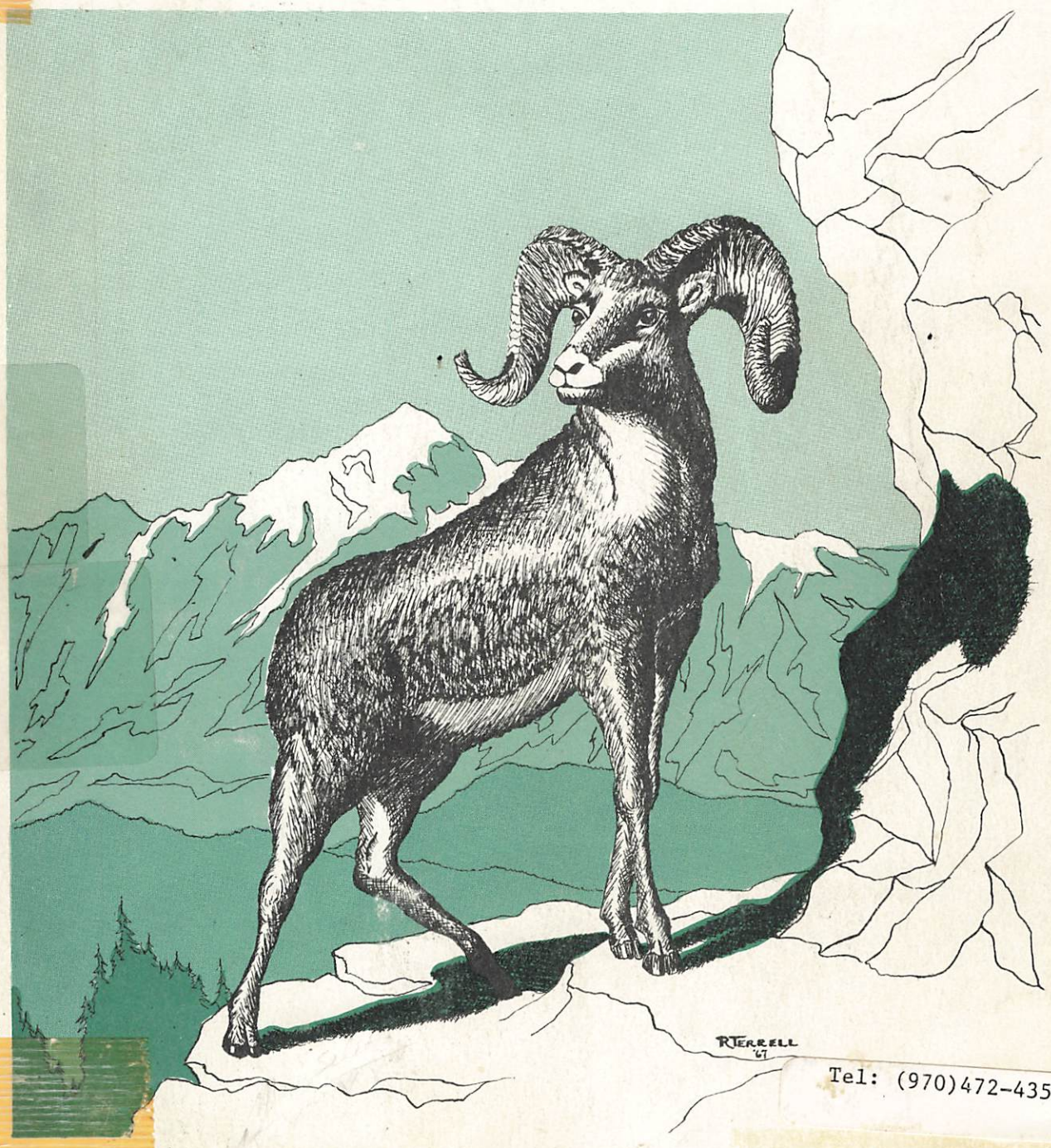
# BIGHORN SHEEP, ELK, MULE DEER RANGE RELATIONSHIPS





A Review Of Literature

JOHN C. CAPP






Rocky Mountain Nature Association
Colorado State University

# BIGHORN SHEEP, ELK, MULE DEER

# RANGE RELATIONSHIPS

## A Review of Literature

John C. Capp

Including A Brief History of Bighorn Sheep In

Rocky Mountain National Park, Colorado

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A Contribution of the Rocky Mountain Nature Association,
Estes Park, Colorado, and the

Department of Fishery and Wildlife Biology
Colorado State University, Fort Collins, Colorado

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# HISTORY OF BIGHORN SHEEP IN ROCKY MOUNTAIN NATIONAL PARK

## Introduction

The Rocky Mountain bighorn sheep, Ovis canadensis canadensis Shaw, is part of the native fauna of Rocky Mountain National Park. First explorers of that region reported an abundance of wildlife. Bighorn Sheep were common during the late 1800's but Sheep were judged diseased and few in number by around 1900. Elk were rare by 1890, mainly because of market hunting. The bighorn and elk populations of the region began to increase after creation of Rocky Mountain National Park[1/] in 1915. Since then, sheep have fluctuated little in numbers while elk have increased to a high population within the Park.

Following is a brief history of native wild ungulates in Rocky Mountain National Park as recorded by various authors. Bighorn sheep will be emphasized. Most material has been extracted from unpublished data on file at the Park because no recent work summarizes data concerning the history of bighorn sheep there. Guse (1966) presented a comprehensive history of elk in the area of Rocky Mountain National Park, and emphasized National Park Service policy for elk management.

## Early History (1850-1880)

Mule deer, elk, and bighorn sheep were present in Rocky Mountain National Park when modern man first came. These ungulates were significant influences on the lives of the most recent Indians in the area, the Utes and Arapahoes, who made non-limiting use of wild ungulate populations there.

Early estimates vary concerning such populations in Rocky Mountain National Park. Quaintance (1934) stated that Jobe Baker, a pioneer of 26 years in the area, said that in the early days it was a common sight to see bands of 50 to 60 sheep on mountains of the Never Summer Range in the western part of the Park. Gifford (1939) lived in that area and worked on the Grand Ditch which collects runoff from the Never Summer mountains. He stated there were "thousands of sheep" in the Park area before white men came. Packard (1939) reported that Abner Sprague, another early pioneer, stated that in 1875 it was a common sight in the spring and fall to see as many as 100 bighorn sheep grazing in Moraine Park. Sprague said sheep appeared in Moraine Park during summer but in smaller groups and less often. He observed bands of sheep in Horseshoe Park and the Mary's Lake area also. Bands in the three areas were of similar size.

Estes (1939) was the first recorded white man to enter the valley now called Estes Park in 1859. He stated that game was very abundant

1/ Hereafter often referred to as "the Park", including reference to "the Rocky Mountain National Park area before 1915.

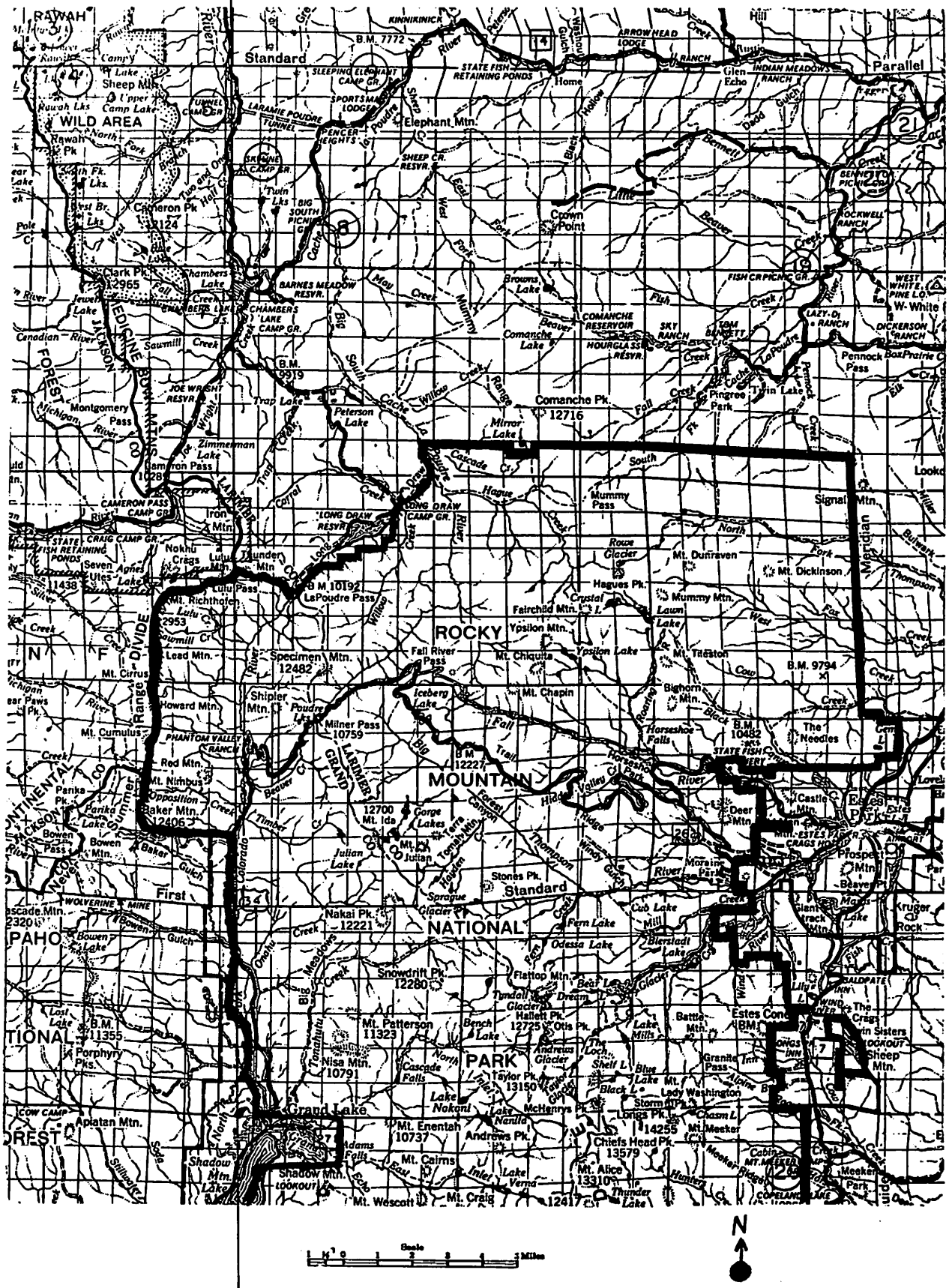


Fig.1. Northern Rocky Mountain National Park and surrounding area.

in the region before white men came and that large herds of deer, elk, and bighorn sheep were seen everywhere in the region of what is now Rocky Mountain National Park. Guse (1966) stated wildlife were quite abundant and well-distributed in the Estes Park area before settlement by early residents. Packard (1947) said deer were moderately plentiful in the Estes Park area while the valley was being settled in the 1860's. This statement was supported by Packard's review of historical data.

These reports included no precise data on population levels and the extent of ungulate distribution. It is certain that sheep, elk, and deer were present around Estes Park and the Never Summer Range. Undoubtedly these species were present throughout the northern one-half of what is now Rocky Mountain National Park. Some authors believed bighorn sheep, elk, and deer were present between what is now Rocky Mountain National Park and the foothill area immediately west of the present town of Loveland, Colorado. Packard (1946) stated: "Considerable evidence supports the belief that at least until late in the nineteenth Century the bighorns and other game, except some elk, left the mountains for the foothills in winter." He added that some wild ungulates wintered along the "hogbacks" at the mouths of the Big Thompson and St. Vrain rivers. This led some people to believe two populations of each species were present -- one a plains-dwelling and another residing high in the mountains. Quaintance (1934) said that Jobe Baker told him some sheep stayed high on the windswept mountains all winter in the late 1800's, and that Mr. and Mrs. Jobe Baker reported that every spring they would see bighorn sunning themselves on Iron Mountain in the Never Summer Range. The Bakers also said that since snow was too deep to allow sheep to get up there in the winter, the sheep must have stayed up all winter.

Other authors reported observations of bighorn at lower elevations during all seasons of the year (Packard, 1939, 1946; Ratcliff, 1941). Ranchers residing along the edge of the foothills east of Estes Park said they observed bighorn sheep in that area. Some saw sheep eating saline mud or utilizing domestic livestock salt licks (Ratcliff, 1941).

The original distribution and movements of bighorn sheep in the present Rocky Mountain National Park and surrounding area will never be accurately determined. Quaintance (1934) stated: "A former workman on Cameron Pass suggests that Medicine Bow sheep (this would include the Never Summer Range) wander all along the mountain range from Clarke's Peak to Nokhu Crags." Quaintance said further that: "Spalding, who trucks into the ditch camps, tells me that Clarke's Peak, farther north of the Never Summers, is famous for its bighorns." Packard (1946) related:

> "The special habitat of the bighorn was the alpine tundra. Most of the bands are believed to have summered there, and, although winter conditions reduced the carring capacity of these ranges, large areas were blown clear of snow most of the winter so that part of the summering population may have remained on the tundra the year around. Some went down almost to the plains. The deep snows kept them down until late spring so that many bighorns spent much of the year in forested terrain."

Simmons (1961) studied bighorn sheep which had been introduced in 1946 in the Cache la Poudre River drainage, north of the Park. After interviewing many local and long-time residents of that area, he concluded there had previously been no relatively large bands of bighorn occupying the suitable area north and south or the Poudre Canyon (Fig. 1). Apparently the Clarke's Peak herd did not move eastward along the Poudre River.

Murie (1941) was primarily concerned with a study of elk in Yellowstone National Park and Jackson Hole, Wyoming, and said:

> "We could not help reaching the conclusion that although the elk assuredly occupied the plains in the early days, they also ranged in the mountains; they were not "driven" to the mountains, but the plains herds were exterminated, and enough remained in the mountains to perpetuate the species; and that the elk behave pretty much today as they did originally, though not over as large a territory."

After visiting several bighorn herds in the Rocky Mountain region in the late 1930's, while involved in the earlier Rocky Mountain Cooperative Bighorn Conferences, Murie (1941;1) stated the following concerning the often proposed theory that bighorn were forced to live in rocky, inaccessible areas:

> "We should be very sure before we state as a fact that the mountain sheep today are occupying an unnatural habitat. To be sure their original range is restricted, their numbers are consequently reduced, but is it not a likelihood, on the face of it, that a part of the original range is still occupied by these animals? This species is particularly adapted to the cliff environment. It has evolved by a slow process of evolution as a creature adapted to rough country primarily. It would be astonishing indeed if such perfect adaption to high rock country were perfected in the last forty years, or a century or two centuries. The present adaption to a particular ecological niche should cause us to hesitate, and to dig very deep into all sources of information before we conclude that the mountain sheep was not originally a mountain animal and that it did not winter on high mountain forage, <u>provided</u>, of course, that the forage was there in sufficient quantity."

## Early Decimation (1880-1910)

Wild ungulate populations in the area of Rocky Mountain National Park began to decrease with the advent of white man. Some disagreement exists as to which of several factors was most significant and when. These factors include disease, parasites, market hunting, sport hunting, reduction in winter range, and mineral deficiencies. Guse (1966) presented a complete account of the decline in the elk population in that

area. He reported that it took only twenty years (1860-1880) from the time white men came until wild ungulates were very scarce. Milton Estes (1939) said that in 1865 and 1866 game was still abundant in the area.

Gifford (1939) stated that the increase in bighorn numbers began in 1867 when a game market opened in Denver and market hunters came into the area. Elk were the primary targets but bighorn were also shot. Market hunting continued until the 1870's and 1880's when game laws were enacted (Gifford, 1939).

Packard (1939), in reviewing conversations with Abner Sprague, an early pioneer there, stated that scabies appeared in 1878 or 1879. Sprague said that sheep "died off" by the hundreds and believed that an epidemic of this disease was a major factor in the decrease of bighorn at the end of the century. He believed that scabies came through the Cache la Poudre River and Laramie Plains country and that the far-wandering habits of the bighorn bands there may have spread it from band to band.

Quaintance (1934) says Jobe Baker concluded that with the immigration of domestic sheep the bighorn population began to "wane". Packard (1946) stated that before Rocky Mountain National Park was established, domestic sheep used the northern part of the Mummy Range and that they may have injured the range there. Quaintance (1934) disclosed that Spalding, a past-worker on the Grand Ditch, said it was possible construction activities and presence of domestic sheep caused the depletion of sheep in the Cameron Pass region. Spalding believed that construction activities may have caused sheep to migrate and that domestic sheep brought in disease.

Ratcliff (1941) asserted that the first serious decline of bighorn in Rocky Mountain National Park was in 1902, due to scabies. Packard (1946) believed that the first significant decrease of bighorn there occurred between 1906 and 1909. He reported the decline was caused by scabies, hunting, and a loss of winter range. Packard stated: "Grazing of cattle and domestic sheep on the winter range, accelerated settlement of the foothills, hunting, and the construction of roads through the canyons forced the bighorns back into the mountains." He believed the lower winter range (canyons east of Estes Park) were abandoned by bighorn around 1900. Packard (1946) and Sprague (in Packard, 1939) asserted that predation was not believed a significant factor in this first decline of bighorn.

Packard (1947) concluded elk were very scarce in the area in 1900, and were the "hardest hit" by market hunters. He stated also that market hunting plus grazing by cattle caused deer to decline "apparently into the early 1900's". He added (Packard, 1947) that:

> The removal of elk as a competitive species before 1900 was doubtless of benefit to the deer. There are no reports that the range was over-utilized by game in the early days; but the reduction of the number of animals using it permitted the maintenance of the luxuriant growth of browse and grass that then existed over much of the area."

Quaintance (1934) reported similarly that in the Never Summer Range, significant with the decrease in bighorn was the "enormous" increase in the deer population, and said "Where formerly deer were a rarity, they now abound in large numbers."

## Restoration, Fluctuation and Stability (1910-1958)

Gifford (1939) and Packard (1946) reported an increase in bighorn numbers between 1909 and 1920. Gifford (1939) stated that this was "possibly the result of removal of all the elk from large suitable ranges by market hunters." He said that by 1915, there were "hundreds of sheep all through the Never Summer Range . . ." and that in 1915, he personally observed 70 bands of bighorn on Specimen Mountain in one day; with each band numbering about 12 animals. Sprague (in Packard, 1939) stated he saw little sign of scabies left in the Park bighorn population in 1915 and 1916. No signs of scabies were observed by him after that time.

Elk were re-introduced into the area of the Park in 1912 and 1913 (Swift, 1945; Packard, 1946). Swift (1945) stated: "The native elk were believed to be nearly extirpated in the Estes Park and adjacent Front Range country by the turn of the century, so a concerted effort was made to re-establish the species through introductions." Elk were released near Estes Park and the towns of Nederland and Rollinsville.

Establishment of Rocky Mountain National Park and the adjacent Colorado State Game Preserve in 1915 was very important because hunting was made illegal there. The Never Summer Range was not included in the Park until 1930, however. A predator control program was initiated after the Park was established and continued until 1926 (Packard, 1947; Guse, 1966). The effect of this control program on ungulate populations is unknown (Guse, 1966).

The wild ungulate populations of the Park began to increase with the cessation of hunting. Bighorn sheep, elk, and deer increased in numbers between 1909 and 1920. Packard (1946) believed that by 1920 elk were again competing on the range, and (1947) reported deer increased immediately after the Park was established.

With all three species increasing in the revised environment, changes were bound to occur. Ratcliff (1941) and Packard (1946) reported a second decline of bighorn in the Park, beginning around 1921. The reasons and degree of decline are obscure. Ratcliff (1941) stated there was a second appearance of scabies then. Gifford (1939) stated that poaching and grazing by domestic sheep increased after World War I (1918) in the Never Summer Range, which at that time was not within Park boundaries. He believed that this factor was the major reason for the second decline of bighorn. Gifford (1939) reported that during every spring in the 1920's he found carcasses of "full bands of sheep that had died of winter starvation, due to the ruin of their range by domestic sheep." He believed this decline continued in the Never Summers until that area was included inside the Park boundary in 1930; and that the range was severely overused by domestic sheep. Gifford reported that he did not observe scabies on these bighorn then. Contrary to this Husted (1939) stated that he found "alot" of scabies in the Never Summer Range bighorn in 1927. If this disease was present, it probably had a profound effect on bighorn sheep.

Another significant factor in this second decline of the bighorn population was range competition among wild ungulates. Packard (1946) stated that by 1926 and 1927 it became evident that there was a danger of elk crowding sheep off the range in certain areas of the Park. According to Packard, this condition was apparently in full force during 1933. Packard (1947) and Cahalane (1948) reported that signs of an over-population of deer in the Park appeared in 1930. Packard (1946) believed that the decline in the bighorn population reached a rapid rate in 1930.

Population estimates of bighorn in Rocky Mountain National Park are first recorded in 1923. The accuracy of early estimates (pre-1936) is questionable. Potts (1936) stated that these early estimates were probably too high. Potts (1936) stated:

> "The census of 1935, based on an accurate survey of the entire Park totalled only 192. This figure is much lower than previous counts, probably not so much because the decrease in population has been so rapid, but because previous estimates have been too high."

The population estimates of bighorn, elk, and deer in the annual census reports of the Park are presented in Table 1. Various individual estimates of the bighorn population are presented in Table 2. The accuracy of these population estimates is questionable because of variation in census techniques, of variation in personnel conducting census work, and the extent of such work.

Factors affecting the bighorn population of the Park between 1935 and 1958 are obscure. Potts (1935) made an extensive survey of the distribution of bighorn sheep during the spring, summer and early fall, 1935. These data are presented in Table 3. Table 3 is believed to point out main areas of use by bighorn then. Comments made by Potts (1935) at the time of observations are presented also. After making this survey of bighorn in the Park, Potts (1935) stated:

> "Sheep range in almost every section of the Park; both above and below timberline, in winter and summer. It is impossible to designate any section as winter or summer range. Sheep range at low altitudes in both seasons alike, a few undoubtedly stay above timberline throughout the year."

Potts (1935) asserted further that range conditions were uniformly good in the Park except for the Never Summer Range. This area, he said, was improving after severe grazing by domestic sheep before 1930. Ratcliff (1941) and Potts (1935) stated that hemorrhagic septicemia was first discovered in Park bighorn in 1935. They asserted that pneumonic Pasteruella oviseptica and Corynebacterium pyogenes were found also. Potts (1935) concluded that the first urgent step in bighorn management recovery was the need for adequate range, both winter and summer. Second was full protection from hunting.

