ECOLOGY OF SHIRAS MOOSE IN MONTANA

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ABSTRACT - A study to determine basic habitat relationships, food habits, reproduction, productivity and population dynamics of Shiras moose was conducted in southwestern Montana from 1965 through 1972. Intensive study was carried out on two study areas, with more extensive data collected from throughout southwestern Montana. Historical records indicate that moose distribution during Montana's early settlement was essentially the same as at present. Moose numbers apparently reached a low point at about the start of the present century. Population recovery and overpopulation, with resultant range deterioration, was noted in some areas by the 1930's. Data on use of vegetation types by moose on the Lower Gallatin Study Area near Bozeman showed that the Douglas-fir type was most important in all seasons except summer when it ranked second to the lodgepole pine type. The three moose population segments on the Upper Madison Study Area near West Yellowstone made differential use of available cover types. Two resident population segments existed, one associated with the spruce-fir type at higher elevations, and the second associated with the willow and adjacent lodgepole pine at lower elevations. The latter area was used in winter by a migratory population segment which summered in the upland types at higher elevations. Other Montana moose populations appear to fit one of these basic patterns of vegetation type use. Seasonal home ranges of moose on the Lower Gallatin Study Area were relatively small (mostly 1.5 square miles or less) although they often were separated by several miles. Individuals also traditionally used seasonal home ranges year after year. Rutting season movements of bulls appeared to be erratic and were often extensive in nature. All bulls returned to more familiar terrain after the rut, however. Browse was the most important forage class for moose in all seasons and areas studied with the exception of one wet summer in the Gravelly-Snowcrest area when forbs assumed first place. Forbs assumed importance only in spring and summer, while grass was a minor dietary component in all seasons. Forage species important to moose in Montana are presented and discussed by area and season. Measurement of key browse species in several southwestern Montana areas showed generally moderate to high utilization levels and percentages of severely hedged and decadent plants. Improved plant condition was noted in some areas in recent years. This was related to increased natural moose mortality in a few cases, but increased harvests and mild winters were responsible in most cases. Plant succession, snow depth, competition with other animals, logging and human development all affect moose forage supplies. Quantity of available forage progressively declines as plant succession advances from seral to climax stages. Snow depth regulates distribution and local density of moose, and limits forage availability, while the duration of deep snow determines the length of time animals are restricted to winter range areas. Interspecific competition may have locally important effects on moose forage supplies, with domestic livestock being potentially most detrimental in the majority of cases although elk and other wildlife may be locally important. Human activities have the greatest impact on moose populations through habitat alterations, and range from very beneficial to extremely detrimental depending on individual circumstances. Controlled burning and tree cutting to improve moose habitat by setting succession back to seral stages should be investigated further. Prehunting season moose classifications showed 77 bulls and 29 calves per 100 cows on the Lower Gallatin Study Area and 74 bulls and 58 calves per 100 cows on the Upper Madison and Centennial Valley Area. Differences in observed cow-calf ratios between these areas are the result of several interacting factors. Primary among these are differences in visibility because of greater proportions of dense timber types on the Lower Gallatin. Nutritional inadequacies, acting through increased loss of young calves, appear to contribute to lower cow-calf ratios on the Lower Gallatin as well. Due primarily to hunter selectivity, harvest composition differs considerably from that observed in the population prior to the hunting season. Statewide harvest collections for the years 1965 through 1971 included 55 percent bulls, 40 percent cows and 6 percent calves. Winter composition from areas with samples of 200 or more animals varied from 27 to 38 calves per 100 adults, with twinning rates of 1 to 12 percent. Areas with low twinning rates and calf-adult ratios probably indicate deteriorated ranges with subsequently lowered reproduction and increased post-natal calf mortality. Analysis of female reproductive tracts showed that calves were not reproductively active. Forty-three percent of the yearling cows had ovulated (48 ova per 100 cows), 32 percent were pregnant and none contained twins. Among adults, 92 percent had ovulated (115 ova per 100 cows), 86 percent were pregnant and 16 percent had twins. Rate of increase, gross productivity and net productivity (34, 25 and 20 percent, respectively) of Montana moose compare favorably with those reported from other North American areas, indicating that 20 percent of the population can be removed annually without diminishing the adult population. The low incidence of twins observed in the field versus *in utero* twinning rates, plus lower than anticipated fall cow-calf ratios in some areas, appears to result from nutritional inadequacies among cows, with resultant increased losses of young calves. The peak of the rut occurred in early October, while calving peaked in late May and early June. A 235 day gestation period seems more applicable to Montana moose than the longer (240 to 246 days) period generally given for moose in the literature. Parasites, diseases, accidents and predation, either singly or in combination, appear to have little direct bearing on Montana moose mortality rates. Harvest removals and natural mortality (primarily nutritionally related) are the most important population controlling mechanisms. Recommendations for managing Montana moose populations as a renewable natural resource to be utilized through recreational hunting are made.

INTRODUCTION

Initial studies of Shiras moose *(Alces alces shirasi)* in Montana (Knowlton 1960; Smith 1962; Peek 1961, 1962, 1963) provided much insight into the life history of this magnificent game animal, but also indicated that additional research was needed before adequate management could be accomplished. Findings of Knowlton (1960) and Peek (1962) indicated that moose in the Gravelly-Snowcrest area of southwestern Montana ranged over relatively small areas in summer, and probably were more restricted on winter concentration areas. These early studies also showed a high moose population in that area, that moose browsing pressure was severe, and important browse species on both summer and winter ranges were in poor condition. Peek's (1961) limited reproductive tract collections indicated that reproduction and twinning rates of moose in the Gravelly-Snowcrest area were considerably below those reported for moose in other areas of North America. He suggested that this might be related to population structure and poor range condition. Although his data also were limited, Smith (1962:22) felt that reproduction in the Rock Creek area of Granite County was comparable to other areas. Knowlton (1960) and Smith (1962) both provided food habits data for moose wintering in the willow *(Salix* spp.) bottom vegetation type and pointed out possible moose competition with other wildlife or domestic livestock, at least seasonally. This could result from direct competition for resources and/or usurpation of bottom lands solely for livestock use, through conversion from shrub and tree cover to pasture or hay land.

These findings also raised several questions with management implications. If seasonal and yearly ranges of moose were indeed small, perhaps management could be improved by reducing the size of hunting units. Knowlton (1960:169-170) pointed out that animals were harvested primarily in easily accessible areas. A reduction in the size of hunting units would force hunters into some areas largely avoided before. If reproduction and productivity differed between areas, what were the causes and could they be remedied to increase harvests without reducing base populations? A knowledge of food habits, range relationships and possible competition with other animals would be important for land use planning and decision making.

Although these questions had been partially resolved for population segments wintering in the willow bottom type, information was not sufficient for refined management, and little was known of the substantial populations which are year-round residents in upland forest types throughout Montana's moose range. In 1965 a comprehensive study was initiated to determine basic habitat relationships, food habits, reproduction, productivity and population dynamics of moose in southwestern Montana to provide a better basis for management of this resource. Some of the initial results were previously published (Stevens 1970). These data, as well as unpublished data collected by Stevens from 1965 to 1967, have been incorporated into this report.

TAXONOMY

A taxonomic review of the living representatives of the genus *Alces* (North American moose and Old World elk) was provided by Peterson (1952) who concluded that North American moose are conspecific with Old World *Alces alces*. He recognized within the species two, or possibly three, Old World races, and four North American races. The North American subspecies probably originated in unglaciated areas or *refugia* during the last maximum expansion of the ice sheets during the Wisconsin stage of glaciation (Peterson 1955:14). This occurred approximately 10,000 years ago (Geist 1971:125). The Shiras moose was first described as a distinct species by Nelson (1914) and named for George Shiras III who had studied and photographed the moose in Yellowstone National Park in the summers of 1908-1910. According to Peterson (1952:24), this race appears to represent the extreme among North American forms in light coloration along the back. However, he utilizes differences in cranial measurements for separating the various moose subspecies.

Skull measurements obtained from the two distinct Montana areas (northwest and southwest) inhabited by moose indicated that only the Shiras subspecies occurs. Measurements of nine adult males in this study were generally smaller than those from nine middle-aged males used by Peterson (1952:9) to help distinguish subspecies. However, averages for the three oldest males were equal to, or slightly larger than, those of Peterson, indicating undue weight was given younger animals in this study.

SHIRAS MOOSE DISTRIBUTION

The Shiras moose is currently found throughout the mountainous regions of southeastern British Columbia, southwestern Alberta, northern and eastern Idaho, western Montana, northeastern Utah, and western Wyoming. Occasional occurrence in Colorado has been reported by Bailey (1940, 1944).

Durrant (1952:461) reported that moose occurred in the Uinta and Wasatch Mountains of Utah, but considered their occurrence accidental. Since that time, however, Utah's moose populations have grown considerably and limited hunting has been allowed since 1958 (Stapley and John 1971). Wilson (1971:49) predicted that the Uinta Mountains moose population would reach the carrying capacity of the key browse species by spring, 1972.

Early Accounts of Moose in Montana

The earliest written reports of moose in Montana are from the accounts of the Lewis and Clark Expedition. Although neither Lewis nor Clark personally encountered moose, two members of the expedition reported in their independent diaries that hunters "Saw some mooce Deer which was much larger than the common deer," on May 10, 1805, a few miles above the mouth of the Milk River (Burroughs 1961:139-140). While camped on Lander's Fork, near present-day Lincoln on July 7, 1806, Lewis wrote "Reuben Fields wounded a moos deer this morning near our camp".

Moose apparently were not uncommon in wooded bottoms along larger streams and rivers of the prairie regions just east of the Rockies in earlier times. In July of 1833 Prince Maximillian recorded "The Moose Deer or Orignal *(Cervus alces Amer.)* is said to be common towards the upper part of Milk River, and Dechamp himself had killed several of these animals on the Missouri, in the vicinity of this river." (Thwaites 1906a:46). England and de Vos (1969:91) cite the journal of Anthony Hendry in which he records killing 48 moose in the grassland regions of southern Alberta and Saskatchewan between August 13 and October 29, 1754.

During the fall of 1824 Alexander Ross visited the west side of the Bighole Valley. In the vicinity of Lemhi Pass he stated that "We were at the same time surrounded on all sides by herds of buffalo, deer, moose and elk. . ." (Ross 1956:291). Moose remained numerous in this area at least through the 1870's as indicated by the following statement by Teddy Roosevelt, "In the Big Hole Basin, in southwest Montana, moose were quite plentiful in the late seventies." (Roosevelt 1902:243).

Following his visit to the Bitterroot Valley in 1841-42, Father DeSmet wrote, "The moose is found here, but is seldom caught, on account of its extraordinary vigilance, for, on the slightest rustling of a branch it leaves off eating, and will not return to its food for a long time afterwards." (Thwaites 1906b:334). Other early accounts of moose in this general area are one shot by Charles Rumley in September of 1862 just west of present day Frenchtown (Howard 1939), and two shot by Teddy Roosevelt in 1887, one in the Bitterroot Mountains and one in the ranges southeast of them (Roosevelt 1902:228-237).

Only one early reference to moose in or near the northwestern part of Montana was found. John Palliser saw "a splendid moose" while observing Chief Mountain (near the northeast corner of Glacier National Park) from "a little north of east" of it on August 8, 1858 (Spry 1968:263-264). The journals of the veteran explorer David Thompson (Tyrrell 1916) do not include records of moose in the portions of northwestern Montana which he visited, although they were frequently seen not too far to the north in Canada.

In and north of Yellowstone National Park moose were still to be found in fair numbers until at least the mid-1870's (Cook et al. 1965, Ludlow 1876). The first chronicled trip to the head of the Yellowstone River in 1869 recorded a moose at the mouth of Meadow Creek on the East Gallatin River (Cook et al. 1965). Moose were "quite abundant" in Yellowstone Park in 1875 although they had been "...driven away from the neighborhood of the trail by the constant passage of travelers." (Ludlow 1876:69). He also reported seeing "...signs of its presence in the Bridger Mountains..." and was told of"...a famous country for moose about fifteen miles from the mouth of Trail Creek." (Southwest of Livingston).

A brief review of common names of lakes and streams, although subject to error, offers some insight into local abundance, or at least presence, of moose during the early settlement period when most were named. This review reveals at least 18 Moose Creeks, a Little Moose Creek, Moose Meadows Creek, Moose Gulch, Big Moosehorn Creek and Little Moosehorn Creek, 4 Moose Lakes, a Big Moose Lake and Moose Creek Sloughs. These occur in most of the area presently inhabited by moose, indicating little change in distribution from the period of early settlement.

History of Montana Moose in the Last 100 Years

Moose hunting in Montana was first regulated (an annual closed season from February 1 to August 15) in 1872, the same year that Yellowstone National Park was established. Following an apparent decline in moose numbers, hunting was closed year-round in 1897 (Stevens 1971:89). Statewide moose populations apparently reached a low ebb about 1900. The 1909-10 biennial report (State of Montana 1910) reported that"...ten years ago, these animals were practically extinct in the state. Today, after ten years of careful protection, there are probably 300 moose in Montana...". The largest herd (approximately 40 animals) was reported from the Ross Fork area of Rock Creek in Granite County. At about the same time, Shiras (1912, 1913), estimated that 1,500 moose lived throughout the year in Yellowstone National Park. Most people consider this estimate to be high, but from his own experiences in the area Bailey (1930:36) felt that Shiras' estimate was more accurate than others from this period because of his familiarity with both the animal and the region. Bailey also felt that moose numbers in Yellowstone Park were much lower in the late 1920's than in 1910.

According to McDowell and Moy (1942) the Forest Service estimated 25 and 308 moose on the Absaroka National Forest (now part of the Gallatin National Forest) in 1921 and 1936, respectively. They also report that the *Absaroka Winter Game Studies*, conducted by the Forest Service in the winter of 1935-36, found seriously overgrazed areas with a high percentage of dead willows which forced the moose to forage on the higher slopes. At about the same time, other areas of moose concentrations were recognized in the Flathead, Bitterroot, Bighole, Ruby, Madison and Gallatin drainages (Stevens 1971:89). Increased moose populations in areas adjacent to Yellowstone Park has been attributed to overflow from the Park (McDowell and Moy 1942, Denniston 1956, Houston 1968), although Denniston (1956) points out that the naturally favorable habitat is probably of almost equal importance. It is also likely that a few moose remained in these areas throughout the period of low populations.

Montana's first positive approach to moose management was the study of McDowell and Moy (1942) who found signs of further range deterioration in the Absaroka Primitive Area and recommended a controlled moose harvest. Despite this, legislation enabling the Fish and Game Commission to set moose seasons was not enacted until 1945. Intensive scientific studies of Shiras moose were begun in Yellowstone Park in 1947 (McMillan 1953, 1954). The first intensive moose studies in Montana were initiated in 1958, one in the upper Ruby River area (Knowlton 1960, Peek 1961, 1962, 1963) and a second in the Rock Creek drainage in Granite County (Smith 1962). These and other Shiras moose studies (Denniston 1956; Harry 1957; Altmann 1958, 1959, 1960; Houston 1968; Dorn 1969, 1970a; Stevens 1970; Stone 1971 and others) have provided information on which existing management practices are based.

Montana experienced its first open moose season in nearly 50 years in 1945 when 90 bull-only permits were issued; 40 for the Absaroka area, 30 for the upper Gallatin and 20 for the Bighole drainages. With additional knowledge of moose populations, distribution and habitat requirements, permit quotas have been increased. Recently, approximately 600-700 either-sex permits have been issued annually resulting in annual harvests of approximately 400-500 animals. Annual hunter success from 1945 through 1971 averaged 73 percent (range 63 to 86 percent).

Current moose distribution in Montana probably differs little from when white men first visited the region, except for their absence from most of the large intermountain valleys and river bottoms east of the mountains. Present abundance may be greater than at any time since the Lewis and Clark expedition visited the region.

METHODS

Vegetation was classified principally by reconnaissance and direct observation, although quantitative measurements were made on several types important to moose. The point-center-quarter method (Cottam and Curtis 1956) was used to determine tree density and record long-term changes in the willow type. The line intercept method (Canfield 1942) was used to measure canopy coverage of shrubs and forbs taller than 1 foot, while a spherical densiometer (Dealy 1960) was used to obtain canopy coverage of trees over 8 feet tall.

Plant nomenclature follows Dorn (1970b) for the genus *Salix*, and Booth (1950) and Booth and Wright (1966) for other species.

Seasonal moose distribution and use of habitat types, sex and age composition of population segments, plus gross seasonal movements, were determined primarily through aerial observation. A Piper Super-cub was used on nearly all flights with a three-place Bell helicopter occasionally utilized for classification and comparison with findings from fixed-wing flights. Location, sex and age, vegetation type, elevation, exposure and animal activity were recorded for most observations.

Moose were immobilized using a dart gun from a helicopter as described by Nielson and Shaw (1967). Dosages of 16-20 milligrams of succinylcholine chloride per adult animal were generally effective. The lower doses were used in late winter and early spring.

Radio telemetry was used in the latter part of the study to more precisely determine seasonal movements and use of habitat types by individual animals and to obtain data on size of home ranges. Radio transmitters were similar to those described by Cochran and Lord (1963) and operated in the VHF range. Receivers were of the double conversion, crystal-controlled, superheterodyne type. A two-element directional antenna was utilized both on the ground and from the air. Ground to ground reception range varied from approximately one-half to over 5 miles, depending on terrain. By utilizing favorable terrain it averaged 2-3 miles. Ground to air reception was obtained from as far as 16-18 miles under ideal conditions but ordinarily was in the vicinity of 5-6 miles. Because of terrain and the lack of a suitable road system in much of the area, most relocations were from the air.

Food habits were studied by examination of feeding sites and analysis of rumen samples (Knowlton 1960:163). When snow was present, feeding site examinations were made by back-tracking the animal to its previous bed. Rumen samples were collected from hunter and accidental moose kills as the opportunity arose. Food habits data were compiled by the aggregate volume method (Martin, Gensch and Brown 1946).

Range condition and trend were determined from browse survey transects (Cole 1959) established in 1967 or earlier on important moose wintering areas. Each transect consisted of 25 to 50 individually tagged plants which were classified as to degree of hedging, age, decadence (25 percent or more of crown dead), and percentage of current years growth used annually.

Initially, lower mandibles and female reproductive tracts of moose were collected in the field. Beginning in 1966 a letter was sent to all moose permit holders in southwestern Montana requesting that these parts be saved and left at designated collection stations near their hunting area. Mandibles were assigned to age classes using the tooth-wear criteria of Passmore et al. (1955) as modified by the use of four known-age samples. Ovaries and uteri were macroscopically examined to determine incidence of ovulation, and ovulation, pregnancy and twinning rates of Shiras moose in Montana. Moose weights were obtained whenever practical, usually at game checking stations. These are presented separately in Appendix .

LOCATION AND DESCRIPTION OF STUDY AREAS

Intensive studies were conducted on two areas; one at the north end of the Gallatin Mountain Range south of Bozeman (Lower Gallatin Study Area), and the second in the Upper Madison River drainage between Earthquake Lake and Yellowstone National Park (Upper Madison Study Area). Less intensive study was conducted throughout most of southwestern Montana. Montana moose distribution and location of important areas mentioned in the text are shown in Figure 1.

LOWER GALLATIN STUDY AREA

The Lower Gallatin (Figure 2) was the primary study area. It comprised approximately 220 square miles, bounded on the south and west by the Squaw Creek-Swan Creek divide and West Gallatin River drainages, on the east by

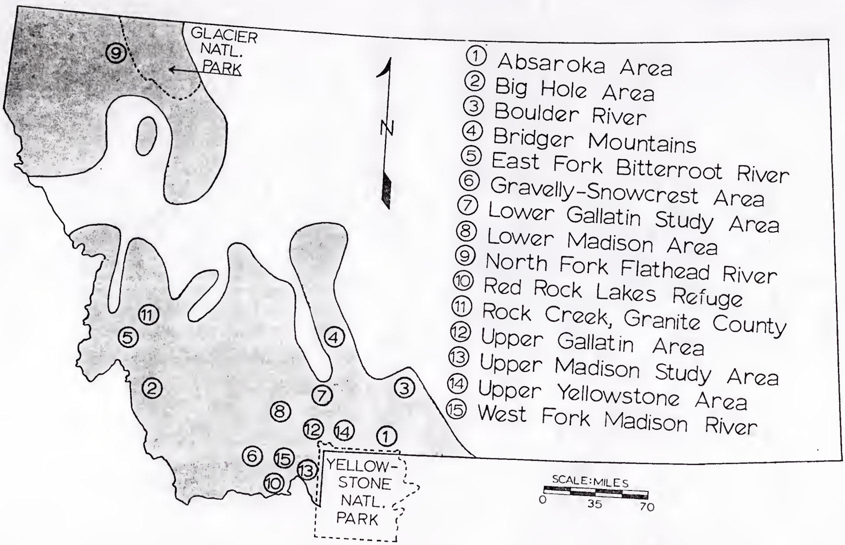

Figure 1. Distribution of Shiras Moose in Montana and Location of Important areas Mentioned in the Text.

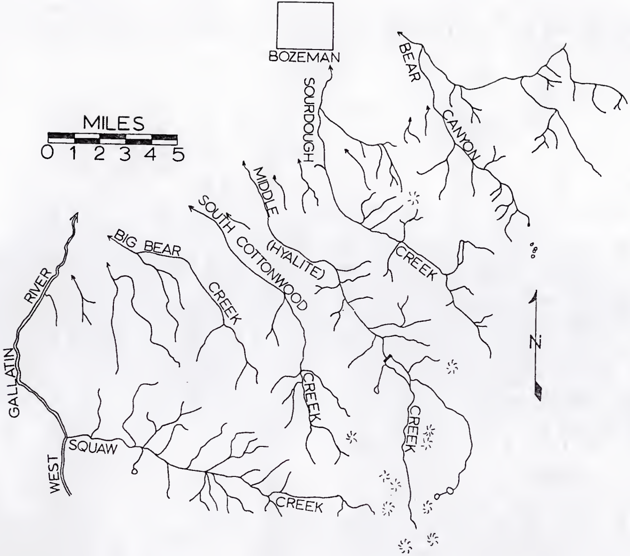

Figure 2. Lower Gallatin Study Area.

the West Gallatin-Yellowstone River divide, and on the north by the open Gallatin Valley where human habitation and the lack of suitable habitat limits moose distribution. The area slopes generally towards the northwest, with drainages cutting relatively steep-sided canyons toward their lower ends. The entire area is underlain by Precambrian metamorphic rock. Rock outcrops along canyon walls reveal a thick sedimentary strata with extrusions of igneous rock lying above (Tysdal 1966). Elevations range from peaks over 10,000 feet to foothills at 5,000 feet.

United States Department of Commerce, Weather Bureau records for Bozeman (elevation 4,856 feet) indicate average monthly temperatures of 20 and 66 F for January and July, respectively. Annual precipitation is just over 17 inches, coming primarily in the spring. Total snowfall at Bozeman averaged 95 inches annually (range 74-119 inches) during the years of study (1965-72). Annual precipitation increases as elevation increases on the study area.

