

BIGHORN SHEEP OF THE TETON RANGE, WYOMING: ECOLOGY OF A REMNANT POPULATION

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ABSTRACT

Man's activities in the Teton Range since settlement in the late 1800's have drastically altered bighorn sheep (*Ovis canadensis canadensis*) numbers, distribution, and habitat conditions in the Range. Major historical impacts were domestic livestock grazing and associated diseases, excessive hunting, restriction of winter ranges, curtailment of natural wildfire, and loss of genetic communication with other bighorn populations. Today's Teton Range bighorn population is restricted to two small portions of its former range. On summer ranges, Teton Range sheep select habitat with greater terrain roughness, gentler slopes, and closer proximity to escape terrain than found randomly, or than reported from other studies of bighorns. Teton Range sheep are more generalized foragers than reported from other populations, with shrubs used to a high degree in summer. Bighorns avoid areas of concentrated recreational use. In winter, sheep are isolated on patches of high, windswept tundra. Teton bighorn display many characteristics associated with low quality, relict populations, and inbreeding is probable. Continued domestic sheep grazing and hunting, increased recreational activity, and potential competition with introduced mountain goats (*Oreamnos americanus*) may threaten the long-term existence of bighorn sheep in the Teton Range.

INTRODUCTION

Man and wild sheep have coexisted throughout the Rocky Mountains for over 9,000 years (Miller 1972). At the appearance of Euro-Americans in Wyoming and Idaho, bighorn sheep were among the most successful ungulate found (Honeess and Frost 1942, Smith 1954). However, settlement in the late 1800's brought about the general decline of wild sheep populations throughout the west (Buechner 1960).

Geist (1971) observed how natural bighorn populations use their habitats through occupation of as many as six seasonal home ranges. However, bighorn use of the habitats available to them varies greatly among localities (Blood 1963, Woolf et al. 1970, Johnson 1980). Remnant populations, such as that of the Tetons, lose portions of their former ranges, with resultant losses in long-term viability (Woodard et al. 1974). Low-quality bighorn populations, which exhibit slow-growing rams (Geist 1971), low survivorship of lambs to yearling age (Buechner 1960), and relatively small group sizes (Leslie 1977), may learn inefficient traditions of habitat use (Geist 1971).

At the initiation of our study in 1976, little was known about the bighorn sheep of the Teton Range. Our objectives were to document a historical perspective of bighorns in the Tetons, to delineate seasonal distributions, and to measure how seasonal distributions are related to selected biotic and abiotic factors.

This study resulted from cooperation among three agencies. The authors acknowledge S. Johnson, Targhee National Forest, G. Roby, Wyoming Game and Fish Department, and W. Barmore, Grand Teton National Park for advice and assistance throughout the study. S. Gregory collected and identified most of the plants. J. Anderson, T. Ore, and J. Baily reviewed the manuscript. The University of Wyoming-National Park Service Research Centre funded winter flights.

STUDY AREA

The Teton Range is in the northwest corner of Wyoming adjacent to the Idaho/Wyoming State boundary. The range is approximately 25 km east-west by 60 km north-south. Elevations vary from 1230-4198 m. The range trends north-south with lands of Targhee National Forest (TNF) on the west slope and Grand Teton National Park (GTNP) on the east slope.

A westerly dipping fault block, the Tetons feature jagged crystalline peaks of Precambrian gneiss and schist at their center. Eroded limestone of Mississippian age is 1,000 feet thick in the north, west, and south of the range. Soils are typically thin, dark loams which rest over weakly-developed, stony subsoils (Nelson 1971). The Teton Mountains are typically warm in summer (27°C maximum) and cold in winter (-45°C minimum), with snow depths commonly in excess of 4 m at elevation 2440 m.

Daubenmire (1978) described a subalpine fir (*Abies lasiocarpa*)/Engelmann spruce (*Picea engelmannii*) province above 2450 m on the south and west slopes. A shrub belt, dominated by currants (*Ribes* spp.), marks the transition between subalpine fir/Engelmann spruce and alpine tundra associations (Daubenmire 1978). Above 3050 m, the alpine tundra zone is vegetated by a diversity of graminoids, forbs, and dwarf willows (*Salix* spp.) (Spence and Shaw 1981). Potential bighorn competitors include elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and introduced mountain goats. Potential predators include coyote (*Canis latrans*), mountain lion (*Felis concolor*), grizzly bear (*Ursus arctos*), and golden eagle (*Aquila chrysaetos*).

