Relations of moose, cattle, and willows in southwestern Montana

by Robert Donald Dorn

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Fish and Wildlife Management
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Abstract:
The Shiras moose {Aloes aloes shirasi) was studied on Red Rock Lakes National Wildlife Refuge in southwest Montana from June 10, 1968 to March 17, 1969 to determine use of vegetation types, food habits, sex and age ratios, and the extent of moose-cattle competition. A means for checking the adequacy of a sample obtained by the feeding site method of food habits analysis was presented. Vegetation of the study area was analyzed quantitatively. The average height of a willow (Salix) species was related to its most common habitat. Observations of moose in the willow type accounted for 84 percent of the total in summer and 93 percent in winter. Food habits primarily determined the use of vegetation types. Browse accounted for 98.3 percent of all forage used by moose in summer with Salix myvtillifolia, Betula glandulosa, Salix geyeriana3 and Salix planifolia accounting for 58.1, 11.8, 9.6, and 6,7 percent, respectively. In winter browse accounted for 99.8 percent of the forage used by moose with S. myvtillifolia, S. planifolia, S. bebbiana, and S. geyeriana accounting for 25.0, 24.2, 15.4, and 10.5 percent, respectively. The factors determining the amount of various plant species in the diet of moose were availability, adaptation, palatability, and habit. It appeared that all species of willow present in this study were potentially important as forage for moose at some time during the year, especially in winter. Salix Wolfii, S, myrtillifolia, S. geyeriana, and S. bebbiana accounted for 50.2, 15.9, 11.2, and 10.9 percent, respectively, of all browse used by cattle in the willow and sedge types in summer. Forage competition between moose and cattle was not significant under conditions prevailing during this study. Competition would be expected under certain conditions. Forage competition between moose and beaver (Castor canadensis) was greater than competition between moose and cattle but was not significant. Observation data show that in summer bulls were more readily identified from the ground than cows and that many calves were not observed from the ground. The data also show that observed sex and age ratios were influenced by home range and migration patterns and differential use of vegetation types between sexes. September ratios obtained from aerial observations were probably most reliable for the composition of the breeding population. Only a small proportion of adult bulls wintered on the study area. Resident, summer, winter, and transient population segments appeared to be using the area. The importance to management of movements and twinning rates was discussed. The range appeared to be in satisfactory condition during the study except for one local area. Management recommendations were given.

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of

MASTER OF SCIENCE

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Approved:

Head, Major Department

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MONTANA STATE UNIVERSITY
Bozeman, Montana

June, 1969

ACKNOWLEDGMENT

Appreciation is extended to the following for their assistance or cooperation during the study: Dr. D. C. Quimby, Montana State University, for setting up the study and for guidance and suggestions in preparing the manuscript; Dr. R. J. Graham and Dr. R. L. Eng, Montana State University, for reading the manuscript and offering suggestions for its improvement; Dr. W. E. Booth, Montana State University, for many hours at verification of plant specimens; Dr. G. W. Argus, University of Saskatchewan, Saskatoon, for verification of willow specimens; Mr. Thomas Mussehl and Mr. Philip Schladweiler, Montana Fish and Game Department, for assistance in various phases of the study; Mr. Kenneth Greer and staff, Montana Fish and Game Department, for gross separation of rumen samples; other personnel of Montana Fish and Game Department for assistance and cooperation; U. S. Fish and Wildlife Service personnel and residents of Lakeview, Monida, and the Centennial Valley for assistance, cooperation, and hospitality; and Mr. George Kamps, Montana State University, for making available feeding site data for mule deer and white-tailed deer. The study was financed by the Montana Fish and Game Department under Federal Aid Projects W-98-R-9 and W-73-R-14.

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ABSTRACT

The Shiras moose (*Alces alces shirasi*) was studied on Red Rock Lakes National Wildlife Refuge in southwest Montana from June 10, 1968 to March 17, 1969 to determine use of vegetation types, food habits, sex and age ratios, and the extent of moose-cattle competition. A means for checking the adequacy of a sample obtained by the feeding site method of food habits analysis was presented. Vegetation of the study area was analyzed quantitatively. The average height of a willow (*Salix*) species was related to its most common habitat. Observations of moose in the willow type accounted for 84 percent of the total in summer and 93 percent in winter. Food habits primarily determined the use of vegetation types. Browse accounted for 98.3 percent of all forage used by moose in summer with *Salix myrtillifolia*, *Betula glandulosa*, *Salix geyeriana*, and *Salix planifolia* accounting for 58.1, 11.8, 9.6, and 6.7 percent, respectively. In winter browse accounted for 99.8 percent of the forage used by moose with *S. myrtillifolia*, *S. planifolia*, *S. bebbiana*, and *S. geyeriana* accounting for 25.0, 24.2, 15.4, and 10.5 percent, respectively. The factors determining the amount of various plant species in the diet of moose were availability, adaptation, palatability, and habit. It appeared that all species of willow present in this study were potentially important as forage for moose at some time during the year, especially in winter. *Salix wolfii*, *S. myrtillifolia*, *S. geyeriana*, and *S. bebbiana* accounted for 50.2, 15.9, 11.2, and 10.9 percent, respectively, of all browse used by cattle in the willow and sedge types in summer. Forage competition between moose and cattle was not significant under conditions prevailing during this study. Competition would be expected under certain conditions. Forage competition between moose and beaver (*Castor canadensis*) was greater than competition between moose and cattle but was not significant. Observation data show that in summer bulls were more readily identified from the ground than cows and that many calves were not observed from the ground. The data also show that observed sex and age ratios were influenced by home range and migration patterns and differential use of vegetation types between sexes. September ratios obtained from aerial observations were probably most reliable for the composition of the breeding population. Only a small proportion of adult bulls wintered on the study area. Resident, summer, winter, and transient population segments appeared to be using the area. The importance to management of movements and twinning rates was discussed. The range appeared to be in satisfactory condition during the study except for one local area. Management recommendations were given.

INTRODUCTION

This investigation was another segment of the ecological studies of the Shiras moose in southwestern Montana. Field work was conducted full-time in summer and winter and part-time in fall from June 10, 1968 to March 17, 1969. The main objectives were to determine use of vegetation types, food habits, sex and age ratios, and the extent of moose-cattle competition in a predominantly willow-sedge area. Previous studies in southwestern Montana were by Knowlton (1960), Peek (1962), Stevens (1965), and Stevens (1967). McMillan (1953), in Yellowstone National Park, and Denniston (1956), Harry (1957), and Houston (1968), in Jackson Hole, Wyoming, also studied the Shiras moose.

AREA DESCRIPTION

The study area, about 22 square miles, was mainly on the Red Rock Lakes National Wildlife Refuge in the Centennial Valley, Beaverhead County, Montana (Figure 1). The Red Rock Lakes lie in a down-dropped basin at 6,600 feet elevation (Banko 1960:40-41). The Centennial Mountains rise abruptly to nearly 10,000 feet immediately to the south and the foothills of the Gravelly Range lie to the north. Alden (1953) discussed area geology and Nielson and Farnsworth (1965) classified area soils.

The area has long, cold winters and short, cool summers. Climatological data for Lakeview, on the study area, are presented in Table I. Snow cover is variable from extensive drifting.

TABLE I. CLIMATOLOGICAL DATA FOR LAKEVIEW, MONTANA (U. S. DEPARTMENT OF COMMERCE, WEATHER BUREAU 1965, FARNES 1969).

Average annual precipitation	19.96 inches
Average annual snowfall	142.1 inches
Mean temperature	
Annual	34.6°F
January	10.3°F
July	58.9°F
Temperature extremes	
Maximum	91° F
Minimum	-44° F
Snow cover 1/	
January 2, 1969	26 inches
January 31, 1969	71 inches
March 3, 1969	78 inches

1/ Data from Farnes (1969) for snow survey course in Douglas-fir--spruce-fir ecotone at 6,930 feet elevation.

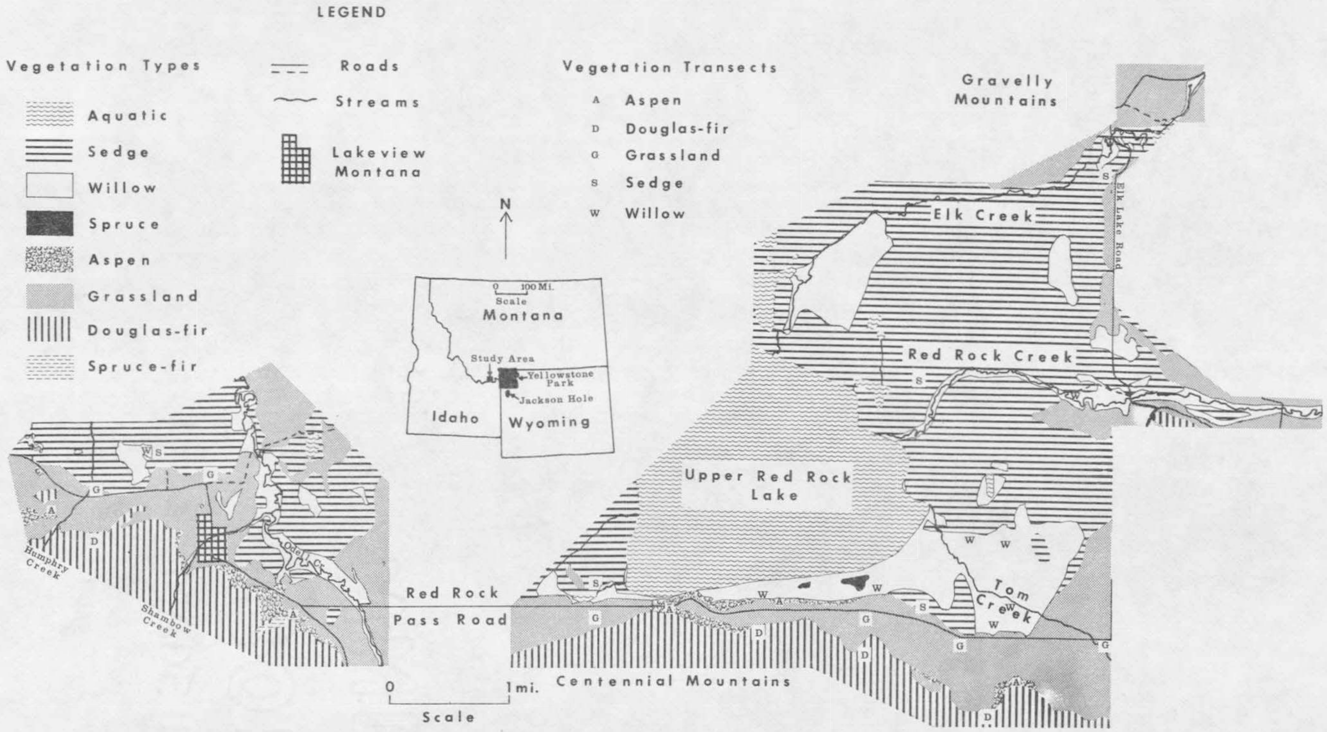


Figure 1. Location of the study area, vegetation types, and vegetation transects.

Red Rock Lakes Refuge, now about 40,000 acres, was established in 1935 to preserve the trumpeter swan (*Olor buccinator*). The primary land uses in non-swan habitat are cattle grazing and haying. Recreational use is heavy in some areas.

Moose were observed in the Centennial Valley shortly after 1900 but were not numerous until after 1940. A conspicuous increase occurred about 1950 (Banko 1951:1). Houston (1968:16-17) described this same pattern for Jackson Hole, Wyoming. Houston (1968:13, 35) also reported a progressive increase in mean annual snowfall in Jackson Hole from 122 inches in the 1912-1930 period to 179 inches in the 1951-1966 period. Data for Lakeview (U. S. Department of Commerce, Weather Bureau 1955:40, 1965:42) show a similar increase from 132 inches in the 1943-1952 period to 159 inches in the 1951-1960 period. This may have resulted in conditions which increased favorable habitat for moose at the same time that the grizzly bear (*Ursus horribilis*) and timber wolf (*Canis lupus*), the primary predators of moose (Houston 1968:79, Mech 1966:114), were being reduced. Changes in land use may also have influenced the increase.

Over-utilization of browse resulted from the population increase on the refuge around 1950 (Banko 1951:2). A die-off of willows occurred shortly after from unknown causes. The refuge was opened to moose hunting by permit in 1952 when the moose population at peak use was about 60 animals. A total of 128 moose was killed over eight successive seasons. A closure of 5 years followed. Five permits were issued annually from 1965 to 1968 and 19 moose were killed (Refuge records). The population at peak use in 1968-69 was about 55 animals.

METHODS

Vegetation

The canopy-coverage method (Daubenmire 1959), line-intercept method (Gates 1949:36-38), point-centered quarter method (Cottam and Curtis 1956), and habitat inventory technique (Webster 1965) were used to sample vegetation types. Sampling dates, sample size, and methods for each vegetation type are presented in Table II. Sample transects were mostly selected in areas frequented by moose and near section lines or landmarks (Figure 1). Transects were 300 feet long with 33 feet 4 inches between plots or points. Upper Red Rock Lake, randomly sampled by the refuge biologist, represented the aquatic type. Vegetation types were mapped from ground observations and aerial photos.

Willow heights were measured with an 11-foot pole marked in feet. Heights over 20 feet were estimated. The closest plant sampling technique (Cole 1963:7) was used for common species. Less common species were merely sought out. Heights were first measured within about 50 yards of the transects in the willow type. Insufficient samples were then completed in areas at least one-quarter mile from any transect. The degree of difficulty in locating plants of a species to measure was proportional to the relative abundance of that species. Frequency indices for each species could then be determined. If at least ten plants of a species were found within about 50 yards of each of the ten transects in the willow type, the frequency index was 100. The obtainable sample was also considered for rare species. Only ten plants of one species were found, but all were near a transect for a frequency

TABLE II. SAMPLING DATES, SAMPLE SIZE, AND METHODS USED FOR VEGETATION TYPE ANALYSES.

