SOME MOOSE–WILLOW RELATIONSHIPS IN THE
INTERIOR OF ALASKA

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INTERIOR OF ALASKA

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THESIS

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SOME MOOSE-WILLOW RELATIONSHIPS IN THE

INTERIOR OF ALASKA

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ABSTRACT

Some moose-willow relationships were studied on several moose ranges in Alaska's interior. Certain species of willows were found to be preferred by moose over others--S. interior, S. alaxensis, S. arbusculoides, and S. pulchra being the most highly preferred. The results of a chemical analysis of several species suggest a possible relationship between the chemical compositions and palatabilities of willow species. S. alaxensis and S. pulchra, by virtue of their high palatability, wide distribution, and relatively high abundance, are probably the most important browse species. Moderately palatable willow species are eaten to a greater degree by moose when occuring with highly preferred species than when occurring in "pure" stands. In a given area neither the relative density nor relative abundance of a species visibly affect its degree of use. The densest of the willow stands that were studied apparently do not physically hinder moose movements sufficiently to cause such stands to be utilized less intensively than are sparse stands. The degree of browsing that is sustained by a given species seems to be positively correlated with plant height, but species preferability is evidently determined more by inherent palatability than by mean height.

The total amount of available browse on one study area was 4.5 pounds (oven-dried weight) per 100 square m. The percentages of available browse removed by moose from the various willow species during one winter ranged from 33.8 to 0.1 percent.

ACKNOWLEDGMENTS

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INTRODUCTION

The importance of willows as a food source for moose has been well documented. Willows are considered the most important food items for moose in Montana (Knowlton, 1960), Wyoming (Baker et al., 1953; Harry, 1957), and south-central Alaska (Chatelain, 1951). Pimlott (1961) sums up the situation by stating that in western Canada and the western United States, willows and moose are inseparable.

Due to the lack of adequate willow keys and the difficulties involved in species identification, most of the literature refers only to Salix spp. as being preferred by moose. The resulting implication is that all species of willows are equally preferred and, hence, of equal importance. Several workers (McMillan, 1953; Murie, 1961; Seiskari, 1956), however, have noted a species preference by moose. Murie's observations, which were made in Mt. McKinley National Park, and observations made by personnel of the Alaska Department of Fish and Game (R. A. Rausch, Alaska Department of Fish and Game, pers. comm.) have indicated that some willow species in Alaska are browsed by moose more intensively than are others.

The primary purpose of this study was to determine the identity and possible preferability to moose of the various willow species occurring on some of the important moose ranges in Alaska's interior. Secondarily, an attempt was made to explain the reasons for selection preference, if such was found to exist. Some of the data that were collected while pursuing these goals also made it possible to investigate other topics, such as effects of plant height, density, and

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location, on browsing intensity.

The study was conducted during the summers of 1967 and 1968. Since the same methods were not employed during both summers, the discussion of methods and results have been divided into two parts, each corresponding to one summer's work.

PART I

STUDY AREAS

The areas investigated were chosen on the basis of their impor-
tance to moose in interior Alaska and because they were known to
support stands of willows suitable for study. During the course of the
study, a helicopter, small, single engine aircraft, automobile, and
canoe were used to gain access to the study areas.

Dry Creek

The Dry Creek study area (Fig. 1) is located in the extreme south-
ern portion of the Tanana River flats, which lie north of the Alaska
Range. (The location of the study area on the map is shown by the
broken lines. The numbers refer to the locations of study plots.) At
one time the study area was a black spruce (Picea mariana) muskeg, but
a fire, occurring at some undetermined time in the past, destroyed the
spruce. The stand of willows studied, which is approximately 2500 m
long and 150 m wide, apparently is a seral community.

The composition of the willow stand varies with its proximity to
the creek. The species Salix alaxensis, S. lasiandra, S. arbusculoides,
S. padophylla, and S. myrtillifolia occur in a "belt" that is adjacent
to Dry Creek. This "belt" of willows varies between 20 and 60 m in
width and is closely associated with the stream levee, which normally
is relatively dry. A marshy condition occurs on the floodplain further
from the creek, and, here, S. pulchra, which grows in dense patches,
and S. arbusculoides are the dominant species of willows present. S.

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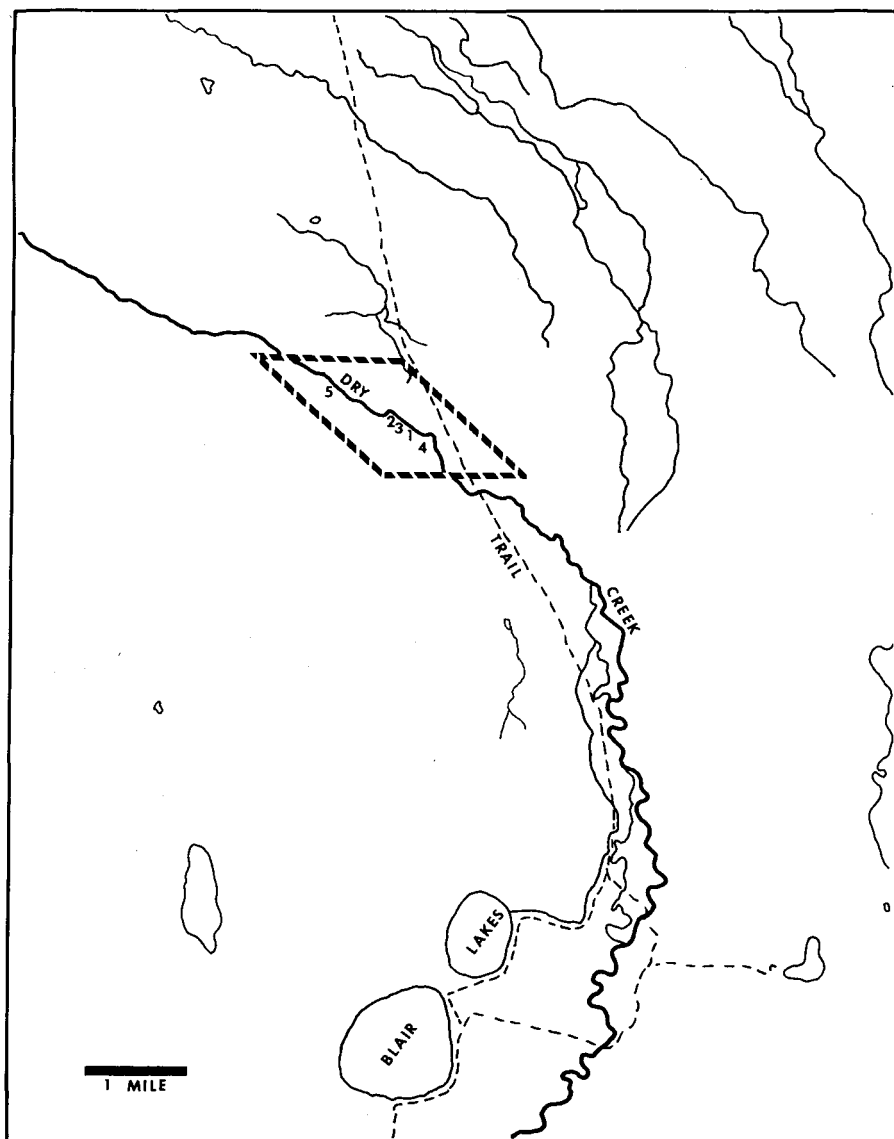
Figure 1. Dry Creek study area; 64°27' N, 147°22' W (From U. S. Geological Survey map B-1, Fairbanks quadrangle).

depressa is occasionally found on the drier sites in this marshy area. The texture of the soil underlying the marshy area is finer than that of the stream levee.

Paxson Lake

Paxson Lake is located in the Alaska Range, approximately 150 miles southeast of Fairbanks (Fig. 2). Dwarf birch (Betula nana) and black spruce are the most abundant plant species in the area surrounding the lake, and willow stands suitable for study are rare. The most extensive willow stand in this region occurs in the marshy areas bordering the Gulkana River, which flows into the north end of Paxson Lake. The marsh near the lake was the only portion of this area examined, and S. pulchra, S. lanata, and S. Barclayi were the only willow species encountered. The soil in this region is finely textured and highly organic.

One other area, located along a section of the old Richardson Highway east of Paxson Lake, was examined. The most abundant plant species on the wet sites along this road are S. pulchra, S. Barclayi, S. lanata, S. reticulata, horsetail (Equisetem sp.) and sphagnum moss (Sphagnum sp.), whereas S. alaxensis, S. glauca, S. depressa, and seedling black cottonwood (Populus trichocarpa) occur on the dry sites. Generally, the soil on the wet sites has a finer texture than that occurring on the dry sites.

Little Clearwater Creek

Little Clearwater Creek is a glacier-fed stream that intersects the Denali Highway 54 miles west of Paxson, Alaska (Fig. 3). Dwarf
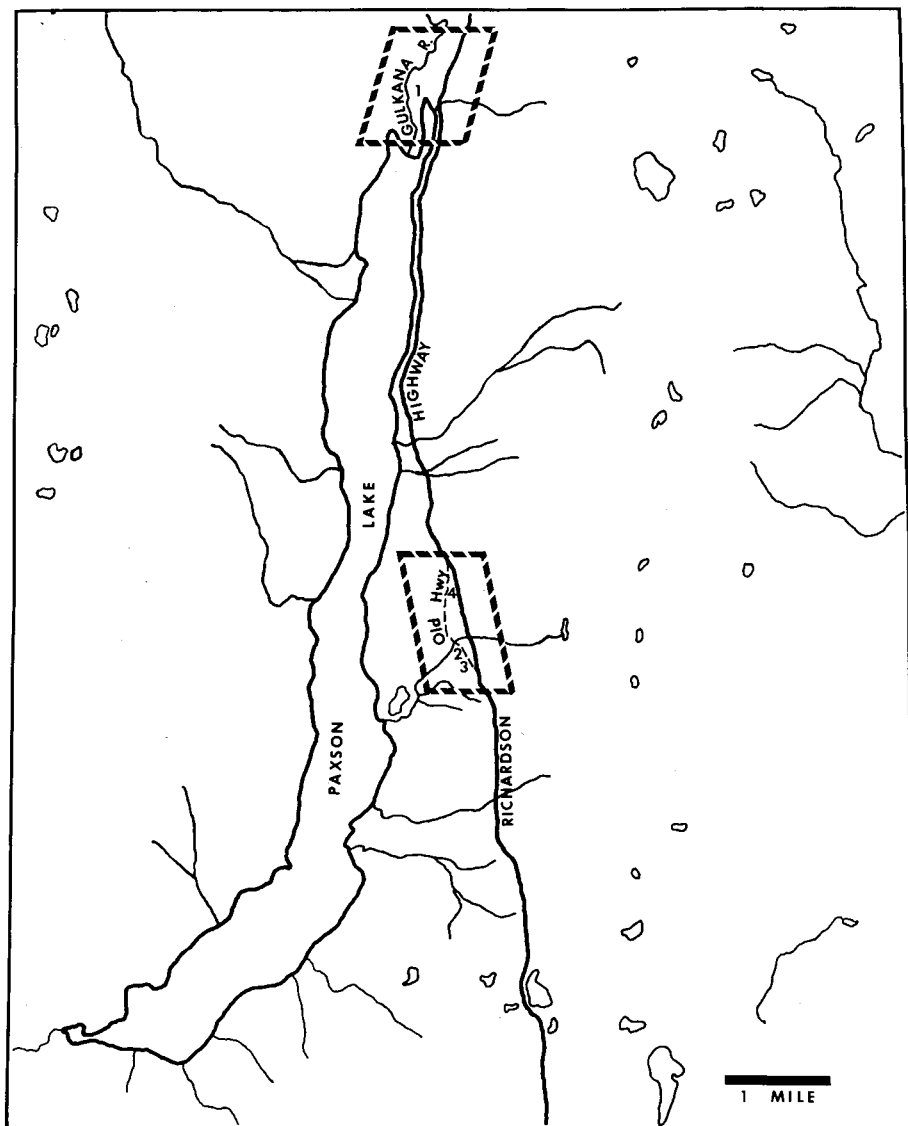
Figure 2. Paxson Lake study area; 62°55' N, 145°30' W (From U. S. Geological Survey maps D-3 and D-4, Gulkana quadrangle).
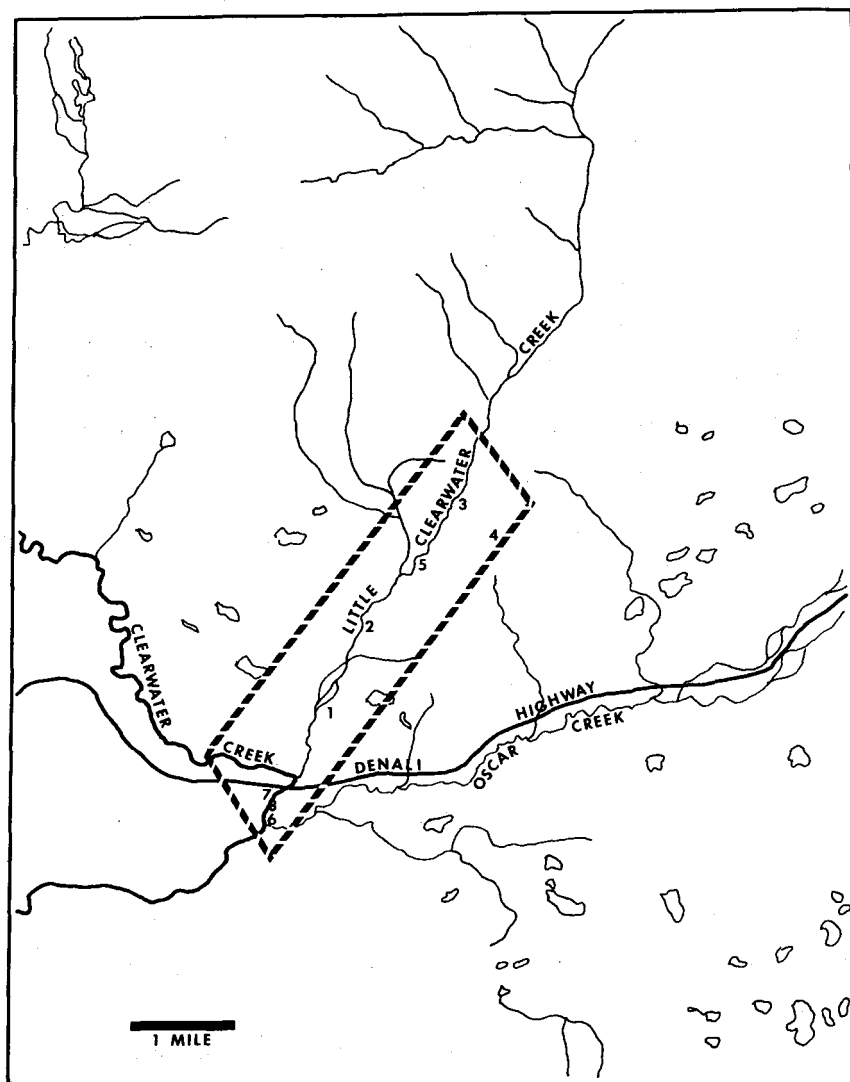
Figure 3. Little Clearwater Creek study area; 63°03' N, 146°52' W
         (From U. S. Geological Survey map A-6, Mt. Hayes quadrangle).

birch is the dominant plant species on most of this hilly region. The
overstory on the floodplain of the creek, however, consists primarily
of willows.