Potts (1936) reported on the ungulate situation in Rocky Mountain National Park in his 1936 annual wildlife report: "The bighorn, Ovis

Table 1. Annual estimates of ungulate populations in Rocky Mountain National Park, Colorado. Taken from Annual Census Reports, Superintendent's report to the Director, Rocky Mountain National Park, 1923-1962, incomplete series. (Table compiled by Neal G. Guse, Jr.)

| YEAR | SUMMER RANGE ESTIMATE | | | WINTER RANGE ESTIMATE | | HIGHEST ACTUAL COUNT | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | Winter | | Summer |
| | Elk | Deer | Bighorn | Elk | Deer | Elk | Deer | Bighorn |
| 1915 | 30 | 600 | - | 30 | - | 30 | - | - |
| 1916 | - | - | - | - | - | - | - | - |
| 1917 | 27 | - | - | 27 | - | 27 | - | - |
| 1918 | 60 | - | - | - | - | - | - | - |
| 1919 | 80 | - | - | - | - | - | - | - |
| 1920 | - | - | - | - | - | - | - | - |
| 1921 | - | - | - | - | - | - | - | - |
| 1922 | - | - | - | - | - | - | - | - |
| 1923 | 2-400 | 3-500 | 3-600 | - | - | - | - | - |
| 1924 | 2-400 | 3-500 | 4-600 | - | - | - | - | - |
| 1925 | 2-400 | 3-500 | 4-600 | - | - | - | - | - |
| 1926 | 200 | 3000 | 400 | - | - | - | - | - |
| 1927 | 200 | 3000 | 400 | - | - | - | - | - |
| 1928 | 200 | 3000 | 400 | - | - | 165 | 486 | - |
| 1929 | 300 | 3500 | 450 | - | - | 282 | 429 | - |
| 1930 | 330 | 3600 | 400 | - | - | 312 | 672 | 287 |
| 1931 | 430 | 2500 | 400 | - | - | 228 | 887 | 139 |
| 1932 | 335 | 2625 | 380 | - | - | 237 | 749 | 121 |
| 1933 | 335 | 2690 | 360 | - | - | 256 | 749 | 115 |
| 1934 | 375 | 3000 | 360 | 435 | 1740 | 390 | 786 | 111 |
| 1935 | 495 | 2900 | 190 | 555 | 725 | 443 | 744 | 154 |
| 1936 | 645 | 1220 | 175 | 675 | 1000 | 273 | 884 | - |
| 1937 | 785 | 1480 | 165 | 750 | 1410 | 368 | 1021 | - |
| 1938 | 865 | 2600 | 145 | 1100 | 800 | 504 | 918 | - |
| 1939 | 1210 | 1400 | 333 | 900 | 1200 | 632 | 871 | 316 |
| 1940 | 1200 | 1400 | 330 | 900 | 1200 | 652 | 734 | 243 |
| 1941 | 1525 | 1750 | 330 | 800 | 800 | 535 | 712 | - |
| 1942 | 1525 | 1750 | 330 | 800 | 800 | 706 | 717 | 58 |
| 1943 | 1000 | 1400 | 100 | - | - | 766 | 399 | 66 |
| 1944 | 1000 | 1400 | 125 | 800 | 800 | 349 | 342 | - |
| 1945 | 700 | 1000 | 125 | - | 700 | 481 | 395 | - |
| 1946 | 800 | 1000 | 200 | - | - | 414 | 405 | - |
| 1947 | 800 | 1000 | 200 | - | 700 | 508 | 551 | 171 |
| 1948 | 932 | 1267 | 200 | 800 | 800 | 550 | 359 | 113 |
| 1949 | 1272 | 969 | 200 | 500 | 675 | 274 | 329 | - |
| 1950 | 736 | 960 | 225 | 500 | 700 | 297 | 422 | 118 |
| 1951 | 700 | 1000 | 225 | 500 | - | 205 | 331 | - |
| 1952 | 700 | 900 | 225 | 500 | - | - | - | - |
| 1953 | 700 | 900 | 225 | 500 | 350 | - | - | - |
| 1954 | 700 | 900 | 230 | 500 | - | - | - | - |
| 1955 | 700 | 900 | 200 | 500 | - | - | - | - |
| 1956 | 700 | 900 | - | - | - | - | - | - |
| 1957 | 700 | 900 | - | - | - | - | - | - |
| 1958 | 700 | 800 | 225 | 466 | 324 | - | - | 191 |
| 1959 | 700 | 800 | 225 | 450 | 200 | - | - | - |
| 1960 | 666 | 800 | 225 | 728 | - | 607 | 91 | - |
| 1961 | 1200 | 600 | 225 | 800 | 400 | 510 | 126 | - |

Table 2. Comparative estimates of the bighorn sheep population in Rocky Mountain National Park, Colorado.

| LOCATION | Potts (1935) | Packard (1939) | Contor (1958) |
|---|---|---|---|
| Mount Craig, Mount Adams | 60 | 12 | 13 |
| Speciman Mountain | 24 | 40 | 51 |
| Never Summer Range | 16 | 83 | 109 |
| Mount Chapin, Sheep Lakes | 15 | 50 | 28 |
| Mount McGregor | 10 | 30 | 0 |
| Hallet Peak, Flattop Mountain | 9 | 11 | 0 |
| Marys Lake | 8 | 6 | 0 |
| The Needles, Lumpy Ridge | 6 | 15 | 0 |
| Trail Ridge | 3 | 26 | 0 |
| Mount Ida | - | 18 | 2 |
| Hague's Peak | - | 10 | 4 |
| Castle Mountain | - | 4 | 0 |
| Sheep Mountain, McGraw Ranch | - | 13 | 4 |
| Moraine Park | - | 7 | 0 |
| Totals | 154 | 325 | 211 |

Table 3. Bighorn herd observations in Rocky Mountain National Park, Colorado, 1941-1955. Taken from Annual Game Count and Census Reports. Superintendent's Reports to the Director, Rocky Mountain National Park, 1941-1955, Incomplete series.

| YEAR | LOCATION | INDIVIDUALS OBSERVED | COMMENTS MADE |
|---|---|---|---|
| 1943 | Lily Mountain; Specimen Mountain, Bighorn Mountain Mount Ida | - | 4 bands: not large |
| 1944 | Park-wide | - | Encouraging no. lambs noted |
| 1945 | - | - | Few bighorn at Sheep Lakes in recent years |
| 1946 | Never Summer Range | 50 | - - - - |
| | Specimen Mountain | 40 | |
| | Mummy Range (east end) | 25 | |
| | Wild Basin | 20 | |
| | South-east of Grand Lake | 20 | |
| | Mount Ida | 15 | |
| | Trail Ridge (east end) | 10 | |
| | West of Mummy Range | 10 | |
| | Snowdrift Peak | 6 | |
| | Beach Lake | 4 | |
| 1947 | Never Summer Range | 81 | - - - - |
| | Horseshoe Park | 28 | |
| | Milner Pass | 24 | |
| | Trail Ridge | 16 | |
| | Mummy Range | 16 | |
| | Flattop Mountain | 6 | |
| 1948 | Mount Chapin | 12 | - - - - |
| 1950 | Park-wide | - | sizeable lamb crop |
| 1951 | Park-wide | - | normal lamb crop |
| 1952-53 | Park-wide | - | lamb crop normal; larger bands noted |
| 1954-55 | Park-wide | - | competition with elk and deer on winter and summer ranges apparently limiting bighorn. No disease. |

canadensis canadensis, population of the Park continues to decline; even the most optimistic observers feel that the herd is no more than holding it's own." He stated also that:

> "The discouraging feature which has been noted again and again is the scarcity of lambs and yearlings in the various bands. There may be a number of explanations for this: predators, disease, sterility, but lack of proof forces us to regard these explanations as theory only. I am more certain than ever that the decrease in the bighorn population may be directly traced to the failure of most of the lambs to reach maturity."

Potts (1936) reported that in 1936 the summer range and the deer and elk of the Park were in "fine" condition. He speculated that elk were steadily increasing throughout the Park. Also, he reported that elk displayed a tendency to migrate to the higher country after the rut and that some wintered above timberline. Such wintering by elk on alpine range was recorded along Trail Ridge Road and the Mummy Range. Concerning deer, Potts (1936) said: "At the present rate of increase, the deer herd will soon exceed the carrying capacity of the Park winter range, and some method of reduction in numbers will be necessary."

Possible causes for the continuing decline of bighorn in the Park were disease, predation, poor range conditions, competition for forage among wild ungulates, loss of winter range to domestic activities, and a deficiency of minerals. These factors appeared to be causing a decrease in the survival of young bighorn. Differences of opinion were expressed by several authors, however.

The creation of the first Rocky Mountain Cooperative Bighorn Conference in 1939 represented a new emphasis on the study of bighorn sheep. Biologists were involved from Colorado, Idaho, Montana, and Wyoming. Discussions concentrated on the decline of bighorn in those states. The Conference concluded that the loss of lambs within the first few months of life was a major factor in this decline (Dixon, 1940).

Several reports of factors limiting bighorn in Rocky Mountain National Park were presented in 1939. Packard (1947) said that in 1939 there were relatively more deer on the range during the summer than the previous year (1938). He believed also that elk had increased and that winter range deterioration was evident. Browse was more heavily used than grass and forbs. Ratcliff (1941) reported that elk and deer were using conifers to a point where a definite "browse line" was present and pine reproduction was damaged. Gifford (1939) stated: "Domestic sheep range today to the north boundary at Comanche Peak, and storms doubtless drift them into the Park as far as Hague's Peak, where they used to range regularly."

The proximate cause of the second decline in ungulates was the encroachment of civilization, according to Dixon (1940) and Ratcliff (1941). Bighorn, elk, and deer were restricted to less habitat by private land ownership along the eastern boundary and within the Park; and they were forced into competition with domestic livestock inside and outside the Park. The wild ungulates were over-using their winter range. Extensive grazing of meadows occurred within the Park from 1939 through 1941 (Ratcliff, 1941). Dixon (1940) reported that livestock were then

grazing the historical bighorn winter range which he believed to include the pastures at the base of the granite ridge east of Mount McGregor, The Needles, and the area around Mary's Lake. He believed bighorn were forced to remain on the granite walls, ledges, and the high country during the winter.

Deficiency of minerals was believed another factor then significantly limiting the bighorn population. Concern over mineral deficiency was expressed although this factor was apparent probably because some other limiting factor was active, i.e., over-use of range. Early workers frequently watched bighorn using natural and domestic livestock salt licks. Dixon (1940) observed sheep "eating" at edges of "dry ponds". Dixon (1940) and Ratcliff (1941) believed that a deficiency of minerals was causing weakness and consequently low survival of lambs. Dixon (1940) asserted that bighorn formerly went to the foothills to sedimentary-rock salt licks, and that the encroachment of man prevented this, causing the bighorn to be deprived of their "natural mineral supply". Ratcliff (1941) revealed that mineral salt blocks were placed in 1939 at The Needles, near Estes Park, and at Sheep Rock, near Milner Pass. Bighorn displayed a preference for sodium chloride in blocks, and used all blocks to some degree (Ratcliff, 1941).

Analysis of samples taken from Fall River in Horseshoe Park showed water too low in dissolved minerals to sustain the life of bighorn sheep as a sole source of minerals. Even at locations such as Sheep Lakes, in Horseshoe Park, where these minerals were naturally concentrated by evaporation, the supply of minerals was believed inadequate as a sole source (Ratcliff, 1941).

All limiting factors discussed previously were probably interacting to cause a decline of bighorn sheep then. Important here is to realize that bighorn sheep, elk, and deer were present originally. Predation, disease, and parasites were there before the influence of white men. If inter-specific competition among ungulates and additional decimating factors were to eliminate bighorn sheep in the Park, they would have long ago. Activities of man caused these original factors to become limiting. Foremost would be reduction of available forage through competition with domestic livestock and loss in availability of former winter ranges. Effects of disease, parasites, and predators on bighorn sheep would be greatly intensified on weak or unhealthy animals on poor range. Murie (1941) stated that range conditions were the key to the decline of bighorn sheep in the Rocky Mountains during this period. He believed the affinity of sheep for mineral licks occurred on poor and good condition ranges, and by unhealthy and healthy animals. He asserted that it was obvious to him that the bighorn range had been reduced. He further recommended that in areas where bighorn were in competition with other animals, competing animals should be removed in favor of the bighorn.

Elk and deer continued to increase in the Park after 1939 (Table 1). Ratcliff (1941) reported the number of wintering elk above tree-line increased during the winters of 1939-40 and 1940-41. He stated that forage was being consumed to a "marked degree". In the 1943 Annual Game Count and Census Report (Anonymous, 1941-1960) David Condon stated: "That our previous quotation (1942 Animal Census Report) of 330 bighorn for this

Park has been much to high is conceded by everyone who is at all familiar with the wildlife of the area." This accounts for the drop in bighorn population estimates from 1942 to 1943 given in Table 1.

Cahalane (1948) reported that during the winter of 1944-45, 113 deer and 301 elk were removed by shooting in a ranger conducted control program. Swift (1945) stated that elk had increased to where range damage was occurring inside and outside the Park in 1945. He said that the reduction program that year allowed improvement of winter range conditions. Buttery (1955) studied the wild ungulate winter range in the eastern part of the Park. He concluded that these areas had been damaged considerably in the past (pre-1955), especially along Fall River in Horseshoe Park. He stated: "The fact that as a whole, these concentration areas (Horseshoe Park and Beaver Meadows) are in a fair range condition is due, no doubt, to the introduction of the elk-deer reduction program in December, 1944."

Packard (1946) said:

> "In summer, elk and deer are to be found on the alpine meadows in some numbers, but there is such an abundance of vegetation there that it is doubtful that they have any serious effect on the bighorns. Large bands of elk migrate across the bighorn habitat, but most of them are there so short a time that the effect is negligible. In the opinion of the qualified members of the Park staff, during their migration season deer and elk deprive the bighorns of forage they need, an effect that may be aggravated by excessive consumption by deer and elk in summer of grasses that would otherwise be available to the sheep in winter."

Between 1944 and 1953, 1045 elk and 318 deer were killed in the Park by rangers (Gysel, 1960). Buechner (1960) stated that reductions of deer and elk in Rocky Mountain National Park had been very helpful in alleviating competitive pressures on bighorn.

Improvement in Park winter range was noticed in the 1954-55 Annual Game Count and Census Report (Anonymous, 1941-1960). The improvement was believed due to open winters, elk and deer migration outside of the Park caused by the reduction program, or summer rains. A post-season on elk was held immediately east of the eastern Park boundary during that year (Anonymous, 1941-1960). That season plus others held during the period, were believed to reduce over-use of Park winter ranges, especially over-utilization by deer. Packard (1947) and Anonymous (1941-1960) reported the deer population of the Park was partially controlled by regular season hunting outside the Park.

Observations of bighorn numbers by Park personnel between 1943 and 1955 reported in the Annual Game Counts and Census Reports (Anonymous, 1941-1960) are presented in Table 3. Accuracy of these estimates is uncertain because they are not based on intensive study.

## Recent History (1958 to Present)

Intensified study of bighorn sheep in Rocky Mountain National Park began in 1957. Contor (1958) began surveying the bighorn range then. Areas first visited were those described by earlier authors as historical bighorn range. Contor (1958) determined that The Needles, Lumpy Ridge, Castle Mountain, Mount McGregor and parts of Bighorn Mountain all displayed no recent use by bighorn sheep although old signs were present. Contor stated that Bighorn Mountain, Mount McGregor, Castle Mountain, and the Needles-Lumpy Ridge area apparently had been abandoned since 1939 (when Packard surveyed these areas); and that there were no recent reports of sheep observed in Moraine Park, Mary's Lake area, and along Trail Ridge (Contor, 1958).

Contor surveyed the high peaks of the Mummy Range during June and July, 1958. He reported no recent sign of bighorn use on Mount Ypsilon, Mount Fairchild, and the south slope of Hague's Peak. Many elk were observed high on the flanks of Mount Ypsilon and Mount Fairchild. Little total use by ungulates and "excellent" forage conditions were observed on all of Hague's Peak and Mummy Mountain. No sign of regular use by bighorn was seen in all of these areas. As a result of that survey he listed three limiting factors of the bighorn sheep population in Rocky Mountain National Park (Contor, 1958):

1) Range restriction and isolation from former winter range
2) Lungworm, coccidiosis and hemorhagic septicema - causing steady death of sheep, especially lambs
3) Competition with elk in the high country - elk increase and sheep do not

Basic premises were that the bighorns were highly mineral deficient and that predation on sheep was insignificant. A reduction of elk wintering above treeline, distribution of mineral salt blocks, and a park-wide census of sheep every year were recommended (Contor, 1958).

Contor's 1958 report is summarized in the 1958 Annual Game Count and Census Report (Anonymous, 1941-1960). The report stated that the general decline of bighorn sheep numbers was continuing, because Contor found that only one of five formerly used areas was presently occupied by bighorns. It was proposed that the decline was partially due to continued reduction in available winter range at lower elevations. More people were moving into the area.

The 1960 Annual Game Count and Census Report (Anonymous, 1941-1960) explained some important characteristics regarding movements of ungulates in the Park and surrounding area plus the annual population estimates. Concerning bighorn sheep, it was reported that:

> "Recent observations by rangers indicate a small upward trend in numbers with no great disease troubles apparent at present. They (bighorn) are principally found in the more remote sections such as the Never Summer Range, Shipler, and Specimen Mountains, and the North Fork of the Thompson River."

Deer and elk population estimates fluctuate considerably between summer and winter due to ungulate migratory habits. Meadows and other areas of lower elevation are shared during the winter by deer and elk. Guse (1966) reported annual elk and deer reductions were held in the Park between 1951 and 1962. The numbers of animals taken varied. Guse presented a complete account of reductions and summarized reports of gradual improvements in condition of winter range. Herds of elk and deer on the winter range were reduced to approximate the estimated carrying capacity of those ranges (Guse, 1966).

Gysel (1960) studied winter range in the eastern part of the Park. He compared current conditions with 25 year old records of twelve exclosures. In ten of the exclosures, the amount of cover of shrubs and trees was judged much greater; while in two the cover was judged equal to cover outside. He estimated also that grasses and forbs were more abundant outside the exclosures than inside. He speculated that this was due to heavy use of browse by deer. He reported that elk ate grass and forbs during the winter then. Guse (1962-1965) stated that ranger observations of bighorn in 1962 indicated a static sheep population. A gradual decrease in the number of lambs was apparent. Elk were reported close to the estimated carrying capacity while deer were believed below carrying capacity (Guse, 1962-1965).

Guse (1962-1965) reported in 1963 that over 1,000 ungulates occupied alpine range in the Park during summer. One-half of them migrated outside of Park boundaries during fall and early winter. Most deer were reported to summer in the east-central portion of the Park, below 10,000 feet in elevation. Cold temperatures and wind were reported to exert the greatest influence on deer and elk use of open areas during periods of cold weather. Snowfall alone had little influence on movements and feeding by ungulates (Guse, 1962-1965). Approximately 1,000 elk were observed on high tundra ranges of the Park in 1964 (Guse, 1962-1965). He reported also that most elk summered in the northwest corner of the Park, i.e., north of Trail Ridge Road and west of the Mummy Mountains.

A slightly higher bighorn lamb survival rate was observed at Sheep Lakes in late summer. Guse (1962-1965) stated:

> "There is available information to suggest that visitor impact on wildlife species is reaching the point where reconsideration of physical development planning will be necessary to insure intact habitats. With recent observations disclosing species distribution confined to the more remote, inaccessible areas and with minor vegetative damage appearing on certain of these sites, the possibility of animal crowding due to visitor pressures is very real."

After reviewing Guse's Annual Wildlife Census Reports (1962-1965) it is evident that migration of deer and elk in the Park is dependent primarily on weather conditions. Increased snowfall combined with snow packing, high winds, and low temperatures, caused deer and elk to leave high ranges. Soon after high range became snowfree ungulates vacated the winter range.

# BEHAVIOR

## Feeding and Bedding - Bighorn Sheep

### Introduction

Moser (1962) stated: "The bighorn, unlike the deer and the elk, is an animal of the most erratic and unpredictable habits." He continued in saying: "The only two habits which they (bighorn) follow consistently are the noon-day rest and the seeking out of an established bedground for the night." Lack of routine in bighorn behavior was reported also by Smith (1954). Thomas (1957) stated: "From the observations made up to this time it would appear that bighorn sheep are among the most erratic and unpredictable of Wyoming's game animals." In this chapter, behavior patterns most important in inter-specific range relationships during the spring, summer, and fall will be described.

### Feeding Time

Bighorn sheep are diurnally active (Green, 1949; Blood, 1963). They feed during the day and alternate feeding periods with rest during all daylight hours in the Tarryall Mountains of Colorado (Spencer, 1943), along the Cache la Poudre River, Colorado (Simmons, 1961), in Colorado generally (Moser, 1962), in Banff National Park, Canada (Green, 1949), in the Sierra Nevada Mountains, California (Jones, 1950), and in British Columbia, Canada (Blood, 1963). Moser (1962) and Blood (1963) reported that ewe-lamb-yearling groups always had some members feeding and some resting at the same time during daylight hours, although the number displaying each behavior pattern varied at any one time. Blood (1963) concluded that this was typical of ram groups also; but Moser (1962) stated that ram groups, remaining separated from the ewes, lambs, and yearlings, were frequently found all feeding or all lying down at the same time.

In contrast to this pattern of frequent alternation of feeding and resting during daylight hours, Honess and Frost (1942) reported bighorn in the Gros Ventre Mountains of Wyoming began feeding at daybreak, and fed mainly during mid-morning and mid-afternoon; with more feeding at noon than did elk and deer. Mills (1937), David (1938), Ellis (1941), Couey (1950), and Smith (1954) reported this same pattern in bighorn behavior in Yellowstone National Park, Idaho, and Montana. Those authors reported that sheep rested during mid-day between the two feeding periods and then fed until late evening when they selected a bedground for the night.

### Feeding Location

Bighorn fed on top of plateaus along Crystal Creek, in the Gros Ventre Mountains. Some feeding occurred along rim rocks or timbered benches or basins (Honess and Frost, 1942). Couey (1950) reported bighorn in Montana fed near heavy grass areas or on protected rocky areas and talus slopes, where forage was scant. Jones (1950), reported that sheep in the Sierra fed on open slopes or meadows adjacent to rugged areas and bedgrounds. McCann (1956) stated that Gros Ventre bighorn preferred to feed on high

plateaus above timberline even though there was an abundance of forage everywhere during the summer. He found sheep definitely preferred green, grassy vegetation when obtainable. Sheep restricted their grazing to spots still green when the lawn-like mesa tops began to dry out. They fed along sides of plateaus when plateau tops became brown.

McCann (1956) concluded, concerning location of summer feeding that:

> "It is rather doubtful that the particular type of forage available in any area has any delimiting effect on the distribution of the mountain sheep. Their ability to utilize such a wide variety of plant foods would seem to indicate an ability to get along in any suitable place where a sufficient quantity of food is available. The forage, however, must be procurable within their cruising radius, which is definitely limited."

Feeding Movements and Techniques

Green (1949) reported bighorn in Banff National Park scattered while grazing, "leisurely picking here and there". He further stated that sheep there did not clip herbage closely, except in the spring, when sheep utilized green shoots in preference to "carryover" vegetation, and occasionally browsed leaves and tender twigs of certain shrubs. Couey (1950), McCann (1956), Sugden (1961), and Moser (1962) reported similar delicate feeding behavior by bighorn. They concluded bighorn tend to nibble and prefer the tenderest of plants. Couey (1950) stated "when bighorns feed, it appears that they just nip the tips off of some plants or nuzzle for the very choicest bits of grass leaves." (Moser (1962) concluded "when feeding on grass, sheep usually utilize the seed heads and tips of grass leaves and, as the season progresses into the winter months, they crop the bunchtype grasses down to the root crowns in some cases." Honess and Frost (1942), Couey (1950), and Sugden (1961) reported sheep travel rapidly while feeding - sometimes running between bites. This is in contrast to the leisurely movements while feeding reported by other authors.

Bighorn seem to feed during normal daily movements. Daily movements vary considerably and will be discussed intensively under the movements section of this review. Simmons (1961) found that bighorn along the Cache la Poudre Canyon spend the night and most of the day high above the river, along the canyon sides. Feeding was most intense along the river and less intense while bighorn moved down to meadows or salt licks. Movements to lower areas were steady and directional. (Simmons, 1961).

Bedding Location and Characteristics

Most authors made clear distinction between bedgrounds used at night and areas where sheep rested during the day. I define resting at night as bedding, while reclining during the day is resting. Bedgrounds are specific areas and are usually found in rocky, precipitous locations, affording a good view of the area below and protection from predators.

Smith (1954) stated that daytime resting areas were selected anywhere sheep were feeding; but that night bedgrounds were carefully chosen and located on steep, rocky sites near a crest of a ridge. David (1938) asserted that bighorn on Mount Washburn, Yellowstone National Park, followed this

same pattern. Spencer (1943) stated that Tarryall Sheep bed in rough, sheltered areas. Honess and Frost (1942) related that each section of the Gros Ventre Range contains bedgrounds and that sheep used bedgrounds most often which offer the best protection. Couey (1950) stated that in primary bighorn sheep areas of Montana, bedgrounds were numerous, and sheep moved to one at end of daylight. Couey described the characteristic bedground as a scooped out area on a gravely ridge. Moser (1962) and Green (1949) reported this method of bighorn selection of a bedground, i.e. using bedgrounds to which the animals are closest at nightfall. Moser (1962) stated that sheep, as evening approaches, grazed in the direction of the nearest bedground, and grazed around that bedground until dark.