METHODS

PAST POPULATIONS

Journals, letters, and narratives of trappers, topographers, and hunters hinted at presettlement sheep distribution. Information on postsettlement bighorn distribution came from personal interviews with longtime residents of the valleys that surround the Teton Range. This information is supplemented from records filed at Grand Teton National Park, Moose, Wyoming and Targhee National Forest, Ashton and Driggs, Idaho.

PRESENT SEASONAL DISTRIBUTIONS

Seasonal distributions were assessed by ground reconnaissance of the entire range and periodic helicopter and fixed-wing flights along preselected routes. Ground travel routes were planned to allow maximal survey with a 25-40 power spotting scope. Sex and age classification followed Geist (1971).

HABITAT CHARACTERISTICS

In the southern portion of the Range a study area which met generalized habitat criteria (Honeess and Frost 1942, Geist 1971) was divided into 200 x 200 m grids on 7.5-minute topographic maps. We randomly selected 81 intersection points from these grids for habitat analysis samples. At each sample point, we measured elevation with an altimeter, percent slope (general area) with a clinometer, and general aspect as a compass bearing. We estimated the straight line distance to areas subjectively defined as escape terrain. Topographic roughness was expressed as the square root of the summed deviations of four defined slopes from the general slope (T. Ore pers. comm.). The four defined slopes were 50 m to the right and left of the sample point perpendicular to the general slope, and 50 m up slope and 50 m down slope. Possible values ranged from 0 to 180. As an example, a value of 60 could result if the general slope of a canyon wall and the specific right, left, and up slope values were 30°, and a vertical cliff (90°) was located 50 m down slope from that sample point. Soil samples were analyzed for percent of key elements.

Ground cover was sampled on a 50 m transect along the contour in a standardized direction from the sample point. Cover transects were actually completed at 42 of the 81 randomly selected points during summer (1 July - 15 September), although transects were completed at all 81 points in spring (15 June - 1 July). During summer cover transects were completed at 12 additional sites where bighorns were observed in winter. Canopy cover was estimated for all plant species in 20 2 x 5 dm frames placed at regular intervals along the transect, and midpoints were recorded for percent-class intervals (Daubenmire 1959). We recorded cover by litter, bare ground, and rock in the same percent classes. Two 1/10 m² biomass plots were clipped from each spring and summer sample transect. Tree cover was measured in 5 x 20 m rectangles which originated at a sample point. Fecal pellets were collected for microhistological analysis to determine food habits (Sparks and Malechek 1968) at Colorado State University. Bighorn fecal pellet groups were counted within a 2 x 50 m belt along each transect line. Observations or evidence of human activity, domestic animals, and wildlife were recorded.

We recorded habitat features at 57 specific sites where bighorns were observed feeding or bedding during the summers of 1976-1983. At these sites, we measured physical features as described above, recorded major plant species, and estimated percent cover by major growth form.

Summer recreational use of the West Slope of the Tetons was characterized through concurrent recreation studies from 1976-1979. Visitor use from late June to mid-September was estimated through randomized trailhead and backcountry route samples. At trailheads we used 12 h samples correlated with infrared traffic counters. In the backcountry, we walked defined routes through destination areas on randomly selected evenings to estimate camper use.

RESULTS AND DISCUSSION

PAST POPULATIONS

Precise estimates of presettlement and early postsettlement bighorn populations in the Tetons are not available. Several journals and 87 old-timer reports point to the early and immediate effect of settlement on Teton Range sheep. Settlement of Teton Valley, Idaho, and Jackson Hole, Wyoming, began in the 1880's, and by 1900 at least 1,000 people lived in Teton Valley (Green 1974). Human activity in the West Slope of the Tetons was more widespread than at any time before or since the settlement era. Small sawmills sprang up in most of the canyon bottoms. Prospectors scoured the mountains and developed mines in Berry Creek, Moran Canyon, Bitch Creek, Death Canyon, Darby Canyon, and Fox Creek, all within or near bighorn habitat. Immense numbers of domestic sheep grazed the entire West Slope and portions of present day GTNP. Trappers and big game hunters were active throughout the Range in all seasons.

Bighorn sheep populations in areas which adjoin the Tetons-the Gros Ventre, Snake River, and Big Hole Mountains-declined or became extinct early in the postsettlement era. These populations had probably exchanged genetic material with Teton Range sheep. Bighorns were effectively eliminated from most low elevation habitat by 1900. Teton Range sheep made sporadic winter use of the Gros Ventre Buttes, lower Rendezvous Mountain, Bitch Creek, and Fox Creek into the 1930's, but were eliminated from these ranges by continued human developments. In the northern West Slope, bighorns were restricted to rugged, inaccessible terrain on the crest of the Range. At the extreme southern end of the Tetons, a notable concentration of bighorns was eliminated by 1960. Clearly, the bighorn sheep habitat available in the Tetons prior to settlement may have supported several times the number of sheep found in the much smaller area occupied today.