Vegetation Type	Sampling Dates	No. of Transects	No. of Plots or Points	METHOD[1]		
				Tree Group	Shrub Group	Herb Group
Aquatic	8/24		50			Habitat inventory
Sedge	8/27-28	5	50		Line-intercept	Canopy-coverage
Willow	7/3-7	10	100	Line-intercept	Line-intercept	Canopy-coverage
Spruce	7/23-25	3	30	Line-intercept Point-quarter	Line-intercept	Canopy-coverage
Grassland	6/25-7/2	6	60		Canopy-coverage	Canopy-coverage
Aspen	7/15-18	5	50	Line-intercept Point-quarter	Line-intercept	Canopy-coverage
Douglas-fir	7/19-20	4	40	Line-intercept Point-quarter	Line-intercept	Canopy-coverage
Spruce-fir	7/19	1	10	Line-intercept Point-quarter	Line-intercept	Canopy-coverage

1/ See text, page 5, for citation.

index of 10. For another species 35 plants were found, but only 5 were near a transect for a frequency index of 5. The larger number of plants found of the latter species indicated a higher abundance than for the former despite the frequency index figures.

Representatives of most plant species were collected and are filed in my personal collection, in the herbarium at Montana State University, and/or at Red Rock Lakes Refuge. Plant nomenclature follows Porter (1967) for the genus *Salix* and Booth (1950) and Booth and Wright (1966), with some unpublished corrections, for other plants unless otherwise noted.

Ninety-one willows identified in summer were tagged to facilitate identification of willows in winter. General distribution of willow species was determined from field observations.

Vegetation Type Use

Observations of moose in summer, June 10 to September 30, were mostly from roads and were aided by a 7 x 50 binocular and a 25X spotting scope. A regular route was traversed nearly every day shortly after sunrise. Observed moose were recorded by vegetation type and location. Few evening observations were made. Observations in winter, December 20 to March 17, were incidental to the study of food habits except for an intensive survey twice each month by snowmobile. Nearly all animals present were probably observed during these surveys except in December and January. A feeding site examined while snow tracking without observing the animal was considered an observation.

Food Habits

Food habits of moose and cattle in summer and of moose in winter were determined from feeding site observations (Knowlton 1960:162-163). An instance of use on browse was utilization of one leaf or one leader in summer and one leader in winter and on forbs, grass, and grass-like plants was utilization of one leaf or one stem. An instance of use on bark was utilization of a volume estimated to be equivalent to an average leader. Food habits data of cattle included only browse use in the willow and sedge types. Food habits of moose in fall were determined from rumen samples from hunter-killed moose. Rumen analysis was as described by Knowlton (1960:163) except measurements were to the nearest 0.5 cc. In winter each vegetation type was surveyed for feeding sites in approximate proportion to its occurrence on the study area. Winter data from the spruce-fir and Douglas-fir types were partly from areas immediately adjacent to the study area. Data from feeding sites and rumen samples were compiled by the aggregate volume method (Martin, *et al.* 1946).

The adequacy of a sample obtained by the feeding site method can be determined with a plotted curve similar to the species:area curve used by plant ecologists (Oosting 1956:44-47). The accumulated total of instances of use on all plant species is plotted on the x axis. The percent of the accumulated total of instances of use that is accounted for by an important species is plotted on the y axis (Figure 2). The three plant species with the most use should each be used for plotting

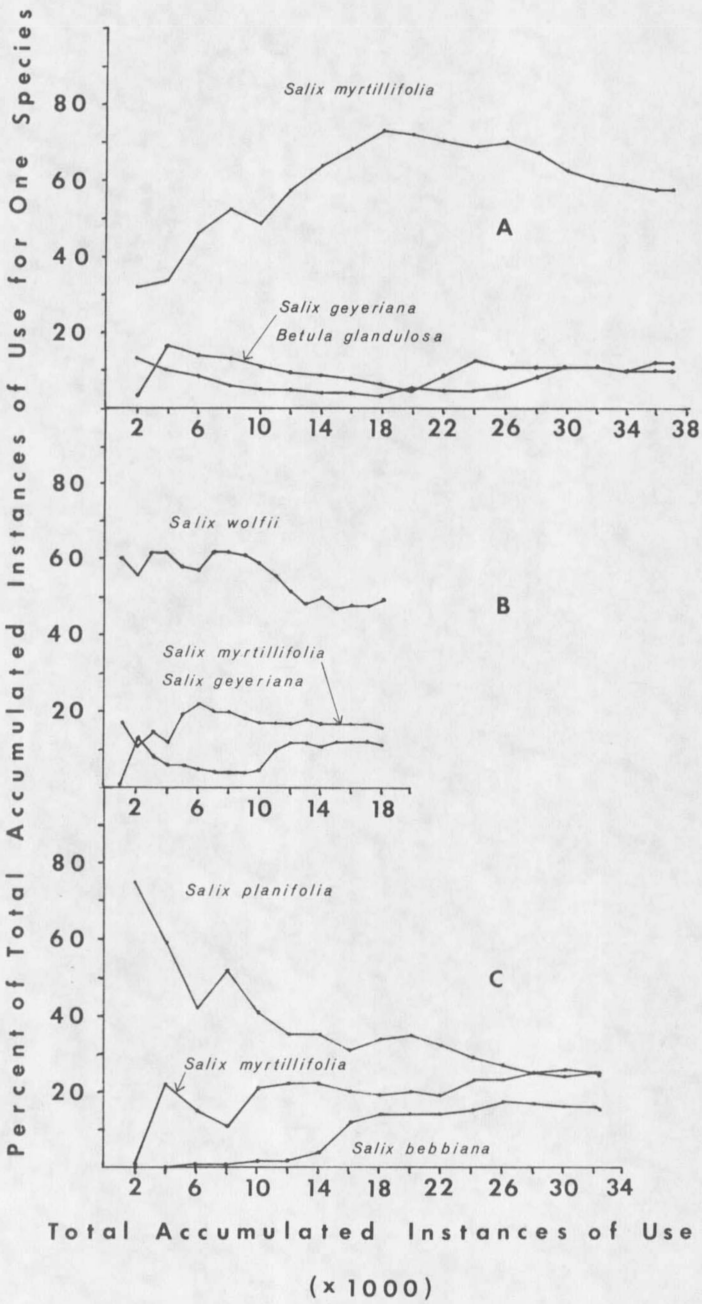


Figure 2. Instances-of-use curves for determining the adequacy of a sample obtained by the feeding site method of food habits analysis: A, moose in summer; B, cattle in summer; C, moose in winter.

a separate curve. This minimizes misinterpretations which are more probable when only one curve is used. The sample is adequate when the curves level off. Arbitrary values, depending on the confidence desired, can be selected for determining when the curves level off. In general, the smaller the average number of instances of use per feeding site, the more demanding should be the criteria. An example is: no more than a 3 percent change with an added 5,000 instances of use for feeding sites averaging about 1,000 instances of use. This point can be determined in the calculations without plotting a curve (Korschgen 1963:320), but a curve helps to minimize misinterpretations of calculated results by providing a continuous, developing pattern which can be examined visually, and it also facilitates the estimation of the amount of additional data that are needed. If food habits data are segregated by vegetation type, curves are needed for each type. The basic unit of instances of use on the x axis should be about twice the average number of instances of use per feeding site. In this study the averages, for total use, were 920 for moose in summer, 594 for cattle, and 928 for moose in winter. The basic units selected were 2,000, 1,000, and 2,000 instances of use, respectively. Small intervals between the unit divisions on the x axis and a long y axis, within limits, give the best curve.

Sex and Age Ratios, Population Trends, and Movements

Data on sex and age ratios, population trends, and movements were recorded with data on the use of vegetation types. Four aerial surveys were flown in fixed-wing aircraft to supplement these data. Nearly all moose that were present were probably observed during the aerial surveys except those in the coniferous timber types. This agrees with Stevens' (1965:31) observations. Yearlings were considered adults and individual moose were not knowingly recorded more than once daily.

Most cows without calves were sexed by the presence of a light-colored patch of hair around the vulva. This method, previously used by refuge personnel, Houston (1968:7), and others, appears to be reliable in this area. In all ground observations, only one cow was noted with an obscure patch and no bulls were observed with a patch.

RESULTS AND CONCLUSIONS

Vegetation

Quantitative results of the vegetation analysis are presented in Tables III and IV and in Tables IX-XVIII in the appendix. Eight vegetation types were differentiated (Figure 1).

Aquatic Type

This type was mainly in Upper Red Rock Lake. It was dominated by *Potamogeton richardsonii*, *Chara* sp. (follows Hotchkiss 1967:52), and *Myriophyllum spicatum*. Respective volumes were 36, 33, and 15 percent of the total and respective frequencies were 70, 46, and 28 percent (U. S. Department of Interior 1968). This type comprised about 15 percent of the study area.

Sedge Type

This type was in wet lowlands and was dominated by *Carex* spp. (mostly *C. rostrata*, *C. simulata*, and *C. nebraskensis*), Class Musci (follows Jaques 1949:160), and *Juncus balticus*. It succeeded the aquatic type and comprised about 35 percent of the study area.

Willow Type

This type was in wet lowlands and along streams. It was dominated by *Salix myrtillifolia*, *S. planifolia*, *S. wolfii*, *S. geyeriana*, and *Betula glandulosa* in the shrub group and by *Carex* spp., Class Musci, and *Juncus balticus* in the herb group. This type succeeded the sedge type and comprised about 15 percent of the study area.

Spruce Type

This type was in wet lowlands and was dominated by *Picea engelmanni*, *Linnaea borealis*, and *Cornus canadensis* in the tree and shrub groups and

TABLE III. INTERCEPT, CANOPY-COVERAGE, AND FREQUENCY OF IMPORTANT PLANTS ON THE STUDY AREA BY VEGETATION TYPE. A SINGLE VALUE INDICATES PERCENT INTERCEPT AND TWO VALUES SEPARATED BY A SLASH INDICATE PERCENT CANOPY-COVERAGE AND FREQUENCY, RESPECTIVELY. T DENOTES LESS THAN 0.5 PERCENT AND + DENOTES PRESENT BUT NOT OCCURRING IN PLOTS.

	VEGETATION TYPE[1/]						
Taxon	SE	WI	SP	AS	DF	SF	GR
Abies lasiocarpa	–	–	–	+	2	60	–
Picea engelmanni	–	T	49	1	1	28	–
Pinus contorta	–	–	–	–	12	–	–
Pseudotsuga menziesii	–	–	–	7	71	–	+
Populus tremuloides	–	+	+	75	+	19	+
Salix myrtillifolia	+	15	T	+	–	–	–
Salix planifolia	1	14	1	+	–	–	–
Salix wolfii	1	9	1	+	–	–	–
Salix geyeriana	T	5	–	–	–	–	–
Betula glandulosa	1	5	T	+	–	–	–
Linnaea borealis	–	T	13	+	–	–	–
Cornus canadensis	–	–	4	–	–	–	–
Symphoricarpos oreophilus	–	–	–	3	2	T	T/2
Spiraea betulifolia	–	–	–	T	6	T	–
Clematis columbiana	–	–	–	1	3	3	–
Berberis repens	–	–	–	2	T	6	+
Salix bebbiana	T	1	2	1	+	–	–
Salix drummondiana	+	T	–	–	–	–	–
Carex spp.	66/100	52/98	40/86	1/22	1/5	–	T/9
Class Musci[2/]	35/62	20/39	27/66	1/6	2/25	3/20	–
Juncus balticus	15/46	5/21	T/3	–	–	–	–
Aster foliaceus	6/34	1/14	+	+	–	–	T/2
Equisetum arvense[3/]	–	1/26	18/56	5/12	–	–	–
Fragaria virginiana	–	1/6	10/50	5/32	1/8	2/20	T/2
Geranium richardsonii	–	T/7	9/43	8/20	+	4/30	–
Actaea rubra	–	+	7/30	7/40	6/45	6/60	–
Smilacina stellata	–	2/13	6/43	3/32	+	T/10	–
Glyceria elata	T/4	+	6/20	–	–	–	–
Taraxacum spp.	1/20	1/17	3/20	13/76	T/3	T/10	11/87
Thalictrum venulosum	–	1/6	1/7	11/44	6/35	12/80	–
Trifolium longipes	1/10	1/6	–	9/26	–	–	1/17
Calamagrostis rubescens	–	–	–	8/38	25/80	10/60	–
Lupinus argenteus var. *parviflorus*[4/]	–	–	–	7/40	1/10	T/10	–
Geranium viscosissimum	–	–	–	7/34	2/13	–	1/2
Arnica cordifolia	–	–	–	6/24	22/85	4/60	–

TABLE III. (CONTINUED)

Taxon	VEGETATION TYPE						
	SE	WI	SP	AS	DF	SF	GR
Phleum pratense	T/12	+	+	5/32	-	-	+
Aster conspicuus	-	-	-	2/6	7/18	11/70	-
Ligusticum filicinum	-	-	-	1/8	+	7/30	-
Festuca ovina	-	-	-	-	-	-	16/73
Lupinus spp.	-	T/1	-	+	-	-	9/68
Microseris nigrescens	-	-	-	-	-	-	6/54
Besseya wyomingensis	-	-	-	-	-	-	5/56
Galium boreale	T/2	1/12	T/?	2/30	1/10	1/40	5/39

1/ SE = sedge, WI = willow, SP = spruce, AS = aspen, DF = Douglas-fir, SF = spruce-fir, and GR = grassland.
2/ Follows Jaques (1949:160).
3/ Follows Davis (1952:51).
4/ Follows Hitchcock and Cronquist (1961:302).

by *Carex* spp., Class Musci, and *Equisetum arvense* (follows Davis 1952:51) in the herb group. It succeeded the willow and aspen types and comprised less than 1 percent of the study area.