Spencer (1943) found bedground areas over-used in the Tarryall Mountains of Colorado. Green (1949) reported that when bighorn remain in one locality for any length of time, there was no evidence that indicated the same bed was used each night sheep were there. Apparently any comfortable place was selected where sheep were at nightfall although beds were usually in the open, near protective cover.

## Feeding - Elk

### Feeding Time

Feeding behavior of elk during spring, summer, and fall seems similar to that of bighorn. The type of area occupied apparently affects elk activities while feeding. Elk were observed feeding intensively early and late in the day in most areas. Other authors observed elk moving and feeding during most of the day. Most authors report elk do not feed at night, but are found then in sheltered areas. Altmann (1952) stated that elk feed in the early morning and late afternoon high on the Jackson Hole summer range. Resting occurred during the middle of day and middle of night. Elk in New Mexico (Lang, 1958) and in the Little Belt Mountains, Montana (Kirsch, 1962) were observed moving gradually toward timber during early morning. Active feeding had greatly decreased by 7 a.m. Most intense feeding by elk in those two areas, was observed just before darkness in grassland openings. Roosevelt elk on the Boyles Prairie, California, displayed this same pattern (Harper, 1962) with the addition that elk began feeding after sunrise on cool days in contrast to "hot summer" days when feeding ended before sunrise. Harper stated that on rainy days or when barometric pressure was very low, elk fed sporadically, were very nervous, and moved constantly while feeding.

Altman (1952) reported that elk on high summer range plateaus fed until several hours after sunrise due to strong winds at high altitudes. She determined sunny areas were used for resting and rumination.

Harper (1962) found that cows and calves displayed different feeding behavior. Calves moved from plant to plant grazing three or four species during one feeding period. Cows fed steadily and often grazed one vegetative species only during one feeding period. Regarding selection of specific plant species eaten (more information on this is discussed under food habits ) Murie (1951) stated:

> "It has been noted how non-selective elk are in their feeding habits. Grasses, other herbaceous plants, and browse are all greatly relished, and any of the three plant groups may receive particular attention where one of them is dominant in the vegetation."

## Feeding - Deer

Dorrance (1965) studied deer summer behavior within ten miles of the northern boundary of Rocky Mountain National Park. The area studied was at an elevation of approximately 10,000 feet and was considered typical of the spruce-fir zone in this region. Dorrance reported:

> "There were two major feeding periods during daylight hours. Feeding commenced at daylight (sunrise then between 0435 and 0540 or just prior to daylight and continued until between 0600 and 0800. During the day deer moved into the timber. The evening period commenced between 1600 and 1800 hours and continued until after dark (sunset between 1735 and 1816)."

Dorrance (1965) reported deer fed in an unhurried manner, browsing "on one clump of willow for one to two minutes before ambling from two to six steps to another clump of willow." Individual feeding periods were highly variable. Deer use of parks gradually diminished during daylight hours and evenings through the summer. Night feeding occurred frequently in meadows during August and September. Precipitation had no apparent effect upon deer feeding activity. Deer fed the same way during rains, fog, and mist as they did on bright, sunny days (Dorrance, 1965).

Sheppard (1960) studied mule deer in the Bow River Forest Preserve in Alberta, Canada. Most of that area was located between 4500 and 7500 feet elevation. Common overstory trees were lodgepole pine and white spruce. The terrain was rough, and high foothills were present cut by deep canyons of shale. Sheppard observed deer feeding in the open during any part of the day although feeding was most intense during mornings and afternoons in spring and during early mornings and late evenings in summer. Deer fed rarely during mid-day in summer and usually bedded down in dense cover then.

## Movements - Bighorn Sheep

### Seasonal Migration

Bighorn sheep migrate seasonally in several areas. The extent of migration varies greatly, causing some authors to label such movement as seasonal drift. Bighorn migrations are less extensive as in earlier years; but separate summer and winter ranges exist in almost all localities, although the degree of separation varies greatly.

Mature bighorn rams occupy separate areas from ewes, lambs, and young bighorn year-around except during the late fall and early winter breeding season. This separation influences time of migration for each type of group, differences in occupancy of range, and daily activities. The environment also affects seasonal migration, especially in the initiation and extent of migration.

Bighorn sheep occupy different seasonal ranges in Colorado (Spencer, 1943; Moser 1962); in Idaho (Godden and Gutzman 1938, Ellis, 1941; and Smith 1954); in Wyoming (Honess and Frost, 1942; McCann, 1956; Thomas, 1957); in Montana (Couey, 1950); in British Columbia (Sugden, 1961; Blood, 1963); and in California (Jones, 1950; McCullough and Schneegas, 1966). Seasonal

use of range varies from occupancy of low elevations during summer to alpine range during winter. More discussion of specific uses of range is presented under food habits and habitat preferences.

Moser (1962) characterized bighorn sheep of Colorado while Spencer (1943) studied the Tarryall herd and Simmons (1961) the Cache la Poudre River bighorn. Moser (1962) reported seasonal drift between summering and wintering areas "is much in evidence"; but that the original pattern of migration between distinct summer and winter ranges was blocked by encroachment of civilization whereby winter ranges were utilized for domestic purposes. Today, in many areas, seasonal ranges are very close together in mileage. Spencer (1943) estimated that one-third of the Tarryall herd remained on summer range all year long except under severe conditions while the balance migrated to lower altitude winter ranges. Simmons (1961) related that in the Cache la Poudre River Canyon, sheep were found year-around at approximately 7000 feet elevation. There, bighorn occupied high areas (below tree-line) during the snow-free months between June and December. Most were found lower in the Canyon between January and May (Simmons, 1961).

In Wyoming, McCann (1956) intensively studied bighorn sheep in the Gros Ventre Range; Honess and Frost (1942) studied most of the state but concentrated on the Gros Ventre Mountains; while Thomas (1957) conducted aerial surveys for sheep across the majority of the State. All three authors reported a loss of the original seasonal migration extending to the plains; but that bighorn altered their distribution seasonally. Honess and Frost (1942) stated: "Seasonal migrations of bighorn sheep are almost non-existent in the present-day herds of Wyoming. There is, however, some seasonal drift". They concluded that bighorn occupied two distinct ranges one summer and one winter, in the Gros Ventre Mountains, specifically along Crystal Creek. Sheep did not migrate abruptly between the two ranges and some, at least, were found on both ranges any time of the year. McCann (1956) and Mills (1937) concurred with these conclusions. Thomas (1957) stated that in Wyoming, no bighorn herd migrated more than 15 miles between summer and winter ranges. He concluded also that in most areas bighorn sheep can be found on both summer and winter ranges at any time of the year.

Smith (1954) found bighorn using summer, winter, and intermediate ranges along the Salmon River in Idaho. He determined that most sheep migrated ten to twelve miles between winter and summer ranges. Some moved only two to five miles. That area displayed great elevational changes within short distances. Smith (1954) reported one-fourth of the sheep occupied winter range during summer. Animals observed there during summer were usually small to medium-sized bands of ewes, lambs, and yearlings. Rams were observed rarely on the winter range during summer (Smith,1954). Gooden and Gutzman (1938) studied bighorn in the Lemhi Valley area of Idaho. They determined that definite winter and summer ranges existed. Sheep left the summer range (8000-9000 feet elevation) in November and returned in late March.

Bighorn migrated seasonally from summer to winter range in the Sun River Game Range of Montana (Couey, 1950). Some sheep were found during summer near winter range. Couey (1950) stated also that the migration back to summer range occurred in late April and May, prior to lambing. He concluded that this was a gradual movement, over regular routes, and ended on higher range.

Blood (1963) and Sugden (1961) studied California bighorn (Ovis canadensis californicus) in British Columbia. Sugden worked inthe Churn Creek area while Blood studied the Ashnola region. They found distinct summer and winter ranges in each area. Summer ranges were located in the alpine zone. Rams preceded ewes in spring migration. Ewes left the winter range in early July while rams moved to higher elevations in late May and early June. Sugden reported a range of 15-30 miles between summer and winter ranges in the Churn Creek area. Jones (1950) and McCullough and Schneegas (1966) found bighorn concentrated in higher elevations during spring, summer, and fall in the Sierra Nevada Mountains of California and migrated to lower ranges in winter. McCullough and Schneegas (1966) asserted that bighorn winter range was separated from the summer range along the crest of the Sierra by about 4000-5000 feet elevation. The distance between was short, three to seven miles, due to extreme slope.

Sex Separation

Rams remain separated from ewes, lambs, yearlings, and young rams year around except during breeding season. States or provinces where this was reported were Colorado (Spencer, 1943; Moser, 1963), Wyoming (McCann, 1956), Idaho (Godden and Gutzman, 1938; Ellis, 1941; Smith, 1954), Montana (Couey, 1950), British Columbia (Sugden, 1961; Blood, 1963) and California (Jones, 1950; McCullough and Schneegas, 1966). The general concensus is that rams remain with ewes until four years of age.

Mature rams are usually first to return to summer range and last to arrive on the winter range to join ewes, lambs, yearlings, and young rams (Ellis, 1941; Couey, 1950; Smith, 1954; McCann, 1956; Sugden, 1961; Moser, 1962; Blood, 1963). Spencer (1943) reported older ewes were first to leave the winter range in the Tarryall Mountains. Rams waited sometimes until June to leave. McCann (1956) concluded that the two sexes appeared to make a positive effort to remain separated during summer and early fall.

Ewes usually lamb on winter range before they move to higher areas. They may lamb on higher areas. Spencer (1943) and Couey (1950) reported ewes left winter range prior to lambing. In contrast, Smith (1954),Sugden (1961), and Blood (1963) observed ewes lamb prior to leaving winter range. Blood attributed this to presence of heavy snow in alpine areas during the lambing season. Smith (1954) believed ewes lambed on winter range because of availability of good lambing habitat. Movements of ewes and newborn lambs from winter range were described by Blood (1963) as more distinct than displayed by rams. He said rams displayed a gradual drift from winter range in spring. Sugden (1961) and Blood (1963) determined ewes, lambs, and yearlings remained usually on winter range after lambing, until July, while Smith (1954) stated that some leave immediately while others wait. Smith (1954) believed some sheep may delay leaving or remain on winter range due to presence of a relatively better salt supply and presence of favorable lambing habitat.

Rams usually occupy rough, precipitous areas at high elevations after leaving the winter range. McCann reported that in the Gros Ventre Mountains, mature rams dispersed at high elevations during summer and occupied the "most inaccessible, craggy canyons and basins", either singly or in small groups. Smith (1954) observed rams on one side of the Middle Fork of the Salmon River during spring, summer, and fall, and not on the other side. Rams were found on both sides of the river during the winter.

## Causes of Seasonal Migration

Reasons for seasonal migration concern mainly physical environment. Winter precipitation and seasonal growth of vegetation is most important. Most authors reported that bighorn leave summer range in response to storms and snowfall (Moser, 1962; Honess and Frost, 1942; Jones, 1950; McCullough and Schneegas, 1966; Sugden, 1961; Blood, 1963; Smith, 1954; McCann, 1956). Most of these authors believed bighorn left summer range because permanent snow covered the needed, low-growing vegetation. Smith (1954) stated: "their (bighorn) preference for high country habitat apparently induces them to remain on sub-alpine pastures until the first snowstorm." Smith believed fall storms caused a more rapid migration in bighorn than in elk or mule deer. He attributed this to food habits; that elk and deer were able to forage on taller browse species after low growing vegetation favored by sheep was covered with snow.

Exceptions exist concerning fall migration. Spencer (1943) determined bighorn migrations occurred at the same time over the same routes year after year, regardless of weather in the Tarryall Mountains of Colorado. Blood (1963) postulated that since breeding does not take place until sheep are on the winter range, fall migration could be motivated partly by reproductive urge. Many authors believed some bighorn remained on summer ranges during winter. This will be discussed more under habitat preferences.

Most authors conceded that during the spring migration, bighorn follow the retreat of melting snow, apparently seeking vegetation in earliest growth stages. Jones (1950) reported this to occur in the Sierra; Smith (1954) for Idaho; Blood (1963) in British Columbia; and Moser (1962) for Colorado. Blood (1963) added, however, that spring migration of bighorn is not well-explained. He believed altitudinal migrations by animals are undertaken to make use of different environments so that adverse conditions are reduced to a minimum. Blood (1963) and Moser (1962) stated that this following the snowline and use of new spring growth occurs mainly on south-facing slopes. Smith (1954) mentioned that vegetation not utilized during winter and uncovered in the spring is utilized also by sheep migrating in spring. Moser (1962) determined sheep movement back to summer range is Colorado was slower than movement during fall migration. In contrast to this, Smith (1954) determined that spring migration was more rapid than fall movement from summer to winter ranges.

## Daily Movements

Data are limited concerning daily movements of bighorn sheep. Apparently the distance bighorn move each day varies considerably, depending on the activity and destination of the animals. It is often reported that bighorn sheep move considerable distances to find water and salt. Sheep do not seek water and salt each day, however. Simmons (1961) calculated a mean daily cruising radius of 832 yards for Cache la Poudre bighorn sheep. These data displayed considerable variability, i.e. one standard error of the mean equaled 109 yards. He reported also that movement of sheep decreased during stormy days; and sheep greatly increased daily movements between early summer and late summer relative to between spring and early summer. This increase was displayed in early morning and early afternoon. Simmons (1961) attributed this increase to the decrease in availability of desired forage.

Bighorn sheep moved an average of 150 yards each day during summer in the Sierra range of California (Jones, 1950). Davis (1938) studied bighorn sheep on Mount Washburn in Yellowstone National Park, Wyoming. He determined a maximum daily movement of two miles. Further complicating this question of expressing bighorn daily movements, Couey (1950) stated that:

> "Rams have been seen wandering great distances from known bands of sheep. This wandering habit should insure a mixture of breeding stock in most bands."

## Movements - Elk

Elk migrate seasonally in the western United States. These movements are similar to those of bighorn sheep. Few studies of the two species in the same area have been conducted, however. Definite elk summer and winter ranges exist in most areas. Some authors reported intermediate ranges. Occupancy of seasonal ranges depends on time of year plus antecedent and current weather conditions.

Mature bulls remain separated from cows, calves, and younger animals throughout spring and summer. As with bighorn sheep these two groups also display different occupancy of range, different timing in migration, and different activities.

### Seasonal Migration

Definite seasonal migrations of elk are reported for: Rocky Mountain National Park (Guse, 1966; Gill, 1966), the White River in Colorado (Harris, 1958), along the Gallatin River, Montana (Brazda, 1953), in the Sun River, Montana area (Picton, 1960), in the Gravelly Mountains of Montana (Rouse, 1957), along Crow Creek, Montana (Stevens, 1965), Montana in general (Cole, 1958), along the Selway River, Idaho (Dahlke,et al. 1965) and in Jackson Hole by Altmann (1952, 1956), Murie (1951), and Anderson (1954). Cole (1958), Harris (1958), Picton (1960), and Dalke (1965) reported use of intermediate ranges by elk. Cole (1958) concluded intermediate ranges may be used during winter, when mild conditions persist. Most authors reported that spring migration began in late May and the fall movement to winter ranges was initiated approximately the first of September.

Distance between elk summer and winter ranges varies among areas. Wild ungulates utilize the same winter range in most localities, at least during severe conditions. Rouse (1957) estimated that elk in the Gravelly Mountains of Montana moved from two to eight miles between summer and winter range. Dalke, et al (1965) reported a maximum movement between elk seasonal ranges of 20 miles. The average was eight to ten miles. Gill (1966) reported some elk have moved great distances in Rocky Mountain National Park and the surrounding area. Seasonal movements of elk varied between one mile and twelve miles.

Altmann (1952, 1956), Brazda (1953), Anderson (1954) and Picton (1960) reported mature bull elk separated from nursery groups (cows, calves, yearlings, and young elk) by being first to leave winter range in spring. Bull groups move toward summer range and arrive there before nursery groups. Cows, calves, yearlings, and younger elk arrive later. This separation persists apparently until the fall breeding season. Brazda (1953), Anderson (1954) and Altmann (1956) reported that cows calve before occupying summer

ranges. Anderson and Brazda believed spring migration was delayed by calving more than by any other factor. Altmann said cows calve in secluded areas, away from the rest of the herd.

Reasons For Migration

Blood (1963) believed altitudinal migrations of ungulates are made to escape unfavorable conditions. The two factors, highly correlated by most authors were snow conditions and the relative growth stage of vegetation (Murie, 1951; Brazda, 1953; Anderson, 1954; Altmann, 1956; Nichols, 1957; Cole, 1958; Harris, 1958; Picton, 1960; Dalke et al., 1965; and Stevens, 1965). Elk followed the retreat of snow in spring and preceded permanent snow in fall. (Murie, 1951; Anderson, 1954; Altmann, 1956; Nichols, 1957; and Dalke et al., 1965). New growth is initiated when vegetation is uncovered by melting snow in spring. Probably new green growth plus the now-available carry-over vegetation are sought by elk.

Altmann (1956) reported some bull groups reach summer range in the Jackson Hole area before the snow cover is depleted. South slopes were used most, even though forage was scarce sometimes. She concluded the small size of these bull groups allowed them to utilize small patches of grass vegetation recently exposed.

Some disagreement exists among authors concerning why elk migrate when they do. Some authors (Nichols, 1957; Picton, 1960; Dalke et al., 1965) believed elk migrate to utilize new vegetation after snow melts. Brazda (1953) and Murie (1951) believed elk move for different reasons although they realized migration was correlated highly with snow melt and vegetative development. Dalke et al. (1965) related that:

> "Elk followed the retreating snowline but descended to the lower slopes with the first appearance of new growth of grasses, sedges, and forbs. Following this distinct downward trend in April, elk gradually worked upward to the summer range. The advent of herbaceous spring vegetation had a greater effect on elk movements than did artificial salt during April and May."

Elk use of high mountain meadows was negligible during summer inthe White River National Forest, Colorado, until vegetation had attained a certain level of growth. (Nichols 1957).

Brazda (1953) studied possible causes of elk migration in the Gallatin River area of Montana. He concentrated on vegetative development relative to elk movements back to summer range by collecting and analyzing plants for determining stage of development, Brazda correlated development with elk movements. He stated cow elk did not follow plant development while migrating back to summer range. Plants collected throughout the upper winter range during the calving period when many elk were present, indicated vegetation was in an early stage of development. Later collections from summer range, when large numbers of elk were first appearing there, indicated vegetation was in a later stage of development. We believed this suggested that the period of parturition was more important in governing the upward movement of cow elk than plant development. Cows, then, were apparently delayed in the spring migration by calving duties.

Delay in spring migration was reported by Anderson (1954) and Altmann (1956). Murie (1951) suggested that elk may move to summer range in spring before new vegetation is present in any significant quantities. He believed dried grasses may still be an important part of the diet when movement is initiated. He stated further that green vegetation did not predominate in the diet until migration had proceeded for one to three weeks. Delay may have partly been due to increased availability of green vegetation then. Many elk left luxuriant vegetation of valley bottoms and persistently followed the snow line back into the mountains.

Brazda (1953) revealed a second phenomenon which indicated elk did not follow development of vegetation in migration. He determined that the emergence of horseflies (Tabanidae)apparently caused elk and deer along the Gallatin River to move to higher elevation in spring, before vegetation was developed there. Deer and elk occupied windy ridges during the day to escape flies.

Murie (1951) and Stevens (1965) believed two additional factors possibly affected elk migration to summer range. Murie (1951) stated:

> "Elk are quite susceptible to heat. Even early in the spring, when the snow is disappearing, they often bed down on snowdrifts, and they seek the highlands early, traveling over snow to reach high ranges, even though the valley below is green. In summer, even at high altitudes, the elk often seek the shade of trees or lie in wet meadows, where they chew cuds and fight flies."

Stevens (1965) found that in one instance snowfall caused an elk here migrating to summer range to withdraw to winter range for approximately two weeks. Anderson (1954), concluded, however, that storms had little effect on elk spring migrations around Jackson Hole, Wyoming.

Inconsistency exists concerning factors causing elk migrations in the fall. Anderson (1954) believed time of migration to winter range is much more directly dependent upon weather conditions than spring migration. He determined snow depth was the primary ecological factor affecting fall migration. Temperature, wind, and other climatological factors had no noticeable effect; although a warm pause between fall snowstorms often temporarily halted fall migration. Anderson (1954) concluded: "Apparently most of the elk remain on the summer range as long as snow does not cover the forage." Cole (1958) asserted that snow and other winter weather patterns forced deer and elk to concentrate on winter range in Montana.

Altmann (1956) determined Jackson Hole elk grazed summer range plateaus to bare soil by late August when snowdrifts had melted and sources of water were scarce. Large elk herds then divided into smaller herds and grazed less-desirable slopes and creek bottoms. Summer ranges become deserted then.

Stevens (1965) found that elk moved out of large open parks, on the summer range during late July, into forested areas. He believed this movement was due to the decrease in succulence of forage in parks. This suggested that elk possibly leave high summer range in an effort to obtain more succulent vegetation at lower elevations or in more protected areas. Guse (1961-65) reported elk in Rocky Mountain National Park first leave

the summer range for breeding purposes, and that mating takes place on upper parts of the winter range. He reported further that elk returned to parts of the summer range after the mating period. Elk remained on the summer range for varying periods of time before being forced to the winter range by inclement weather.

## Movements - Deer

Siglin (1965) studied mule deer seasonal migrations and daily movements in the Cache la Poudre River headquarter area, Colorado. Deer were tagged and radio transmitters were placed on individual deer. He believed deer returned to the same summer range each year. Deer crossed major ridge tops between drainages during migration. Deer migrated an average of 12.8 miles. Maximum seasonal movement was 23 miles.

Dorrance (1965) studied deer in the same area as Siglin (1965). Dorrance concluded deer arrive at the Long Draw Reservoir summering area each year about the second week in June and depart for the winter range before the third week of October. Deer arrived on summer range both years within several days while departure was spread over several weeks. Dorrance (1965) recognized an "altitudinal stratification" by sex and age on summer range. Bucks occupied areas above or close to tree-line, and spent most of the summer there. Does, fawns, and young deer occupied lower elevations during summer, in timbered areas with numerous open parks. This stratification was not absolute, however.

Sheppard (1960) studied mule deer in the Sheep River region of Alberta. This area varied in elevation between 4500 and 7500 feet. Most of the area was lodgepole pine covered foot-hills cut by canyons of shale. Some northern alpine meadow vegetation was present. Deer were relatively non-migratory; although they moved to south-west-facing slopes in spring where snow melted first and grass began to grow. Does with fawns occupied lower portions of the range while bucks, yearlings, and barren does were found on higher areas. Buck groups were often observed in open alpine meadows during summer. No fawns were observed above tree-line. Deer movements during summer were confined to the morning and evening periods (Sheppard, 1960).

Siglin (1965) and Dorrance (1965) concluded the ultimate cause of deer fall migration was inclement weather. Siglin believed physical discomfort and the covering of vegetation by snow were most important. Dorrance (1965) stated:

> "It appears that existing weather conditions are not the proximate cause of migration although they may be the ultimate cause. During both years of the study, deer migrated at least two weeks prior to any inclement weather which would cause them hardships. I believe that the migration is in response to some factor, as for example, duration of daylight or angle of incidence of the sun's rays".

Siglin (1965) concluded spring movement of deer was correlated to development of vegetation and indirectly related to snow-melt. Dorrance (1965) stated the development of new vegetation is the ultimate cause in determining arrival time on summer ranges. Factors or combination of factors listed above by him were believed the proximate causes. He stated that "Deer must

arrive on the summer range very close to the same date every year, for there is only a period of a few days between the date of arrival and parturition."