UPPER MADISON STUDY AREA

The Upper Madison area (Figure 3) includes approximately 155 square miles, exclusive of Hebgen Lake (about 22 square miles). The northern portion is a rugged mountainous area drained by three major tributaries of the Madison River. These arise in relatively open basins and flow through rather deep, steep-sided canyons. The southern portion is a broad valley characterized by extremely sandy soils. Elevations range from over 10,600 feet in the mountainous northern part, to below 6,500 feet where the Madison River leaves the study area. Geologically, the area is underlain by Precambrian metamorphic rock with folded and faulted sedimentary deposits above. Glaciation and massive earth movements have altered the surface in recent times.

Deep snow and long, cold winters are characteristic of this area. Weather Bureau records for West Yellowstone (elevation 6,662 feet) indicate mean monthly temperatures of 12 and 60 F for January and July, respectively. Annual precipitation averages just over 21 inches, with much of it occurring as snow between November and April, inclusively. Total annual snowfall averaged nearly 160 inches (range 130-209 inches) during the winters of study (1965-72). In five of these eight winters for which records are complete, Hebgen Dam, approximately 18 airline miles from West Yellowstone, received an annual average of 74 inches (range 42-96 inches) more snowfall than West Yellowstone. This indicates the wide variation in snowfall that often occurs over short distances in mountainous terrain.

Vegetation

The vegetation in the general vicinity of the two study areas is a complex intermingling of several plant communities. Eight basic vegetation types discernable from the air were recognized.

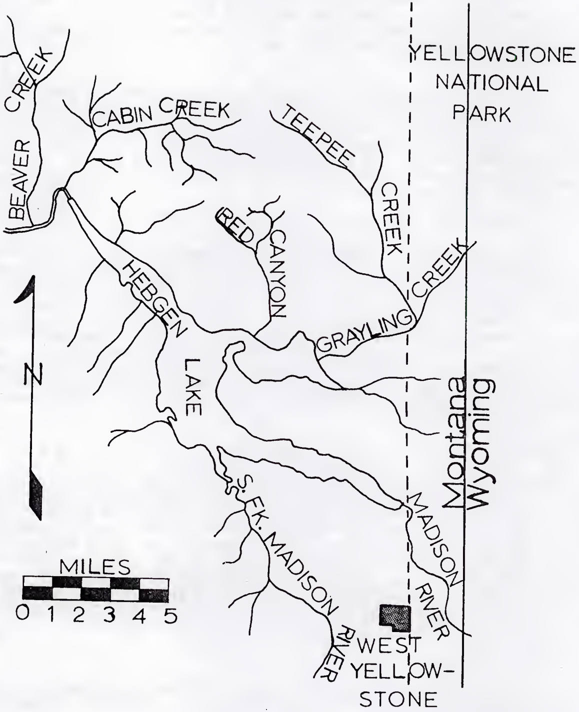

Figure 3. Upper Madison Study Area.

The most extensive vegetation type on both the Lower Gallatin (about 44 percent of the area) and Upper Madison (about 54 percent of the area) Study Areas is lodgepole pine *(Pinus contorta)*. This type is found at almost all elevations but is uncommon above 8,500 feet. It is considered seral to climax spruce-fir and Douglas-fir *(Pseudotsuga menziesii)* communities (Oosting 1956:298). Lodgepole pine in varying density is the most characteristic species. The understory varies from almost non-existent to profuse, with pinegrass *(Calamagrostis rubescens)* at lower elevations being replaced by low red huckleberry *(Vaccinium scoparium)* in higher areas. In many areas lodgepole pine is represented only by large decadent trees that are being replaced by spruce and fir in the understory. Numerous clearcut-logged areas in this type are dominated by various age-classes of lodgepole pine reproduction with a grass and sedge understory.

A Douglas-fir type occupies 18 and 12 percent of the Lower Gallatin and Upper Madison Study Areas, respectively. It generally occurs below 7,000 feet but extends considerably higher under favorable exposure and moisture conditions. Pinegrass, heartleaf arnica *(Arnica cordifolia)* and white spiraea *(Spiraea betulifolia)* are major understory species. A semi-open canopy type exists on south and southwest exposures with arrowleaf balsamroot *(Balsamorhiza sagitatta)* characterizing the understory. The understory on northern exposures at lower elevations is characterized by a dense shrub-union of ninebark *(Physocarpus malvaceus)*, snowberry *(Symphoricarpos albus)* and rose *(Rosa woodsii)*. Past selective logging has opened the canopy in some areas.

A spruce-fir type, dominated by Engelmann spruce *(Picea engelmanni)* and alpine fir *(Abies lasiocarpa)*, occurs primarily above 7,000 feet. The understory is primarily low red huckleberry and mosses. This type covers approximately 21 and 9 percent of the Lower Gallatin and Upper Madison Study Areas, respectively, extending into lower vegetation types along streams and northern exposures.

Approximately 12 and 19 percent of the Lower Gallatin and Upper Madison Study Areas, respectively, are unforested. The most common non-forest type is sagebrush-grassland which occurs as parks scattered throughout the area, generally on southwest exposures, ridgetops and at lower elevations. (Patten 1969:239) considers this an early seral stage in a successional series terminating in a mixed conifer climax forest. In the Lower Gallatin, large openings occur toward the northern edge of the study area, while vast open expanses surround parts of Hebgen Lake in the Upper Madison Study Area. Idaho fescue *(Festuca idahoensis)* and bluebunch wheatgrass *(Agropyron spicatum)* characterizes this type on xeric sites, with big sagebrush *(Artemisia tridentata)* often present as an overstory. Timothy *(Phleum pratense)*, mountain brome *(Bromus marginatus)* and sticky geranium *(Geranium viscossissimum)* are common in mesic swales, with sedges and grasses dominating wet meadows.

Approximately 4 to 5 percent of each study area is occupied by quaking aspen *(Populus tremuloides)* which is common on high-moisture sites, primarily within and below the Douglas-fir type. Aspen characterizes the type, with ninebark, rose, snowberry and spiraea common understory shrubs. Chokecherry *(Prunus virginiana)*, western serviceberry *(Amelanchier alnifolia)* and Scouler willow *(Salix scouleriana)* are also represented.

Willow communities occur on approximately 2 and less than 1 percent of the Upper Madison and Lower Gallatin Study Areas, respectively. They are mainly restricted to streambanks and relatively small bottom areas. Primary species are *Salix novae-angliae*, *S. drummondiana* and *S. geyeriana*, with *S. monticola*, *S. wolfii* and *S. phylicifolia* also being common. Grasses and sedges are the chief understory plants with shrubby cinquefoil *(Potentilla fruticosa)* and scrub birch *(Betula glandulosa)* common on drier sites.

The cottonwood type is of limited occurrence, occupying less than 1 percent of the Lower Gallatin Study Area and being virtually nonexistent on the Upper Madison Study Area. It occurs as a gallery formation along streams at lower elevations and is characterized by cottonwood *(Populus* spp.) with a dense shrub-union of alder *(Alnus incana)*, red dogwood *(Cornus stolonifera)*, mountain maple *(Acer glabrum)* and willow. Douglas-fir reproduction is locally abundant.

Hawthorn *(Crataegus* spp.) occurs in isolated patches on the Lower Gallatin Study Area, primarily in the eastern half. It occupies only a trace of the overall area. It was not noted on the Upper Madison Study Area.

Since moose were occasionally observed in water, either feeding or travelling in open streams during deep-snow periods, an aquatic type was included. This type appears to be insignificant to moose in Montana as discussed later.

RESULTS

HABITAT RELATIONSHIPS

Seasonal Elevational Distribution and Use of Vegetation Types

Relative seasonal and yearly use of vegetation types by moose was determined from 2,474 and 887 moose observations on the Lower Gallatin and Upper Madison Study Areas, respectively. Most observations were from systematic aerial flights.

Lower Gallatin Study Area - Relative seasonal use of vegetation types on the Lower Gallatin Study Area is shown in Table 1. Cutover areas were distinguished as separate types because of differences in ground cover in logged as compared with adjacent undisturbed habitats. The majority of the logging has involved clearcutting of lodgepole pine, with only minor amounts of the Douglas-fir and spruce-fir types having been cut.

Table 1. Relative Seasonal Use of Vegetation Types by Moose on the Lower Gallatin Study Area, 1965-1972. T = less than 0.5 percent.

Vegetation Type	Percent of Use by Period				
	September-October	November-December	January-February	March-April	May-August
Douglas-Fir	46	26	46	45	25
Spruce-Fir	18	23	5	3	8
Lodgepole Pine	18	14	9	9	34
Aspen	6	8	28	27	3
Logged	10	20	1	--	19
Willow	1	2	6	9	8
Sage-Grass	1	6	1	2	2
Cottonwood	--	--	4	2	--
Hawthorn	1	--	1	2	--
Aquatic	--	--	--	T	1
Total Observations	558	176	831	765	144

The Douglas-fir type received the highest use during all periods except May-August when it ranked second to lodgepole pine. The lodgepole pine, spruce-fir and aspen types ranked second in observed use in September - October, September - December, and January - April, respectively. Logged areas assumed importance in the May - August and November - December periods. The willow type was relatively important during all periods except early fall through early winter. The remaining types were of minor importance in all seasons. Differences in seasonal use of vegetation types occurred between years, primarily a result of the influence of snow depth on elevational distribution (see later discussion), which influences the relative availability of vegetation types for use by moose.

Aerial observations on the Lower Gallatin indicated that moose were widely scattered from late spring through early winter (Table 2). Approximately 70 percent of the animals were found between 6,000-7,000 feet from May through December, while over half of the January through April observations were below 6,000 feet. Moose were rarely found above 7,000 feet during winter (January-April) on the Lower Gallatin Study Area.

Although some moose arrived in winter range areas earlier, the main downward movement began in December and continued into March if snow continued to accumulate on upper and middle portions of winter ranges. Annual snow accumulation on winter ranges varied, resulting in differential concentration and use of various portions of the winter range between years. In general, fall migration resulted in progressively increasing local densities and dramatically increased use of the aspen type.

Initial upward movement on the Lower Gallatin Study Area is gradual, and strongly influenced by snow depth. In some years it had begun by mid-February. Edwards and Ritcey (1956) and Houston (1968:47) have also reported that movement onto and off of wintering areas coincided with increased and decreased snow depths, respectively. Both these studies identified migratory and non-migratory or resident population segments. A few moose remained at both high and low elevation year-round on the Lower Gallatin Study Area, indicating that both migratory and resident population segments probably existed in this area as well.

Upper Madison Study Area - Distributional patterns of moose on the Upper Madison Study Area differed slightly from the Lower Gallatin. Two resident populations plus a migratory herd apparently existed on the Upper Madison Area. One resident population occurred at high elevation (7,500 plus feet) in the spruce-fir type and the other at lower elevations (below 6,800 feet) in the willow and surrounding lodgepole pine types along the major tributaries draining into Hebgen Lake. Each resident segment comprised about one-fourth of the total animals in this area while approximately half of the animals were migratory. Migratory animals wintered primarily in the willow type around Hebgen Lake, and summered in coniferous forest types at higher elevations. Relative use of vegetation types on the Upper Madison is shown in Table 3.

Table 2. Elevational Distribution of Moose on the Lower Gallatin Study Area, 1965-72. T = less than 0.5 percent.

Elevation (Feet)	Percent of Observations by Period				
	September-October	November-December	January-February	March-April	May-August
5,000-5,499	2	--	11	9	3
5,500-5,999	12	13	42	42	6
6,000-6,499	38	42	31	41	32
6,500-6,999	30	31	13	6	37
7,000-7,499	15	12	4	1	22
7,500-7,999	2	2	--	T	1
8,000 plus	--	--	--	T	--
Total Observations	433	131	582	678	142

Table 3. Relative Seasonal Use of Vegetation Types by Moose on the Upper Madison Study Area, 1965-1972.

Vegetation Type	Percent of Use by Period			
	November-December	January-February	March-April	May-September
Spruce-Fir	19	23	26	32
Lodgepole Pine	12	9	15	7
Douglas-Fir	--	6	11	--
Willow	36	55	41	34
Sage-Grass	30	5	2	27
Aspen	--	2	2	--
Aquatic	2	--	4	--
Total Observations	92	502	252	41

Observations from late spring through early fall (May - September) were too few to accurately indicate use of vegetation types during this period. Use of vegetation types from November through April indicates movement from the lodgepole pine and sagebrush-grassland (mainly open parks within coniferous timber types at higher elevations) types to the willow, Douglas-fir, and aspen types at lower elevations.

Early winter (November - December) observations showed that 85 percent of the moose on the Upper Madison were above 8,500 feet, while nearly 60 percent of the January through April observations were below 7,000 feet (Table 4).

Movement to winter range in this area normally began in late November or early December and was essentially complete by mid-January. Return to higher elevation normally began around mid-April. Montana sightings and/or harvest of animals marked in Idaho during winter (Nielson and Shaw 1967) indicate that some moose from the Upper Madison winter in Idaho but spend considerable time in Montana during other seasons. The longest recorded movement for a moose marked in Idaho was approximately 54 miles, from the Juniper Butte area (April, 1962) to the Madison River north of West Yellowstone where it was seen November 7, 1962. Two other animals, marked near Henry's Lake, Idaho, were reported from the South Fork of the Madison River within the Upper Madison Study Area. One of these, a bull marked on February 11, 1967, was shot on October 22nd of the same year. The other was an unclassified animal observed on February 29, 1968, which had been marked either in March, 1966 or April, 1967. The distance from the marking site to the South Fork of the Madison River was 9 to 10 miles.

Other Southwestern Montana Areas - Knowlton (1960:164-166) reported that movement of moose onto willow bottom concentration areas in the Gravelly Mountains continued through March. While using willow bottoms, these moose utilized adjacent coniferous timber when disturbed or during winter storms. In the present study, nearly 80 percent of the animals observed in the Gravelly range during the winters (November - March) of 1965 through 1971 were in the willow type, with the remainder well scattered throughout the other types. By the first week of June, Knowlton (1960:166) found many moose at the lower limit of coniferous timber, and after mid-June most observations were made above 8,000 feet. During summer he found most feeding moose in sub-alpine meadows and adjacent willow bottoms, with coniferous timber used for resting and escape cover. Moose remained at high elevations through fall as indicated by hunter kill locations. Some of the moose which summered in the Gravelly Mountains apparently wintered on or near the Red Rock Lakes National Wildlife Refuge (Dorn 1969:35-36). These animals must move a minimum of 10-15 miles between seasonal ranges.

Dorn (1969:19) presented data (summarized in Table 5) on vegetation type use for the Red Rock Lakes National Wildlife Refuge. He pointed out that due to differences in observability between types use of timber

Table 4. Elevational Distribution of Moose on the Upper Madison Study Area, 1965-1972.

Elevation (Feet)	Percent of Observations by Period		
	November-December	January-February	March-April
6,000-6,499	3	20	15
6,500-6,999	12	39	43
7,000-7,499	40	22	16
7,500-7,999	28	10	12
8,000-8,499	17	5	12
8,500 plus	--	4	3
Total Observations	98	471	247

Table 5. Use of Vegetation Types by Moose for Feeding and Bedding, Red Rock Lakes National Wildlife Refuge, 1968-1969, (from Dorn, 1969). T = less than 0.5 percent.

Vegetation Type	Percent of use by Period	
	Summer	Winter
Willow	84	93
Aspen	6	3
Sedge	6	T
Grassland	3	T
Aquatic	1	0
Douglas-fir	T	3
Spruce	T	T
Spruce-fir	T	T
Total Observations	581	413

types was probably heavier than indicated during summer, while use of grassland and sedge types was probably less. Some animals present in summer moved long distances to winter, as evidenced by summer sightings of animals marked in Idaho during the winter. Red Rock Refuge personnel, Dorn (1969:34) and this study have all reported sightings of these marked animals. One bull marked near Henry's Lake, approximately 15 miles to the east, was observed 3 times in September, 1968, by Dorn (personal communication). A bull marked near Juniper Butte, approximately 45 miles to the south, was repeatedly observed by Refuge personnel and Dorn (1969:32,34) prior to winter 1968-1969. Another bull marked in the same area on February 14, 1969, was discovered blind on the Refuge and dispatched by Montana Fish and Game Department personnel on October 8, 1970.

Moose wintering in the Rock Creek area of Granite County generally forage in the stream bottom willow type and utilize the surrounding upland forest (primarily Douglas-fir and lodgepole pine) for bedding and escape cover (Smith 1962, Stone 1971).

The spruce-fir forest type is apparently important to moose year-round in the northwestern part of Montana (Jonkel 1963).

Seasonal Movements and Home Ranges of Individual Animals

Between July, 1968 and August, 1970, 10 moose were captured and marked on the Lower Gallatin Study Area. Nine were marked with ear tags and radio transmitter collars, while one bull whose neck was too large to take a collar was ear tagged only. Subsequent relocations of eight of these animals provided considerable information on seasonal movements and home ranges of Shiras moose in the upland forest types typical of much of the moose range in southwestern Montana.

Summer-Fall Movements and Home Range Characteristics

An adult bull captured and instrumented on April 7, 1970, remained on his winter home range until early June. On June 22 he was relocated nearly 4 miles south-southeast. After moving another 3.5 miles northwest, he remained in an area of approximately 0.75 square miles until early October. Sixty-eight and 25 percent of this area was covered by the lodgepole pine and Douglas-fir types, respectively, while 7 percent was non-forested. Two of four summer observations of this bull were in the Douglas-fir type, one was in Douglas-fir with lodgepole pine as a secondary overstory species, and the other was in the lodgepole pine type.

Another adult bull, tracked from mid-February 1969 through early April 1971, summered in the same vicinity during 2 successive years. In 1969, he occupied the summer range in mid-May and remained in an area of 1.5 square miles until late September. Eighty-five percent of this area was covered by the lodgepole pine type, some of which contained relatively large amounts of Douglas-fir in the overstory. Douglas-fir covered 13 percent of the area, while stream bank forest, primarily a mixture of aspen and various other tree species, comprised the remaining 3 percent. Only two visual observations were obtained during this period, one in mixed Douglas-fir—lodgepole pine, and the other in the stream bank type. This bull reoccupied the summer home range in late May of 1970. Except for one brief round-trip to his winter home range in mid-August, he remained in this area until mid-September, utilizing an area of 0.6 square miles. Slightly more than half of the area used was also used the previous summer. Douglas-fir, lodgepole pine and non-forested types, comprised 71, 27 and 2 percent, respectively, of the vegetation of the 1970 range. Five of seven visual observations were in the Douglas-fir type while two were in lodgepole pine.

Two of three animals seen together in a 25 acre willow bottom were instrumented on July 28, 1969. A yearling cow and a young adult bull were captured, while a larger bull escaped.

The instrumented bull was found 1.5 miles south of the capture site on the following day, and then moved 2.3 miles north-northeast where he utilized an area of approximately 1.5 square miles for the next 8 weeks. Approximately 4 percent of the area used by this animal was non-forested, 30 to 35 percent consisted of various aged clearcuts, and the remainder was covered by lodgepole pine. Considerable spruce and fir occurred as subdominate canopy species in the older lodgepole pine stands, while younger stands had considerable spruce in the understory. Seven and two observations were made in mature and cutover lodgepole pine types, respectively, while one observation was made in the willow-meadow type. Some use of clearcut areas was undoubtedly missed since visual observations were mainly made during midday when animals are mostly inactive. Early morning and late evening moose observations in general (Table 1) support this contention. This bull was reportedly observed in November, 1972, approximately 5-6 miles northeast of his capture site.

The yearling cow used an area of approximately 1.1 square miles for 11½ weeks following instrumentation, but was never found with the above bull again. Slightly more than five percent of the area used was non-forested, most of which was occupied by the willow bottom at the capture site. Spruce-fir, mature and cutover lodgepole pine occupied 17, 74 and 4 percent of the area, respectively. Of ten subsequent relocations for which vegetation type could be determined, four were in the spruce-fir type, three in the lodgepole pine type and one each in cutover lodgepole pine, willow and willow-lodgepole pine edge. This cow was killed by a hunter on November 5, 1970, approximately 1 mile outside the area in which she had been tracked during the previous fall.

A yearling cow and an adult bull were captured and instrumented approximately 1 mile apart on August 16, 1970. The yearling cow used an area of approximately 1.0 square mile for the next 5 weeks, after which the transmitter malfunctioned. Lodgepole pine, Douglas-fir and cutover lodgepole pine conprised 81, 14 and 5 percent of this area, respectively.

Three and two visual observations were in the Douglas-fir and lodgepole pine type respectively. This cow was seen with a calf on March 13, 1972, within 0.25 miles of the area she had previously utilized, providing further indication that some animals are year-round residents of lower elevation ranges.

The adult bull was located 3.2 miles to the northeast 2 days after capture. He remained in that vicinity until mid-October, utilizing an area of approximately 2.25 square miles. Lodgepole pine, Douglas-fir and an old burn revegetating to Douglas-fir comprised 87, 12 and 1 percent, respectively, of the area. Six of eight visual observations of this bull in this area were in the Douglas-fir type with two in the lodgepole pine type.

Fall movements were, for the most part, within areas utilized during summer. Movements to wintering areas were accomplished in relatively short time spans. Data from observations during the fall of 1970 indicated that bulls may make extensive movements during this period. These probably are directly attributable to the rut, which peaks in early October in this area. The bull currently under discussion moved 7.0 miles south of his summer home range in mid-October, then remained relatively sedentary for several weeks prior to onset of winter.

The bull tracked during three winter and two summer periods was in his summer home range until mid-August, 1970, when he moved to his winter home range (2 miles to the northeast) and returned again within six days. He remained within the summer home range for three additional weeks, before again moving to a point near his winter area where he stayed until late September. In late September he was found 1.0 mile northwest of his summer home range and spent 2½ weeks in an area of approximately 0.3 square miles. He was next located on October 28, after moving 5.3 miles northeast. The next relocation, on December 10, 1970, found him within his winter use area.

A third bull (instrumented on April 7, 1970, see below) remained within his summer home range until October 5, 1970. On October 8 and 9 he was found 1.8 and 2.3 miles, respectively, west of the October 5 location. He was observed 5.0 miles east of the October 9 location on October 19, and was shot by a hunter in the same area 2 days later.

Summer habitat use data (Table 6) for radio-equipped moose indicates that use of the Douglas-fir, spruce-fir and non-forested (mainly willow in this case) types was much greater than their occurrence on summer ranges of these animals. Aspen and logged types received use approximately proportional to their occurrence, while lodgepole pine was used much less. The Douglas-fir, spruce-fir, non-forested and aspen types are better producers of forage than either the logged or lodgepole pine types, which probably accounts for their greater use.

Table 6. Seasonal use of habitat types by radio-equipped moose on the Lower Gallatin Study Area, February, 1969- April, 1971. T = less than 0.5 percent.