The species S. alaxensis, S. Barclayi, S. hastata, S. lanata, and
S. Barrattiana are present on the islands and along the creek in a strip
that is approximately 50 m wide. Beyond this strip and extending to
the outer boundaries of the floodplain the overstory consists of a
dense stand of S. pulchra and S. Barclayi. This latter willow type
is particularly evident in the region north of the highway and east of
the creek, where it covers an area about 3500 m long and 300 m wide.
The differences in plant composition are probably due to the differences
in soil texture and moisture content; the soil on those areas bordering
the creek is of finer texture and drier than that occurring on the
other areas of this region.

Gunn Creek Flat

Gunn Creek flat is a level area located just beyond the toe of the
Gulkana Glacier, approximately 13 miles north of Paxson, Alaska (Fig. 4).
This flat area is triangular shaped with sides that are four miles
long; the apex is located at the glacier, and the base extends along
the Richardson Highway. The area was formed by the deposition of
glacial drift and outwash.

The surface material of the region located just beyond the glacier's
terminus is very rocky, and S. alaxensis grows here in pure stands.
Southeast of this area, where the soil is less rocky, the willow
community consists primarily of S. alaxensis, S. glauca, S. lanata, and
S. Barclayi. This willow type grades into a pure S. Barclayi type that
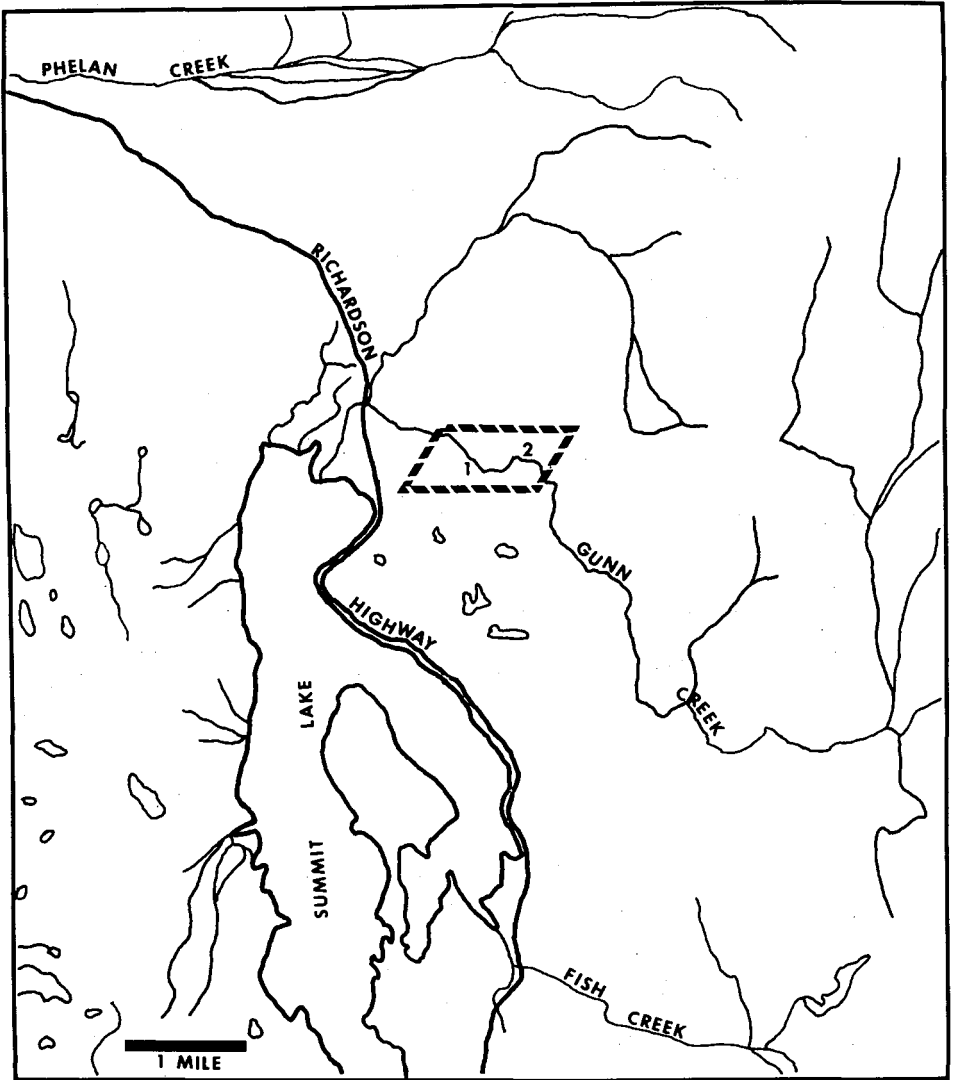
Figure 4. Gunn Creek study area; 63°10' N, 145°29' W (From U. S. Geological Survey maps A-3 and A-4, Mt. Hayes quadrangle).

extends all the way to the highway and nearly to Gunn Creek. This is a moderately wet area with finely textured soils. The region bordering Gunn Creek supports a stand of willows consisting of S. alaxensis, S. pulchra, S. Barclayi, and some S. lanata and S. hastata. The portion of the flat lying south of Gunn Creek is marshy, and S. pulchra predominates.

Taylor Highway

The Taylor Highway is located in eastern Alaska, and it intersects the Alaska Highway at Tetlin Junction, approximately 200 miles southeast of Fairbanks. Most of this mountainous region is densely timbered with white spruce (Picea glauca) and maintains few large willow stands. Mount Fairplay (Fig. 5), however, with an elevation of 1690 m (5545 feet), supports alpine tundra vegetation, and many of the small drainages radiating from this peak contain dense stands of S. pulchra interspersed with Calamagrostis sp. and dwarf birch. The rocky slopes extending into these "draws" are sparsely vegetated with S. glauca, dwarf birch, bog blueberry (Vaccinium uliginosum), and cranberry (Vaccinium vitis-idea).

Small stands of willows also grow adjacent to several of the major streams located north of Mount Fairplay (Fig. 6). A willow stand consisting mainly of S. pulchra, S. arbusculoides, S. glauca, and S. alaxensis is located next to Logging Cabin Creek, which intersects the Taylor Highway 43 miles north of Tetlin Junction. Salix pulchra is the most abundant willow species growing along the banks of the West Fork of the Dennison River at mile 49. A flat area just south of this river and west of the highway supports S. pulchra, S. alaxensis, S. arbuscu-
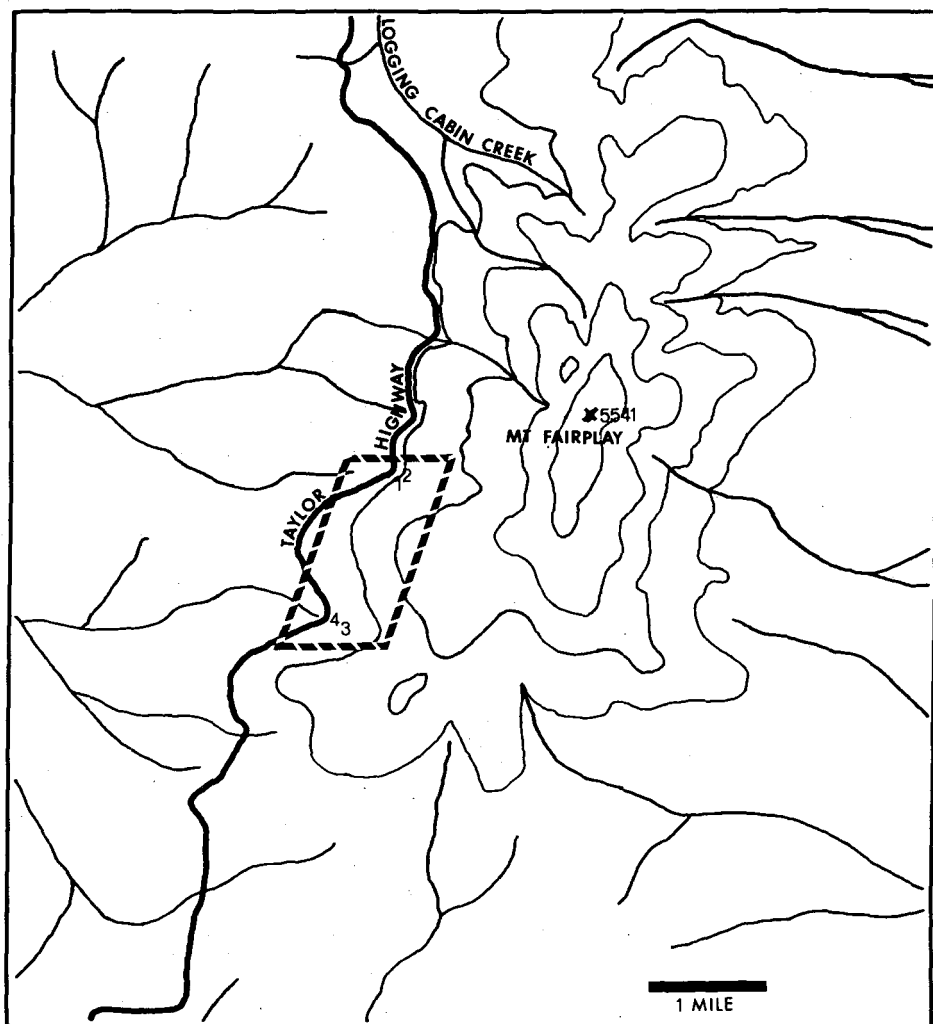
Figure 5. Taylor Highway (Mt. Fairplay) study area; 63°40' N, 142°15' W (From U. S. Geological Survey map C-3, Tanacross quadrangle).
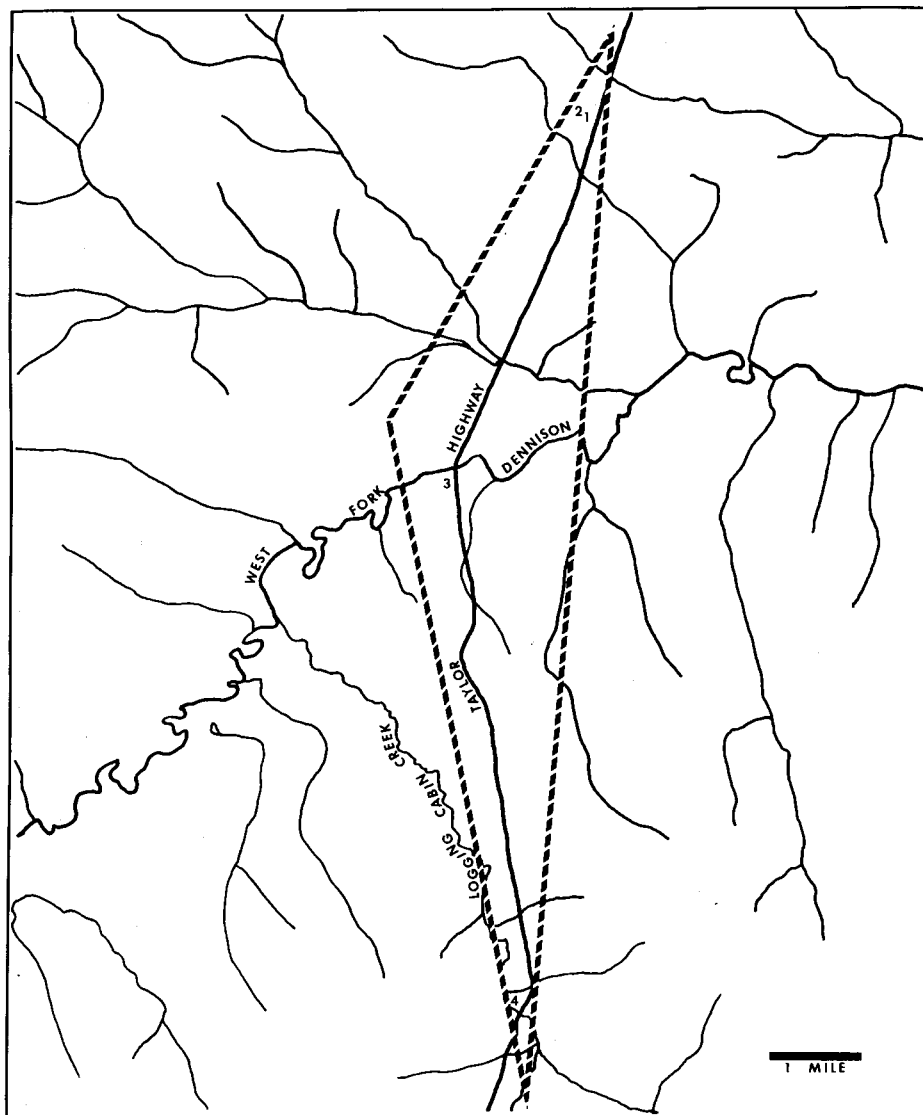
Figure 6. Taylor Highway (Other) study area; 63°55' N, 142°15' W (From
U. S. Geological Survey map D-3, Tanacross quadrangle).

loides, S. glauca, and S. depressa, in addition to dwarf birch and
bog blueberry. The species of willows occurring at a dry, rocky,
roadside site north of this area are S. arbusculoides, S. depressa, S.
Scouleriana, S. alaxensis, S. glauca, and S. pulchra.

Wood River

Wood River is a glacier-fed river that flows out of the Alaska
Range in a northwesterly direction and enters the Tanana River about
30 miles southwest of Fairbanks. Only the extreme upper portion of the
river, located approximately 30 miles east of Mt. McKinley National Park,
was examined; study plots were established along a four-mile stretch of
the river beginning at the mouth of Young Creek and extending upstream
(Fig. 7). This is a very mountainous region, with many peaks having
elevations exceeding 2000 m.

The willows of importance to moose in the upper Wood River area
are found on the old river floodplain and on the lower slopes of the
mountains bordering the river valley. The active river floodplain,
which often exceeds 100 m in width, is overlain with coarse gravel and
does not support vegetation. The old river floodplain, with its finer
textured soils, maintains a plant community comprised of S. alaxensis,
S. glauca, S. arbusculoides, S. lanata, S. hastata, and scattered S.
Barclayi, S. pulchra, white spruce, black cottonwood, and dwarf birch.