## Daily Weather Conditions

### Bighorn Sheep

Bighorn sheep seek natural shelter during severe hail, rain, or snow storms (Davis, 1938; Ratcliff, 1941; Green, 1949; Couey, 1950; Smith 1954; Sugden, 1961). Davis (1938), Green (1949), and Smith (1954) reported bighorn used forested areas for protection from severe storms. Use of caves and protected areas at the base of cliffs by bighorn during harsh storms was reported by Green (1949), Couey (1950) and Smith (1954).

Moderately severe storms apparently have little effect on bighorn, especially when wind velocity is low. Smith (1954) believed sheep were indifferent to moderately severe weather conditions. Sugden (1961) reported that rain, snow, or hailstorms with no wind had no visible effect on bighorn behavior. He believed high winds of any kind, with rain or snow, made sheep nervous, especially when moving objects were sighted. Ratcliff (1941) determined protected areas were grazed more heavily than areas exposed to winds on winter range in eastern Rocky Mountain National Park. Those areas were located in meadows and on hillsides with southern and eastern exposures. Schallenberger (1965) reported bighorn used only Douglas-fir timbered areas and canyon bottoms on days when strong winds and cold temperatures "forced" them to seek shelter.

Smith (1954) concluded sheep differed from elk and deer because bighorn did not seek shade during the heat of the day on summer range. Bighorn were observed sunning themselves on exposed areas. Smith stated further, however, that bighorn often sought shade on winter range occupied during summer. He added that during the summer bighorn were most active during sunny weather following rain. Simmons (1961) reported that bighorn daily movements along the Cache la Poudre River, Colorado, decreased during stormy days.

### Elk

Elk usually seek shelter during severe storms. Altmann (1956) and Murie (1951) concluded that harsh storms, especially where high winds were present, caused elk to enter forested areas or dense aggregates of trees. Murie (1951) reported some elk fed in open areas during storms, but never when high winds were active. Altmann (1956) stated that during bad weather elk grazed in a cluster formation, preceding the seeking of shelter. She reported also that elk quickly entered shelter areas during sudden storms.

Murie (1951) believed elk were quite susceptible to heat. He reported elk on high summer range often lay in the shade of trees or in wet meadows. The effects of physical environment on elk feeding behavior have been discussed under a previous section of this chapter. Harper (1962) related that Roosevelt elk on the Boyles Prairie of California became very nervous, fed sporadically, and increased their movements on rainy days or where barometric pressure was low. Harper determined also that elk began feeding before sunrise and bedded between mid-morning and late afternoon to escape the mid-day heat. Dalke et al. (1965) concluded elk sought vegetative cover

more in summer than winter. Harper (1962) correlated colder weather during summer with feeding by elk after sunrise and earlier in the afternoon. Altmann (1952) reported: "characteristic formations of elk groups on the slopes of the summer range are the 'windrow' formation in which all animals of a group graze parallel in a long-drawn-out row, and the formation in which they stand close, but not touching each others flanks, in a limited stretch of sunshine on a slope."

Deer

Dorrance (1965), studied deer during summer north and west of Rocky Mountain National Park. He concluded:

> "Precipitation had no apparent effect upon (deer) activity. Deer were observed feeding in fog, mist, light rain, downpours, and snowstorms just as they were on bright, sunny days."

He determined no significant correlation of deer use of meadows with weather changes and characteristics.

In contrast to Dorrance's findings, Sheppard (1960) determined that mule deer in Alberta were inclined to bed earlier and arise later in the day during hot days. He found also that during cold, wet weather or during high winds, mule deer were confined to heavy cover.

## Herding - Bighorn Sheep

### Herd Composition

Bighorn rams remain separated from ewes, lambs, yearlings, and younger individuals all year except during portions of fall and winter. This was reported in Colorado by Spencer (1941), Simmons (1961), Moser(1962), and Tileston (1962); in Wyoming by McCann (1956) and Thomas (1957); in Utah by Barmore (1962); in Idaho by Smith (1954); in British Columbia by Blood (1963); and in Alberta by Green (1949). Blood (1963), Moser (1962), Thomas (1957) and Simmons (1961) reported that rams separated from ewes and young animals during summer while Spencer (1941), Green (1949), Jones (1959), and McCann (1956), stated rams separated from ewes and young animals immediately after the breeding season and before the spring migration. Tileston (1962) concluded rams separated from ewe groups in April.

The age of rams which leave ewe - lamb - yearling groups varies. Simmons (1961) and Jones (1950) stated rams became members of ram groups at the age of two years. Green (1949) reported rams remained with ewe groups until four years of age. Blood (1963) stated that yearling sheep were observed in three of 107 rams groups encountered in Banff National Park, Canada; and that two year old rams were slightly less common in ewe groups than ram groups. Three year old rams occurred in 37 percent of the observed ram groups and in nine percent of ewe groups. No lambs were observed in any ram group. Blood determined also that 12 percent of the ewe groups contained mature ewes only. Tileston (1962) reported that in April, pregnant ewes "drive off" the yearlings; thus small groups of yearlings only were seen during spring. Smith (1954) found that in Idaho, yearlings and lambs banded together after the breeding season and remained separated from ewes until late spring. He concluded this separation caused low lamb and yearling spring census counts.

Ewe groups and ram groups occupy different habitat types during summer and fall, after separation. Rams occupy higher, more inaccessible areas while ewes remain at lower altitudes in lambing areas. Spencer (1941), McCann (1956), and Moser (1962) stated that rams occupy higher ranges than ewe groups while Thomas (1957), Simmons (1961) and McCullough and Schneegas (1966), reported that ram groups spend the summer and fall in more rugged and inaccessible areas than ewes. Blood (1963) reported that rams preferred rolling mountain areas during summer in British Columbia. He stated also that differences in topography between ram and ewe summer ranges suggested protection of lambs was a significant factor in selection of summer range by ewe groups. Ewes usually select habitat with more readily available escape terrain. Moser (1962) reported that during summer, in Colorado, ewe groups are found at lower elevations than rams. In contrast, Thomas (1957) reported ewe groups occupied high, open mesas and plateaus during summer in Wyoming.

Green (1949) and Simmons (1961) stated rams may join ewe groups in lower altitudes for brief periods during summer; but that little to no mixing or show of interest occurred. Blood (1963) observed both ram and ewe groups on alpine range in British Columbia, but never together. Simmons (1961), Barmore (1962), and McCullough and Schneegas (1966) reported rams were difficult to locate during summer due to occupancy of inaccessible ranges.

Group Size

Green (1949) and Sugden (1961) asserted that bighorn sheep is a gregarious species, and that herd size varies. Sugden stated that herd size appeared to vary directly with total number of sheep present instead of populations having constant herd sizes. Green (1949) reported that bighorn bands in Banff National Park varied from groups of 15 or fewer to congregations of more than 100.

Variations in herd size occur for several reasons. Changes in herd size and composition occur mainly during the breeding season, and in some areas during severe winters. Rams join ewe groups during mating. Green (1949) stated bighorn bands were loosely associated and may merge wholly or partly with other herds. McCann (1956) found Gros Ventre bighorn split into various small bands in summer and winter. Bands were separated sometimes by a distance of up to ten to twelve miles. He believed interband migrations sometimes occurred where distance between herds was not great. The number of sheep observed in any one band varied from day to day. He believed this was due to the tendency of small sub-groups to split off from the main group, to feed.

Ram groups are small when separated from ewes. Ewe groups are larger (Table 4). Thomas (1957) said rams occur in small isolated bands during the summer and fall but he gave no data concerning this. Many authors reported observing solitary bighorn, with most stating that sightings of single sheep were usually of rams. Green (1949) stated that old and senile sheep usually were solitary.

Blood (1963) stated, after evaluating herd size during the entire year, that bighorn occurred in larger size groups during the months of June, July, and August. Ewe groups were largest during these three months while ram groups were larger during April, May, and August.

Table 4. Comparative estimates of bighorn herd size, in North American populations. 1/

| AUTHOR | AREA STUDIED | AVE. HERD SIZE | SIZE RANGE | | |
|---|---|---|---|---|---|
| | | | Male | Female | Total |
| Honess and Frost (1942) | Gros Ventre Mountains Wyoming | - | - | - | 1-25 |
| McCann (1956) | Gros Ventre Mountains | - | 2-12 | - | - |
| Smith (1954) | Salmon River, Idaho | 7.3 | - | - | 1-46 |
| Blood (1963) | Ashnola area, British Columbia | 9.3 | - | - | 1-46 |
| Green (1949) | Banff National Park | - | 2-15 | - | - |
| Simmons (1961) | Cache la Poudre River | - | 1-4 | - | - |
| Moser (1962) | Colorado (state-wide) | - | - | 5-20 | - |
| McCullough and Schneegas (1966) | Sierra Nevada Range, California | 7-6 | - | - | 1-18 |
| Jones (1950) | Sierra Nevada Range, | - | 1-3 | 1-15 | - |

1/ counts made when mature rams separated from rest of herd

## Herding - Elk

Elk separate during spring and summer as bighorn do, i.e. bulls remain apart from cow-calf-young groups (Altmann, 1952, 1956). Altmann (1952) determined bulls joined cow groups during the rutting season, September to November, and stayed with female groups part of the winter. Altmann (1956) described elk herd structure as follows:

winter - very large aggregates containing both sexes.

spring - small to medium bands (5-50). Sexes separated on the normally long migration.

summer - cows form large herds with calves and yearlings. Bulls form small groups.

fall - Bulls form cow harems of five to fifteen animals. One bull present. Pre-rut-one and two year old males are driven from bull and cow groups. Bulls remove velvet and increase their use of wallows.

Rouse (1957) studied elk in the Gravelly Mountains of Montana. He determined the average size of cow groups between June and October was 21 while between December and March herds averaged 32 individuals. Kirsch (1962) found that during summer, in the Little Belt Mountains of Montana, elk groups averaged 7.9 animals. The largest group sighted contained 56 individuals. Stevens (1965) surveyed elk on the Elkhorn Mountain Range of Montana during summer. Elk averaged 9.1 animals per group, based on ground census. After conducting aerial surveys, both helicopter and fixed-wing, over the same area during the same period, Stevens determined that elk averaged 13.9 individuals per group.

## Bighorn Lambing

### Time of Lambing

Bighorn ewes bear young usually between May and June. Some lambing occurs in April and July. Spencer (1941), Packard (1946) and Blood (1963), stated lambing occurred between late April and mid-June, with the peak about June first. Davis (1938) and Moser (1962) concluded that the peak in lambing in Colorado and Yellowstone National Park was mid-June. Some births occurred in early July. Couey (1950) believed the lambing peak occurred during the last week of May in Montana.

McCann (1956) determined lambing occurred in the Gros Ventre Mountains approximately the same time bighorn migrated back to summer range. He stated that ewes expecting lambs remained on the winter range, and those not pregnant moved on. Some ewes and lambs remained on the winter range lambing grounds for a few days after lambing before moving to summer range. This may explain reports by Davis (1938) and Packard (1946) who observed new ewes and lambs on the summer range as summer progressed.

### Location

Lambing grounds are precipitous, rugged areas and usually contain cliffs and rock outcroppings. Such lambing grounds were found in Colorado

(Spencer, 1941; Packard, 1946, and Moser, 1962), in Wyoming (McCann, 1956), in Idaho (Smith, 1954), in Montana (Couey, 1950) and in British Columbia (Blood, 1963). Protection of young is the main reason for lambing in rugged areas, (Smith, 1954; Packard, 1946; McCann, 1956). Smith (1954) and Blood (1963) found lambing areas only on south exposures, next to a source of food. Smith believed the distance to water from lambing areas was insignificant. Most lambing areas found by Blood were void of trees. Few were partly forested. Moser (1962) determined lambing grounds were used year after year in Colorado.

Lamb Care and Growth

Spencer (1941), McCann (1956) Moser (1962) and Blood (1963) reported that ewes gave birth to lambs in secluded spots on lambing areas, and that the ewe and lamb remain close together in this spot for the first few days to one week. Moser (1962) asserted that this time interval was closer to two weeks in Colorado herds.

Spencer (1941) and Moser (1962) stated that following the period of ewe and new born lamb isolation after parturition, the ewe and lamb join other ewes with lambs to form small bands. Moser reported those bands then began to migrate to higher summer range. Spencer (1943) concluded lambs were perfectly at home on rocks at one week of age in the Tarryall Mountains of Colorado.

Murie (1940), Couey (1950), and McCann (1956) concluded that when lambs were very young, ewes may cache their very young lambs or leave them with other ewes while they go off alone to feed or to drink. Murie (1940) and McCann (1956) observed single ewes caring for two or more lambs. Spencer (1941) believed lambs follow ewes and are not cached like fawns. Spencer was probably considering lamb behavior after the first few weeks of life, however.

Lambs develop rapidly after birth. Spencer (1941) observed lambs grazing when one month of age. Spencer (1941) concluded lambs are weaned by November while Blood (1963) estimated weaning time as five to six months after birth. Honess and Frost (1942) reported that lambs may double their size in one month, and that fastest growth occurs during the first summer. They estimated the normal lamb was three-fourths the size and one-half the weight of its mother by the end of fall. Moser (1962) estimated lambs attained one-half the size of their mothers during fall and ceased nursing by late fall. Moser observed that during the fall, lambs were considerably darker in pelage than ewes and yearlings.

Number of Lambs and Breeding Age

Honess and Frost (1942), Green (1949), Moser (1962) and Tileston (1962) reported twins occur in bighorn sheep but they found no record of this in their study areas. Green (1949) concluded the extent of twinning in Banff National Park bighorn sheep was very difficult to determine due to the loose association between ewes and lambs. These authors concluded one lamb per ewe giving birth is the rule. Spalding (1966) found four of eleven pregnant ewes killed by vehicular traffic in southern British Columbia were carrying twins during winter.

# FOOD HABITS

## Bighorn Sheep

Bighorn sheep are varied feeders, although most authors believed sheep eat mainly grasses and grass-like plants. Food habits of bighorn vary with relative availability and succulence of vegetation. Plant composition changes with differences in site; thus availability of plant species varies among locations. Succulence of vegetation depends on time of year and antecedent weather factors. Bighorn definitely prefer green, succulent vegetation and will seek it when available.

Food habits studies are difficult and accuracy is often questioned. Too often, sampling is insufficient to allow proper statistical analysis. This is due to difficulty in studying free-ranging wild ungulates, whose diets change according to vegetative availability and succulence. Many times, the determined diet of ungulates is not related to plant availability. Composition of diet is used commonly to indicate vegetative preference instead of percent utilization of what is available. Cook and Stoddart (1953) stated that measurement of preference must be based on availability of each plant species relative to other species and total forage available. They believed palatibility and preference can be determined by comparing degree of utilization with abundance and production of species.

Reported food habits studies on bighorn sheep are numerous and varied. Several different herds have been studied, with different methods used. A summary of these studies and their findings is presented in Table 5. It is valuable, however, to know more about each study, the locality, vegetation, and animals present. I will discuss these studies by states.

### Colorado

Moser (1962) and Tileston (1962) presented analysis of 81 bighorn stomach samples collected during the 1953 and 1954 September hunting seasons. Samples were collected from several herd localities. Data are presented in Table 6. Most areas contained alpine vegetation, and bighorn may have been using alpine areas during September.Grass occurred most frequently in the diet (Table 6). Total mean percent frequency of occurrence of all samples showed grass comprised 74.7 percent, browse 19.1 percent, and forbs 6.2 percent. Moser (1962) described the contents of the samples. He reported all samples contained grass. Seventeen species of grass were found. Most significant species were Carex nigricans, Festuca idahoensis, Festuca ovina, Muhlenbergia montana, Poa alpina and Poa rupicola. Nine species of browse were identified. Most frequently occurring were Potentilla fruticosa and Salix glauca. Eight species of forbs identified included Trifolium nanum, Mertensia alpina, and Senecio fendleri.

Spencer (1941, 1943) studied sheep in the Pike National Forest of Colorado, especially the Tarryall Mountains. By direct observation and "snow trailing" of sheep, he determined bighorn food habits were similar to elk there. Sheep occupied high elevations in summer. Alpine sedges and clovers comprised most of the diets. Other species eaten were: Festuca idahoensis, Trisetum spicatum, Muhlenberia montana, Deschampsia caespitosa Koeleria cristata, Calamogrostis canadensis, Poa pratensis, Polygonum douglasii (flowers only), Cersium spp., Mertensia siberca, Caltha sp.,

Table 5. Food habits of North American bighorn sheep populations.

| AUTHOR | LOCATION OF STUDY | FOOD HABITS | | | | FOOD HABITS DETERMINATION TECHNIQUE |
|---|---|---|---|---|---|---|
| | | Fall | Winter | Spring | Summer | |
| Schallenberger, 1965 | Sun River Canyon, Montana | *G-86%<br>*B-2nd<br>*F-3rd | B-43%<br>G-36%<br>F-21% | - | - | Fall-15 stomach samples - (% volume)<br>Winter-feeding site exam |
| Couey, 1950 | Sun River area, Montana | G-1rst<br>F-2nd<br>B-3rd | C1rst<br>B-2nd<br>F-3rd | - | - | Stomach samples -6 (% volume) |
| McCullough and Schneegas 1966 | Sierra Nevada Mountains | - | G-35%+ | - | - | Direct Observation |
| Riegelhuth, 1965 | Sierra Nevada Mountains | - | B-1rst | - | - | Direct observation |
| Jones, 1950 | Sierra Nevada Mountains | F-1rst<br>B-2nd<br>G-3rd | - | - | - | Grazed plant tally along transect line |
| Smith, 1954 | Salmon River, Idaho | F -66%<br>G<br>B-25% | F -56%<br>G<br>B-39% | F -77%<br>G<br>B-22% | F -86%<br>G<br>B-14% | Direct observation - % feeding time of group |
| Ellis, 1941 | Lemhi Valley, Idaho | G-60% | ---------- | ---------- | F-2nd | ---------- |
| Gooden and Gutzman, 1938 | Salmon River, Idaho | - | GL-1rst<br>B-2nd<br>FG-3rd | - | GL-1rst<br>BF-2nd<br>G-3rd | Intuitive estimates |
| Flook, 1962 | Banff and Jasper National Parks, Canada | - | - | - | G-50%<br>F-2nd<br>B-3rd | ---- |
| Cowan, 1947 | Jasper National Park Canada | - | G-83%<br>F-10%<br>B- 7% | - | - | Direct observation - % feeding time |
| Sugden, 1961 | Churn Creek, British Columbia | - | B-62%<br>G-29%<br>F- 9% | - | - | Band trailing - % observations |
| Moser, 1962 and Tileston,1962 | 14 Colorado herds | G-75%<br>B-19%<br>F- 6% | - | - | - | Stomach samples -81 (% volume) |

Table 5 concluded -

| AUTHOR | LOCATION OF STUDY | FOOD HABITS | | | | FOOD HABITS DETERMINATION TECHNIQUE |
|---|---|---|---|---|---|---|
| | | Fall | Winter | Spring | Summer | |
| Wasser, 1940 | Milner Pass & Specimen Mtn. Rocky Mountain Nat'l Park | - | - | - | GL-65%<br>G-25%<br>F-10% | Site inspection - % utilization x % composition |
| Honess and Frost, 1942 | Gros Ventre Mountains Wyoming | G-1rst<br>F-2nd<br>B-3rd | - | G-1rst<br>B-2nd<br>*CF-3rd | F-1rst<br>G-2nd<br>GB-3rd | Stomach samples -8 (% volume) |
| Davis, 1938 | Mt. Washburn, Yellowstone National Park, Wyoming | - | - | - | G-1rst | Direct observation - time spent by herd |
| Oldemeyer, 1966 | Yellowstone National Park, Wyoming | G-57%<br>B-34%<br>F- 9% | G-1rst<br>F-2nd<br>B-3rd | - | - | Direct observation and band-trailing |
| +Averages | Seasonal | G-60¢<br>F-24%<br>B-16% | G-60%<br>B-26%<br>F-14% | - - - | G-51%<br>F-38%<br>B-12% | |
| | Year-long<br>Grass-57%<br>Forbs-25%<br>Browse-12% | | | | | |

* - G=grasses B=browse F=forbs C=conifers GL-grass-like CF=conifers & forbs BF=browse & forbs GB=grass & browse

\+ - averaged data in season to get seasonal average and seasonal averages to get year-long average; if data by rank only and not in %, then assigned the rank a (averaged) % value by computing a average % value of all first place % values given by author, in numerical order, within each season.

" - not used in computing averages

Table 6. Analysis of 81 Colorado Rocky Mountain Bighorn Sheep stomach samples, September 1953 and September 1954. From Tileston (1962;31).

| NO SAMPLES | LOCATION | PERCENT FREQUENCY OF OCCURRENCE | | |
|---|---|---|---|---|
| | | Grass | Browse | Forbs |
| 27 | Buffalo Peaks | 70.2 | 20.6 | 9.2 |
| 11 | Arkansas River | 80.2 | 13.7 | 6.1 |
| 7 | Taylor River | 84.1 | 12.6 | 3.3 |
| 6 | Cimarron River | 76.2 | 12.5 | 11.3 |
| 5 | Pikes Peak | 67.2 | 24.5 | 8.0 |
| 5 | Pole Mountain | 90.9 | 9.1 | 0.0 |
| 4 | Collegiate Range | 78.3 | 11.4 | 10.3 |
| 4 | Georgetown Triangle | 55.4 | 38.7 | 5.9 |
| 3 | Clarke's Peak | 82.7 | 13.1 | 4.2 |
| 3 | Glenwood Canyon | 73.5 | 26.5 | 0.0 |
| 2 | Antero Peak | 78.4 | 9.3 | 12.3 |
| 2 | Kenosha Range | 76.5 | 23.5 | 0.0 |
| 1 | Sangre De Cristo Range | 63.4 | 20.3 | 16.3 |
| 1 | Tarryall Range | 68.0 | 32.0 | 0.0 |
| Averages | | 74.7 | 19.1 | 6.2 |

Eriogonum spp.(flowers only), Myostis alpestris, Populus tremuloides, Ribes inebrians, Jamesia americana, Rosa spp, Salix glaucops, and Picea engelmanii (buds mainly).

Potts (1936) and Wasser(1940) briefly studied bighorn food habits in Rocky Mountain National Park. Wasser observed bighorn foraging habits at Sheep Rock (elevation approximately 10,500 feet) and on the West slope of Speciman Mountain (at elevation of 11,500 to 12,000 feet). Tree-line averaged approximately 11,400 feet. He found bighorn around Sheep Rock highly preferred (species composition times species utilization) alpine dryland sedges, primarily Carex pyrenaica. Alpine sheep fescue, alpine bluegrass, black-headed sedge and western yarrow were preferred also. Dryland sedges were preferred most on Specimen Mountain with wet sedges, alpine sheep fescue, black-headed sedge, alpine poa, and moss used significantly in that order. Wasser estimated composition of bighorn diets as grasslike plants 65-70 per cent, grasses 20-25 percent, and forbs 5-10 percent.

Potts(1936) observed bighorn at Sheep Lakes in Rocky Mountain National Park. This area, at an elevation of approximately 8500 feet, was known for bighorn use of natural concentration of minerals. Minerals may be the sole reason sheep came there. Potts determined that during one visit by seven sheep during summer, Muhlenbergia sp. was utilized extensively. Carex sp., Poa sp., Artemisia frigida, Calamogrostis sp., and Ribes cereum were eaten also.

Simmons (1961) studied bighorn sheep along the Cache la Poudre River. Sheep did not inhabit high ranges during summer. Bighorn occupied montane zone areas between 7500 and 9500 feet elevation during summer. Characteristic tree species were ponderosa pine and Douglas-fir. Browse and grass-covered south slopes and north slopes were occupied by conifers, aspen, and bare rock. Grass species varied, big sagebrush and bitterbrush were the main browse species. Sheep utilized several browse species "and a variety of grasses." Distribution of grasses and browse were believed to affect sheep distribution. Browse distribution did so significantly. Sheep avidly sought salt and traveled "considerable" distances to get it (Simmons, 1961).

