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SUMMER HABITAT AND FOOD UTILIZATION BY DALL'S SHEEP
AND THEIR RELATION TO BODY AND HORN SIZE

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SUMMER HABITAT AND FOOD UTILIZATION BY DALL'S SHEEP
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A
THESIS

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ABSTRACT

Investigations of Dall's sheep summer habitat and food utilization were conducted during 1977 and 1978 in the eastern Alaska Range near Tok, Alaska, to investigate the hypothesis that nutrition is the major factor influencing body and horn size differences among Alaskan sheep populations. Nutritional quality of forage is greatest in early stages of plant growth. No significant differences in plant chemical composition were found between this study and other studies of Dall's sheep range. Sheep summer diets consisted primarily of grasses, sedges, *Dryas octopetala*, willows, and a few forbs. Patterns of use of vegetation types by sheep indicated preference for early growth stages of plants. The length of the plant growing season, topographic variability, and the extent of altitudinal migration determine the spatial and temporal availability of plants in early growth stages. These factors are proposed as determiners of body and horn size differences in Alaskan sheep populations.

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INTRODUCTION

Nutrition is an important factor in the lives of mountain sheep. Growth of extravagant social paraphernalia in the form of horns and survival in rigorous alpine habitats demand a high plane of nutrition during at least part of the year. Considerable information has been gathered on nutrition of bighorn sheep (*Ovis canadensis*) (Blood 1967; Demarchi 1968; Constan 1972; Hebert 1972, 1973; Todd 1972, 1975; Todd and Hansen 1973; Stelfox 1976) and of Dall's sheep (*O. dalli dalli*) (Murie 1944; Jones 1963a,b; Viereck 1963; Heimer 1973, 1978; Hoefs 1974, 1975; Nichols 1974; Whitten 1975; Hoefs and Brink 1978). Recently, investigations have focused on relationships between bioenergetics and body and horn growth in different sheep populations. Geist (1966, 1971) noted differences in horn size, growth rates, life expectancy, and fecundity in bighorn and Stone's sheep (*O. d. stonei*), and he expressed these patterns in terms of population quality. Since then, Shackleton (1973) has examined several aspects of Geist's population quality hypothesis for different populations of bighorns. Heimer and Smith (1975) examined ram horn growth measurements and percent glacial cover (hypothesized by Geist [1971] as an indicator of range quality) for Dall's sheep populations in Alaska. Most recently, Bunnell (1978) demonstrated a strong correlation between horn growth and precipitation, suggesting primary productivity and thus range quality strongly influences horn growth in Dall's sheep.

The purpose of this study was to examine the hypothesis that nutrition is the underlying factor influencing differences in body and horn size in different populations of Dall's sheep in Alaska. Data collected during this study and from other studies were compared. Three primary objectives were: (1) to determine if forage quality (chemical composition) varied among sheep ranges; (2) to determine if forage species eaten by sheep varied among populations; and (3) to determine if differences in the extent and timing of altitudinal migration existed among populations.

The Tok area was chosen for this study for several reasons. Relatively large bodied and large horned sheep are found in the area (Heimer and Smith 1975). The area is accessible, approximately 2.5 km from the Alaska Highway. A large mineral lick used by many sheep is in the area, which virtually assures that sheep would be present for observations during the summer months. In addition, some data for sheep populations in the area are available, and continuing studies of these sheep are being conducted by the Alaska Department of Fish and Game.

STUDY AREA

The study area is located on the north side of the Alaska Range in east-central Alaska, approximately 240 km southeast of Fairbanks. The area is approximately 2.5 km southwest of the Alaska Highway at its closest point (Figure 1).

The mountains of the eastern Alaska Range are composed of metamorphic and igneous rocks, mantled with various thicknesses of alluvium, colluvium, and drift (Holmes and Foster 1968). Precambrian Birch Creek Schist, a metamorphic bedrock unit composed primarily of schist, gneiss, quartzite, and amphibolite, underlies the study area. Surficial geology has been modified by Pleistocene glaciations as indicated by U-shaped valleys, cirques, and moraines (Holmes 1964). The area is characterized by steep and, in places, precipitous slopes with peaks approaching 2200 m above sea level. Elevation within the study area ranges from a low of about 850 m (treeline in much of the area) to a maximum of 2166 m.

The study area is divided by a narrow ridgeline. The creeks draining the northern portion of the study area empty directly into the Tanana River, whereas the creeks to the south drain into the Robertson River which ultimately flows into the Tanana River. For convenience, these portions of the study area will be called the Tanana and Robertson drainages, respectively.

The climate of the area is generally typical of the continental subarctic climate of interior Alaska; long, cold winter, moderately

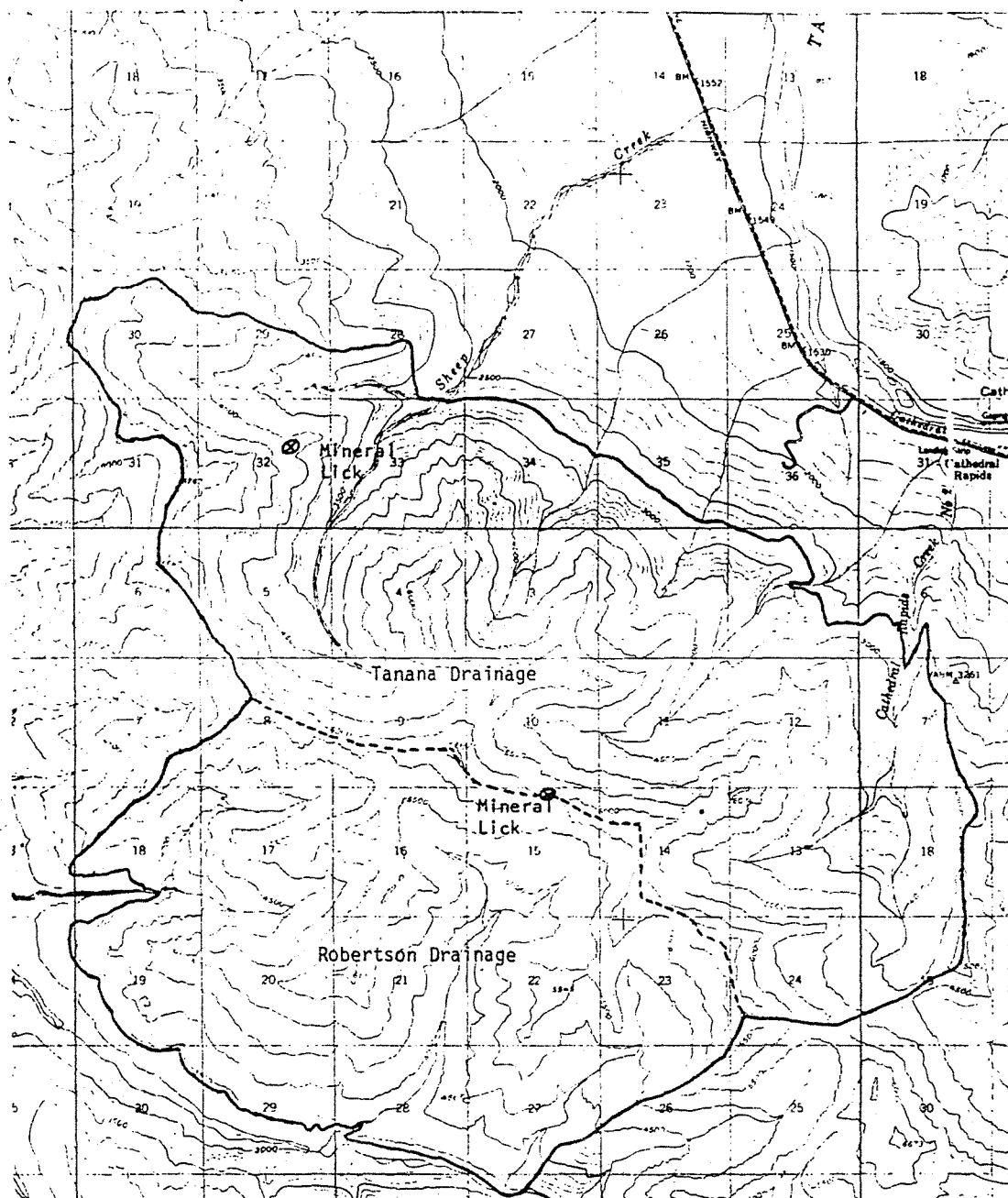


Figure 1. Map of the Sheep Creek study area.
 (The dashed line indicates the divide between the drainages)

1 km

warm summers, and light precipitation, mostly in the form of summer rain (Holmes 1964). Weather data for 1977 and 1978 are summarized in Table 1. The nearest weather recording station operative on a yearly basis is at Tok, approximately 40 km southeast of the study area. Weather data are also recorded at Tanacross, approximately 21 km east of the study area, but only for the period May to September. Both of the stations are in the lowlands of the Tanana River valley and therefore do not indicate actual weather values found on the sheep range. They should, however, indicate the general weather patterns that occur on the study area throughout the year.

The study area is contained within the Tok Management Area, a portion of the eastern Alaska Range managed by the Alaska Department of Fish and Game for high quality trophy hunting of Dall's sheep. Such hunting is by permit for full curl rams; permits are also issued for harvesting ewes.

The Tok Management Area is judged to have high quality sheep populations with that estimate of quality based on indices derived from ram horn volume, maximum attainable horn volume, maximum sustained horn growth rate, and diameter of horn curl (Heimer and Smith 1975). Rams within that area, when compared with rams in 17 other areas of Dall's sheep range within Alaska, rank second, fifth, third, and second in quality for the above parameters (Heimer and Smith 1975).

Dall's sheep are present throughout the study area during the summer. Their distribution within the study area, both temporal and

Table 1. Weather data for Tok and Tanacross, 1977 and 1978¹.

Month	Tok						Tanacross				
	Temperature (°C) ²			Precipitation (mm) ³			Temperature (°C) ²		Precipitation (mm) ³		
	Max	Min	Ave	Total	Snow		Max	Min	Ave	Total	
					Total	Max on Ground					
1977 Jan	--	--	--	--	--	--	--	--	--	--	--
Feb	- 8.3	-21.4	-14.8	9.9	121.9	330.2	--	--	--	--	--
Mar	- 3.9	-21.7	-12.8	0.8	12.7	330.2	--	--	--	--	--
Apr	6.1	- 8.5	- 1.8	11.9	119.4	330.2	--	--	--	--	--
May	14.9	- 2.1	6.4	29.0	0.0	0.0	14.9	-0.6	7.8	23.9	--
Jun	20.6	3.7	12.8	73.2	0.0	0.0	20.6	4.1	12.4	51.6	--
Jul	23.3	4.6	14.0	65.0	0.0	0.0	22.4	5.3	13.9	11.7	--
Aug	24.1	5.3	14.7	6.6	0.0	0.0	26.1	5.5	15.8	4.8	--
Sep	13.5	- 0.7	6.4	22.1	0.0	0.0	--	--	--	--	--
Oct	- 0.3	-10.4	- 5.3	4.3	152.4	101.6	--	--	--	--	--
Nov	-19.1	-30.4	-24.8	6.9	78.7	152.4	--	--	--	--	--
Dec	-26.0	-34.3	-30.2	0.0	0.0	152.4	--	--	--	--	--
1978 Jan	--	--	--	--	--	--	--	--	--	--	--
Feb	-12.3	-25.8	-19.1	5.1	53.3	330.2	--	--	--	--	--
Mar	--	--	--	--	--	--	--	--	--	--	--
Apr	8.2	- 9.9	- 0.8	1.5	63.5	279.4	--	--	--	--	--
May	16.5	- 3.3	6.6	0.0	0.0	0.0	15.7	0.1	7.9	24.4	--
Jun	--	--	--	--	--	--	18.8	4.9	11.8	23.6	--
Jul	24.9	5.6	15.3	--	--	--	23.3	6.9	15.1	20.3	--
Aug	23.0	1.9	12.5	--	--	--	22.1	2.9	12.5	32.8	--
Sep	14.5	- 1.4	6.6	--	--	--	--	--	--	--	--
Oct	--	--	--	--	--	--	--	--	--	--	--
Nov	-12.3	-24.0	-18.2	0.0	0.0	228.6	--	--	--	--	--
Dec	-14.5	-26.1	-20.3	2.0	53.3	330.2	--	--	--	--	--

¹Data from U. S. Dept. of Commerce (1977-1978) and Bureau of Land Management, respectively

²Converted from °F

³Converted from inches

spatial, is influenced by a number of factors, including mineral licks. One large mineral lick and several smaller mineral licks are found within the study area and are used by sheep throughout the summer.