Grassland Type

This type was on dry to moderately moist uplands and was dominated by *Festuca ovina*, *Taraxacum* spp., and *Lupinus* spp. An overstory of *Artemisia tridentata* and/or *Chrysothamnus* spp. was present in some areas. This type succeeded the sedge and willow types and comprised about 20 percent of the study area.

Aspen Type

This type was on moderately moist uplands and in wet lowlands. It was dominated by *Populus tremuloides*, *Symphoricarpos oreophilus*, and *Berberis repens* in the tree and shrub groups and by *Taraxacum* spp., *Thalictrum venulosum*, and *Trifolium longipes* in the herb group. This type succeeded the willow type in the lowlands and the grassland type in the uplands and comprised less than 1 percent of the study area.

Douglas-fir Type

This type was on moderately moist uplands mostly below 7,500 feet. It was dominated by *Pseudotsuga menziesii*, *Spiraea betulifolia*, and *Clematis columbiana* in the tree and shrub groups and by *Calamagrostis rubescens*, *Arnica cordifolia*, and *Aster conspicuus* in the herb group. This type succeeded the aspen and grassland types and is considered the climax on drier sites mostly below 7,500 feet (Patten 1963:378, 386, 398). It comprised about 10 percent of the study area.

Spruce-fir Type

This type was on wet uplands and was dominated on the study area by *Abies lasiocarpa*, *Berberis repens*, and *Clematis columbiana* in the tree and shrub groups and by *Thalictrum venulosum*, *Aster conspicuus*, and *Calamagrostis rubescens* in the herb group. This type is considered the climax on moist sites mostly above 7,500 feet (Daubenmire 1943, Patten 1963:378, 397-398). It comprised less than 1 percent of the study area.

Data on willow heights are presented in Table IV and in Figure 5 in the appendix. The average height of a willow species was related to its most common habitat with respect to soil moisture, microclimate,

TABLE IV. HEIGHTS AND FREQUENCY INDICES OF WILLOWS ON THE STUDY AREA.

Species	Sample Size	HEIGHT (ft.) Average	Maximum	Minimum	Frequency Index[1/]
S. candida	50	2.2	5.0	1.0	14
S. wolfii	100	2.9	5.5	1.0	80
S. exigua	50	3.4	7.0	1.0	10
S. rigida	10	3.5	7.0	2.0	10
S. planifolia	100	3.7	13.5	1.0	100
S. drummondiana	100	4.9	9.0	2.0	22
S. monticola	50	5.3	14.0	1.5	14
S. myrtillifolia	100	5.6	14.0	1.5	90
S. lasiandra	35	5.7	19.5	2.0	5
S. bebbiana	100	6.2	18.0	1.5	23
S. geyeriana	100	7.8	18.5	2.0	90
S. scouleriana	20	19.6	40.0	3.0	-

1/ See text, page 5, for explanation.

or both (Figure 3). Generally, the shortest species were in areas with the most moisture and the greatest temperature extremes while the tallest species were in areas with the least moisture and the least temperature extremes during the growing season. Streams apparently upset this relationship. All species were within an elevational range of 150 feet. *S. rigida* was too rare for evaluation.

This height-habitat relationship parallels the dwarfing of willows with increasing elevation and latitude. The wet, mossy bogs roughly correspond to subalpine slopes in the mountains and the lower tundra in the north. Raup (1959:20), referring to willows in boreal western America, stated that most prostrate willows grow in the arctic or

Greatest Temperature Extremes ———————————— Least Temperature Extremes

Wet Mossy Bog	Moderately Wet Lowland	Drier Lowland Edges	Dry Upland Forest
S. candida 2.2	*S. planifolia* 3.7	*S. bebbiana* 6.2	*S. scouleriana* 19.6
S. wolfii 2.9	*S. monticola* 5.3	*S. geyeriana* 7.8	
	S. myrtillifolia 5.6		

Stream Bank Group

S. exigua	3.4
S. drummondiana	4.9
S. lasiandra	5.7

Figure 3. Most common habitat of willow species with respect to soil moisture and microclimate. The numbers are average heights of the species in feet.

alpine tundra, most medium-sized species are in swales or along streams in the tundra or on open land of forest areas, and most tall species are in forests or on the margins of forests. This relationship is apparently only evident under nearly ideal conditions because of the many factors influencing the heights. Patten (1968:1112) discussed the effects of browsing on several species of willow. Many of the factors listed by Hanson (1953:139) as influencing the development, maintenance, or changes of the species composition within vegetation types also influence willow heights. Under less than ideal conditions, dwarfing is most apparent with increasing latitude, somewhat less apparent with increasing elevation, and least apparent on a small area. The smaller the area, the more pronounced are the effects of influencing factors in masking the height relationship. The high mountain valley with significant temperature changes over a small area, a gradual change in soil moisture, a variety of willow species, moderate browsing, and other factors provided nearly ideal conditions for expression of this height-habitat relationship on the study area.

The most common habitat (Figure 3) does not reflect the range of distribution. In general, *S. candida*, *S. scouleriana*, and the stream bank group were mostly restricted to mossy bogs, upland forests, and stream banks, respectively. The remaining species mostly ranged between the positions of *S. wolfii* and *S. geyeriana*, including the stream bank position (Figure 3).

Vegetation Type Use

Observations of moose feeding or bedded in summer and winter totaled 581 and 413, respectively. Observations in the willow type accounted for 84 percent of the total in summer and 93 percent in winter (Table V). Use of the timber types was probably more in summer than the data indicate. Seven percent of all observations were of moose moving to and from the Douglas-fir type in the morning and evening, respectively, suggesting more use of this type than observed. Use of the sedge and grassland types was probably less in summer than the data indicate due to excellent visibility in these types.

The differences in the use of types between summer and winter were mainly due to snow cover influencing availability of forage and visibility. Food habits primarily determined the use of vegetation types which explains the importance of the willow type. Different areas have different patterns of use because food habits usually differ by area.

TABLE V. USE OF VEGETATION TYPES BY MOOSE FOR FEEDING AND BEDDING. NUMBER OF OBSERVATIONS IS IN PARENTHESES. T DENOTES LESS THAN 0.5 PERCENT.

Vegetation Type	PERCENT USE	
	Summer(581)	Winter(413)
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	100	99

The distribution of moose within the willow type differed between summer and winter (Figure 6 in the appendix). This may have been due to differences in availability of forage, cover requirements, remaining in the first stand of suitable willows encountered after leaving timbered areas in winter, or a combination of these. This difference in distribution helped reduce the browsing pressure on the winter forage supply.

Moose were sometimes observed bedded on the ice of Upper Red Rock Lake possibly to take advantage of solar radiation. This was considered use of the adjacent willow type.

Food Habits

Moose-summer

Browse accounted for 98.3 percent of all forage used by moose in summer (Table VI). Knowlton (1960:166) and Houston (1968:26) reported percentages of 29 and about 75 percent, respectively. The abundance in quantity and variety of willows in this study largely accounted for the heavy use of browse.

Salix myrtillifolia, *Betula glandulosa*, *Salix geyeriana*, and *Salix planifolia* accounted for 58.1, 11.8, 9.6, and 6.7 percent, respectively, of all forage used (Table VI). Other investigators found varying degrees of use of one or more of these species except *S. planifolia* (McMillan 1953:103, Denniston 1956:106, Peek 1963:228-229, Houston 1968:27,101).

TABLE VI. FOOD HABITS OF CATTLE AND MOOSE. VALUES ARE PERCENTAGES. T DENOTES LESS THAN 0.05 PERCENT AND NA DENOTES NOT AVAILABLE. PLANTS WITH LESS THAN 2 PERCENT USE (EXCLUDING THE GENUS *SALIX*) IN ALL CATEGORIES EXCEPT FREQUENCY FOR RUMEN SAMPLES APPEAR IN TABLE XIX IN THE APPENDIX.

	SUMMER				FALL					WINTER			
	Cattle	Moose			Moose					Moose			
Area of Use[1/]:	Al 30	Ca 19	Al 40	As 8	Al 8[2/]		Wi 7[2/]		Ti 1[2/]	Al 35	Wi 24	Df 9	As 5
Taxon / Instances of Use :	17,813	12,271[2/]	36,812	2,221[2/]	Vol.	Freq.	Vol.	Freq.	Vol.	32,480	26,748	3,487[2/]	1,627[2/]
Abies lasiocarpa	NA	NA	0.0	0.0	1.3	25	0.2	14	7.1	2.5	NA	17.1	10.9
Acer glabrum	NA	NA	0.0	0.0	0.0	0	NA	-	0.0	2.2	NA	20.2	0.6
Betula glandulosa	2.7	5.1	11.8	0.0	0.0	0	0.0	0	NA	0.7	0.9	NA	0.0
Populus tremuloides	0.0	2.0	3.3	42.3	0.9	25	1.1	29	0.0	3.1	0.0	11.9	36.2
Populus tremuloides (bark)	0.0	T	T	0.0	5.3	13	0.0	0	34.6	1.5	0.0	14.3	0.0
Prunus virginiana	NA	NA	0.4	6.7	0.0	0	NA	-	0.0	0.3	NA	0.5	4.7
Pseudotsuga menziesii	NA	NA	0.0	0.0	0.0	0	NA	-	0.0	0.6	NA	4.8	1.7
Rosa woodsii	0.0	0.0	0.1	1.5	0.0	0	0.0	0	0.0	1.7	T	1.5	30.1
Salix bebbiana	10.9	2.0	2.6	17.9	-	-	-	-	-	15.4	17.5	8.7	2.2
Salix candida	0.5	0.0	0.0	NA	-	-	-	-	-	T	T	NA	NA
Salix drummondiana	2.9	6.3	2.8	NA	-	-	-	-	-	0.9	1.0	NA	NA
Salix exigua	0.3	0.2	0.1	NA	-	-	-	-	-	0.1	0.1	NA	NA
Salix geyeriana	11.2	21.0	9.6	NA	-	-	-	-	-	10.5	12.8	NA	NA
Salix glauca[3/]	NA	NA	0.2	NA	-	-	-	-	-	-	-	-	-
Salix lasiandra	NA	NA	0.0	NA	-	-	-	-	-	2.0	2.4	NA	NA
Salix monticola	0.3	2.4	0.8	NA	-	-	-	-	-	0.7	0.8	0.0	NA
Salix myrtillifolia	15.9	45.6	58.1	15.4	-	-	-	-	-	25.0	30.4	0.0	0.0
Salix pentandra[3/]	NA	NA	0.0	NA	-	-	-	-	-	1.8	NA	NA	NA
Salix planifolia	4.8	10.3	6.7	12.5	-	-	-	-	-	24.2	29.4	NA	0.0
Salix rigida	NA	NA	0.1	0.0	-	-	-	-	-	0.0	0.0	NA	0.0
Salix scouleriana	NA	NA	T	0.0	-	-	-	-	-	1.9	NA	17.1	1.5
Salix wolfii	50.2	0.0	0.1	0.0	-	-	-	-	-	2.5	3.1	NA	0.0
Salix spp.	-	-	-	-	85.2	100	96.6	100	22.2	1.1	1.3	0.3	-
Symphoricarpos oreophilus	NA	NA	0.1	0.9	0.1	13	NA	-	0.4	0.8	NA	3.4	8.2
Unidentified browse	-	-	-	-	1.9	38	0.8	29	7.5	-	-	-	-
Total Browse[4/]	100.0[5/]	95.4	98.3	99.0	95.5	100	99.6	100	72.2	99.8	99.8	100.0	100.0
Aster conspicuus	-	NA	0.0	0.0	3.8	13	NA	-	24.8	0.0	NA	0.0	0.0
Lupinus argenteus var. *argenteus*[6/]	-	4.5	1.5	0.0	0.0	0	0.0	0	0.0	0.0	0.0	NA	0.0
Total Forbs[4/]	-[5/]	4.5	1.5	1.0	3.8	50	0.1	43	24.8	T	T	0.0	0.1
Gramineae and *Carex* spp.	-	-	-	-	0.7	75	0.3	71	3.0	-	-	-	-
Total Grass, Grass-like[4/]	-[5/]	0.0	0.2	T	0.7	75	0.3	71	3.0	0.1	0.2	0.0	0.0

1/ Al = all areas, Ca = cattle areas, As = aspen type, Wi = willow type, Ti = upland timber types, and Df = Douglas-fir type. Numbers are total feeding sites for summer and winter and total rumen samples for fall.

2/ Insufficient sample.

3/ Recorded in an area adjacent to the study area.

4/ Includes plants in Table XIX in the appendix.

5/ Cattle use on non-woody plants was not recorded.

6/ Follows Hitchcock and Cronquist (1961:306).

Forage use in the willow type was similar to overall use. The sample in the aspen type was not sufficient for reliable percentages, but the data suggest possible proportions of use. *Populus tremuloides* was most important followed by three species of willow (Table VI).

Moose-fall

Three rumen samples from hunter-killed moose were collected October 19, 1958 (Knowlton 1960:167), one was collected November 21, 1959 by Montana Fish and Game Department personnel, and I collected four on October 20, 1968. This sample was not sufficient (Hanson and Graybill 1956), but it does suggest possible food habits in fall. The use of browse in all vegetation types was 95.5 percent of the total use (Table VI) compared to over 85 percent in other studies (Knowlton 1960:166, Stevens 1967:13, Houston 1968:26). Species of *Salix* accounted for 96.6 percent of the use in the willow type. One rumen sample representing the upland timber types contained only 72.2 percent browse, mostly *P. tremuloides* bark and species of *Salix*. One forb, *Aster conspicuus*, accounted for 24.8 percent of the total of this sample.