Wyoming

Mills (1937), Davis (1938), and Oldemeyer (1966) studied bighorn sheep food habits in Yellowstone National Park. The first two authors studied foraging habits during July while the latter determined bighorn food habits during winter. Quantitative data presented by Mills and Oldemeyer are presented in Table 5. Oldemeyer (1966) stated Agropyron spicatum, Carex sp., Phlox sp., Eurotia lanata and Chrysothamnus viscidiflorus were species utilized most by sheep during winter. Davis (1938) observed bighorn on Mount Washburn avoid most abundant forbs and sedges and seek grasses and other plants presumably more palatable. He estimated sheep grazed 95 percent of feeding time during July. Green vegetation was preferred over dried plants at all times. He stated (Davis, 1938): "as the season advanced, additional plants doubtless took the places of those maturing." Relative palatability of each species changed during summer.

Honess and Frost (1942) studied bighorn ecology in the Gros Ventre Mountains. Eight stomach samples were collected and the data are presented in Table 5. Areas occupied by bighorn sheep during the summer were high

plateaus covered by alpine vegetation. Rocky, bluff-type edges provided escape. McCann (1956) also studied bighorn in the Gros Ventre Mountains. He concurred with Honess and Frost (1942) by reporting bighorn occupied high, plateau-like mountain tops, well above timberline during the summer, where they found an abundance of forage. He believed available minerals were necessary for bighorn and that sheep did not take free water, but utilized snow instead.

Idaho

Smith (1954) studied bighorn sheep along the Salmon River, typically on cliffs with related talus. The Salmon River flowed at an elevation of approximately 3000 feet. Bighorn occupied canyon sides during the winter. Smith (1954) described sheep summer range: "The high country is characterized by sub-alpine valleys surrounded by ridges which are studded with spires of jagged rock." Glaciated basins were rimmed with talus and outcroppings of barren granite. Higher peaks varied between 8000 and 11,000 feet in elevation (Smith, 1954).

He concluded bighorn were versatile in their diet, and usually favored succulent and tender forms of forage. Results of his observations on bighorn food habits are presented in Table 5. Sheep ate grasses most, some forbs, and little browse year-around. Grasses and forbs were used less in the fall and winter. Presumably, this was due to a loss in palatability. Use of grasses and forbs increased markedly in spring. He reported that bighorn occupied open, grassy, south-facing slopes during spring. Grasses, grasslikes, and forbs comprised 86 percent of the summer diet.

Smith (1954) concluded sedges, bluebunch wheatgrass, rushes, little ricegrass and curlleaf mountain mahogany were most important forage species taken during summer. Bighorn used bluebunch wheatgrass, curlleaf mountain mahogany, and Idaho fescue during fall. Bighorn ate mainly curlleaf mountain mahogany, bluebunch wheatgrass, big sagebrush, Idaho fescue, rubber rabbitbrush and golden currant during winter. During spring, bighorn fed mostly on curlleaf mountain mahogany, bluebunch wheatgrass, arrowleaved balsamroot, and Idaho fescue.

Ellis (1941) studied bighorn in the Lemhi Valley. He determined bighorn consumed 60 percent grass year-around. Principal grass species eaten year long were Agropyron spicatum, Festuca idahoensis, and Poa secunda. Calamogrostis canadensis was utilized extensively during summer. Sheep used all browse species present, but most infrequently. Cercocarpus ledifolius was the staple browse species year-around; while Ceonothus velutinous and C. sanquinius were taken during fall, winter, and early spring. Twenty of 71 forb species present were utilized by sheep. Species most commonly used during the summer were Lupinus caudatus, Trifolium rhydbergii, and Anaphalis subalpina.

Gooden and Gutzman (1938) studied bighorn sheep along the Salmon River prior to Smith's 1954 study. Along the Middle Fork they found most sheep summered at elevations between 8000 and 9000 feet, in small parks and glades adjacent to cliffs and other protective areas. Bighorn wintered at lower altitudes adjacent to the river. Bighorn ate primarily Equisetum sp., sedges, rushes, browse, and forbs, and a small amount of grass during summer. They determined bighorn used little grass year-around. Winter food habits

indicated preference for Equisetum sp., sedges, rushes, and possibly more browse than during summer.

Montana

Couey (1950) studied bighorn sheep state-wide in Montana; but most intensively on the Sun River Game Range. He estimated trees covered 75 percent of the range and grass covered 15-20 percent. Eight vegetative types were identified. Types included: 1) mature spruce - sub-alpine fir; 2) mature Douglas-fir; 3) limber pine-whitebark pine - reef; 4) lodgepole pine; 5) burn; 6) grassland; 7) aspen; and 8) brush. The mature spruce - sub-alpine fir type occurred at high elevations (6000-7500). Sheep migrated between separate summer and winter ranges and occupied high elevations during summer. Couey determined the greatest use by bighorn during summer and fall occurred in the limber pine-whitebark pine-reef type. This type occurred on rocky, wind-swept areas, and was extensive. Apparently, sheep used these areas year-around. Trees were scattered, and a sparse understory of scrubby willow, mountain maple, snowberry, and bearberry was present. Ground cover consisted of widely-scattered clumps of bunchgrasses and forbs. Sheep used edges of grassland areas (some alpine) adjacent to reef types during summer (Couey, 1950).

Couey (1950) estimated bighorn food habits on the range. The results of analysis of six stomach samples collected between late November and March are presented in Table 5. Grasses comprised most of the diet then (63 percent by volume); while browse constituted 17 percent, forbs 14 percent, and miscellaneous forage 6 percent. Forb utilization increased during summer. Use of forbs during winter was reportedly difficult to measure. Concerning browse present on escape areas, Couey (1950; 35) stated: "Most of the reef-type browse plants are used slightly by bighorns but none of them seem to enter largely into their diet." He stated further that grass formed the bulk of the diet during winter; although Artemisia frigida was the preferred species then. Vegetation of the limber pine-whitebark pine-reef type was preferred by bighorn.

Schallenberger (1965) also studied wild ungulate range relationships in the Sun River area. The analytical results of 15 stomach samples collected during October and November, 1964, and results of winter feeding site examinations are presented in Table 5. Observations of wild ungulates were conducted on the winter range. Bighorn ate mostly grass during fall and winter. Winter food habits were determined by feeding site examinations.

Schallenberger (1965) determined bluebunch wheatgrass, Idaho fescue, Poa spp. and Juncus spp. comprised the greatest percent of total grasses in all habitat types except valley bottoms. Bighorn preferred the most succulent vegetative species present.

Bighorn occupied the bunchgrass habitat type most between January and March. Seventy-nine percent of sheep observed during that period were on south-facing slopes.

California

Jones (1950) studied bighorn in the Sierra Nevada Mountains between July and December. Rugged and precipitous mountain peaks between 12,000 and 14,500 feet in elevation were present. Tree-line on the eastern slope

of the Sierra was approximately 11,400 feet in elevation. Jones found forbs were preferred (composition times utilization) most by grazing animals, primarily bighorn sheep. Grasses were a distant second.

Riegelhuth (1965) observed bighorn food habits in the Sierra Nevada Mountains. No quantitative measure of food habits was given. Both Riegelhuth (1965) and McCullough and Schneegas (1966) reported browse was the main food of Sierra bighorn during winter. The latter authors reported (Table 5) grasses comprised less than 35 percent of the diet during winter.

Canada

Food habits of bighorn sheep in Canada have been studied by Cowan (1947), Sugden (1961), and Flook (1962). The general diet of bighorn sheep during winter in Jasper National Park, Alberta, (Cowan, 1947) is presented in Table 5. Grass was utilized most by sheep on a winter range believed inadequate for over-populations of elk, moose, deer, and bighorn sheep. Competition for winter forage among these ungulate species was believed severe. Bighorn occupied marginal areas of the winter range.

Flook (1962) studied range relationships of wild ungulates native to Jasper National Park and Banff National Park, Alberta. He found the summer diet of bighorn quite variable; but that grass comprised slightly less than 50 percent of the total diet then (Table 5). Legumes were grazed commonly in summer. The winter diet of bighorn was mostly of grass-like plants. Flook concluded bighorn move extensively in sub-alpine and alpine zones during summer, always close to rugged terrain. Forbs and browse were second and third, respectively, in importance during summer and winter.

Flook (1962) described areas used by bighorn and their patterns of use. Most areas of these two Parks were alpine and subalpine; with elevations, park-wide, varying between 3200 and 12,300 feet. Tree-line occurred at approximately 7,000 feet in elevation. Most bighorn in the subalpine (forested) zone, usually on southern exposures, where snow depth did not eliminate availability of forage. Some sheep wintered on alpine areas.

Bighorn ate approximately 60 percent browse during winter along Churn Creek in British Columbia (Sugden, 1961). Grass and grass-like species comprised approximately 29 percent of the diet while forbs contributed approximately nine percent. (Table 5). Pasture sage (Artemisia frigida) comprised most of the winter diet. Pasture sage and beardless wheatgrass (Agropyron spicatum var. inerme) were eaten most during winter. Pasture sage was the most preferred grass species. (Sugden, 1961).

Sugden determined that the winter ranges for Churn Creek bighorn were located in the Douglas-fir zone while the summer range was comprised of alpine and sub-alpine areas. He concluded wheatgrass, sheep fescue, alpine bluegrass and a variety of sedges were the most important forage species for bighorn during summer.

Salt and Water

Bighorn sheep seek salt and minerals avidly in Colorado (Simmons, 1961) and in Idaho (Ellis, 1941; Smith, 1954). In contrast, Sugden (1961) stated California Bighorn in British Columbia displayed no evidence they need or prefer extra salt beyond a normal vegetative diet. Smith (1954) and

Simmons (1961) stated movements of bighorn were influenced by location of salt sources. Smith (1954) related: "Some of the local drift (of bighorn) in summer seems to be influenced by the presence of salt." He continued by saying that: "The actions of non-migratory bighorn suggest that their habit of frequently visiting licks at low elevations during the summer may be a factor influencing them not to migrate." Smith concluded by reporting bighorn displayed greatest eagerness for salt in spring; but that they sought salt year-long. Simmons (1961) reported sheep traveled considerable distances to obtain salt in the Cache la Poudre River area of Colorado. Simmons and Ellis (1941) believed bighorn preferred soil with high salt content over conventional salt blocks distributed for livestock use.

Smith (1954) determined bighorn ate snow on summer range rather than descending to natural sources of water below. Ellis (1941) reported bighorn traveled long distances to obtain water, eat snow, or drink free water. McCann (1956) concluded that bighorn in the Gros Ventre Mountains of Wyoming, preferred to obtain water by eating snow. He did not observe sheep drinking free water. Jones (1950) said that he was unable to determine where or when bighorn obtained water in the high Sierra of California.

## Elk

Elk eat more grass than browse or forbs throughout the year in most areas of the United States (Table 7). Forb and browse combined usually comprised less than one-half of the year-long diet.

Elk prefer green and succulent vegetation similar to bighorn sheep. It has been determined that protein and other essential forage constituents are most abundant in growing plants. Plants vary in time of greatest succulence; consequently elk shift their food preferences during different seasons of the year. Grasses are first to produce available forage in the spring, so elk consume mostly grass then. Forbs are abundant and produce a great variety of forage during summer; consequently elk utilize mostly forbs during summer. Browse and forbs are not succulent during fall and winter; so elk eat mainly grasses then because grasses are most abundant and available.

Availability of different species affects food habits of elk as other wild ungulates. Low-growing forbs are usually unavailable under winter snow cover. Browse plants are most available during winter relative to snow cover depth, but are less abundant than grasses in total plant composition.

More range and consequently more different habitat types are available to elk during summer. Different habitat types are occupied by different vegetative species. Male elk occupy different areas than female and young elk then. Thus, the locality individual elk occupy changes forage availability and consumption. Habitat preferences of elk and other wild ungulate species, will be discussed further in chapter three. Fall, winter, and spring feeding is more restricted in area, thus limiting the availability of different species.

Elk food habit studies are discussed separately under the state where located. Additional ecological information is given to make food habits data more meaningful. Winter food habits data are presented generally.

Table 7. Food habits of North American elk populations

| AUTHOR | LOCATION OF STUDY | FOOD HABITS | | | | FOOD HABITS DETERMINATION TECHNIQUE |
|---|---|---|---|---|---|---|
| | | Fall | Winter | Spring | Summer | |
| Kirsch, 1962 | Little Belt Mountains Montana | G-74%<br>F-13%<br>B-13% | G-88%<br>F- 7%<br>B- 5% | G-88%<br>F-11%<br>B- 1% | F-86%<br>B- 7%<br>B- 6% | Inspection after observed use; plus stomach sample analysis (41) |
| Rouse, 1957 | Gravelly Mountains, Montana | G-80%<br>F-14%<br>B- 3% | G-90%<br>B- 7%<br>F- 3% | G-90%<br>F- 6%<br>B- 4% | F-91%<br>G- 6%<br>B- 3% | Inspection after observed use; grazed plants along transect; stomach samples |
| Mackie, 1962 | Missouri Breaks area Montana | G-69%<br>F-19%<br>B-12% | G-91%<br>B- 5%<br>F- 4% | G-82%<br>F-14%<br>B- 4% | F-76%<br>B-22%<br>G- 2¢ | |
| Knight, 1962 | Sun River area, Montana | G-66%<br>F-19%<br>B-15% | B-85%<br>G-14%<br>F- 1% | G-1rst<br>F-2nd<br>B-3rd | F-67%<br>G-2nd<br>B-3rd | Direct observation; stomach samples (19). |
| Schallenberger, 1965 | Sun River Canyon, Montana | - | B-42%<br>G-37%<br>F-21% | - | - | Inspection after observed use |
| Stevens, 1965 | Elkhorn Mountains Montana | - | - | G-77%<br>F-2nd<br>B-3rd | F-76%<br>G-17%<br>B-3rd | Inspection after observed use |
| Cole, 1958 | Montana (state-wide) | - | - | - | F-1rst | - - - - - |
| Nichols, 1957 | White River National | - | - | - | G-58%<br>F-31%<br>B- 1% | Comparative production-utilization plots |
| Tileston, 1962 (Riordan,1948) | Rocky Mountain National Park, Colorado | G-66%<br>B-20%<br>F-14% | G-70%<br>B-18%<br>F-12% | G-86%<br>B- 9%<br>F- 5% | G-68%<br>B-17%<br>F-15% | Stomach samples - Fall (16); Winter (15); Spring (16); Summer (16). |
| Young and Robinette, 1939 | Selway Game Preserve Idaho | G-40%<br>B-40%<br>F-20% | - | - | G-45%<br>B-37%<br>F-18% | Production-utilization plots |
| Denio, 1938 | Bitterroot National Forest, Idaho | - | G-65%<br>B-27%<br>F- 8% | - | - | Stomach samples (53) |

Table 7 concluded -

| AUTHOR | LOCATION OF STUDY | FOOD HABITS | | | | FOOD HABITS DETERMINATION TECHNIQUE |
|---|---|---|---|---|---|---|
| | | Fall | Winter | Spring | Summer | |
| Jeffrey, 1963 | Fishlake National Forest, Utah | - | - | G-1rst | F-1rst | Direct observation |
| Anderson, Crump & Baker, 1956 | Wyoming-various areas | G-44%<br>F-32%<br>F-24% | - | - | - | Stomach samples (18) |
| Murie, 1951 | north Yellowstone National Park, Wyoming | - | G-93%<br>B-2nd | - | - | Stomach samples (48) |
| Cowan, 1947 | Jasper National Park, Alberta, Canada | - | G-97%<br>B- 3% | - | - | Direct observation |
| Harper, 1962 | Boyles Prairie, California | G-57%<br>F-23%<br>B-20% | G-76%<br>B-22%<br>F- 2% | G-61%<br>F-34%<br>B- 5% | G-58%<br>F-22%<br>B-20% | Direct observation - % minutes feeding on vegetative class. |
| Pickford and Reid, | Whitman National Forest, Oregon | - | - | - | F-80%<br>G-2nd | Production-utilization plots |
| Lang,1958 | Pecos Wilderness (fall) and Gila National Forest (winter), New Mexico | G-77%<br>B-21%<br>F- 2% | B-95%<br>G- 5% | - | - | Stomach samples - Fall (4); Winter (7). |
| +Averages | Seasonal | G-64%<br>B-19%<br>F-17% | G-66%<br>B-29%<br>F- 5% | G-81%<br>B-11%<br>F- 8% | F-53%<br>G-33%<br>F-14% | |
| | Year-long | Grass 61%<br>Forbs 21%<br>Browse 18% | | | | |

*G=grasses B=browse F=forbs

+Averages were compiles by averaging percentage data in seasonal columns for seasonal average and by averaging seasonal averages for year-long average.

Food habits information presented here should be related to movements and habitat preferences information presented in other sections.

Colorado

Nichols (1957) studied elk and domestic sheep use of the 400 acre Lost Solar Park in the White River National Forest. The Park was approximately 11,000 feet in elevation. Vegetation consisted chiefly of grasses, grass-like plants, and low-growing forbs. Bettle-killed spruce and fir enclosed the Park. Nichol's estimates of elk summer diet are presented in Table 7. He determined elk consumed forage species mainly in relation to their abundance, without significantly preferring any particular species. Tufted hairgrass (Deschampsia caespitosa), miscellaneous forbs, white marsh-marigold (Caltha leptosepala), and Baltic rush (Juncus balticus) comprised, in order, most of the elk diet.

Elk were observed frequently feeding in the Park. Through observations of individual animals, tracks, and other sign, it was learned elk used the surrounding dead timber areas, where succulent vegetation was abundant in summer. Those areas received the majority of elk use in August, presumably due to a presence of more succulent forage than in the open Park.

Montana

Numerous studies have been conducted on Montana elk. Food habits information pertaining to all seasons of the year is presented by Rouse (1957), Kirsch (1962), Knight (1962), Mackie (1962). Schallenberger (1965) studied elk winter food habits; while Stevens (1965) surveyed elk food habits during summer. Their findings are presented in Table 7. Grasses comprised most of the elk diet during the fall, winter, and spring in these areas. Forbs were taken in greater amount than grasses or browse during summer. Forbs were utilized more than browse during spring and fall; while browse was second only to grasses in amount taken by elk in winter. Brazda (1953) and White (1958) studied elk summer food habits but presented no quantitative data concerning utilization totals per vegetative class.

Knight (1962) presented data concerning elk food habits year-around in the Sun River area. There, grasses and grass-like plants comprised most forage eaten by elk during spring (Table 7). Grasses were most abundant on elk spring range, however, and most elk observed during spring were in grassland areas. Major vegetative species utilized by elk then were Festuca scabrella and Festuca idahoensis. Elk fed most often during summer where forbs were most abundant. Four forbs, Ranunculus spp., Astragalus miser, Achillea lanulosa and Aster spp., comprised 67 percent of the elk diet. The most important single species during summer, however, was Poa arctica, which comprised 19 percent of the total diet. Fall range for elk was divided equally between grass and timber areas. Feeding on grasses increased during fall from summer, until a reported 94 percent of the elk observed during fall were located in grassland areas.

Kirsch (1962) studied elk food habits in the Little Belt Mountains. This mountain range displayed a maximum elevation of 9,175 feet and was surrounded by plains. The Range is characteristically low and plateau-like cut by deep and narrow canyons. Locally, there were rugged, rocky crests with prominant cliffs and talus slopes. Four major plant communities were recognized: 1) ponderosa pine woodland and grassland (below 5300 feet

elevation); 2) ponderosa pine; 3) Douglas-fir; and 4) the spruce-fir. He recognized no definite tree-line. The spruce-fir community was found at the upper edge of the Douglas-fir community, approximately 7,200 feet in elevation.

Kirsch (1962) concluded that year-around use by elk of one forage class was related to availability or composition that class comprised of the total forage present. Elk occupied the ponderosa pine woodland-grassland community in the foothills area mostly during spring. Elk use of the Douglas-fir community increased during late May and early June. The spruce-fir community was the most heavily used community during July and August. Kirsch concluded the high use of forbs during summer (Table 8), may have been due to presence of logged areas and consequent high growth and availability of forbs.

The Gravelly Mountains varied in elevation between 6,500 and 10,500 feet. Rouse (1957) studied elk ecology there. He recognized six vegetative types. The subalpine fir-Engelmann spruce type occurred between 8,000 and 9,500 feet elevation. The Douglas-fir type occurred between 7,000 and 8,500 feet. The sedgerush zone occupied many areas between 6,500 and 9,500 feet; the sagebrush type was encountered between 6,500 and 8,800 feet, the fescue-wheatgrass type occurred between 6,500 and 10,500 feet and aspen groves were found between 7,000 and 8,500 feet in elevation. Most elk were found in the Douglas-fir and fescue-wheatgrass types during summer and early fall. Between December and March, 93 percent of the elk observed were in the sagebrush type. No elk were observed in the subalpine fir-Engelmann spruce and aspen types then. Food habits data are presented in Table 7. Grasses comprised the great majority of the elk diet during all seasons of the year except summer, when forbs were utilized more than grasses or browse.

Stevens (1965) studied elk, cattle, and domestic sheep range relationships in the Elkhorn Mountain Range. That mountain range, approximately 21 miles long by 18 miles wide with a high point of 9,414 feet, was surrounded by plains varying in elevation between 4,000 and 5,000 feet. The Crow Creek study area varied from foothills adjacent to the plains to a large basin at an elevation of 6,500 and 8,000 feet surrounded by rocky ridges. Upper elevations were forested while a grassland formation covered lower areas. Two zones were recognized in the forest formation. The Douglas-fir zone occupied approximately 37,000 acres between 5,800 and 7,200 feet in elevation and the Engelmann spruce-subalpine fir zone occurred at higher elevations. The spruce-fir zone covered about 28,000 acres between 7,000 and 9,000 feet. The dominant genera in the grassland formation, which occurred up to 6,500 feet in elevation, were Festuca and Agropyron. Numerous forbs, sedges, and rushes were present in the grassland formation. Open areas of grasses and forbs appeared within the spruce-fir formation. The dominant plant groups found in open areas were fescues, sedges, bluegrasses, and timothy (Stevens, 1965).

Elk first used dry vegetation, from the previous summer, during early spring. They later utilized green plants as they became available. Between May 1 and May 16,elk ate 95 percent grasses, primarily Idaho fescue, while from May 16 to May 31, grasses comprised 35 percent of the elk diet. Elk ate mainly new-growing forb species then. More elk were observed in the fescue-wheatgrass and the Douglas-fir zones than any other zone during May

and June. This higher use of forbs continued through summer (Table 7). All elk observed during July were located in the spruce-fir zone and in grassy parks of the Douglas-fir zone. The main forbs taken during summer were dandelion (Taraxacum sp.), arnica (Arnica fulgens), pale agoseris (Agoseris glauca), clover (Trifolium repens), and cinquefoil (Potentilla spp.). Grasses and grass-like plants were a minor part of the elk diet during summer relative to forbs. Forb utilization decreased in August, browse use increased, while use of grasses remained relatively stable. Most elk observed during August were located in the spruce-fir zone. The primary browse species used then were willow and huckleberry. Elk definitely selected certain plants while feeding (Stevens, 1965).

Mackie (1962) surveyed deer and elk food habits and range relationships in the Missouri Breaks area. That region was characterized by numerous rolling or near-flat hills cut by many canyons. Slight elevational changes were reported. Uplands were covered by extensive but inter-mingled areas of sagebrush, juniper, pine, grassland, and greasewood with several combinations of tree species and understory types together. Food habits and range use data were collected through extensive year-long observations on deer and elk. Conclusions from observations of food habits are presented in Table 7. He reported elk used grasses more than forbs or browse during fall, winter, and spring. Forbs were the most important source of forage during summer. Elk used browse moderately during summer and fall and lightly during winter. Summer droughts caused caused elk to increase their use of grass.

Mackie (1962) studied elk patterns of use in the Missouri Breaks area, to complement food habits data. He determined the sagebrush-grassland habitat type was used most by elk during late fall, winter, and spring. Elk heavily used canyon bottoms during late summer, where numerous wet meadows were located. Elk occupied distinct summer and winter ranges which required extensive movements between. Mule deer were relatively evenly distributed over the study area.