METHODS

Field work for this study was conducted during the summers of 1977 and 1978, with occasional trips to the study area during the intervening winter. Field work during the summer of 1977 was conducted only in the Tanana drainages of the study area. The period 4 May through 30 June 1978 was spent within the Tanana drainages. During the period 1 July 1978 to 23 August 1978, when field research was completed, periods of five to eight days were spent alternating between the Robertson and Tanana river drainages. During such periods, observations of the vegetation and of sheep, primarily feeding habits and use of vegetation types, were recorded within the study area. Trips from base camps were usually for a single day. Occasional trips of two to three days were undertaken to reach more distant portions of the study area.

Sheep were observed with the unaided eye, 7x35 or 8x24 binoculars, or, most frequently, a 15-60 power spotting scope. Sheep were classified into distinct classes on the basis of sex, age, and horn size. These classes were lambs, yearling females, adult females, yearling males, and adult males. Adult rams were further classified by degree of horn curl, using one-quarter curl increments. Activity (feeding, resting, or ruminating), altitude, and vegetation type used by sheep were recorded. Durations of lamb nursings were recorded whenever possible. Time spent feeding versus ruminating was

also noted. Observations of plant species, the stages of growth, and parts of plants eaten were recorded. Feeding sites were examined in a manner similar to that used by Hjeljord (1971), after sheep left the immediate area. Percent cover, plant coverage removed as a percent of the total coverage for that species, percentage of plant tissue removed, and the part of the plant eaten were recorded for each species present in ten randomly placed 0.5 x 0.5 m plots. Plant coverage removed and percent plant tissue removed were estimated by comparison with ungrazed plants in the area.

Two sheep rumen samples, collected during June and July 1978, were obtained from the Alaska Department of Fish and Game. The samples were washed over 12.7 mm, 6.35 mm, and 2.0 mm screens, and the plant parts were identified to species where possible. The amount of each species or larger grouping (e.g., woody twigs, grass-sedge) was determined by volumetric displacement in water and recorded as percent of the washed sample.

Sheep habitat was classified into vegetation types based either on dominant flora or on physiographic characteristics. Vegetation within various vegetation types was sampled quantitatively to describe more accurately the types and to make possible comparisons between sites in various portions of the study area. Percent cover, in 5 percent increments, was estimated for each species in 10 randomly placed 0.5 x 0.5 m plots. If vegetation was layered, cover for each species in each layer was recorded and the values summed,

thus allowing total coverage values greater than 100 percent.

Visual estimates of the percent of each vegetation type in a particular drainage were recorded. These values were summed for comparisons between the Tanana and Robertson River drainages.

Phenology of plant growth was recorded for each vegetation type. Phenological data included date of first flowering, length of new leaves for some grasses and sedges at the start of the growing season, and date of appearance of leaves on various shrub species.

Many plants were collected for nutrient analysis. Emphasis was placed on those species seen eaten by sheep, although abundant species not eaten to any great extent by sheep were also sampled. Plants for nutrient analysis were collected at approximately monthly intervals during the summer to assess temporal changes in plant chemical composition. A few winter samples were also collected. The parts of plants eaten by sheep were handpicked in randomly located 1 m² plots; four samples of approximately 15 grams (wet weight) were collected for each species sampled at these sites. These four samples were later grouped into one composite sample for a given species from a given site. While in the field, plant samples were air-dried in a plant press. These plants were later oven-dried at 65°C for 48 hours and ground in a Wiley mill to pass through a 40 mesh screen in preparation for analysis.

All plant samples were analyzed for nitrogen, phosphorus, calcium, and magnesium content. Total nitrogen was determined by the

micro-Kjeldahl procedure (Jackson 1958). Total phosphorus was determined on a perchloric acid digest of a plant sample using the ammonium molybdate technique with an amino-naphtholsulfonic acid reducing agent (Jackson 1958). Total calcium and magnesium were determined from aliquots of the perchloric acid digest using an atomic absorption spectrophotometer. Strontium chloride was added to calcium and magnesium aliquots to suppress anion interference. All analyses were duplicated.

Selected plant samples were analyzed for total nonstructural carbohydrate, acid detergent fiber, neutral detergent fiber, cellulose, lignin, silica, and ash by the University of Alaska Institute of Agricultural Sciences' Palmer Research Center, Palmer, Alaska.

All plants were identified by the author except *Draba* spp. which were identified by Dr. D. F. Murray, Curator of the University of Alaska Herbarium. Plant nomenclature followed that of Hultén (1968) except for *Salix* spp.; *Salix* nomenclature followed that of Viereck and Little (1972). Voucher plant specimens are conserved at the University of Alaska Herbarium.

VEGETATION ANALYSES

Qualitative Vegetation Analysis

Within the study area, sheep habitat was classified into general vegetation types based on the dominant plant species that were present, or on physiographic properties of the site. Vegetation types were described such that all areas could be assigned to a particular vegetation type. The following is a list of the major vegetation zones and their component vegetation types used in this study, including the features characteristic of each type:

Forest Zone

This zone serves as the lower altitudinal boundary of the study area and was not subdivided into vegetation types. Continuous stands, composed primarily of conifers, reach elevations of 820 to 1060 m, depending on aspect, with scattered individual conifers occurring up to 1300 m. White spruce (*Picea glauca*) is the dominant species with lesser amounts of black spruce (*Picea mariana*), quaking aspen (*Populus tremuloides*), and cottonwood (*Populus balsamifera*) also present. Sheep were not observed in this zone and consequently detailed examination of this area was not conducted.

Shrub Zone

This zone is found immediately above treeline and ranges in

altitude from approximately 760 to 1400 m. Most vegetation types within this zone contain 0.5 to 4 m tall shrubs as dominant plant species. Continuous, well developed stands of shrubs occur to approximately 1370 m with small, isolated stands or occasional individual shrubs reaching 1430 m, particularly in sheltered, moist areas. Three vegetation types were recognized in this zone.

Willow-alder - Willows (*Salix alaxensis*, *S. barclayi*, *S. glauca*, and *S. planifolia* ssp. *pulchra*) and alder (*Alnus crispa*), 1.5 to 3 m tall, are the dominant life forms with the grasses *Calamagrostis canadensis* and *Festuca altaica*, the sedge *Carex podocarpa*, and the forbs *Boykinia richardsonii*, *Mertensia paniculata*, and *Epilobium angustifolium* forming the major portion of the understory. Willows and alder occur together or separately in large areas immediately above timberline or in isolated thickets.

Low shrub - Low growing shrubs 0.5 to 1.5 m high characterize this type. Resin birch (*Betula glandulosa*) is the most abundant shrub species with lesser amounts of blueberry (*Vaccinium uliginosum*), willows, Labrador tea (*Ledum palustre* ssp. *decumbens* and *L. p.* ssp. *groenlandicum*) also present. Mosses, lichens, crowberry (*Empetrum nigrum*), bunchgrass (*Festuca altaica*) and forbs such as *Pyrola grandiflora*, *Linnaea borealis*, and *Lycopodium annotinum* grow beneath the shrub layer.

Grass-sedge meadow - This vegetation type is found on steep morainal deposits along streams at elevations less than 900 m, well

within the shrub zone. The grasses, *Festuca altaica*, *Elymus innovatus*, *Calamagrostis purpurascens*, *Poa glauca*, and the sedge *Carex scirpoidea* are the dominant members of this type. Also present in limited amounts are *Dryas octopetala*, *Juniperus communis*, *Arctostaphylos uva-ursi*, *Zygadenus elegans*, *Oxytropis boreale*, and *Potentilla hookeriana*.

Alpine Zone

Vegetation in this zone, composed primarily of low growing alpine species, extends from approximately 950 to 2166 m, the maximum elevation within the study area. In places, continuous vegetation reaches 1800 m; above 1800 m only small, scattered patches of vegetation occur. Eight vegetation types were recognized within this zone.

Festuca-Dryas - This vegetation type is commonly found at the border between the shrub and alpine zones. *Festuca altaica* and *Dryas octopetala* jointly form 50 to 80 percent of the cover. Numerous forb species including *Anemone parviflora*, *Artemisia arctica*, and *Lupinus arcticus* are present with scattered alder and willow occasionally present.

Dryas mat - This type is characterized by a fairly continuous mat of *Dryas octopetala* through which are interspersed mosses, lichens, the sedge *Carex microchaeta*, the grasses *Poa alpina*, *Hierochloe alpina*, and *Calamagrostis purpurascens*, and many forbs, notably *Epilobium latifolium*, *Anemone parviflora*, and *Geum rossii*.

Dryas-moss-Cassiope - Nearly equal amounts of *Dryas octopetala*,

Cassiope tetragona, and mosses compose this vegetation type which is usually restricted to north-facing slopes. Many species, including *Carex microchaeta*, *Salix reticulata*, *Vaccinium uliginosum*, *Boykinia richardsonii*, *Festuca altaica*, and willows 1 to 2 m tall are scattered throughout the sites.

Wet sedge meadow - The dominant members of this vegetation type are *Eriophorum angustifolium*, *Carex membranacea*, and *C. misandra*. *Salix reticulata*, *S. polaris* ssp. *pseudopolaris*, and mosses are also important members of this vegetation type. The soil is usually saturated and flowing water from underground seeps is common.

Wet low-Salix meadow - This vegetation type is also characterized by high soil moisture, ranging from very moist to saturated with standing or even flowing water. Low growing willows, particularly *Salix polaris* ssp. *pseudopolaris* and to a lesser extent *Salix reticulata*, are the most important components of this type. Mosses and sedges are also important components. Forbs such as *Ranunculus nivalis*, *Anemone parviflora*, *A. richardsonii*, *Geum rossii*, and *Boykinia richardsonii* are common.

Small-rock scree - Small-rock scree slopes are characterized by small, unstable rocks less than 150 mm in diameter, usually on steep slopes. Widely spaced individual plants or small clumps of plants are found growing on small-rock scree. Common species include *Silene acaulis*, *Epilobium latifolium*, *Saxifraga oppositifolia*, *Oxyria digyna*, and *Poa alpigena*.

Large-rock scree - Slopes with rocks larger than those found in small-rock scree are defined as large-rock scree. Vegetation on large-rock scree is limited to widely spaced plants or small clumps of plants. Common species include *Dryas octopetala*, *Carex microchaeta*, *Papaver alboroseum*, *Hierochloe alpina*, *Silene acaulis*, *Arnica alpina*, and *Saxifraga bronchialis*.

Cliffs - Cliffs are areas of near vertical terrain steeper than 70 degrees. The vegetation present on these areas varies, generally conforming to that present on the adjacent non-cliff terrain.