Moose-winter

Browse accounted for 99.8 percent of all forage used by moose in winter (Table VI). Knowlton (1960:167), Stevens (1967:15), and Houston (1968:25) reported similar percentages.

S. myrtillifolia, *S. planifolia*, *S. bebbiana*, and *S. geyeriana* accounted for 25.0, 24.2, 15.4, and 10.5 percent, respectively, of all use.

These percentages were 28.4, 17.2, 22.6, and 15.0, respectively, during the period of deep snow in February and March. The importance of the tall species increased while that of the shortest species, *S. planifolia*, decreased. *S. wolfii* was important early in the winter while it was available. Houston (1968:28, 103) reported varying degrees of use of all these species except *S. planifolia*.

Use in the willow type was similar to overall use. Use in the Douglas-fir and aspen types was only suggestive because of the small samples. *P. tremuloides* and *Rosa woodsii* were important in the aspen type and *P. tremuloides*, *Acer glabrum*, *Abies lasiocarpa*, and *Salix scouleriana* were important in the Douglas-fir type.

Cattle-summer

S. wolfii, *S. myrtillifolia*, *S. geyeriana*, and *S. bebbiana* accounted for 50.2, 15.9, 11.2, and 10.9 percent, respectively, of all browse used by cattle in summer (Table VI). All these species have been reported as used by cattle or other livestock (Van Dersal 1938:245-254, Houston 1968:45).

Conclusions

Availability was one factor determining the amount of various plant species in the diet of moose. In this study *S. planifolia* was important. In Jackson Hole it apparently was not present (Houston 1968). *Cornus stolonifera* was important in the diet of moose in winter in Jackson Hole (Houston 1968:29, 32) but was not important in this study due to its limited availability. Moose were observed using aquatics only twice in this study. Both periods of feeding were brief. Peterson (1955:140) found that *Potamogeton richardsonii* was the most important aquatic food in a study in Ontario. This species was the most abundant aquatic on this study area. Moose apparently use few aquatics if willows are abundant.

Many factors influence availability. The most important in this study was snow cover. Extensive drifting resulted in complex influences. Drifts covered some plants 10 feet high, but because these drifts could support a moose, they made available some plants over 15 feet high. Most plants less than 4 feet high were unavailable by mid-winter. Winter use of *B. glandulosa* and *S. wolfii*, both low-growing shrubs, was limited to early winter. *S. bebbiana*, of minor importance in summer and early winter, became important in late winter partly through an increase in relative availability due to its tall height (Figure 2C).

Adaptation was a second factor determining the amount of various plant species in the diet. Flerov (1960:174) and McMillan (1953:109) discussed the adaptations of moose for browsing. The efficiency with which moose strip the leaves from willow twigs illustrates one adaptation. Most use of browse by moose in summer was by leaf stripping. This adaptation largely accounted for the light use of *S. wolfii* by moose in summer. Most leaf stripping was over 3 feet above ground level, apparently the area for most efficiency. This was above most *S. wolfii* plants. Since use in winter was by nipping leaders, often close to the snow level, *S. wolfii* became important to moose while it was available because it could be as efficiently utilized as other species. Use of *S. wolfii* by cattle in summer was heavy. Cattle, being adapted for grazing, are inefficient browsers. The low form of growth of *S. wolfii* put it in a grazing position. McMillan (1953:104) found that moose used *S. wolfii* less than *S. geyeriana* in summer and suggested it was partly due to its low form of growth making it more difficult to browse. He also noted more use of *S. wolfii* by elk (*Cervus canadensis nelsoni*) which are more adapted for grazing than moose.

Palatability was a third factor determining the amount of various plant species in the diet. In the Douglas-fir type in winter *Abies lasiocarpa* was used much more than *Pseudotsuga menziesii* which was much more abundant (Tables III and VI). Use of *A. lasiocarpa* was limited to certain trees which were often severely hedged. Houston (1968:30) also noted this pattern of use of *A. lasiocarpa*. Consistent use of decadent willows, especially *S. planifolia* and *S. bebbiana*, with use of growth as old as 7 years, rather than the previous year's growth, was observed in this study.

A fourth factor determining the amount of various plant species in the diet was habit (Leopold 1933:255-258). A suitable species will not be used unless an animal has learned to use it through training or experience (Leopold 1933:258, Kendeigh 1961:188-189). Individual variation is included here. My data were insufficient to demonstrate this factor.

Availability was most important in determining the composition of the diet followed by adaptation and palatability. Evaluation of the absolute importance of individual plant species was difficult because these factors were all interrelated. It appeared that all species of willow that were present in this study were potentially important as forage for moose at some time during the year, especially in winter. Relatively low availabilities kept most species from being important. The probable most important factor determining the amount of use for five important forage species of moose in this study is presented in Table VII. The growth form of *S. myrtillifolia* probably allowed it to be used more efficiently than other species in summer, therefore accounting for its heavy use. Besides willows, two other species were potentially important in winter. These were *P. tremuloides* and *A. lasiocarpa*. They were important in Jackson Hole (Harry 1957:55, Houston 1968:28, 33, 44) and *P. tremuloides* was important in parts of Alaska (Spencer and Chatelain 1953:542).

TABLE VII. PROBABLE MOST IMPORTANT FACTORS DETERMINING THE AMOUNT OF USE OF IMPORTANT FORAGE SPECIES OF MOOSE IN THIS STUDY.

	FACTOR	
Taxon	Summer	Winter
Salix myrtillifolia	Adaptation	Availability
Salix planifolia	Availability	Palatability
Salix bebbiana	Availability	Availability
Salix geyeriana	Availability	Availability
Betula glandulosa	Palatability	Availability

Moose-Cattle Competition

Forage competition (Smith and Julander 1953:101) between moose and cattle was not significant under the conditions prevailing during this study. *S. wolfii*, accounting for 50.2 percent of all browse used by cattle, was rarely used by moose except in early winter (Table VI). The abundance of this species acted as a buffer to reduce the use by cattle of *S. myrtillifolia*, *S. bebbiana*, and *S. geyeriana*. Competition would be expected to increase in areas with a low availability or absence of *S. wolfii* or where moose must depend on *S. wolfii* due to absence of other willows. Houston (1968:44-45) reported moose-cattle competition on *S. myrtillifolia*. In this study cattle used little browse before the more palatable forbs, grasses, and grass-like plants were largely utilized. A lesser availability of these would increase the use of browse. Most of the browse used by cattle was less than 5 feet above ground level. Most of this was covered with snow in winter so was unavailable to moose. Elimination of cattle use would probably have little effect on allowing more willows to reach above the snow in winter on the study area. *S. wolfii* rarely grows over 4 feet tall and cattle use on other willows was mostly on lower lateral shoots. Forage competition caused by trampling and rubbing could become significant with heavier stocking. The approximate stocking rate was one animal per 5 acres for a period of 82 days in an area with the following percentages of vegetation: willow type 50, sedge type 45, grassland type 3, aspen type 1, and aquatic type 1. "Disturbance competition," as noted by Denniston (1956:114), whereby moose move out when cattle move in, was not observed. Moose and cattle were observed feeding within 10 feet of each other with no apparent concern except curiosity.

Other Competition

Forage competition between moose and beaver was greater than competition between moose and cattle. Damage to willows by cutting and flooding was apparent in several areas but was not significant. It could become significant with a small increase of the beaver population. Most aspen close to suitable water areas has been eliminated so willow was the primary woody food and construction material for beaver. Packard (1947:227) and Rudersdorf (1952:37, 51) reported that beaver turn to willow after aspen has been eliminated and apparently accept it as a satisfactory substitute.

Sex and Age Ratios, Population Trends, and Movements

Sex and age ratios of moose in summer determined from aerial observations were more accurate than from ground observations. Comparison of data from ground observations from June through September and combined aerial observations from July and September (Table VIII) indicates that bulls were more readily identified from the ground than cows. Knowlton (1960:168-169) observed this also. The sex of 16 percent of all moose observed from the ground in summer was not determined. Most were probably cows. Adding these to the cow group gives a ratio of 73 bulls to 100 cows which is nearly the same as the ratio from aerial observations in summer of 74:100. The same comparison indicates that many calves were not observed from the ground. Part of the difference was due to transient cows, which rarely had calves, appearing in the ground data. The major difference resulted from difficulty in seeing the smaller calves. Knowlton (1960:169), Edwards and Ritcey (1958:261), Pimlott (1959a:392), and Houston (1968:21) noted that observed calf to cow ratios were not reliable at least in summer.

TABLE VIII. OBSERVED SEX AND AGE RATIOS OF MOOSE ON THE STUDY AREA. NUMBER OF MOOSE OBSERVED IS IN PARENTHESES.

	AERIAL OBSERVATIONS					GROUND OBSERVATIONS	
	April (50)1/	July (23)	Sept. (31)	Oct. (16)	July-Sept. (54)	June-Sept. (674)	Mar. (46)2/
Bulls:Cows	-	60:100	85:100	57:100	74:100	105:100	15:100
Calves:Cows	-	60:100	54:100	71:100	57:100	34:100	56:100
Calves:Adults	35:100	35:100	29:100	45:100	32:100	13:100	48:100 3/

1/ Two months before start of study.
2/ Snowmobile survey.
3/ Nine male and six female calves were observed.

The data on sex and age ratios from aerial and snowmobile observations (Table VIII) and data on the number of moose observed by periods throughout the study (Figure 4) indicate that observed sex and age ratios were influenced by home range and migration patterns and differential use of vegetation types between sexes. Peek (1962:361-362) noted that differential use of vegetation types between sexes and differential

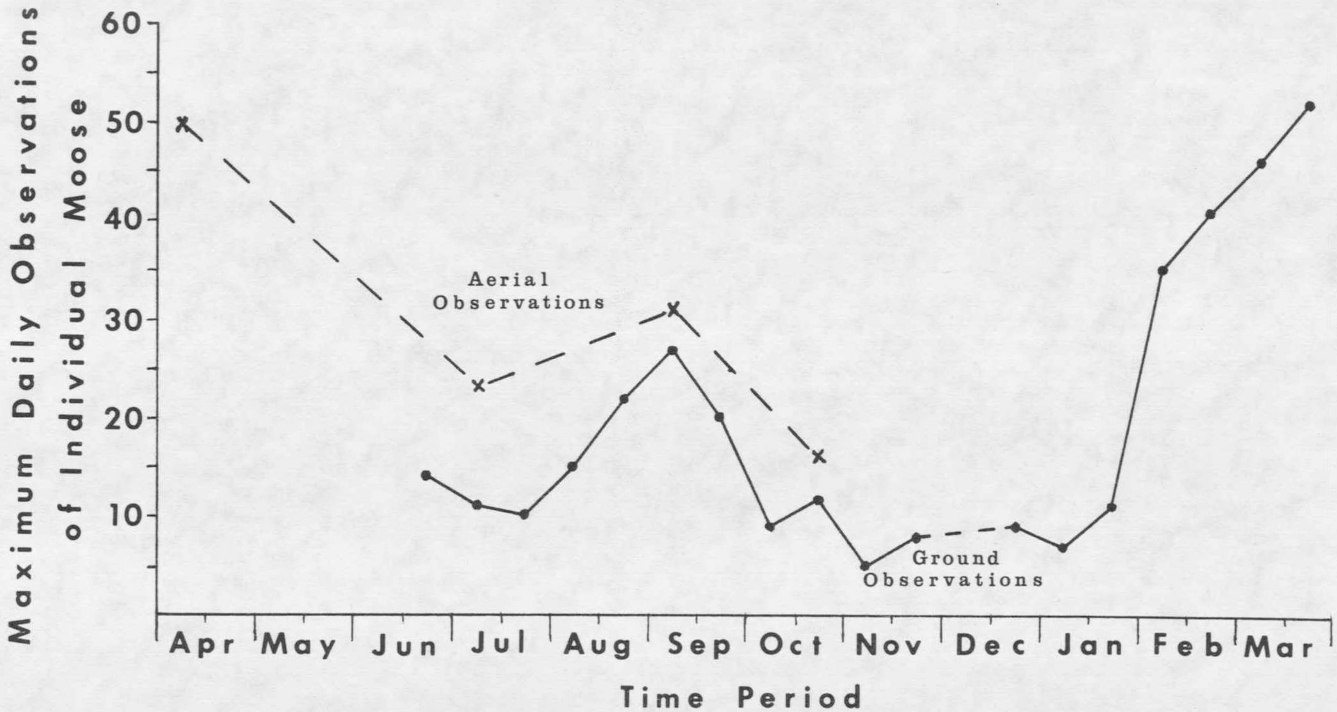


Figure 4. Maximum daily observations of individual moose by semimonthly periods.

movements from year to year influenced sex and age ratios and Pimlott (1959b:442) noted that sex ratios were influenced by differential use between sexes of open habitats. September ratios from aerial observations were probably most reliable for the composition of the breeding population. The most bulls and the most moose, except for winter, were observed on the study area in September. This period coincided with the early rut. Most bulls apparently ranged the timbered uplands during most of the summer and moved down to the lowlands in late August and September. Cowan (1950:583) noted that many bulls ranged at higher elevations than the main herds. Altmann (1959:421-422) noted use of willow flats by larger bulls in summer until August when they moved to the timbered slopes. In September they returned to the willow flats for the rut. Peek (1962:363) observed an increased use of willow bottoms by bulls in late August and early September. Ratios observed at other times of the year gave different results. In winter when moose are on wintering areas and readily observable, the composition of the population on a given area may be different from the breeding population. An intensive ground survey by snowmobile in March indicated that only a small proportion of adult bulls wintered on the study area (Table VIII). Comparison of ratios from different areas is probably meaningless because of differences in the movement patterns of each population. Until more is known about movements of moose, sex and age ratios are best used as indices for determining trends in a given area.