Brazda (1953) studied elk movements in the Gallatin River area. Of particular concern was how vegetative development affected herd seasonal migrations. Elk movements were traced from summer range areas in the northwest corner of Yellowstone National Park and the Selway Game Preserve to winter range areas along the Gallatin River in Montana. The most prominant plant species present were ranked relative to preference by elk during spring and summer. The seven most preferred grasses and grass-likes were Carex rubicola, Carex raynoldsii, Poa epilis, Phleum alpinum, Festuca ovina, Festuca idahoensis, and Poa secunda. Forbs sought most by elk were Agoseris serieus, Delphinium stachydeum and Rumex pauciflorus. The least preferred forbs included Taraxacum officianale, Viola muttallii, Ranunculus glaberrimus, Aquilega falvescens, Balsamorhiza saggitata, and Heracleum lanatum.

Wyoming

Eighteen elk stomach samples were collected during fall from various parts of Wyoming by Anderson, Crump, and Baker (1956). These samples were analyzed and the grass and grass-like, forb, and browse composition is presented in Table 7. Sixteen browse and fifteen forb species were identified. Grasses were not identified to genus. Over 27 percent of contents of samples was unidentified forbs. All identified forbs occurred in trace amounts. Sedges were found in moderate amounts.

Murie (1951) described elk in the Jackson Hole-Yellowstone National Park area. He reported grasses were a staple part of their diet year-long, especially winter (Table 7). Elk summered in subalpine and alpine habitat types. Willows were not grazed extensively during summer, although palatable plants were common. Summering elk displayed distinct preferences among grass species. Murie (1951) stated:

> "Even in summer, when the vegetation present is all available, the elk do not confine themselves to grass by any means; nor do they appear to seek dense grassy meadows for feeding. Often they bed down in a heavy patch of reedgrass (Calamogrostis) or sedge (Carex) without utilizing it for food to any noticeable extent".

Murie (1959) determined summer range was characterized by "luxuriant" vegetation which made available "a wealth of food choice for elk". Plant growth reportedly culminated during July and elk occupied high, open, relatively bare slopes then, where a variety of green vegetation was present. Plants in some areas began to cure during August. Elk then occupied areas, usually forested, where plants were still green. Elk were more selective while foraging during September due to loss of palatability in many species. Species low in preference earlier became preferred in late September because they remained greener than others. Palatability and preference varied among areas for one species. (Murie, 1951).

Anderson (1953) concurred generally with Murie (1951) concerning elk foraging habits in the Jackson Hole area. Anderson stated elk utilized the latest growing, more succulent plants. He concluded elk preferred grass during spring and early summer, forbs during summer, and browse which remained green after most grasses and forbs had dried out.

Idaho

Young and Robinette (1939) studied elk use of range in the Selway Game Preserve. Plant composition and density were measured in plots located between 5,000 and 8,300 feet in elevation. Plots were located on summer range on open hillsides and hillsides occupied by scattered timber. Tree species, at plot locations, included Douglas-fir, white fir, Engelmann spruce, subalpine fir, and mountain alder. A variety of forbs and several browse species were present, especially abundant on open slopes. Forage utilization by elk of major vegetative classes during summer and early fall is presented in Table 7. Elk displayed a decided preference for browse most of summer even though desirable grasses were present. Palatability studies (Young and Robinette, 1939) concluded key species for elk on the summer range were Salix spp., Acer glabrum, Bromus carinatus, Elymus glaucus, and Carex geyeri. Carex geyeri was the most important herbaceous forage species due to its abundance and palatability. Palatability varied considerably among species and each species varied in palatability from season to season.

Other States

Pickford and Reid (1943) reviewed elk and domestic sheep range relationships in the Whitman National Forest. On summer range, where heavy growth of sedges (primarily elk sedge) and minor quantities of forbs and

grasses were found, elk and domestic sheep displayed preference for the same forage species. Succulent forbs were utilized heavily by elk and domestic sheep. Sedges were used less. Sedges were utilized more on drier, open slopes and non-timbered areas than on other areas. Most forage taken by elk and domestic sheep was not the choicest plants. A relatively small group of plant species furnished the bulk of forage. Pickford and Reid concluded competition was keen between domestic sheep and elk for choice forage plants. Elk ate more forbs than grasses or grass-like plants and were quite selective in choice of forbs. Forb species comprised more than 80 percent of the summer elk diet (Table 7). They estimated summer range vegetation consisted of 76 percent forbs, 14 percent grasses, sedges, rushes, and 10 percent browse.

Harper (1962) studied elk in the coastel redwood belt of northwest California. Food habits of elk are presented in Table 7. Perennial grasses were the most abundant vegetative species on the Boyles Prairie study area. The area is surrounded by dense stands of coastal redwood (Sequoia sempervirens) and sitka spruce (Picea sitkensis). Forbs did not comprise most of the summer diet although they did reach a peak in use during summer and fall. Harper determined also that diets of female elk and bulls differed in spring, summer and winter, presumably due largely to difference in areas occupied.

Flook (1962) studied range relationships of wild ungulates in Jasper and Banff National Parks, Alberta. He reported elk subsisted primarily on grass-like plants year-around. Browse was second in importance during summer and minor importance in winter. Flook (1962) concluded that on ranges where over-use in recent history has altered vegetative composition: "elk are able to adjust their foraging habits to a marked degree". He concluded elk in Banff and Jasper National Parks were found in the widest variety of habitats of any ungulates there. Elk occurred throughout the subalpine zone and occasionally in the lower alpine areas in summer.

## Mule Deer

Mule deer diets change seasonally also. Generally, it is believed mule deer are browse and forb eaters. This seems true in most areas. The deer winter diet, like other wild ungulates on mule deer range, is often partly a maintenance diet. Little choice of forage is present. Animals are on restricted range then. Many species are not available for use. Browse comprises the bulk of the deer winter diet (Table 8 ). Coniferous species may become an important food source.

Deer change their food habits after winter has passed. Mule deer begin to utilize the new growth in early spring, when green vegetation is first appearing. Grasses may then be a significant part of the diet. Later, in the spring, as forbs and browse begin to grow, deer decrease use of grasses and utilize green forbs and browse. A great variety of succulent forbs and browse are available during summer. Deer then utilize them, in varying amounts among different areas, but are more selective in species taken. Forbs are utilized most during summer, with use of grasses minor then.

Selective choice of forbs and browse continues through summer. Browse species increase in composition of diet toward the end of summer. Browse may comprise more of the diet than forbs during fall. This shift is due

Table 8. Food habits of North American mule deer populations

| AUTHOR | LOCATION OF STUDY | FOOD HABITS | | | | FOOD HABITS DETERMINATION TECHNIQUE |
|---|---|---|---|---|---|---|
| | | Fall | Winter | Spring | Summer | |
| Lovaas, 1958 | Little Belt Mountains Montana | *F-53%<br>*B-44%<br>*G- 3% | B-77%<br>F-17%<br>G- 6% | B-42%<br>F-38%<br>G-20% | F-63%<br>B-30%<br>G- 7% | Feeding site examination and stomach samples |
| Wilkins, 1957 | Bridger Mountains, Montana | - | - | - | F-77%<br>B-22%<br>G- 1% | Feeding site examination; Direct Observation; stomach samp. |
| Cowan, 1947 | Jasper National Park, Alberta, Canada | - | B-79%<br>G-13%<br>F- 8% | - | - | Direct observation |
| Sugden, 1961 | Sheep Flats, British Columbia, Canada | - | B-90%<br>F- 5%<br>G- 5% | - | - | Direct observation; band trailing |
| Smith and Julander, 1953 | Fishlake National Forest, Utah | - | - | - | B-54%<br>G-24%<br>F-22% | Production-utilization estimates |
| Tileston, 1962 | Colorado (state-wide) | "B-68%<br>F-26%<br>G- 6% | B-95%<br>G- 3%<br>F- 2% | B-63%<br>G-19%<br>F-18% | B-89%<br>F-10%<br>G- 1% | Stomach samples - Fall(23); Winter(106: Spring(45); Summer(30) |
| Ferrell and Leach, 1950 | Jawbone deer herd, California | - | B-89%<br>G- 9%<br>F- 2% | - | B-90%<br>F- 9%<br>G- 1% | Stomach samples - Winter(24); Summer(16) |
| Anderson, Crump, and Baker, 1956 | Wyoming (state-wide) | B-74%<br>F-22%<br>G- 4% | - | - | - | Stomach samples (11) |
| Smith, 1952 | Fishlake National Forest, Utah | - | - | G-90% | F-60%<br>B-35%<br>G- 5% | ----- |
| Cole, 1958 | Montana (state-wide) | *FB-1rst | B-1rst | *FB-1rst | F-1rst<br>B-2nd<br>G-3rd | Intuitive estimates |

Table 8 concluded -

| AUTHOR | LOCATION OS STUDY | FOOD HABITS | | | | FOOD HABITS DETERMINATION TECHNIQUE |
|---|---|---|---|---|---|---|
| | | Fall | Winter | Spring | Summer | |
| Sheppard, 1960 | Sheep River region, Alberta, Canada | B-1rst | B-1rst | - | F-1rst<br>B-2nd | Feeding site examination; stomach samples |
| Mace, 1957 | Oregon (state-wide) | - | B-1rst | - | - | Intuitive estimate |
| Lang, 1957 | New Mexico (state-wide) | FB-1rst | B-1rst | FB-1rst | - | Intuitive estimate |
| +Averages | Seasonal | B-62%<br>F-34%<br>G- 4% | B-86%<br>F- 7%<br>G- 7% | B-49%<br>F-30%<br>G-21% | F-48%<br>B-46%<br>G- 6% | |
| | Year-long | Browse 61%<br>Forbs 30%<br>Grass 9% | | | | |

* B=browse F=forbs G=grass FB=forbs and browse

" Includes miscellaneous foods and conifers

+ Averages were compiled by averaging percentage data in seasonal columns for seasonal average and by averaging seasonal averages for year-long average

apparently to extension of browse succulence beyond maturation of most forb species. Also, deer may occupy different areas then to compensate for lack of succulent plants at higher elevations or in other specific sites.

Studies of deer food habits are presented. Review of deer studies was limited, due mainly to the relative concern of deer as a summer range competitor. Also, deer are more varied in their seasonal use of range than elk or bighorn. Most summer range studies on mule deer were not conducted on alpine range. Species listed in literature as part of mule deer winter diets are not presented here.

Colorado

Tileston (1962) summarized analyses of deer stomach samples reported in Colorado Federal Aid Quarterly Reports between 1938 and 1957. (Table 8). Browse comprised 74 percent of the total deer diet during summer. Serviceberry, chokecherry, and oak were species taken in greatest amount. Use of those species was very low in winter, low in spring, and low in fall after high summer use. Deer utilized browse species during summer that were used heavily during winter and moderately during spring and fall. No conifers were eaten during summer, although they were utilized significantly during all other seasons. Forb use was highest during fall. Greatest use of grasses was in spring.

Wyoming

Anderson, Crump, and Baker (1956) reported analyses of deer stomach samples collected in Wyoming. Eleven samples were analyzed, none from fall collections and two taken in summer (Table 8). These authors determined no significant differences in sample contents between fall and summer. The browse species utilized most during fall was Pachystima myrsinities. Balsamorhiza sp. displayed greatest composition of identified forbs. Most of the forb contents were unidentified.

Montana

Cole (1958) described deer food habits statewide. He concluded deer used mostly browse in winter and browse and forbs during fall, winter and spring. Use of forbs was reported greatest during summer. Grasses were a minor source of food year-around, and greatest use occurred in spring (Table 8).

Lovaas (1958) studied mule deer food habits and range use in the Little Belt Mountains. This area was described by Kirsch (1962), presented under elk food habits. Four vegetative types were recognized: 1) prairie (below 5,000 feet in elevation); 2) ponderosa pine (between 5,000 and 6,000 feet elevation); 3) lodgepole pine (between 6,000 and 7,000 feet); and 4) spruce-fir (above 7,000 feet in elevation). Lovaas observed deer occupancy of vegetative types. He determined deer used the spruce-fir, lodgepole pine, and ponderosa pine types about equally during June. Deer occupied the lodgepole pine type over twice as much as the spruce-fir type (60 percent vs. 27 percent) during July. Few deer were observed during July at lower elevations (13 percent). Observations in August showed deer used the spruce-fir zone most often (45 percent) with occupancy of the lodgepole pine type a close second (34 percent) Sixty-eight percent of deer observed in September, were in the ponderosa pine type. The prairie type (15 percent),

lodgepole pine type (9 percent), and spruce-fir type (7 percent) featured the balance of observations.

Lovaas (1958) concluded forbs were utilized most by deer during summer (Table 8). Browse was second in use, and grass use was minor.

White (1958) studied summer range ecology of mule deer in the spruce-fir zone of the Rattlesnake Creek region. Subalpine fir (Abies lasiocarpa) was the principal tree species present. Englemann spruce (Picea engelmanni) was abundant on north slopes and canyon bottoms. Smooth menziesia (Menziesia glabella) formed a near complete understory under areas dominated by Englemann spruce. South-facing slopes were occupied by lodgepole pine, whitebark pine, and limber pine, with vaccinium, Xerophyllum, and sedges the most common understory plants there.

Deer preferred flowers of bear grass and paintbrush and leaves of Aster laevis. Willow (Salix spp.) and mountain ash (Sorbus scopulina)were utilized whenever available "to the point of serious damage". Deer used Menziesia glabella and Vaccinium membranaceum heavily. Vaccinium scoparium was not used heavily due to its low-growing form (White, 1958).

Deer rumen samples collected during summer were analyzed and related to physical site occupied by the collected animal. Rumen contents showed a browse to forb ratio of 1:0.70 on south-facing slopes and level benches. The ratio was 1:0.01 on north-facing slopes and Creek bottoms. Rumen samples collected on talus slopes were found to contain a browse-forb ratio of 1:1.13.

Wilkins (1957) described food habits in the Bridger Mountains relative to vegetative types present: mountain meadow, montane forest, sagebrush-bitterbrush, and bunchgrass-prairie. Seasonal importance of grass, browse and forbs species is presented in Table 8. The mountain-meadow vegetative type reached the highest elevations of the four types given. This type included some sub-alpine areas. The high altitude and presence of numerous springs kept high areas wet most of summer. Chief species present in high areas (mainly mountain meadows) were oniongrass (Melica spectibilis), Idaho fescue (Festuca idahoensis), and sedges (Carex spp.). Other numerous species were Douglas-fir, subalpine fir (Abies lasiocarpa) and a variety of forbs.

Utah

Smith (1952) described deer food habits in the Fishlake National Forest. Mule deer summer range included four recognized vegetative types: spruce-fir, aspen, browse and silver sage-grass. The spruce-fir zone, characteristically at elevations around 9,300 feet on steep north-facing slopes, was occupied mainly by Engelmann spruce, white fir, aspen, and Douglas-fir. Herbaceous understory species included snowberry (Symphoricarpas spp.) mahonia (Mahonia repens), myrtle pachistima (Pachistima sp.), heartleaf arnica (Arnica cordifolia), clover (Trifolium sp.), penstemon (Penstemon spp.), sedge (Carex sp.) and nodding brome (Bromus animolus).

Production-utilization estimates were recorded for 104 plant species (23 browse, 64 forb, 17 grasses and sedges) as part of the four year study conducted during July, August, and early October. Forbs comprised most forage utilized during summer (Table 8), and decreased greatly from then through fall. Browse utilization was low in July and increased greatly in

fall. Grass use was minor except during early spring when it comprised as high as 90 percent of the diet. Species most prominent in the summer diet in all vegetative types were: aspen, chokecherry, oak, Elderberry, snowberry, painted cup, ligusticum, lupine, penstemon, and clover. Plants low in abundance but showing high utilization were: monkshood (Aconitum columbianum) bittercress (Cardimine cordifolia), geranium (Geranium spp.), Agoseris (Agoseris spp.), and Phacelia (Phacelia spp.)

Alberta

Sheppard (1960) determined that mule deer altered their food habits seasonally in the Bow River Forest Preserve, Sheep River region (Table 8). Deer used new grass growth on south-west-facing slopes in early spring. Grass first appeared there, although initiation of growth was very dependent on spring weather. As forbs and browse sprouted later, deer shifted their diet to these, which were in a great variety. Deer occupied north-facing slopes and utilized forbs and browse which just then became green in late spring. Forbs comprised the bulk of the diet during summer. A great variety of forb species was present during summer. The proportion of forbs to browse in the diet decreased in late summer until browse formed the main part of the diet in fall. The most important forbs taken during summer were: dandelion, milkvetch, fireweed, hedysarum, and late-yellow locoweed. Summer browse use occurred on rose, chokecherry, willow, and elder (Sheppard, 1960).

The area was rough in topography. Most was high foothills with rock outcroppings. Elevations varied between 4500 and 7500 feet. Deep canyons, cut in shale, were present. Lodgepole pine and white spruce covered most of the area, which were especially thick on north and east-facing slopes. South and west-facing slopes were characteristically a mixture of grassland, aspen, and lodgepole pine vegetation. Some higher areas were occupied by alpine meadow species, subalpine fir, spruce, and larch. Sheppard estimated lodgepole covered approximately 70 percent of the study area, aspen 10 percent, aspen-lodgepole mixture 8 percent, and other vegetative types 12 percent.

Other

Lang (1957) described food habits of deer in New Mexico. He concluded (Table 8) forbs and browse comprised most of the diet year-around. Grasses comprised a large part of the diet for short periods of time, however, especially during early spring. Deer were more selective in diet during summer when more green species were available. Deer were restricted to late growing (green) browse and forbs in fall. Browse and conifers were utilized most during winter.

Mace (1957) summarized food habits of Oregon mule deer. Deer used more grass than in other states. Grass and forbs comprised most of the spring diet. Grasses were utilized also during late summer and fall. No quantitative data were presented. Deer became selective in species utilization in winter and utilized most browse. (Mace, 1957).

Ferrel and Leach (1950) described seasonal use of forage by mule deer on the west slope of the California Sierra range. Results were presented in Table 8. The summer range extended from 4,000 to 10,000 feet in elevation. Deer were restricted between the elevations of 1500 and 4000 feet during winter.

# BIGHORN HERD COMPOSITION

## Factors Affecting Census for Sex and Age

Sex and age composition of bighorn herds has been used in many areas to gauge herd status. Data have been analyzed and used in many ways. Accuracy of these estimates varies considerably. Bighorn are very difficult to census since they are found in rugged, inaccessible areas. Aerial censusing has provided probably the most accurate estimates.

Problems involved in bighorn census are extensive. Stokes and Balph (1965) asserted how census and other study of animals can be biased considerably if a knowledge of the species' behavior patterns is not acquired first. The time of year the census is conducted is of primary importance. Ram groups and ewe-lamb-yearling-young ram groups occupy different ranges seasonally. Differentiation in areas occupied by bighorn groups must be recognized and accounted for; since accurate estimate of herd composition depends on sampling of an adequate cross section of the herd. Age and relative appearance of young bighorn vary also with time of year. Accurate identification of varying ages and sex of bighorn is very important since natality, lamb survival, and sometimes mortality are based on recognized herd composition. There is a significant difference between the ratio of lambs per breeding and non-breeding ewes.

Other important variables are involved concerning the accuracy of bighorn census work. The aging of older sheep in the field is difficult and relatively inaccurate. This is due to error involved in recognizing annual growth rings on horns. Horn ring counts are the lone technique available in determining age of individual free-ranging sheep except for marked animals of known age. Bighorn herd reproduction and survival of lambs vary from year to year. This variation may be great between two successive years. Therefore, population census work becomes much more meaningful when considered on a long term basis.

In the following pages I will describe these factors as they were reported by various authors. Also, results of bighorn census work in several areas will be presented. To conclude, applications of census data in describing herd status are described.

Lambs usually are called lambs through the first winter after birth. During the first spring after birth they normally are called yearlings. Green (1949) followed this pattern, by calling them lambs through December 31. He then classified them as yearlings through the next calendar year. In each succeeding calendar year, sheep were called two, three, or four, etc., year old animals. Animals older than two years of age were termed ewes and rams. Rams are generally classified according to length of horn, i.e. 1/2 curl, 3/4 curl, full curl. Rams displaying horns of 3/4 curl or larger usually are classified as mature rams.

Difficulties have been encountered in identifying age of individual bighorn sheep. The yearling class is probably the most significant age group to identify. Yearlings are difficult to distinguish, from older ewes, as yearlings approach two years of age. Honess and Frost (1942), Thomas (1957), Buechner (1960), Sugden (1961), and McCullough and Schneegas (1966) reported difficulty in identification of sheep then. Buechner (1960) stated:

"Two-year-old ewes are not distinguished readily in the field , even at close range". Sugden (1961) concluded fall census counts gave the most accurate data on herd composition but that then it was very difficult to distinguish one and one-half year old ewes from adult ewes. Smith (1954) found yearlings often separated from ewes and lambs between March and August. He eliminated identification error by discarding data from partially identified groups. Honess and Frost (1942), Couey (1950) reported younger ewes could not be distinguished from adult ewes after the second summer following birth. Honess and Frost (1942) believed yearlings grow rapidly their second summer and become nearly as large as older sheep by fall. They reported "after ewes have passed their second winter they are difficult to distinguish from mature animals and they can no longer be readily classified in the field; rams of the same age may be mistaken for adult ewes."

Apparently, lambs are identified easily in the field, at least during the first six months of life. Thomas (1957), after extensive aerial census work on bighorn, stated lambs were distinguishable from the air between birth and nine months of age. He believed aerial identification of lambs over nine months of age was largely guess work. Lambs then were approaching the size of yearlings. Buechner (1960), however, believed everyone is liable to mistake yearlings for lambs.

Several authors reported effects on census data caused by differentiation in range occupied by ram groups and ewe-lamb-yearling groups. Most authors stated bighorn rams were less observable. Schallenberger (1965) reported the number of ram-only groups was low relative to other groups. Also, ram groups were found in more rugged areas, so observer travel was more difficult and opportunities to observe rams was reduced. Couey (1950) concluded his counts of rams were too low relative to ewe and younger-animal counts. Rams occupied different areas.

Cowan (1950), Smith (1954), Sugden (1961), and Moser (1962) reported error in herd sex ratio counts due to rams occupying separate ranges. Cowan (1950) stated sex ratio counts must be obtained frequently by observing all areas occupied by bighorn. Moser (1962) concluded sex ratio data from hunter questionnaires taken during fall were inaccurate. Hunters experienced more difficulty in locating rams then. Smith (1957) stated:

> "With the exception of the fall rutting season and early winter period, when rams are closely associated with bands of ewes and young animals, it was found that mature rams were consistently less 'observable' than females and juveniles. Among factors responsible for low ram counts was their inclination to utilize inaccessible areas, early dispersal from winter ranges, and the habit of breaking into small bands when not in the company of ewes and lambs."

Smith considered only ewe-ram ratios taken in winter were accurate.

Aging bighorn sheep by counting horn growth rings on free-ranging animals is difficult but sometimes reliable. Only rams can be accurately aged this way. Ewes reportedly can not. Geist (1966), studied marked rams and ewes of known age. Twenty-one rams showed near perfect correlation between visual counts of rings from very close range and known age. Geist reported also that horn rings were very difficult to count on ewes. Some rings on

ewes were hidden from view. Doubt was expressed concerning time of one horn ring per year. Another problem encountered was differentiation of true annual rings from more numerous non-annular depressions. Woodgerd (1964) studied a bighorn population confined to an island. He was convinced ewes could not be aged accurately in the field using physical characteristics. He concluded annual horn growth of ewes is negligible after four to five years of age.

Woodgerd (1964) summed up bighorn census work by stating:

> "Accurate sex and age ratios are difficult to obtain. The tendency of bighorns to associate with individuals of similar sex and age and the lack of stability of group composition render a sampling technique unreliable."