Type	SUMMER Percent of Total Area	SUMMER Percent of Observations	WINTER Percent of Total Area	WINTER Percent of Observations
Lodgepole Pine	74	37	60	18
Douglas-fir	14	39	28	55
Logged	7	7	2	0
Spruce-fir	2	9	1	20
Non-forested	2	7	4	0
Aspen	1	2	2	7
Old Burn	T	0	4	0
Cottonwood	-	-	T	0
Total Acres	5,575		7,180	

Summer-fall movement data indicate that the majority of moose on the Lower Gallatin Study Area have summer home ranges of limited size, mostly under 1.5 square miles. Knowlton (1960:166) found limited summer movement among moose in the Gravelly Mountains. Summer home ranges shown by Knowlton (1960:165) were all under 1.5 square miles in area. Moose movements in the Gravelly-Snowcrest area during the two summers following Knowlton's study increased, apparently due to dry summer conditions (Peek 1962:362). In the Centennial Valley, south of the Gravelly-Snowcrest area, Dorn (1969:32) repeatedly observed cows and calves in areas of one-half to 2 square miles throughout summer and into fall. His summer observations of solitary cows showed that some used small areas while others did not. Dorn (1969:32) attributed this to the possibility of younger animals (probably mostly yearlings) moving more than older ones. In Jackson Hole, Wyoming, Houston (1968:53) found that over half the observed summer areas used by nine yearlings exceeded 2¼ square miles, the largest being 24 square miles.

Dorn (1969:32-33) did not observe bulls using limited areas for extended periods during summer. Portions of summer home ranges of many animals, especially bulls, apparently were in upland timber types adjacent to the more open cover that comprised over 85 percent of his study area. Seven percent of all observations made by Dorn (1969:19) were of moose moving between open types and the Douglas-fir type. Summer observations of a marked bull seen between mid-June and mid-September were within an area having maximum dimensions of approximately 2.8 x 1.0 miles (Dorn 1969:74). This bull was never seen on more than 3 consecutive days, and the intervals between sightings ranged from 1 to 3 weeks (Dorn 1969:32-33), indicating considerable use of timbered areas.

Working in Jackson Hole, Wyoming, Houston (1968:51) also found that Shiras moose had limited summer ranges. Over 95 percent of the observed summer home ranges of 25 adults in his study covered 1.5 square miles or less. In northeastern Minnesota, Van Ballenberghe and Peek (1971:69) found primary summer use of an area of less than 1 square mile, with less frequent use of a larger area for each of two cows, and a larger home range for one bull. Phillips *et al.* (in press), working in northwestern Minnesota, report mean summer-fall home ranges of 5.6 and 6.9 square miles for bulls and cows, respectively. These home range sizes are generally larger than found in the other studies cited, and are probably directly related to the open cover types and extremely flat terrain of their study area (mean drop of 1.5 feet per mile).

Winter Movements and Home Range Characteristics

Following extensive mid-October movements, the adult bull captured on August 16, 1970 remained in an area of approximately 2.2 square miles until mid-January. Seventy-seven, 8, 8 and 4 percent of this area are in lodgepole pine, cutover lodgepole, Douglas-fir and spruce-fir types, respectively, with 3 percent non-forested. Four visual observations were all in the spruce-fir type. On January 22, 1971 this bull was found in a small natural opening in the Douglas-fir type nearly 5 miles north-northwest of, and approximately 1,200 feet lower than, his location 1 week earlier. Two weeks later he was over 5½ miles to the east-northeast, within the area he had utilized the first 8 weeks he was tracked. He remained in this area (1 percent old burn, 12 percent Douglas-fir and 87 percent lodgepole pine) until signal loss in early April, but utilized only about half of the total area (approximately 1.1 square miles) used during late summer and early fall. Of four visual observations made between early February and early April, two were in the Douglas-fir type, one was in the lodgepole pine type and one was in a small aspen patch within the Douglas-fir type.

A young adult bull was captured and instrumented on April 7, 1970 in a small stringer of mixed aspen, Douglas-fir and brush along a small creek about 0.5 mile from the nearest continuous timber. He was re-observed in the same spot on the following day, and then moved about 1.5 miles southeast where he remained until early June. He utilized an area of 0.5 square mile during this time, 60, 19 and 5 percent of which was in the Douglas-fir, lodgepole pine and aspen types, respectively. Sixteen percent of the area was non-forested. All three visual observations of this bull during this period were in the Douglas-fir type.

A cow followed by a calf was instrumented on February 12, 1969, and followed for 10 weeks. These animals intensively used a relatively small area (0.25 square mile or less) for 1 to 2 weeks, then moved a half mile to a mile and repeated this use. During the first 4 weeks they moved 3.5 miles southward and 900 feet higher in elevation. The use pattern during the next 6 weeks was similar except distances between areas of restricted movement were somewhat shorter, and they tended to use an area longer before moving on. Overall, an area of approximately 4.0 square miles was utilized. Aspen, occurring as small scattered groves in the lower part, occupied less than one percent of the area. Lodgepole pine and Douglas-fir comprised 65 and 30 percent of the area respectively, with about 4 percent non-forested. Five of eight visual observations of these animals were in the Douglas-fir type, two were in lodgepole pine having considerable Douglas-fir as a co-dominant overstory tree, and one was in the aspen type. Three subsequent winter observations were obtained, one on March 6, 1970 approximately 2.0 miles east of the original capture site and two in 1971 (February 6 and April 5) 1.5 and 0.5 miles southeast of the original capture site, respectively.

Three fall observations of this same cow were also obtained, one each in 1969, 1970 and 1971. These were 2.3 to 4.5 miles south and southeast of the original capture site. One was within the area used during early 1969, while the other two were less than a mile east of where she was last located in early May 1969.

Two adult bulls were captured together on February 12, 1969, in the same aspen patch that the above cow and calf were using when captured on the same date. Following slight initial movement, the first bull used an area of approximately 0.75 square mile for 8 weeks. Ten percent of the area used during that time was non-forested, with Douglas-fir, aspen and cottonwood types comprising 70, 15 and 5 percent, respectively. Three of five visual observations were in the Douglas-fir type, one in the aspen type, and one in mixed Douglas-fir and aspen. Two reobservations of this bull were made the following winter, one in early January near the original capture site, and one in early March, approximately 2.0 miles northeast of the area utilized the previous winter. Hunters also reported seeing this bull in mid-October and early November 1969, just east of the area used the previous winter. Three observations obtained in the fall of 1970 were between 1.75 and 3.25 miles south and southeast of the area in which he was tracked during the winter of 1968-1969.

The second bull exhibited erratic movements for 10 to 12 days after being captured. He first moved south 1.75 miles, but 3 days later was 3.75 miles to the northeast. By February 24 he had moved 1.0 miles southeast of that location, and remained in this vicinity until mid-May, utilizing an area of approximately 0.8 square mile. Lodgepole pine, Douglas-fir, spruce-fir and non-forested types comprised 54, 40, 4 and 2 percent of this area, respectively. Three of six visual observations during this period were in the Douglas-fir type, two were in the lodgepole pine type and one was in the spruce-fir type. In 1969, this bull returned to the same area between September 19 and 25 and remained there until mid-May 1970, utilizing approximately 1.1 square miles, including most of the area covered the previous winter. Lodgepole pine, Douglas-fir, an old burn (mostly non-vegetated during winter), spruce-fir and aspen types occupied 49, 29, 19, 2 and 1 percent, respectively, of the area utilized the second winter. Six visual observations were made during this period under what were considered winter conditions. Three were in the spruce-fir type, and one each in the Douglas-fir, aspen and lodgepole types. In 1970, the bull again reoccupied this area sometime between October 28 and December 10, 1970, after the rutting season movements previously discussed. Between December 10 and April 1, when he was last contacted following transmitter failure, this bull utilized an area of approximately 0.8 square mile, completely with the area utilized the previous two winters. Lodgepole pine, Douglas-fir, old burn and spruce-fir types occupied 53, 21, 24 and 2 percent of the area, respectively. Five, two and one visual observations were in the Douglas-fir, lodgepole pine and spruce-fir types, respectively.

Visual observations, tracks and locations from the air without actually seeing the animal all indicated that a small dense spruce-fir patch (approximately 15 acres) and the lodgepole pine immediately surrounding it received heavy late winter use (late March on) by this bull in all 3 years.

Figure 4 shows the movements and areas used by this bull during the 26 months he was followed.

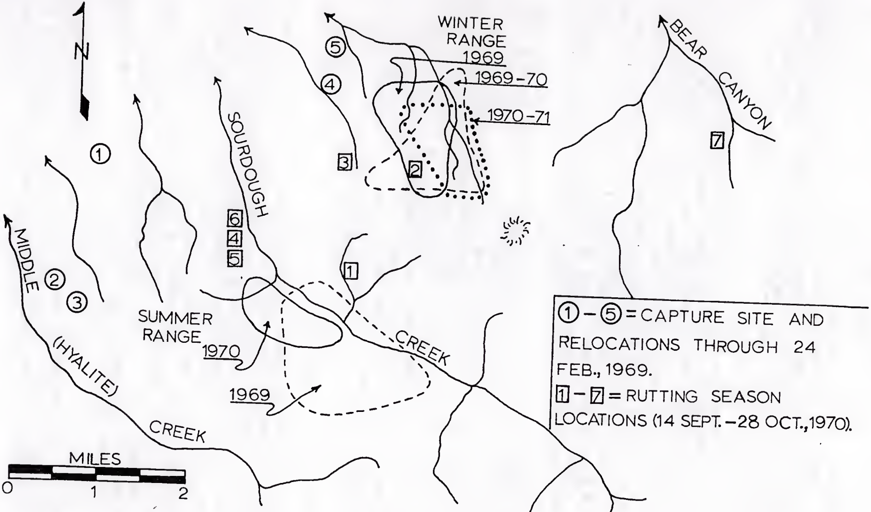

Figure 4. Movements and Seasonal Home Ranges of an Adult Bull Moose Radio-tracked between February 12, 1969 and April 1, 1971.

Winter habitat use data (Table 6) for instrumented moose shows that use of the spruce-fir, aspen and Douglas-fir types was considerably greater than their occurrence, while lodgepole pine received considerably less use. Open types (non-forested, old burn and logged) were not used, probably because both food and cover are lacking when snow covers the ground.

All marked animals on the Lower Gallatin Study Area were relatively sedentary on restricted winter home ranges except the one cow and her calf. This corresponds to the findings of Houston (1968:51) who reported that nearly 90 percent of 39 adult winter ranges in the Jackson Hole, Wyoming region were 1.5 square miles or less in area. Phillips *et al.* (in press) found winter home ranges in northwestern Minnesota averaged 1.4 and 1.2 square miles for cows and bulls, respectively. In Finland, Loisa and Pulliainen (1968) followed a cow and 1 year-old calf for nearly 1 month during late winter within an area of slightly under 1 square mile. During this period the same route was covered twice, and their old tracks were often used on the second circuit.

The movement pattern of the cow and calf tracked during winter in the present study corresponds to those of 2 cows (an adult and a yearling) radio tracked in northeastern Minnesota by Van Ballenberghe and Peek (1971:64-67), who concluded that winter home ranges consist of a series of high-use areas connected by wanderings of varying distances. They suggested that part of this movement may have been the result of the road system in that area. Two additional adults (a cow and a bull) radio tracked for shorter periods during winter by Van Ballenberghe and Peek (1971:67) used small areas, similar to most animals in this and other studies cited. It appears that most moose have limited winter home ranges with a small percentage not following the general rule for one reason or another.

Movements Between Seasonal Ranges

Summer and winter home ranges of most migratory moose in Montana are separated by several miles. One marked calf observed by Knowlton (1960:164) moved over 6½ miles to a wintering area. Moose which leave the Gravelly Mountains to winter in the Centennial Valley travel at least 10-15 miles, while some animals which summer in the Centennial Valley apparently winter up to 50 miles distant in Idaho. Houston (1968:53) found that some migrants in Jackson Hole, Wyoming, moved at least 20 miles between summer and winter ranges. Barry (1961) reports moose in Canada's Northwest Territories summering as far as 108 miles from timbered portions of valleys where they apparently wintered. Phillips *et al.* (in press) found moose moving 9-21 miles between summer and winter home ranges in northwestern Minnesota.

Movements of instrumented bulls greatly increased during the rutting season, with no apparent pattern to these movements. Houston (1968:51) found increased movements of bulls at this time also, and Phillips *et al.* (in press) report that all bulls radio tracked during the rut left their "normal" home range and travelled over "strange" territory. The extent of rutting season movements may be related to both overall population density and density of breeding males. Houston (1968:51) suggests that the latter might also influence cow movements at this season. Phillips *et al.* (in press) suggest that a scarcity of receptive cows after most breeding is completed may have further increased bull movements.

Data from marked moose on the Lower Gallatin Study Area agree with those of Houston (1968:45-51) which showed that adult moose return to established summer and winter home ranges. Severe winters may force some migratory animals to use lower parts of winter home ranges than they would in normal or mild winters, as also reported by Houston (1968:49). Although based on meager data, Geist (1963:411) suggested that moose may return each year to accustomed summer range. Ritchie (1970:9) had data on marked moose in Idaho which suggested that individuals generally return to the same wintering areas each year. Phillips *et al.* (in press) found that movement patterns of individuals were very traditional, with several marked animals relocated in successive years less than 0.15 mile from where they had been 1 year earlier. LeResche and Davis (1971b) present data on marked Alaskan moose *(A. a. gigas)* which also suggest that individuals use the same specific areas seasonally year after year, and that they follow stereotyped circular migration paths for more than 1 year. Peterson (1955:113) cautions that ecological conditions and population pressure largely govern movements and home range size. However, Goddard (1970:444) found no evidence that marked moose moved from a relatively unhunted to an adjacent heavily hunted area. This suggests that tradition probably has more to do with movements of individuals than population pressure. A possible exception to this would be yearling animals prior to home range establishment.

FOOD HABITS

Like most large ungulates, moose have the capability of sufficiently decimating forage supplies to reduce their own populations through decreased productivity and malnutrition losses (Murie 1934, Aldous and Krefting 1946, Krefting 1951). Before moose can be effectively managed the interaction between moose populations and their habitat, especially food relations, must be understood.

Moose food habits have been extensively examined in Montana. Prior studies (McDowell and Moy 1942, Knowlton 1960, Peek 1961, Smith 1962, Jonkel 1963, Dorn 1969, and Stone 1971) have provided food habits data from general observations, analysis of over 200 moose rumen samples and feeding site examinations recording nearly 170,000 instances of plant use by moose. In addition, studies of Shiras moose in nearby states (McMillan 1953, Harry 1957, Houston 1968, Ritchie 1970, 1972, Wilson 1971) offer food habits data applicable to some Montana ranges or of value for comparative purposes.

Moose are primarily browsers and feed on stems and leaves of a large variety of trees and shrubs. Winter feeding is primarily by browsing accessible stems of both deciduous and coniferous trees and shrubs. Larger branches may occasionally be broken to reach desired browse (Geist 1963:387-388). In summer, browsing is primarily on leaves though some stems are taken. Grass and forbs are taken by grazing, and occasionally moose must kneel to reach low growing plants, most commonly in early spring as plant growth commences.

In the following discussions, seasonal food habits data collected during the present study, together with some previously unpublished rumen sample data obtained from the files of the Montana Fish and Game Department's Wildlife Laboratory at Bozeman, are summarized by study area. In addition, some previously published rumen sample data were obtained and re-analyzed according to seasonal breakdowns used in this study, or to incorporate additional data. Although seasonal sample sizes from some areas may be insufficient to precisely express food habits, they should be indicative of important food species and seasonal trends.

Lower Gallatin Study Area. Seasonal food habits on the Lower Gallatin Study Area were determined from analysis of 60 rumen samples and from 75 feeding site examinations totaling 21,102 instances of plant use. Seasonal use of plant species comprising at least 5 percent of the total use in any one season is shown in Table 7, along with the total percentage comprised by each major forage class. Browse formed the bulk of the diet in all seasons, ranging from just over 66 percent of the summer total to over 99 percent in winter. Grasses and grass-like plants made up less than 1 percent of the total in all seasons.

Fall (Mid-September through November)-Early fall food habits (Table 7) may not be indicative of the overall moose diet on the study area at this time, due to the small sample size and possible sampling bias (five of seven feeding sites examined were from the same general area in 1 year). However, they may indicate important forage classes and provide a general idea of food habits at this time.

Fall rumen samples represent all parts of the study area and the entire fall period, making them the best indicator of fall food habits for this area. Willow, Douglas-fir, alpine fir and huckleberry (*Vaccinium* spp.) comprised 21.8, 18.0, 15.6 and 13.2 percent of the aggregate volume of these samples, respectively. Groundsel *(Senecio* spp.) and thistle *(Cirsium* spp.) were the only other items that approached or exceeded 5 percent of the total volume. Although desirable, separation of the data by vegetation type was not always feasible. Where vegetation types were known, huckleberry and alpine fir were most important in rumens from the spruce-fir type, while Douglas-fir, willow and huckleberry were most important in the Douglas-fir and lodgepole pine types. Willow, red dogwood and *Populus* spp. were important in the aspen and cottonwood types, and willow was used most heavily in the willow type.

Table 7. Seasonal food habits of Shiras moose on the Lower Gallatin Study Area as determined by rumen sample analysis and feeding site examination, 1965-1972. Only species comprising at least 5 percent of the total for one season are included. T denotes less than 0.05 percent. Species comprising less than 5 percent in all seasons are listed in Appendix Table 3.

Plant Species and Forage Class	EARLY FALL (Late Sept.)	FALL (Sept. — Nov.)	WINTER (Dec. — March)		SPRING (April — Mid-June)	SUMMER (Mid-June — Mid-Sept.)
	(7-2,830)[1]	(50)[2]	(40-11,834)[1]	(8)[2]	(20-4,770)[1]	(8-1,668)[1]
Abies lasiocarpa	--	34/15.6	12/2.0	12/2.9	--	--
Acer glabrum	29/5.9[3]	2/0.1	22/5.6	12/5.0	10/0.4	--
Alnus incana	71/43.6	14/2.6	10/0.2	--	5/T	--
Amelanchier alnifolia	--	4/T	40/11.1	12/0.3	40/7.3	--
Cornus stolonifera	--	12/1.7	32/25.0	25/8.1	15/3.6	--
Populus spp.	--	10/0.7	38/5.4	25/1.7	10/0.6	--
Prunus virginianus	--	12/3.0	40/7.5	25/1.6	15/4.7	--
Pseudotsuga menziesii	--	56/18.0	8/2.6	75/40.0	15/0.3	--
Ribes spp.	29/1.5	40/2.0	35/4.7	50/5.3	35/14.8	12/0.1
Rosa woodsii	14/0.7	12/0.2	12/0.4	12/0.2	20/1.2	25/8.2
Rubus parviflorus	14/1.9	--	--	--	--	25/19.7
Salix spp.	57/8.9	76/21.8	62/32.8	88/30.4	50/44.3	75/36.2
Spiraea betulifolia	71/9.0	--	--	--	10/1.3	12/0.5
Vaccinium scoparium	43/16.8	--	--	--	20/12.8	--
Vaccinium spp.	--	60/13.2	--	--	5/0.1	--
Total Browse	100/92.8	100/86.6	100/99.8	100/99.2	100/97.2	88/66.4
Epilobium angustifolium	--	--	--	--	5/0.6	50/28.4
Senecio spp.	43/1.1	10/6.7	--	--	--	25/2.5
Total Forb	57/7.2	35/12.6	2/0.2	12/0.2	42/2.2	88/33.6
Total Grass, Grass-Like	--	42/0.7	--	25/0.6	10/0.5	--

[1]Feeding sites - Instances of use.
[2]Number of rumens examined
[3]Percent frequency of occurrence/Percent of total identifiable forage.

Winter (December through March)-Winter food habits on the Lower Gallatin Study Area were determined from 40 feeding sites recording 11,834 instances of plant use, and 8 rumen samples. While feeding sites covered most vegetation types and major drainages in the study area, the majority were from the accessible, lower portions of the study area. Because of unequal sampling of available vegetation types, serviceberry and red dogwood were probably less important, and Douglas-fir was probably considerably more important, than indicated by feeding site examinations.

Within the limitations of sample sizes and methods, important winter forage species for moose on the Lower Gallatin Study area were willow, Douglas-fir, red dogwood, mountain maple, *Ribes* and serviceberry. Alpine fir was extensively utilized by, and important only to, the relatively small number of animals which wintered at higher elevations in the spruce-fir type.

Cottonwood appeared to be very palatable and readily taken, but was largely unavailable due to the size of the trees. Use noted on this species was primarily on branches of wind thrown trees, with minor use on basal sprouts.

Spring (April through mid-June)-Browse continued to make up over 97 percent of the diet through spring, as determined from 20 feeding sites totaling 4,770 instances of plant use. Willow remained the most important single item, comprising over 44 percent of the total. Low red huckleberry, serviceberry and *Ribes* were other important species in the spring diet. Several species of green forbs were taken, but they remained unimportant as a group, partly because they appeared at the same time that new green leaves appeared on shrub species. The latter are available in much greater volume, are easier for moose to reach, and are apparently more palatable than many forbs. A single spring rumen contained the following species and approximate percentages: willow, 84; red dogwood, 12; alder, 4; and forbs, 1.

Summer (Mid-June through mid-September)-Moose were very difficult to observe during the summer months, and in many instances when they were found, no evidence of recent feeding could be detected. Summer food habits data included only 8 feeding sites totaling 1,668 instances of use. This was the only season in which forbs assumed importance, comprising nearly one-third of the overall diet. Fireweed *(Epilobium angustifolium)* comprised most of the forb portion of the diet, with the remainder divided between several other species. Willow was still the single most important item in the diet. Other important browse species were thimbleberry *(Rubus parviflorus)* and rose. Utilization of the latter two species was on new stems and young plants which were essentially non-woody, more resembling forbs at this season. One summer rumen from a streambank willow area contained approximately 99 percent willow and 1 percent unidentified forbs.

Upper Madison Study Area. Food habits on the Upper Madison Study Area were determined from 29 rumen samples and 26 feeding site examinations totaling 5,517 instances of use (Table 8). Fall and winter use of major forage categories was very similar to that for the lower Gallatin. Spring and summer use of forbs on the upper Madison was greater than

Table 8. Seasonal food habits of Shiras moose on the Upper Madison Study Area as determined by rumen sample analysis and feeding site examination, 1965-71, plus 4 fall and 6 winter rumens collected earlier (1956-1963). Only species comprising at least 5 percent of the total for one season are included. T denotes less than 0.05 percent. Species comprising less than 5 percent in all seasons are listed in Appendix Table 3.