The validity of the September ratios is questionable. The small sample gives a wide confidence interval. If it is assumed that the sampling was random and that the population was stable, the 95 percent confidence interval for the bull to cow ratio would be 66:100 to 94:100 (Spiegel 1961:158-163). The same applies for the other ratios. Moose not observed in the coniferous timber types could cause this large variation.

Cows with calves were repeatedly observed in areas of one-half to two square miles throughout the summer and into fall. During this period the calf to cow ratio was small when the total number of animals observed was large and vice versa (Table VIII and Figure 4) indicating a relative constancy of cow-calf groups. On the July, September, and October flights, six, seven, and five calves were observed, respectively. A cow with twin calves was observed in the same area in July and September but was not observed in October. Some solitary cows were repeatedly observed in the same areas in summer but others were observed in an area for only short periods. This may have been due to age differences with the younger animals moving the most.

No bulls were observed for any extended period in any one area during summer. They usually were on the study area for a short period and then left, apparently into the upland timber, for a longer period. A bull with a red neck band, put on by Idaho Fish and Game Department personnel (Nielson and Shaw 1967), was observed on the study area irregularly throughout the summer (Figure 6 in the appendix). He was never observed on more than three consecutive days and the intervals when he was not observed ranged from 1 to 3 weeks. The bull to cow ratio was largest when the total number of animals observed was largest and vice versa (Table VIII and Figure 4) indicating that bulls ranged over greater areas than cows during summer.

Movements reported in other studies vary (Denniston 1956:110, Knowlton 1960:166, Peek 1962:362, Houston 1968:51-53). Home ranges apparently vary with the area as suggested by Peterson (1955:113) and with changing environmental conditions as suggested by Peek (1962:362).

The fewer observations of bulls apparently was not due to use of timber types during the day only but rather to continuous use of these types. Cow-calf groups accounted for 62 percent of all observations of moose crossing between the lowlands and upland timber. Groups including bulls accounted for 19 percent of the total. Some cows with calves used the timber for cover during the day and returned to the lowlands to feed in the evening and early morning. This habit occasionally causes calf mortality on fences. Adult moose easily jump most fences but calves usually have difficulty and sometimes become entangled.

Migration patterns appeared to be complex. The sharp decline in the number of animals observed in early October (Figure 4) resulted from migration or a shift back to the timbered areas of home ranges. The decline corresponded with two natural phenomena which could cause a temporary shift. Willow leaves were killed at this time which may have made them unpalatable. Hosley (1949:16) cited Cooney as stating that moose returned to timbered slopes at the end of September after willow leaves, which are preferred to the browse, were killed. Thin ice was also formed at this time which may have made travel in the lowlands difficult or even painful for moose. These phenomena could also stimulate migration. The small change of the calf to cow ratio between July and September and the large change from September to October (Table VIII) indicated that both solitary cows and bulls moved out in October. The presence on the study area of the marked bull for several summers but not in winter (O. H. Vivion, personal communication), the season when he was banded in Idaho, indicates that some of the moose present in summer winter elsewhere, probably in Idaho. The low proportion of bulls on the study area in winter (Table VIII) indicated that most of the bulls winter elsewhere. Cowan (1950:583) noted that many bulls ranged at higher elevations in winter than the main herds and Stevens (1967:11) observed over 20 percent of the moose in one area wintering in the spruce-fir community which is mostly at higher elevations. If a summer population segment exists, the definition of migrations presented by Edwards and Ritcey (1956:487), whereby different environments are utilized to minimize detrimental conditions, may need re-examination. Conditions in probable wintering environments off the study area are possibly more detrimental.

The constancy of cow-calf groups into October and their predominating presence in early winter suggested that a resident population segment was present made up mostly of cow-calf groups. Peterson (1955:110) indicated that some moose, especially cows, calves, and yearlings, remained in the lowlands all year.

A winter population segment was present in this study as indicated by the many moose observed by late winter and the sharp decline in spring (Figure 4). The sharp increase in the number of moose observed on the study area in early February (Figure 4) occurred after a series of storms which increased the snow cover in the lower timbered areas from about 3 to 6 feet. Movements to winter ranges in response to increasing snow depths were observed by Edwards and Ritcey (1956:493), Peek (1963:229), and Houston (1968:47). Snow in the lowlands did not restrict movements except for a few days after heavy snowfalls. Settling and wind action compacted the snow sufficiently to support the moose.

Recognition of individual moose, mostly yearlings, over short periods indicated that a transient population segment was also present in summer. Houston (1968:17, 21) observed resident, winter, and transient segments in Jackson Hole. He did not consider a summer population segment, if present, to be significant (personal communication).

Since the condition of the winter range is important in the management of moose, it is desirable to know where the winter population segment is during the hunting season, about October 20 to December 15, and what part of the population segment present during the hunting season is also present in winter. The appearance of moose on both the north and south sides of the study area in winter suggested that part of the winter population segment summered in the Gravelly Mountains and part in the Centennial Mountains. The animals present during the hunting season were probably mostly residents. Excessive harvest of this group would have little effect on the winter range unless animals from the other population segments moved in to take their places and were subjected to subsequent harvests. The apparent reduction of all population segments after intensive hunting in the 1950's (Refuge records) suggests that this replacement did take place. Houston's (1968:56) observations suggest that vacant areas would quickly be filled by yearlings.

The increasing evidence that orphaned calves rarely survive the winter (Denniston 1956:112, Altmann 1958:158, Houston 1968:77) and that twinning rates and the occurrence of triplets may be genetically controlled (Pimlott 1959a:388, Houston 1968:69-71), although nutrition apparently is also involved (Pimlott 1959a:397-399), suggests that a regulation or request to protect cows followed by a calf or calves may benefit productivity and yield. Pimlott (1959b:428) cited Mäki as indicating that this regulation was in effect in Finland. The apparent reduction in the twinning rate in the surrounding area in recent years (Bailey 1930:41, Denniston 1956:108, Peek 1962:362, Knowlton 1960:169, Stevens 1965:31, Houston 1968:69) may be partly due to selection against productive cows in "any moose" hunting seasons. The occurrence of cows with calves in accessible lowland areas would facilitate such selection.

Data of Edwards and Ritcey (1958:263-264) suggest a possible selection against lowland moose. Moose summering at higher elevations had a higher twinning rate and did not always arrive on winter areas soon enough to be harvested. They thought some environmental factor at higher elevations might be responsible for the higher twinning rate there. Deterioration of the range probably caused the decline in the twinning rate in areas where hunting has been prohibited. Bailey (1930:39, 41) observed a high twinning rate in Yellowstone National Park and an abundance of willows although in some areas they were severely browsed. Poor reproduction was observed by de Vos (1956:520) on a refuge where moose were protected and he thought it might be due to poor range conditions. Houston (1968:70) suggested a possible mechanism for changes in the twinning rate in response to changes in environmental stresses. There was little evidence of environmental stress in this study.

The twinning rate found in this study was higher than in surrounding areas in recent years. The rate varied from 18 percent in April, 1968 to 17 percent in September, 1968 to 13 percent in March, 1969; these percentages involve only two, one, and two sets of twins, respectively. Stevens (1965:21) observed two sets of twins on the study area in 1965. Houston (1968:69) observed a rate of 4.5 percent in Jackson Hole. Knowlton (1960:169) observed no twins and Peek (1962: 362) observed only two sets in one year and none in two other years.

Nutrition apparently is as important as a genetic control since the higher twinning rates were reported from areas with a higher availability of willows. Pimlott (1959a:386) reported North American twinning rates ranging from 2 to 28 percent. Although there is some chance for error in comparing rates from different areas, the variables between areas as discussed earlier are considerably less because only cows with calves are being considered.

Range Survey

Four transects for the Cole (1963) range survey were established on the study area in 1965. They are of little value in determining the condition of the range. All tagged plants were not key species and only one transect was in a representative location in a key area. *S. myrtillifolia* appeared to be the key species on the study area. Houston (1968: 87) considered this the key species in Jackson Hole. The status of *S. planifolia* was uncertain. Its growth was generally lower than *S. myrtillifolia* so was less available in winter, it produced less forage because of its growth form, and it was generally in poor condition. *S. myrtillifolia* was the predominant species tagged in only two transects. All transects had more than one species tagged. Stevens (1965:31-32) indicated that only one species of willow should be sampled in a transect.

The availability zones on willows were difficult to establish because of differential snow depths. The variation in data recorded by different individuals is often due to this. A fixed zone for each transect would largely eliminate this variation.

Cole (1963:8) suggested an allowable use of leaders for willow of 50, 75, and 95 percent in mild, average, and severe winters, respectively. Houston (1968:85) suggested allowable use of 50, 70, and 90 percent in mild, average, and severe winters, respectively, for *S. myrtillifolia*. These percentages appear satisfactory.

Qualitative observations on the condition of the range should also be a part of the survey as suggested by Stevens (1965:32). The range appeared to be in satisfactory condition during the study except for the area of willows south of Upper Red Rock Lake which was overused. The winter population appeared to be approaching the carrying capacity of the range.

Management Recommendations

Stocking rates of cattle should take into account the availability of palatable forbs, grasses, and grass-like plants and of *Salix wolfii* on any given area to prevent significant moose-cattle competition. The possibility of trampling damage should also be considered. Fences should be constructed and located to minimize hazards to moose. Beaver should be harvested regularly to minimize competition with moose.

Until reliable information is obtained on movements, a hunting season starting about September 20 seems preferable to the present season because of the composition and size of the population at that time on the study area. Cows followed by calves should be protected and the annual quota should be raised from five to eight.

New range survey transects should be established to replace three of the four existing transects. The existing transect on Red Rock Creek is satisfactory. An additional one should be established on this creek to the east and two should be established south of Upper Red Rock Lake between the main *Picea engelmanni* stand and Shambow Pond.

APPENDIX

TABLE IX. PERCENT VOLUME AND FREQUENCY OF AQUATIC TYPE TAXA (U. S. DEPARTMENT OF INTERIOR, 1968).

Taxon	Volume	Frequency
Potamogeton richardsonii	36	70
Chara sp.1/	33	46
Myriophyllum spicatum	15	28
Potamogeton praelongus	5	12
Potamogeton pectinatus	5	10
Sagittaria cuneata	4	14
Elodea canadensis	1	12
Najas flexilis	1	10
Lemna trisulca	T2/	2
Total	100	

1/ Follows Hotchkiss (1967:52).
2/ T denotes less than 0.5 percent.

TABLE X. PERCENT CANOPY-COVERAGE, FREQUENCY, AND INTERCEPT OF SEDGE TYPE TAXA. T DENOTES LESS THAN 0.5 PERCENT.

Taxon	Canopy-Coverage	Frequency	Intercept
Salix planifolia			1
Salix wolfii			1
Salix candida			1
Betula glandulosa			1
Salix geyeriana			T
Salix bebbiana			T
Potentilla fruticosa			T
Arctostaphylos uva-ursi			T
Carex spp.	66	100	
Class Musci 1/	35	62	
Juncus balticus	15	46	
Aster foliaceus	6	34	
Polemonium occidentale	3	26	
Swertia perennis	2	20	
Pedicularis groenlandica	2	14	
Unidentified Forbs	2	8	
Galium trifidum	1	32	
Taraxacum spp.	1	20	
Poa spp.	1	14	
Muhlenbergia racemosa	1	12	
Potentilla gracilis	1	12	
Trifolium longipes	1	10	
Arenaria lateriflora	T	16	
Phleum pratense	T	12	
Viola nephrophylla	T	10	
Deschampsia caespitosa	T	10	
Parnassia parviflora	T	8	
Hordeum brachyantherum	T	8	
Achillea millefolium	T	6	
Stellaria longifolia	T	6	
Festuca rubra	T	4	
Agropyron bakeri	T	4	
Claytonia chamissoi	T	4	
Veronica americana	T	4	
Glyceria elata	T	4	
Muhlenbergia filiformis	T	2	

TABLE X. (CONTINUED).

Taxon	Canopy-Coverage	Frequency	Intercept
Calamagrostis neglecta	T	2	
Allium schoenoprasum	T	2	
Solidago canadensis	T	2	
Galium boreale	T	2	
Alopecurus alpinus	T	2	
Equisetum laevigatum 2/	T	2	
Phleum alpinum	T	2	
Antennaria anaphaloides	T	2	
Habenaria hyperborea	T	2	
Litter	47	94	
Water	3	4	
Bare	1	8	

1/ Follows Jaques (1949:160).
2/ Follows Davis (1952:53).

TABLE XI. PERCENT CANOPY-COVERAGE, FREQUENCY, AND INTERCEPT OF WILLOW TYPE TAXA. T DENOTES LESS THAN 0.5 PERCENT.

Taxon	Canopy-Coverage	Frequency	Intercept
Salix myrtillifolia			15
Salix planifolia			14
Salix wolfii			9
Salix geyeriana			5
Betula glandulosa			5
Potentilla fruticosa			2
Salix bebbiana			1
Ribes inerme			1
Lonicera involucrata			1
Rhamnus alnifolia			1
Salix drummondiana			T
Salix monticola			T
Salix candida			T
Arctostaphylos uva-ursi			T
Linnaea borealis			T
Cornus stolonifera			T
Picea engelmanni			T
Rosa woodsii			T
Carex spp.	52	98	
Class Musci[1/]	20	39	
Juncus balticus	5	21	
Swertia perennis	3	22	
Pedicularis groenlandica	3	17	
Smilacina stellata	2	13	
Equisetum arvense[2/]	1	26	
Taraxacum spp.	1	17	
Aster foliaceus	1	14	
Polemonium occidentale	1	13	
Galium boreale	1	12	
Geum macrophyllum	1	12	
Castilleja miniata	1	9	
Fragaria virginiana	1	6	
Trifolium longipes	1	6	
Thalictrum venulosum	1	6	

TABLE XI. (CONTINUED).

