow deer, with special reference to Drummond Hill Forest, Scotland. J. Anim. Ecol. 29:375-384.

Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. Sci. Am. 225:86-93.

Berger, J. 1978. Group size, foraging, and antipredator ploys: an analysis of bighorn sheep decisions. Behav. Ecol. Sociobiol. 4:91-99.

Berger, J. 1979. Predator harassment as a defensive strategy in ungulates. Am. Midl. Nat. 102:197-199.

Buechner, H. K. 1960. The bighorn sheep in the United States, its past, present, and future. Wildl. Monogr. 4. 174pp.

Capp, J. C. 1968. Bighorn sheep, elk, mule deer range relationships: a review of literature. Rocky Mt. Nat. Assoc. and Colorado State Univ., Fort Collins. 75pp.

Caraco, T. 1979. Time budgeting and group size: a test of a theory. Ecology 60:618-627.

Caswell, B. 1900. Caswell Diary 1895-1900. Idaho State Historical Collection, Boise, Idaho.

Claar, J. J. 1973. Correlation of ungulate food habits and winter range conditions in the Idaho Primitive Area. M. S. Thesis. Univ. of Idaho, Moscow. 85pp.

Collins, W. B., and P. J. Urness. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. J. Wildl. Manage. 47:646-663.

Constan, K. J. 1972. Winter foods and range use of three species of ungulates. J. Wildl. Manage. 36:1068-1076.

Cooperrider, A. Y., S. A. McCollough, and J. A. Bailey. 1980. Variation in bighorn sheep food habits as measured by fecal analysis. Proc Bienn. Symp. North. Wild Sheep and Goat Counc. 2:29-41.

Cowan, I. McT. 1947. Range competition between mule deer, bighorn sheep, and elk in Jasper Park, Alberta. Trans. North Amer. Wildl. Conf. 12:223-227.

Dale, A. R., and J. A. Bailey. 1982. Application of optimal foraging theory for bighorn sheep habitat evaluation. Proc. Bienn. Symp. North. Wild Sheep and Goat Counc. 3:254-261.

Fitzgibbon, C. D. 1990. Mixed species grouping in Thomson's and Grant's gazelles: the antipredator benefits. Anim. Behav. 39:1116-1126.

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

Geist, V. and R. G. Petocz. 1977. Bighorn sheep in winter: do rams maximize reproductive fitness by spatial and habitat segregation from ewes? Can. J. Zool. 55:1802-1810.

Haas, W. L. 1979. Ecology of an introduced herd of Rocky Mountain bighorn sheep in southcentral Wyoming. M. S. Thesis. Colorado State Univ., Fort Collins. 343pp.

Hamilton, W. D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31:295-311.

Hediger. 1940. Page 76, cited in W. Leuthold. 1977. African ungulates: a comparative review of their ethology and behavioral ecology. Eighth ed. Springer-Verlag, Berlin. 307pp.

Hobbs, N. T., D. L. Baker, and R. B. Gill. 1983. Comparative nutritional ecology of montane ungulates during winter. J. Wildl. Manage. 47:1-16.

Hobbs, N. T., and R. A. Spowart. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. J. Wildl. Manage. 48:551-560.

Horejsi, B. 1975. Page 103 in J. B. Trefethen, ed. The wild sheep in modern North America: Proceedings of the workshop on the management biology of North American wild sheep. The Winchester Press, NY. 302pp.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monogr. 21. 39pp.

Hunter G. and R. E. Pillmore. 1954. Mountain sheep drive mule deer from food. J. Mammal. 31:193.

Idaho Department of Fish and Game. 1981. Species management plan, trophy species: moose, bighorn sheep, mountain goat, pronghorn antelope, 1981-1985. IDF&G, Boise, ID.

Idaho Department of Fish and Game. n.d. Miscellaneous records from spring greenup counts of bighorn sheep, mule deer, and elk in the Big Creek drainage, 1960-1992. Unpublished reports, McCall Subregion IDF&G, McCall, ID.

Keating, K. A., L. R. Irby, and W. F. Kasworm. 1985. Mountain sheep winter food habits in the upper Yellowstone Valley. J. Wildl. Manage. 49:156-161.

Kindel, F. et al. 1949-1970. Idaho game populations census and range study. F. A. Idaho Project No. W-85-R. Boise.

Kramer, A. 1973. Interspecific behavior and dispersion of two sympatric deer species. J. Wildl. Manage. 37:288-300.

Lauer, J. L. and J. M. Peek. 1976. Big game-livestock relationships on the bighorn sheep winter range, East Fork Salmon River, Idaho. Forest and Wildl. Range Exp. Sta. Bull. No. 12. 44pp.

Leuthold, W. 1977. African ungulates: a comparative review of their ethology and behavioral ecology. Eighth ed. Springer-Verlag, Berlin. 307pp.

Leuthold, W. 1978. Ecological separation among browsing ungulates in Tsavo East National Park, Kenya. Oecologia 35:241-252.

Lewis, D. n.d. Dave Lewis historical collection of letters and documents. University of Idaho Archives, Moscow, ID.

Lipetz, V. E. and M. Bekoff. 1982. Group size and vigilance in pronghorns. Z. Tierpsychol. 58:203-216.