Plant Species and Forage Class	FALL (Oct.-Nov.)	WINTER (Dec. — Mid-April)		SPRING (Mid-April — Mid-June)		SUMMER (August)
	(11)[1]	(16)[1]	(13-2,871)[2]	(2)[1]	(10-2,435)[2]	(3-211)[2]
Abies lasiocarpa	9/0.6	25/2.3	23/12.0	--	--	--
Betula glandulosa	--	--	--	--	10/7.3	--
Pinus contorta	64/2.1	50/9.0	--	--	--	--
Populus tremuloides	18/4.9	31/0.5	23/5.1	--	--	--
Prunus virginiana	9/T	--	8/7.0	--	--	--
Pseudotsuga menziesii	18/3.1	69/9.3	--	--	--	--
Ribes spp.	9/T	19/0.3	31/6.3	--	40/7.1	--
Salix spp.	82/64.7	88/71.6	77/62.7	100/99.0	80/64.3	100/45.0
Vaccinium spp.	36/10.0	--	--	--	--	--
Total Browse	100/90.1	100/99.4	100/98.9	100/98.9	80/82.2	100/45.0
Epilobium angustifolium	--	--	--	--	--	67/18.5
Geranium viscossissimum	--	--	--	--	20/4.9	100/34.6
Lupinus spp.	27/6.2	--	--	--	--	--
Mertensia spp.	--	--	--	--	40/9.3	--
Total Forb	82/8.8	25/0.5	8/1.1	100/1.0	70/17.5	100/54.1
Total Grass, Grass-Like	36/1.1	13/T	--	50/0.1	30/0.3	33/0.9

[1]Number of rumens examined.
[2]Feeding sites -- instances of use.
[3]Percent frequency of occurrence/Percent of total identifiable forage.

found on the lower Gallatin. Willow was the single most important food item in all seasons, comprising from 45 to over 70 percent of seasonal totals.

Fall (October, November)-Fall food habits were determined from 11 rumen samples. Browse made up over 90 percent of the total, with over two-thirds of all browse being willow. Huckleberry and aspen were the only other browse species approaching or exceeding 5 percent of the fall total. Lupine *(Lupinus* spp.) was the only forb of importance.

Winter (December through mid-April)-Sixteen rumens and 13 feeding sites totaling 2,871 instances of use were available from winter. Douglas-fir and lodgepole pine each occurred in at least half the rumen samples, but neither was used at feeding sites. Similarly, chokecherry was relatively important (based on high use at one feeding site) at feeding sites, but was absent from rumen samples. Overall, willow, Douglas-fir and alpine fir were the most important winter forage species in this area, with aspen, *Ribes* and possibly lodgepole pine and chokecherry of limited importance. Forbs, and grass and grass-like plants were very minor dietary components by both methods.

Spring (mid-April through mid-June)-Spring food habits were determined from 10 feeding sites recording 2,435 instances of use, supplemented by two rumen samples. Browse, primarily willow, comprised over 82 percent of the total instances of use with scrub birch, *Ribes* and honeysuckle *(Lonicera* spp.) being secondarily important, and the only other browse species utilized. Bluebell *(Mertensia* spp.) and sticky geranium *(Geranium viscossissimum)* were the only important forbs although several species were utilized. Both spring rumens were from the willow type, and willow comprised 99 percent of the aggregate volume.

Summer (mid-June through mid-September)-Summer data for this area include only three August feeding sites totaling 211 instances of use. Willow, sticky geranium and fireweed comprised 45.0, 34.6, and 18.5 percent of the total instances of use from this small sample.

Other Montana Areas. A considerable volume of Shiras moose food habits data is available from other Montana studies. Most of this information has been published, primarily in theses and Federal Aid Job Progress Reports. In some instances additional data have been obtained and incorporated into the previously published data presented here.

ABSAROKA AREA - McDowell and Moy (1942) studied moose food habits in the Absaroka Mountains just north of Yellowstone National Park, estimating the amounts of different foods eaten by observing feeding animals with binoculars. Willows were the most important food item, with three species, *S. subcoerulea, S. pseudocordata* [*S. drummondiana and S. novae-angliae* of Dorn (1970b)] and an unidentified species listed. Other important summer browse species listed were buffaloberry *(Shepherdia canadensis)*, huckleberry, bearberry *(Arctostaphylos uva-ursi)*, honeysuckle, elderberry *(Sambucus melanocarpa)*, and snowberry. In all, McDowell and Moy (1942) list 26 browse, 21 forb (including 3 aquatics), and 24 grass and grass-like species as being taken by moose during summer in this area. They estimated the monthly percentage of the total diet that each major forage class comprised between June and October. Browse led the list in all months, accounting for 64 (June) to 93 (October) percent of the total diet for individual months. Ranges for other forage groups were: forbs, 2 to 14 percent; aquatics, 2 to 5 percent; and grass and grass-like plants, 3 to 20 percent.

GRAVELLY-SNOWCREST AREA - Knowlton (1960) quantified summer, fall and winter food habits of moose in the Gravelly and Snowcrest Mountains. These data, supplemented by 26 additional fall rumen samples, are presented in Table 9.

Summer (mid-June through August)-Summer food habits were based on 34 feeding site examinations totaling 6,770 instances of use. Forbs comprised over 70 percent of the total use, with sticky geranium providing the bulk of the forb use. Willow and *Ribes* comprised approximately 19 and 5 percent of the total use, respectively, and were the only important browse species used in summer. Use of grass and grass-like plants was insignificant.

Although his data are not quantitatively presented, Peek (1961:11-12; 1963:229-230) reported that summer food habits in this area in 1959 and 1960 were markedly different from those found by Knowlton in 1958. He also found a decided preference for browse, mainly willow, during the summers of 1959 and 1960. Some sampling bias, particularly in 1958, apparently occurred (Peek, personal communication), and Knowlton (1960: 168) pointed out that difficulty in finding feeding animals in timber types might have precluded recording substantial browse use. However, Peek (1961:11-12) also felt that forbs may be preferred in wet summers (1958), when they would possibly be more numerous and remain succulent longer, with browse being used more in dry summers (1959 and 1960).

Fall (October, November)-Knowlton (1960) presented data from 14 fall rumen samples, which were supplemented by the addition of 26 rumens collected in 1959 (Table 9). The four most important browse species did not change with the increased sample. However, percentages and order of importance did change, and three species were added to the list of minor fall food items. Browse accounted for nearly 96 percent of the total fall diet. Alpine fir, aspen, willow and *Ribes* were most important, in that order. Only two forbs were identified, each comprising less than three percent of the total fall sample. Grass and grass-like plants were again insignificant.

Winter (December through March)-The same four browse species continued to be the most important dietary components during early winter while most animals remained above 7,000 feet in elevation (Table 9). However, willow comprised over two-thirds of the diet, followed, in order of importance, by alpine fir, *Ribes* and aspen, each of which totaled less than 10 percent of the diet. Forbs and grass and grass-like plants were insignificant during this period.

Table 9. Seasonal food habits of Shiras moose in the Gravelly-Snowcrest area as determined by rumen sample analysis and feeding site examination, 1958-1960. Only species comprising at least 5 percent of the total for one season are included. T denotes less than 0.05 percent. Species comprising less than 5 percent in all seasons are listed in Appendix Table 3. Data are from Knowlton (1960) plus 26 additional fall rumen samples.

Plant Species and Forage Class	SUMMER (34-6,770)[1]	FALL (40)[2]	EARLY WINTER (Above 7,000 feet) (13-14,540)[1]	LATE WINTER (Below 7,000 feet) (6-17,496)[1]
Abies lasiocarpa	--	90/27.0	9.6	--
Alnus tenuifolia	--	--	0.5	10.7
Eleagnus commutata	--	--	--	26.6
Populus tremuloides	1.7	38/25.4	4.3	0.6
Ribes spp.	5.0	70/14.5	8.9	0.2
Salix spp.	19.3	72/24.6	67.4	59.2
Total Browse	28.6	100/95.9	96.9	100.1
Geranium viscossissimum	64.2	--	--	--
Total Forb	70.6	70/3.6	2.9	T
Total Grass, Grass-Like	0.6	68/0.5	0.2	--

[1]Feeding sites -- instances of use
[2]Number of rumens examined
[3]Frequency of occurrence/Percent of total identifiable forage for Fall, percent of total forage used for other seasons.

Late winter food habits (when moose were below 7,000 feet in elevation) determined by Knowlton were based on six feeding sites totaling 17,497 instances of use. Browse formed 100 percent of the late winter diet and willow was again the single most important item, forming almost 60 percent of the total. Silverberry *(Eleagnus commutata)* and alder comprised nearly 27 and 11 percent of the total, respectively, with no other species being important.

RED ROCK LAKES NATIONAL WILDLIFE REFUGE - This area is located just south of the Gravelly-Snowcrest area, and moose food habits were studied there by Dorn (1969), with emphasis on moose-cattle competition.

Summer (mid-June through mid-September)-Browse accounted for over 98 percent of the summer moose diet determined by Dorn (1969) from 40 feeding site examinations totaling 36,812 instances of use (Table 10). Willow formed over 80 percent of the total diet, with *S. novae-angliae, S. geyeriana* and *S. phylicifolia* [nomenclature follows Dorn (1970b), and differs from that presented by Dorn (1969) in some instances], accounting for 58.1, 9.6 and 6.7 percent, respectively. Scrub birch was the only other important summer food item, forming 11.8 percent of the total.

Fall (October, November)-Fall food habits reported by Dorn (1969:22) were based on four rumen samples he collected, and four collected by Fish and Game Department personnel in years prior to his study. Seven additional rumen samples were subsequently obtained. Willow accounted for 89 percent of the fall diet, being the only important item. Eight other species brought the browse total to 94.3 percent of the aggregate volume. Most samples were obtained in the willow type, while one was from the upland timber and at least three were from animals moving between the willow and Douglas-fir types. Contents of several rumens from the willow type indicated that these animals had also been using upland timber types.

Winter (December through March)-Browse accounted for 99.8 percent of all forage used in winter (Dorn 1969:22), based on 32,480 instances of use at 35 feeding sites. *Salix novae-angliae, S. phylicifolia, S. bebbiana* and *S. geyeriana* accounted for 25.0, 24.2, 15.4 and 10.5 percent, respectively, of all use. Use of *S. phylicifolia,* the shortest species, decreased during the deep snow period, while use on the three taller species increased. *Salix wolfii* was important in early winter while available above the snow. Based on small samples, aspen and rose were important in the aspen type, and aspen, mountain maple, apline fir and Scouler willow were important in the Douglas-fir type.

ROCK CREEK, GRANITE COUNTY-(Fall and Winter)-Two investigators (Smith 1962 and Stone 1971) have presented data on fall and/or winter food habits of moose in Granite County's Rock Creek drainage. Original rumen sample data was recalculated to get seasonal figures. Because of differences in presentation, winter feeding site data from these two studies could only be compared on a monthly basis (Table 11). Browse formed nearly 84 percent of the total fall diet with forbs and grass

Table 10. Seasonal food habits of Shiras moose on the Red Rock Lakes National Wildlife Refuge as determined by rumen sample analysis and feeding site examination 1958, 59, 65, 68-71. Only species comprising at least 5 percent of the total for one season are included. T denotes less than 0.05 percent. Species comprising less than 5 percent in all seasons are listed in Appendix Table 3. Data are from Dorn (1969) plus 7 additional fall rumens.

Plant Species and Forage Class	SUMMER (40-36,812)[1]	FALL (15)[2]	WINTER (35-32,480)[1]
Betula glandulosa	11.8[3]	--	0.7[3]
Salix bebbiana	2.6	--	15.4
Salix geyeriana	9.6	--	10.5
Salix myrtillifolia	58.1	--	25.0
Salix planifolia	6.7	--	24.2
Salix spp.[4]	4.1	100/89.0[3]	11.0
Total Browse	98.3	100/96.4	99.8
Total Forb	1.5	53/3.1	T
Total Grass, Grass-Like	0.2	47/0.5	0.1

[1]Feeding sites -- instances of use

[2]Number of rumens examined

[3]Figures for Summer and Winter are percentages. Fall figures are frequency of occurrence/Percent of total identifiable forage.

[4]Includes all species of *Salix* reported by Dorn (1969) which are not included above.

Table 11. Fall and winter food habits of Shiras moose in the Rock Creek Drainage, Granite County, as determined by rumen sample analysis and feeding site examination, 1958-60, 1971. Only species comprising at least 5 percent of the total for one season are included. T denotes less than 0.05 percent. Species comprising less than 5 percent in all seasons are listed in Appendix Table 3. 1960 and 1971 data are from Smith (1962) and Stone (1971), respectively.

Plant Species and Forage Class	FALL (Sept. - Nov.) (21)[1]	WINTER (Dec. - Jan.) (7)[1]	(January[2]) 1960	(January[2]) 1971	(February[2]) 1960	(February[2]) 1971	(March[2]) 1960	(March[2]) 1971
Cornus stolonifera	33/12.3[3]	29/1.7	--	--	--	10.3[3]	16.0	--
Lonicera spp.	5/5.0	--	1.3	1.3	1.8	1.6	1.7	1.0
Populus tremuloides	19/5.8	14/3.3	--	2.5	--	0.6	--	0.3
Pseudotsuga menziesii	24/2.2	100/11.1	--	--	1.4	T	0.3	--
Rhamnus alnifolia	10/5.8	--	--	--	--	--	--	--
Salix spp.	71/31.2	100/67.6	94.9	91.9	89.9	80.2	76.5	86.6
Shepherdia canadensis	10.0.4	43/6.9	--	T	T	--	--	--
Vaccinium spp.	48/5.9	--	--	--	--	--	--	--
Total Browse	100/81.8	100/99.1	100.0	99.2	103.7	98.4	100.0	99.9
Total Forb	57/9.0	57/0.3	0	0.7	0	1.2	0	T
Total Grass, Grass-Like	71/7.6	100/0.6	0	0	0	0	0	0

[1]Number of rumens examined. Rumen samples were collected by Smith (1962) and the original data re-tabulated for this presentation.

[2]Instances of use for 1960 were: January 1,410; February and March (combined) 5,878; Monthly totals for 1971 were 9,422, 6,539 and 11,947 for January, February and March, respectively. February 1960 figures given by Smith (1962) totaled over 100 percent.

[3]Figures are frequency of occurrence/percent of total identifiable forage for rumen samples and percent of total instances of use for feeding sites. Moss and fungus together formed slightly over 1 percent of the volume of fall rumens.

and grass-like plants forming approximately 9 and 6 percent, respectively. The most important fall food was willow, followed by red dogwood, huckleberry, aspen, buckthorn *(Rhamnus alnifolia)* and honeysuckle, in that order.

Winter food habits were based on seven December and January rumen samples and 35,196 instances of plant use at over 50 feeding sites from January through March. Both Smith (1962) and Stone (1971) confined their winter studies primarily to the willow type. Willow formed the bulk of the use at feeding sites in both studies, and no other browse species formed 5 percent of the winter diet with the possible exception of red dogwood in 1960. Smith (1962:3-4) stated that herbaceous plants, including various grasses, sedges and forbs, were snow-covered while moose were on winter range, and he recorded no use on forage classes other than browse. Stone recorded minor use on forbs and stated (Stone 1971:28) that grass was sometimes taken, but in unknown amounts. Grass was not included in his list of utilized plants. Winter rumen contents indicated that all samples were from the willow type. Presence of a relatively high percentage of Douglas-fir in all winter rumen samples indicates that most moose wintering in the willow type in this area probably make extensive use of adjacent upland timber types for food as well as cover. Presence of other plant species characteristic of uplands (Table 11) strengthens this conclusion. This use is not apparent in the feeding site data which may represent a very important sampling bias which under-emphasizes the importance of upland types to moose wintering primarily in willow types. Douglas-fir is probably a more important winter food in this area than indicated by the feeding site data, and would undoubtedly be much more important to animals wintering away from willow flats.

NORTH FORK OF FLATHEAD - Seventeen moose rumen samples were collected from the spruce-fir type in this area in the fall of 1962 (Jonkel 1963). When the original data were recalculated the results differed slightly from that presented by Jonkel (1963:4). Browse was the most important forage class, forming approximately 99 percent of the aggregate volume. The single most important species was myrtle pachistima *(Pachistima myrsinites)* which formed over 75 percent of the total. Willow and *Populus* spp. formed approximately 13 and 5 percent of the total, respectively. Other species utilized appear in Appendix Table 4. A single winter sample obtained about 20 miles from the area where fall samples were collected had Douglas-fir, larch *(Larix occidentalis)* and cedar *(Thuja plicata)* comprising 78, 8 and 8 percent of the plant material, respectively.

SOUTH BIGHOLE AREA - Moose in this area winter in the willow type which intermingles with numerous hay fields. Haystacks in these fields are annually damaged by moose to some extent due to the poor condition of the willow (Stevens 1967:14). A special limited moose hunt (15 permits) was held in this area in January, 1967, to alleviate haystack damage. Browse formed only about 75 percent of the aggregate volume of 10 rumen samples obtained during this hunt, with willow being the only important species. Forbs were unimportant, but grasses and grass-like species formed just over 25 percent of the total. Most, if not all, of the latter was probably obtained from haystacks since these plants were generally unavailable at this time due to snow depth. Other species utilized are shown in Appendix Table 4.

MISCELLANEOUS AREAS - Additional rumen samples were obtained from many areas throughout southwestern Montana. These will be presented by habitat type rather than locality, both to increase sample size and provide a more accurate representation of food habits.

Eleven fall-early winter (mid-September through early December) rumen samples were obtained from the Douglas-fir type. These were from widely separated areas, including the Boulder River south of Big Timber (one sample), several tributaries of the Yellowstone River south of Livingston (five), the Bridger Mountains (three), the West Fork of the Madison River (one), and from southwest of Monida (one). Browse formed over 96 percent of the aggregate volume, with Douglas-fir, willow, huckleberry and *Ribes* comprising 45.4, 19.1, 10.9 and 6.0 percent of the total volume, respectively. Nine other browse and six forb species, plus grass and grass-like plants made up the remainder (Appendix Table 4).

Four fall rumens were collected from the willow type, three from the East Fork of the Bitterroot River and one from southwest of Butte. Willow comprised 99.5 percent of the total volume of these samples, with *Populus* spp., lodgepole pine, moss and grass and grass-like plants also identified. Red dogwood formed over 94 percent of the volume of two fall rumens from the cottonwood type. Other species utilized, in order of importance, were thistle, cottonwood and willow.

Discussion of Food Habits

Several factors influence the amounts of various plant species moose utilize as food. Most important are availability, palatability and adaptation of moose as discussed by Dorn (1970a:562-563). Evaluating absolute importance of plant species is difficult because of the interrelationships of these factors.

General agreement exists between the Montana data and that for Shiras moose from other areas in regards to relative seasonal importance of forage classes (Table 12).

Browse was the most important forage class in all seasons, and in all Montana areas studied and reviewed here, with the exception of one summer (1958) in the Gravelly-Snowcrest area as discussed above. Summer data from the Upper Madison Study Area also showed greater use of forbs than browse but were too few to provide an accurate indication of summer food habits in this area.

Most previous Shiras moose studies have shown that various willow species provide the majority of the browse diet, especially in winter. However, this and other recent studies have investigated Shiras moose food habits in a variety of vegetation types, revealing that other browse species assume importance where willow is of limited availability. These different types may cover extensive areas of important moose range where

Table 12. Relative seasonal importance of major forage classes to Shiras moose in various parts of their range.

AREA[1]	FALL	WINTER	SPRING	SUMMER
	SEASON			
MONTANA				
Lower Gallatin	87-93/7-13/0[2]	99+/<1/<1	97/2/<1	66/34/0
Upper Madison	90/9/1	99/1/0	82/18<1	45/54/1
Gravelly-Snowcrest	96/4/<1	97+/3/<1	-	29/71/<1
Red Rock Lakes	96/3/<1	99+/<1/<1	-	98/2/<1
Rock Creek	82/9/8	99+/<1/<1	-	-
N. Fk. Flathead	99/<1/<1	-	-	-
South Big Hole	-	75/<1/25	-	-
YELLOWSTONE PARK	-	-	-	75/18/7
JACKSON HOLE, WYO.	-	99+/<1/<1	-	-
JACKSON HOLE, WYO.	91/7/2	99/<1/<1	62/28/10	79/17/4
SOUTHEAST IDAHO	79-95/4-5/<1-16	99+/<1/0	-	-
NORTHEAST UTAH	-	100/0/0	-	-

[1]Montana areas are discussed in the text; the other areas, in the order listed are from McMillan 1953, Harry 1957, Houston 1968, Ritchie 1970 and 1972, and Wilson 1971.
[2]Percentages of: browse/forbs/grass and grass-like plants.

willow is poorly represented, such as the Lower Gallatin Study Area. Also, some browse species appear to be more palatable to moose than willow, at least in some seasons, as evidenced by heavier use on these when they occurred with willow. Species in the latter category on the Lower Gallatin Study Area included red dogwood and possibly serviceberry. In many habitat types willow was taken when available, but was not the most important fall and/or winter forage due to its limited availability or to the greater relative abundance of more palatable species.

Mountain ash *(Sorbus scopulina)*, reportedly a highly preferred food (Peterson 1955:135-136 and 148-149, Aldous and Krefting 1946:305), especially on eastern ranges, occurred on the Lower Gallatin Study Area as rare, scattered plants. Moose browsed some of these heavily each year, while others were not used. Its limited availability makes it unimportant to moose in this area, and probably in other Montana areas. Houston (1968) listed mountain ash among those species receiving 1-14 percent of the use in summer, and over 15 percent in fall, on the spruce-fir type in Jackson Hole, Wyoming.

Silverberry apparently is also highly preferred (Harry 1957; Knowlton 1960:168), but was not observed on the two major study areas covered by this study. It is one of the key browse species in the Gravelly-Snowcrest area, and where available in any quantity is probably important to wintering moose.

Whether the heavy use of myrtle pachistima in northwestern Montana is a function of availability or palatability is unknown at this time. Probably it is a combination of these factors. Myrtle pachistima did not occur on areas included in this study, and apparently was absent from areas covered by the other Montana studies cited. It is another example of heavier use of a more available and/or more palatable species than willow. Hatter (1948) (cited by Peterson 1955:148-149) included this species in a list of the most palatable food plants in central British Columbia, and Houston (1968) recorded minor use (1-14 percent) of this species in the aspen type in both spring and summer.

Bitterbrush *(Purshia tridentata)* is apparently highly preferred by moose and taken whenever available (Harry 1957; Houston 1968; Ritchie 1970, 1972). This species is probably of little importance to moose in Montana due to its absence or limited availability in most areas inhabited by moose. It could conceivably assume local importance in some areas with an increase in moose populations, and moose-deer competition might occur in situations where this happens.

Aquatics are reportedly important summer foods in many areas (Peterson 1955:118-120; de Vos 1958:136-139; Ritcey and Verbeek 1969; Van Ballenberghe and Peek 1971:67; and others), but they appear to be unimportant to Montana moose. On the Lower Gallatin Study Area only 1 percent of the summer observations were in the aquatic type (Table 1), while the small summer sample from the Upper Madison Study Area included no observations in this type. McDowell and Moy (1942) estimated that aquatics comprised 2 to 5 percent of the monthly diet between June and October just north of Yellowstone National Park. Within the Park, McMillan (1953:104) found that aquatic plants constituted a minor part of the summer moose diet. Of all Montana study areas, the one studied by Dorn (1969) apparently has the best and most extensive aquatic habitat, with a large amount of shoreline adjacent to shallow water and abundant aquatic vegetation. However, Dorn (1969:23-24) reports only two brief feeding periods on aquatics. The most abundant aquatic species in this area *(Potamogeton richardsonii)* corresponds to the most important aquatic food in Peterson's (1955:140) Ontario study.