He found marked individuals moved frequently among different bands of sheep on the four-square mile Wildhorse Island.

## Results of Studies

The sex and age composition of many bighorn herds in North America is presented in Tables 9 and 10. The date herd composition counts were taken and number of animals observed are presented where possible. Such information is important when considering significance of composition estimates. Sex and age ratios within the same herd apparently vary considerably from year to year.

Table 10 presents results of bighorn herd composition surveys conducted by Smith (1954). Variables encountered in census work were presented in the preceding section. Smith suggested correlation between severity of winters and successful bearing of young. During post-lambing counts in summer, lamb-ewes ratios varied from year to year with the severity of the preceding winter. Smith considered winter census surveys most accurate because rams joined ewe groups only in late fall and winter.

Tileston (1962) described two Colorado herds that were studied relatively intensively. He stated the Pike's Peak herd "suffered a severe population reduction due to a lungworm infestation in 1952." The Georgetown herd was considered a stable herd for several years previous to the census and during census...Moser (1962) stated census was difficult due to the large size and inaccessibility of areas studied.

Other authors reported problems encountered in census work. Contor (1958) observed bighorn in Rocky Mountain National Park and was unable to classify many as to age or sex. Couey (1950) and Schallenberger (1965) reported known duplication in counting and classifying bighorn. Sugden (1961) believed differences in ewe-lamb ratios between two British Columbia herds was due to varying lamb production or fluctuating lamb mortality.

## Management Applications

Several authors utilized bighorn herd composition data in estimating population status. Sugden (1961) stated:

> "....sex and age composition of a game population will often indicate its trend in size and sometimes suggests factors

Table 9. Comparative estimates of sex and age composition of various bighorn sheep populations in North America.

| AUTHOR | AREA STUDIED | RATIOS | | | PERCENT OF HERD | | | | WHEN COUNTED | NUMBER COUNTED |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Ram:Ewe | Lamb:Ewe | Yrlg:Ewe | Ewe | Ram | Lamb | Yrlg. | | |
| Moser (1962) | Pikes Peak, Colorado | - - - | 48:100 | - - - | - | - | - | - | July, 1949 | 133 |
| | | - - - | 49:100 | - - - | - | - | - | - | July, 1950 | 118 |
| | | - - - | 79:100 | - - - | - | - | - | - | July, 1951 | 77 |
| | | - - - | 65:100 | - - - | - | - | - | - | July, 1952 | 170 |
| | | - - - | 7:100 | - - - | - | - | - | - | June, 1953 | 30 |
| | | - - - | 85:100 | - - - | - | - | - | - | July, 1954 | 26 |
| | Georgetown,Colorado | - - - | 95:100 | - - - | - | - | - | - | 1950 | 37 |
| | | - - - | 48:100 | - - - | - | - | - | - | 1951 | 40 |
| | | - - - | 72:100 | - - - | - | - | - | - | 1953 | 19 |
| | | - - - | 84:100 | - - - | - | - | - | - | 1955 | 35 |
| | | - - - | 43:100 | - - - | - | - | - | - | 1956 | 60 |
| Contor (1958) | Rocky Mountain National Park, Colorado | 30:100* | 58:100* | - - - | - | - | - | - | Nov. 1957-Oct. 1958 | 211 |
| Thomas (1957) | Wyoming (state-wide) | 54:100*# | 49:100* | - - - | - | - | 23 | - | June, 1956-June,1957 | 1151 |
| | | 39:100*+ | - - - | - - - | - | - | - | - | year-long | - |
| Barmore(1962) | Dinosaur National Monument, Colorado | 16:100# | 44:100 | 43:100 | - | - | - | - | summer, 1959 | - |
| | | 49:100 | 33:100 | - - - | - | - | - | - | fall, 1959 | - |
| | | 73:100 | 46:100 | - - - | - | - | - | - | winter, 1960 | - |
| | | - - - | - - - | 50:100 | - | - | - | - | summer, 1960 | 127 |
| Woodgerd (1964) | Wildhorse Island Montana | 109:100 | 100:100 | - - - | - | - | - | - | June, 1951 | 38 |
| | | 81:100 | 100:100 | - - - | - | - | - | - | June, 1952 | 66 |
| | | 104:100 | 68:100 | - - - | - | - | - | - | June, 1953 | 83 |
| | | 75:100 | 67:100 | - - - | - | - | - | - | June, 1954 | 100 |
| | | 145:100 | 74:100 | - - - | - | - | - | - | June, 1959 | 137 |
| | | 156:100 | 70:100 | - - - | - | - | - | - | June, 1960 | 131 |
| | | 112:100 | 76:100 | - - - | - | - | - | - | June, 1961 | 125 |
| | | 102:100 | 85:100 | - - - | - | - | - | - | June, 1962 | 132 |

Table 9 Concluded

| AUTHOR | AREA STUDIED | RATIOS | | | PERCENT OF HERD | | | | WHEN COUNTED | NUMBER COUNTED |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Ram:Ewe | Lamb:Ewe | Yrlg:Ewe | Ewe | Ram | Lamb | Yrlg. | | |
| Ellis (1941) | Lemhi Valley, Idaho | 81:100 | 71:100 | - - - | - | - | - | - | March-May, 1941 | 138 |
| Couey (1950) | Sun River, Montana | - - - | 78:100 | - - - | - | 47 | 26 | 9 | winter | - |
| | | 40:100 | 56:100 | - - - | 58 | 42 | - | - | summer | - |
| Sugden (1961) | Churn Creek, British Columbia | - - - | - - - | - - - | 61* | 28 | 11 | - | 1952 | 83 |
| | | - - - | - - - | - - - | 60* | 25 | 15 | - | 1953 | 68 |
| | Risk Creek, British Columbia | - - - | - - - | - - - | 46 | 33 | 21 | - | 1953 | 165 |
| | | - - - | - - - | - - - | 47 | 31 | 22 | - | 1954 | 194 |
| Schallenberger (1965) | Sun River, Montana | 50:100 | 40:100 | - - - | - | - | - | - | Jan.-March, 1965 | - |
| Cowan (1950) | Banff and Jasper National Parks, Canada | 53:100 | - - - | - - - | - | 35' | - | - | winter | - |
| Green (1949) | Banff National Park, Alberta | - - - | - - - | - - - | - | - | 16 | - | summer-fall | - |
| McCullough and Schneegas (1966) | Sierra Nevada Range, California | - - - | 34:100 | 12:100" | - | - | - | - | Jan.-May | - |
| Riegelhuth (1965) | Sierra Nevada Range, California | 45:100* | 35:100* | - - - | - | - | - | - | winter-spring | - |
| Jones (1950) | Sierra Nevada Range, California | - - - | 50:100* | - - - | - | - | - | - | summer-fall | - |

* - includes yearlings with ewes
\# - includes all males two years old or more
\+ - includes only males with 3/4 curl
' - percent males in adult herd only
" - includes only female yearlings

Table 10. Bighorn sheep sex and age ratios as determined by classification of animals observed. From Smith (1954:88).

| | TOTAL NUMBER OF ANIMALS IN COMPLETELY CLASSIFIED GROUPS | | | | RATIOS* | | | |
|---|---|---|---|---|---|---|---|---|
| | 1949 | 1950 | 1951 | 1952 | 1949 | 1950 | 1951 | 1952 |
| Post-lambing Counts (June 15 - Aug. 18) | | | | | | | | |
| Ram-ewe | 101 | 114 | 18 | 35 | 2.26 | 15.29 | 2.00 | 3.37 |
| Ewe-lamb | 108 | 191 | 21 | 47 | *0.54 | *0.78 | *0.75 | *0.74 |
| Ewe-yearling | 88 | 121 | 13 | 35 | 0.26 | 0.13 | 0.08 | 0.30 |
| Winter Counts (Nov. 14 - Jan. 18 | | | | | | | | |
| Ram-ewe | 113 | 81 | 119 | | *1.35 | *1.61 | *1.13 | |
| Ewe-lamb | 93 | 85 | 96 | | *0.41 | *0.70 | *0.52 | |
| Ewe-yearling | 76 | 69 | 82 | | *0.24 | *0.38 | *0.30 | |
| Pre-lambing Counts (Mar. 15 - April 29) | | | | | | | | |
| Ram-ewe | | 96 | 218 | 235 | | 1.34 | 2.46 | 3.12 |
| Ewe-lamb | | 75 | 230 | 241 | | *0.36 | *0.48 | *0.35 |
| Ewe-yearling | | 65 | 202 | 202 | | 0.18 | 0.30 | 0.13 |

* - indicates ratios most representative of true herd status

> controlling the population. Lamb to ewe ratios indicate the relative reproductive success in a bighorn herd."

Couey (1950) reported: "A ewe-lamb ratio of 1 to .54 is indicative of an increasing herd" when comparing his data with information concerning other herds. Thomas (1957) used ram-ewe ratios to estimate allowable hunting pressure.

It is apparent, however, that adequate herd composition data taken during a limited number of years are of less value than information covering many and successive years. Long-term composition records are necessary to establish herd trend, especially since reproduction and survival of young fluctuate widely from year to year in most bighorn populations. McCullough and Schneegas (1966) stated: "The absence of long-term records makes it difficult to assess population trend. The ewe-lamb ratio of 34:100 for the 1964-65 winter would seem to be relatively low . . ." They reported further: "Taking into account these ratios (sex-age ratios of bighorn herd in Sierra), range analysis and the reports of a few informed local residents, we believe the recent trend has been more or less static".

Buechner (1960) compiled information on bighorn herds of the United States. His publication is very extensive. He discussed problems involved in estimating herd status through consideration of sex and age ratios. He believed natural populations are never static and stated:

> "Arbitrarily, a stable population is considered to be one in which the level fluctuates not more than 20 percent from one year to the next. Mortality and replacement rates must, therefore, be considered in terms of annual averages."

Buechner (1960) concluded: "... in order to know whether a population is increasing at near maximum rate, prior information of the sort one seeks to determine is required."

Buechner (1960) discussed validity of estimating herd status by utilizing adult-young ratios. He reported: "Field lamb to ewe ratios provide only a measure of natality at the time of year when the observations are made; and without data on mortality, the rate of population increase cannot be determined." He stated further (Buechner, 1960;86):

> "As a population reaches stability and mortality increases, the rate of increment diverges more and more from the rate of population increase, and the use of lamb-to-ewe ratios becomes progressively more inaccurate as a measure of population increase. Since most natural populations of bighorn sheep probably approach a steady state, rather than the maximum rate of increase, the use of lamb to ewe ratios by which to judge rate of population increase in most populations, it is necessary to know something about mortality rates. Unbiased data on age structure would provide a basis for calculating the mean annual mortality rate in a relatively stable population, but such data are available only under exceptional circumstances, as in Muries horn collection in Mount McKinley National Park or the age distribution obtained after a catastrophic mortality. The best measure of mortality available under ordinary circumstances is the rate of change between lamb-to-ewe and yearling-to-ewe ratios.

> Such data provide some idea of lamb mortality; but mortality is likely to remain comparatively high among yearlings. The inevitable conclusion is that in stable populations yearling-to ewe ratios are the best indication of the approximate rate of population increase, but without information on mortality (total) these ratios may be mis-leading."

Buechner added, however, that in rapidly increasing populations, mortality is very low and then age ratios can provide an accurate estimate of herd increase. This is contingent on accurate census data which Buechner believed are best obtained in late fall or winter, after summer mortality and when lambs and yearlings are still recognizable. He believed also that it is best to determine lamb-breeding ewe ratios when possible. The percentage of young entering the population must be small in relatively stable population with a low turnover rate, due to either low reproduction or high lamb mortality (Buechner, 1960).

Cowan (1950) compared the sex ratio of all bighorn with the sex ratio of adult animals in Banff National Park. The ratio of all age classes are 78 males to 100 females in this unhunted herd. He stated: "This (sex ratio of all age classes) is almost identical with the ratio determined for the adult herd and suggests that the discrepancy arises before the end of the first year of life." The population studied was experiencing heavy competition for forage with other ungulate species. Buechner (1960) concluded: "In all probability the number of rams is approximately equal to the number of ewes in natural populations of bighorn sheep."

Other characteristics of natural populations of bighorn were listed by Buechner. He estimated a mean life expectancy of approximately seven and one-half years. He predicted also that high mortality occurs in the first year of life and high survival is expected between the ages of one and nine years; also recruitment to the population is relatively slow.

## HABITAT PREFERENCES AND USE

### Introduction

Wild ungulates of the United States are found in certain types of habitats more often than in others. Within relatively small geographical areas, as a mountain range or even an individual mountain, apparent preferences in habitat occupancy are displayed. Such preferences and how they are displayed in given sets of conditions must be realized in studying range relationships. Factors adversely affecting availability of preferred habitat types include losses in accessibility, competition for forage and space, and weather.

Mountainous areas offer a variety of habitat types. Taber and Hoffman (1964) stated: "Characteristic elements of the mountain environment are instability due to lightning fires, land-slips, avalanches, wind throw and erosion; meteorological extremes such as strong isolation, radiation, and wind - - great diurnal temperature extremes and great extremes between sun and shade; seasonal regularity; well land-marked for orientation and learning; and close juxtaposition of strong contrasts due to changes in altitude, aspect and shading, and differences due to air drainage, soil and snow accumulation." Due to the great variety of specific habitat types present within relatively small areas, these authors predicted wild ungulates move

regularly to occupy preferred environmental situations. Taber and Hoffman (1964) reported further that:

> "A striking aspect of the behavioral responses of mammals in mountains is their wide range of adaptability to various habitat conditions over a large geographic range. This is coupled with a pronounced restriction of some species to specific habitats in portions of their ranges in response to the presence of closely related species."

They continued: "Mountain mammals are thus both adaptable to a wide range of environmental conditions (broad niches), and highly adapted specifically to limited habitats (restricted niches) depending upon their behavioral responses to closely related competitors."

It is most important to know the relationship between ungulate use of range and the range itself since ungulate species have certain habitat preferences, and herds must usually be managed on a sustained basis. The carrying capacity of an area or habitat type is estimated usually, and trends in animal use of range are compared.

Mitchell (1941) listed important considerations in evaluating utilization and carrying capacity of summer ranges. He discussed mainly the importance of and procedures in determining this relationship; but other important information was presented. He reported:

> "On every summer range there are usually areas characterized by three degrees of use, namely, concentration spots, generally frequented areas and those little used. The concentration spots occur around salt licks, watering places, and dust wallows - and in any place, in fact, where the animals naturally congregate."

Cowan and Brink (1949) described salt licks used by wild ungulates in the national parks of Canada. Ungulates utilized salt licks usually during summer only. Bighorn frequented dry licks almost exclusively although wet licks were used occasionally. Mule deer used wet licks more than dry ones; and elk visited both types almost equally.

Specific uses or preferences for use of certain habitat types by bighorn sheep, elk, and mule deer will be discussed in the following sections of this chapter. Seasonal movements and lambing habitat preferences are not included because they were discussed previously. Winter range activities are excluded. Some information concerning habitat preferences of bighorn sheep, elk, and mule deer was presented previously under "food habits."

Bighorn Sheep

It is generally accepted that bighorn prefer rocky, inaccessible terrain. Areas not containing such habitat are usually not occupied by sheep. Honess and Frost (1942) studied Gros Ventre bighorn. They stated:

> "Typical bighorn terrain is made up of sheer and broken rimrocks which command a good view of the surrounding country. These are utilized by sheep for bed-grounds and places of retreat. Jutting shoulders, ledges, and small patches of

> timber furnish protection from inclement weather; talus slopes and mesa or ridge tops adjacent to rim rocks are their pastures."

In that area, high altitude ranges are characteristically flat or rolling-topped mesas bordered by rugged areas. Honess and Frost (1942) stated further: "Sheep seem to have little fear of coyotes and pay slight attention to them when they are near or in the rim rocks; but when feeding on the mesa tops they always watch a coyote warily and if the snow is deep they will usually retreat to the cliffs." Green (1949), Couey (1950), Smith (1954), McCann (1956), Flook (1962), Schallenberger (1965), and McCullough and Schneegas (1966) reported a similar dependence by sheep on rocky, rugged, broken areas.

Bighorn sheep seem to avoid areas without escape cover. Extension of range to suitable areas is prevented often. McCann (1956) stated Gros Ventre Mountain Range bighorn seemed to fear extensive heavily-timbered areas and broad expanses of open country when escape cover was not present. He stated further: "They (bighorn) appear to completely refrain from entering upon any open stretches in which cliffy conditions are not at least distantly visible." Apparently, rugged escape terrain was needed within distance for a "quick, short dash" by bighorn before they would cross any open area. He believed, however, that in cliffy areas regularly frequented by bighorn, they would occasionally enter small wooded patches nearby. McCann reported several instances where bighorn traversed openings between cliff areas and believed their behavior indicated sheep considered such open conditions highly dangerous. Bighorn moved as if "feeling their way; advancing only short distances at a time, and interspersing each advancement with long pauses." He believed bighorn clung to cliff areas until absolutely necessary to break away (McCann, 1956).

Green (1949) in discussing necessary characteristics of suitable bighorn habitat, reported: "The nearness of escape cover such as rock slides, cliffs and steep ledges, especially on or about grazing areas, appears to be a consideration where frequented terrain is more or less closely confined or enclosed by forest growth." Flook (1962) stated bighorn in Banff and Jasper National Parks of Canada frequently occupied grassed slopes adjacent to rough, escape terrain. He reported further that escape terrain consisted sometimes of banks of clay or shale.

Preference for rocky, rugged areas seem to exist while bighorn travel among different areas. McCann (1956) stated that when bighorn migrated between winter and summer ranges, they avoided forested areas as much as possible, and followed open ridges and crags. He concluded routes between winter and summer range must be characterized by a continuous series of cliffs and steep ridges; and bighorn cannot be expected to traverse vast open areas or through continuous, dense, stands of timber to reach suitable habitat. Dixon (1940) observed bighorn in Rocky Mountain National Park and stated: "In traveling from their summer to their winter range, the Rocky Mountain Bighorn have certain cities of refuge or safety stations. These consist of broken rocky cliffs and rounded, granite domes." He concluded these areas were used for protection.

In contrast to the much reported need for close escape cover, a possible exception was reported by Green (1949). He determined bighorn in Banff National Park needed immediately available escape cover while occupying

heavily timbered areas; but the presence of escape cover was apparently not a consideration in choice of grazing areas in large alpine meadows. He concluded this was because sheep have unobscured vision of surroundings in such alpine areas, permitting detection of approaching enemies and decreasing the hazard of surprise.

As has been discussed in previous sections, bighorn are found usually at high altitudes in spring, summer, and early fall. High ranges occupied by bighorn were above or near tree-line in most areas studied. McCann (1956) stated:

> "Sheep obviously prefer cool conditions. Where alpine areas are available, they make annual summer migrations; in part to take advantage of cool conditions."

Flook (1962) reported bighorn in Banff and Jasper National Parks range extensively in subalpine and alpine zones. Additional reports of sheep use of high ranges were presented previously when discussing seasonal migrations and food habits. Couey (1950) believed areas of standing dead timber make "excellent summer range for bighorn."

Bighorn are reported to prefer south-facing slopes in periods of restricted forage availability and cold weather. This occurs during winter and spring, according to the literature. Smith (1954) stated: "There is a very noticeable movement of bighorn onto grassy slopes once the snow has melted in the spring." He reported three-fourths of bighorn observed in early spring were occupying south-facing slopes. Schallenberger (1965) stated south-facing slopes provided 79 percent of bighorn observations during winter in the Sun River area of Montana. He determined also that bighorn used south-facing slopes more than any other ungulate species present there, which included elk, mule deer, white-tailed deer, and horses. Schallenberger believed the preference for rocky,inaccessible areas and south-facing slopes acted to limit winter distribution of sheep. McCann (1956) determined east and south-facing slopes were most preferred locations by sheep during winter in the Gros Ventre Range of Wyoming. Green (1949) concluded bighorn in Banff National Park preferred south and south-west exposed slopes, where vegetation was more dense and of greater variety. Longer hours of sunlight were available there. McCullough and Schneegas (1966) concluded large south-facing slopes and steep, rocky areas are necessary for bighorn winter range in the wierra Nevada Mountains.

Preference for slopes without southern exposures seems variable among areas. Green (1949) reported bighorn were seldom observed on north facing slopes, unless they were traveling, or on eastern exposures unless the slope was at least south-east-facing. Smith (1954) stated 75 percent of bighorn observations during late summer and fall were on north-facing slopes. He believed north-facing slopes were preferred then due to presence of more shade and a higher availability of succulent vegetation.

Bighorn sheep, usually rams, winter occasionally in alpine areas. Moser (1962) believed high velocity winds keep many alpine ridges snowfree in Colorado. Rams were observed feeding on those slopes in many areas of the state. Dixon (1940) asserted this occurred in Rocky Mountain National Park. Flook (1962) concluded some sheep wintered in the alpine zone of Banff and Jasper National Parks, but at least one-half the population wintered in the subalpine zone.

Elk

Elk occupy many areas jointly with bighorn in western United States; but generally, it can be concluded that the two species prefer somewhat different types of habitat. Elk evade enemies in timbered areas instead of using rocky, relatively inaccessible areas of escape. Elk and bighorn feed in open grassy areas most of the year; but elk use is more restricted to areas close to trees and water. Apparently, elk seldom occupy steep, rugged areas, especially during spring, summer, and fall. Subalpine areas are used extensively by elk, especially where wet meadows, drier slopes, and forested areas are inter-mingled, or in close proximity to each other. Information concerning elk use of specific vegetative types has been presented previously under food habits and seasonal migrations.

In general, elk use areas of high elevation during summer. They usually occupy the highest vegetative type available during summer, although relative use of alpine areas may vary greatly among areas. Flook (1962) reported this occurred in Banff and Jasper National Parks. He determined elk occur throughout the subalpine and lower alpine areas of those Parks; although some elk remained year-around at relatively low elevations. Elk in Yellowstone National Park - Jackson Hole area (Murie, 1950; Anderson, 1954; M. Altman, 1956; Casebeer, 1961), Gros Ventre Mountains of Wyoming (Honess and Frost, 1942), Rocky Mountain National Park (Packard, 1947) and Montana (Brazda, 1953; Rouse, 1957; Cole, 1958; Picton, 1960), are reported to utilize alpine areas during summer. Most other authors stated elk occupied the subalpine zone when available.

Elk prefer to occupy open slopes or parks during summer at least while feeding. Elk fed frequently during summer in a large subalpine park along the White River in Colorado (Nichols, 1957). Occupancy of the Park ceased during late summer when elk occupied adjacent forested areas where succulent vegetation was more abundant then. Some elk occupied adjacent forest areas during summer. Kirsch (1962) determined elk fed in logged areas in the Little Belt Mountains of Montana. He reported also that elk used forested areas more in late summer. Elk use of openings decreased greatly then. Dalke et al. (1965) found that during late spring and early summer, elk in the Selway Preserve of Idaho used areas predominantly covered by grasses and sedges more often than other areas. Calving occurred on those open slopes.

Reynolds (1962) studied elk use of openings, adjacent forest borders, and cut over forests in a ponderosa pine dominated area of the Apache National Forest, Arizona. Elk preferred openings. Elk pellet groups were one-half as numerous in forested borders surrounding parks. Elk occupied cut over areas least. Most pellet groups were found approximately 400 feet into openings. Fewer pellet groups were found in the centerof parks of greater size than 45 acres. Elk use was distributed relatively equally in openings between one and 45 acres in size.

Elk seem to prefer wet or moist areas during late spring and summer. Mackie (1962) reported elk remained close to water and wet areas in the Missouri Breaks area of Montana. Kirsch (1962) stated elk in the Little Belt Mountains favored habitats "closely associated with water." He determined that the most mesic sites were located within the spruce-fir zone. Anderson (1954) reported elk in the Jackson Hole area utilized grass in meadows and creek bottoms during early spring (where green vegetation was

first available) and later fed on drier slopes when forbs began growing. When slopes dried out, elk fed in wet meadows. This same feeding pattern was reported in Montana by Kirsch (1962).