Quantitative Vegetation Analysis

During 1977 and 1978, I collected plants from a variety of sites for nutrient analysis. At each of these sites, I also analyzed percent cover and frequency of occurrence for each species in ten plots. In 1978, I examined several feeding sites and recorded percent cover and frequency of occurrence for those plant species within the site. These sites were typical of the areas within which sheep fed and were generally representative of the vegetation type classifications. These sites did not, however, represent the entire range of vegetation types used by sheep throughout the summer. Descriptions of each site follow in Tables 2 and 3, with locations of each site presented in Figure 2.

Of the 13 vegetation types I have described, only one, the wet sedge meadow, was not included in this analysis. I saw no sheep

Table 2. Description of sites from which plants were collected for nutrient analysis.

Site	Drainage	Description and Location	Slope (°)	Elevation (m)
1	Tanana	South-facing grass-sedge meadow, west fork of Sheep Creek	45	850
2	Tanana	Southwest-facing <i>Dryas</i> mat, 0.75 km south of the fork of Sheep Creek	50	1275
3	Tanana	Southwest-facing <i>Festuca-Dryas</i> meadow below site 2	30	1100
4	Tanana	South-facing willow-alder area, 1.5 km up the west fork of Sheep Creek	40	1075
5	Tanana	South-facing low shrub area, directly above site 4	40	1125
6	Tanana	North-facing willow thicket, slightly upstream and across the creek from sites 4 and 5	30	1100
7	Tanana	North-facing <i>Dryas</i> -moss- <i>Cassiope</i> mat, 250 m upstream from site 6	30	1200
8	Tanana	Northeast-facing <i>Dryas</i> mat, 1.4 km west of Cathedral Rapids Creek No. 2	20	1375
9	Tanana	Northeast-facing small-rock scree slope, 250 m southeast of site 8	50	1375

Table 2. (continued)

Site	Drainage	Description and Location	Slope (°)	Elevation (m)
10	Tanana	South-facing large-rock scree slope 1.6 km northwest of site 8	40	1425
11	Tanana	North-facing large-rock scree slope opposite site 10	40	1425
12	Robertson	Northeast-facing small-rock scree slope, 1 km southeast of the fork of creek A	50	1375
13	Robertson	Northeast-facing <i>Dryas</i> mat, 250 m north of the fork of creek A	25	1400
14	Robertson	South-facing large-rock scree slope, most rocks less than 1 m across, 1.9 km northeast of the mouth of creek C	30	1425
15	Robertson	South-facing large-rock scree slope and ridgetop, 0.7 km northeast of the junction of creeks D and E	40	1425
16	Robertson	West-facing <i>Dryas</i> mat, 0.7 km east of the junction of creeks D and E	45	1250
17	Robertson	Southwest-facing <i>Festuca-Dryas</i> strip along a large-rock scree slope, 400 m downstream of site 16	20	1125

Table 2. (continued)

Site	Drainage	Description and Location	Slope (°)	Elevation (m)
18	Robertson	South-facing low shrub area, 200 m downstream of site 16	35	1150
19	Robertson	North-facing willow thicket, 100 m upstream of the junction of creeks D and E	30	1075
20	Robertson	South-facing willow-alder thicket directly across from site 19	20	1075
21	Robertson	Dry, rocky, west-facing <i>Dryas</i> mat 1 km east of the fork of creek A	10	1625
22	Robertson	Rocky, south-facing <i>Dryas</i> mat just below the ridgetop between creek E and the west fork of creek A	45	1825
23	Robertson	Southwest-facing large-rock scree slope, most rocks 0.3 m or less in diameter, 300 m northwest of site 22	30	1825

Table 3. Feeding site descriptions.

Site	Drainage	Description and Location	Slope (°)	Elevation (m)	Date
a	Tanana	East-facing small cliffs adjacent to creek, 0.7 km upstream from the fork of Sheep Creek	70	850	8 May 1978
b	Tanana	South-facing <i>Dryas</i> mat, 2.8 km up the west fork of Sheep Creek	50	1375	30 May 1978
c	Tanana	East-facing <i>Dryas</i> mat, 2.8 km up the main fork of Sheep Creek	30	1275	10 Jun 1978
d	Tanana	North-facing <i>Dryas</i> -moss- <i>Cassiope</i> mat, 1.5 km up the west fork of Sheep Creek	20	1150	11 Jun 1978
e	Tanana	Northeast-facing low shrub area, 2 km up the main fork of Sheep Creek	15	1100	13 Jun 1978
f	Tanana	Northeast-facing <i>Festuca</i> - <i>Dryas</i> meadow with scattered willow, 100 m south of site e	15	1100	13 Jun 1978
g	Tanana	Northeast-facing wet low- <i>Salix</i> meadow, 50 m west of site f	15	1100	13 Jun 1978
h	Tanana	North-facing willow-alder thicket, 250 m east of site 6	30	1025	19 Jun 1978

Table 3. (continued)

Site	Drainage	Description and Location	Slope (°)	Elevation (m)	Date
i	Tanana	Northeast-facing <i>Dryas</i> -moss- <i>Cassiope</i> mat, 500 m east of site c	20	1150	20 Jun 1978
j	Tanana	Northeast-facing <i>Dryas</i> -moss- <i>Cassiope</i> mat, 200 m northwest of site 7	15	1225	22 Jun 1978
k	Robertson	Same as nutrient site 21	10	1625	28 Jul 1978

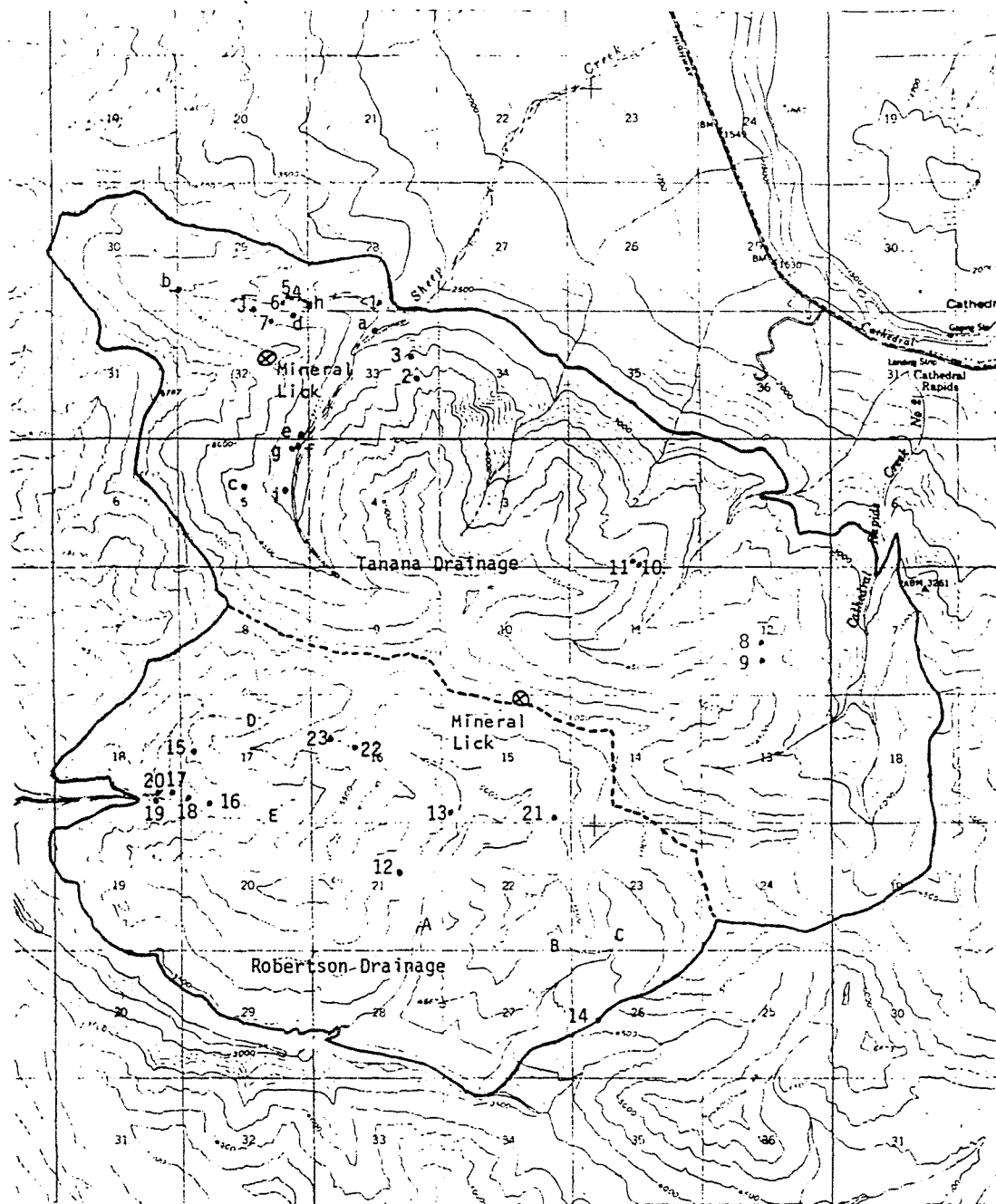


Figure 2. Locations of feeding and nutrient sites in the Sheep Creek study area.
(The dashed line indicates the divide between the drainages)

1 km

feeding in this type; consequently I did not collect plants for nutrient analysis, nor did I examine the area quantitatively as a feeding site.

Plant coverage values and frequency of occurrence were recorded at sites to compare the flora of nutrient sites in both the Robertson and Tanana drainages. Tables 4, 5, 6, 7, and 8 present the coverage and frequency values at the nutrient and feeding sites. The sites are grouped under the vegetation type headings for convenience and do not represent grouping along any environmental gradient.

The coverage values of the above sites were also compared quantitatively by the ordination technique of Bray and Curtis (1957) to assess the floristic similarity of sites whose nutrient values were directly compared. Floristic differences could represent differences in site parameters not measured (soil moisture, pH) which would influence the nutrient content of plants.

A matrix of similarity was constructed for all sites (Table 9). The similarity index was calculated as follows:

$$C = 2w \cdot (a+b)^{-1}, \text{ where,}$$

C = the similarity index
 a = the sum of the coverage values in one site,
 b = the sum of the coverage values for a second site, and
 w = the sum of the lesser coverage values for those species which are common to both sites.