The decline of Teton Range bighorns resulted from several factors which may have acted in concert. Chief among these factors were competition from domestic sheep, diseases, excessive hunting, restriction of winter ranges, and curtailment of wildfire.

During the late 1800's and early 1900's, large numbers of domestic sheep grazed throughout the Teton Range. U.S. Forest Service records (Fig. 1) indicate that from 1910 to 1915, over 25,000 permitted sheep grazed the southern half of the Range for nearly 70,000 Animal Unit Months (AUMS) each

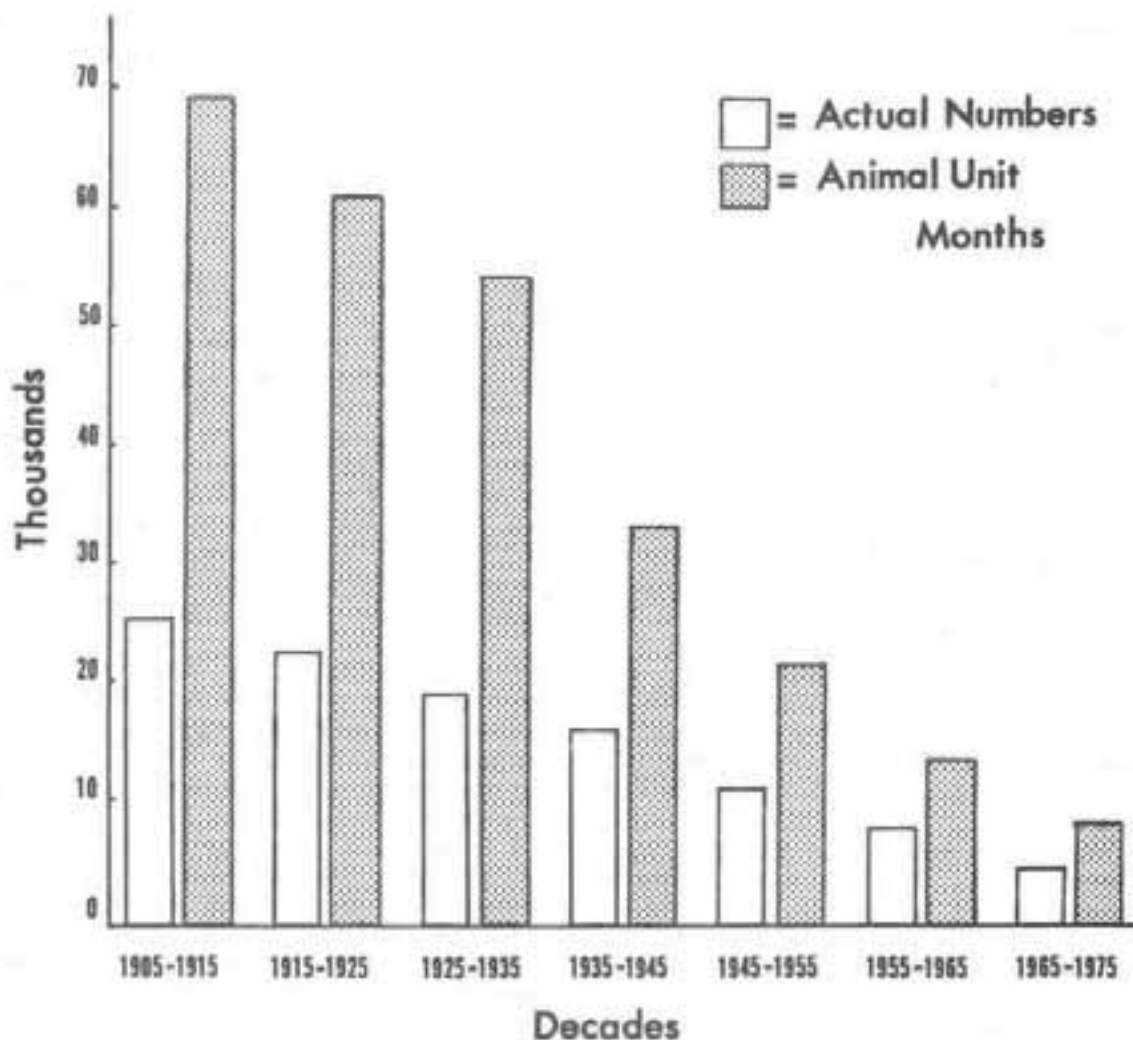


Fig. 1. History of domestic sheep use (actual, not permitted) on the West Slope of the Teton Mountain Range, Bitch Creek to Coal Creek. Use estimates may be inaccurate due to many gaps in the records and changes in allotment boundaries. As nearly as possible, estimates are intended to reflect the average actual use during the decade. In areas where history is lacking, use is assumed to be the same as that indicated for the earliest year in the time period. Years of non-use are considered in averages. For this discussion, one Animal Unit Month (AUM) is equal to one animal month, or one ewe with lamb for one month.