Dwarf birch and bog blueberry are the most abundant species on the
lower slopes of the mountains bordering the river valley, but S. glauca
and S. lanata occasionally occur in stands and as scattered individual
plants. More substantial and diverse willow stands are found along the
small streams that flow down these slopes and enter the river. Several
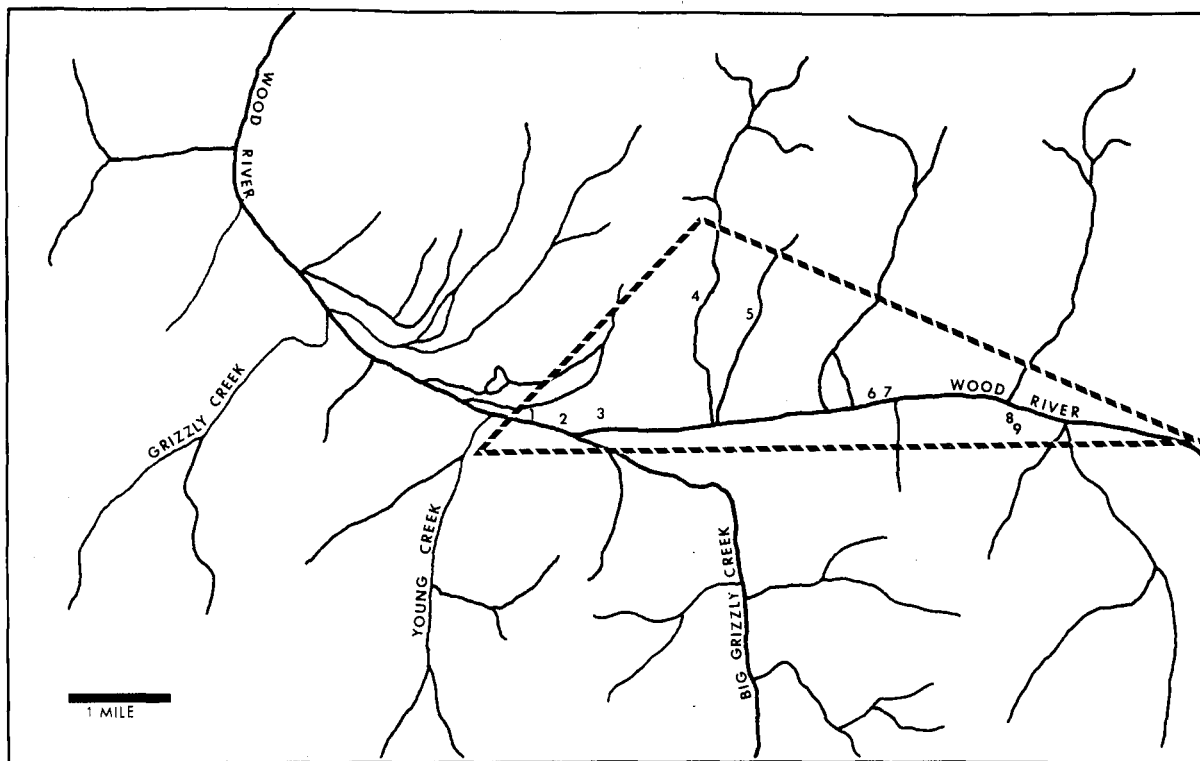
Figure 7. Wood River study area; 63°45' N, 147°55' W (From U. S. Geological Survey maps C-2 and D-2, Healy quadrangle).

small streams, which enter this section of Wood River from the north, are bordered by S. alaxensis, S. glauca, S. pulchra, and S. hastata. Bog blueberry, dwarf birch, black cottonwood, and soapberry (Shepherdia canadensis) also grow along these small drainages. The substrate along these small drainages is quite rocky in comparison to that occurring on other areas of these lower slopes.

METHODS

The purpose of this part of the study was to obtain information
on browsing over a wide geographical area. Since time was limited,
the methods were designed for acquiring only general data on a rather
gross level. An IBM 360 computer was used to analyze the huge quantity
of raw data that was collected.

Species Identification

After arriving in a study area, a general reconnaissance was made
to identify the species of willows present. Specimens of all species
were collected, preserved, and eventually stored in the University of
Alaska herbarium. Unfamiliar species were identified with the aid of
a key to the willows of boreal western America (Raup, 1959). It should
be noted here, however, that the nomenclature used follows Hultén's
(1968) flora, which was not available until after the field work was
completed. Hultén's taxonomic system is slightly different from that
of Raup; the three species S. lanata L., S. depressa L., and S. hastata
L. of Hultén are synonymous with Raup's S. Richardsonii Hook., S.
Bebbiana Sarg., and S. Farrae Ball, respectively.

Locating Study Plots

Following the initial reconnaissance of a study area, a survey was
made to determine the location, size, and apparent variability of each
willow type. The decision as to the number of study plots to be estab-
lished within a willow type was made on the basis of the plant size and
density variability that were present; the greatest numbers of plots

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were used in the most variable types. After the size of a willow type
was estimated by pacing, a map of its boundaries was roughly sketched
on paper; the map was then divided into rectangular sections, which
were scaled in proportion to the size of the study plots to be used.
The sections were numbered consecutively, and several, the actual
number depending upon the number of study plots to be used, were chosen
from a list of random digits. The rectangular study plots, which cor-
responded to the sections chosen, were then located, and their bound-
aries were established.

The size of the study plots was generally based on the variability
of the willow type in which they were located; the largest plots were
used in those willow types displaying the greatest amount of variabil-
ity in plant size or density. In some instances, however, the size of
the plots was limited by the size of the willow stand. The study plots
varied in size from 1,200 to 6,000 square m, although 3,000 square m was
the most common size.

Locating Sample Frames

The collection of data in the study plots was made within a
two-by-two meter wood frame. These four square meter sample frames
were located according to the example in Fig. 8. If, for example, the
study plot measured 100 by 30 m, one of the 100 m boundaries was used
as a baseline and marked with stakes every 20 m. For each 20 m length,
two numbers from zero to 20 were chosen from a list of random digits,
and two stakes were located on each 20 m segment of baseline at a dis-
tance from the starting point of that segment equal in meters to the
numerical values of the numbers chosen; 11 and 18 m in the example
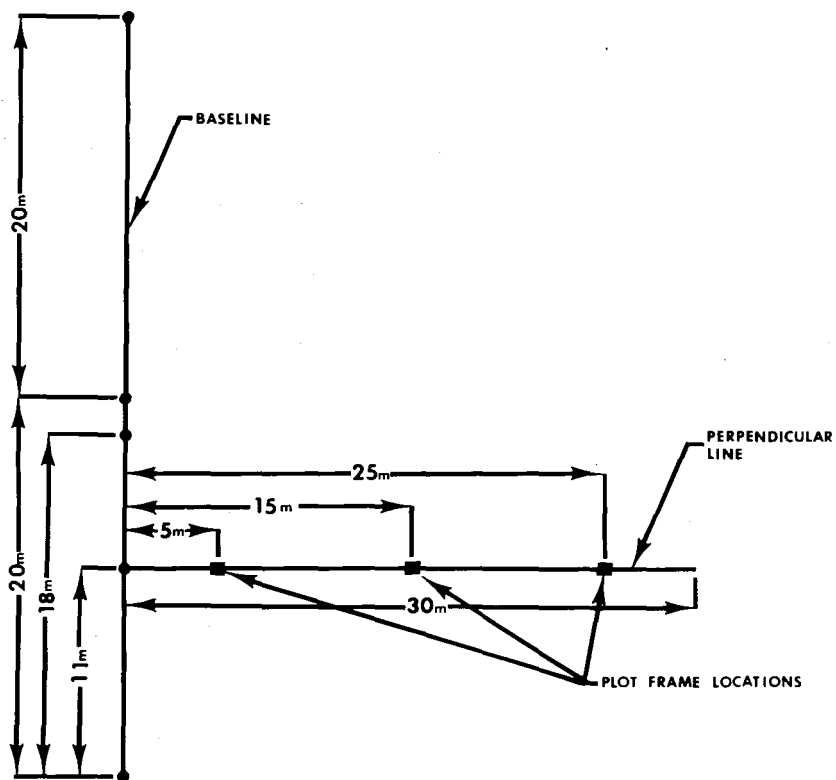
Figure 8. Example of the method used for locating sample frames.

shown. With the aid of a staff compass, a line was run perpendicular
to the baseline at each of these stakes and extended across the width
of the study plot. For each perpendicular line, a certain number of
digits from zero to the width of the study plot in meters was chosen
from a table of random digits, the actual number of digits chosen de-
pending upon the number of sample plots to be used. If, for example,
the study plot was 30 m wide, the determined number of digits would be
randomly chosen within the range of zero to 30 for each perpendicular
line, and if the numbers chosen for the first line were 5, 15, and 25,
three stakes would be located at those corresponding distances in meters
from the baseline (Fig. 8). The stakes on the perpendicular lines
marked the location of that corner of the four square meter sample
frame which was nearest the baseline starting point when the inside
edge of the frame was lined up parallel to the baseline. The number of
sample frames used in a study plot was based upon the size of the study
plot and the variability of the willow stand; the greatest number of
sample frames was used in the largest plots and the most variable willow
stands. Generally, from three to six percent of each study plot was
sampled.

Information Recorded

Each willow plant encountered within a sample frame was recorded
as to species, height, measured to the nearest five cm, and browse class.
A plant was considered to be that entity whose base was surrounded by
soil, even though it was often obvious that a number of such plants
had a common underground source. The criteria used in browse class
determination were the percentage of the twigs browsed and the per-

centage of the plant growing within the available browse zone. The
characteristics of each browse class are shown in Table 1.

A twig was judged as having been browsed if a portion of it had
been removed or if it had been stripped of bark or leaves, although
stripping was rarely encountered during this study. The determination
of the percentage of a given plant available for browsing was based upon
the minimum height at which browsing had occurred on that study plot.
Prior to taking measurements on a study plot, a reconnaissance was made
of the area, and the minimum browsing height, defined as the height
below which browsing did not occur, was recorded. Every study plot had
a particular minimum browsing height, which appeared not to be species-
specific. If, for example, the minimum browsing height on a study plot
was 50 cm, the following browse class scheme would be used: less than 50
cm in height--unavailable (browse class 8); 50 to 74 cm in height--1 to
33 percent available (browse classes 7-1 to 7-3); 75 to 149 cm in height--
34 to 66 percent available (browse classes 4 to 6); greater than 149 cm
in height--greater than 66 percent available (browse classes 1 to 3).
None of the plants on any of the study plots appeared to be growing
beyond the reach of moose; browsing was observed at heights exceeding four
m. Browsing at such heights is possible since moose are known to "ride
down" tall plants by straddling them and walking forward until the young,
upper twigs are available. Also, snow accumulations on the upper branches
cause them to droop and, thus, become more readily available. It should
be noted that the term "percentage of plant available," as used here,
does not refer to the percentage of plant mass available to browsing, but
refers to the percentage of the linear height of the plant growing within
the browsing zone on the study plot.

Table 1. Browse class characteristics

Browse class	Twigs browsed (%) (previous annual growth)	Portion of plant available (%)
1	less than 33	greater than 66
2	34–66	greater than 66
3	67–100	greater than 66
4	less than 33	34–66
5	34–66	34–66
6	67–100	34–66
7–1	less than 33	1–33
7–2	34–66	1–33
7–3	67–100	1–33
8	---	0

DISCUSSION OF RESULTS

A compilation of the data from each study plot is listed in Appendix 1; the plot numbers listed under each study area correspond to the plot location numbers on the study area maps. The various categories of information listed will be dealt with separately under the appropriate subheadings of the discussion. For the sake of expediency, code letters are substituted for species names in all tables and graphs. The following code scheme is used: S. alaxensis = ALA; S. arbusculoides = ARB; S. Barclayi = BAR; S. Barrattiana = ZZZ; S. depressa = DEP; S. glauca = GLA; S. hastata = HAS; S. interior = INT; S. lanata = LAN; S. lasiandra = LAS; S. myrtillifolia = MYR; S. padophylla = PAD; S. pulchra = PUL; S. Scouleriana = SCO.

Species Preference

Very little information is recorded in the literature concerning selection preference by moose for certain species of willows. This probably is primarily due to the difficulties involved in willow species identification. McMillan (1953), however, notes that of the two willow species encountered during a study in Yellowstone National Park, one was eaten by moose three times more frequently than was the other. Murie (1961) indicates that of the more than 20 species of willows in Mt. McKinley National Park, three species were particularly well liked by moose. He mentions that S. pulchra and S. Richardsonii (= S. lanata) were special favorites, and that S. alaxensis was browsed intensively along Igloo Creek. Murie's observations are particularly noteworthy since they agree closely with my findings.

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To aid in evaluating a species' selection preferability, a
quantity, which I have called the Browsing Intensity Index (BII), was
calculated for each species on every study plot. To calculate the BII
for a species, the percentage of plants in each browse class from 1
through 7-3 was determined by using the total number of plants in these
browse classes and the number in each class. Using these percentages,
the BII for a given species was obtained as follows: $BII = 1[X(1) +
X(4) + X(7-1)] + 2[X(2) + X(5) + X(7-2)] + 3[X(3) + X(6) + X(7-3)]$,
where $X(i)$ = percentage of plants in the ith browse class. The smallest
BII possible is 100 (i.e., 100% of the plants utilized from 0 to 33%),
and the largest possible BII is 300 (i.e., 100% of the plants utilized
from 67 to 100%). The BII, therefore, is based on the degree of browsing
sustained by a species, and a comparison of the BIIs of the various
species should indicate the relative degrees of browsing sustained by
them.

Several factors that affect the accuracy of BII values should be
discussed before proceeding further with the analysis. The BII value,
for example, is influenced by plant form, as is indicated by the fol-
lowing hypothetical example: suppose that two equally palatable species
of approximately the same height occur on a study area. Species A
is represented by ten plants, each of which supports only one browsable
twig, and species B is represented by just one plant that supplies ten
available twigs. A comparison of the BII values for the two species
under a range of browsing intensities (Table 2) indicates that species
which maintain only a few browsable twigs may tend to have larger BII
values than bushy species when the browsing is light and smaller BII
values than bushy species when the browsing is intensive. The influence

Table 2. Comparison of the BIIs of species having different growth
forms

Species	BII values									
	10%#	20%	30%	40%	50%	60%	70%	80%	90%	100%
A*	120	140	160	180	200	220	240	260	280	300
B**	100	100	100	200	200	200	300	300	300	300

\# Percentage of twigs browsed
* Ten plants, each with one available twig
**One plant with ten available twigs

of plant form on the BII values, therefore, represents a source of error in the species preference analysis, although with large sample sizes and with random browsing of twigs within each species this error approaches zero. This source of error could have been eliminated if the numbers of available and browsed twigs had been estimated and recorded for each sampled plant. The percentage of available twigs that had been browsed could then be tallied for each species, and a comparison of these percentages would indicate the relative degrees of browsing that had been sustained by the various species. I believe, therefore, that an analysis of the numbers of available and utilized twigs, rather than an analysis of browse classes (as was done in this study), would probably be a better method of determining browsing intensity.