Similarity values could range from 0 for sites with no species in common to 100 for two sites with identical species composition. The similarity values were then used to graphically illustrate

Table 4. Species coverage (C) and frequency of occurrence (F) values in percent for the *Dryas*-moss-*Cassiope* nutrient and feeding sites in the Sheep Creek study area, 1977 and 1978. (T=trace)

Species	Site	<i>Dryas</i> -moss- <i>Cassiope</i>							
		7		d		i		j	
		C	F	C	F	C	F	C	F
<i>Dryas octopetala</i>		26.0	100	24.5	100	27.0	100	23.5	100
Mosses		28.0	100	18.0	100	31.3	100	19.5	100
Lichens		3.3	90	4.0	100	5.0	100	0.5	40
<i>Cassiope tetragona</i>		18.0	90	30.5	100	18.5	90	11.0	90
<i>Carex microchaeta</i>		2.7	80	0.5	80	3.2	70	5.0	80
<i>Salix reticulata</i>		T	10	3.0	70	3.0	50	4.0	70
<i>Salix phlebophylla</i>		--	--	0.5	20	1.5	50	--	--
<i>Salix polaris</i> ssp. <i>pseudopolaris</i>		--	--	--	--	--	--	2.0	20
<i>Festuca altaica</i>		1.0	10	2.2	50	--	--	5.5	40
<i>Poa alpina</i>		--	--	--	--	--	--	0.5	20
<i>Equisetum scirpoides</i>		--	--	T	20	T	60	T	50
<i>Arctostaphylos alpina</i>		--	--	--	--	--	--	5.0	30
<i>Vaccinium uliginosum</i>		1.0	30	0.2	40	7.0	60	14.5	100
<i>Vaccinium vitis-idaea</i>		--	--	--	--	1.0	20	4.0	70
<i>Stilene acaulis</i>		0.9	30	--	--	0.2	10	--	--
<i>Senecio atropurpureus</i>		--	--	--	--	--	--	T	10
<i>Diapensia lapponica</i>		0.5	10	1.5	10	T	10	--	--
<i>Minuartia arctica</i>		1.0	30	--	--	0.1	30	0.5	10
<i>Tofieldia coccinea</i>		1.5	40	0.5	10	0.3	30	--	--
<i>Cardamine purpurea</i>		--	--	--	--	T	20	--	--
<i>Anemone parviflora</i>		0.1	60	0.2	50	T	20	--	--
<i>Boykinia richardsonii</i>		2.0	50	2.5	40	--	--	--	--
<i>Oxyria digyna</i>		T	10	--	--	--	--	--	--
<i>Oxytropis nigrescens</i>		--	--	--	--	0.7	40	--	--
<i>Astagalus umbellatus</i>		--	--	--	--	0.6	60	0.8	50
<i>Geum rossii</i>		--	--	--	--	T	30	--	--
<i>Dodecatheon frigidum</i>		0.5	20	0.1	20	--	--	0.3	10
<i>Pedicularis capitata</i>		--	--	0.2	20	T	10	T	10
<i>Loiseleuria procumbens</i>		--	--	--	--	--	--	0.5	10
<i>Parrya nudicaulis</i>		--	--	0.1	10	--	--	T	20
<i>Pyrola grandiflora</i>		--	--	--	--	0.1	20	0.9	60
<i>Empetrum nigrum</i>		--	--	T	10	--	--	1.5	20
<i>Ledum palustre</i> ssp. <i>groenlandicum</i>		--	--	--	--	--	--	0.5	30
<i>Luzula confusa</i>		--	--	--	--	--	--	T	10
<i>Lloydia serotina</i>		T	10	--	--	--	--	--	--
<i>Androsace chamaejasme</i>		T	10	--	--	--	--	--	--
<i>Lycopodium annotinum</i>		T	10	--	--	--	--	0.5	10
Rock		13.0	60	11.5	40	1.0	20	--	--

Table 5. Species coverage (C) and frequency of occurrence (F) values in percent for the *Dryas* nutrient and feeding sites in the Sheep Creek study area, 1977 and 1978. (T=trace)

Species	Site	<i>Dryas</i>															
		2		16		8		13		21		22		b		c	
		C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
<i>Dryas octopetala</i>		40.5	80	28.0	70	25.0	100	20.0	90	21.0	100	51.0	100	56.1	100	41.0	100
Mosses		6.0	90	3.2	50	1.1	50	3.0	50	13.5	100	--	--	--	--	1.5	20
Lichens		5.5	70	4.3	70	0.7	30	--	--	16.0	100	5.0	100	--	--	3.0	50
<i>Cassiope tetragona</i>		--	--	--	--	3.2	40	1.5	10	1.0	20	--	--	--	--	7.0	70
<i>Carex microchaeta</i>		5.0	80	3.0	40	8.0	90	8.5	100	4.1	80	1.3	70	--	--	1.1	70
<i>Carex scirpoides</i>		--	--	0.1	20	--	--	--	--	--	--	--	--	0.6	10	--	--
<i>Salix reticulata</i>		--	--	--	--	7.0	70	16.5	90	--	--	--	--	--	--	--	--
<i>Salix phlebophylla</i>		--	--	--	--	--	--	--	--	--	--	9.0	90	2.5	20	T	20
<i>Salix polaris</i> ssp. <i>pseudopolaris</i>		--	--	--	--	3.2	40	8.5	70	--	--	--	--	--	--	--	--
<i>Salix arctica</i>		T	10	--	--	--	--	--	--	2.6	60	--	--	--	--	--	--
<i>Calamagrostis purpurascens</i>		--	--	0.5	10	--	--	--	--	--	--	--	--	2.1	50	--	--
<i>Calamagrostis canadensis</i>		--	--	--	--	--	--	1.5	20	--	--	--	--	--	--	--	--
<i>Hierochloa alpina</i>		2.5	90	--	--	--	--	--	--	1.6	90	T	50	--	--	--	--
<i>Festuca altaica</i>		T	10	--	--	--	--	4.0	60	--	--	--	--	--	--	T	10
<i>Poa alpina</i>		--	--	--	--	T	30	1.7	60	--	--	--	--	--	--	--	--
<i>Juncus castaneus</i>		0.5	80	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<i>Equisetum scirpoides</i>		--	--	--	--	T	60	T	80	--	--	--	--	--	--	--	--
<i>Epilobium latifolium</i>		1.6	40	0.1	20	0.2	10	--	--	--	--	--	--	--	--	--	--
<i>Saxifraga bronchialis</i>		1.0	20	1.0	20	--	--	--	--	--	--	--	--	--	--	--	--
<i>Saxifraga eschscholtzii</i>		--	--	0.5	10	--	--	--	--	--	--	--	--	--	--	--	--
<i>Saxifraga flagellaris</i>		--	--	--	--	--	--	--	--	--	--	T	10	--	--	--	--
<i>Saxifraga hibernica</i>		--	--	--	--	--	--	0.5	10	--	--	--	--	--	--	--	--
<i>Saxifraga trienspidata</i>		--	--	--	--	--	--	--	--	--	--	--	--	0.9	30	--	--
<i>Arctostaphylos alpina</i>		2.5	10	--	--	--	--	--	--	--	--	--	--	--	--	3.0	30
<i>Vaccinium uliginosum</i>		--	--	--	--	--	--	--	--	--	--	--	--	0.1	10	9.5	90
<i>Vaccinium vitis-idaea</i>		--	--	--	--	--	--	--	--	0.3	40	--	--	T	40	3.5	60
<i>Silene acaulis</i>		1.5	30	0.2	10	--	--	0.5	10	--	--	1.8	90	--	--	--	--
<i>Arnica alpina</i>		1.0	20	0.2	20	--	--	--	--	--	--	--	--	--	--	--	--
<i>Senecio atrorubescens</i>		T	10	--	--	--	--	--	--	--	--	0.5	20	--	--	--	--
<i>Petasites frigidus</i>		--	--	--	--	--	--	0.9	40	--	--	--	--	--	--	--	--
<i>Gnaphalium borealis</i>		0.7	20	--	--	--	--	--	--	1.0	50	--	--	--	--	--	--
<i>Diapensia lapponica</i>		0.5	10	--	--	--	--	--	--	--	--	--	--	8.1	60	0.5	10
<i>Mimulus arctica</i>		0.5	20	--	--	T	10	--	--	0.1	10	--	--	--	--	--	--

Table 5. (continued)

Species	Dryas															
	2		16		8		13		21		22		b		c	
	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
<i>Tofieldia coccinea</i>	0.1	20	--	--	--	--	--	--	--	--	--	--	T	40	--	--
<i>Cardamine purpurea</i>	0.5	20	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<i>Campanula lasiocarpa</i>	T	20	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<i>Anemone parviflora</i>	--	--	--	--	10.0	100	7.5	100	--	--	--	--	T	20	--	--
<i>Aconitum delphinifolium</i>	--	--	--	--	--	--	0.2	20	--	--	--	--	--	--	--	--
<i>Artemisia arctica</i>	--	--	--	--	0.3	20	2.6	50	--	--	--	--	--	--	--	--
<i>Martensia paniculata</i>	--	--	--	--	--	--	1.5	20	--	--	--	--	--	--	--	--
<i>Boykinia richardsonii</i>	--	--	--	--	--	--	2.0	30	--	--	--	--	--	--	--	--
<i>Oxyria digyna</i>	--	--	--	--	1.3	40	0.1	20	--	--	--	--	--	--	--	--
<i>Polygonum viviparum</i>	--	--	--	--	--	--	--	--	--	--	T	80	--	--	--	--
<i>Oxytropis nigrescens</i>	--	--	--	--	--	--	--	--	0.5	20	--	--	2.0	80	T	20
<i>Astragalus umbellatus</i>	--	--	--	--	6.5	70	--	--	--	--	--	--	--	--	--	--
<i>Geum rossii</i>	--	--	--	--	17.5	80	17.0	80	--	--	0.5	10	--	--	0.5	30
<i>Dodecatheon frigidum</i>	--	--	--	--	13.2	90	3.5	50	--	--	--	--	--	--	--	--
<i>Pedicularis capitata</i>	--	--	--	--	T	20	T	30	--	--	--	--	--	--	T	30
<i>Pedicularis langsdoeffii</i>	--	--	--	--	--	--	--	--	--	--	T	10	--	--	--	--
<i>Loiseleuria procumbens</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2.5	30
<i>Linnaea borealis</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	--	T	10
<i>Claytonia samentosa</i>	--	--	--	--	--	--	T	20	--	--	--	--	--	--	--	--
<i>Thysotis alpestris</i>	--	--	--	--	--	--	T	10	--	--	--	--	--	--	--	--
<i>Parrya nudicaulis</i>	--	--	--	--	0.1	10	--	--	--	--	--	--	--	--	--	--
<i>Pyrola grandiflora</i>	--	--	--	--	0.1	10	--	--	--	--	--	--	--	--	--	--
<i>Empetrum nigrum</i>	--	--	--	--	--	--	--	--	--	--	--	--	--	--	11.0	70
<i>Ledum palustre</i> ssp. <i>groenlandicum</i>	--	--	--	--	--	--	--	--	--	--	--	--	0.4	10	--	--
Rock	30.6	100	58.1	100	2.6	40	--	--	38.4	100	28.2	100	27.1	90	15.9	60

Table 6. Species coverage (C) and frequency of occurrence (F) values in percent for the large-rock scree and small-rock scree nutrient sites in the Sheep Creek study area, 1977 and 1978. (T=trace)