year. Annual use of this same area in recent years is below 5,000 sheep for 9,000 AUMs. During the first two decades of domestic livestock use of the Tetons, 1890-1910, when no records were kept, use probably exceeded the high levels recorded in 1910-1915. In this era of no-control, which preceded establishment of Targhee National Forest in 1908, herders pushed huge bands of sheep in a season-long race for the choicest grazing areas (E. Winger, pers. comm.). From their homes in Teton Valley, shepherd's families were often able to trace the mountain locations of domestic sheep herds by observation of campfires at night and dust columns during the day (S. A. Stevens, pers. comm.). Forest Service records and herder observation (L. Henrie, pers. comm.), indicate that these domestic herds often grazed in habitats used by bighorns.

In reaction to forage depletion and soil erosion, permitted livestock numbers were gradually decreased (Fig. 1). Despite livestock closures, previously overgrazed slopes in several drainages were subject to severe flooding in the early 1950's (Baird in litt.). Decades of overgrazing in the Tetons have left numerous scars within former bighorn habitat: extensive areas with thin soil cover, vegetative communities dominated by ruderal species, and erosion channels and pavements. Social intolerance to the large domestic herds, with associated dogs and herders, may have stressed bighorn sheep psychologically. Today's bighorn population is distinctly limited to rough, high elevation terrain along the crest of the Range and peaks in GTNP. The southern Tetons, which were notably overgrazed into the 1950's, are no longer inhabited by bighorn sheep.

A die-off of thousands of bighorn sheep from scabies occurred throughout the western United States between 1870 and 1890 (Buechner 1960). No conclusive proof has been presented to determine if bighorns died from contact with the scab mite of domestic sheep or a similar mite endemic to wild sheep. Scabies in mountain sheep in the 1880's was reported from every section of Wyoming (Hones and Frost 1942).

Post (1971) indicated that a major factor in the decline of bighorn populations has been lung diseases. He suggested that pneumonia may have been involved in the extensive die-offs attributed to scabies. The pneumonia complex, which consists of several bacterial species, usually associated with lung nematodes of the genus *Protostrongylus*, was implicated as the prime mortality factor in bighorn die-offs since 1900. Unnaturally high lungworm infections, which may have led to death of bighorns, occurred when sheep wintered and summered in the same area (Spraker 1974) or were pushed onto winter range early by human disturbance (Wishart et al. 1980). Such unnatural use of winter ranges may make sheep more subject to infection when snail activity at concentration sites is high (Wishart et al. 1980). Teton Range bighorns have long been forced to summer and winter in the same high elevation habitat. Such year-around use of the same range may be a particularly significant factor in late-winter lamb mortality in Colorado (Spraker 1974).

Sheep herders occasionally observed wild bighorn rams mixed with their domestic herds (L. Henrie and W. Christensen, pers. comm.). Thus, the avenue for disease spread, from domestic sheep to wild sheep, existed. Although no record of major bighorn die-offs in the Tetons was found, W. Stone (pers. comm.) observed the remains of many bighorns south of Rendezvous Mountain in the early 1940's. He did not determine the cause of death.

Excessive, unregulated hunting of bighorn sheep for meat and horns was a major factor in the decline of bighorn sheep in many of their former ranges (Buechner 1960, John 1975, Tsukamoto 1975, Hickey 1978). Buechner (1960) credited persistent hunting of populations already decimated by disease with continued decreases in sheep numbers. Early hunting of sheep in the Tetons and adjacent ranges removed relatively few sheep from the presettlement populations. A thorough review of the journals of explorers, trappers, and hunters revealed few encounters with wild sheep presettlement (Whitfield 1983). The more important effect of the arrival of the Euro-American era may have been the elimination of bighorn migration routes which crossed major human travel-ways. Opportunistic hunting along these travel-ways may have curtailed genetic communication with other bighorn populations. Poaching may have been a more direct threat in the 1930 to 1970 era, after Teton Range bighorns were reduced to a small, remnant population (A. Murie in. litt.).