Aquatic feeding sites accounted for only about 3 percent of the total instances of use in Jackson Hole, Wyoming, ranging from less than 1 percent in winter to approximately 8 percent in fall (computed from Houston 1968:27-28 and 98-99). Two and 4 percent of the November-December and March-April observations, respectively, on the Upper Madison Study Area were in the aquatic type (Table 3). Tracks and observations both indicated that many of these animals were using open, flowing streams as travel routes during deep snow periods with little or no actual feeding on aquatics. Some individuals undoubtedly utilized aquatics in these situations, but they did not account for a significant part of the overall winter diet.

Limited availability apparently accounts for the low use of aquatics by Shiras moose, but it also appears that little use may be made of aquatics if abundant willow browse is available in summer (McMillan 1953:104;

Dorn 1969:24). This might be related to the efficiency with which moose can strip leaves from willows as opposed to feeding in shallow water. Other factors, such as habit, may also contribute to the low use of aquatics in such situations. Telfer (1967:422) reported that aquatics are scarce in areas of Nova Scotia where moose are common.

Utilization and condition trends of important forage species.

Condition trends and estimates of utilization of important forage plants provide a basis for determining whether range carrying capacity is being exceeded. Since available winter range is limited in mountainous areas, winter is normally the season when available forage is also most limited. Because the winter forage supply determines maximum moose populations, perpetuation of these forage sources becomes critical.

Plant condition, based on degree of hedging and decadence (25 percent or more of the crown dead), and percentage utilization of the current year's leaders were determined for important moose forage species on approximately 90 browse transects (Cole 1959) established in 1967 or earlier. Willow was the key species on most transects, with aspen, scrub birch, silverberry, red dogwood, serviceberry and chokecherry also sampled. Although all transects were not read annually, the time span covered was sufficient to indicate trends in plant condition. Since factors other than browsing (old age, disease, insects, etc.) account for some dead crown, the percent of plants severely hedged was probably a better indicator of condition than was the percent of plants decadent. Lonner (1972:55) also concluded that estimates of percent dead crown may have only limited value in assessing the effects of browsing on most browse species he studied on Montana big game ranges. Measured use on most transects was primarily by moose although mule deer *(Odocoileus hemionus)*, elk *(Cervus canadensis)* and domestic stock occasionally used some of the areas.

No satisfactory method of assessing browsing on fir has been devised. General observations (Stevens 1970:44 and this study) show that when available, use of alpine fir and Douglas-fir was often heavy. Availability of Douglas-fir is limited on many lower elevation winter ranges. Winter utilization of alpine fir appears to be limited to small areas where one or a few animals are restricted by deep snow during winter. In such situations nearly all available browse is utilized and these areas may be unsuitable for moose for many years (Stevens 1970:44). Houston (1968:30) reported only a small percentage of alpine fir trees browsed, but that those browsed were often heavily used.

Relationship of Snow to Browse Utilization

Snow is the single most important weather factor influencing browse utilization and condition. Snow depth limits winter forage availability and also influences forage supplies by more or less regulating winter distribution and local moose densities. Duration of deep snow governs the length of time animals are restricted to winter ranges and snow depth may also limit general distribution of moose. Formozov (1946:133) indicated that moose are limited to forested areas of the USSR where average snow depth does not exceed 90 centimeters (approximately 36 inches). Peterson (1955: 109) reported that 30 inches of uncrusted snow presents little hindrance to moose. Kelsall (1969:308) found moose to be severely restricted by snow depths of 70 to 99 cm. (approximately 28-29 inches) in New Brunswick and cited Nasimovich (1955) as reporting Eurasian moose impeded by 60 to 70 cm. (approximately 24 to 28 inches) of snow, but traveling freely in 40 to 50 cm. (16 to 20 inches).

Pruitt (1959) reported thresholds of sensitivity to depth, density and hardness of snow among caribou which, if exceeded, resulted in the animals moving until snow of lesser hardness, density or thickness was encountered. Similar thresholds and reactions probably occur with moose.

Telfer (1970) in New Brunswick and Peek (1971) in Minnesota both reported late-winter moose activity largely restricted to dense conifer dominated stands, after spending fall and early-winter in more open types. In Quebec it was found (de Meules 1964) that moose also shifted to more dense types when snow depth reached 77 to 86 cm. (30-34 inches), and that they normally did not use areas where soft snow exceeded 107 to 122 cm. (42-48 inches). These late-winter shifts to more dense cover were largely responses to increased snow accumulation, but may have also occurred when a difference in snow depth, hardness and/or density occurred between open and dense canopy types (Peek 1971:42). Such shifts are generally into cover having less available food. Similar shifts apparently occurred on the Lower Gallatin Study Area but did not show up in the vegetation use data (Table 1). They are inferred from the fact that, especially in some years, numbers of moose observed on similar flights in late-March and April were substantially fewer (often less than half) than in January or earlier.

Verme and Ozoga (1971:21) have pointed out that extreme mid-winter severity is not, in itself, especially deadly for deer since they are physiologically "geared down" at this time. Physically devastating winters are those beginning unusually early and ending late, which subject animals to prolonged, unrelenting attrition. The same is undoubtedly true for moose and other ungulates whose winter forage supply and movements are largely restricted by depth and duration of snow cover.

Moose wintering on willow bottom areas often make heavy use of adjacent timber types for daytime bedding and also during winter storms (Knowlton 1960:166; Stone 1971:67). Dense types provide protection from wind, have more uniform temperatures and retard heat loss (Moen 1968).

In some areas relatively large numbers of moose winter in the spruce-fir type at high elevations where snow depths average 4 to 5 feet and may reach over twice that depth. In this situation moose feed almost exclusively on alpine fir and remain in a small area until most available browse is utilized (Stevens 1970:44). Lesser snow depth in the dense cover and the animal's activity in a restricted area compact the snow sufficiently to negate or reduce the adverse impact of the deep snow. At the same time, compaction of increased snow accumulations allows moose to obtain forage from previously unavailable higher branches. Later in the winter the snow becomes sufficiently settled and crusted to support moose, at least at night, enabling them to reach better forage areas. Since snow depth exceeding approximately 30 inches apparently restricts moose movements, duration of snow of at least this depth was used to rate the relative severity of winters during the period of study. This system was felt to better represent winter rigor than others, since available weather data are largely from points at some distance from study areas, generally at lower elevations where conditions are quite different than those experienced on the study areas. Measurements from three snow courses (Farnes 1970a and b, Farnes and Clagett 1971, Farnes and Shafer 1972) located on upper portions (6,600 to 6,860 feet) of the Lower Gallatin Study Area winter range were used to calculate annual and long term means for number of days with snow at least 30 inches deep. Measurements were begun on these courses in 1935, 1939 and 1964. All three are measured on or near the first of February, March and April, while two were also measured on or near the first of January, May and June and on or near May 15. Snow courses at Hebgen Dam and West Yellowstone, both initially read in 1934, were considered representative of winter conditions on the Upper Madison Study Area. These are read on or near the first of each month from January through May, inclusively. Records from most other snow courses near moose winter range areas do not date back far enough to allow calculation of long term means. Winters with ± 20 days of the long term mean value for snow depth 30 inches or greater were considered average (Table 13). Although snow density and hardness are also important factors, no measures of these parameters are available for comparison.

Table 13. Relative winter severity based on number of days with snow of 30 inch depth or greater. An average winter is one within ± 20 days of the long-term mean.

	LOWER GALLATIN STUDY AREA		UPPER MADISON STUDY AREA	
WINTER	NUMBER OF DAYS WITH 30 INCHES OR MORE SNOW DEPTH	RELATIVE SEVERITY	NUMBER OF DAYS WITH 30 INCHES OR MORE SNOW DEPTH	RELATIVE SEVERITY
1963-64	100	Average	87	Average
1964-65	104	Average	114	Severe
1965-66	0	Mild	0	Mild
1966-67	105	Average	115	Severe
1967-68	130+	Severe	86	Average
1968-69	71	Average	108	Severe
1969-70	142+	Severe	100	Average
1970-71	99	Average	115+	Severe
1971-72	38	Mild	97	Average
Mean	85	--	80	--

Transect Measurements

LOWER GALLATIN STUDY AREA - Seven willow transects were established on spring-summer-fall ranges on this area in 1965. The percentage of both severely hedged and decadent plants indicated only fair condition at that time. A downward trend in condition was noted through 1967. The slight improvement noted in both 1968 and 1969 became more marked in subsequent years (Table 14). Condition in 1972 still appeared to be lower than desirable.

Transects on moose winter ranges on this area included 11 on willow, five on aspen reproduction (under 8 feet tall), two on serviceberry and one each on red dogwood and chokecherry. Willow was in poor condition when transects were established in 1965. Condition declined through 1967 and then remained relatively stable through 1969. Slight improvement occurred in 1970, with increased improvement noted through 1972 (Table 14). Condition in 1972 was somewhat better than in 1965 but was still considered poor.

Using Houston's (1968:85) criteria of 50, 70 and 90 percent allowable utilization of willow during mild, average and severe winters, respectively, the moose population on the Lower Gallatin Study Area was probably excessive for the first 2 years, and near carrying capacity for most of the remainder of this study. However, excessive utilization occurred on most willow transects in the eastern half of the Study Area, while use on transects in the western half was generally below acceptable levels.

Condition trends of other forage species (Table 15) sampled on this area were similar to willow, with the exception of red dogwood which showed no improvement. Utilization of red dogwood remained high through 1972, while utilization of the other species generally decreased. Aspen, although utilized below reportedly excessive levels, was in poor condition throughout the study. It became progressively harder to find a sample of 25 aspen plants to read on most transects due to death of plants. Discussing small cutover areas, Smith *et al.* (1972:29-30) point out that intermixed unharvested timber may inhibit maximum sprouting, resulting in slow growing sprouts of poor vigor which are more susceptible to browsing damage. This appears to be the situation in most, if not all, aspen stands on the Lower Gallatin Study Area where aspen reproduction is primarily restricted to small, naturally occurring openings. Point-center-quarter measurements in five aspen stands on the Lower Gallatin Study Area in 1967 showed an average of 654 aspen per acre, 14 percent of which (92 per acre) were under 8 feet high. This contrasts to 30,000 to 50,000 sprouts produced per acre one year following aspen removal (Smith *et al.* 1972:10). By the fourth year after cutting, few treatments, including complete protection, retained over 25 percent of the initial number of sprouts, and all treatments, except unrestricted domestic sheep use, had ample sprouts for stand establishment (Smith *et al.* 1972:12).

Periodic cutting and/or prescribed burning in portions of these aspen stands on the Lower Gallatin Study Area would probably improve them for moose and other wildlife. Domestic livestock, if properly managed, could also benefit.

Table 14. Condition and utilization of willow on important moose ranges on the Lower Gallatin Study Area, as determined from seven transects on spring-summer-fall range, and eleven transects on winter range.

YEAR	PERCENT OF PLANTS SEVERELY HEDGED		PERCENT OF PLANTS WITH 25 PERCENT OR MORE OF CROWN DEAD		AVERAGE PERCENT OF CURRENT YEARS LEADERS UTILIZED	
	Winter Range	Spring-Summer-Fall Range	Winter Range	Spring-Summer-Fall Range	Winter Range	Spring-Summer-Fall Range
1965	60	44	57	28	80	39
1966	61	48	49	40	54	29
1967	80	72	62	66	65	61
1968	75	66	60	64	70	60
1969	83	59	61	55	78	60
1970	72	30	59	41	67	46
1971	63	32	56	29	68	42
1972	38	23	42	29	50	39

Table 15. Condition and utilization of important forage species other than willow on moose winter ranges, Lower Gallatin Study Area, as determined from five aspen*, two serviceberry, one red dogwood and one chokecherry transect.

YEAR	PERCENT OF PLANTS SEVERELY HEDGED				PERCENT OF PLANTS WITH 25 PERCENT OR MORE OF CROWN DEAD				AVERAGE PERCENT OF CURRENT YEARS LEADERS UTILIZED			
	Aspen	Service-berry	Red Dogwood	Choke-cherry	Aspen	Service-berry	Red Dogwood	Choke-cherry	Aspen	Service-berry	Red Dogwood	Choke-cherry
1965	--	--	80	--	--	--	40	--	--	--	83	--
1966	--	92	80	88	--	36	40	68	--	62	80	31
1967	69	100	100	92	61	100	52	84	50	50	76	40
1968	61	98	100	96	61	86	8	88	49	72	85	38
1969	78	96	96	96	86	62	28	88	63	84	84	43
1970	76	100	88	92	65	32	20	64	64	75	69	45
1971	53	98	92	80	43	36	12	68	59	83	88	45
1972	42	84	100	44	42	34	28	36	55	63	81	35

*Only plants less than 8 feet high were sampled.

UPPER MADISON STUDY AREA - Six willow transects were established on this area between 1963 and 1965: two in Beaver Creek and four on the major moose wintering area at the mouth of Grayling Creek. Plants on the two transects (one on each area) were in extremely poor condition when read in 1963. Beaver Creek transects remained in poor condition through 1967, after which they showed considerable improvement, especially in 1971 (Table 16). Utilization on these transects decreased from 1963 through 1968, remained relatively stable through 1970, and decreased markedly the following year. The upper part of this area was probably over-used in most years prior to 1970, with earlier improvement primarily restricted to lower Beaver Creek.

The increased number of transects on Grayling Creek in 1965 indicated fair range condition. Condition remained fairly stable through 1968, after which noticeable improvement occurred. Utilization on this area was light to moderate in all years. Condition on both areas in 1971 was considered good to excellent.

Overall, the area has probably been stocked below carrying capacity. The Big Sky Snowmobile Trail goes through the upper part of Cabin Creek and appears to have caused decreased use of this part of the drainage by wintering moose. Use has shifted to other parts of the area, and the overall effects are probably minimal. However, off-trail snowmobile use in upper Cabin Creek could be detrimental and should be prohibited.

OTHER SOUTHWESTERN MONTANA AREAS - Browse transects in other areas are more difficult to evaluate in terms of allowable annual utilization since winter severity cannot be rated in most of these areas. However, condition and utilization can indicate over-use, even when winter severity cannot be ascertained.

UPPER GALLATIN AREA - Transect measurements on this area date from 1957 (Table 17), and all transects have willow as the key species. Four to nine transects were read annually between 1957 and 1964, while 14 to 17 transects were read annually from 1965 through 1972. Excessive use apparently occurred on some transects in most years, and on others in at least some years. The presence of the Gallatin elk herd, its migration habit and often heavy utilization of browse during severe winters (Lovaas 1970) complicates the assessment of moose-browse relationships in this area. Lovaas (1970:31-37) described the winters of 1961-62 to 1964-65, inclusively, as severe, mild, mild and severe, respectively. Utilization on transects read in those years indicate excessive use only in the 1963-64 winter. The 1965-66 winter was probably mild in this area as it was to the north and south. Utilization generally reflected the mild winter, with only the West Fork transects showing slightly excessive use.

Gallatin River Bottom transects were within and adjacent to Yellowstone National Park and were used primarily by elk, with only minor use by moose; they were unimportant to moose during the period of measurement.

All Taylor Fork transects were used by moose, and three also received varying elk use. These transects remained in good to excellent condition, and were normally utilized near or below levels which would cause declining trends in condition.

Table 16. Condition and utilization of willow on important winter moose range on the Upper Madison Study Area, as determined from 4 transects in Grayling Creek and 2 in Beaver Creek.

YEAR	PERCENT OF PLANTS SEVERELY HEDGED		PERCENT OF PLANTS WITH 25 PERCENT OR MORE DEAD CROWN		AVERAGE PERCENT OF CURRENT ANNUAL GROWTH UTILIZED	
	Grayling Creek	Beaver Creek	Grayling Creek	Beaver Creek	Grayling Creek	Beaver Creek
1963*	100	100	100	96	25	82
1965	46	92	42	76	40	68
1966	56	96	70	94	28	62
1967	36	90	52	86	44	50
1968	42	62	69	78	34	43
1969	24	40	40	60	31	46
1970	1	38	22	30	13	44
1971	5	0	18	34	21	11

*Only one transect on each area.

Table 17. Condition and utilization of willow on important winter moose range in the Upper Gallatin Area as determined from 4 to 9 transects read annually in 1957-64, and 14 to 17 transects read annually from 1965-72.

	PERCENT OF PLANTS SEVERELY HEDGED					PERCENT OF PLANTS WITH 25 PERCENT OR MORE DEAD CROWN					AVERAGE PERCENT OF CURRENT YEARS LEADERS UTILIZED				
YEAR	Gallatin River Bottom	Taylor Fork	Porcupine Creek	Cinnamon Creek	West Fork Gallatin	Gallatin River Bottom	Taylor Fork	Porcupine Creek	Cinnamon Creek	West Fork Gallatin	Gallatin River Bottom	Taylor Fork	Porcupine Creek	Cinnamon Creek	West Fork Gallatin
1957	56	42	81	--	--	84	70	95	--	--	58	19	61	--	--
1958	49	0	32	--	--	81	52	98	--	--	58	9	27	--	--
1959	12	0	53	--	--	79	48	95	--	--	58	23	64	--	--
1960	45	6	87	--	--	83	46	95	--	--	78	41	53	--	--
1961	97	0	33	--	--	100	50	100	--	--	90	20	60	--	--
1962	95	0	53	--	--	93	66	99	--	--	68	68	89	--	--
1963	81	0	35	--	--	99	76	71	--	--	43	2	29	--	--
1964	0	20	--	--	--	88	88	--	--	--	68	82	--	--	--
1965	80	58	96	84	100	60	40	78	44	38	40	12	74	36	80
1966	41	24	94	52	77	33	26	79	16	83	7	28	16	30	52
1967	8	26	66	100	85	55	71	90	100	85	30	19	60	76	79
1968	5	14	37	100	96	33	44	88	100	82	33	23	42	46	76
1969	1	5	37	52	93	37	15	76	72	69	53	31	71	76	82
1970	4	7	33	64	52	27	12	74	60	25	63	44	50	66	66
1971	48	12	61	32	72	42	26	80	52	41	68	48	74	61	73
1972	--	10	40	52	47	--	10	68	48	27	25	25	40	73	63

Two Porcupine Creek transects were used primarily by elk, one primarily by moose, and two others by both species although moose use was predominate in most years. Plants on these transects have been in fair to very poor condition over the years, with major variations resulting from fluctuations in elk use. Moose use has probably also been excessive in some years.

Cinnamon Creek and West Fork transects are used almost exclusively by moose, although deer and elk may use one of the latter. Willows were in poor to very poor condition and received generally excessive utilization throughout the period of measurement. The over-used condition in the West Fork area may be aggravated by recreational development in that area causing a decrease in available winter habitat (see section on land use implications).

Point-center-quarter measurements made in 1965 and 1970 on one Porcupine Creek and one West Fork transect indicate that willow density decreased on both areas (Table 18). Other measurements indicate that total browse production on the West Fork transect declined substantially between 1965 and 1970 while very little change was evident for the Porcupine Creek transect.

Table 18. Data from point-center-quarter measurements on two willow browse transects in the Upper Gallatin Area.

	PORCUPINE CREEK		WEST FORK	
	1965	1970	1965	1970
Willow density[1]	1,675	1,031	2,591	1,341
Mean Crown Area[2]	9.2	13.9	5.5	4.3
Mean Canopy coverage[3]	35	33	33	13
Mean basal area[2]	2.5	2.5	1.8	0.8
Mean basal coverage[3]	10	6	11	2

[1]Plants per acre.
[2]Square feet.
[3]Percent

UPPER YELLOWSTONE AREA - Seven willow transects were established in the upper Yellowstone in 1965 (Table 19). Three transects, located on private land, were sprayed with herbicides during the 1966 growing season to convert the vegetation from brush to grass to benefit cattle.

Assuming severe and mild winters in 1964-65 and 1965-66, respectively, (corresponding to those in the upper Gallatin), and no mild winters from then through 1970-71, utilization was within allowable limits in all years. Willow on unsprayed transects was in very poor condition in 1965 and remained so through 1968, with some improvement noted in subsequent years.

Table 19. Condition and utilization of important browse species on winter moose range in the upper Yellowstone Drainage.

YEAR	PERCENT OF PLANTS SEVERELY HEDGED		PERCENT OF PLANTS WITH 25 PERCENT OR MORE DEAD CROWN		AVERAGE PERCENT OF CURRENT YEARS LEADERS UTILIZED	
	Sprayed[1]	Unsprayed[1]	Sprayed	Unsprayed	Sprayed	Unsprayed
1965	32	83	19	45	52	82
1966	43	85	30	82	27	35
1967	66	86	84	89	48	69
1968	75	80	97	80	51	62
1969	27	53	92	60	44	61
1970	29	78	99	54	32	55
1971	1	42	88	65	27	52

[1]Three transects sprayed, four unsprayed. Dashed line indicates when spraying occurred.

Average plant condition on these transects in 1971 was still considered only poor to fair. Red dogwood was measured in 1969, 1970 and 1971 adjacent to one of the unsprayed willow transects. These plants were in extremely poor condition, with all plants severely hedged all 3 years and an average of 68 percent of the plants decadent. Utilization averaged over 86 percent for the 3 years.

Transects which were later sprayed were in fair to good condition in 1965, with a sharp decline in condition noted following spraying. The great increase in decadent plants was expected, while the increase in severely hedged plants reflects only the living stems and probably resulted from increased use of available living plants or parts of plants. The percentage of decadent plants remained near 90 percent through 1971. Severely hedged plants increased through 1968, and improved greatly thereafter. Following spraying, utilization remained at about the same level as before, indicating continued moose use of the area. No increase in utilization following significant reductions in available forage suggests that relatively few animals used the area and/or spent considerably less time there. The abundance of browse in the surrounding area and the imcomplete kill lessened the impact of this spray program on moose. More complete removal, and/or relatively less area of adjacent suitable winter browse could eliminate large areas of important moose winter range, with drastic consequences for the moose population. However, periodically spraying small portions of an extensive area to promote resprouting might actually improve the area for moose by providing more available forage. Both the spray operation and livestock would have to be well managed for this to be successful, however.

LOWER MADISON AREA - A 10-year record of browse transect readings exists for the Madison River drainage between Earthquake and Ennis Lakes (Table 20). Included are three willow and one red dogwood transect in Hunting District 33 (west of the Madison River) and one red dogwood transect in Hunting District 36 (east of the Madison River).

Although utilization appeared to be within allowable limits for all or most winters, willow plants in Area 33 were mostly in poor condition throughout the sampling period, with fluctuations probably reflecting variations in winter severity. These plants apparently were of low vigor and could not tolerate the level of browsing which vigorous plants could. Many red dogwood plants on the transect in this area were short enough to be unavailable during periods of deep snow, resulting in wide variations in utilization and condition. Red dogwood plants in Area 36 were in very poor condition throughout the period, with some improvement noted in 1972.

Recent increased use of snowmobiles on the road up the bottom of the West Fork of the Madison River appears to have caused reduced use of parts of this area by moose. The overall effect is unknown but presently it appears to have caused a shift in use of available habitat rather than shifts to less suitable habitat. Increased snowmobile use in the future might necessitate restrictions on their use.