Species	Site	Large-rock scree										Small-rock scree			
		10		11		14		15		23		9		12	
		C	F	C	F	C	F	C	F	C	F	C	F	C	F
<i>Dryas octopetala</i>		2.0	30	1.0	20	10.5	60	3.0	40	0.2	10	0.2	10	--	--
<i>Hierochloa alpina</i>		0.9	70	0.7	50	1.0	40	0.7	70	--	--	--	--	--	--
Lichens		0.9	50	1.5	60	2.0	50	2.0	30	0.9	60	--	--	--	--
<i>Carex microchaeta</i>		1.1	40	1.0	40	0.1	20	3.0	60	0.8	50	--	--	--	--
<i>Carex scirpoidea</i>		--	--	--	--	0.5	20	--	--	--	--	--	--	--	--
Mosses		1.2	20	1.2	30	T	10	0.7	30	--	--	--	--	--	--
<i>Festuca altaica</i>		--	--	--	--	2.0	20	2.0	30	--	--	--	--	--	--
<i>Poa arctica</i>		--	--	--	--	--	--	1.4	60	T	20	--	--	--	--
<i>Poa alpigena</i>		--	--	--	--	--	--	--	--	--	--	T	10	0.1	20
<i>Salix phlebophylla</i>		--	--	--	--	--	--	--	--	4.5	70	--	--	--	--
<i>Salix polaris</i> ssp. <i>pseudopolaris</i>		--	--	--	--	--	--	--	--	--	--	0.3	20	--	--
<i>Papaver alboroseum</i>		--	--	--	--	--	--	0.3	10	0.4	60	--	--	--	--
<i>Papaver macounii</i>		--	--	1.2	30	--	--	--	--	--	--	--	--	--	--
<i>Saxifraga bronchialis</i>		0.4	20	0.2	10	T	10	1.0	20	--	--	--	--	--	--
<i>Saxifraga oppositifolia</i>		--	--	--	--	--	--	0.8	30	1.2	70	0.1	20	0.1	30
<i>Silene acaulis</i>		1.0	30	--	--	1.0	10	1.0	20	2.7	90	0.3	20	0.5	50
<i>Mimartia arctica</i>		0.2	30	0.5	30	--	--	--	--	0.4	30	--	--	--	--
<i>Arnica alpina</i>		0.8	50	--	--	--	--	2.1	50	--	--	--	--	--	--
<i>Geum rossii</i>		--	--	T	10	--	--	--	--	0.8	20	--	--	--	--
<i>Potentilla hookeriana</i>		0.5	10	--	--	--	--	2.5	40	--	--	--	--	--	--
<i>Dryopteris fragans</i>		--	--	0.2	10	--	--	--	--	--	--	--	--	--	--
<i>Synthlipsis borealis</i>		--	--	--	--	--	--	0.8	30	--	--	--	--	--	--
<i>Rhododendron lapponicum</i>		--	--	--	--	0.5	10	--	--	--	--	--	--	--	--
<i>Polygonum viviparum</i>		--	--	--	--	T	10	--	--	--	--	--	--	--	--
<i>Oxyria digyna</i>		--	--	--	--	--	--	--	--	--	--	0.5	40	0.1	30
<i>Epilobium latifolium</i>		--	--	--	--	--	--	--	--	--	--	0.7	60	0.1	20
<i>Boykinia richardsonii</i>		--	--	--	--	--	--	--	--	--	--	--	--	T	10
<i>Oxytropis nigrescens</i>		--	--	--	--	--	--	--	--	--	--	T	20	--	--
<i>Stellaria laeta</i>		--	--	--	--	--	--	--	--	--	--	0.1	20	--	--
<i>Cuscuta tetragona</i>		--	--	1.0	20	6.0	70	--	--	--	--	--	--	--	--
Rock		91.0	100	91.5	100	77.9	100	79.5	100	87.9	100	97.8	100	99.0	100

Table 7. Species coverage (C) and frequency of occurrence (F) values in percent for the willow-alder and low shrub nutrient and feeding sites in the Sheep Creek study area, 1977 and 1978. (T=trace)

Species	Site	Willow-alder										Low shrub					
		4		20		6		19		h		5		18		e	
		C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
<i>Salix alaxensis</i>		--	--	6.5	30	22.5	80	3.5	30	1.0	10	--	--	--	--	--	--
<i>Salix barclayi</i>		26.5	80	2.5	10	1.5	30	14.0	60	1.0	10	--	--	--	--	--	--
<i>Salix glauca</i>		--	--	--	--	--	--	2.5	10	--	--	--	--	--	--	--	--
<i>Salix planifolia</i> ssp. <i>pulehra</i>		2.5	20	6.0	20	--	--	--	--	4.5	20	--	--	3.5	20	--	--
<i>Salix reticulata</i>		--	--	--	--	0.5	30	7.1	70	2.5	20	--	--	--	--	T	20
<i>Alnus crispa</i>		22.5	50	21.0	40	9.5	40	--	--	36.5	100	--	--	--	--	--	--
<i>Betula nana</i>		--	--	3.0	50	0.5	10	2.0	50	--	--	19.5	90	32.0	100	38.5	100
<i>Vaccinium uliginosum</i>		--	--	3.0	20	T	10	--	--	4.0	70	31.9	100	22.0	90	6.0	60
<i>Vaccinium vitis-idaea</i>		--	--	0.5	20	--	--	1.0	40	3.5	80	--	--	9.0	80	7.0	90
<i>Cassiope tetragona</i>		--	--	--	--	--	--	9.5	80	12.0	90	--	--	--	--	3.0	60
<i>Empetrum nigrum</i>		--	--	1.0	10	--	--	6.5	60	1.5	20	22.5	100	11.5	90	12.5	100
Mosses		0.5	10	5.5	50	32.5	90	12.8	100	39.0	100	13.8	40	13.5	90	19.5	100
Lichens		--	--	--	--	--	--	--	--	--	--	2.8	50	12.0	70	--	--
<i>Carex microchaeta</i>		--	--	--	--	--	--	--	--	--	--	--	--	--	--	6.5	90
<i>Carex podocarpa</i>		1.5	20	1.5	60	7.0	90	--	--	2.0	80	--	--	--	--	--	--
<i>Calamagrostis canadensis</i>		35.0	100	26.5	90	--	--	T	10	--	--	--	--	--	--	--	--
<i>Elymus innovatus</i>		--	--	--	--	--	--	--	--	--	--	--	--	--	--	T	10
<i>Festuca altaica</i>		6.0	50	--	--	3.0	40	3.0	30	T	20	2.5	20	9.5	60	15.5	100
<i>Poa alpina</i>		--	--	--	--	--	--	--	--	--	--	--	--	--	--	T	10
<i>Dryas octopetala</i>		--	--	--	--	--	--	6.5	40	1.0	30	0.5	10	0.5	10	7.5	40
<i>Arctostaphylos alpina</i>		--	--	--	--	--	--	--	--	0.5	10	16.9	100	--	--	--	--
<i>Ledum palustre</i> ssp. <i>decumbens</i>		--	--	--	--	--	--	--	--	1.0	10	0.5	60	--	--	2.5	60
<i>Ledum palustre</i> ssp. <i>groenlandicum</i>		--	--	6.0	60	--	--	0.1	20	--	--	--	--	5.0	80	--	--
<i>Spiraea beauverdana</i>		0.1	10	11.5	30	--	--	--	--	--	--	--	--	--	--	--	--
<i>Poa lanata</i>		--	--	--	--	1.0	20	--	--	--	--	--	--	--	--	--	--
<i>Equisetum scirpoides</i>		--	--	--	--	T	50	T	60	--	--	--	--	--	--	--	--
<i>Anemone parviflora</i>		--	--	--	--	1.8	80	T	10	--	--	--	--	--	--	0.1	10
<i>Anemone richardsonii</i>		--	--	--	--	T	10	--	--	--	--	--	--	--	--	--	--
<i>Hierochloa alpina</i>		--	--	--	--	--	--	--	--	T	30	--	--	--	--	--	--
<i>Boykinia richardsonii</i>		--	--	--	--	18.0	70	29.0	60	8.5	50	--	--	--	--	--	--
<i>Lycopodium annotinum</i>		--	--	4.0	80	--	--	--	--	0.5	10	--	--	1.0	60	1.0	30
<i>Mertensia paniculata</i>		21.0	100	10.5	70	5.5	90	1.5	30	--	--	--	--	0.5	20	--	--
<i>Oxyria digyna</i>		--	--	--	--	4.1	100	--	--	T	10	--	--	--	--	0.1	10

Table 7. (continued)

Species	Site	Willow-alder										Low shrub					
		4		20		6		19		h		5		18		e	
		C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
<i>Pyrola grandiflora</i>		--	--	--	--	--	--	--	--	T	30	0.1	10	T	20	0.2	10
<i>Artemisia arctica</i>		--	--	--	--	1.0	20	0.5	20	--	--	--	--	--	--	T	10
<i>Linnaea borealis</i>		--	--	--	--	--	--	--	--	0.5	30	--	--	3.0	60	--	--
<i>Lupinus arcticus</i>		--	--	--	--	--	--	13.0	50	--	--	--	--	1.0	20	--	--
<i>Polemonium acutiflorum</i>		--	--	--	--	0.7	50	1.0	20	0.2	30	--	--	--	--	--	--
<i>Epilobium angustifolium</i>		6.2	80	3.0	60	--	--	--	--	--	--	--	--	1.0	20	--	--
<i>Potentilla fruticosa</i>		--	--	--	--	--	--	--	--	--	--	--	--	0.5	10	--	--
<i>Saxifraga bronchialis</i>		--	--	--	--	--	--	--	--	0.8	10	--	--	--	--	--	--
<i>Stellaria monantha</i>		0.1	10	T	40	--	--	T	60	--	--	--	--	--	--	--	--
<i>Aconitum delphinifolium</i>		--	--	T	30	1.1	70	--	--	--	--	--	--	--	--	--	--
<i>Delphinium glaucum</i>		6.1	80	0.5	10	0.5	10	--	--	--	--	--	--	--	--	--	--
<i>Cornus canadensis</i>		--	--	2.0	30	--	--	--	--	--	--	--	--	--	--	--	--
<i>Rosa acicularis</i>		--	--	2.0	20	--	--	--	--	--	--	--	--	--	--	--	--
<i>Dodecatheon frigidum</i>		--	--	--	--	0.2	20	--	--	--	--	--	--	--	--	--	--
<i>Petasites frigidus</i>		--	--	--	--	0.5	10	--	--	--	--	--	--	--	--	--	--
<i>Corydalis pauciflora</i>		--	--	--	--	T	40	--	--	--	--	--	--	--	--	--	--
Rock		4.5	40	--	--	8.5	20	4.0	10	3.0	20	--	--	--	--	0.5	10

Table 3. Species coverage (C) and frequency of occurrence (F) values in percent for the *Festuca-Dryas*, grass-sedge, cliff, and wet low-*Salix* nutrient and feeding sites in the Sheep Creek study area, 1977 and 1978. (T=trace)

Species	Site	<i>Festuca-Dryas</i>						Grass-sedge		Cliff		Wet low- <i>Salix</i>	
		3		17		f		l		a		g	
		C	F	C	F	C	F	C	F	C	F	C	F
<i>Festuca altaica</i>		35.0	100	33.5	100	19.0	100	17.5	100	0.5	10	2.0	20
<i>Dryas octopetala</i>		32.0	100	39.5	100	24.0	90	1.0	20	--	--	--	--
<i>Potentilla fruticosa</i>		--	--	3.0	60	2.0	10	--	--	2.8	50	--	--
<i>Salix alaxensis</i>		--	--	--	--	22.0	80	--	--	1.5	10	--	--
<i>Salix reticulata</i>		--	--	--	--	3.5	50	--	--	--	--	4.0	80
<i>Salix arctica</i>		1.0	30	--	--	--	--	--	--	--	--	--	--
<i>Salix polaris</i> ssp. <i>pseudopolaris</i>		--	--	--	--	0.5	10	--	--	--	--	21.5	100
<i>Betula nana</i>		--	--	--	--	T	10	--	--	--	--	--	--
<i>Vaccinium uliginosum</i>		--	--	T	30	4.0	30	--	--	--	--	--	--
<i>Vaccinium vitis-idaea</i>		--	--	--	--	0.5	30	--	--	--	--	--	--
<i>Alnus crispa</i>		--	--	4.0	40	--	--	--	--	5.5	20	--	--
Mosses		13.5	80	--	--	15.5	100	--	--	0.5	10	33.1	100
Lichens		2.3	60	--	--	--	--	--	--	0.1	10	--	--
<i>Empetrum nigrum</i>		--	--	0.5	20	0.5	10	--	--	--	--	--	--
<i>Juniperus communis</i>		--	--	1.0	10	T	10	--	--	3.5	30	--	--
<i>Carex microchaeta</i>		2.5	70	--	--	5.7	80	--	--	--	--	4.0	50
<i>Carex scirpoides</i>		--	--	1.6	70	3.8	60	13.4	100	26.5	80	10.5	80
<i>Arctostaphylos alpina</i>		3.5	30	--	--	--	--	--	--	--	--	--	--
<i>Podocatheon frigidum</i>		--	--	--	--	2.0	50	--	--	--	--	0.1	20
<i>Anemone parviflora</i>		1.5	50	4.0	60	4.0	80	--	--	--	--	2.8	100
<i>Artemisia arctica</i>		T	30	--	--	0.7	70	--	--	--	--	0.6	70
<i>Astragalus umbellatus</i>		--	--	--	--	0.6	30	--	--	--	--	T	10
<i>Aconitum delphinifolium</i>		T	30	--	--	0.5	60	--	--	--	--	0.1	50
<i>Linnaea borealis</i>		--	--	--	--	2.5	10	--	--	--	--	--	--
<i>Pyrola grandiflora</i>		--	--	--	--	2.0	40	--	--	--	--	--	--
<i>Elymus imrovatus</i>		--	--	--	--	0.5	10	19.7	90	11.2	80	9.3	60
<i>Poa alpina</i>		--	--	--	--	1.0	20	--	--	--	--	2.5	40
<i>Oxyria digyna</i>		--	--	--	--	T	10	--	--	--	--	1.1	60
<i>Artemisia tilevii</i>		--	--	--	--	1.0	20	--	--	--	--	--	--
<i>Pedicularis capitata</i>		T	10	--	--	T	20	--	--	--	--	T	40
<i>Lechen palustre</i> ssp. <i>groenlandicum</i>		--	--	4.0	50	--	--	--	--	--	--	--	--
<i>Zygadenus elegans</i>		--	--	0.5	70	--	--	2.5	100	0.1	10	--	--
<i>Hartemita paniculata</i>		--	--	4.1	60	--	--	--	--	--	--	--	--
<i>Polemonium acutiflorum</i>		--	--	0.5	30	--	--	--	--	--	--	--	--
<i>Asler nibiricus</i>		--	--	T	20	--	--	--	--	--	--	--	--