Teton Range bighorns once migrated seasonally to lowland winter ranges (Whitfield 1983). Human encroachment upon winter ranges, and developments which blocked migration routes, gradually eliminated bighorn use of almost all the lower elevation habitats. At low and midslope elevations, the exclusion of wildfire in the Tetons over the past 80 years has allowed conifer invasion of seral forb and grass communities which were maintained in presettlement days by frequent wildfires (Whitfield 1983).

PRESENT SEASONAL DISTRIBUTIONS

Some 1279 observations of bighorn sheep were recorded in the Teton Range from 1969 to 1981. Twenty-eight study flights and 228 days of field effort were used to learn seasonal movements. We found most sheep in two population centers; one in the northern end of the range, and a second on the south-central portion of the range. Geist (1971) noted separate seasonal ranges for ram and ewe groups. Bighorn groups in the Tetons were significantly segregated by sex in spring and summer ($p < 0.05$, χ^2 test). Sheep were generally found at or near treeline in all seasons but spring, when many bighorn descend to lower elevations. Values for the mean observed elevation throughout the entire year were 2992 m (+ 395 m, 95% C.L.) for ewe groups, and 3025 m (+ 343 m, 95% C.L.) for ram groups. These means were not significantly different ($p > 0.05$, Group Comparison t).

Whereas study efforts in spring were limited, some range-use patterns were evident. By early April, hard snow allowed bighorns to scatter widely throughout the Teton Range. Although some sheep, predominantly rams, remained on high elevation winter ranges, many spring observations were at elevations below 2600 m, where green-up begins. Several unusual observations of bighorns in forested areas at low elevations 6-12 km from recognized habitat in the northern Tetons suggest more widespread use of low elevations than we detected. Bighorns were also found in lower elevation granitic areas at the center of the range where few sheep were seen in other seasons. Lambing ranges were in steep, rugged limestone cliffs on the lower south exposures of three major drainages.

Spring-like conditions lingered into July, with extensive snow cover above 2700 m. Bighorns at higher elevations focused upon southerly exposures, where plant growth progressed rapidly. In early summer sheep were often seen on green benches and around lake basins frequented by backpackers. These sheep shifted

to more remote areas as recreation use peaked in late July and August. Although ewe groups remained in rugged terrain near the major crest trail, ram groups predominated in areas little used by recreationists.

In late July and August, sheep shifted to east and north exposures. Throughout the Range in August and September most sheep were observed near Krummholz at about 3050 m elevation. Heavy frosts occurred in early September. We observed equal use of north and south exposures in early September, but in later fall, sheep strongly favored eastern and southern exposures. Large, sexually-mixed groups became prominent by late September, a reversal from the pronounced spatial segregation of ewe and ram groups in summer. This mixing of sex and age classes preceded the rut by two months. Lasting snow fell in the Tetons by late September.

We recorded no observations of Teton Range bighorns on historic low-elevation winter ranges. All observations from mid-November to mid-March were on isolated patches of windswept alpine tundra or snow-free Krummholz ridges above 2800 m elevation. Sheep generally restricted themselves to small snow-free areas with southern aspects. These areas were often over 300 m from escape terrain. Sheep dispersed more widely over high ridges or into adjacent cliffs during the heavy, wet snowfalls of late winter. Winter observations were at an average elevation of 3034 m. Mixed groups were frequently seen.

POPULATION CHARACTERISTICS

The population dynamics of Teton Range bighorns were inferred primarily from five key flights or series of flights between 1969 and 1981 when 42 to 75 sheep were observed per flight (Table 1). We also attempted to assess all summer observations with probable duplications eliminated, although this information is less reliable. Observations from the May-June lambing period and the November-December rut were not included because of probable bias in the observabilities of sex- and age-cohorts.

Caughley (1974) cautioned against the casual interpretation of age ratio data to determine population dynamics in the absence of information on population rate of increase. Buechner (1960) added the further complication of separating yearlings and two-year-old females from reproductive ewes (three years plus), particularly when observed from aircraft. Two-year-old females were difficult to differentiate from older ewes. Corrected ratios (Table 1) assume that 23% of classified ewes were actually non-breeding two-year-old females, and that all lambs, yearlings, and two-year-old males were accurately classified (Buechner 1960). Use of the reported observation data to develop sex- and age-ratios further assumes no bias in observability of individual cohorts.

Actual lamb:ewe ratios lay somewhere between observed and calculated values. If it is accurate to assume that there were equal numbers of two-year-old females and two-year-old males in the population, our ram classifications suggest that two-year-old females made up only 7-11 percent of classified ewes. Total summer observation ratios, as adjusted to avoid duplication, yielded a range of lamb:ewe ratios from 0.29-0.85. These ratios suggest sometimes poor, but generally high lamb production. Some years of poor lamb production would be expected from sheep that live in the harsh winter and spring environment of the Tetons. The fall, 1980 flight (24-25, Sept.) showed

Table 1 Sex/age ratios from unduplicated bighorn sheep observations in the Teton Mountain Range, Wyoming, 1969-1981.