Table 20. Condition and utilization of willow and red dogwood on moose winter ranges in the Madison River Drainage between Earthquake and Ennis Lakes.

YEAR	PERCENT OF PLANTS SEVERELY HEDGED			PERCENT OF PLANTS WITH 25 PERCENT OR MORE DEAD CROWN			AVERAGE PERCENT OF CURRENT YEARS LEADERS UTILIZED		
	Area 33		Area 36	Area 33		Area 36	Area 33		Area 36
	Willow	Dogwood	Dogwood	Willow	Dogwood	Dogwood	Willow	Dogwood	Dogwood
1963	92	64	100	60	16	72	66	27	77
1964	--	--	100	--	--	84	--	--	79
1965	28	56	--	36	0	--	35	59	--
1967	65	96	100	93	100	100	59	78	70
1968	60	100	96	66	100	92	55	76	67
1969	52	100	100	65	40	48	51	87	85
1970	17	40	92	55	12	28	31	63	74
1971	52	52	92	56	24	56	58	33	83
1972	54	48	76	48	20	28	60	59	69

GRAVELLY-SNOWCREST AREA - Browse transect readings on this area date from 1959 and included both winter and summer ranges. Transects included 12 on willow and 3 on scrub birch above 7,000 feet (spring-summer-fall range), and three on willow and two on silverberry on the restricted winter range below 6,500 feet. Moose remain on spring-summer-fall range for 8 to 10 months each year (Peek 1961:23). Based on the percentage of plants severely hedged, plants on winter range along the Ruby River were in good condition when first read in 1959 (Table 21). This may have been the temporary result of a mild winter since a high percentage of plants were decadent. Condition of both willow and silverberry rapidly deteriorated on this winter range area during the next two years. Utilization did not appear heavy enough to have caused this in healthy plants, suggesting poor range condition and plants of low vigor. Both species remained in very poor condition through at least 1963. Readings were not made in 1964, and by 1965 condition had improved to fair-good, and remained so through 1971.

Plants on summer range were in fair condition in 1959 and poor to very poor through 1963. Willow condition improved considerably after this, with scrub birch remaining in poor condition through 1967 (Table 21). Following substantial improvement in condition of browse plants on summer ranges, these transects were read less frequently (only every three to five years, or sooner if use on winter range areas appeared heavy enough to warrant it).

Peek (1961:3) stated that heavy utilization of willow by moose was noted in this area as early as 1952 and 1953. Peek (1963) and Stevens (1966) provided data from browse transects in this area and discussed their findings in relation to moose populations. It appears that past over-use of both summer and winter ranges may have caused low plant vigor, resulting in increased plant deterioration under normally acceptable levels of use, and in subsequent range deterioration and declining moose populations. This will be discussed more fully in the section on population dynamics.

Five willow transects were established on winter range on the west side of the Snowcrest Mountains in 1961, four on the East Fork of Blacktail Creek and one on Ledford Creek (Table 22). Although these transects have not been read annually, the data appear to be useful. Transects on both areas indicated that willow was in poor to very poor condition during the 1961-1965 period, with probable over-use prior to 1963. A gradually improving condition was noted to 1965 with considerable improvement noted in subsequent years. Moose population segments which winter in these areas appear to have undergone declines similar to those in the rest of the Gravelly-Snowcrest area.

RED ROCK LAKES NATIONAL WILDLIFE REFUGE - Four willow transects were established on the Refuge in 1965 (Table 23). Condition was fair to excellent on these transects since 1965, with a declining trend from 1965 to 1967, improvement through 1970, and another decline in 1971.

Dorn (1969:38-40) felt these transects were of little value in determining range condition because the key species was the dominant tagged plant

Table 21. Condition and utilization of important moose forage species in the Gravelly-Snowcrest area. Winter range includes areas below 6,500 feet, and summer range areas over 7,000 feet in elevation.

YEAR	PERCENT OF PLANTS SEVERELY HEDGED				PERCENT OF PLANTS WITH 25 PERCENT OR MORE DEAD CROWN				AVERAGE PERCENT OF CURRENT YEARS LEADERS UTILIZED			
	Winter Range		Summer Range		Winter Range		Summer Range		Winter Range		Summer Range	
	Willow	Silver-berry	Willow	Scrub Birch	Willow	Silver-berry	Willow	Scrub Birch	Willow	Silver-berry	Willow	Scrub Birch
1959	4	16	23	--	98	0	42	--	53	70	40	--
1960	72	28	63	100	76	0	46	56	66	66	50	--
1961	100	100	66	--	81	50	54	--	57	67	26	--
1962	97	74	54	99	100	46	92	93	79	71	39	54
1963	97	98	76	99	93	12	58	97	2	21	34	27
1965	11	16	26	79	61	44	45	95	24	10	20	17
1966	23	0	26	37	80	28	62	88	24	2	40	3
1967	21	18	31	68	85	40	59	97	37	48	46	22
1968	8	12	2	0	24	2	34	40	38	35	9	2
1969	12	8	10	--	21	24	38	--	39	13	27	--
1970	8	32	0	--	45	14	32	--	42	12	3	--
1971	29	22	0	--	40	10	32	--	48	16	1	--

Table 22. Condition and utilization of willow on moose winter ranges in Ledford Creek (one transect), and the East Fork of Blacktail Creek (four transects).

YEAR	PERCENT OF PLANTS SEVERELY HEDGED		PERCENT OF PLANTS WITH 25 PERCENT OR MORE DEAD CROWN		AVERAGE PERCENT OF CURRENT YEARS GROWTH UTILIZED	
	Blacktail Creek	Ledford Creek	Blacktail Creek	Ledford Creek	Blacktail Creek	Ledford Creek
1961	93	60	95	48	61	57
1963	80	--	100	--	44	--
1965	58	64	97	20	31	25
1967	23	4	61	16	46	26
1968	36	--	74	--	28	--
1971	11	12	35	24	9	54

Table 23. Condition and utilization of willow on four transects on year-round moose range, Red Rock Lakes National Wildlife Refuge.

YEAR	PERCENT OF PLANTS SEVERELY HEDGED	PERCENT OF PLANTS WITH 25 PERCENT OR MORE DEAD CROWN	AVERAGE PERCENT OF CURRENT YEARS GROWTH UTILIZED
1965	22	34	51
1966	33	55	39
1967	37	55	51
1968	23	49	24
1969	12	22	27
1970	8	19	23
1971	29	32	43

on only two transects, only one of which he considered to be in a key area. He recommended replacing three of these transects with new transects in other locations. I would abandon only two of these, and would retain both transects on which the key willow species predominates. Winter aerial observations within approximately 1 mile of the second of these transects showed 10, 1, 8, 10 and 9 moose in 1965 through 1968, inclusively, and 1971. This suggests that this probably is a key area, at least in winter, and should be retained. Replacement locations suggested by Dorn (1969:40) appear to be properly located.

This range appeared to be in satisfactory condition through 1969 with the exception of one over-used willow area (Dorn 1969:39). Increased utilization and decline in condition in 1971 is attributable to increased numbers of wintering moose. Transects should continue to be read in this area.

ROCK CREEK (GRANITE COUNTY) - Although no moose browse transects exist in this area, the winter range apparently was not over-used in 1958 through 1960 (Smith 1962:46) or 1969 through 1971 (Stone 1971:69). These investigators also made no mention of apparent past over-use.

Effects of Browsing on Plants

A number of factors affect the condition of browse plants. Of primary concern here is the effect of animal browsing. The effect of browsing on shrubs depends on the browse species and its age, as well as the season, intensity and frequency of use. Also important are weather conditions and site factors such as soil fertility, moisture and overstory crown closure.

Various studies (Julander 1937, Young and Payne 1948, Aldous 1952, Krefting *et al.* 1966, Shepherd 1971) have shown that browse species differ greatly in their ability to withstand browsing.

Julander (1937:281) reported that aspen reproduction in northern Arizona could withstand 65 to 70 percent utilization during summer and improve from an overbrowsed condition. With summer use of 70 to 75 percent aspen reproduction could almost maintain itself, but not recover from overbrowsing. Smith *et al.* (1972:29) reported that aspen sprouts appeared to be most palatable to browsing animals in the first year following emergence and decline in palatability after that. They concluded that aspen regeneration in Utah was possible under heavy use by both wild and domestic animals, and that frequent failure of aspen to reproduce was the result of faulty timber and/or livestock management. Neither of these studies reported whether aspen reproduction could withstand heavier utilization during dormant periods as many other browse species can.

In northern Idaho Young and Payne (1948:38) found that removal of 50 percent of the new growth from serviceberry during spring or summer induced a small decrease in forage the next year. A slight increase occurred following the same rate of removal in fall. Plants clipped 75 percent showed definite forage reduction trends for treatments applied in all three seasons. Shepherd (1971) also studied the response of serviceberry to simulated browsing. His results suggested that late summer-early fall use of up to 60 percent of current annual growth stems 1 centimeter or more in length increased production, but sustained utilization of 80 percent or over was harmful and would eventually kill the plants.

Aldous (1952:407-408) reports that willow in northeastern Minnesota responded more to heavy clipping (100 percent removal of current annual growth) than any of the other species he studied. Annual browse production (based on fresh weight) increased steadily through five years of clipping, but the number of stems was greatly reduced. Total browse production was less under moderate use (50 percent removal of current growth) but twig numbers were much more stable. A longer period of time would be required to determine complete effects of sustained heavy utilization. Cole (1963:8) suggests allowable levels of use of 50, 75 and 95 percent for willow in mild, average and severe winters, respectively. Houston (1968:85) suggested similar levels (50, 70 and 90 percent) of use for *Salix novae-angliae*. These suggestions are apparently based on general observations and are for vigorous, mature plants. Lower levels of use would probably be required to allow improvement in condition of severely hedged plants as suggested by Yorgason (1967, cited by Houston 1968:85). Individual willow transects on the Lower Gallatin Study Area winter range suggested that the percentage of severely hedged plants did not decrease until utilization fell below approximately 75 to 80 percent. Utilization at or above this level maintained or increased the percentage of severely hedged plants. Lower levels of use would probably be required to allow plants which have been severely hedged for a number of years to fully recover their vigor and produce maximum amounts of forage. Houston (1968:30-35) reported periodic heavy use of vegetation, with short-term fluctuations in willow condition. However, snow depth and the growth form of willow in Jackson Hole prevented permanent damage to these plants.

Stevens (1965:31-32) presented some criteria for willow browse transects which appear to increase their value for determining range condition and trends. Among these were: a given transect should sample only a single willow species; the area and degree of availability should be taken into account; individual plants should be tagged; and overall range use in the area should be noted. Dorn (1969:38-39) made similar suggestions. Due to the great individual variation among willows it is difficult for management personnel to assure that all plants selected for a transect are the same species. Establishing transects and tagging plants after they are fully leafed-out would help solve this problem. There is also the difficulty of determining which should be the key willow species in an area. The area and degree of availability are often difficult to determine, especially when utilization is light. They also vary between locations and between years on the same area due to varying snow depths. Assessment of overall range use in the area would largely eliminate this problem.

Aldous (1952:407) reported that red dogwood in northeastern Minnesota cannot withstand repeated heavy use (100 percent removal of annual growth).

However, even complete elimination of this species from Montana's moose ranges would most likely have little, if any, effect on moose populations because of its limited distribution and abundance. Red dogwood plants examined during this study produced little forage in most years due to past heavy utilization. They did not appear to be in danger of dying, however, and the severely hedged form made much of the new growth unavailable. Some of these plants are short enough to receive periodic rest from browsing while snow covered.

Shepherd (1971) clipped more than the current years growth from some plants, and although this happens infrequently from browsing animals, it could have serious local consequences if it occurs too frequently.

Cowan *et al.* (1950) reported that palatable browse species decreased and unpalatable ones increased greatly as logged forests in central British Columbia matured. These and other authors (for a review see Halls and Epps 1969:1028) have reported varying effects of overstory canopy on quality of browse growing beneath it. As a general rule, browse quality decreases as overstory canopy increases. Cole (1959:184) also states that, in general, plants under timber will not tolerate as high a degree of hedging or remain as productive as those receiving full sunlight.

Interspecific Relations

The most important ecological implication stemming from the relationship between moose and other animals appears to be competition for forage. Many wild and domestic animal species are actual or potential competitors for forage with moose, depending on the situation.

Beaver - Beaver *(Castor canadensis)* activities may prove either beneficial or detrimental to moose forage supplies depending on individual circumstances. Primary beaver foods are aspen and willow (Hall 1960:493), and one or both must be present before beaver will colonize an area. Beaver flooding may drown out conifers and other less desirable moose forage and create desirable moose habitat by setting plant succession back. On the other hand, beaver characteristically overutilize both aspen and willow within the immediate vicinity of the colony (Hall 1960: 494-494) and benefits to moose may be negative or may not be realized until after the beaver vacate a colony. Low density beaver populations probably do not significantly conflict with moose. Dorn (1969) felt that a small increase in beaver numbers could result in serious moose-beaver competition on the Red Rock Lakes National Wildlife Refuge, and recommended regular beaver harvests on the area. Although locally high beaver populations may compete with moose on some winter ranges, most wintering areas are readily accessible to trappers, which in most cases prevents development of large beaver populations.

Elk - Elk forage both by grazing and browsing, but apparently prefer grass when or where available during fall through spring. Significant amounts of browse are utilized only when or where grass is in limited supply. In general, browse plants comprise a major portion of the winter elk diet only on heavily forested ranges in western Montana.

Several browse species important to moose are also readily eaten by elk, and direct competition for forage could occur where both species depend on browse winter-long, or where elk are forced to utilize browse during periods of deep snow.

With some local exceptions, such as the upper Gallatin, moose-elk competition appears to be minimal, either as a result of differences in distribution or diets. Where overlaps regularly occur, one or both species probably have been reduced in numbers.

Deer - Mule and/or white-tailed *(Odocoileus virginianus)* deer share both summer and winter ranges with moose over much of Montana. Both species of deer browse extensively in winter, eating many of the same plants as moose. These overlaps probably result in competition in some areas, However, due to their smaller size deer cannot browse as high on plants, are more restricted by deep snow and pose much less of a competitive threat to moose than elk. Overall, moose-deer competition would probably affect deer more drastically than moose.

Domestic Livestock - Domestic livestock utilize moose ranges in many areas of Montana. On public lands (primarily National Forests) this usually occurs as summer livestock use on both summer and winter moose ranges. Where livestock are properly managed this use generally is not directly detrimental to moose. Problems are created by excessive livestock use of stream bottom areas on moose winter ranges and can occur even under proper livestock stocking rates. Though costly, fencing livestock out of these over-used bottoms could help prevent competition and also lessen the impacts of overgrazing (stream sedimentation, etc.) on other values being damaged by overuse.

Private lands are grazed at any and all seasons. Those of value to moose are mostly stream bottom willow flats adjacent to, or below forested areas. These are normally used by moose in winter and represent areas of greatest actual or potential moose-livestock competition. Cattle activities may greatly reduce the forage available to moose, both through feeding and by physically damaging the plants. Although the Centennial Valley was devoted primarily to cattle raising, Dorn (1969:27) found moose-cattle competition to be insignificant under stocking rates (approximately one animal per 5 acres for 82 days) prevailing during his study. He pointed out conditions which would be expected to increase competition.

Indirect, as well as direct, moose-cattle competition has been reported by Houston (1968:44-45), Smith (1962:27) and Stone (1971:56). Both Denniston (1956:114) and Stone (1971:56) reported that moose moved out of an area when cattle moved in. This appeared to occur on parts of the Lower Gallatin Study Area. Moose were commonly observed on cattle-use areas both before and after the period (mid-June to mid-October) when cattle were present, but were infrequently observed in the same areas along with the cattle. Dorn (1969:27-28) reports moose and cattle feeding together with no apparent concern. The reaction of moose to the presence of cattle may be related to the availability of suitable adjacent moose habitat. Where it is ample moose may avoid cattle-use areas.

However, if cattle occupy most, or all, of the suitable moose habitat, the moose would be forced to use the area along with the cattle.

Land-Use Implications

A number of factors affect moose habitat in addition to natural plant succession and animal use. Most are directly related to human activities or endeavors and affect moose populations in various ways.

Logging - Timber harvest has often been considered favorable to big game populations, including moose (Bergerud and Manuel 1968:730, Peterson 1955:160-161, Markgren 1969:272-273). However, the location, size of cutting unit, cutting system employed and habitat type (Daubenmire 1969:31) in which cutting occurs all influence whether logging will be beneficial or detrimental to big game in the area.

Elevation, slope and exposure largely determine the amount of potential big game winter range in Montana. Location of the logging operation, therefore, is critical. Generally speaking, secondary succession following logging in the Montane Taiga and Mesophytic Forest provides very little good browse except in habitat types having a *Pachistima myrsinites* understory (Daubenmire 1969:33-37). These two factors severely limit the benefits of logging for moose populations in Montana.

There are some negative aspects of logging regarding moose as well. Road development associated with logging in an area normally increases human activity, especially in winter since they provide easy snowmobile access. Where roads follow major stream bottoms, increased distrubance and harassment from uncontrolled snowmobile use can conflict with wintering moose populations when they are least mobile and in poorest physical condition. Another aspect of logging negatively affecting moose was reported by Markgren (1969:273); large clearcut operations resulted in a gradual drying-up of the soil with a negative influence on nutrition through vegetation changes.

To determine relative use of different aged clearcuts moose pellet groups were counted on summer range in the Lower Gallatin Study Area. Ten clearcut areas, ranging in age from 5 months to over 21 years, and six adjacent uncut areas were sampled. Two timber types, spruce-fir and lodgepole pine, were included. These counts were made in 100-square-foot circular plots which sampled approximately 0.35 percent of the total area of each cut. Adjacent uncut areas were sampled at slightly less than half the intensity of clearcuts.

Although the results (Table 24) did not give a clear indication of the relationship between age of clearcuts and use by moose, a few generalized conclusions may be drawn. Uncut spruce-fir appeared to be more preferred by moose than uncut lodgepole pine, possibly reflecting the greater amount and diversity of understory vegetation in the spruce-fir type. Moose use appeared to decrease for at least the first few years following clearcut logging in the lodgepole type. After approximately 10 to 12 years, clearcuts in this type received greater use than surrounding uncut timber. This may be correlated with the development of a more profuse understory, along with lodgepole regeneration in the clearcuts becoming tall enough to provide adequate cover.

Table 24. Moose pellet groups counted in different aged clearcuts in the spruce-fir and lodgepole pine timber types and adjacent uncut timber, Lower Gallatin Study Area.

TIMBER TYPE	YEARS SINCE LOGGED	ACRES SAMPLED	PELLET GROUPS PER 100 ACRES
Spruce-fir[1]	Uncut	70	27
Spruce-fir[1]	5-6	150	7
Lodgepole pine	Uncut	150	3
Lodgepole pine	<2	230	0
Lodgepole pine	14-21	165	7

[1]Included up to approximately 40 percent lodgepole pine in the canopy.

Use of 5 and 6 year old cuts in the spruce-fir type was approximately one-fourth that in adjacent uncut timber. Cutting in the spruce-fir type normally results in replacement by lodgepole pine. This, plus the fact that the level of use in older lodgepole clearcuts was approximately the same as in 5 and 6 year old spruce-fir cuts, indicated that clear-cutting in the spruce-fir type was detrimental to moose. Whether clear-cutting of spruce-fir on moose summer range is likely to reach a level significant to moose populations is questionable, particularly under present cutting practices.

Overall, the effects of logging on Montana moose populations is probably more or less neutral, being favorable in some instances and detrimental in others.

Human-related Activities and Developments - A number of human activities not fitting previously discussed categories have caused loss of winter forage supplies or upset plant succession in important stream bottom areas.

Natural stream channels are continually eroding and depositing material and cutting new channels. This natural cutting action provides a continuous source of newly bared areas on which seral vegetation can develop. Straightening, deepening and/or widening of stream channels reduces or eliminates these bare areas and upsets plant succession. These activities might also increase drainage and lower the water table sufficiently to reduce the amount of important plant species such as willow. Besides hastening or otherwise upsetting plant succession, additional habitat is lost through the decrease in total channel length.

Loss of moose forage through moose-cattle competition was previously discussed. In addition, brush removal to benefit livestock (through herbicide spraying, burning and/or mechanical means) has been carried out on several Montana areas important to wintering moose. This is immediately and directly detrimental to the moose dependent on these areas for winter forage.

The increasing trend toward locating cabins, homes and recreational facilities in stream bottom areas important to moose in winter poses another potentially significant source of direct habitat loss. Many of these facilities are not used during the critical winter period, although growing use of snowmobiles may increase this use, and therefore their impact is dependent on the amount of habitat directly damaged or removed. Areas receiving year-round human use present the added factor of human disturbance during the critical winter period. Effects of this type of disturbance on moose can run the gamut from insignificant to drastic.

The Big Sky Recreational Area, currently under construction on the West Fork of the West Gallatin River, is a potentially damaging development in terms of winter moose habitat. Recent development has damaged or removed some of the willow on one browse transect on the West Fork near the mouth of the North Fork. More extensive willow damage has occurred below this transect. Although the number of wintering moose involved is not large (normally 6 to 12), effective elimination of the willow below the mouth of the North Fork (through physical removal and/or intolerably high human activity accompanying development) can only be detrimental to this moose population segment. A secondary effect of Big Sky is the peripheral development accompanying its construction. These secondary developments are seldom planned as well, and are probably equally or more important in habitat loss than the primary development.

Human activities have the greatest impact on moose through habitat alterations and losses. Currently, effects of human activities on moose primarily range from relatively neutral to very detrimental, with very few being beneficial. However, human activities may also offer the greatest potential for creating additional moose habitat. Tree cutting (either commercial logging, or cutting of non-commercial species such as aspen) and controlled burning are two tools which can be used to improve or enlarge present winter ranges or create new ones. Effects of controlled burning and timber harvest in different cover types should be determined by research designed specifically for moose habitat improvement.

POPULATION DYNAMICS

Although aerial observation is an effective technique for determining general moose distribution and use of habitat types, it is not effective for censusing moose populations in most of southwestern Montana (Stevens 1970:44). The extent of actual under-estimation of moose populations from aerial observations is unknown. However, some marked animals known to be present on the Lower Gallatin Study Area in 1968 through 1972 were missed on all flights, regardless of season or observing conditions. In Alaska, LeResche and Davis (1971*a*) found that only two-thirds to three-fourths of the animals known to be present within 1-square-mile enclosures were seen under ideal conditions (excellent snow conditions and currently experienced observers). Considerably less than half the animals were often observed under poor snow conditions and/or using inexperienced observers or observers having considerable past experience but no current (within one year) experience. Two observers in a helicopter saw slightly more animals than a single observer in a Super-cub, but not enough to justify the considerably higher costs.

Because of these limitations we made no attempt to enumerate total populations on study areas. Rather, we attempted only to evaluate annual reproduction and changes in productivity.

SEX AND AGE COMPOSITION

Sex and age composition of moose populations were determined by late summer-early fall (pre-hunting season), and winter aerial observations. The latter provided only calf:adult ratios due to the large number of unclassified adult animals. Hunter questionnaires and hunting season collections provided data on sex and age composition of the harvest for comparison.