Another possible difficulty is that BII values may be influenced by variations in the pattern of browsing, which result in conditional probabilities of twigs being browsed. An example will illustrate this point. Suppose that there are two plants of a species, each of which supplies four available twigs. If one twig was browsed on each plant, the BII would be 100, whereas if two twigs were browsed on one plant and none browsed on the other, the BII would be 150. Since the intensity of browsing on the species is the same in both cases, it seems evident that variations in the pattern or distribution of browsing would introduce a presently unmeasurable error in the analysis of BII values. It is possible that once a twig of a given plant is browsed, the probabilities of other twigs being browsed on the same plant are changed. It could be postulated, for example, that, when an animal browses a twig of a highly preferred plant, the probabilities of the other twigs

being browsed by that animal are increased. Conversely, it also seems
possible that if an animal browses a twig of a non-preferred plant,
the probabilities of other twigs of that plant being eaten are reduced.
If the probabilities of twigs being browsed were conditional in this
manner, the browsing on non-preferred species might tend to be more
uniform than that on preferred species. If this were true, the gap
between the BII values of preferred and non-preferred species might be
wider than it should be.

The mean BII for each species on a study area was calculated by
using the BIIs of those study plots in which the species occurred at
densities greater than 0.4 plants with available twigs (i.e., plants
in browse classes 1 through 7-3) per sample frame. Since the BII
contains sources of error that were not realized at the time the study
was made, only the relative ranking of the species as derived from
comparisons of their BIIs, and not the absolute BII values, will be
employed in the discussion. The ranking of the species, according
to the decreasing sizes of their BII values, is shown for each study
area in Table 3.

The table suggests that on most study areas S. alaxensis, S.
arbusculoides, S. pulchra, and S. interior are generally browsed more
intensively than are other willow species associated with them. Con-
versely, S. glauca, S. Barclayi, and S. hastata seem to be almost with-
out exception the most lightly browsed species. On the study plots, it
was common to see well-utilized S. alaxensis or S. arbusculoides plants
surrounded by untouched S. Barclayi or S. hastata plants, or to see
a stand of substantially browsed S. pulchra adjacent to a stand of
unbrowsed S. glauca.

Table 3. Ranking of species for each study area in the order of decreasing BII values

Wood R.	Paxson L.	Gunn Ck.	L. Clearwater Ck.	Taylor Hwy. (other)	Taylor Hwy. (Mt. Fairplay)	Dry Ck.
ARB	ALA	ALA	ALA	ARB	PUL	INT
ALA	LAN	LAN	PUL	PUL	GLA	PUL
PUL	PUL	PUL	BAR	DEP		LAS
LAN	GLA	BAR	HAS	GLA		ARB
GLA	BAR					
BAR						
HAS						

These differences in browsing intensity were also observed in areas where study plots were not established. Much of the Gunn Creek flat north of Gunn Creek, for example, is covered with a nearly pure stand of unbrowsed S. Barclayi. Adjacent to this area and just beyond the base of the Gulkana Glacier, however, is a stand of willows comprised almost entirely of S. alaxensis, which has been utilized so intensively that it is virtually impossible to find a single plant that has not been severely browsed. The Gulkana River near Paxson, Alaska, is bordered by intensively utilized S. alaxensis plants, a number of which are dead probably as a result of overbrowsing, and S. hastata plants, most of which have not been touched by moose. The bottoms of the gullies on the slopes of Mt. Fairplay support well-utilized stands of S. pulchra, whereas the sides of these gullies are covered with stands of S. glauca that have not been browsed.

On nearly all of the study areas, the same species of willows are apparently browsed to a greater degree than are the other species with which they occur, and it is my contention that this indicates a species selection preference shown by moose. Therefore, the following species list, which is ordered according to decreasing magnitudes of the overall mean BII values, could be interpreted as approximating the order of decreasing preference for those willow species occurring on some of the important moose ranges in Alaska's interior: S. interior, S. alaxensis, S. arbusculoides, S. lasiandra, S. pulchra, S. depressa, S. lanata, S. Barclayi, S. glauca, and S. hastata. It should be noted that in the one study area where S. lasiandra occurs with S. pulchra, it does not appear to be browsed as intensively as is S. pulchra. For this reason, S. lasiandra probably should not be regarded as being preferred

over S. pulchra.

Species Importance

The importance of a willow species to moose depends not only upon its degree of preferability, but also upon the amount of usable plant material that it supplies; e.g., some species, although high on the preference list, are not abundant or not frequently encountered and are not, therefore, of great importance to moose as a source of food. Although the data will not permit accurate quantification of the relative importance of the various species, some generalizations concerning this topic are possible.

Willow species of the greatest importance to moose should be those that are highly palatable and that supply a large amount of available plant material over a wide geographical area. It is notable that S. alaxensis and S. pulchra appear to be two of the most preferred and most widely distributed willow species in the interior of Alaska; S. pulchra is well represented on all seven study areas, S. alaxensis is relatively abundant on all but the Taylor Highway study areas, and both species are common on many areas not studied. During the study, these two species were encountered more frequently than any others. S. interior and S. arbusculoides, the other highly preferred species, occur on only one and three study areas, respectively, although S. arbusculoides often is abundant where it does occur. S. lanata, although not a highly preferred species, is abundant and moderately browsed in some areas, such as the mountain slopes that border upper Wood River.

It is my opinion that S. alaxensis and S. pulchra, by virtue of their high preferability, wide distribution, and relatively high abun-

dance, are the two willow species of the greatest importance to moose in the general study area. S. arbusculoides and S. lanata, although not as widely distributed, appear also to be important sources of food for moose in some areas.

Relative Species Abundance and Browsing Intensity

It is possible that the relative rarity or abundance of a species can affect its degree of utilization to a greater extent than does its inherent palatability. For example, a fairly unpalatable species that is rare in a given area might be browsed more intensively than the abundant species because of its demand to satisfy food variety or nutritional requirements. Since it would be very difficult to accurately determine the effects of relative abundance on browsing intensity from my data, a discussion of this topic must be primarily based on personal observations.

Certain species of willows, such as S. Barclayi and S. glauca, are poorly utilized, regardless of their relative abundance, on all of the study areas in which they occur. For example, S. Barclayi is browsed very lightly at Paxson Lake and along Little Clearwater Creek, where it is abundant, and at upper Wood River, where it is poorly represented. S. glauca is poorly utilized on the study areas where it is abundant, such as the upper Wood River and Taylor Highway areas, and also on those where it is scarce, like the Paxson Lake region.

Other willow species, such as S. alaxensis and S. pulchra, are well utilized on nearly all of the study areas. S. alaxensis is browsed intensively at Paxson Lake, where it is not well represented, and at Little Clearwater Creek and upper Wood River, where the species

is quite abundant. S. pulchra is also heavily browsed whether it is very abundant, as it is at Dry Creek, or whether it is relatively uncommon, such as at upper Wood River.

An analysis of the data also suggests that species utilization is not inversely correlated with species density. Table 4 shows a comparison of the BIIs of the least dense and most dense species that occur on six of the study areas; the Mt. Fairplay area was not analyzed, since only two willow species occur in this region. The table indicates that on four of the six study areas the BII of the least dense species is smaller, instead of larger, than that of the most dense species.

The lack of correlation between the degree of utilization and the relative abundance of the species can also be observed in individual willow stands. The preferred willow species seem to be browsed intensively whether they are the dominant species in a stand or whether they are represented by only a few scattered individuals. On the other hand, the non-preferred species are browsed lightly in all stands, regardless of their relative abundance.

There is at least one possible source of error in this analysis. It is quite possible that neither the abundance nor the density of a species is a good measure of the amount of browse that it supplies. For example, a tall, bushy species, although it may not be abundant, might provide more edible plant material than a relatively abundant, low-growing species that maintains only a few branches. If this were true, the short species would actually be the "rarer" in terms of the amount of available browse that is supplied.

The only conclusion that can be drawn from my observations and data, therefore, is that neither the relative abundance nor density of

Table 4. Comparison of the BIIs of least dense species with those of
most dense species

Study area	BII of least dense species	BII of most dense species
Dry Creek	244	181
Little Clearwater	105	161
Paxson Lake	127	141
Gunn Creek	120	116
Taylor Highway (other)	107	145
Wood River	114	120

a species observably affect its degree of utilization. The probable explanation for this is that the inherent palatability of a species overrides the effects of relative abundance or density on browsing intensity. This appears to be an example of the important role that species identity plays in determining the amount of browsing that occurs.

Effects of the Presence of Highly Preferred Species

It was sometimes evident during the course of the study that the presence of a highly preferred species affected the degree of utilization sustained by other species. In the Dry Creek area, for example, S. interior, which grew most abundantly along the banks of the creek, sometimes occurred in small, isolated patches on the floodplain. These small patches were always heavily browsed, but it was also apparent that other species of willows occurring in proximity to these patches were utilized to a greater degree than was normal for them. This same phenomenon was also observed in other study areas. Quite often a S. glauca or a S. lanata plant that was growing very near a S. alaxensis or S. arbusculoides plant was browsed more intensively than was usual for a plant of these species. It seemed, however, that species occurring very low on the preference list were not utilized to a greater extent under these circumstances.

One possible explanation for this phenomenon becomes evident when a browsing moose is observed closely. A cow moose I observed browsing in the Wood River area, after browsing on a S. alaxensis plant for a period of time, would leave it and wander along until encountering another plant of this species before stopping to feed again. She

rarely browsed on the other species present, S. lanata and S. glauca, while traveling between S. alaxensis plants. Occasionally, however, before leaving a S. alaxensis plant from which only a small proportion of the available browse was removed, she would briefly browse those plants of the other species that occurred within easy reach. It appeared as if she browsed on the non-preferred species only because she was standing still at the time, and they happened to be readily available. This type of feeding behavior suggests a possible explanation for the abnormal amount of browsing on the lower preference species that occur in the vicinity of a highly preferred plant.

The greater utilization of moderately preferred species when occurring near highly preferred species also occurs on a larger scale. It has been noted in the literature that Artemesia tridentata (Stoddart and Smith, 1955) and Agropyron smithii (Tomanek et al., 1958) are eaten more heavily by livestock when occurring in small quantities throughout a "better" forage than when growing in pure stands. Likewise, the nearly pure stands of S. glauca occurring on the lower slopes of Mt. Fairplay are not browsed, although moose frequent the area, as is evidenced by the substantial use of S. pulchra patches present in the draws. When S. glauca grows with S. pulchra and S. arbusculoides, however, as occurs on a dry roadside site along the Taylor Highway (mile 53.2), it is browsed to some extent. In the same manner, willow stands of S. glauca and S. lanata that occur on the slopes bordering upper Wood River are browsed very lightly. On the old floodplain, where these same species grow with S. alaxensis and S. arbusculoides, however, they, particularly S. glauca, are used more frequently.

These observations might be explainable by the apparent manner in

which moose, and possibly livestock, feed. If animals generally stop to feed only when encountering a well-liked species, it would not be surprising to find poorly utilized stands of moderately preferred species. Where these same species grow with more preferred species, however, they might be occasionally eaten by animals that are using the area to procure the preferred species. If this explanation were correct, the presence of preferred species would enhance the possible forage value of an area in two ways: (1) the preferred species would themselves be valuable sources of food, and (2) their presence would entice animals into the area with the result that some moderately pre-ferred species would also be utilized.

There is another possible explanation of the observations that moderately preferred species are utilized to a lesser degree where they occur in pure stands than where they occur in mixed stands with highly preferred species. The browsing sustained by individual species varies with the soil types on which they occur; this being probably due to differences in soil fertility and the resulting variation in the nutri-tive contents of the plants (Hurd and Pond, 1958). It is possible that preferred species grow only on fertile sites, and that their high palatability is due to their relatively high nutrient contents. Those moderately preferred species that also occur on these fertile sites might also be fairly palatable and, therefore, be utilized to some degree. Moderately preferred or non-preferred species might grow most successfully on the more infertile sites, where there is an absence of competition from preferred species. The moderately preferred species might be less nutritious when growing on these infertile sites and, consequently, be browsed to a lesser degree than when occurring on

fertile soils. If this explanation were correct, the greater use of
moderately preferred species when occurring in stands with highly
preferred species would be a result of higher nutrient contents and
not a result of the presence of preferred species.

There is at least one other possible explanation of this phenomenon.
It would seem that stands comprised of one or two moderately preferred
species might be poorly utilized in relation to mixed stands, because
moose may prefer to browse in stands where they can obtain a mixture
of foods. It is interesting, however, that the nearly pure stands of
S. pulchra at Dry Creek, the pure stands of S. pulchra on the lower
slopes of Mt. Fairplay, the stand of willows located just beyond the
base of the Gulkana Glacier, which is comprised almost entirely of S.
alaxensis, and the stands of S. alaxensis occurring along the banks
of Wood River are heavily browsed. Since moose do browse in pure stands
of willows, the lack of food variety is probably not the reason why
stands comprised of one or two moderately preferred species are lightly
browsed.

Plant Height and Browsing Intensity

One method of determining whether there is a relationship between
plant height and browsing intensity is to analyze each species separ-
ately. Each species received a BII value for every study plot in
which it occurred on a study area. Consequently, a comparison could
be made of the BIIs for those plots in which each species had the
highest and the lowest mean heights; the results of such an analysis
are shown for three study areas in Table 5. The table shows that in
nearly all instances a species received a higher BII value where it

Table 5. Species BIIs for plots on which individual species have the lowest and the highest mean heights

Study area	Species	BII values	
		Plot on which species is shortest	Plot on which species is tallest
Dry Creek	ALA	139	151
	ARB	199	118
	INT	227	262
	LAS	143	220
	PUL	145	183
Little Clearwater	ALA	270	280
	BAR	107	159
	HAS	102	106
	PUL	140	166
Wood River	ALA	206	241
	ARB	276	210
	BAR	109	118
	GLA	108	129
	HAS	100	115
	LAN	100	148

was tallest than where it was shortest. This would seem to indicate
that tall plants are browsed to a greater degree than are short plants.