Date	Observed ^a Lamb to Ewe Ratio	Calculated ^b Lamb to Ewe Ratio	Observed ^a Yearling to Ewe Ratio	Calculated ^b Yearling to Ewe Ratio	Observed ^a Ram to Ewe Ratio	Calculated ^c Ram to Ewe Ratio
July, 1969	0.85	1.10	0.00	0.01	0.85	0.85
Jan.- March, 1976	0.57	0.74	0.00	0.01	0.74	0.74
Summer, 1976	0.67	0.87	0.25	0.32	1.42	1.42
Summer, 1977	0.29	0.38	0.00	0.01	1.13	1.13
Summer, 1978	0.53	0.69	0.13	0.17	0.47	0.47
Jan., 1979	0.40	0.52	0.12	0.16	0.56	0.56
Summer, 1979	0.50	0.65	0.05	0.06	0.70	0.70
Sept., 1980	0.69	0.90	0.00	0.01	1.08	1.08
March, 1981	0.44	0.57	0.00	0.01	0.48	0.48

^a Observed ratios derived from observations shown in Whitfield (1983).

^b Calculated lamb-to-ewe ratios and yearling-to-ewe ratios assume that breeding ewe numbers equal classified ewes minus 23 percent for two-year-old ewes (Buechner 1960).

^c Ram-to-ewe ratios assume that equal numbers of nonbreeding animals were classified with each sexual cohort.

little to no decline in lamb:ewe ratios from the average summer observations from other years. The late winter flights pointed to a loss of 13-25 percent of summer lamb crops.

Lamb:ewe ratios may provide little insight into actual rates of population increase, but merely indicate a rate or productivity (Buechner 1960). In the Teton Range, extremely high lamb mortality apparently occurred in late winter and early spring. Few yearlings were observed, and high lamb:ewe ratios indicated that few yearlings were misclassified in ewe groups. Ram age class ratios also suggested poor lamb to yearling survival. Yearling:ewe ratios averaged about 0.10 in our observations.

Ram:ewe ratios approached or exceeded 1 in most Teton Range surveys. An even ram:ewe ratio is expected in a non-hunted population, or in a population where all age classes are hunted equally. Between the January, 1976 and January, 1979 flights, five 3/4 curl rams were removed from the population by legal hunting (G. Roby pers. comm.). Two more 3/4 curl rams were taken before the March, 1981 flight. A decline in winter ram:ewe ratios of 26% between January, 1976 and March, 1981 suggested minor ram mortality apart from hunting. We found relatively few bighorn remains despite considerable time in bighorn habitats. This low mortality rate among bighorns over yearling age fits well with models of stable or slowly declining populations (Geist 1971). K. Becker (pers. comm.) found many bighorn remains in the habitat of a high quality population.

Brody (1945, as cited by Geist 1971) first discovered the inverse relationship between growth rate and life expectancy as an indicator of population quality. A low-quality bighorn population associated with a stable or declining population size, should have rams with relatively small bodies, slow horn growth, late sexual maturity, little social activity, and long lives (Geist 1971). Lambs in a low quality population should have relatively low survivability to yearling age (Buechner 1960). Low quality populations result from relatively poor forage availability (Geist 1971). Group sizes in areas of poor forage quality should be relatively small (Morgan 1970, Leslie 1977).

Teton Range bighorns exhibited many of the characteristics of a low quality population. Harvested Teton Range rams had relatively tighter horn curls, smaller horns, and more stress rings in all age classes than did rams from other Wyoming populations (G. Roby pers. comm.). Several 11-year-old rams were barely 3/4 curls when harvested. The population turnover rate appeared to be low. We saw little of the lamb play behavior described from other populations (Geist 1971), and lamb mortality late in the first winter of life was high. Average group sizes (4.6 overall) were smaller than observed for most Rocky Mountain bighorn populations (Skiba 1981).

HABITAT RELATIONSHIPS

In 1978-1979, we recorded bighorn use at 42 randomly selected points during summer as a use index based upon evidence of use and actual observations. Extensive use by sheep occurred at only seven of the summer sites, not enough to characterize bighorn preferences. We returned to the Tetons in August, 1983, to record habitat features at 57 sites where we had recorded bighorn observations during the summers of 1976-1983.