Fall (pre-hunting season) - Fall classifications on the Lower Gallatin Study Area from 1966 through 1971 showed little annual variation and averaged 37 percent bulls, 48 percent cows and 14 percent calves. Ratios were 77 bulls and 29 calves:100 cows (Table 25). Fall calf: cow ratios probably were minimal since some calves, as well as some cow-calf groups, were apparently missed on fall flights. Pimlott (1953:571) believed that observers did not see cows with calves in the same proportion that they occurred in the population during summer and early fall, and Peek (1962:361) observed more cows with calves than lone cows in dense cover during summer. General observations seemed to verify this moose behavior pattern, which could account for the low number of calves in the fall observations.

Fall classifications obtained from the Upper Madison (including the West Fork) and the adjacent upper Centennial Valley were combined for analysis because of limited individual samples. The sex ratio (74 bulls:100 cows) was similar to that for the Lower Gallatin Study

Table 25. Fall (pre-hunting season) and winter sex and age ratios obtained in various Montana areas, 1965-1972. Only areas having samples of 200 or more animals are included.

	FALL		WINTER		
	Bulls: 100 Cows	Calves: 100 Cows	Calves: 100 Adults	Calves: 100 Cows[1]	Twinning Rate (Percent)
Lower Gallatin Study Area	77	29	27	49	1
Upper Madison-Centennial	74	58	-	-	-
Upper Madison Study Area	-	-	27	49	3
Upper Centennial	-	-	35	64	12
Upper Gallatin	-	-	22	40	5
Gravelly-Snowcrest	-	-	38	69	4
Big Hole	-	-	33	60	3

[1]Assuming 55 percent of the adult population to be composed of females.

Area, but the calf:cow ratio (58:100) was double that of the Lower Gallatin (Table 25). Much of this difference may be attributed to the fact that the area sampled was generally more open than the Lower Gallatin, permitting a more representative sample to be obtained.

Hunting Season - Sex and age composition of the harvest, determined from hunter questionnaires and mandible and reproductive tract collections, are not representative of the sex and age of fall populations. However, they do indicate the degree of hunter selectivity that exists for or against certain sex or age groups.

Questionnaires from the years 1966 through 1971 indicated a harvest of 54 percent bulls, 36 percent cows and 9 percent calves. Mandibles collected during the same years included similar percentages (55, 40 and 6) of bulls, cows and calves, respectively.

Age composition of the harvest, determined from mandible collections, indicated no great changes in age structure from 1966 through 1971 (Table 26). The proportion of calves in the harvest (less than 10 percent) was always much smaller than their proportion in the population (approximately 24 percent). Analysis of the data for 1966 through 1971 to estimate the percentage of yearlings in the population (Simkin 1965:747) indicated that percentages of yearlings in the harvest were similar to their estimated occurrence in the population in most years

Table 26. Wear class distribution of hunter-killed moose examined in Montana (1963, 1965-1971).

	PERCENT OF ADULTS (YEARLING AND OLDER)								
Wear Class	1963	1965	1966	1967	1968	1969	1970	1971	1966-1971 Combined
I	15.7	15.3	19.2	19.8	20.4	14.4	25.2	22.7	20.4
II			18.1	24.2	22.2	24.9	17.9	24.2	21.6
III	37.1	43.9	18.9	15.9	14.5	14.4	14.6	14.7	15.6
IV			12.4	8.8	13.1	12.4	13.4	12.6	12.3
V			7.6	8.2	5.9	7.0	7.3	5.1	6.8
VI	34.3	31.6	5.7	4.4	5.4	4.0	4.1	5.0	4.8
VII			5.3	6.0	6.8	7.0	7.3	8.1	6.7
VIII	12.9	9.2	6.4	8.8	5.0	9.4	7.3	6.1	7.1
IX			6.4	3.9	6.8	6.5	2.9	1.5	4.7
Adult Sample Size	70	98	265	182	221	201	246	198	1,313
Calf Sample Size	12	5	25	12	5	9	19	13	83
Total Jaws "Aged"	82	103	290	194	226	210	265	211	1,396

(Table 27). Pimlott (1959:394-396) noted that calves were harvested in less than actual proportions in Newfoundland, while yearlings comprised a higher percentage of the harvest than their occurrence in the population. Simkin (1965:746-747) reported similar findings in Ontario. Lower percentages of calves and yearlings in Montana harvest collections, when compared to either Newfoundland or Ontario, probably reflects the fact that Montana's moose hunting districts, although varying greatly, are comparatively small in size and have restricted numbers of permits.

Table 27. Percent yearlings in the harvest, in the population, and yearling vulnerability factors for Shiras moose in Montana (1966-1971).

Year	Percent Yearlings in Harvest	Estimated Percent Yearlings in Population	Vulnerability Factor
1966	19.25	19.41	0.99
1967	19.78	20.24	0.98
1968	20.36	19.83	1.03
1969	14.43	17.68	0.82
1970	25.20	21.01	1.20
1971	22.73	22.66	1.00
All Years Combined	20.41	20.15	1.01

It is also apparent that although a few hunters seek a specific type of animal (trophy bull, cow for meat, etc.), the majority capitalize on their first opportunity to bag an animal, regardless of sex or age. However, when two or more animals are encountered together the average hunter normally selects a large bull over a smaller one, any bull over a cow, and a cow over a calf. This appears to be the major cause of differences between pre-season and harvest sex and age data.

Winter - Composition of winter populations is generally modified from fall ratios by differentially greater harvest of adults, especially bulls, and increased observability of calves. Classifications on the Lower Gallatin Study Area from 1965 through 1972 indicated an average winter ratio of 27 calves per 100 adults (yearlings included as adults) and a one percent twinning rate (Table 25).

Adequate pre- and post-hunting season samples were obtained in 1968 through 1970, inclusively. In each of these years, post-season flights showed more total calves and higher calf:adult ratios than pre-season flights. Twins were not observed on any fall flights, but were observed in several winters, again indicating that fall flights missed some calves and probably cow-calf groups as well.

Winter observations on the Upper Madison Study Area (1965-1972) showed a calf:adult ratio identical to that on the Lower Gallatin (27:100), but with a high twinning rate (3 percent).

Assuming approximately 55 percent of the adult moose population in winter is composed of cows (fall observations showed 57 percent cows), calf:adult ratios for both the Lower Gallatin and Upper Madison would be 49 calves:100 cows in winter. This indicates a large increase over the fall ratio on the Lower Gallatin and is probably attributable to both differential harvest and increased calf observability. The winter ratio on the Upper Madison appears to be similar to that for fall. Terrain makes hunting in this area more difficult, with differential harvest being less pronounced than in most areas, resulting in little change between fall and winter ratios.

Classifications were obtained from several other areas during the winters of 1965 through 1971, but only 4 areas had sample sizes considered adequate (Table 25). Winter ratios in areas inadequately sampled (not included in Table 25) ranged from a low of 16 calves:100 adults with no twins observed (Upper Yellowstone), to as high as 41:100 with at least a 17 percent twinning rate (a very small sample in a restricted area south of Anaconda). The overall winter calf:adult ratio (32:100) for all these other areas combined compares to a ratio of 58 calves:100 cows, based on an adult sex ratio of 55 percent cows.

Reproduction

The following discussion summarizes reproductive data obtained in this study. Additional details on methods and terminology are presented by Schladweiler and Stevens (1973). Statistical significance is based on chi-square tests and the 5 percent probability level (Steele and Torrie 1960).

A total of 424 female reproductive tracts were collected from southwestern Montana in 1963 and from 1965 through 1971. Collections from 1966 through 1971 were obtained from an average of 39 percent (range 31 to 57 percent) of the total female harvest. Although collections sampled several reasonably discrete moose populations, small individual sample sizes and lack of knowledge concerning most of these populations necessitated treating the data as if from a single population.

Ovulation Rates - None of 21 pairs of calf ovaries showed any sign of ovarian activity (Table 28). This agrees with the findings of Pimlott (1959:385), Simkin (1965:742) and Markgren (1969:197).

Among cows older than calves, regional, and even local variation exists in the age at which reproduction first becomes possible (Markgren 1969: 197). Although Edwards and Ritcey (1958) concluded that female moose bred first as 2-year-olds on their study area in British Columbia, all other studies have reported at least some yearlings ovulating (Table 29).

Table 28. Incidence of ovulation and ovulation rates of Shiras moose in Montana as determined from counts of primary corpora lutea (1963, 1965-1971).

Age Class	Time Period	Sample Size	Percent Ovulating	Ovulations Per 100 Cows
Calf	September on	21	0.0	—
Yearling	September	6	0.0	—
	October on	51	43.1	48.3
Adult	September	21	4.8	4.8
	October on	304	92.1	114.8

Table 29. Incidence of ovulation and ovulation rates of moose from different areas.

Area[1]	Yearlings			Adults		
	Sample Size	Percent Ovulating	Ovulation Rate[2]	Sample Size	Percent Ovulating	Ovulation Rate[2]
United States						
Montana	51	43.1	48.3	304	92.1	114.8
Wyoming	12	25.0	25.0	72	88.9	94.4
Canada						
Newfoundland	69	47.8	53.6	188	85.1	104.8
Ontario	68	35.3	36.8	140	86.4	127.1
Sweden						
Gävleborg Coast	77	50.6	54.5	135	94.8	156.3
Gävleborg Inland	37	8.1	8.1	128	91.4	111.7
Åmot	24	33.3	33.3	63	92.1	114.3
Malingsbo	8	12.5	12.5	20	100.0	115.0

[1]Newfoundland, Ontario, Wyoming, Swedish and Montana data are from Pimlott (1959), Simkin (1965), Houston (1968), Markgren (1969) and this study, respectively.
[2]Ovulations per 100 cows.

The incidence of yearlings ovulating, the proportion of multiple ovulations among yearling cows, and the yearling ovulation rate in the Montana sample were statistically similar to these data from most studies elsewhere (Table 30).

Table 30. Statistical comparison of incidence of ovulation (left column), proportion of ovulations which were multiple (center column) and ovulation rates (right column) for Montana moose and those from other areas. 0 = not significantly different, + = significantly higher than for Montana, - = significantly lower than for Montana.

Area[1]	Yearlings			Adults		
United States						
Wyoming	0	0	0	0	-	0
Canada						
Newfoundland	0	0	0	-	0	0
Ontario	0	0	0	0	+	0
Sweden						
Gävleborg Coast	0	0	0	0	+	+
Gävleborg Inland	-	0	-	0	0	0
Åmot	0	0	0	0	0	0
Malingsbo	0	0	0	0	0	0

[1]See footnote to Table 5.

Pimlott (1959:398) and Markgren (1969:268) have suggested that the nutritional plane during their first winter probably determines whether or not female moose breed as yearlings. Forage conditions in some areas and/or years may provide female calves with winter nutrition sufficiently above sustenance levels to allow breeding the following fall. Markgren (1969:200-201) concluded that most yearlings ovulate during the same general period as adults, with a few ovulating at a decidedly later date.

The incidence of ovulation among adult moose in Montana (Table 28) was statistically similar to that for all other areas for which data are available except Newfoundland (Table 29 and 30). Multiple ovulations among Montana adults were significantly higher than in Wyoming, and significantly lower than in Ontario or coastal Swedish adults. No significant differences occurred between Montana and the other areas (Table 30).

The ovulation rate of Montana adults (Table 28) was statistically similar to all but the coastal Swedish area (Tables 29 and 30).

Pregnancy Rates - Pregnancy rates of yearling moose in Montana and Newfoundland (Table 31) were significantly higher than for British Columbia and Wyoming, with no differences between the rest. Although twins were found in the Newfoundland yearling sample (Table 31), no significant differences occurred between any of the areas in yearling twinning rate.

Table 31. Pregnancy rates of moose from five North American studies.

Area[1]	Yearling			Adults		
	Sample Size	Percent Pregnant	Percent Twins	Sample Size	Percent Pregnant	Percent Twins
British Columbia	15	0	0	169	76	22
Newfoundland	78	46	3	239	81	14
Ontario	12	17	0	87	87	29
Wyoming	35	6	0	41	90	11[2]
Montana	22	32	0	73	86	16

[1]Data from Edwards and Ritcey (1958), Pimlott (1959), Simkin (1965), Houston (1968) and this study, respectively.
[2]Based on a sample of 18 uteri.

Beuchner and Swanson (1955) attributed a high incidence of pregnant yearling elk in southeastern Washington to better nutrition resulting from greater forage availability per individual following herd reduction.

Pregnancy and twinning rates of adult moose in Montana (Table 31) were not significantly different from those reported from any other North American areas.

Data from this study showed *in utero* reproductive rates (including twinning rates) of both yearlings and adults compared favorably to those reported for most other areas. Using these figures plus the age structure of the female harvest, expected calf:cow ratios of around 65:100 are indicated. Observed ratios are frequently much lower than this, and observed twinning rates seldom approach the level found in reproductive tract collections. These facts raise questions as to why some areas have low observed calf:cow (or calf: adult) ratios, and why so few field observations of Shiras moose with twins are made (Knowlton 1960, Peek 1962, Houston 1968, Stevens 1970 and this study).

Pimlott (1959:398) and Houston (1968:70-71) have suggested that genetic factors might control the incidence of twins and triplets among moose. It does not seem possible that genetic factors would cause the great difference between *in utero* incidence of twins and field observations in this study. Rather, our results suggest that calf loss, either late in pregnancy or immediately *post partum*, is occurring. A *post partum* loss as reported by LeResche (1968), who also found significantly lower survival of calves with twin siblings, seems most likely. Rausch and Bratlie (1965:143) also concluded that calf mortality, and not variations in fertility rates, were responsible for variations in calf production between areas. This is probably related to nutrition of the cow, as suggested by several moose investigators (Hosley 1949:6, de Vos 1956:520, Edwards and Ritcey 1958:266-267, Pimlott 1959:398-399, Markgren 1969:266-269) and demonstrated for captive white-tailed deer receiving deficient diets. Does fed diets of 7 and 11 percent protein lost 42 and 27 percent, respectively, of their fawns to malnutrition, as opposed to no fawn loss for does on control diets (Murphy and Coates 1966). Does on low winter diets followed by a high spring ration lost more than one-third of the fawns produced (Verme 1962:21). It has also been suggested that size difference in twin siblings may result in an unequal division of nutrients, enabling one twin to survive where the probability that both would survive is remote (Verme 1963:437).

Data from this study indicate that reproductive figures reported by Peek (1962) for the Gravelly-Snowcrest area probably were not representative of statewide moose populations. The Gravelly-Snowcrest moose population was substantially reduced between 1961 and 1963 with resultant recovery of important browse species (Stevens 1966). Subsequently, moose numbers have been held relatively low, forage supplies appear to have improved further, and increased *in utero* reproduction has been demonstrated (Table 32). Observed occurrence of twins from this area are less conclusive since observations were not obtained in some years and sample sizes in recent years were small. However, it appears that twins are more frequently observed now than when winter populations were much higher.

An indication of probable nutritional control of twinning rate is available from the moose population which winters on approximately 5.5 square miles of the Red Rock Lakes National Wildlife Refuge. Aerial counts in the winters of 1965, 1966, 1968, 1969 and 1971 (Dorn 1969 and this study) showed populations of 43, 31, 50, 55 and 64, respectively with corresponding twinning rates of 20, 17, 18, 13 and 7 percent. Dorn (1969:39) concluded that this range generally appeared to be in satisfactory condition although winter carrying capacity was

Table 32. Data from the Gravelly-Snowcrest area of Montana showing improved range condition and increased *in utero* reproduction of adult moose following population reduction.

Years[1]	Relative Population Size	Range Condition	Percent Ovulating	Ovulations: 100 cows	Multiple Ovulation Rate
1958-59	High	Poor	71	71	0
1962-65	Low	Poor-Good	85	100	18
1968-71	Low	Good	87	107	23

[1]Data are from Peek (1962), Stevens (1966) and this study, respectively.

being approached in 1968-69. Increased wintering populations since 1969 appear to have resulted in range deterioration and a declining twinning rate. Despite increasing harvest quotas from 5 in previous years to 10 in 1971 and 1972 (recent hunter success has consistently been 100 percent of those hunting), no twins were observed on flights in February and March of 1973 (total counts of 29 and 42, respectively) although at least 2 pair were present the previous summer (Planz, personal communication). These twins may have belonged to cows which winter elsewhere, but in any event, winter comparisons show a further decline in observed twinning rates. Range assessment should be continued in this area to attempt to document what is occurring.

Productivity and Rate of Increase

The rate of increase, gross productivity and net productivity of Montana moose (Schladweiler and Stevens 1973) compare favorably with other areas. Rates of increase of Newfoundland, British Columbia, Ontario and Montana moose were 33, 36, 34 and 34 percent, respectively. Gross productivity of the same populations was 25, 26, 25 and 25 percent respectively. Net productivity, based on the proportion of yearlings in the yearling and older segment of the population, was 23, 24 and 20 percent for Newfoundland, Ontario and Montana, respectively. The latter statistic is also the percentage of the population which can be harvested annually without diminishing the base herd.

Although reproduction among males was not investigated in this study, available evidence indicates that yearling males are capable of breeding. Markgren (1969:209-210) concluded that male moose normally reach puberty as yearlings, but generally do not actively participate in the rut. Peek (1962:363) found sperm in the testes and epididymides of 2 yearling and 13 older bulls killed after mid-October in the Gravelly-Snowcrest area of Montana, and Houston (1968:60-61) found 92 percent of the yearlings taken after 20 September in the Jackson Hole area of Wyoming had developed sperm in their testes. The latter two investigators assumed yearlings to be physiologically capable of breeding, although Peek (1962:364) reports definite dominance of large, aggressive bulls over others. Markgren's (1969:210) conclusion that practically all antlered bulls are potential members of the breeding population probably applies to Montana moose as well.

Breeding Season, Gestation Period and Calving Season

Possible methods of determining the time of estrus are listed by Markgren (1969:162) as: (1) observed matings, (2) back-dating from calving dates, (3) ovarian studies, and (4) aging of embryos and embryonic tissue. These data also provide information on the calving season if the gestation period is known. Hosley (1949:6) considered the gestation period to be about eight months, while Peterson (1955:99) stated that it generally is conceded to be 240 to 246 days. Verme (1970:403) gives an average gestation period of 242 days for three Michigan calves born in captivity. Markgren (1969:162-163) summarized Swedish and Russian studies of confined or semi-confined cows indicating an average gestation period of 235 days for 24 pregnancies.

In this study, breeding and calving season determinations were based on calving data and aging of embryos or embryonic tissue following Markgren (1969:180-190). After assigning an age to an embryo, conception dates were determined and birth dates calculated using both 235 and 242 day gestation periods. The same method, in reverse order, was applied to field observations of calves estimated to be less than 10 days old. Checking these two approaches against one another indicated that a 235 day gestation period may be more nearly correct for Shiras moose. The majority of birth dates based on aged embryos and a 235 day gestation period fall in the same period as those based on observations of very young calves. Likewise, conception dates based on calf observations agree very well with those based on aged embryos when a 235 day gestation period is used. The 242 day gestation period gave birth dates 1 week later and conception dates 1 week earlier than they appeared to be.

Further evidence for a 235 day gestation period was obtained from ovulation data which showed a significantly higher incidence of ovulation in October versus September samples among both yearlings and adults (Table 28). Using a 242 day gestation period and calving data from field observations would put a much higher percentage of the cows ovulating in September than is supported by the data.

Conception and birth dates estimated from both embryos and calving data, and a 235 day gestation period show the peak of the rut to be in early October, with the peak of calving in late May and early June (Figure 5). These rutting season dates agree with those given for

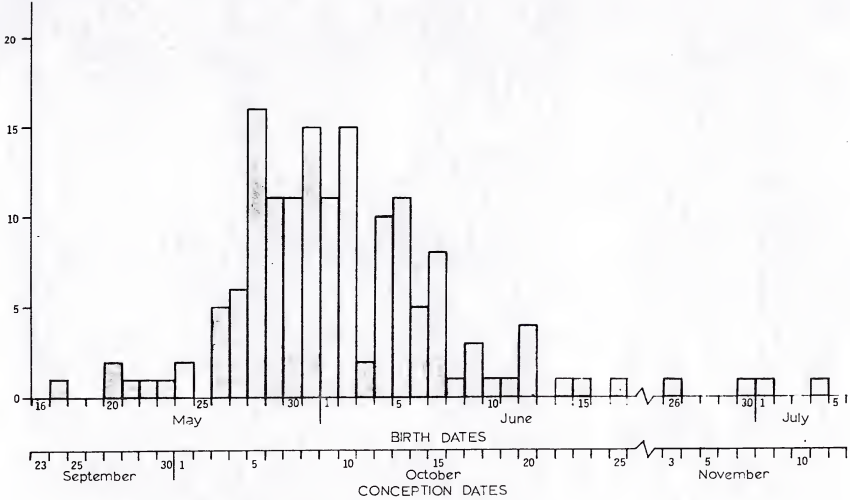

Figure 5. Conception dates (lower line) and corresponding birth dates (upper line) for Shiras Moose in Montana, based on estimated ages of embryos and calves less than 10 days old, and a 235 gestation period.

Shiras moose by Altmann (1959), Denniston (1956) and Peek (1962). Peterson (1955:62), Markgren (1969:191), LeResche (1968:954) and Altmann (1959:420) all noted calving in the period indicated by our data. Denniston (1956), however, believed calving occurred mainly in late April and May in Jackson Hole, Wyoming, which seems unlikely if, as he states, the rut occurs from mid-September through early November.

Our four late calving dates probably resulted from matings during recurrent estrus (Markgren 1969:166-170), though late breeding may also reflect delayed estrus among some younger animals. Late breeding through recurrent estrus appears to be an uncommon occurrence in Montana although Markgren (1969:170) felt that it was comparatively common in some parts of Sweden.

Decimating Factors

Malnutrition - Effects of forage quantity and quality on calf production and survival were previously covered. Actual starvation generally affects calves of both sexes and older animals, especially females (Houston 1968:71). In the absence of hunter harvest, most moose populations would probably be regulated by such malnutrition related losses. In these situations it appears that few calves would survive in most years but that survival of those reaching yearling age would probably be high, with low calf survival being balanced by low adult mortality. However, carrying capacity on ranges where hunting is not helping control populations would probably be lower than with hunting.

Predation - Predators capable of regularly taking moose are relatively scarce or absent from most Montana moose ranges. Timber wolves *(Canis lupus)*, formerly found throughout much of the state, currently occur with regularity only in the vicinity of Glacier National Park, although a few recent sightings have been reported from Yellowstone National Park. Where they occur, wolves are too few to have much impact on Montana moose populations. Black bears *(Ursus americanus)* have been reported as important predators on moose calves in Alaska (Chatelain 1950:231, Spencer and Chatelain 1953:550). However, another Alaskan study (LeResche 1968:956) concluded that they were unimportant predators although brown bears *(Ursus arctos)* were observed preying on moose. Black and grizzly bears *(Ursus arctos horribilis)* have been reported feeding on moose carcasses in Montana (McDowell and Moy 1942) but evidence was insufficient to determine cause of death. Black bears are considered ineffectual predators on Montana moose, although they may take an occasional young calf. Grizzly bear populations in Montana are of low density and too scattered to be a threat to any moose population. Mountain lion *(Felis concolor)* populations, although widely distributed throughout mountainous portions of the state, are also of low density and they are unimportant moose predators. Overall, natural predation appears to be a negligible part of Montana's annual moose mortality, just as Houston (1968:79) concluded for Jackson Hole, Wyoming.