Loveland, R. 1971. Tape recorded interview of Jess Taylor. University of Idaho Wilderness Research Center Collection, Moscow, ID.

Mackie, R. J. 1981. Interspecific relationships. Pages 487-507 in O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln. 605pp.

Mangel, M. 1990. Resource divisibility, predation, and group formation. Anim. Behav. 39:1163-1172.

McCollough, S. A., A. Y. Cooperrider, and J. A. Bailey. 1980. Impact of cattle grazing on bighorn sheep habitat at Trickle Mountain, Colorado. Proc Bienn. Symp. North. Wild Sheep and Goat Counc. 2:42-59.

McCullough, D. R. and E. R. Schneegas. 1966. Winter observations on the Sierra Nevada bighorn sheep. Calif. Fish and Game 52:68-84.

Murie, O. J. 1941. The elk of North America. Stackpole Co., Harrisburg, Pa. 376pp.

Nelson, J. R. 1982. Relationships of elk and other large herbivores. Pages 415-441 in J. W. Thomas and D. E. Toweill, eds. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pa. 698pp.

Nievergelt, B. 1981. Ibexes in an African environment: ecology and social system of the Walia ibex in the Simen Mountains, Ethiopia. Springer-Verlag, Berlin. 189pp.

Oldemeyer, J. C., W. J. Barmore, and D. L. Gilbert. 1971. Winter ecology of bighorn sheep in Yellowstone National Park. J. Wildl. Manage. 35:257-269.

Ott, L. 1984. An introduction to statistical methods and data analysis. 2nd ed. Duxbury Press, Boston, Mass. 775pp.

Pfister, J. A., F. San Martin, L. Rosales, D. V. Sisson, E. Flores, and F. C. Bryant. 1989. Grazing behaviour of llamas, alpacas and sheep in the Andes of Peru. Appl. Anim. Behav. Sci. 23:237-246.

Ratcliff, H. M. and L. Sumner. 1945. National park wildlife ranges. Trans. North Amer. Wildl Conf. 10:246-250.

Risenhoover, K. L., and J. A. Bailey. 1980. Visibility: an important habitat factor for an indigenous, low-elevation bighorn herd in Colorado. Bienn. Symp. North. Wild Sheep and Goat Counc. 2:18-28.

Risenhoover, K. L., and J. A. Bailey. 1985. Foraging ecology of mountain sheep: implications for habitat management. J. Wildl. Manage. 49:797-804.

Rubenstein, D. I. 1978. On predation, competition, and the advantages of group living. Pages 205-231 in P. P. G. Bateson and P. H. Klopfer, eds. Perspectives in ethology. Plenum Press, New York.

SAS Institute, Inc. 1988. SAS/STAT user's guide, release 6.03 ed. SAS Institute, Inc., Cary, NC. 1028pp.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. BioScience 37:789-799.

Severson, K. E. and A. L. Medina. 1983. Deer and elk habitat management in the southwest. J. Range Manage. Monog. No. 2. 64pp.

Simmons, N. M. 1962. Daily and seasonal movements of Poudre River bighorn sheep. Trans. Desert Bighorn Council 9:89-92.

Sinclair, A. R. E. 1985. Does interspecific competition or predation shape the African ungulate community? J. Anim. Ecol. 54:899-918.

Smith, D. R. 1951. The life history and ecology of the bighorn sheep in Idaho. M. S. Thesis. Univ. Idaho, Moscow.

Smith, D. R. 1953. Idaho bighorn sheep studied. Idaho Wildl. Review 5:4-7, 10.

Smith, D. R. 1954. The bighorn sheep in Idaho, its status, life history and management. Idaho Fish and Game Dep. Wildl. Bull. 1. 154pp.

Spowart, R. A., and N. T. Hobbs. 1985. Effects of fire on diet overlap between mule deer and mountain sheep. J. Wildl. Manage. 49:942-946.

Steele, R., R. D. Pfister, R. A. Ryker, and J. A. Kittams. 1981. Forest habitat types of central Idaho. USDA For. Serv. Gen. Tech. Rep. INT-114, Intermt. For. and Range Exp. Sta., Ogden, Utah. 138pp.

Thomas, F. S. 1985. Mountain sheep and mountain sheep hunters. M. S. Thesis. Univ. of Idaho, Moscow.

Tilton, M. E., and E. E. Willard. 1981. Winter food habits of mountain sheep in Montana. J. Wildl. Manage. 45:548-553.

Trefethen, J. B., ed. 1975. The wild sheep in modern North America: Proceedings of the workshop on the management biology of North American wild sheep. Boone and Crockett Club, The Winchester Press, NY. 302pp.

Underwood, R. 1982. Vigilance behaviour in grazing African antelopes. Behavior 79:81-107.

U. S. Forest Service. 1940. Report of spring big game census of Big Creek. Unpublished document, Krassel Ranger District, McCall, ID.

Wilson, L. O. 1975. Pages 103-104 in J. B. Trefethen, ed. The wild sheep in modern North America: Proceedings of the workshop on the management biology of North American wild sheep. The Winchester Press, NY.