Taxon	Canopy-Coverage	Frequency	Intercept
Poa pratensis	1	5	
Class Hepaticae[1/]	1	3	
Rubus acaulis	1	2	
Arenaria lateriflora	T	17	
Poa spp.	T	12	
Gramineae	T	9	
Stellaria longifolia	T	8	
Pyrola asarifolia	T	8	
Geranium richardsonii	T	7	
Viola nephrophylla	T	7	
Galium trifidum	T	5	
Equisetum laevigatum[2/]	T	4	
Veronica americana	T	4	
Parnassia fimbriata	T	4	
Unidentified Forbs	T	4	
Habenaria hyperborea	T	3	
Agropyron repens	T	3	
Parnassia parviflora	T	2	
Thalictrum sparsiflorum	T	2	
Angelica arguta	T	2	
Epilobium glandulosum	T	2	
Mimulus guttatus	T	2	
Achillea millefolium	T	2	
Potentilla anserina	T	2	
Potentilla gracilis	T	2	
Cirsium foliosum	T	1	
Allium schoenoprasum	T	1	
Compositae	T	1	
Juncus saximontanus	T	1	
Claytonia chamissoi	T	1	
Glyceria striata	T	1	
Angelica pinnata	T	1	
Alopecurus alpinus	T	1	
Lupinus argenteus var. *argenteus*[3/]	T	1	
Polygonum amphibium	T	1	
Epilobium angustifolium	T	1	

TABLE XI. (CONTINUED).

Taxon	Canopy-Coverage	Frequency	Intercept
Solidago multiradiata	T	1	
Stellaria sp.	T	1	
Litter	46	84	
Water	7	16	
Bare	1	6	

1/ Follows Jaques (1949:160).
2/ Follows Davis (1952:51-53).
3/ Follows Hitchcock and Cronquist (1961:306).

TABLE XII. PERCENT CANOPY-COVERAGE, FREQUENCY, AND INTERCEPT OF SPRUCE TYPE TAXA. T DENOTES LESS THAN 0.5 PERCENT.

Taxon	Canopy-Coverage	Frequency	Intercept
Open Overstory			51
Picea engelmanni			49
Linnaea borealis			13
Cornus canadensis			4
Salix bebbiana			2
Lonicera involucrata			2
Cornus stolonifera			2
Salix planifolia			1
Ribes hudsonianum			1
Salix wolfii			1
Rhamnus alnifolia			1
Ribes inerme			T
Juniperus communis			T
Betula glandulosa			T
Arctostaphylos uva-ursi			T
Salix myrtillifolia			T
Carex spp.	40	86	
Class Musci[1/]	27	66	
Equisetum arvense[2/]	18	56	
Fragaria virginiana	10	50	
Geranium richardsonii	9	43	
Unidentified Forbs	7	59	
Actaea rubra	7	30	
Smilacina stellata	6	43	
Glyceria elata	6	20	
Parnassia fimbriata	3	53	
Galium spp.	3	40	
Taraxacum spp.	3	20	
Polemonium occidentale	2	13	
Pyrola virens	2	13	
Epilobium angustifolium	2	13	
Angelica arguta	2	13	
Allium brevistylum	1	13	
Epilobium glandulosum	1	10	
Geum macrophyllum	1	10	
Veronica americana	1	7	
Thalictrum venulosum	1	7	

TABLE XII. (CONTINUED).

Taxon	Canopy-Coverage	Frequency	Intercept
Antennaria anaphaloides	1	7	
Pyrola asarifolia	1	3	
Claytonia chamissoi	1	3	
Senecio triangularis	1	3	
Angelica pinnata	1	3	
Thalictrum sparsiflorum	1	3	
Calamagrostis canadensis	T	7	
Pedicularis groenlandica	T	7	
Stellaria longifolia	T	7	
Bromus ciliatus	T	3	
Cinna latifolia	T	3	
Class Hepaticae 1/	T	3	
Barbarea orthoceras	T	3	
Zizia aptera	T	3	
Juncus balticus	T	3	
Gentiana affinis	T	3	
Poa spp.	T	3	
Listera borealis	T	3	
Gramineae	T	3	
Habenaria hyperborea	T	3	
Litter	64	92	
Bare	1	3	

1/ Follows Jaques (1949:160).
2/ Follows Davis (1952:51).

TABLE XIII. PERCENT CANOPY-COVERAGE AND FREQUENCY OF GRASSLAND TYPE TAXA. T DENOTES LESS THAN 0.5 PERCENT.

Taxon	Canopy-Coverage	Frequency
Festuca ovina	16	73
Taraxacum spp.	11	87
Lupinus spp.	9	68
Unidentified Forbs	6	61
Microseris nigrescens	6	54
Besseya wyomingensis	5	56
Galium boreale	5	39
Cerastium arvense	4	48
Poa secunda	4	41
Agropyron spp.	3	53
Arnica sororia	3	37
Achillea millefolium	2	48
Viola nuttallii	2	39
Antennaria rosea	2	26
Phlox longifolia	2	20
Anemone patens	2	15
Agropyron dasystachyum	2	14
Artemisia tridentata	2	12
Potentilla gracilis	2	12
Arenaria congesta	1	36
Gramineae	1	31
Arabis nuttallii	1	29
Zygadenus venenosus	1	20
Saxifraga rhomboidea	1	19
Trifolium longipes	1	17
Poa spp.	1	15
Poa cusickii	1	15
Astragalus miser	1	12
Phlox hoodii	1	12
Antennaria anaphaloides	1	10
Linum perenne	1	9
Leguminosae	1	9
Geum triflorum	1	7
Chrysothamnus viscidiflorus	1	7
Frasera speciosa	1	7

TABLE XIII. (CONTINUED).

Taxon	Canopy-Coverage	Frequency
Umbelliferae	1	7
Eriogonum umbellatum	1	7
Koeleria cristata	1	5
Agropyron bakeri	1	2
Geranium viscosissimum	1	2
Allium cernuum	T	17
Ranunculus glaberrimus	T	12
Carex spp.	T	9
Solidago multiradiata	T	9
Muhlenbergia sp.	T	9
Carex filifolia	T	7
Androsace septentrionalis	T	7
Danthonia intermedia	T	5
Castilleja sulphurea	T	5
Senecio lugens	T	3
Solidago nemoralis	T	3
Draba nemorosa	T	3
Haplopappus integrifolius	T	3
Penstemon radicosus	T	3
Aster occidentalis	T	3
Iris missouriensis	T	2
Symphoricarpos oreophilus	T	2
Fragaria virginiana	T	2
Anemone multifida	T	2
Erigeron glabellus	T	2
Erigeron compositus	T	2
Mertensia oblongifolia	T	2
Dodecatheon sp.	T	2
Arabis sp.	T	2
Solidago missouriensis	T	2
Gaillardia aristata	T	2
Agoseris glauca	T	2
Aster foliaceus	T	2
Rosaceae	T	2
Bare	12	99

TABLE XIV. PERCENT CANOPY-COVERAGE, FREQUENCY, AND INTERCEPT OF ASPEN TYPE TAXA. T DENOTES LESS THAN 0.5 PERCENT.

Taxon	Canopy-Coverage	Frequency	Intercept
Populus tremuloides			75
Open in Overstory			24
Pseudotsuga menziesii			7
Picea engelmanni			1
Symphoricarpos oreophilus			3
Berberis repens			2
Rosa woodsii			1
Salix bebbiana			1
Clematis columbiana			1
Shepherdia canadensis			1
Spiraea betulifolia			T
Lonicera involucrata			T
Taraxacum spp.	13	76	
Unidentified Forbs	11	50	
Thalictrum venulosum	11	44	
Trifolium longipes	9	26	
Calamagrostis rubescens	8	38	
Geranium richardsonii	8	20	
Lupinus argenteus var. *parviflorus*[1/]	7	40	
Actaea rubra	7	40	
Geranium viscosissimum	7	34	
Arnica cordifolia	6	24	
Fragaria virginiana	5	32	
Phleum pratense	5	32	
Equisetum arvense[2/]	5	12	
Smilacina stellata	3	32	
Astragalus miser	3	26	
Galium boreale	2	30	
Achillea millefolium	2	24	
Elymus glaucus	2	16	
Poa palustris	2	16	
Fragaria vesca	2	12	
Castilleja miniata	2	6	
Aster conspicuus	2	6	

TABLE XIV. (CONTINUED).

Taxon	Canopy-Coverage	Frequency	Intercept
Aquilegia flavescens	2	4	
Carex spp.	1	22	
Poa spp.	1	20	
Allium brevistylum	1	16	
Arenaria lateriflora	1	16	
Gramineae	1	12	
Agropyron trachycaulum	1	10	
Ligusticum filicinum	1	8	
Antennaria rosea	1	6	
Class Musci[3/]	1	6	
Solidago canadensis	1	4	
Bromus marginatus	T	14	
Pyrola secunda	T	6	
Androsace septentrionalis	T	6	
Collomia linearis	T	6	
Stipa columbiana	T	6	
Bromus sp.	T	4	
Potentilla spp.	T	4	
Osmorhiza occidentalis	T	4	
Cruciferae	T	4	
Aster occidentalis	T	2	
Geum sp.	T	2	
Geum triflorum	T	2	
Agropyron sp.	T	2	
Poa pratensis	T	2	
Silene sp.	T	2	
Arnica chamissonis	T	2	
Phleum alpinum	T	2	
Veronica americana	T	2	
Barbarea orthoceras	T	2	
Arabis sp.	T	2	
Agrostis scabra	T	2	
Senecio serra	T	2	
Hordeum sp.	T	2	

TABLE XIV. (CONTINUED).

Taxon	Canopy-Coverage	Frequency	Intercept
Agropyron bakeri	T	2	
Viola adunca	T	2	
Pedicularis paysoniana	T	2	
Poa nervosa	T	2	
Anemone multifida	T	2	
Carex rossii	T	2	
Clematis hirsutissima	T	2	
Koeleria cristata	T	2	
Litter	75	96	
Bare	5	20	
Rock	2	4	

1/ Follows Hitchcock and Cronquist (1961:302).
2/ Follows Davis (1952:51).
3/ Follows Jaques (1949:160).

TABLE XV. PERCENT CANOPY-COVERAGE, FREQUENCY, AND INTERCEPT OF DOUGLAS-FIR TYPE TAXA. T DENOTES LESS THAN 0.5 PERCENT.

Taxon	Canopy-Coverage	Frequency	Intercept
Pseudotsuga menziesii			71
Open in Overstory			19
Pinus contorta			12
Abies lasiocarpa			2
Picea engelmanni			1
Spiraea betulifolia			6
Clematis columbiana			3
Symphoricarpos oreophilus			2
Salix scouleriana			1
Acer glabrum			1
Juniperus communis			T
Berberis repens			T
Ribes viscosissimum			T
Lonicera utahensis			T
Rubus parviflorus			T
Calamagrostis rubescens	25	80	
Arnica cordifolia	22	85	
Aster conspicuus	7	18	
Actaea rubra	6	45	
Thalictrum venulosum	6	35	
Unidentified Forbs	4	35	
Antennaria racemosa	4	28	
Fragaria vesca	4	25	
Aquilegia flavescens	3	8	
Class Musci[1/]	2	25	
Mitella stauropetala	2	23	
Astragalus miser	2	13	
Geranium viscosissimum	2	13	
Poa palustris	1	18	
Pyrola secunda	1	15	
Goodyera oblongifolia	1	13	
Viola adunca	1	10	
Galium boreale	1	10	
Lupinus argenteus var. *parviflorus*[2/]	1	10	

TABLE XV. (CONTINUED).

Taxon	Canopy-Coverage	Frequency	Intercept
Fragaria virginiana	1	8	
Geum spp.	1	5	
Carex rossii	1	5	
Valeriana dioica	1	3	
Calypso bulbosa	T	5	
Antennaria anaphaloides	T	5	
Disporum trachycarpum	T	5	
Arenaria lateriflora	T	5	
Achillea millefolium	T	5	
Taraxacum spp.	T	3	
Antennaria rosea	T	3	
Gramineae	T	3	
Collomia linearis	T	3	
Potentilla gracilis	T	3	
Litter	92	95	
Bare	T	3	
Rock	T	3	

1/ Follows Jaques (1949:160).
2/ Follows Hitchcock and Cronquist (1961:302).

TABLE XVI. PERCENT CANOPY-COVERAGE, FREQUENCY, AND INTERCEPT OF SPRUCE-FIR TYPE TAXA. T DENOTES LESS THAN 0.5 PERCENT.

Taxon	Canopy-Coverage	Frequency	Intercept
Abies lasiocarpa			60
Picea engelmanni			28
Open in Overstory			23
Populus tremuloides			19
Berberis repens			6
Clematis columbiana			3
Spiraea betulifolia			T
Symphoricarpos oreophilus			T
Thalictrum venulosum	12	80	
Aster conspicuus	11	70	
Calamagrostis rubescens	10	60	
Ligusticum filicinum	7	30	
Actaea rubra	6	60	
Arnica cordifolia	4	60	
Geranium richardsonii	4	30	
Class Musci 1/	3	20	
Fragaria virginiana	2	20	
Unidentified Forbs	2	10	
Galium boreale	1	40	
Viola adunca	1	30	
Allium brevistylum	1	20	
Pyrola secunda	T	10	
Achillea millefolium	T	10	
Taraxacum spp.	T	10	
Astragalus miser	T	10	
Elymus glaucus	T	10	
Smilacina stellata	T	10	
Lupinus argenteus var. *parviflorus* 2/	T	10	
Litter	88	90	

1/ Follows Jaques (1949:160).
2/ Follows Hitchcock and Cronquist (1961:302).