Elk seem to prefer south-facing slopes during winter and early spring. Kirsch (1962) noted a preference for southern exposures in early spring. Preferred were usually grassy areas used for feeding. Schallenberger (1965) stated 67 percent of his winter and early spring elk observations were of animals occupying south-facing slopes. Flook (1962) believed south-facing grassed slopes in the subalpine zone of Banff and Jasper National Parks have been occupied more by elk than other sites. He concluded elk used those slopes heavily during winter and early spring. Mackie (1962) determined elk preferred level to gentle slope areas during most of the year.

Elk use of alpine areas during winter is not well documented. Such use is known to occur in some areas. Packard (1947) believed some elk, probably bulls, remained on alpine slopes in Rocky Mountain National Park through the winter. Schwan and Costello (1951) stated elk wintered in some alpine areas of the Rocky Mountains.

Jeffrey (1963) intensively studied elk in the Fishlake National Forest of Utah. He considered all major factors possibly affecting elk use of range, i.e. vegetative type, range condition and utilization, distance to water, soil development, physical site, etc. Single factors could not be isolated as a cause of specific elk distribution. He concluded occupancy of range was determined by complex interaction of several factors. Factors varied in effect during different periods of spring and summer. Cover type or plant composition failed to show statistical significance.

Jeffrey made several conclusions. Elk preferred high ranges in spring and summer, low ranges in fall and winter, and edges of vegetative types and north-east-facing slopes in summer. He stated (Jeffrey, 1963): "Even though the animals (elk) shade up in dense patches of timber during the heat of the day, they are generally found quite close to the edge." Elk preferred drier slopes during a wet spring and wet areas during a dry fall. Elk did not prefer steep, rugged slopes. Areas with water within one-third mile away were preferred. Elk avoided marshy areas and frequented gravelly locations. The best habitat for elk was where several varied and interspersed cover types were present. A good production of forbs was necessary and grass and browse were desirable. (Jeffrey, 1963).

Mule Deer

The seasonal distribution of mule deer was discussed previously. It has been reported deer are found from winter range areas to alpine sites during summer.

Mule deer seem to prefer edges of vegetative types on summer (higher) ranges; however, significant variations were reported. Jeffrey and Julander (1964) reported deer use decreased with less ledge or as the distance away from edge increased. They concluded edge effect influenced deer more than for cattle or elk on summer range. Mackie (1962) concluded mule deer utilized timbered vegetative types most in summer and early fall. Reynolds (1962) determined deer occupied openings, opening-forest edges, and cut-over timber areas about equally in a ponderosa pine - open park area of Arizona. There, signs of deer occupancy in openings decreased greatly beyond 700 feet from

the edge. Cowan (1947) reported mule deer preferred to remain close to the edge of forested-open areas on winter range in Jasper National Park. Deer occupied openings less than elk or bighorn.

Mule deer apparently do not consistently prefer specific slopes or exposures. Deer use of certain exposures and slope graduents varies among areas. The probable reason, realizing the lack of available information, is due to factors such as food availability and presence of other ungulate species. Jeffrey and Julander (1964) concluded: "... deer made more use of range on the steeper slopes than the gentler slopes, particularly in summer and fall." They believed this possibly was due to a greater amount of available forage on steep slopes (due to cattle utilization on gentle slopes). In this study, they concluded deer favored south-west facing slopes in summer. White (1958) determined mule deer occupied and preferred south-facing slopes more than other exposures in the spruce-fir zone in Montana. He presumed this was due to occurrence of warmer temperatures on such slopes. White observed little deer use on dry, south-facing, rocky slopes where vegetation was sparse. Schallenberger (1965) reported south-facing slopes provided 75 percent of his winter observations of mule deer. Mackie (1962) found greatest mule deer use during winter and early spring on level to gentle slopes.

## UNGULATE INTER-SPECIFIC COMPETITION

### Introduction

Competition is an often misused and misunderstood term. Usually competition is defined as a struggle or quest for some need that is in short supply.

Accurate evaluation of competition is difficult. Inter-specific competition among wild ungulates is complex. Many factors are involved. Much data must be collected to accurately gauge species status in situations of competition.

Cole (1958) listed four necessary components of inter-specific competition: 1) the species use the same area; 2) they use the same forage plants; 3) the forage species used are important sources of food for either or all species and; 4) the forage plants being used are in a limited supply or are deteriorating in production as a result of combined use. Buechner (1960) listed types of information needed when total competition is to be evaluated: 1) the food habits of species involved; 2) the numbers of each species present; 3) comprehensive and statistically adequate sampling of the vegetation; 4) a knowledge of the seasonal and annual variation in forage production; 5) the distributional habits of the animals; and 6) the history of each area with special reference to grazing and fire.

In most areas where inter-specific competition for forage occurs, the critical period, or period when competition is most active is during winter. Stoddart and Rasmussen (1945;252) stated:

> "Snow on the high ranges forces seasonal migration of both big game and domestic stock. The grazing capacity of the seasonal range units must balance with the time the animals spend on each unit. The least productive unit, therefore, limits the capacity as a whole."

They (Stoddart and Rasmussen, 1945;252) stated further that:

> "The winter range almost everywhere in the West is the area of limited feed for game. Regardless of abundant summer feed, the maintenance of big game herds is dependent upon winter range capacity."

Insufficient winter range causes conspicuous losses of animals, especially where winters vary greatly in severity; or where the summer range supports a much greater number of animals than can be carried on the winter range.

The effects of competition may be subtle, although a population is being limited. Herd productivity declines on poor condition ranges. Effects of disease, parasites, predation, and human activity become intensified where animals are competing.

Competition itself may be subtle. Competing species may occupy the same areas during different periods.

Historical Population Displacement

Displacement of one ungulate species by another, through superior foraging ability and productivity, has been documented in several localities. Elk seem most successful in competition situations. Murie (1951) stated competition with elk is all the more intense because they tend to congregate in large numbers. Ratcliff and Sumner (1945) concluded loss of available winter range in Rocky Mountain National Park caused elk to occupy areas formerly used only by bighorn. Elk increased over what the range could support on a sustained basis, so competition for forage resulted. As a result of competition, bighorn were believed forced to remain above timberline for a "large portion of the year", whereas they formerly migrated earlier to lower winter ranges. Lower winter ranges were overused by increased populations of deer and elk. Elk wintered above timber-line in increasing numbers thereby using forage badly needed by bighorn (Ratcliff and Sumner, 1945).

Elk out-competed deer in the Selway area of Idaho. Case (1938) reported deer were originally abundant there but elk were scarce. At that time, deer apparently occupied areas of lesser snow depths on "favorable" exposures, and elk occupied higher areas with greater snow depths. The elk population increased and soon began frequenting sites occupied by deer. Case (1938) stated: "Here the elk, being the larger and stronger animals, were able to reach higher and paw deeper snow to obtain adequate food." Case reported that in 1938, elk were out-competing deer and that the deer population was decreasing. Deer were believed less healthy and experiencing greater losses to predators.

Smith (1954) believed Idaho bighorn have not been able to thrive in areas where deer or elk were "overly" abundant. He reported (Smith, 1954;90):

> "Where common game use has not deteriorated the range, there is evidence that mountain sheep can live harmoniously with the other inhabitants. It is from abused areas that bighorn 'disappear', leaving elk and deer to multiply and further deplete the vegetation.

> The requirement for thrifty range is not peculiar, of course, to bighorn sheep; but they do appear to be more immediately and adversely affected by mis-management than either elk or deer."

He believed bighorn numbers could be increased on some ranges by favoring sheep production without increasing range carrying capacity.

Jones (1950) concluded deer numbers had increased greatly along the eastern side of the Sierra Nevada range since the early 1900's. He believed competition for forage and damage to winter range had resulted. Winter range competition was most intense during severe winters - when bighorn were forced to use the same areas as deer. He stated (Jones, 1950): "In areas under such competition the higher reproductive rate of the deer has insured their continued presence over that of the bighorn." He believed distribution of bighorn year-around was restricted to areas where deer were not plentiful, where deer were being limited by factors other than winter range forage.

Cowan (1950) reported moose, bighorn sheep, and mule deer were originally present in Banff and Jasper National Parks of Canada. No significant competition occurred then. Elk were introduced in 1917 and 1920, and began utilizing the same plant species the three former species used. Competition for forage increases as elk increased. Over use of range began in 1930 and continued until at least 1949. The mule deer and moose populations decreased as elk increased. Bighorn decreased in marginal areas only. As deer, moose, and bighorn decreased, malnutrition, parasitism and predation became evident causes of death. Malnutrition apparently affected fecundity and sex ratios of these species. Bighorn appeared most vulnerable to climatic conditions associated with severe winters. Elk experienced a greater loss of animals in normal winters than did sheep. Bighorn lost more in severe winters, especially yearlings. (Cowan, 1950), Green (1949) and Flook (1962), concurred with this history of competition in these Parks.

Summer, Spring, Fall Competition

Significant inter-specific competition occurs usually on winter ranges, where species are forced to utilize the same restricted ranges. Few reports exist of competition on other areas or at other times of year. Effects of competition other than on winter ranges are obscure and difficult to gauge.

Deer and elk probably occupy alpine areas during summer where bighorn winter. Ratcliff and Sumner (1945) reported this occurred in Rocky Mountain National Park to the detriment of bighorn. Green (1949) reported "All known areas of alpine meadowland in Banff National Park frequented by bighorn, with one exception, are utilized by elk either seasonably or throughout the year." He reported further that excessive utilization of range by elk occurred on many bighorn ranges and range competition affected the bighorn population. He stated (Green, 1949): "The elk pressure on all ranges, especially those of limited extent, has had the effect of confining sheep to range edges where forage is inferior, or driving them to less-favorable localities nearby where elk do not occur." Apparently the increase in the elk population caused bighorn to break up into smaller bands. Ranges shared with elk would not support former numbers of bighorn (Green, 1949).

Flook (1962) reported that on south-facing, grassed, subalpine slopes used jointly by elk and bighorn during winter and spring, where grasses and

sedges had been depleted, there was direct competition for food. Mackie (1962) believed elk and mule deer did compete for food in early spring, late summer and fall where their ranges overlapped. Both authors determined competition for food during spring, summer, and fall occurred for succulent forage species. Competition was most intense in spring when open slopes provided early growth by grasses.

Sheppard (1960) reporting on Wishart's (1958) work on bighorn sheep in Alberta, stated: "Wishart (1958) found little evidence of competition between mule deer and bighorn sheep except in spring, when both species are eating grass." Sheppard (1960) stated further:

> "In April and May, however, both animals are feeding on new grass, the supply of which is, at first, limited. The competition involved may be responsible for slower spring recovery on the part of both species, perhaps causing the deaths of some weakened animals, that might have recovered, had the spring competition been less severe."

Sugden (1961) reported bighorn did not compete for forage although deer utilized high, exposed ridges in summer which were occupied by bighorn in winter. Food habits of the two species were different. Murie (1951) reported elk utilized preferred plant species on talus slopes and ridge tops in the Jackson Hole area of Wyoming, during fall and early winter. Bighorn occupied the same areas in winter. Riegelhuth (1965) reported evidence of elk occupancy in summer occurred where bighorn wintered along the Sierra Nevada. He judged this detrimental to sheep.

## Winter Competition

Bighorn sheep, in almost every area where they occur, appear in competition for forage with other wild ungulates. Such interspecific competition was reported present in Colorado (Spencer, 1941; Ratcliff and Sumner, 1945; and Packard, 1946), Wyoming (Honess and Frost, 1942; Cahalane, 1948; Murie, 1951; Craighead, 1952; McCann, 1956; Beetle, 1962, and Oldemeyer, 1966), Montana (Couey, 1950, 1955; Cooney, 1952; Knight, 1962; and Schallenberger, 1965), in Idaho (Smith, 1954), Oregon (Cliff, 1939), California (Jones, 1950; Riegelhuth, 1965; and McCullough and Schneegas, 1966), and in Canada (Cowan, 1947, 1950; Green, 1949; and Sugden, 1961). Most reports described restriction of ungulate populations due to lack of suitable winter range. Most often this competition was most significant during severe winters, when all species were forced to use the same areas.

### Wyoming

High starvation losses of bighorn, deer, and elk occur during severe winters in the Gros Ventre Mountains of Wyoming. All three species used the same winter range areas. Such areas were overused. Scarcity of forage caused deer and elk to use rougher areas, where bighorn wintered. Competition between elk and bighorn was more intense because their food habits (grass) were similar. Deer utilized rougher (sheep) areas more than elk (Honess and Frost, 1942).

McCann (1956) expressed similar beliefs concerning ungulate competition in the Gros Ventre Range. He stated (McCann, 1956):

> "Mountain sheep tend to suffer disproportionately in any competition from other grazing animals. Whereas most other herbivores are able to range widely in search of forage, the mountain sheep seem psychologically bound to their restricted niche, and are forced to find forage within very limited boundaries."

He reported that as snow depth increased, elk and deer fed more on wind-swept ridges and flats and other snow-free areas, which were preferred by bighorn as feeding sites. Deer occupied rocky, rough areas, more than elk, in direct and constant competition with bighorn. Craighead (1952) reported the same situation for this area.

Beetle (1962) surveyed range in the Teton Wilderness area. He determined mountain sheep were severely reduced in numbers. Few sheep occupied alpine meadows during summer. He believed restriction of winter range and competition with elk caused a reduction in the sheep population.

Montana

Cooney (1952) reported serious competition in the Sun River area between elk and deer or browse winter ranges and between elk and bighorn on other winter ranges. Couey (1950) stated that in severe winters in Montana, elk and bighorn competed for forage but that bighorn were not affected "abnormally". He believed that deer and elk did not compete significantly with bighorn in the Sun River area because sheep occupied precipitous sparsely vegetated areas with little cover. Deer and elk did not frequent those rough areas. Couey, (1955) reported that bighorn herds of Montana were then in the best condition ever. This he attributed to the better balancing of utilization with capacity of ranges.

Schallenberger (1965) also studied winter range relationships among ungulates in the Sun River area. He determined serious interspecific competition between mule deer and bighorn occurred where winter ranges were shared. Food habits were very similar on those areas. Elk and bighorn competed for forage to some degree on bunchgrass ranges in winter.

California

Jones (1950) stated bighorn may have competed with deer for browse on winter range in the Sierra Nevada Mountains. Riegelhuth (1965) reported bighorn, elk, and deer possibly competed for forage during winter on one area of the Sierra Nevada Range. He believed bighorn usually wintered at higher elevations than elk or deer however. McCullough and Schneegas (1966) believed bighorn and deer wintered in different areas along the east slope of the Sierra Nevada Mountains. On the west slope, where deer and bighorn winter in close proximity, these two species preferred sites with different vegetative and physical characteristics. Bighorn utilized rougher areas. Tule elk, also present there, used some areas jointly with deer and bighorn in the winter; but most bighorn winter range was judged too rough for elk (McCullough and Schneegas, 1966).

Canada

Cowan (1947) made an intensive study of ungulate relationships in the

Athabasca Valley of Jasper National Park during December. Mule deer, bighorn, and elk were using the same winter ranges. He determined elk were in serious competition for food with deer and bighorn. Deer and sheep were in minor competition. Elk and bighorn competed for grass. Elk had overused willow to the extent that it was unavailable (out of reach) to deer. Large herds of elk on range during periodic thaws caused,through trampling, icy crusts to form on the snow cover. Vegetation in those areas was judged unavailable to deer and bighorn (Cowan, 1947).

Cowan (1950) reported winter competition for forage among wild ungulates in Banff, Jasper, Kootenay, and Yoho National Parks of Alberta and British Columbia. Bighorn, elk, moose, and mule deer were present on winter ranges. Green (1949) reported ungulate competition on Banff National Park winter ranges. Elk were out-competing bighorn. Sugden (1961) concluded bighorn and mule deer probably competed only during severe winters in the Churn Creek area of British Columbia.

Cliff (1939) surveyed ungulate relationships on the Whitman National Forest of Oregon. He determined winter feeding habits of deer and elk were similar. Ungulate competition occurred when the range carrying capacity was exceeded. He believed deer were unsuccessful competitors with elk because elk had a physical advantage. He thought this would cause a gradual replacement of deer by elk.

Inter-specific Social Competition

It seems difficult to assess the effects of social inter-specific competition or competition for space. Very little has been written concerning social interactions among wild ungulates. Altmann (1952, 1956 a and 1956b) described behavior of elk and ungulate inter-specific social relationships. Her reports are the most comprehensive concerning elk behavior.

Elk, bighorn, and mule deer apparently are compatible socially in most areas. Guse (1963) stated he often observed deer and elk feed in close proximity in Rocky Mountain National Park. Simmons (1961) reported deer and bighorn often fed and bedded together during spring and summer along the Cache la Poudre River in Colorado. McCann (1956) reported that during winter in the Gros Ventre Mountains of Wyoming: "For weeks, bands of elk were seen side by side with the sheep, and in direct competition for the same forage." Feeding by all species was restricted to small, snow-free areas there. Kirsch (1962) stated deer and elk were often found together during all seasons of the year in Montana. White (1958) stated: "Deer and elk were observed many times feeding within 100 yards of one another, with no apparent concern for each other." Schallenberger (1965) frequently observed bighorn and deer grazing close together.

Smith (1954) believed bighorn were most compatible socially with mule deer in Idaho. He often observed deer and sheep feeding together in spring. Elk were observed twice feeding with bighorn. Sugden (1961) asserted mule deer and bighorn sheep were "commonly associated on winter and spring ranges" in British Columbia's Churn Creek area. Sheep and deer intermingled frequently while feeding; but they fed apart most often. Sheppard (1960), studied mule deer in Alberta. He found no positive or negative association of deer and bighorn, physically or socially, on spring range. Groups of both species fed together often with no apparent concern. He believed those associations were due to chance alone.

Green (1949) believed bighorn have an apparent intolerance for the presence of elk. He rarely observed sheep mingle with elk. He postulated this may be to "fouling" of range by elk, a condition he believed objectionable to bighorn. Green surmised also that intolerance may be the reason bighorn were forced to occupy fringes of areas dominated by elk. Young and Robinette (1939) determined that in the Selway area of Idaho, deer and moose visits to salt licks decreased when elk visits increased. Also deer and moose visited "less-desirable" licks when elk increased their use of the main licks. Hunter and Kinghorn (1950) reported bighorn displaced mule deer during winter in north-central Colorado on one occasion. There, deer arrived at a cache of salt and hay placed in an opening. Bighorn, rams and ewes, were bedded nearby. The sheep walked to the cache in a group after sighting the deer. The deer promptly retreated (Young and Kinghorn, 1950).

Some information has been presented concerning social relations among wild ungulates and livestock. Nichols (1957) reported an apparent intolerance by elk for domestic sheep in Colorado. Packard (1946) stated bighorn in Rocky Mountain National Park appeared not to mind the presence of horses and cattle. Jeffrey (1963) believed elk were tolerant of cattle to a certain point, and then elk would leave the area. He studied summer range in the Fishlake National Forest of Utah.

## UNGULATE RESPONSE TO RANGE CONDITION

Wild ungulate populations become restricted or limited as competition for forage becomes established or increases. Presumably, where natural causes increase the decimation of a population (i.e. starvation, predation, disease), lack of food is the proximate cause. However, populations have existed a long time under the influence of natural controls. Natural population controls become most limiting where ungulates occupy inadequate range.

Poor range conditions or poor animal nutrition may limit populations indirectly. Population productivity may be decreased greatly by poor nutrition of animals. Since competition for forage usually results in poor range conditions and inadequate forage consumption, cues to presence of poor range conditions or poor animal nutrition are important. These two factors are present usually on winter ranges, but also may occur on other areas.

Longhurst (1951) and Lang (1958) discussed studies of domestic livestock which have produced information on the effects of nutrition on productivity. Lang (1958) concluded studies of livestock show poor nutrition decreases breeding potential and increases winter death losses. Longhurst (1951) stated: "Food shortages before and during the time of ovulation have been considered detrimental to the rate of ovulation in livestock . . ." He stated also that (Longhurst, 1951) "Nutritional deficiencies encountered during pregnancy are reported in livestock to contribute to the birth of weak or still-born young."

Wild ungulate diets change as animals occupy different seasonal ranges. Longhurst (1951) stated: "In most northern or mountainous areas, particularly where animals show a seasonal shift in range, the late winter and early spring is the period of shortest food supply." He continued (Longhurst, 1951): "Studies of plant phenology indicate that the nutrients such as proteins and vitamin A which appear to be the most critical for ruminant well-being (Longhurst, 1950) are most abundant during the growing season and

diminish during the dormant season." Taylor (1956, ed.) concurred with this. Taylor believed succulent, green vegetation is always preferred by deer over cured or woody vegetation. Lang (1958) asserted wild ungulates seasonally seek out plants with the highest protein content.

Forage of limited nutritional value is present during the winter dormant period since vegetation is highest in nutrient content while growing. Taylor (1956, ed.) said:

> "At best the winter ranges furnish only maintenance rations. Stored body fat are essential to bring the deer through cold winters. So, not only is good winter range necessary, but the summer range must provide forage in quantity and quality that will build adequate storage reserved to the animal's body."

Most growth of animals, including fetuses, occurs during summer. Adequate summer range is just as important as winter range.

Buechner (1960) concurred by stating:

> "The abundance of summer range probably contributes greatly to the maintenance of good survival through the winter. The condition of animals shifting to low-plane diets of winter ranges greatly affects survival. Winter diet is hardly more than a maintenance diet, regardless of whether quantity is unlimited...".

Range condition and availability of vegetation year around therefore are the keys to the status of wild ungulate herds. Buechner (1960) stated:

> "Bighorn sheep are dependent more on vegetation than on other components of their environment. Populations can recover from epizootic mortalities, either natural or induced from domestic stock if the vegetation is in sufficiently good condition to support the adults in good health and to permit successful reproduction and survival."

Buechner studied several populations of bighorn sheep in the Rocky Mountain area. He concluded almost all were occupying winter ranges in poor condition and herd productivity was decreasing.

Buechner (1960) concluded also that high mortality among lambs constituted a major loss in sheep populations. He believed that if poor nutrition contributes to high lamb mortality, "it may function through nutritional deficiencies acquired from ewes suffering malnutrition during wintertime." He speculated this occurred in some Wyoming bighorn herds.

Couey (1955) related range condition and bighorn populations in Montana. He concluded that most often, where bighorn were unthrifty, the range or part of the range they occupied was in poor condition. He (Couey, 1955) stated: "In general it appears that the lack of sufficient range during severe winters could have a basic effect upon the thriftiness of our bighorns."

Most studies of wild ungulate nutrition have been conducted with deer rather than bighorn or elk. Cowan (1950) reported inadequate winter ranges

caused competition for forage among mule deer, bighorn sheep, elk, and moose in four National Parks of Canada. The effective reproduction of those ungulate species was low. Elk displayed heavy prenatal and "natal phase" losses. Bighorn and mule deer experienced higher reproductive rates than elk. Elk and bighorn suffered heavy short-yearling losses during winter and deer showed a reduction in fawn production in spring.

Jones, Robinette, and Julander (1956) studied two deer herds in Utah. One herd occupied a summer range in poor condition and the other herd utilized a summer range believed near optimum for deer. Both herds were judged wintering under very similar conditions. The authors determined that reproduction (ovulation rate and fetal rate) plus mean weight of individual animals decreased for the herd occupying the poor condition summer ranges. They concluded also that a high loss of fawns at birth or shortly thereafter occurred if does did not recover from effects of inadequate winter forage.

Robinette and Gashwiler (1955), after studying Utah mule deer, concluded:

> "It seems probable that the condition of summer range is of far greater importance in determining the reproductive success of older does than is winter range, whereas in the case of yearlings the two ranges may assume near equal importance."

They believed mature does could attain peak condition by the rutting season if summer range was adequate even though the previous winter was detrimental to the animal. If summer range was poor, all forage consumed was utilized for growth of the doe. They believed the doe would thus not be able to conceive.

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