Another method of investigating the effects of plant height on
utilization is to compare the Height Utilization Indices (HUIs) of the
availability classes; 1-33%, 34-66%, and greater than 66% available.
The HUI for the 1-33% available class was calculated by using the
numbers of plants in each of the browse classes from 7-1 through 7-3
as follows: $HUI = Y(7-1) \times 100 + Y(7-2) \times 200 + Y(7-3) \times 300/[Y(7-1) +$
$Y(7-2) + Y(7-3)]$, where $Y(i)$ = number of plants in the ith browse class.
The HUIs for the 34-66% and the greater than 66% available classes were
calculated in the same manner, except that the numbers of plants in
browse classes 4 through 6 and 1 through 3, respectively, were used in
the calculations. A HUI for each availability class was obtained for
every species and for the sum of all plants, regardless of species,
on each study plot.

The HUI is calculated in such a manner that the greater the amount
of browsing sustained by plants of a given availability class, the
larger will be the HUI for that class. By comparing the HUIs of the
three classes, it should be possible to determine the size or avail-
ability range of plants most intensively utilized by moose. The mean
HUI for each availability class is shown in Fig. 9 for all plants,
regardless of species, on each of the study areas.

The graph indicates that plants in the greater than 66% available
class are generally browsed most intensively, whereas plants in the
1-33% available class usually receive the least amount of browsing.
This information may also indicate that moose prefer to browse tall
plants, although this cannot be definitely concluded. It is quite
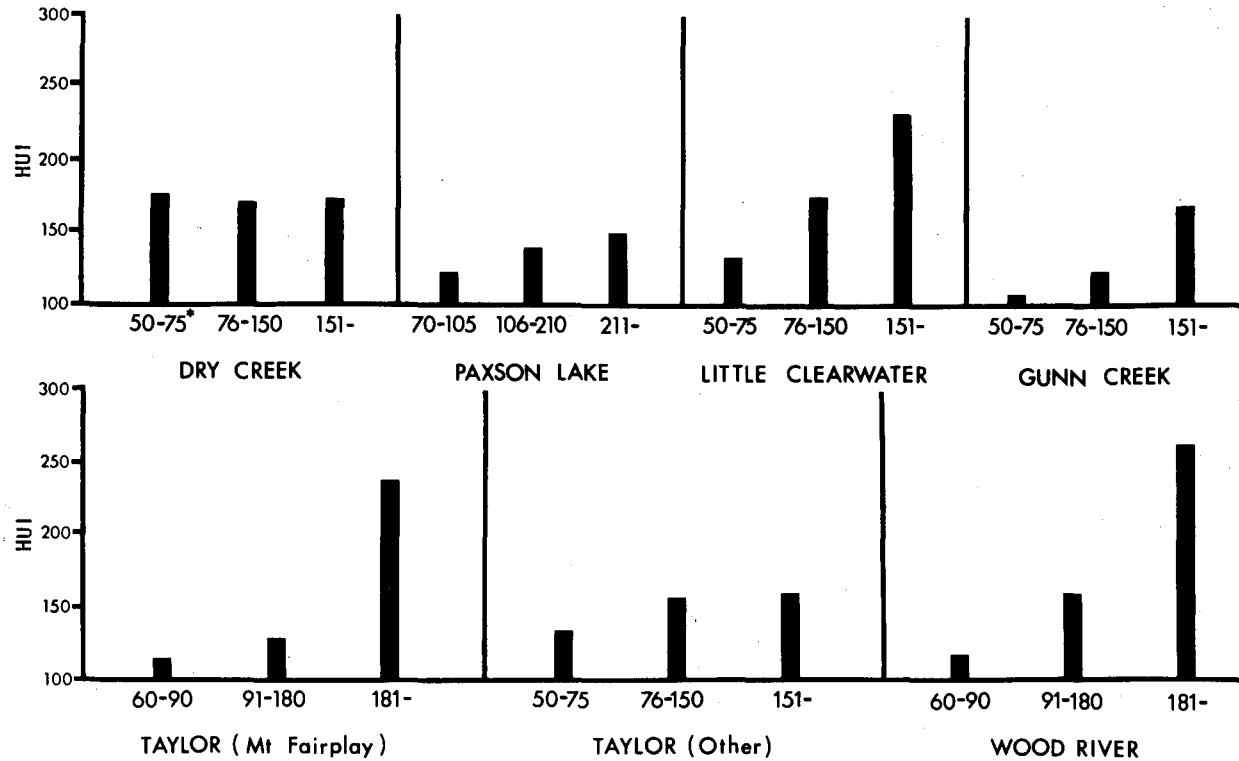
Figure 9. Comparison of study area HUIs (Height Use Indices).

*Height in centimeters

possible that the intensive browsing on the tall, highly preferred species, such as S. alaxensis and S. arbusculoides, might strongly influence the HUI values for many study areas. Since the inverse occurs at Dry Creek—i.e., the low-growing species S. interior and S. pulchra are browsed more intensively than are the tall-growing ones—this might explain why the relationship between the HUI values for this study area is different from that of the other study areas.

Willow Stands as Physical Barriers

It would seem possible that, although a moose is a large animal, a stand of willows could be dense enough to impede the movements of moose. If this were the case, such stands would not be as effectively utilized as sparse stands. The data were examined to determine whether density was a factor in determining utilization by moose. For each species, the BII that was calculated for the study plot with the highest total density of plants over one m tall was compared with the BII that was obtained for the plot that supported the lowest total density of plants over one m tall; it was felt that plants shorter than one m in height would be totally ineffective in hindering the movements of moose. This analysis was made for three study areas (Table 6), and the results show that in nine instances the species BIIs for areas with the highest total density of plants over one m tall were greater than those for areas with the lowest density; in the remaining six cases, just the converse was true. In other words, the data indicate that in a majority of cases individual species were actually browsed more intensively where the total plant density was highest than where the density was lowest.

This information seems to suggest that the densest willow stands

Table 6. Species BIIs for plots supporting the lowest and the highest
          total densities of plants over one m tall

| Study area | Species | BII values | |
		Plot with lowest density	Plot with highest density
Dry Creek	ALA	204	128
	ARB	199	118
	INT	227	262
	LAS	220	188
	PUL	201	179
Little Clearwater	ALA	252	280
	BAR	107	157
	HAS	110	100
	PUL	149	157
Wood River	ALA	206	249
	ARB	276	262
	BAR	110	119
	GLA	108	129
	HAS	100	102
	LAN	108	136

are not effective as physical barriers. It should be noted, however, that the highest densities of plants over one m tall at Dry Creek, Little Clearwater Creek, and Wood River are 16.9, 14.6, and 7.6 plants per sample frame, respectively. The majority of species at Dry Creek received smaller BIIs on plots with the highest total plant density than on plots with the lowest density of tall plants, and it might be argued that the densest stand was not utilized well because it effectively impeded the movements of moose. On the other hand, the highest density of tall plants at Little Clearwater Creek is nearly equal to that at Dry Creek, but at Little Clearwater Creek the species BIIs are larger where the total density is highest than where the total density is lowest. This seems to suggest that factors other than total plant density are causing browsing intensity variation in these areas.

Another method of investigating the effects of total plant density on browsing intensity is to analyze the amount of utilization on all plants, regardless of species. An index of the total browsing intensity, which I have called the Area Preference Index (API), was first computed for each study plot in the same manner as was the BII for each species, except that all plants occurring on the plot were used in the computation instead of just those plants of a particular species. The mean API for each study area is shown in Fig. 10. Calculations were then made to determine the degree of correlation between the study plot APIs and densities of plants over one m tall on the three study areas with the greatest number of plots. If dense stands are not utilized as effectively as sparse stands, there would be a negative correlation between total density and utilization. The correlation coefficients obtained--+0.26, +0.63, and -0.93--seem to indicate that such a relation-
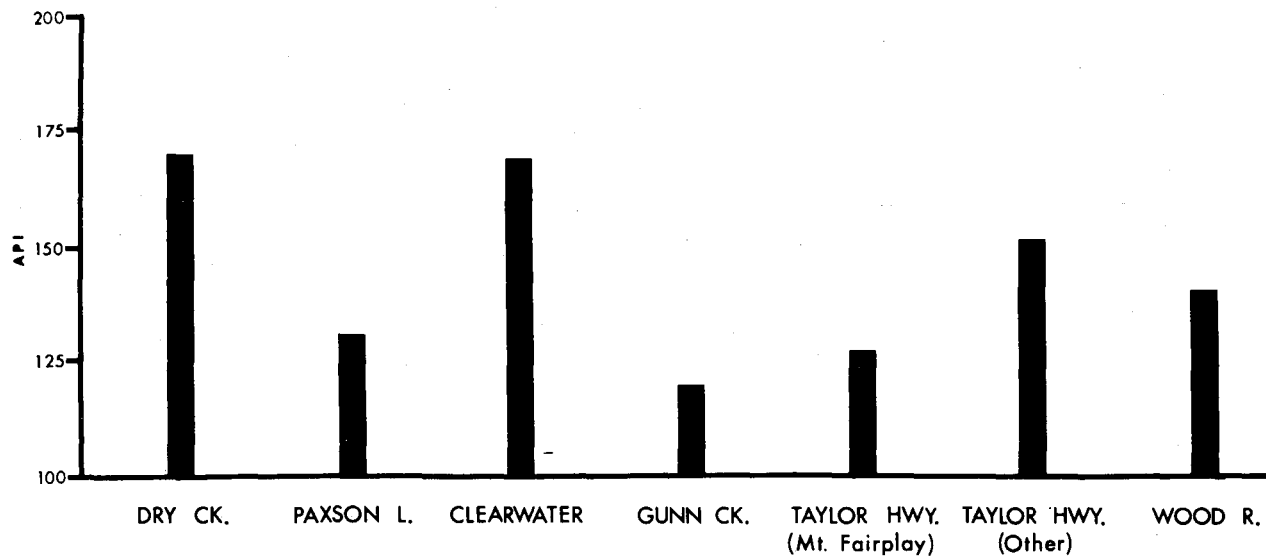
Figure 10. Study area APIs (Area Preference Indices).

ship does not exist.

Perhaps of greater significance is the fact that on five of the seven study areas the study plots supporting the highest density of plants over one m tall had larger APIs than the plots having the lowest density of plants exceeding one m in height. In other words, instead of there being a decrease of browsing pressure in the dense stands, as would occur if the dense stands were effective as barriers, they were actually browsed more intensively on a majority of the study areas. The total browsing intensity was probably high in the dense stands because the density of the tall, highly preferred species, such as S. alaxensis and S. arbusculoides, was high.

In general, the data suggest that the densest willow stands on the study areas are not effective as physical barriers. This does not necessarily mean, however, that moose are physically unhindered by plants in the dense stands. It is possible that these stands are particularly attractive because of the high density of preferred species in them, and that moose browse in dense stands despite being physically hindered. This possibility opposes the conclusion made by McMillan (1953) from observations in Yellowstone National Park. He found that the amount of browsing occurring in the center of willow clumps was equal to that occurring on their edges and concluded that moose were not impeded physically by the plants. It is possible, however, that plants growing in the center of willow clumps are somewhat more nutri-tious than those growing on the edges where the conditions for growth may be marginal, and that the central plants would be browsed to a greater degree than the peripheral ones if moose movements were not impeded. In view of these comments, it is only safe to conclude that

if the densest willow stands on the study areas acted as physical

barriers, the hindrance to moose movements was apparently not effective

in reducing the amount of browsing below that which was sustained by

sparse stands.

PART II

STUDY AREA

The Tanana River study area is located on an island in the Tanana River about one mile south of Fairbanks (Fig. 11). The study area is 17,600 square m (4.4 acres) in size, representing approximately three-fourths of the total area of the island. The soil of the island, which is composed of silt-sized material, seems to have been formed in well defined stages. This interpretation is based on differences in the vegetational composition on the island.

S. alaxensis, some plants of which reach heights exceeding four m, and alder (Alnus sp.) dominate on the oldest and highest portion of the island. The other species found here, S. niphoclada, S. interior, S. myrtillifolia, and S. lasiandra, are represented mainly by small plants. On a somewhat younger portion of the island, alder and S. niphoclada predominate, although S. interior and S. myrtillifolia are also fairly abundant; many of the willows here are over 1.5 m tall. S. interior is the most abundant species on an even younger part of the island, although the other species are also present. Only a few of the plants in this area are over one m tall. The most recently deposited portion of the island supports the five species of willow already mentioned, but S. lasiandra is more abundant here than in the other areas. Since most of the plants here are under 0.5 m in height and, probably as a result of being buried under snow, are not utilized, this area was not sampled.
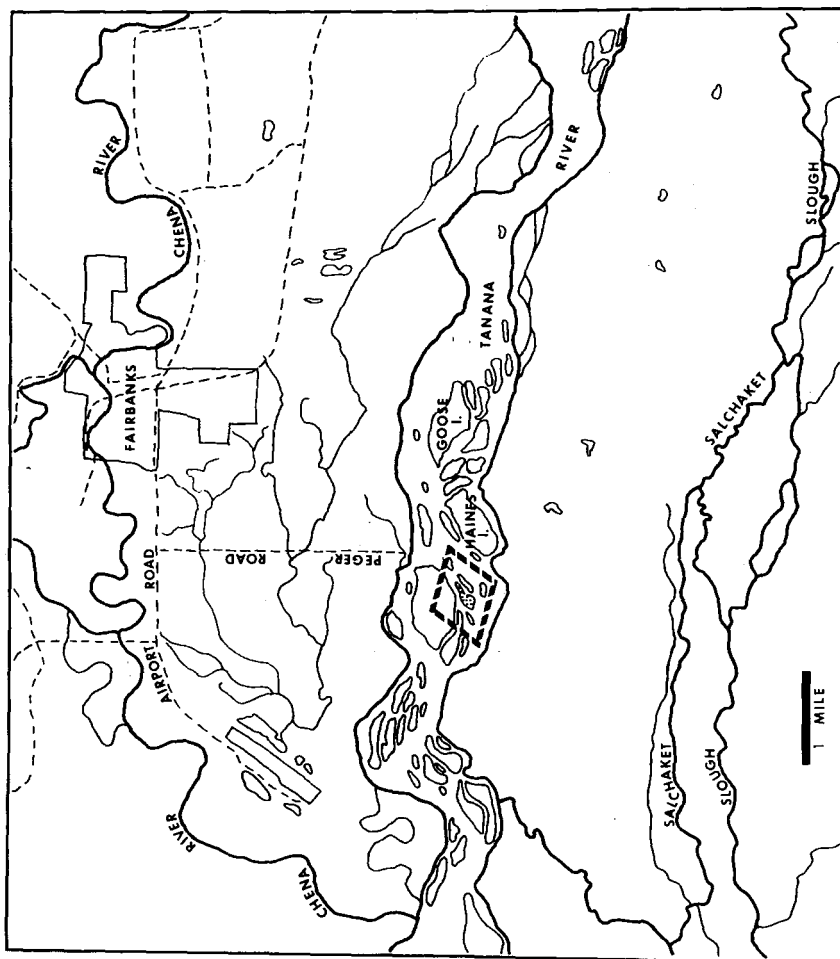
Figure 11. Tanana River study area; 64°47' N, 147°49' W (From
U. S. Geological Survey maps C-2 and D-2, Fairbanks
quadrangle).