TABLE XVII. RESULTS OF POINT-CENTERED QUARTER METHOD ANALYSES OF TREES.

Vegetation Type and Taxon	Relative Frequency	Relative Density	Relative Dominance	Importance Value
Spruce				
Picea engelmanni	100	100	100	300
Aspen				
Populus tremuloides	79.4	90.5	96.5	266.4
Pseudotsuga menziesii	15.9	7.0	3.0	25.9
Picea engelmanni	4.8	2.5	0.6	7.9
Total	100.1	100.0	100.1	300.2
Douglas-fir				
Pseudotsuga menziesii	78.0	85.0	94.0	257.0
Pinus contorta	16.0	11.3	4.9	32.2
Abies lasiocarpa	6.0	3.8	1.1	10.9
Total	100.0	100.1	100.0	300.1
Spruce-fir				
Abies lasiocarpa	66.7	70.0	77.2	213.9
Populus tremuloides	20.0	20.0	14.9	54.9
Picea engelmanni	13.3	10.0	7.9	31.2
Total	100.0	100.0	100.0	300.0

TABLE XVIII. PLANT DISTRIBUTION BY VEGETATION TYPE ON THE STUDY AREA (AQ = AQUATIC[1], SE = SEDGE, WI = WILLOW, SP = SPRUCE, AS = ASPEN, DF = DOUGLAS-FIR, SF = SPRUCE-FIR, GR = GRASSLAND, MI = MISCELLANEOUS[2]). X DENOTES PRESENCE.

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
EQUISETACEAE[3]									
Equisetum arvense[3]	X		X	X	X				
laevigatum[3]		X	X	X	X			X	
palustre[3]	X								
PINACEAE									
Abies lasiocarpa					X	X	X		
Picea engelmanni			X	X	X	X	X		
Pinus contorta						X			
flexilis					X	X		X	
Pseudotsuga menziesii					X	X		X	
CUPRESSACEAE									
Juniperus communis				X	X	X		X	
scopulorum						X			
TYPHACEAE									
Typha latifolia	X	X							
SPARGANIACEAE									
Sparganium multipedunculatum	X								
POTAMOGETONACEAE									
Potamogeton filiformis	X								
pectinatus	X								
praelongus	X								
pusillus	X								
richardsonii	X								
zosteriformis	X								
Zannichellia palustris	X								
NAJADACEAE									
Najas flexilis	X								
JUNCAGINACEAE									
Triglochin maritima		X							
ALISMACEAE									
Sagittaria cuneata	X								
HYDROCHARITACEAE									
Elodea canadensis	X								

TABLE XVIII. (CONTINUED).

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
GRAMINEAE									
Tribe Festuceae									
Bromus anomalus								X	
ciliatus			X	X	X				
inermis								X	X
marginatus					X	X		X	X
tectorum									X
Catabrosa aquatica	X								
Dactylis glomerata									X
Festuca ovina								X	
rubra		X							
Glyceria borealis	X								
elata		X	X	X					
grandis	X								
striata			X						
Melica spectabilis								X	
Poa ampla								X	
compressa								X	
cusickii								X	
epilis		X							
nervosa					X				
palustris		X			X	X			
pratensis		X	X		X			X	X
secunda						X		X	
Puccinellia distans									X
Tribe Hordeae									
Agropyron bakeri		X			X			X	
dasystachyum								X	
desertorum								X	
pseudorepens								X	X
repens			X					X	
trachycaulum					X			X	
Elymus cinereus		X						X	
glaucus					X	X	X		
macounii								X	
Hordeum brachyantherum		X						X	X
jubatum	X	X						X	X
Tribe Aveneae									
Danthonia intermedia								X	
Deschampsia caespitosa		X							
Koeleria cristata					X			X	
Trisetum spicatum						X			X

TABLE XVIII. (CONTINUED).

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
Tribe Agrostideae									
Agrostis alba		X							
diegoensis			X	X					
exarata	X								
scabra					X			X	
Alopecurus aequalis	X	X							
alpinus		X	X		X				
Calamagrostis canadensis	X		X	X					
inexpansa	X		X						
neglecta		X							
rubescens					X	X	X		
Cinna latifolia				X					
Muhlenbergia filiformis		X							
racemosa		X							
Phleum alpinum		X			X	X		X	
pratense		X	X	X	X			X	X
Stipa columbiana					X	X		X	
williamsii								X	
Tribe Chlorideae									
Beckmannia syzigachne	X	X							
Spartina gracilis		X							
Tribe Phalarideae									
Hierochloe odorata		X							
Phalaris arundinacea	X	X							
CYPERACEAE									
Carex									
Section Divisae									
Carex douglasii		X							
simulata		X							
Section Bracteosae									
Carex vallicola								X	
Section Heleonastes									
Carex disperma			X	X					
Section Stellulatae									
Carex interior		X	X	X	X				
Section Ovales									
Carex athrostachya	X								
festivella		X							
microptera					X				
xerantica								X	
Section Filifoliae									
Carex filifolia								X	

TABLE XVIII. (CONTINUED).

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
Section Montanae									
Carex rossii					X	X			
Section Firmiculmes									
Carex geyeri						X			
Section Bicolores									
Carex aurea		X							
Section Hirtae									
Carex lanuginosa		X							
Section Atratae									
Carex raynoldsii					X	X			
Section Acutae									
Carex nebraskensis		X							
Section Vesicariae									
Carex rostrata		X	X	X	X				
Eleocharis acicularis	X								
macrostachya	X	X							
Eriophorum angustifolium		X							
Scirpus acutus	X								
LEMNACEAE									
*Lemna minima*4/	X								
minor	X								
trisulca	X								
JUNCACEAE									
Juncus balticus	X	X	X	X					
bufonius	X								
confusus	X								
effusus	X								
longistylis	X	X							
saximontanus	X	X	X	X	X				
Luzula parviflora				X					
LILIACEAE									
Allium brevistylum			X	X	X		X		
cernuum						X		X	
schoenoprasum		X	X						
Calochortus nitidus								X	
nuttallii								X	
Camassia quamash								X	
Disporum trachycarpum				X	X	X			
Fritillaria atropurpurea					X				
pudica								X	

TABLE XVIII. (CONTINUED).

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
Smilacina racemosa						X		X	
stellata			X	X	X	X	X		
Zygadenus elegans		X	X						
venenosus								X	
IRIDACEAE									
Iris missouriensis		X			X			X	
Sisyrinchium angustifolium		X	X					X	
ORCHIDACEAE									
Calypso bulbosa						X			
Goodyera oblongifolia						X			
Habenaria hyperborea		X	X	X	X				
unalascensis						X			
Listera borealis				X					
SALICACEAE									
Populus acuminata		X							X
tremuloides		X	X	X	X	X	X	X	X
trichocarpa									X
Salix bebbiana	X	X	X	X	X	X			
candida		X	X						
drummondiana	X	X	X						
exigua	X	X	X						X
fragilis									X
geyeriana	X	X	X						
lasiandra	X		X						
monticola	X	X	X	X		X			
myrtillifolia	X	X	X	X	X	X			
planifolia	X	X	X	X	X				
rigida			X		X				
scouleriana					X	X			
wolfii	X	X	X	X	X				
BETULACEAE									
Betula glandulosa		X	X	X	X				
URTICACEAE									
Urtica dioica	X		X	X	X				X
SANTALACEAE									
Comandra umbellata								X	
POLYGONACEAE									
Eriogonum umbellatum								X	
Polygonum amphibium	X	X	X						
aviculare									X

TABLE XVIII. (CONTINUED).

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
bistortoides								X	
douglasii								X	
lapathifolium	X								
Rheum rhaponticum									X
Rumex crispus									X
maritimus		X							
occidentalis		X							
paucifolius								X	
salicifolius	X								
CHENOPODIACEAE									
Chenopodium album									X
rubrum					X				
Monolepis nuttalliana	X								
PORTULACACEAE									
Claytonia chamissoi		X	X	X					
CARYOPHYLLACEAE									
Arenaria congesta								X	
lateriflora		X	X		X	X			
Cerastium arvense								X	
vulgatum		X							
*Sagina occidentalis*3/	X								
Silene parryi					X				
Stellaria longifolia		X	X	X					
RANUNCULACEAE									
Actaea rubra			X	X	X	X	X		
Anemone multifida					X			X	
patens								X	
Aquilegia flavescens					X	X		X	
Clematis columbiana					X	X	X		
hirsutissima					X			X	
Delphinium glaucescens			X		X			X	
*nelsoni*5/								X	
Ranunculus acriformis		X							X
aquatilis	X								
cymbalaria	X	X							X
glaberrimus								X	
gmelinii	X								
inamoenus								X	
natans	X			X					
sceleratus	X	X							
Thalictrum sparsiflorum		X	X	X					
venulosum			X	X	X	X	X		

TABLE XVIII. (CONTINUED).

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
BERBERIDACEAE									
Berberis repens					X	X	X	X	
FUMARIACEAE									
Corydalis aurea									X
CRUCIFERAE									
Arabis hirsuta									X
nuttallii								X	
Barbarea orthoceras		X		X	X				
Capsella bursa-pastoris								X	X
Cardamine breweri	X								
Descurainia richardsonii									X
Draba nemorosa								X	
Erysimum cheiranthoides		X						X	
Lepidium densiflorum									X
Rorippa islandica		X		X					
lyrata	X								
nasturtium-aquaticum	X								
Sisymbrium loeselii									X
Thelypodium sagittatum		X	X						
Thlaspi arvense								X	X
CRASSULACEAE									
Sedum lanceolatum						X		X	
SAXIFRAGACEAE									
Heuchera parvifolia						X		X	
Mitella stauropetala						X			
Parnassia fimbriata		X	X	X	X				
parviflora		X	X						
Saxifraga arguta				X					
rhomboidea								X	
GROSSULARIACEAE									
Ribes hudsonianum			X	X	X				
inerme			X	X	X				
setosum			X						
viscosissimum					X	X			
ROSACEAE									
Amelanchier alnifolia					X	X		X	X
Fragaria vesca					X	X			
virginiana			X	X	X	X	X	X	
Geum canadense						X		X	
macrophyllum		X	X	X	X	X		X	
triflorum					X			X	

TABLE XVIII. (CONTINUED).

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
Potentilla anserina			X					X	X
fruticosa		X	X	X					
gracilis		X	X			X		X	
norvegica									X
plattensis								X	
Prunus virginiana					X	X		X	X
Rosa woodsii			X		X	X		X	X
Rubus acaulis			X						
idaeus									X
parviflorus						X			
Spiraea betulifolia					X	X	X		X
LEGUMINOSAE									
Astragalus canadensis									X
dasyglottis								X	X
eucosmus			X						
inflexus								X	
miser					X	X	X	X	
terminalis								X	
Caragana arborescens			X					X	X
Hedysarum boreale								X	
sulphurescens								X	
Lupinus argenteus var. *argenteus*[6/]			X		X			X	
parviflorus[6/]					X	X	X		
sericeus								X	
Medicago lupulina									X
sativa								X	
Melilotus alba								X	X
officinalis								X	X
Oxytropis deflexa									X
sericea								X	
Trifolium longipes		X	X		X			X	
pratense									X
repens		X							X
GERANIACEAE									
Geranium richardsonii			X	X	X	X	X		
viscosissimum					X	X		X	X
LINACEAE									
Linum perenne								X	
CALLITRICHACEAE									
Callitriche hermaphroditica	X								
verna	X								

TABLE XVIII. (CONTINUED).

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
ACERACEAE									
Acer glabrum					X	X			
RHAMNACEAE									
Rhamnus alnifolia			X	X	X				
MALVACEAE									
Iliamna rivularis								X	X
VIOLACEAE									
Viola adunca					X	X	X	X	
nephrophylla		X	X	X	X				
nuttallii								X	
ELAEAGNACEAE									
Shepherdia canadensis		X	X	X	X	X			
ONAGRACEAE									
Epilobium angustifolium			X	X	X				X
glandulosum	X	X	X	X	X				X
palustre			X						
Oenothera flava								X	X
HALORAGIDACEAE									
Myriophyllum spicatum	X								
HIPPURIDACEAE									
Hippuris vulgaris	X								
UMBELLIFERAE									
Angelica arguta		X	X	X	X				
pinnata		X	X	X	X				
Bupleurum americanum								X	
Heracleum lanatum			X	X	X				X
Ligusticum filicinum					X	X	X		
Lomatium cous								X	
triternatum								X	
Musineon divaricatum								X	
Osmorhiza occidentalis					X	X			
Perideridia gairdneri						X		X	
Sium suave		X	X						
Zizia aptera		X	X	X					
CORNACEAE									
Cornus canadensis				X					
stolonifera			X	X	X	X			

TABLE XVIII. (CONTINUED).