The areas from which we randomly selected sample points were defined, in general terms, by literature descriptions of bighorn habitat. However, comparisons of habitat features at these randomly selected sites with features at sites where bighorns were observed revealed that the sheep were selective (Table 2). Bighorns chose rougher terrain, gentler slopes, and greater proximity to escape terrain than found randomly ($p < 0.05$). There were not significant differences in shrub and herbaceous plant cover (Table 2). Several random samples fell within forested areas. Although Teton Range bighorns frequented scattered Krummholz at the edges of forested areas, we never saw bighorns or their sign within dense tree cover.

Bighorn sheep were rarely seen beyond 75 m from escape terrain. Feeding sites averaged 61 m from escape terrain, whereas bedding sites averaged only 7 m from escape terrain, a significant difference ($p < 0.05$, Group Comparison t). On several occasions, we saw bighorns feed in open areas about 60 m from escape terrain, but then move to cliff edges or rough ridge crests to bed. Exceptions to this general observation occurred on several high elevation plateaus, where sheep often bedded in the same areas where they fed. These areas were rarely visited by humans. Bighorns did some feeding at most bed sites, and at some sites, the predominant use was difficult to determine.

Topographic roughness values averaged 24 for feeding sites, and 42.24 for bedding sites, again a significant difference ($p < 0.05$, Group Comparison t). Mean percent slope values were similar for feeding and bedding sites, 31 and 27 respectively. Sheep often fed in relatively flat meadows and bedded on relatively flat ridge tops at cliff edges, but these sites were usually near to escape terrain on slopes of greater steepness than found at the specific observation sites. Feeding areas were significantly better vegetated than were bedding areas ($p < 0.05$), particularly for forbs, with a mean percent canopy cover of 29 on feeding sites and 12 on bedding sites. Lush meadows near escape terrain were heavily used.

Food habit analysis by the microhistological technique was completed on 19 fecal samples. We collected fresh pellet groups from 13 summer areas, 5 from known, classified sheep, between 30 June and 30 August. Six pellet groups were collected from winter ranges. The analysis reported summer diets of 23 percent graminoids, 13 percent forbs, and 64 percent shrubs and trees. Winter diets consisted of 29 percent graminoids, 32 percent forbs, and 38 percent shrubs and trees. Johnson (1980) noted that forbs were underestimated by approximately 20 percent in microhistological analysis when compared with direct feeding observations of tame bighorns. Johnson (pers. comm.) was concerned that important forbs eaten early in development, before cell walls were well lignified, would be easily missed by the fecal analysis technique. The Teton Range results certainly raised this concern, particularly when compared with direct feeding observations of five of the bighorns from which summer pellet samples came. Teton Range sheep were often seen feeding voraciously in forb communities. These communities were notably diverse, with 163 forb species identified in vegetation samples.

The Tetons support an extensive shrub belt at about 3050 m elevation, particularly in association with broken cliffs, and dense stands of dwarf *Salix* at higher elevations. Johnson (pers. comm.) reported a depauperate shrub belt in subalpine areas he sampled in New Mexico, where sheep strongly favored forbs. Teton Range sheep appeared to eat a wide variety of plant species in

Table 2. Comparison of habitat features at randomly selected sites with sites where bighorn were observed during summer in the Teton Mountain Range, Wyoming, 1976-1983.

Habitat Feature	Random Summer Samples \bar{X}^a	Observation Site Samples \bar{X}^b	Test Result ^c
Graminoids (% Canopy Cover)	8.9	8.6	t = 0.09; n.s.
Forbs (% Canopy Cover)	25.3	18.5	t = 1.51; n.s.
Shrubs (% Canopy Cover)	5.6	7.6	t = 1.02; n.s.
Percent Slope	51.9	31.4	t = 4.72; (p<0.05)
Topographic Roughness Index	16.7	32.1	t = -4.23; (p<0.05)
Distance to Escape Terrain (m)	76	36	t = 2.84; (p<0.05)

^a This sample set includes only randomly selected summer samples. Winter range samples are excluded because their selection was based upon bighorn use. Therefore, n = 42.

^b This sample set includes measurements from n = 57 specific sites where bighorn were observed during summer.

^c Mean values of habitat features from randomly selected sample points and bighorn observation sites were evaluated with the two-tailed t test for group comparisons (Zar 1974).

H₀: \bar{X} from random summer samples = \bar{X} from observation site samples for each habitat feature.

^t_{0.05(2),97} = 1.985

n.s. = not significant (p>0.05)

summer, including many shrubs, in contrast to the usual characterization of bighorns as selective grazers. These differences may be due to the relatively rich forb and brush flora of the Tetons, and to preferential use of habitats wherein shrubs are dominant, but appear to be amplified by inherent errors in the fecal analysis technique.