Table 8. (continued)

Species	<i>Festuca-Dryas</i>						<i>Grass-sedge</i>		<i>Cliff</i>		<i>Wet low-Salix</i>	
	3		17		f		l		a		g	
	C	F	C	F	C	F	C	F	C	F	C	F
<i>Oxytropis nigrescens</i>	--	--	T	10	--	--	--	--	--	--	--	--
<i>Lupinus arcticus</i>	4.0	80	--	--	--	--	--	--	--	--	--	--
<i>Epilobium latifolium</i>	1.0	20	--	--	--	--	--	--	--	--	--	--
<i>Mimuartia arctica</i>	--	--	--	--	--	--	0.6	50	3.8	60	--	--
<i>Hierochloa alpina</i>	T	30	--	--	--	--	--	--	--	--	--	--
<i>Arnica alpina</i>	1.0	40	--	--	--	--	0.3	20	0.3	20	--	--
<i>Senecio lugens</i>	0.5	30	--	--	--	--	--	--	--	--	--	--
<i>Saxifraga tricuspidata</i>	T	20	--	--	--	--	--	--	1.0	30	--	--
<i>Calamagrostis purpurascens</i>	--	--	--	--	--	--	3.3	40	5.5	50	--	--
<i>Poa lanata</i>	--	--	--	--	--	--	2.0	20	--	--	--	--
<i>Carex glaciale</i>	--	--	--	--	--	--	0.7	30	--	--	--	--
<i>Populus tremuloides</i>	--	--	--	--	--	--	0.5	20	--	--	--	--
<i>Androsace chamaejasme</i>	--	--	--	--	--	--	1.3	80	0.7	40	--	--
<i>Potentilla hookeriana</i>	--	--	--	--	--	--	0.6	60	T	20	--	--
<i>Pulsatilla patens</i>	--	--	--	--	--	--	0.7	40	--	--	--	--
<i>Saxifraga reflexa</i>	--	--	--	--	--	--	0.1	20	T	10	--	--
<i>Oxytropis boreale</i>	--	--	--	--	--	--	2.9	40	--	--	--	--
<i>Artemisia alaskana</i>	--	--	--	--	--	--	2.1	20	6.8	50	--	--
<i>Artemisia boreale</i>	--	--	--	--	--	--	1.5	20	--	--	--	--
<i>Eritrichium splendens</i>	--	--	--	--	--	--	0.8	30	2.7	50	--	--
<i>Hedysarum alpinum</i>	--	--	--	--	--	--	0.8	20	0.1	20	--	--
<i>Arctostaphylos uva-ursi</i>	--	--	--	--	--	--	10.5	50	--	--	--	--
<i>Senecio contemminus</i>	--	--	--	--	--	--	0.3	10	--	--	--	--
<i>Draba nivalis</i>	--	--	--	--	--	--	--	--	0.6	50	--	--
<i>Solidago multiradiata</i>	--	--	--	--	--	--	--	--	0.2	20	--	--
<i>Lloydia serotina</i>	--	--	--	--	--	--	--	--	--	--	T	20
<i>Epilobium variegatum</i>	--	--	--	--	--	--	--	--	--	--	T	60
<i>Anemone richardsonii</i>	--	--	--	--	--	--	--	--	--	--	T	20
<i>Boykinia richardsonii</i>	--	--	--	--	--	--	--	--	--	--	T	10
<i>Ranunculus nivalis</i>	--	--	--	--	--	--	--	--	--	--	0.7	50
<i>Valeriana capitata</i>	--	--	--	--	--	--	--	--	--	--	0.5	40
Rock	2.0	10	5.8	70	4.0	40	16.9	80	26.7	90	6.5	60

Table 9. Matrix of similarity for the vegetation of nutrient and feeding sites from the Sheep Creek study area.

	<i>Dryas</i>								<i>Dryas-moss -Cassiope</i>				<i>Willow-alder</i>				<i>Low shrub</i>		<i>Festuca- Dryas</i>		<i>Grass- sedge</i>		<i>Cliff</i>	<i>Wet low- Salix</i>	<i>Large -rock scree</i>					<i>Small -rock scree</i>				
Site	2	16	8	13	21	22	b	c	7	d	i	j	4	20	6	19	h	5	18	e	3	17	f	1	a	g	10	11	14	15	23	9	12	
2																																		
16	72																																	
8	38	43																																
13	33	37	70																															
21	59	61	35	34																														
22	69	61	33	26	42																													
b	29	50	29	23	32	75																												
c	64	54	35	27	38	60	53																											
7	52	56	36	33	56	41	33	47																										
d	45	50	36	34	53	37	33	43	79																									
i	49	54	38	31	55	42	34	52	86	74																								
j	45	43	37	40	50	30	27	56	64	63	70																							
4	1	1	0	7	1	0	0	1	1	3	0	5																						
20	6	4	1	6	7	0	1	6	6	6	8	10	56																					
6	7	4	5	13	16	0	0	2	32	24	30	19	18	27																				
19	14	13	17	23	24	7	7	23	32	36	31	36	16	14	38																			
h	9	6	7	9	17	1	1	19	43	38	47	40	23	33	48	33																		
5	13	4	1	6	3	4	1	29	19	20	23	27	3	11	15	22	18																	
18	13	10	2	7	28	6	1	28	18	19	24	36	8	20	15	23	22	62																
e	19	17	13	21	29	9	8	33	34	30	38	50	5	12	20	30	28	48	66															
3	56	52	32	31	51	43	39	44	49	46	46	49	6	5	17	25	19	21	24	36														
17	40	41	30	30	27	48	48	44	30	29	28	30	13	12	14	12	5	3	14	22	69													
f	38	39	39	39	44	27	26	32	44	45	47	56	5	13	39	27	22	19	26	42	57	48												
1	2	3	1	5	2	1	5	1	3	4	1	8	6	0	4	4	1	15	10	16	21	23	23											
a	2	2	1	1	1	1	5	1	3	1	1	2	6	8	9	3	7	1	2	1	1	12	9	42										
g	12	9	17	27	23	2	1	3	36	26	39	33	2	5	37	18	36	16	14	24	41	7	28	25	25									
10	21	28	9	9	18	13	5	11	11	9	10	9	1	2	2	5	3	4	4	7	11	4	24	4	3	2								
11	16	20	9	8	19	9	3	12	13	11	11	10	1	2	2	5	5	5	5	5	9	2	5	3	2	4	59							
14	31	40	24	23	34	29	23	35	37	37	31	31	3	0	3	21	10	7	6	18	24	22	19	7	2	5	24	27						
15	27	32	13	15	23	16	6	13	19	15	15	15	3	1	4	9	4	8	7	12	19	9	13	8	3	6	54	34	39					
23	9	8	5	4	5	22	6	5	7	5	7	3	0	0	0	0	0	2	2	2	4	0	2	1	1	2	30	23	12	24				
9	3	2	2	2	1	1	1	1	1	0	1	1	0	0	1	1	0	0	0	1	1	0	1	1	0	12	9	20	4	5	9			
12	2	1	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	5	0	4	5	9	39		

relationships between sites. Two sites with least similarity (sites 12 and g, with zero similarity) were chosen as reference sites and placed as endpoints on the x-axis. The remaining sites were then positioned relative to the reference sites by rotating two arcs representing the distance (inverse of similarity or $100-C$) of the projected sites from each of the reference stands. From the arcs' intersection, a line was drawn perpendicular to the x-axis, marking the site's position relative to the reference sites. To further separate sites, sites were positioned relative to a second pair of reference sites. The second pair of reference sites, sites 4 and 22, which were close to each other on the x-axis yet had zero similarity, were chosen as the endpoints for the y-axis. Sites were then positioned as described above, only this time the line was drawn perpendicular to the y-axis. Final ordination of the sites is presented in Figure 3.

The final ordination of sites in Figure 3 is based on the similarity of each site relative to the reference sites and not on environmental factors. However, the reference sites for the x-axis, 12, a small-rock scree site, and g, the wet low-*Salix* site, were chosen from several sites with zero similarity on the basis of the amount of soil moisture present at these sites. These sites represent the endpoints of a moisture gradient among the sites. The amount of soil moisture increases as the distance of a site from the y-axis increases.