METHODS

Selection of Study Area

The study island, which lies in the Tanana River south of Fair-
banks, was selected because its vegetation is dominated by willows.
Most of the islands in this area are covered with dense stands of black
cottonwood and alder, and the willow group is poorly represented. Since
the study island is atypical, the findings of this study do not neces-
sarily describe the conditions that occur on the other islands in this
area.

Locating Sample Frames

A baseline was established through the center of the island with
the aid of a staff compass and was marked every 20 m. The line was
terminated at the 240 m mark because the willows growing on the end of
the island beyond this point were too short to be available for browsing.
Four numbers from zero to 20 were chosen from a table of random digits
for each 20 m interval, and the equivalent distances in meters were
marked by stakes on the baseline from the starting point of each
interval. From each of these stakes, lines perpendicular to the base-
line were extended to the edge of the island, two lines being estab-
lished to the left of the baseline and two lines to the right for every
baseline segment. Since the lengths of these perpendicular lines varied,
each line was measured and its length recorded. For each perpendicular
line, two numbers from zero to its length in meters were chosen from a
list of random digits, and each line was marked off with stakes at the
equivalent distances in meters from the baseline. Each of these stakes

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marked the location of that corner of the 1.5 by 1.5 m sample frame
which lay nearest the starting point of the baseline when one side of
the frame was parallel to the baseline.

Information Recorded

The minimum height at which browsing had occurred was determined
first. Every willow plant whose stem emerged from the ground within
the 96 randomly located sample frames was then recorded as to species,
height in centimeters, browse class, and the diameters in millimeters
of the ends of those twigs which had been browsed. The browse class
criteria were the same as those described previously, but class 7 was
not subdivided into classes 7-1, 7-2, and 7-3, as was done on the other
study areas. The browse class scheme used on the island is identical
with that first described by Dasmann (1951). Metal calipers were used
to measure the twig diameters.

Clipping

The mean diameter to which twigs had been browsed was then calcu-
lated for each willow species. Twigs of each willow plant that occurred
within the sample frames were clipped at the appropriate mean diameter
for that species if they extended above the minimum browsing height;
no clipping was done below this height. The clipped twigs from each
species and sample frame were bundled separately and were oven-dried
for 48 hours. The bundles were then weighed separately to the nearest
gram, and these weights were later used to determine the oven-dried
weights of available winter browse supplied by each species; all clipping
was accomplished after the growing season had ended. In addition,

individual dried twigs from each species were selected randomly and weighed to the nearest gram, and the mean individual twig weight of each species was determined. This mean weight is the calculated weight of plant material that has been removed from a browsed twig of a given species.

Utilization Plots

Six utilization plots, each measuring six by six m, were also located randomly on the island during the same summer. The browsed twigs of all willows within these plots were clipped smoothly with shears just below their tips. This made it possible, after returning to the island in June of the next year, to differentiate between twigs that had been browsed during the preceding winter and twigs that had been browsed previous to that time. The number of twigs that had been browsed within the utilization plots during the winter was determined for each species. Since the average weight of the material that is removed from a browsed twig had also been obtained for each species, it was possible to determine the weight of the plant material consumed and the percentage of available browse removed by moose from each species during one winter.

DISCUSSION OF RESULTS

The mean heights, mean densities, and percentages of the various browse classes are shown by Appendix II for all willow species occurring on the island; the remainder of the data will be discussed under the appropriate subheadings. Code letters are substituted for species names on all tables and graphs. The following code system is used: S. alaxensis = ALA; S. interior = INT; S. lasiandra = LAS; S. myrtillifolia = MYR; S. niphoclada = NIP. Since the method of sampling that was employed resulted in unequal sampling probabilities, the data from each sample frame were "weighted" in relation to the probability of selecting that frame location. All results are based on the corrected data.

Species Preference

It is my assumption that the degree of browsing sustained by a given species is indicative of its selection preferability. To be able to quantitatively describe the degree of utilization received by a species, a Browsing Intensity Index (BII) was calculated for each willow species occurring on the island. The BII was calculated by using the percentages of plants in each of the browse classes from 1 through 6, as follows: $BII = 1[X(1) + X(4)] + 2[X(2) + X(5)] + 3[X(3) + X(6)]$, where $X(i)$ = percentage of plants in the ith browse class. This method of BII determination differs slightly from that described previously, because browse class 7 was not subdivided for this portion of the study and could not be incorporated into the calculation. Therefore, the BIIs, as calculated from this method, would tend to have

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higher values, since, as discussed previously, plants in the lowest height class (i.e., browse class 7) are apparently browsed least intensively. The results from both methods range in value from 100 to 300. It should also be restated here that the BII's accuracy is probably affected by plant form and pattern of browsing. Therefore, the relationship between values, not the values themselves, will be considered when estimating the relative degrees of browsing that were sustained by the various species.

The ranking of the species, according to the decreasing sizes of their BII values, is as follows: S. alaxensis, S. interior, S. myrtillifolia, and S. niphoclada. This suggests that S. alaxensis and S. interior have been browsed to a greater degree than have the other willow species and, therefore, are considered to be the preferred species. These results compare favorably with those obtained on the other study areas. Likewise, S. niphoclada, which was not found on the other study areas, would be rated low on a preference list by virtue of the low degree of utilization that it sustained.

The differences between the amounts of browsing received by the various species cannot be overemphasized too strongly. It was difficult to find a S. alaxensis or S. interior plant that had not been browsed intensively; a number of S. interior plants had died and an even greater number were partially dead, probably as a result of over-browsing. In contrast, it was equally difficult to find a S. niphoclada plant that had been utilized to any degree. Such observations make it quite evident that moose show a definite selection preference for certain species of willows.

Factors Affecting Species Preferability

A number of factors apparently influence the relative prefer-
ability of food plants. Heady (1964) discusses the effects of palat-
ability, associated species, climate, soil, topography, kind of animal,
and animal physiology on preference.

Palatability is generally defined as those plant characteristics
or conditions that stimulate a selective response by animals (Heady,
1964). The chemical composition of a plant is one such characteristic
affecting its palatability. A high positive correlation has been ob-
served between the protein content of forage and preference by cattle
and sheep (Cook, 1959; Hardison et al., 1954; Hobbs et al., 1945).
Swank (1956) found that species consistently having a high moisture
content are preferred by deer and cattle. Foods high in sugar content
are preferred by cattle (Plice, 1952) and deer (Mitchell and Hosley,
1936). Studies with livestock have shown a positive correlation be-
tween preferability and fat content or percentage of ether extract
(Hardison et al., 1954; Blaser et al., 1960). Grasses with the highest
phosphate and potash contents are apparently the most acceptable to
livestock (Leigh, 1961), and calcium uptake affects phosphorous re-
quirements (Swank, 1956). A high negative relationship has been noted
between the tannin contents and preference by cattle for the various
varieties of lespedeza (Wilkins et al., 1953). Several researchers
have concluded, however, that the total nutritive value of a plant is
a better indicator of preference than is the content of any single
chemical compound (Albrecht, 1945; Cook et al., 1956).

Two samples of the preceding year's twig growth were collected in
March from each of the willow species occurring on the island, and these

were submitted for chemical analysis. The results of the analysis
(Table 7) indicate that S. alaxensis has the highest moisture, protein,
and caloric contents, S. interior has the highest nitrogen free extract
or carbohydrate content, and S. niphoclada has the lowest moisture and
caloric contents. It would seem that a combination of high moisture,
protein, and caloric contents could be responsible for S. alaxensis
being a highly preferred species, whereas the converse might explain
why S. niphoclada is a non-preferred species. This conclusion supports
the theory that the total nutritive value of a plant is the best
indicator of preference.

There are several reasons, however, why it might be hazardous to
formulate any conclusions based on the chemical analysis results. It
will be noticed, for example, that calcium, potassium, phosphorus, and
tannin, all of which may affect preference, were not analyzed. Further-
more, the nutrient contents of the various species, particularly S.
interior and S. myrtillifolia, are so similar that their association
with preference would seem dubious. In addition, several variables
were not taken into account when the samples were collected, and, as a
result, the samples may not be comparable. Bailey (1967), for instance,
noted that the highest concentration of crude protein is located in
those samples that (1) are clipped nearest to the terminal buds, (2)
are collected from the lower rather than the upper portions of the
crowns, and (3) include flower buds or lateral buds rather than only
terminal vegetative buds. I did not consider the sample locations
in reference to the plant crowns nor the number of buds supported by
the clipped twigs. Swank (1956) stated that the protein content of a
species varies seasonally, which suggests that if the samples had been

Table 7. Results of a chemical analysis of samples collected from the
primary willow species that occur on the Tanana River study
area

Species	Moisture (%)	Protein (%)	Fat (%)	Crude Fiber (%)	Ash (%)	N_2 free extract	Kg cal./ 100 g
ALA	19.6	6.6	2.8	33.4	2.1	55.1	505
	19.6	7.4	2.6	33.7	2.4	53.9	499
	(19.6)*	(7.0)	(2.7)	(33.6)	(2.3)	(54.5)	(502)
INT	14.3	5.8	1.5	27.7	2.0	63.0	478
	14.9	5.2	1.2	30.4	2.2	61.0	499
	(14.6)	(5.5)	(1.4)	(29.1)	(2.1)	(62.0)	(489)
MYR	18.2	6.6	4.2	24.6	3.3	61.3	485
	13.0	6.1	2.8	30.7	2.4	58.0	492
	(15.6	(6.4)	(3.5)	(27.7)	(2.9)	(59.7)	(489)
NIP	10.0	6.6	2.2	30.9	2.4	57.9	492
	11.8	5.5	2.2	33.4	3.5	55.4	478
	(10.9)	(6.1)	(2.2)	(32.2)	(3.0)	(56.7)	(485)

* Mean of two samples

collected at some other time the analytic results might have been completely different. The maturity and health of plants also affect their nutritive composition (Cook and Harris, 1950; McIlvanie, 1942); plant maturity was not considered when collecting samples, and many S. interior plants appeared to be in poor condition, presumably as a result of over-browsing. If the small sample size is added to this list, the magnitude of the difficulties becomes awesome.

Another palatability factor is the external form of a plant. Heady (1964) states that stickiness, position of the leaves, texture, and hairiness probably affect preferability. None of the willow species discussed in this paper have sticky stems or leaves, and I am not able to comment about leaf position or texture differences. Of the species preferred most highly on all study areas, S. alaxensis has extremely hairy twigs and leaves, whereas S. arbusculoides, S. pulchra, and S. interior have glabrous stems and little or no hair on their leaves. Among the non-preferred species, S. glauca and S. niphoclada have quite hairy stems and leaves, while S. Barclayi and S. hastata have glabrous leaves and near-glabrous stems. These observations would seem to rule out hairiness as a factor of palatability among willows. McMillan (1953) mentions that preferability may be associated with the heights of species. He notes that a tall-growing willow species in Yellowstone National Park is browsed more intensively than another species, which rarely exceeds three feet in height, and suggests that this may be a result of moose being able to simultaneously hide in and feed on the tall-growing species. McMillan also reasons that the low-growing species may be less easily browsed upon than the other species. My data from all study areas, however, indicate that S. interior and S.

pulchra, neither of which commonly exceed two feet in height, are two
of the lowest-growing and most highly preferred species. This would
seem to indicate that, although browsing intensity might be correlated
with plant height, the inherent palatability of a species affects its
preferability to a greater degree than does its average height.

It seems possible that an animal might selectively browse a cer-
tain species of plant, regardless of its nutritive value, simply be-
cause it tastes good; a high content of certain nutrients does not
necessarily imply a high palatability. I have tasted all of the willow
species occurring on the study areas and find that they differ in taste.
Although all of them taste bitter, some species taste markedly less so
than others. S. interior, which has a high carbohydrate content
(Table 7), is the sweetest tasting species, but the other preferred
species are quite bitter. I have not been able to distinguish a taste
common to preferred or to non-preferred species and can only conclude
that differences in taste do exist.

Factors that are external to the plants also affect their pre-
ference. The browsing sustained by individual species varies with the
vegetation and soil types in which they occur (Hurd and Pond, 1958),
temperature and rainfall (Castle and Halley, 1953), topography, and the
physiology of the browsing animals (Heady, 1964). Although the willows
that were encountered during this study occurred under a variety of
environmental conditions, certain species were nearly always preferred
over others. This would seem to indicate that certain palatability
factors, and not environmental conditions, are responsible for willow
species preferability, and it is my belief that these factors are
characteristic of individual species.

Amount of Available Browse

The actual amount of plant material available for browsing is
seldom determined by field workers because of the difficulties involved
in obtaining this quantity. The methods employed during this study,
however, made it possible to determine the oven-dried weights of the
available browse supplied by the various species of willows on the
island. The average oven-dried weights of browse available per sample
frame (i.e., 2.25 square m) and per 100 square m is shown in Table 8.

Although the leaves were removed from the clipped stems to simulate
winter conditions and the weights listed are oven-dried weights, the
results indicate that a seemingly small amount of plant mass is available
for browsing on the study area: 2,038.0 g (4.5 pounds) per 100 square
m. These results, however, compare favorably with those obtained by
several other field workers. Taber (1956) states that shrubland
in California supplies 324,160 pounds (oven-dry weight) and chaparral
offers 115,960 pounds of deer browse per square mile; these weights
are equivalent to 12.5 and 4.4 pounds, respectively, per 100 square m.
Harlow (1955) lists the air-dried weights of available deer browse
on a number of areas in Florida, the majority of which range between
100 and 200 pounds per acre or between 2.5 and 5.0 pounds per 100
square m. It should be noted that the average plant heights and den-
sities on the island are quite similar to those occurring on the other
study areas. This may mean that comparable amounts of browse are
available on the other study areas.

Amount of Browse Removed During One Winter

To be able to calculate the amount of browse removed by moose

Table 8. Oven-dried weights of available browse, by species

Species	Wt. (g) per sample frame	Wt. (g) per 100 sq. m
ALA	8.3 (56.7)*	368.5
INT	4.5 (6.8)	199.8
MYR	3.4 (9.4)	151.0
NIP	29.7 (58.0)	1318.7
Total =	45.9	2038.0 (4.5 lbs.)

* Standard deviation

during one winter, a count was conducted in the spring of the number of twigs of each species that had been browsed on the 36 square m utilization plots during the previous winter. Since the mean oven-dried weight of plant material removed from a browsed twig was also determined for each species, the weight of the browse removed during the winter was easily calculated. The mean weight of the plant mass removed from a browsed twig, the number of twigs browsed per utilization plot, the calculated weight of browse removed per 100 square m, and the calculated percentage of available browse removed are shown for each species in Table 9.