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
ERICACEAE									
Arctostaphylos uva-ursi		X	X	X	X	X			
Pyrola asarifolia			X	X					
secunda					X	X	X		
uniflora				X					
virens			X	X					
PRIMULACEAE									
Androsace septentrionalis	X				X			X	X
Dodecatheon conjugens								X	
pauciflorum		X							
Primula incana								X	
GENTIANACEAE									
Frasera speciosa								X	
Gentiana affinis		X	X	X	X			X	
prostrata								X	
Swertia perennis		X	X	X	X				
POLEMONIACEAE									
Collomia linearis					X	X		X	X
Phlox hoodii								X	
kelseyi								X	
longifolia								X	
Polemonium occidentale		X	X	X	X				
HYDROPHYLLACEAE									
Hydrophyllum capitatum					X				
Phacelia hastata						X			X
sericea									X
BORAGINACEAE									
Hackelia floribunda					X	X			X
Lappula echinata								X	X
Mertensia ciliata			X		X				
oblongifolia								X	
Myosotis sylvatica								X	
Plagiobothrys scouleri	X	X							
LABIATAE									
Agastache urticifolia						X			
Mentha arvensis	X	X	X	X	X				
Prunella vulgaris	X								
Scutellaria galericulata		X							
Stachys palustris	X								
SOLANACEAE									
Hyoscyamus niger									X

TABLE XVIII. (CONTINUED).

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
SCROPHULARIACEAE									
Besseya wyomingensis								X	
Castilleja miniata		X	X	X	X	X		X	
sulphurea		X						X	
Limosella aquatica	X								
Mimulus guttatus	X	X	X	X	X				
Orthocarpus luteus								X	
Pedicularis groenlandica		X	X	X	X				
paysoniana					X	X			
Penstemon radicosus								X	
rydbergii		X						X	
Veronica americana	X	X	X	X	X				
arvensis		X							
serpyllifolia			X						
LENTIBULARIACEAE									
Utricularia vulgaris	X								
PLANTAGINACEAE									
Plantago major		X			X				X
RUBIACEAE									
Galium boreale		X	X	X	X	X	X	X	
trifidum		X	X	X					
triflorum			X	X					
CAPRIFOLIACEAE									
Linnaea borealis			X	X	X				
Lonicera involucrata			X	X	X	X		X	
utahensis						X			X
Sambucus pubens					X				X
Symphoricarpos oreophilus					X	X	X	X	X
Viburnum edule			X		X				
VALERIANACEAE									
Valeriana dioica					X	X			
edulis		X	X						
CAMPANULACEAE									
Campanula rotundifolia			X		X	X		X	
COMPOSITAE									
Tribe Heliantheae[3]									
Balsamorhiza sagittata								X	
Bidens cernua	X								
Eriophyllum lanatum						X		X	
Gaillardia aristata								X	X
Helianthella uniflora				X	X	X		X	
Helianthus annuus									X
Iva xanthifolia									X

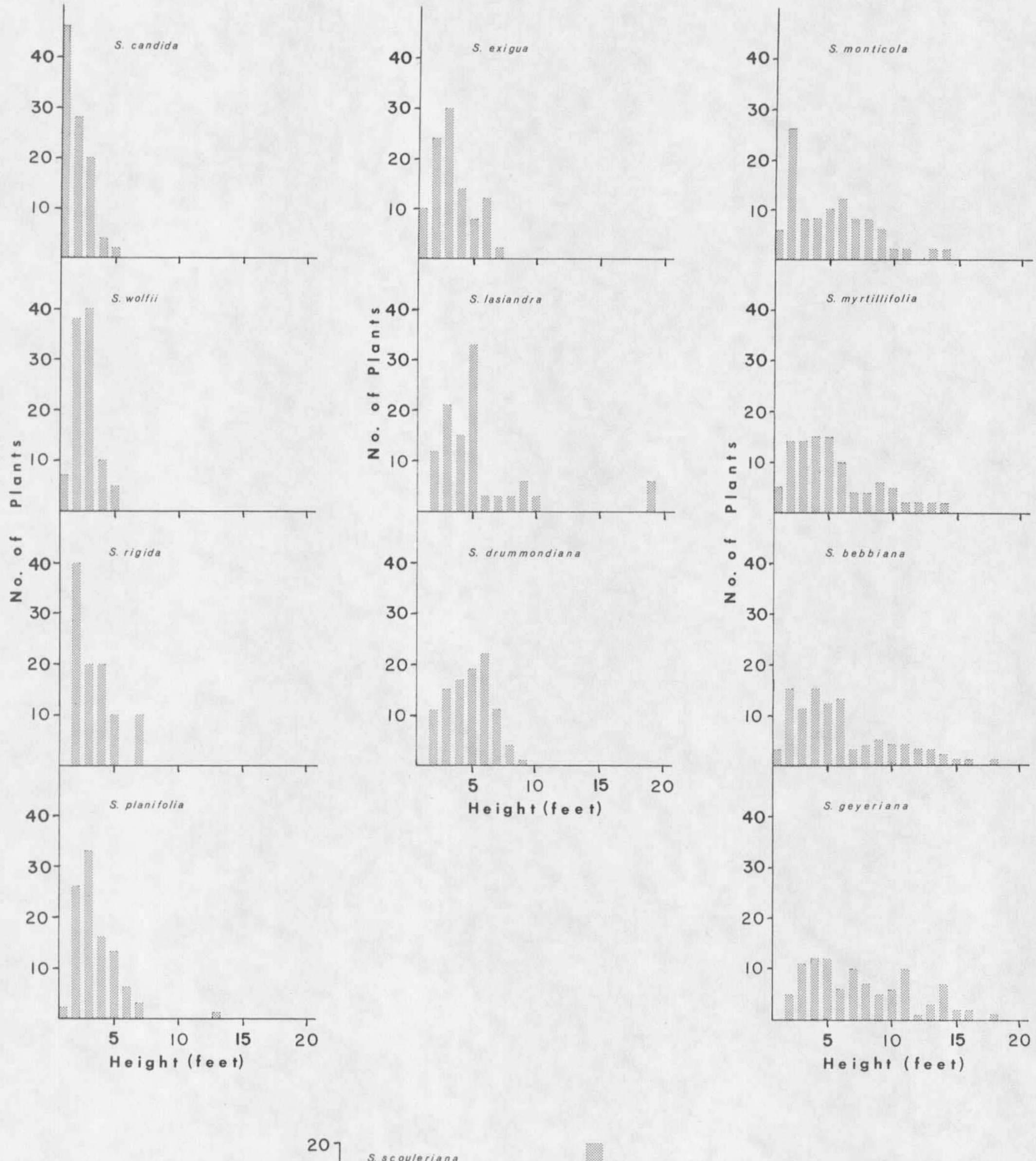
TABLE XVIII. (CONTINUED).

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
Madia glomerata									X
Rudbeckia occidentalis			X		X				X
Wyethia helianthoides								X	
Tribe Anthemideae[3/]									
Achillea millefolium		X	X		X	X	X	X	X
Artemisia biennis									X
dracunculus								X	
frigida								X	
ludoviciana								X	X
tridentata					X			X	X
Chrysanthemum leucanthemum									X
Matricaria matricarioides									X
Tanacetum vulgare									X
Tribe Senecioneae[3/]									
Arnica chamissonis					X				
cordifolia					X	X	X		
sororia								X	
Senecio canus								X	
debilis		X							
hydrophilus		X							
lugens								X	
pseudaureus		X							
serra			X		X	X		X	
sphaerocephalus		X							
triangularis			X	X	X				
werneriaefolius								X	
Tetradymia canescens								X	
Tribe Astereae[3/]									
Aster conspicuus					X	X	X		
engelmanni					X				
falcatus								X	
foliaceus		X	X	X	X			X	
hesperius		X							
occidentalis					X			X	X
perelegans						X			
Chrysothamnus nauseosus								X	
viscidiflorus								X	
Erigeron compositus								X	
corymbosus								X	
glabellus								X	
lonchophyllus		X							
philadelphicus					X				X
speciosus								X	

TABLE XVIII. (CONTINUED).

Taxon	AQ	SE	WI	SP	AS	DF	SF	GR	MI
Grindelia squarrosa									X
Haplopappus acaulis								X	
integrifolius		X						X	
uniflorus		X						X	
Solidago canadensis		X	X	X	X				
missouriensis								X	
multiradiata			X					X	
nemoralis								X	
Townsendia parryi								X	
Tribe Inuleae 3/									
Antennaria anaphaloides		X	X	X		X		X	
racemosa						X			
rosea					X	X		X	
Gnaphalium palustre	X								
Tribe Cynareae 3/									
Cirsium arvense			X						X
foliosum		X	X					X	
vulgare					X				
Tribe Cichorieae 3/									
Agoseris glauca					X			X	
Crepis acuminata								X	
Hieracium albiflorum						X			
cynoglossoides						X			X
Lactuca pulchella									X
Microseris nigrescens								X	
Sonchus uliginosus	X								
Taraxacum laevigatum								X	
officinale		X	X		X	X		X	X
Tragopogon dubius								X	X
pratensis								X	

1/ Includes wet banks, shores, and ditches.
2/ Includes roadsides and other disturbed areas.
3/ Follows Davis (1952).
4/ Follows Fassett (1966:376).
5/ Follows Sawyer (1967).
6/ Follows Hitchcock and Cronquist (1961:302-306).



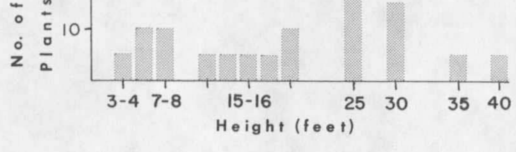


Figure 5. Distribution of willow heights on the study area by species. Samples of less than 100 plants are projected to 100.

TABLE XIX. FORAGE PLANTS WITH LESS THAN 2 PERCENT USE (EXCLUDING THE GENUS *SALIX*) BY MOOSE AND CATTLE IN ALL CATEGORIES EXCEPT FREQUENCY FOR RUMEN SAMPLES. VALUES ARE PERCENTAGES. T DENOTES LESS THAN 0.05 PERCENT AND NA DENOTES NOT AVAILABLE.

	SUMMER				FALL					WINTER			
	Cattle	Moose			Moose					Moose			
Area of Use[1/]:	Al 30	Ca 19	Al 40	As 8	Al 8[2/]		Wi 7[2/]		Ti 1[2/]	Al 35	Wi 24	Df 9	As 5
Taxon / Instances of Use:	17,813	12,271[2/]	36,812	2,221[2/]	Vol.	Freq.	Vol.	Freq.	Vol.	32,480	26,748	3,487[2/]	1,627[2/]
Amelanchier alnifolia	NA	NA	0.0	0.0	0.0	0	NA	-	0.0	0.1	NA	0.2	1.4
Berberis repens	NA	NA	0.0	0.0	0.1	13	NA	-	0.4	0.0	NA	0.0	0.0
Clematis columbiana	NA	NA	0.0	0.0	0.0	0	NA	-	0.0	T	NA	0.0	0.4
Cornus stolonifera	NA	NA	0.1	0.0	T	13	T	14	0.0	0.1	0.1	0.0	0.2
Lonicera involucrata	0.3	0.1	1.1	1.1	0.0	0	0.0	0	0.0	T	0.0	0.0	0.4
Potentilla fruticosa	0.0	0.0	T	NA	0.0	0	0.0	0	NA	0.0	0.0	NA	NA
Ribes inerme	T	0.4	0.3	0.7	-	-	-	-	-	T	T	NA	0.0
Ribes setosum	NA	NA	0.0	NA	-	-	-	-	-	T	T	NA	NA
Ribes spp.	-	-	-	-	0.7	13	0.9	14	0.0	0.1	T	0.0	0.9
Shepherdia canadensis	NA	NA	0.0	0.0	0.0	0	0.0	0	0.0	T	0.0	0.0	0.4
Spiraea betulifolia	NA	NA	0.0	0.0	0.0	0	NA	-	0.0	T	NA	0.0	0.2
Aster foliaceus	-	0.0	0.0	0.0	0.0	0	0.0	0	0.0	T	T	NA	0.0
Epilobium angustifolium	-	0.0	T	0.1	0.0	0	0.0	0	0.0	0.0	0.0	NA	0.0
Fragaria virginiana	-	0.0	T	0.2	0.0	0	0.0	0	0.0	0.0	0.0	0.0	0.0
Geranium richardsonii	-	0.0	T	0.5	0.0	0	0.0	0	0.0	0.0	0.0	0.0	0.0
Geranium viscosissimum	-	0.0	T	0.1	0.0	0	NA	-	0.0	0.0	NA	0.0	0.0
Geum macrophyllum	-	T	T	0.0	T	13	T	14	0.0	0.0	0.0	0.0	0.0
Lupinus argenteus var. *parviflorus*[3/]	-	NA	T	0.1	0.0	0	NA	-	0.0	0.0	NA	0.0	0.0
Rudbeckia occidentalis	-	NA	T	0.0	0.0	0	0.0	0	0.0	0.0	0.0	NA	0.0
Smilacina stellata	-	0.0	T	0.0	0.0	0	0.0	0	0.0	0.0	0.0	0.0	0.0
Taraxacum officinale	-	0.0	T	0.0	0.0	0	0.0	0	0.0	0.0	0.0	0.0	0.0
Unidentified forbs	-	-	-	-	T	25	0.1	29	0.0	T	-	-	0.1
Bromus marginatus	-	0.0	T	T	-	-	-	-	-	0.0	NA	0.0	0.0
Calamagrostis canadensis	-	0.0	T	NA	-	-	-	-	-	0.0	0.0	NA	NA
Carex spp.	-	0.0	0.1	0.0	-	-	-	-	-	0.1	0.2	0.0	0.0
Juncus balticus	-	0.0	0.1	NA	0.0	0	0.0	0	NA	0.0	0.0	NA	NA
Phleum pratense	-	0.0	T	T	-	-	-	-	-	0.0	0.0	NA	0.0
Unidentified Gramineae	-	-	T	-	-	-	-	-	-	T	T	-	-

1/ Al = all areas, Ca = cattle areas, As = aspen type, Wi = willow type, Ti = upland timber types, and Df = Douglas-fir type. Numbers are total feeding sites for summer and winter and total rumen samples for fall.

2/ Insufficient sample.

3/ Follows Hitchcock and Cronquist (1961:302).