The separation of sites along the y-axis appears to be linked

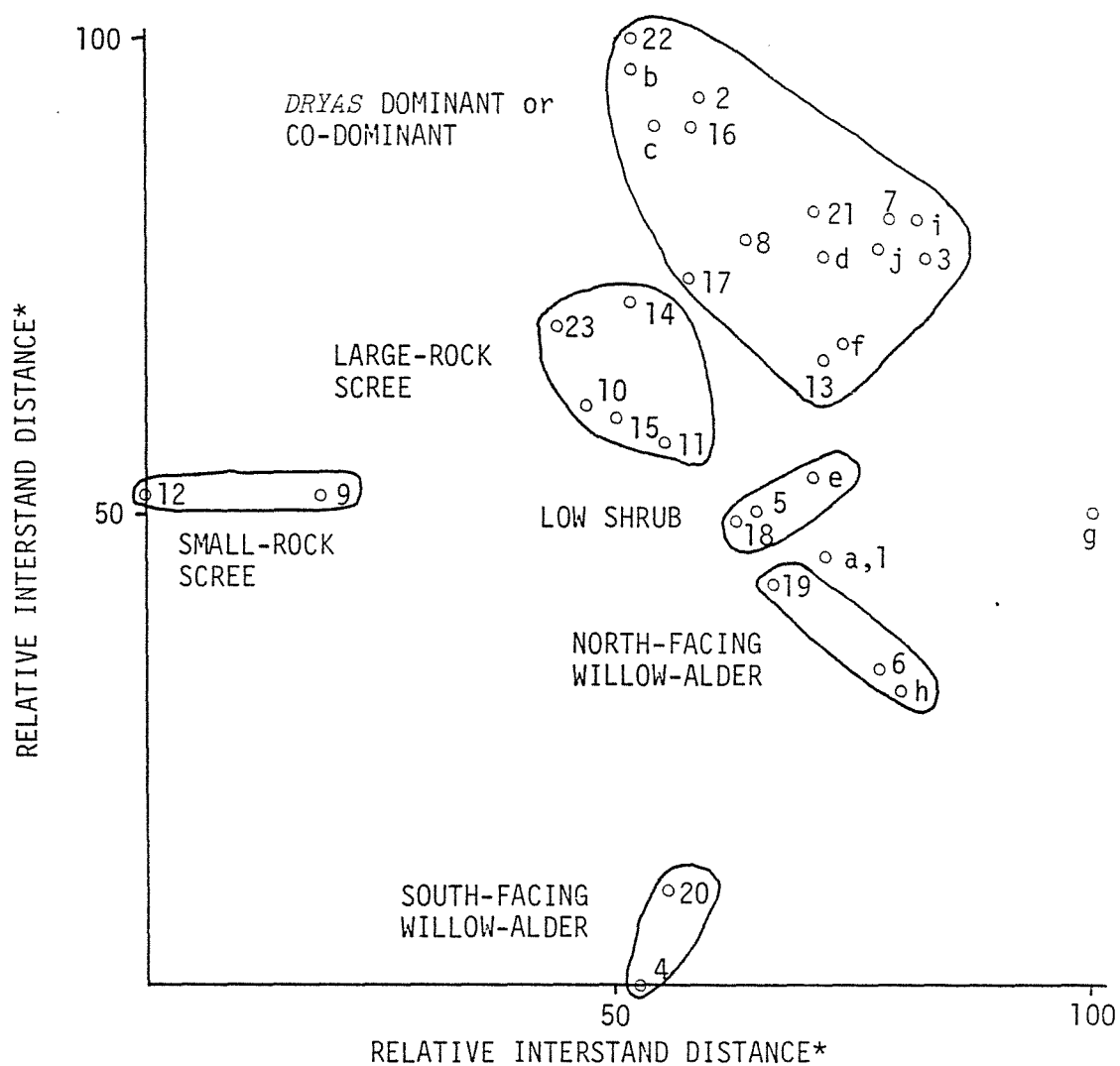


Figure 3. Ordination of nutrient and feeding sites from the Sheep Creek study area.

*inverse of similarity (see text for explanation)

to the amount of *Dryas octopetala* present in a particular site. The amount of *Dryas* present in a site increases as the distance of the site from the x-axis increases; coverage values range from 0 (site 4, a south-facing willow-alder site) at the x-axis to 51.0 percent (site 22, a *Dryas* site) at the point of maximum separation. This pattern is not uniform, however, as several sites have lower *Dryas* coverage values and are positioned farther from the x-axis than are sites possessing greater *Dryas* coverage values. Therefore, the amount of *Dryas* present is not solely determining the separation of sites along the y-axis; the amounts of other species present also has an influence on the separation of the sites.

Sites of a particular vegetation type were generally located close to each other in this scheme of ordination. Substantial dispersion occurred among the large-rock scree sites and among sites where *Dryas octopetala* was the dominant or a co-dominant species. The dispersion of these sites was the result of the variability among sites that were placed into specific vegetation types. Such variability reflects differences in physiographic and biologic properties of the sites, notwithstanding the variability of the ecological requirements of individual species.

Comparable sites in both the Tanana and Robertson drainages showed no major differences in terms of species composition or species coverage. The differences in vegetation that were present probably resulted from slight variations in readily observable

environmental factors (e.g., aspect, slope, or elevation) or slight variations of parameters not measured such as soil moisture, temperature, pH, or soil chemical composition.

Phenology of Plant Growth

The rate of emergence of new growth ranged from slow and subtle to rapid and dramatic. The emergence of leaves on the shrubs of the low shrub and willow-alder areas was rapid and quite dramatic. In 1977, most of the leaves of shrubs emerged between 5 June and 7 June; leaf emergence occurred between 31 May and 2 June in 1978.

The progression of new growth in grasses, sedges, and forbs was less obvious. Growth, particularly in forbs, was often not obvious until the onset of flowering, probably the most easily observed growth stage of forbs. In 1978, dates on which plants were first seen in flower were recorded for each vegetation type (Table 10). Not all vegetation types were traversed daily, particularly those which were seldom used by sheep after early spring (i.e., grass-sedge meadows, *Festuca-Dryas* areas). Consequently, the flowering dates listed may not have been the actual date of first flowering, but the difference between the actual and observed flowering dates was probably less than three or four days, although in the case of *Festuca-Dryas* it may have been as great as three weeks. Lack of flowering dates under certain vegetation type headings indicates either the absence of that plant species from that vegetation type

Table 10. Flowering phenology in selected vegetation types in the Sheep Creek study area, 1978.
(species ordered chronologically by earliest flowering dates [month/day], N = north-facing, S = south-facing)

Species	Vegetation types and dates of first observed flowering												
	Grass-sedge	Dryas	Cliff	Low shrub		Small-rock scree		Dryas-moss -Cassiope	Willow-alder		Festuca-Dryas	Large-rock scree	
				N	S	N	S		N	S		N	S
<i>Pulsatilla patens</i>	5/7												
<i>Carex scirpoidea</i>		5/24	5/8					6/10		6/9	6/24		
<i>Saxifraga oppositifolia</i>	5/9	5/9	5/8				5/9	5/23					5/11
<i>Douglasia gormanii</i>		5/9					5/9						5/11
<i>Arctostaphylos alpina</i>				6/6	5/11			5/24	5/29		5/29	5/29	
<i>Synthlipsis borealis</i>		5/30	6/14	6/6				5/30				6/8	5/11
<i>Anemone parviflora</i>		5/24	5/23			6/8		5/23	6/5	5/12	5/29	5/29	
<i>Androsace chamaejasme</i>	5/25	5/24	5/27			6/8	5/23	6/10					
<i>Oxytropis nigrescens</i>		5/24	5/23			6/8	6/8						6/8
<i>Salix alaxensis</i>			5/5					5/31	5/29		5/7		
<i>Cassiope tetragona</i>		5/24		6/6	5/30			5/31	6/10				6/8
<i>Diapensia lapponica</i>		5/24		6/6	5/31								6/8
<i>Dryas octopetala</i>	5/25	5/24	5/27	6/6	5/30	6/8	5/24	5/31	6/19	5/24			6/8
<i>Geum rossii</i>		5/24						5/31					
<i>Hieracium alpinum</i>	5/25	5/24			5/30			6/13				7/2	6/8
<i>Lloydia serotina</i>		5/24				6/8		6/10				5/29	6/8
<i>Loiseleuria procumbens</i>		5/24		6/6	5/30				6/19				
<i>Salix polaris</i> ssp. <i>pseudopolaris</i>		5/24						6/22					
<i>Saxifraga eschscholtzii</i>		5/24					6/8						6/14
<i>Arctostaphylos uva-ursi</i>	5/25				6/14		5/30						
<i>Draba nivalis</i>	5/25		5/23				5/30					5/29	
<i>Eritrichium splendens</i>	5/25		6/7				5/30						
<i>Mertensia paniculata</i>					5/25				8/2	6/6			6/17
<i>Oxytropis borealis</i>	5/25	6/14	5/27				5/30						
<i>Potentilla hookeriana</i>	5/25	6/8	5/27				6/8					7/2	6/8
<i>Saxifraga reflexa</i>	5/25	7/7				7/7	6/5			6/9			
<i>Potentilla fruticosa</i>	6/6		5/27		6/14					6/19			
<i>Minuartia arctica</i>			7/5	6/24			7/5	6/15	6/19		6/24	5/29	5/29
<i>Salix arctica</i>								6/14		5/29	5/29	7/2	6/14
<i>Salix planifolia</i> ssp. <i>pulehna</i>					5/31			6/12			5/29		
<i>Silene acaulis</i>						6/8				6/6	5/29	5/29	6/8
<i>Vaccinium uliginosum</i>					5/30			6/19	6/23				
<i>Parrya nudicaulis</i>					5/31			6/11	6/15			6/8	

Table 10. (continued)

Species	Vegetation types and dates of first observed flowering												
	Grass- sedge	<i>Dryas</i>	Cliff	Low shrub		Small-rock scree		<i>Dryas</i> -moss - <i>Cassiope</i>	Willow- alder		<i>Festuca</i> - <i>Dryas</i>	Large-rock scree	
				N	S	N	S		N	S		N	S
<i>Arnica alpina</i>		6/14	6/17				6/5			6/19	6/24		6/23
<i>Saxifraga tricuspidata</i>	6/6				6/14		6/5				6/24		6/23
<i>Ledum palustre</i> ssp. <i>decumbens</i>				6/24	6/6			6/19					
<i>Pyrola grandiflora</i>					6/6			6/19			6/24		
<i>Oxyria digyna</i>		6/14				6/8		6/10	6/10			7/7	6/14
<i>Carex podocarpa</i>			6/7					6/12	6/26	6/9	6/24		
<i>Salix bavelayi</i>									6/9	6/9			
<i>Boykinia richardsonii</i>								6/15	6/10				6/23
<i>Dodecatheon frigidum</i>								6/10	6/19				
<i>Salix reticulata</i>								6/11	6/10				
<i>Homnolus nivalis</i>								6/10					
<i>Rhododendron lapponicum</i>								6/11					
<i>Petasites frigidus</i>								6/12	6/15				
<i>Cardamine purpurea</i>						6/23	7/6	6/13	6/19			8/2	6/14
<i>Chrysosplenium wrightii</i>						7/1						6/13	6/14
<i>Pedicularis lanata</i>								6/13					6/14
<i>Castilleja caudata</i>		6/14	7/5				7/5				7/25		
<i>Pedicularis capitata</i>		6/14		6/17			7/1	6/22	6/24		6/24	6/17	
<i>Pedicularis labradorica</i>				6/24	6/14								6/23
<i>Saxifraga flagellaris</i>		7/4										6/14	6/23
<i>Tofieldia coccinea</i>		6/14						6/19			6/24		
<i>Carex microchaeta</i>		7/12						6/15				7/2	7/2
<i>Luzula confusa</i>				6/24				6/15	6/24				7/2
<i>Senecio atropurpureus</i>						6/23	7/1	6/16	6/16				6/20
<i>Stellaria monantha</i>				6/24				6/16	6/16		6/24	6/17	
<i>Spiraea beauverdigiana</i>									6/23				6/17
<i>Aster sibiricus</i>		6/30				6/23	6/18						
<i>Hedysarum alpinum</i>	6/26	6/30	6/25							6/19			
<i>Saxifraga bronchialis</i>								6/19				8/1	6/23
<i>Astragalus umbellatus</i>		6/20											
<i>Polemonium boreale</i>							6/20					8/1	6/20
<i>Claytonia sarmentosa</i>		8/2		6/22			7/6		6/22				8/2
<i>Artemisia arctica</i>	8/2	6/30							6/23		7/8	6/23	
<i>Cerastium beeringianum</i>			6/29				6/23						
<i>Erigeron humilis</i>		6/30				7/8	6/23						

Table 10. (continued)

Species	Vegetation types and dates of first observed flowering												
	Grass-sedge	Dryas	Cliff	Low shrub		Small-rock scree		Dryas-moss -Cassiope	Willow-alder		Festuca-Dryas	Large-rock scree	
				N	S	N	S		N	S		N	S
<i>Ledum palustre</i> ssp. <i>groenlandicum</i>									6/23				6/23
<i>Linnaea borealis</i>									6/23	6/26			
<i>Oxytropis maydelliana</i>		7/4											6/23
<i>Epilobium latifolium</i>			7/5	6/24	6/26	7/16	7/5	7/29			6/24		
<i>Festuca altaica</i>	6/26							7/31			6/24		
<i>Lupinus arcticus</i>		7/10		6/24					6/24		6/24		7/10
<i>Papaver macounii</i>				6/24		7/31			6/24				
<i>Polygonum alaskanum</i>				6/24			6/26		6/24	6/26			
<i>Polygonum bistorta</i>		7/4		6/24				7/16	6/24				
<i>Senecio lugens</i>		6/30		6/24					6/24		6/24		
<i>Solidago multiradiata</i>		6/30	7/24		6/26		7/24			6/26			
<i>Aconitum delphinifolium</i>	6/26	6/30			6/30			7/24	8/2		6/24		
<i>Antennaria pallida</i>	6/26	6/30					6/26			6/26			
<i>Poa alpigena</i>										6/26			
<i>Poa alpina</i>						7/22		7/31		6/26			
<i>Rosa acicularis</i>	6/26				6/26					6/26			
<i>Zygadenus elegans</i>	6/26	6/30	7/24		6/26		7/24			6/26			
<i>Papaver alboroseum</i>						7/1	7/7						7/28
<i>Pedicularis langsdorffii</i>							7/1						7/1
<i>Polygonum viviparum</i>												7/2	7/2
<i>Artemisia capillaris</i>		7/4	7/5				7/5						
<i>Calamagrostis purpurascens</i>	7/4		7/5				7/5	7/31					
<i>Campanula lasiocarpa</i>		7/4	7/5			7/16	7/5				7/25	7/16	
<i>Delphinium brachycentrum</i>									8/2	7/4			
<i>Elymus innovatus</i>	7/4							7/29					
<i>Crepis nana</i>			7/5				7/5						
<i>Poa lanata</i>									7/13	7/23			
<i>Artemisia alaskana</i>			7/24				7/24						
<i>Poa arctica</i>							8/3						7/30
<i>Calamagrostis canadensis</i>	8/2									8/1			

or, if the species was present, failure to observe or record flowering.