The results indicate that extreme differences exist in the percentages of available browse removed from the various species during the winter. Observe, with respect to the various species, that the same general relationship exists between the percentages of available browse removed from the species and their BIIs (Fig. 12). This association would seem to suggest that the relationship between species BIIs approximates the relationship between the degrees of browsing that the species sustained. With respect to the actual values for the species, however, the association between the BIIs and percentages of available browse that was removed is not very close; e.g., the BII for S. alaxensis is 14% larger than that for S. interior, while the percentage of available browse removed from S. alaxensis is 210% greater than that from S. interior. This is not surprising, since the BII is a measure of the percentage of twigs that have been browsed and not a measure of how much of the available browse has been removed from the twigs. It seems probable that a certain percentage of twigs browsed on one species represents the removal of a different percentage

Table 9. Oven-dried weights of clipped twigs, number of twigs eaten per utilization plot, calculated
weights of browse eaten per 100 sq. m, and calculated percentages of available browse removed
during one winter

Species	Wt. (g)/ clipped twig	No. twigs eaten/ utiliz. plot	Calc. wt. (g) eaten/ 100 sq. m	Calc. % avail. browse removed
ALA	3.2 (0.76)*	13.9 (26.89)	124.6	33.8
INT	2.0 (0.44)	3.9 (6.53)	21.8	10.9
MYR	2.0 (0.31)	0.1 (0.40)	0.6	0.4
NIP	2.9 (0.54)	0.2 (0.81)	1.6	0.1

* Standard deviation
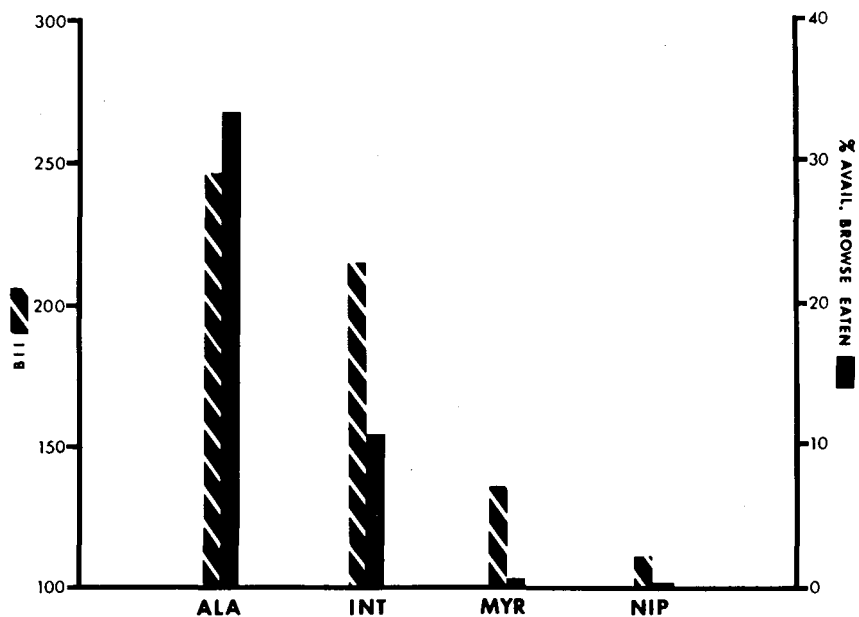
Figure 12. Comparison of BII (Browsing Intensity Index) values and percentages of available browse removed during one winter.

of available plant material than the same percentage of twigs browsed on another species. For example, a browsed twig on a species that maintains numerous, slender twigs will probably represent a smaller removal of available browse than a twig eaten on a species that supports a few, thick twigs. The different relationship between the BII values and the percentages of available browse removed might also be partially due to the fact that the BII represents an average value over a number of years, whereas the percentage of browse removed is based on the browsing that occurred during one winter. Errors in the BII values might also have contributed to this discrepancy.

SUMMARY AND CONCLUSIONS

Following is a summary of the principal results of this study:

1. Certain species of willows are preferred by moose over others. S. interior, S. alaxensis, S. arbusculoides, and S. pulchra are the most highly preferred species on the areas that were studied.

2. Among the various willow species occurring in Alaska's interior, S. alaxensis and S. pulchra, due to their high preferability and wide distribution, are probably of the greatest importance to moose.

3. Moderately palatable species are eaten to a greater extent when occurring in mixed stands with highly preferred species than when growing in "pure" stands. The amount of browsing on species that are located very low on the preference list is not affected in this manner.

4. In a given area, neither the relative abundance nor density of a species noticeably affect its degree of use, this being possibly due to the overriding influence of inherent palatability.

5. The densest of the willow stands that were studied either do not physically hinder moose, or, if they do impede movements, the hindrance does not appear to reduce the amount of browsing on these stands below that which is sustained by sparse stands.

6. Although the degree of browsing that is sustained by a given species seems to be correlated with plant height, species preferability is not related to height; preferability is probably influenced more by inherent palatability than by average plant height.

7. The amount of available browse on one study area is 4.5 pounds (oven-dried weight) per 100 square m.

Results of this study suggest several possible applications to the

future moose management program in Alaska. When assessing moose
range conditions or the relationship of moose density to the food
supply, only the amount of browsing sustained by the highly and moder-
ately preferred willow species should be considered, since even where
these species are severely utilized, certain non-preferred species
will scarcely be touched by moose. When environmental manipulation
becomes possible, only the growth of preferred species should be
encouraged. If possible, the establishment of strips of highly pre-
ferred species within a stand of moderately preferred species could be
beneficial; the highly preferred species would themselves be valuable
sources of food, and their presence might increase the utilization of
those moderately preferred.

This study was, in effect, only a pilot study of some of the
important moose ranges in Alaska's interior. Before range condition
surveys can be accomplished efficiently, a more adequate method of
willow species identification must be developed. A method by which
species can be identified after they have lost their leaves would be
highly beneficial. Further research on the ecology of the various
willow species is needed before moose ranges can be artificially
improved. To estimate the carrying capacities of moose ranges, the
amounts of usable browse that they supply and the food requirements of
moose must first be determined. I believe, from personal observations,
that the various willow species are differentially resistant to browsing.
It would be necessary to know the degree of browsing that the different
species can tolerate before range condition or carrying capacity
analyses can be made. My data suggest that there might be a complex
interaction between plant height, density, volume, form, location, and

palatability that affects utilization; information about this possible interaction could be useful. Finally, if only for academic reasons, it would be of interest to determine how and why a species selection preference occurs.

APPENDIX I. Heights, densities, and percentages of plants in each browse class for all willow species on the study plots

Study area	Study plot	Species	Ht. (cm)	#Stems/ sample frame	Percent in each browse class									
					1	2	3	4	5	6	7-1	7-2	7-3	8
Dry Creek	1	LAS	118.2	11.0	19.5	10.3	2.4	28.3	9.1	4.0	14.0	2.7	2.4	7.3
		INT	77.8	4.6	2.9	0.0	0.7	13.8	6.5	27.5	9.4	5.1	21.0	13.0
		MYR	65.2	1.5	0.0	0.0	0.0	19.6	2.2	0.0	19.6	10.9	23.9	23.9
		PAD	58.0	0.2	0.0	0.0	0.0	20.0	0.0	0.0	20.0	0.0	0.0	60.0
		ALA	130.9	13.9	18.0	8.4	6.0	38.7	6.0	2.4	11.1	1.9	1.7	5.8
		DEP	12.9	0.4	0.0	0.0	0.0	33.3	8.3	8.3	0.0	8.3	0.0	41.7
		PUL	51.5	3.2	0.0	0.0	0.0	3.2	1.1	0.0	34.7	14.7	5.3	41.1
		ARB	97.7	3.8	7.9	0.9	1.8	46.5	9.6	7.0	15.8	2.6	0.9	7.0
	2	LAS	120.0	0.8	21.7	0.0	8.7	21.7	0.0	8.7	26.1	0.0	0.0	13.0
		INT	87.9	0.4	0.0	0.0	0.0	25.0	0.0	50.0	0.0	0.0	25.0	0.0
		MYR	57.5	0.1	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0
		PAD	130.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
		ALA	284.5	6.1	53.6	10.4	16.4	6.0	1.6	1.1	3.8	0.0	0.5	6.6
		DEP	115.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
		PUL	83.1	4.1	4.8	4.0	1.6	16.1	9.7	11.3	16.9	8.9	10.5	16.1
		ARB	105.6	1.2	16.7	5.6	0.0	38.9	5.6	0.0	19.4	0.9	2.8	11.1
	3	LAS	141.2	1.7	23.5	14.7	14.7	17.6	8.8	17.6	2.9	0.0	0.0	0.0
		INT	77.9	0.8	5.9	0.0	0.0	5.9	11.8	11.8	0.0	0.0	58.8	5.9
		MYR	82.9	0.3	0.0	0.0	0.0	57.1	0.0	0.0	14.3	0.0	0.0	28.6

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APPENDIX I (Contd.)

Study area	Study plot	Species	Ht. (cm)	#Stems/ sample frame	Percent in each browse class									
					1	2	3	4	5	6	7-1	7-2	7-3	8
Dry Creek	3	ALA	157.2	12.8	45.3	7.0	3.5	32.4	4.7	3.5	2.0	0.4	0.8	0.4
		PUL	75.8	6.3	0.0	0.0	0.0	26.4	8.8	15.2	20.8	11.2	12.0	5.6
		ARB	127.5	6.5	22.9	3.8	0.0	58.0	3.1	3.1	3.8	3.1	0.8	1.5
	4	LAS	61.9	0.3	0.0	0.0	0.0	15.4	0.0	0.0	61.5	0.0	0.0	23.1
		PAD	35.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
		ALA	46.2	2.0	0.0	0.0	0.0	5.0	0.0	0.0	35.0	0.0	0.0	60.0
		DEP	79.9	1.7	1.4	0.0	0.0	33.3	13.0	10.1	15.9	5.8	0.0	20.3
		PUL	66.4	17.7	0.3	0.1	0.6	7.2	4.9	14.4	26.7	12.6	17.9	15.4
		ARB	113.7	3.3	6.8	4.5	9.8	15.2	18.9	24.2	9.8	0.8	1.5	8.3
	5	LAS	180.3	0.5	20.0	20.0	40.0	0.0	6.7	6.7	6.7	0.0	0.0	0.0
		ALA	197.9	0.9	28.6	14.3	42.9	7.1	3.6	0.0	3.6	0.0	0.0	0.0
		PUL	59.9	28.2	0.0	0.0	0.0	7.1	4.5	5.7	22.4	16.9	24.5	18.9
		ARB	78.6	9.8	0.3	0.7	0.7	21.6	25.0	22.3	12.0	7.2	9.9	0.3
Paxson Lake	1	BAR	55.8	4.4	0.0	0.0	0.0	15.2	0.0	0.0	49.2	0.0	0.0	35.6
		LAN	64.5	20.8	0.2	0.2	0.0	23.8	5.0	1.1	46.9	1.6	0.3	21.0
		PUL	52.1	14.0	0.0	0.0	0.0	10.0	0.0	0.0	47.3	0.7	0.2	41.8
	2	GLA	98.3	1.1	0.0	0.0	0.0	33.3	3.0	0.0	30.3	3.0	3.0	27.3
		BAR	65.6	48.0	0.0	0.0	0.0	5.3	1.0	0.3	24.7	0.8	0.6	67.3
		LAN	79.2	3.8	0.0	0.0	0.0	5.3	0.9	5.3	29.8	2.6	2.6	53.5
		ALA	87.5	12.6	0.0	0.0	0.0	6.6	5.3	9.8	25.4	3.2	5.6	44.2

APPENDIX I (Contd.)

Study area	Study plot	Species	Ht. (cm)	#Stems/ sample frame	Percent in each browse class									
					1	2	3	4	5	6	7-1	7-2	7-3	8
Paxson Lake	2	DEP	148.3	0.1	0.0	0.0	0.0	66.7	0.0	0.0	0.0	0.0	0.0	33.3
		PUL	70.9	38.3	0.1	0.0	0.0	4.3	1.9	1.6	26.2	3.2	2.8	60.0
	3	GLA	115.0	0.1	0.0	0.0	0.0	50.0	0.0	0.0	50.0	0.0	0.0	0.0
		BAR	122.4	15.0	0.0	0.0	0.0	44.9	6.9	3.1	24.9	1.1	1.1	18.0
		LAN	136.6	2.0	0.0	0.0	0.0	15.3	16.9	32.2	28.8	15.1	1.7	0.0
		ALA	101.4	0.2	0.0	0.0	0.0	0.0	0.0	42.9	28.6	0.0	14.3	14.3
		PUL	113.3	26.1	0.0	0.1	0.0	17.9	12.1	12.9	26.6	3.6	5.4	21.4
	4	GLA	75.9	2.6	0.0	0.0	0.0	9.6	3.8	0.0	25.0	1.9	5.8	53.8
		BAR	53.9	4.9	0.0	0.0	0.0	0.0	0.0	0.0	13.1	0.0	0.0	86.9
		LAN	35.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
		DEP	99.7	3.7	0.0	0.0	0.0	29.7	2.7	0.0	31.1	1.4	0.0	35.1
		PUL	51.9	12.6	0.0	0.0	0.0	0.0	0.0	0.0	8.7	5.2	2.4	83.7
Little Clearwater Creek	1	HAS	67.3	5.1	0.0	0.0	0.0	42.2	2.9	1.0	20.6	2.0	0.0	31.4
		BAR	40.8	2.5	0.0	0.0	0.0	5.9	0.0	0.0	21.6	2.0	0.0	70.6
		LAN	70.0	0.1	0.0	0.0	0.0	50.0	0.0	0.0	50.0	0.0	0.0	0.0
		ALA	108.6	9.8	0.0	1.5	18.5	7.7	8.2	44.1	8.7	1.0	1.5	8.7
		PUL	68.3	11.9	0.0	0.0	0.0	24.7	10.9	5.4	26.8	1.3	7.1	23.8
	2	HAS	92.8	8.4	1.2	0.0	0.0	65.7	6.5	3.0	15.4	1.2	0.6	6.5
		BAR	86.5	1.8	0.0	5.4	0.0	37.8	8.1	18.9	16.2	0.0	0.0	13.5

Study area	Study plot	Species	Ht. (cm)	#Stems/ sample frame	Percent in each browse class									
					1	2	3	4	5	6	7-1	7-2	7-3	8
Little Clearwater Creek	2	LAN	105.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
		ALA	106.3	12.8	0.0	1.2	11.7	21.8	16.7	32.3	5.8	1.6	1.9	7.0
		PUL	95.6	6.5	2.3	1.5	0.8	40.5	19.1	14.5	9.9	1.5	5.3	4.6
	3	HAS	66.8	1.5	0.0	0.0	0.0	35.5	0.0	0.0	41.9	0.0	0.0	22.6
		BAR	112.1	9.2	3.3	1.1	1.1	47.3	25.0	13.6	7.1	0.5	0.0	1.1
		LAN	100.0	0.1	0.0	0.0	0.0	33.3	66.7	0.0	0.0	0.0	0.0	0.0
		ALA	137.6	2.9	0.0	1.7	37.3	3.4	11.9	45.8	0.0	0.0	0.0	0.0
		PUL	95.2	16.5	0.3	0.3	0.3	47.4	21.1	15.1	9.7	0.6	0.6	4.5
	4	HAS	92.4	0.8	0.0	0.0	0.0	70.6	5.9	0.0	23.5	0.0	0.0	0.0
		BAR	119.9	8.6	7.0	3.5	0.0	47.7	20.9	16.9	2.3	0.0	0.0	1.7
		PUL	90.0	21.0	0.0	0.5	0.2	35.0	20.7	21.9	8.6	2.9	5.2	5.0
	5	HAS	58.0	6.1	0.0	0.0	0.0	19.2	0.0	0.0	38.4	1.4	0.0	41.1
		BAR	35.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
		ALA	95.0	29.4	0.0	1.1	0.6	19.3	21.2	34.3	11.0	4.8	2.3	5.4
		PUL	63.0	1.8	0.0	0.0	0.0	22.7	4.5	9.1	27.3	4.5	0.0	31.8
	6	HAS	71.4	2.1	0.0	0.0	0.0	50.0	0.0	0.0	19.0	0.0	0.0	31.0
		BAR	96.1	9.3	1.1	0.0	0.0	67.0	9.7	5.4	10.3	1.1	0.5	4.9
		PUL	93.8	20.3	1.2	0.7	0.7	31.3	19.2	29.3	9.6	0.7	1.2	5.9

APPENDIX I (Contd.)