Shannon et al. (1975), through simple and partial correlation analysis of 11 environmental variables, found that vegetation accounted for a large proportion of the variance associated with bighorn distribution in British Columbia. However, in a review of literature on a wide range of animal communities, Schoener (1974) noted that resources are most frequently partitioned through spatial separation on the habitat dimension. Food specialization is less commonly the major mode of dividing resources, particularly for large herbivores. In association with elk, deer, and other ungulates, bighorns were spatially separated from other species through a preference for the more rocky, inaccessible terrain (Hudson et al. 1976, Barmore 1981).

Bighorns from low-quality populations (Stewart 1975, Kopec 1981, Whitfield 1983) appeared to be more closely tied to escape terrain than were sheep from high-quality populations (Frisina 1974, Stewart 1975, Tilton 1977). Low-quality populations result from relatively poor forage availability (Geist 1971) or lack of genetic diversity (Skiba and Schmidt 1982). Learned traditions of restricted habitat use may contribute to poor nutrition (Geist 1971).

We suggest that loss of traditional migration routes and low elevation winter ranges due to human encroachment, habitat degradation due to overgrazing and wildfire suppression, and avoidance of opportunistic poachers and large domestic sheep bands, have taught Teton Range bighorns to remain strictly tied to remote, vegetatively poor terrain. This tradition of habitat use is inefficient in the present era, when most of the historical conflicts no longer exist. Direct evidences for inefficient habitat use are an unusually strong tie to topographically rough escape terrain, and a high level of browse consumption in summer.

REACTIONS TO HUMANS

Man is not inherently an unpleasant stimulus to bighorn sheep. Bighorn from totally unhunted populations may habituate to people to the point of ignoring human presence, or even seeking it (Geist 1975). However, if hunted to even a light degree, rams soon learn to avoid humans (Horejsi 1976). Thorne et al. (1978) noted that rams of the Whiskey Mountain, Wyoming bighorn populations actively avoided people, except during the rut and spring green-up, and were rarely seen in summer. Rams abandoned optimal summer and winter ranges to avoid human contacts (Thorne et al. 1978), although ewe groups reacted much less negatively to humans.

Passive human disturbance may prevent bighorn sheep from exploiting their entire habitat potential, may cause increased energy expenditures, and may lead to increased predation (Horejsi 1976). Activity patterns and distribution on occupied ranges may be altered, and parts of ranges abandoned by bighorns when human use of an area is high (Horejsi 1976).

In the Tetons, areas of high and low recreation use were interspersed. Bighorn sheep significantly avoided high-use areas ($p < 0.05$, Group Comparison t). The sheep were seen within several high-use areas in early summer, but most of these animals moved to more remote areas as recreation use increased in mid-summer.

Since 1976, when hunting was first permitted in the Tetons, the number of ram observations steadily declined, particularly class III and IV rams. These large rams made up 24 percent of the classified observations in summer, 1976. They were easily observed, and we often approached them to within 50 m. By 1978 and 1979, large rams made up only 6 percent of the classified summer observations. Flight distance, the distance from an approaching observer which causes flight in animals (Altmann 1958), increased dramatically. Our appearance in isolated canyons caused displacements of large rams at flight distances up to 2 km.

MANAGEMENT IMPLICATIONS

Survey flights and field observations appear to show a decline in the Teton Range bighorn population from 1976 to 1981. Although this survey information is inconclusive, yearling:reproductive ewe ratios are cause for concern. Simmons et al. (1984) suggest that yearling recruitment rates below 14.8% indicate a declining population. Our observed yearling ratios indicate a need for careful monitoring of yearling recruitment, and of those factors which contribute to it.

Since 1977, exotic mountain goats from an introduced population in the Snake River Range to the south of the Tetons have been sporadically reported throughout the Range (Whitfield 1983). Although mountain goats are not yet established in the Teton Range, there is strong potential for growth of a Teton Range population (J. Hayden pers. comm.). We fear that mountain goats and bighorn sheep may compete for the limited habitat available in the Tetons, to the ultimate disadvantage of the native sheep. Particularly severe competition could develop on the high elevation winter ranges. Mountain goat/bighorn sheep interactions in the Tetons deserve careful monitoring.

Teton Range bighorns are members of a low quality, relict population. However, the genetics which allow them to persist in the most difficult of habitat conditions make this population particularly valuable. We conclude that their continued survival in the Range depends upon decisive management efforts to conserve and expand their occupied habitat, and enhance their genetic base. We recommend specific controls of recreational activity, including hunting, cessation of domestic grazing in several important areas, prescribed burning to reduce conifer and brush cover, and possibly reintroduction of genetically vigorous sheep into abandoned, historical habitats (Whitfield 1983).

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