Parasites and Diseases - A large number of parasites and diseases have been identified from moose throughout their range. Peterson (1955: 181-192) reviewed the North American literature, and Neiland and Dukeminier (1972) presented a bibliography of parasites, diseases and disorders of northern hemisphere ruminants, including moose references, relatively complete through 1969. Many of these afflictions have been reported from moose in Montana or adjacent areas. With one possible exception, however, they are regarded as having little influence on moose populations. The significance of finding *Elaeophora schneideri* in one blind and three apparently healthy Montana moose in 1971 (Worley *et al.* 1972) remains unknown at present. This arterial worm has been shown to cause blindness, central nervous system damage and facial necrosis in elk. It also occurs in deer in several areas, but apparently does not affect them in the same manner. One to three reports of blind moose have been received the past several years, and although several of these animals have been necropsied, this parasite was implicated in only one case. Several additional moose heads collected from hunter harvested animals have also been negative for this parasite.

A number of instances of lesions and necrosis of the lower jaw bone and connective tissue were noted among jaw collections, but no specific records were kept. These normally occurred in older animals, were associated with impacted food, and appeared to have been caused by infection of wounds made by twigs during normal feeding activities. With the possible exception of *Elaeophora schneideri*, parasites and diseases are regarded as of little consequence to Montana moose populations. Houston (1968:79) reached the same conclusion regarding moose in Jackson Hole, Wyoming.

Accidents - Moose, especially young calves, encounter a variety of accidents. Among those listed by LeResche (1968) are drowning, entrapment by vegetation and injury inflicted by the dam. Peterson (1955:193) considered drowning a relatively important mortality factor among calves, and occasionally for adults as well. The most important accidental mortality factor in Montana appears to be collision with motor vehicles, including trains, and also appears to be somewhat selective of calves. Accidental deaths are a minor part of overall moose mortality rates in Montana.

Hunting - Hunter harvest, both legal and illegal, is the most important single mortality factor for most Montana moose populations. Moose hunting is regulated by issuing a limited number of permits valid only for restricted areas. Most allow the taking of one animal of any sex or age with one or two areas restricted to bull-only hunting in some years. Permittees successful in taking a moose may not apply for a permit for the next 7 years.

The extent of the illegal kill (poaching or mistaking moose for other big game) and crippling losses are unknown. The illegal kill does not appear to constitute a very important part of overall mortality except in certain local areas. In the upper Ruby River area, where only five permits have been given in recent years, the known illegal kill has approached or even exceeded the legal harvest in some years. This could be an important factor in the apparent failure of this population to increase in recent years.

Some concern has been voiced in Shiras moose literature that calves orphaned during fall hunting seasons are unable to survive. Dorn (1969: 36), although having no data of his own, reviewed the literature and stated "The increasing evidence that orphaned calves rarely survive the winter (Denniston 1956:112, Altmann 1958:158, Houston 1968:77)...suggests that a regulation or request to protect cows followed by a calf or calves may benefit productivity and yield". My own perusal of this literature showed that the "increasing evidence" was highly speculative and far from conclusive. Denniston (1956:112) offered no first-hand information on the subject, relying on reports of "competent observers". One of those cited was Daniels (1953) who reported that he had never seen an orphaned moose calf survive the feed ground routine. Artificial feed grounds are far from natural situations and his findings can hardly be expanded and applied to wild, free-roaming animals. Also cited were Brown and Simon (1947) whose statements, although not definite, seem to contradict those of Denniston. Altmann (1958:155) stated that in no case could the identity of individual animals under observation be carried through the winter, but she later states that "it is a known fact that if the dam is killed the moose-calf rarely survives the winter" (Altmann 1958:158). Again, no supporting information is given, either from her own or other studies. Houston (1956:77) was the only one who presented quantitative data on this subject. Field observations of one known and three presumably orphaned calves revealed that two died and two were presumed to have died during the winter.

To base a management decision for the protection of productive cows on such sketchy information (as suggested by Dorn 1969:36) appears to be somewhat premature. Sightings of lone calves during mid- to late-winter in the present study suggests that at least some calves survive under natural circumstances. Because the fate of orphaned moose calves was unknown, a proposal was drafted to study this aspect of survival as part of the present study. Unfortunately, several factors prevented its being undertaken. However, until such a study is completed, no restrictions should be imposed on the taking of productive cows in Montana. Since many, if not most, moose populations in the state appear to be harvested at a level below what they can sustain, such a restriction would not benefit moose populations as well as being unenforceable.

Overall mortality rates of moose in Montana are primarily a result of hunter harvest and nutritional inadequacies. The latter includes direct winter starvation losses, post-natal calf mortality, and the effect of inadequate nutrition on the incidence of yearling breeding and on adult pregnancy and twinning rates. In the absence of hunting, moose mortality would almost entirely be a result of malnutrition-related factors. In Montana, hunting serves a useful purpose in maintaining healthy, productive moose populations and helps prevent damage to moose habitat through over-use. Other mortality seems to be a minor factor, both individually and combined.

MANAGEMENT RECOMMENDATIONS

Based on the findings of this study, several management recommendations can be made which consider moose a renewable resource primarily utilized for recreational hunting. Management techniques which benefit moose populations will also enhance the non-hunting publics chances to appreciate this resource. Montana moose hunting is on a limited permit basis with any sex or age animal legal in most areas. No changes in the basic framework for setting seasons and harvest quotas are recommended.

The small home ranges found in this study agree with those from studies in other areas, and indicate that hunting units should be as small as practicable. The initial step toward improving management of moose populations in most of Montana should be determining past harvest distribution from questionnaires and, where feasible, reducing the size and increasing the number of hunting units. This would improve harvest distribution and increase overall harvests in many of our present hunting units by maintaining current harvest levels in accessible portions and directing more pressure to previously lightly-hunted portions by making them separate units. In many instances it appears that a single drainage as small as 50 square miles which has excellent access might constitute a hunting unit. Both the Squaw Creek and Middle (Hyalite) Creek drainages on the Lower Gallatin Study Area are examples of where this could be accomplished.

Study results also indicated that many, if not most, Montana moose populations are affected to some degree by mortality caused by nutritional inadequacies which are primarily reflected in increased early post-natal calf losses. Where such losses appear to be significant, increased harvest removals could substitute for most other mortality factors. Harvest quotas must be adjusted to maintain key browse plants in desired condition (vigorous plants not continually in a severely hedged or decadent state). Utilization levels that maintain desirable conditions in vigorous willow plants (50, 70 and 90 percent in mild, average and severe winters, respectively) need to be reduced to allow recovery of plants in deteriorated condition. Adequate harvest removals could probably have prevented the deterioration of the moose range in the Absaroka Area, which in turn could have supported a relatively stable herd at a much higher level, providing more hunting potential than has been the case in the recent past.

Intensive management, based on maintenance of forage supplies in desirable condition, would result in decreased potential for trophy type hunting unless increased permits were bull-only permits added to the either-sex quota for a unit. Such a system would allow manipulation of sex and age composition while maintaining or increasing current productivity with increased harvests. This level of management will probably be impossible to achieve with population segments in remote areas unless hunter demand increases substantially. However, some of these populations migrate to more accessible winter ranges and could be harvested at that time. Antler shedding begins around the first of December, with older bulls losing their antlers before younger ones, resulting in many, if not most bulls being antlerless during such late hunts. Under intensive management, hunters desiring a trophy would have to spend more time and effort, and/or hunt in the more remote areas where hunting pressure and resultant harvests are lighter.

Very few bulls would be likely to attain "trophy" size antlers under unlimited bull hunting, and such a system is not advocated.

The best license system appears to consist of either-sex permits, with the possibility of adding bull-only permits and/or late hunts when or where additional harvests are deemed necessary. Areas with added bull permits would have fewer large bulls.

The best time to classify moose is late fall-early winter when snow covers the ground, preferably prior to antler shedding, but prior to the shift to heavier cover that occurs in mid-winter.

Post hunting season ratios approaching 40 calves per 100 adults, and twinning rates of 12 to 15 percent appear to be maximums for Montana's moose populations. Adequate winter samples giving ratios below 30 calves per 100 adults probably indicate nutritional inadequacies and the need for increased harvest quota. Limited data indicate that where population reductions have occurred subsequent winter observations have shown increases in these figures.

Where harvest quotas are not based on browse condition and trend, they could be based on the knowledge that there is approximately a 20 percent recruitment of yearlings to the population annually, meaning that this percentage of the population can be removed annually without reducing the base herd. Population surveys and average hunter success would indicate the number of permits needed in a given area to achieve this level of harvest.

Extensive willow bottom areas important to moose on public lands should be considered for protection from domestic livestock grazing.

From an elevational standpoint, most logging in Montana is not located where it could potentially increase winter moose forage. On the other hand, road development associated with logging can be detrimental if roads follow stream bottoms important to wintering moose. Roads in these areas provide increased access and potential for human-moose conflicts, especially from snowmobile use. Placement of roads in critical bottoms should be avoided. Based on limited data, clearcut logging in the spruce-fir timber type on moose summer range appears to be detrimental to moose whereas clearcutting in the lodgepole pine type can result in increased use by moose. Maintaining coniferous cover types adjacent to important moose winter range areas should be a consideration during timber sale planning.

Habitat manipulation, especially tree cutting and/or prescribed burning to rehabilitate or enlarge present moose winter ranges, or to create new ones, should receive additional research effort. Initial efforts would probably be most profitable in the aspen type associated with the Douglas-fir type on lower elevation winter ranges. This is an endeavor in which the aid of sportsmens groups could be enlisted to minimize costs. Treating 20-25 percent of the area every 5-10 years would probably be the most practical technique.

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APPENDIX

WEIGHTS OF SHIRAS MOOSE IN MONTANA

As part of this study, moose were weighed whenever possible. Most moose weighed were from the fall harvest, with some accidentally or illegally killed animals weighed during other seasons. In the following discussion whole weight refers to the weight immediately after death and does not take into account any blood loss. Field-dressed weight is of an animal from which all viscera have been removed. Partial weight refers to an animal from which all viscera, plus head and/or feet, have been removed while carcass weight indicates weight of an animal lacking viscera, head, feet and hide.

Between 1965 and 1971 field-dressed weights were obtained from 158, partial weights from 66 and carcass weights from 4 animals. Whole, field-dressed, and carcass weights were each obtained from five additional animals (one adult male, two adult females, one yearling female, and one female calf). Weights of 18 sets of feet, 34 heads, and 11 hides were obtained from animals for which field-dressed weights were also obtained, providing a basis for estimating field-dressed weights of all animals for which partial weights are available. Weights of heads and feet were with hide (and for bulls, antlers) attached. Heads were removed at the atlas-occipital condyle joint. Hide weights were exclusive of the feet as they are normally removed by hunters. Age estimates of weighed moose were based on mandibular wear criteria of Passmore, *et al.* (1955).

Percent weight loss due to evisceration for the five animals weighed whole were: female calf, 35.5; yearling female, 25.8; adult females, 35.0 and 33.6; adult male, 18.4. The only published data found for weight loss from evisceration of moose (Peterson 1955:78) show losses of 22.0 and 23.0 percent for two adult male *A. a. andersoni* taken in mid-September and mid-October, respectively. Our data, although admittedly very limited was therefore felt to be of value. The calf was the only one of the five animals weighed whole which was obtained during Montana's general big game season. The yearling female and adult male were obtained prior to the rut and would be expected to be in better physical condition, based on whole body weight. The adult females were taken after December 1, and had probably experienced a loss in weight. According to Verme (1970) adults weigh the most just prior to the rut and both sexes, but especially bulls, experience a weight loss during the breeding season, and normally on through the winter as well.

Using our data as a guide, and realizing when these animals were taken in relation to the rut, and that our general hunting season starts after the peak of the rut, some assumptions were made on average weight loss due to evisceration of Shiras moose during Montana's general hunting season. An average weight loss due to evisceration of 30 percent was assumed for adult cows, and calves and yearlings of both sexes. A 25 percent loss was assumed for adult bulls.

Average weight loss from evisceration reported for other ungulates is 26.7 percent for white-tailed deer *(Odocoileus virginianus)* of all sex and age classes (Hamerstrom and Camburn 1950); 32 and 33 percent for adult male and adult female elk *(Cervus canadensis nelsoni)*, respectively (Quimby and Johnson 1951); 25.1 to 28.5 percent for Uganda kob *(Adenota kob)* of various sex and age classes (Ledger and Smith 1964); and 27 to 31 percent for pronghorns *(Antilocapra americana)* from several studies cited by O'Gara (1970).

Head weights averaged 10.0, 8.1, 8.8, and 11.2 percent of the field-dressed weights of calves and yearlings of both sexes, adult females and adult males, respectively. Feet averaged 6.5, 5.7, and 4.7 percent of the field-dressed weights of calves, yearlings and adults, respectively, with no difference between sexes. Hides averaged 9.1 percent of the field-dressed weights of all animals, sample sizes being too small to note any differences between individual sex-age groups. Field-dressed weights, including those calculated from partial or carcass weights using the percentages given above, are presented in Appendix Table 1. Small sample sizes for most individual wear classes necessitated grouping adult age data.

Carcass weights accounted for the following percentages of the whole weights of our five animals: female calf, 47.4; yearling female, 57.1; adult females, 48.2 and 52.0; adult male, 62.0. Peterson (1955:78) gives carcass yield percentages of 55.0 for an adult cow, and 60.0 to 64.0 for three adult bulls of *A. a andersoni*, but these were all obtained prior to when Montana's general hunting season opens. Our calf and two adult females were obtained during the period corresponding to that during which Blood *et al.* (1967) collected their animals (late November to early January), and carcass yields are within the ranges they found. As would be expected from animals taken prior to the peak of the rut, carcass yield of our yearling female was somewhat above, and that of the adult bull considerably above, the ranges presented by Blood *et al.* (1967) for these groups.

Carcass yields (as a percent of whole weight) were computed for all moose weighed using the assumed percentages for loss due to evisceration, and those obtained for heads, feet and hides (corrected to percentage of whole weight). Resultant carcass yields were 52.1, 54.0, 54.1 and 56.2 percent of the whole weight of calves, yearlings, adult cows, and adult bulls, respectively. These percentages are similar to those reported by Skuncke (1949:292) and Blood *et al.* (1967:265) for Swedish and Alberta moose, respectively, and was considered a further indication that our assumptions on weight loss due to evisceration are approximately correct for the period during which Montana moose are hunted. Reported carcass yields of other ungulates (Quimby and Johnson 1951, Hamerstrom and Camburn 1950, O'Gara 1970, Ledger and Smith 1964) are generally similar to those obtained for Shiras moose in Montana.

Using our data for percentages lost due to removal of viscera and other parts, factors were computed for converting partial weights to approximate whole weights (Appendix Table 2). Approximate whole weights included in Appendix Table 1 were calculated using these factors.

Our data indicate that yearling males are heavier than females of the same age, which does not agree with whole weight data presented by Blood *et al.* (1967:265) for yearling moose from Alberta. Skuncke (1949:290), however, indicated that males outweigh females as early as 6 months of age, the weight difference increasing with age. Chi-square tests (Steele and Torrie 1960) of actual whole and dressed carcass weights of yearlings obtained by Blood *et al.* (1967) were not significantly different (P>0.50) between sexes. Our field-dressed weights of yearlings also showed no significant difference (P>0.10) between sexes. Therefore, differences between our data and that of Blood *et al.* (1967) probably relate to sample size, seasonal and individual variation.

Markgren (1969:222) stated that the main increase in weight occurs during the first 2 years of life, with the weight curve flattening out after that and possibly even declining for older-aged females, while the weight curve for bulls apparently continues to rise beyond 10 years of age. The latter statement is apparently based on Skuncke's (1949:293) graphs, which are also presented by Peterson (1955:77). These interpretations are in general agreement with our data (Appendix Table 1) which, however, indicate a possible leveling off in weight of older aged males as well.

Blood *et al.* (1965:267) compared actual and estimated whole weights of the four North American moose races, but only for adults 3 years old or over. They concluded that individual and seasonal differences were probably more significant than racial differences. Including our wear class II animals as adults makes our data not strictly comparable to theirs, and undoubtedly lowered our means for both sexes, and broadened the range for males. The fact that our heaviest weights approach or exceed those for other races further indicates that racial differences probably are not great, and that our conversion factors are probably applicable to other subspecies.

APPENDIX TABLE 1. Field-dressed and approximate whole weights (in pounds) of Shiras moose in Montana.

	MALES					FEMALES				
		Field-Dressed Weights		Approximate Whole Weights*			Field-Dressed Weights		Approximate Whole Weights*	
Wear Class	Sample Size	Mean	Range	Mean	Range	Sample Size	Mean	Range	Mean	Range
Calf	9	219	180-255	313	257-365	14	186	120-225	266	172-322
I(yearling)	28	376	275-458	538	393-655	15	360	278-411	515	398-588
II-IV	51	516	335-840	686	446-1117	35	466	325-630	666	465-901
V-VII	24	593	450-770	789	599-1024	14	504	323-730	721	462-1044
VIII+	11	593	425-770	789	565-1024	15	443	303-560	633	433-801
Unclassified Adults	11	568	425-671	755	565-892	6	449	370-500	642	529-715
All Adults (II+)	97	550	335-840	732	446-1117	70	467	303-730	668	433-1044

*Computed using the factors provided in Appendix Table 2.

APPENDIX TABLE 2. Factors for obtaining approximate whole weights from partial weights of Shiras moose taken during Montana's general hunting season.

Known Partial Weights	Factor to Multiply by To Obtain the Approximate Whole Weight of:			
	Calf	Yearling	Adult Cow	Adult Bull
Field-dressed	1.43	1.43	1.43	1.33
Field-dressed minus Feet	1.53	1.52	1.50	1.40
Field-dressed minus Head	1.59	1.55	1.57	1.50
Field-dressed minus Head and Feet	1.71	1.66	1.65	1.58
Carcass	1.92	1.85	1.85	1.78

APPENDIX TABLE 3. Plant species comprising less than 5 percent of the total moose diet in all seasons in various areas of Montana, as determined by rumen sample analysis and feeding site examination. (See Tables 7-11 for sample sizes and plant species comprising over 5 percent of the total diet in at least one season for these areas).

SUMMER	FALL	WINTER	SPRING
	Lower Gallatin Study Area		
Symphoricarpos spp. *Aquilegia* spp. *Delphinium* spp. *Geranium viscossissimum* *Trifolium* spp.	*Arctostaphylos uva-ursi* *Artemisia tridentata* *Berberis repens* *Ceanothus velutinus* *Crataegus* spp. *Pinus contorta* *Rubus* spp. *Sambucus* spp. *Shepherdia canadensis* *Symphoricarpos* spp. *Aster canescens* *Aster* spp. *Cirsium* spp. *Erigeron* spp. *Geranium viscossissimum* *Lupinus* spp. *Tragopogon dubius* *Verbascum thapsus*	*Alnus* spp. (bark) *Artemisia tridentata* *Berberis repens* *Betula glandulosa* *Ceanothus velutinus* *Crataegus* spp. *Juniperus* spp. *Physocarpus malvaceus* *Pinus contorta* *Populus* spp. (bark) *Rubus* spp. *Sambucus* spp. *Shepherdia canadensis* *Symphoricarpos* spp. *Vaccinium membranaceum* *Cirsium* spp.	*Amelanchier alnifolia* (bark) *Arctostaphylos uva-ursi* *Berberis repens* *Chimaphila umbellata* *Gaultheria* spp. *Rubus* spp. *Symphoricarpos* spp. *Vaccinium membranaceum* *Cirsium* spp. *Fragaria* spp. *Geranium viscossissimum*
	Upper Madison Study Area		
Aster spp. *Potentilla* spp.	*Artemisia tridentata* *Berberis repens* *Rosa* spp. *Shepherdia canadensis* *Symphoricarpos* spp. *Aster* spp. *Cirsium* spp. *Phlox* spp.	*Acer glabrum* *Alnus* spp. *Amelanchier alnifolia* *Cornus stolonifera* *Picea engelmanni* *Pinus flexilis* *Potentilla fruticosa* *Rosa* spp. *Shepherdia canadensis* *Symphoricarpos* spp. *Achillea lanulosa* *Cirsium* spp.	*Berberis repens* *Lonicera* spp. *Rosa* spp. *Rubus* spp. *Caltha leptocephala* *Cirsium* spp. *Fragaria* spp. *Goodyera oblongifolia* *Potentilla* spp. *Rumex* spp. *Taraxacum* spp. *Valeriana dioica*

APPENDIX TABLE 3. Continued

SUMMER	FALL	WINTER	SPRING
	Gravelly-Snowcrest		
Rosa woodsii *Shepherdia canadensis* *Symphoricarpos albus*	*Cornus stolonifera* *Prunus virginianus* *Shepherdia canadensis* *Symphoricarpos albus* *Vaccinium scoparium*	*Cornus stolonifera* *Gutierrezia sarothrae* *Potentilla fruticosa* *Prunus virginianus* *Rosa woodsii* *Sambucus* spp. *Symphoricarpos albus*	
Eriogonum spp. *Delphinium* spp. *Lupinus* spp. *Potentilla gracilis* *Rumex acetosella*	*Cirsium foliosum* *Lemna trisulca* *Lupinus* spp.	*Cirsium foliosum* *Rudbeckia occidentalis*	
	Red Rock Lakes		
Cornus stolonifera *Lonicera involucrata* *Populus tremuloides* *Populus tremuloides* (bark) *Potentilla fruticosa* *Prunus virginianus* *Ribes inerme* *Rosa woodsii* *Symphoricarpos oreophilus*	*Abies lasiocarpa* *Berberis repens* *Cornus stolonifera* *Populus tremuloides* *Populus tremuloides* (bark) *Pseudotsuga menziesii* *Ribes* spp. *Rosa woodsii* *Symphoricarpos oreophilus*	*Abies lasiocarpa* *Acer glabrum* *Amelanchier alnifolia* *Clematis columbiana* *Cornus stolonifera* *Lonicera involucrata* *Populus tremuloides* *Populus tremuloides* (bark) *Prunus virginianus* *Pseudotsuga menziesii* *Ribes inerme* *Ribes setosum* *Ribes* spp. *Rosa woodsii* *Shepherdia canadensis* *Spiraea betulifolia* *Symphoricarpos oreophilus*	
Epilobium angustifolium *Fragaria virginiana* *Geranium richardsonii* *Geranium viscosissimum* *Geum macrophyllum* *Lupinus argenteus* (2 varieties) *Rudbeckia occidentalis* *Smilacina stellata* *Taraxacum officinale*	*Aster conspicuus* *Geum macrophyllum*	*Aster foliaceus*	