Study Area	Study plot	Species	Ht. (cm)	#Stems/ sample frame	Percent in each browse class									
					1	2	3	4	5	6	7-1	7-2	7-3	8
Little Clearwater Creek	7	HAS	72.9	0.6	0.0	0.0	0.0	52.9	0.0	0.0	17.6	0.0	0.0	29.4
		BAR	90.2	7.4	0.0	0.0	0.0	53.6	19.1	7.7	14.5	1.8	0.0	3.2
		ZZZ	37.5	10.1	0.0	0.0	0.0	2.3	0.0	0.0	9.9	0.0	0.0	87.8
		PUL	81.8	18.6	0.0	0.2	1.6	31.0	17.6	11.1	20.1	3.0	0.4	15.1
	8	HAS	66.9	9.9	0.0	0.0	0.0	40.3	2.3	0.0	28.2	0.3	0.0	28.9
		BAR	95.4	12.8	1.0	0.5	1.0	50.5	15.1	10.4	8.1	1.6	0.0	11.7
		LAN	56.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0
		ALA	105.6	3.9	0.8	0.0	5.9	5.1	9.3	72.0	3.4	0.8	0.0	2.5
		PUL	73.5	15.4	0.2	0.4	0.0	30.5	12.1	4.3	22.9	5.6	6.7	17.1
Gunn Creek	1	HAS	55.8	0.4	0.0	0.0	0.0	16.7	0.0	0.0	41.7	0.0	0.0	41.7
		BAR	69.3	18.1	2.2	0.4	0.0	31.9	2.4	0.4	27.3	0.2	0.0	35.4
		LAN	90.6	3.3	1.0	1.0	0.0	57.6	7.1	1.0	22.2	0.0	0.0	10.1
		ALA	97.7	5.9	1.1	3.4	11.4	18.2	10.8	14.8	21.6	1.7	0.0	17.0
		PUL	80.3	43.2	3.0	0.7	0.2	44.8	3.2	0.9	22.8	0.2	0.1	24.1
	2	BAR	74.3	3.3	2.0	0.0	0.0	39.0	6.0	0.0	23.0	5.0	0.0	25.0
		LAN	124.5	1.0	16.7	0.0	3.3	60.0	16.7	3.3	0.0	0.0	0.0	0.0
		ALA	149.1	0.7	4.5	0.0	40.9	13.6	4.5	36.4	0.0	0.0	0.0	0.0
		PUL	88.7	60.7	3.1	1.9	1.2	44.2	8.1	3.7	23.6	0.8	0.3	13.2

Study area	Study plot	Species	Ht. (cm)	#Stems/ sample frame	Percent in each browse class									
					1	2	3	4	5	6	7-1	7-2	7-3	8
Taylor Highway (Mt. Fairplay)	1	PUL	104.1	16.6	0.0	0.0	1.5	21.0	14.5	13.6	24.1	9.6	3.9	11.7
	2	GLA	67.9	8.3	0.0	0.0	0.0	21.4	0.0	0.0	34.7	0.0	0.0	44.0
		PUL	53.8	1.9	0.0	0.0	0.0	3.6	0.0	0.0	30.4	1.8	0.0	64.3
	3	GLA	79.9	2.6	0.0	0.0	0.0	32.5	1.3	0.0	41.6	0.0	0.0	24.7
		PUL	64.3	0.8	0.0	0.0	0.0	13.0	0.0	0.0	34.8	8.7	0.0	43.5
	4	PUL	92.7	18.7	0.0	0.3	0.0	18.7	11.0	4.3	42.2	6.7	0.3	16.6
Taylor Highway (Other)	1	GLA	60.2	3.1	0.0	0.0	0.0	27.0	0.0	0.0	39.2	0.0	0.0	33.8
		ALA	61.9	0.3	0.0	0.0	0.0	25.0	0.0	0.0	50.0	0.0	0.0	25.0
		DEP	81.5	18.0	3.9	2.1	0.0	38.4	9.0	1.4	18.8	2.5	1.2	22.7
		SCO	69.7	0.8	0.0	5.6	0.0	11.1	11.1	0.0	22.2	5.6	11.1	33.0
		PUL	45.8	1.4	0.0	0.0	0.0	6.1	3.0	0.0	24.2	3.0	0.0	63.6
		ARB	82.2	2.9	0.0	1.4	2.9	26.1	5.8	14.5	27.5	7.2	5.8	8.7
	2	GLA	80.0	7.8	2.9	1.4	0.0	48.6	5.0	0.7	22.1	3.6	1.4	14.3
		MYR	82.5	0.3	0.0	0.0	0.0	66.7	0.0	0.0	33.3	0.0	0.0	0.0
		ALA	130.0	0.2	0.0	0.0	25.0	25.0	0.0	50.0	0.0	0.0	0.0	0.0
		DEP	124.9	11.5	9.2	11.6	3.9	22.2	22.2	18.4	2.9	2.9	2.9	3.9
		PUL	73.2	4.5	0.0	0.0	0.0	16.0	13.6	16.0	19.8	1.2	17.3	16.0
		ARB	91.1	6.8	0.8	1.6	1.6	9.0	16.4	45.1	4.1	3.3	14.8	3.3
	3	GLA	71.3	0.1	0.0	0.0	0.0	50.0	0.0	0.0	50.0	0.0	0.0	0.0
		ALA	135.8	0.2	16.7	16.7	0.0	16.7	0.0	33.3	16.7	0.0	0.0	0.0

APPENDIX I (Contd.)

Study area	Study plot	Species	Ht. (cm)	#Stems/ sample frame	Percent in each browse class									
					1	2	3	4	5	6	7-1	7-2	7-3	8
Taylor Highway (Other)	3	DEP	79.7	1.9	5.2	0.0	0.0	44.8	1.7	0.0	19.0	0.0	0.0	29.3
		PUL	51.3	10.8	0.0	0.0	0.0	14.9	0.9	0.0	30.3	0.6	0.0	53.3
		ARB	89.9	2.4	0.0	2.7	0.0	38.4	27.4	2.7	16.4	2.7	0.0	9.6
	4	GLA	153.3	1.3	56.5	0.0	0.0	34.8	4.3	0.0	4.3	0.0	0.0	0.0
		ALA	135.0	0.1	0.0	0.0	50.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0
		DEP	68.1	0.4	0.0	0.0	0.0	12.5	25.0	12.5	12.5	12.5	12.5	12.5
		PUL	72.7	23.1	0.0	0.2	0.0	22.9	16.9	12.3	22.4	2.9	4.6	17.8
		ARB	91.1	4.7	1.2	1.2	0.0	14.3	20.2	39.3	8.3	3.6	11.9	0.0
Wood River	1	GLA	95.1	6.6	1.1	1.5	1.9	43.4	5.3	0.4	34.3	0.4	0.0	11.7
		HAS	38.7	24.4	0.0	0.0	0.0	0.1	0.0	0.0	6.6	0.0	0.0	93.3
		BAR	56.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0	50.0
		LAN	59.2	4.4	0.0	0.0	0.0	8.5	0.0	0.0	41.5	0.0	0.0	50.0
		ALA	203.3	0.1	33.3	0.0	66.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		PUL	41.5	0.3	0.0	0.0	0.0	0.0	0.0	0.0	30.8	0.0	0.0	69.2
		ARB	129.7	5.3	1.4	1.9	19.6	17.3	11.2	21.0	14.0	2.3	1.4	9.8
	2	GLA	79.2	0.1	0.0	0.0	0.0	50.0	0.0	0.0	33.3	0.0	0.0	16.7
		HAS	43.7	31.5	0.0	0.0	0.0	0.7	0.0	0.0	12.7	0.1	0.0	86.5
		BAR	36.4	0.5	0.0	0.0	0.0	0.0	0.0	0.0	4.8	0.0	0.0	95.2
		LAN	61.5	15.2	0.0	0.0	0.0	12.5	4.1	2.8	25.2	2.0	0.5	53.0
		ALA	138.8	7.5	3.6	7.9	11.9	17.2	13.9	18.2	8.3	3.3	5.6	9.9
		ARB	92.9	1.3	0.0	0.0	9.8	9.8	7.8	7.8	21.6	21.6	5.9	15.7

APPENDIX I (Contd.)

Study area	Study Plot	Species	Ht. (cm)	#Stems/ sample frame	Percent in each browse class									
					1	2	3	4	5	6	7-1	7-2	7-3	8
Wood River	3	GLA	97.3	1.7	2.0	4.0	0.0	28.0	8.0	6.0	36.0	2.0	0.0	14.0
		HAS	46.1	18.6	0.0	0.0	0.0	1.4	0.0	0.0	18.1	0.4	0.0	80.1
		LAN	79.2	20.2	0.0	0.0	0.2	19.1	6.9	7.4	40.5	3.6	1.3	20.9
		ALA	194.8	2.1	6.3	6.3	35.9	7.8	20.3	17.2	1.6	1.6	3.1	0.0
		ARB	124.1	2.7	1.2	15.9	3.7	9.8	36.6	3.7	8.5	0.0	11.0	9.8
	4	GLA	103.0	12.0	0.3	1.7	0.8	46.3	13.6	2.2	25.2	0.8	2.2	6.9
		ALA	153.9	2.4	0.0	8.3	20.8	9.7	9.7	41.7	5.6	2.8	1.4	0.0
		PUL	70.5	3.1	0.0	0.0	0.0	10.6	9.6	1.1	33.0	11.7	2.1	31.9
	5	GLA	87.9	11.6	0.0	0.0	0.0	30.5	9.9	6.9	36.5	9.0	2.1	5.2
		HAS	76.4	1.0	0.0	0.0	0.0	14.3	4.8	0.0	66.7	9.5	0.0	4.8
		ALA	99.7	0.9	0.0	0.0	0.0	16.7	16.7	38.9	22.2	0.0	5.6	0.0
	6	HAS	54.3	4.0	0.0	0.0	0.0	3.8	0.0	0.0	37.5	0.0	0.0	58.8
		BAR	60.1	8.8	0.0	0.0	0.0	0.6	0.0	0.0	57.4	5.1	0.6	36.4
		LAN	60.0	9.6	0.0	0.0	0.0	9.8	0.5	0.0	33.2	3.1	0.0	53.4
		ALA	83.3	0.3	0.0	0.0	0.0	0.0	16.7	16.7	16.7	0.0	33.3	16.7
		PUL	62.6	12.0	0.0	0.0	0.0	7.1	4.2	1.3	33.3	11.7	3.3	39.2
	7	GLA	82.2	1.8	0.0	0.0	0.0	43.4	7.5	0.0	26.4	0.0	0.0	22.6
		HAS	48.5	17.5	0.0	0.0	0.0	1.5	0.0	0.0	25.9	0.8	0.0	71.9
		BAR	53.9	8.4	0.0	0.0	0.0	5.1	0.8	0.0	30.4	5.5	0.8	57.3
		LAN	66.1	0.8	0.0	0.0	0.0	17.4	0.0	4.3	30.4	0.0	0.0	47.8

APPENDIX I (Contd.)

Study area	Study plot	Species	Ht. (cm)	#Stems/ sample frame	Percent in each browse class									
					1	2	3	4	5	6	7-1	7-2	7-3	8
Wood River	7	ALA	130.3	6.4	0.0	2.1	15.1	6.3	10.9	42.2	8.3	5.7	5.2	4.2
		DEP	90.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
		PUL	28.9	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
		ARB	94.4	0.6	0.0	0.0	0.0	0.0	11.8	41.2	0.0	11.8	35.3	0.0
	8	GLA	69.7	5.4	0.0	0.0	0.0	21.1	5.0	0.6	34.2	1.2	0.0	37.9
		HAS	30.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0
		LAN	84.2	2.2	0.0	0.0	0.0	21.5	18.5	4.6	23.1	9.2	0.0	23.1
		PUL	41.3	1.5	0.0	0.0	0.0	0.0	0.0	0.0	9.1	0.0	0.0	90.9
	9	GLA	58.3	6.3	0.0	0.0	0.0	10.2	1.6	0.4	32.7	0.8	0.4	53.9
		LAN	60.8	4.5	0.0	0.0	0.0	8.3	3.9	0.0	33.9	3.9	0.6	49.4
		PUL	41.9	2.0	0.0	0.0	0.0	0.0	2.5	0.0	10.0	1.3	0.0	86.3

APPENDIX II. Heights, densities, and percentages of plants in each browse class for all willow species on the Tanana River study area

Species	Ht. (cm)	#Stems/sample frame	Percent in each browse class							
			1	2	3	4	5	6	7	8
LAS	52.5	0.2	0.0	0.0	0.0	27.8	11.1	0.0	33.3	27.8
INT	69.3	3.4	0.9	0.9	1.2	13.5	19.4	22.8	34.2	7.1
MYR	77.3	1.3	10.5	3.2	4.0	29.8	8.1	2.4	29.8	12.1
ALA	131.3	0.6	5.1	1.7	40.7	10.2	8.5	10.2	15.3	8.5
NIP	70.0	5.9	11.2	2.5	0.4	27.8	2.3	0.4	30.1	25.5
ARB	110.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0

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