Although flowering phenology did not proceed in an orderly fashion from one vegetation type to the next, a trend is apparent in Table 10. Although early flowering plants, plants flowering before 1 June, were found in most vegetation types, most of these species were found in the grass-sedge and south-facing *Dryas* vegetation types. Large-rock scree appeared to have the latest flowering flora, although several other vegetation types such as *Festuca-Dryas*, willow-alder, *Dryas-moss-Cassiope*, and small-rock scree had a nearly equal number of late flowering plants.

Considerable variation of physical parameters among and within the vegetation types contributed to the variation in flowering dates. Plant species on dry, exposed, south-facing slopes of a particular vegetation type generally flowered one to two weeks earlier than their north-facing counterparts. Protected sites, with abundant water from persistent snowbeds or seeps, flowered much later in summer. These moist sites, particularly on north-facing slopes, had plants flowering in late July and as late as mid-August. Flowering dates were generally delayed with increasing altitude. Certain species on dry, exposed sites at high elevations flowered simultaneously with those same species at lower elevations. For example, *Saxifraga oppositifolia* was flowering on an east-facing cliff site at 850 m on one day and on south-facing small-rock scree sites at

1225 m one day later. This was much earlier than would be expected using the delay of 3 to 4 days for each 100 m of altitudinal increase suggested by Hopkins (1920) or the delay of 3 to 5 days suggested by Costello and Price (1939).

In 1978, new plant growth was evident as early as 6 May on the low cliffs and grass-sedge meadow of Sheep Creek, areas having elevations of approximately 850 m and which became snow-free very early. Grasses such as *Elymus innovatus*, *Calamagrostis purpurascens*, and *Festuca altaica* had approximately 50 mm of new growth by that date. New basal leaves were present on many forbs and plants of species such as *Pulsatilla patens*, *Saxifraga oppositifolia*, *Salix alaxensis*, and *Carex scirpoidea* were beginning to flower. By mid-May, growth was well underway in most vegetation types, particularly on south-facing slopes. *Dryas octopetala* was producing new leaves by 6 May and began flowering approximately two weeks later. Leaves of *Betula glandulosa*, *Vaccinium uliginosum*, *Alnus crispa*, and *Salix* spp. were emerging on a few plants within the low shrub and willow-alder areas on 24 May, with most shrub leaves emerging between 31 May and 2 June.

June was the month of abundant plant growth and flowering, even at higher elevations and on north-facing slopes. Numerous plants were flowering on large-rock scree slopes at elevations up to 1700 m. June was also a month in which some species began maturing and producing seed. Most *Dryas* plants on south-facing *Dryas* slopes between 1200 and 1400 m had completed flowering and were beginning to release

seed by the end of June. Plants of other species were still flowering, although they were few in number. On north-facing *Dryas*-moss-*Cassiope* slopes between 1100 and 1300 m, approximately 50 percent of the *Dryas* plants were still flowering at the end of June; the rest were starting to set seed, although they had not developed the long styles characteristic of mature seeds.

July brought continued maturation and senescence of vegetation. The willows were shedding seed by mid-July, with many other species also producing mature seed. Plants continued to flower from mid to late July on scree, *Dryas*, and cliff sites above 1700 m, and on those sites below persistent snow patches, on north-facing slopes, or along small streamlets or seeps.

Few new flowers were produced during August. At lower elevations in low shrub and willow-alder areas, a few late flowering species such as *Delphinium brachycentrum*, *Angelica lucida*, and *Aconitum delphinifolium* were flowering in early August. Some of the grasses were also flowering in these vegetation types at this time. Species on the *Dryas* and scree slopes up to 1800 m also had virtually ceased flowering except for occasional plants of such species as *Campanula lasiocarpa*, *Papaver alboroseum*, *Claytonia sarmentosa*, and *Erigeron humilus*, primarily on north-facing or moist sites above 1700 m. By 18 August, the only forb still flowering was *Papaver alboroseum*, again on a north-facing large-rock scree slope at 1900 m. Many of the forbs by this date were turning yellow and withering. Berries

were not ripe and many shrubs had yellowing or falling leaves, indicating the end of another growing season for many species.

Nutrient Composition of Forage Plants

Forage plants were collected from the nutrient sites during 1977 and 1978. Only above ground portions of plants were collected, and in the case of shrubs, only leaves and catkins were collected. All species in all plant samples were analyzed for nitrogen, magnesium, calcium, and phosphorus content. Due to the high cost of analysis, only selected plant species were analyzed for total nonstructural carbohydrates. The results of these analyses are presented in Table 11. Crude protein (percent nitrogen x 6.25) values are included in Table 11, since ruminants can normally use virtually all forage nitrogen for protein synthesis. Fiber analyses were conducted on samples of *Carex microchaeta*, *C. scirpoidea*, *Dryas octopetala*, and *Salix planifolia* ssp. *pulchra*. The results of these analyses are presented in Table 12.

The trends in nutrient changes during the growing season generally agreed with the results reported by other researchers (McLean and Tisdale 1960; Johnston and Bezeau 1962; Johnston et al. 1968; Whitten 1975). It can be seen from Figures 4 and 5 that plant nitrogen and phosphorus reached their highest levels during early plant growth stages and then declined as the plants matured. Willows, alder, and the legume *Astragalus uribellatus* contained the highest

Table 11. Nutrient composition of selected plants from the Sheep Creek study area, 1977 and 1978.
(mean values \pm standard deviation in percent of total weight on a dry matter basis,
except total nonstructural carbohydrate values which are means only; n = 2 for all
nutrient values)

Site description and species analyzed	Date	Nitrogen	Protein (Nx6.25)	TNC ¹	Magnesium	Calcium	Phosphorus
1. South-facing grass-sedge meadow. 850 m.							
<i>Dryas octopetala</i>	25 May 1977	2.76 \pm 0.01	17.22 \pm 0.04	--	0.26 \pm 0.00	0.92 \pm 0.01	0.28 \pm 0.01
	23 Jun 1977	1.85 \pm 0.11	11.56 \pm 0.71	--	0.26 \pm 0.02	0.82 \pm 0.04	0.22 \pm 0.00
	21 Jul 1977	1.75 \pm 0.02	10.91 \pm 0.13	--	0.30 \pm 0.01	1.09 \pm 0.02	0.19 \pm 0.01
	15 Aug 1977	1.63 \pm 0.02	10.16 \pm 0.13	--	0.32 \pm 0.04	1.31 \pm 0.04	0.20 \pm 0.01
	14 Oct 1977	0.83 \pm 0.01	5.19 \pm 0.09	--	0.34 \pm 0.01	1.81 \pm 0.04	0.08 \pm 0.00
	4 Mar 1978	0.93 \pm 0.02	5.78 \pm 0.13	--	0.28 \pm 0.01	1.64 \pm 0.04	0.06 \pm 0.00
	25 May 1978	2.87 \pm 0.01	17.94 \pm 0.09	--	0.21 \pm 0.01	0.88 \pm 0.03	0.30 \pm 0.00
<i>Carex scirpoides</i>	25 May 1977	2.57 \pm 0.01	16.03 \pm 0.03	9.0	0.18 \pm 0.01	0.39 \pm 0.04	0.25 \pm 0.00
	23 Jun 1977	1.70 \pm 0.03	10.63 \pm 0.18	10.6	0.13 \pm 0.01	0.44 \pm 0.00	0.16 \pm 0.00
	21 Jul 1977	1.41 \pm 0.01	8.81 \pm 0.09	11.0	0.14 \pm 0.00	0.53 \pm 0.01	0.13 \pm 0.01
	15 Aug 1977	1.19 \pm 0.01	7.41 \pm 0.04	11.3	0.14 \pm 0.01	0.84 \pm 0.01	0.10 \pm 0.00
	14 Oct 1977	0.48 \pm 0.01	3.00 \pm 0.09	1.5	0.13 \pm 0.00	0.82 \pm 0.01	0.03 \pm 0.01
	4 Mar 1978	0.46 \pm 0.02	2.84 \pm 0.13	0.1	0.22 \pm 0.01	1.05 \pm 0.02	0.03 \pm 0.01
	25 May 1978	2.16 \pm 0.11	13.47 \pm 0.66	--	0.15 \pm 0.01	0.37 \pm 0.02	0.20 \pm 0.00
<i>Elymus innovatus</i>	25 May 1977	3.12 \pm 0.07	19.50 \pm 0.44	9.7	0.12 \pm 0.00	0.25 \pm 0.01	0.27 \pm 0.00
	23 Jun 1977	2.36 \pm 0.01	14.72 \pm 0.04	10.1	0.13 \pm 0.01	0.42 \pm 0.00	0.18 \pm 0.00
	21 Jul 1977	2.04 \pm 0.08	12.75 \pm 1.15	7.8	0.12 \pm 0.01	0.47 \pm 0.01	0.17 \pm 0.00
	15 Aug 1977	2.18 \pm 0.01	13.59 \pm 0.04	6.5	0.13 \pm 0.01	0.59 \pm 0.01	0.14 \pm 0.00
	14 Oct 1977	0.56 \pm 0.01	3.47 \pm 0.04	3.3	0.14 \pm 0.01	0.65 \pm 0.01	0.04 \pm 0.00
	4 Mar 1978	0.58 \pm 0.01	3.59 \pm 0.04	1.6	0.11 \pm 0.00	0.76 \pm 0.00	0.05 \pm 0.00
	25 May 1978	3.02 \pm 0.08	18.84 \pm 0.49	--	0.09 \pm 0.01	0.40 \pm 0.00	0.21 \pm 0.00
2. Southwest-facing <i>Dryas</i> mat. 1275 m.							
<i>Dryas octopetala</i>	8 Jun 1977	2.80 \pm 0.01	17.47 \pm 0.04	8.3	0.21 \pm 0.01	0.98 \pm 0.01	0.28 \pm 0.00
	12 Jul 1977	2.06 \pm 0.01	12.34 \pm 0.04	8.2	0.18 \pm 0.00	1.11 \pm 0.02	0.21 \pm 0.00
	19 Aug 1977	1.97 \pm 0.01	12.28 \pm 0.04	9.6	0.15 \pm 0.00	1.43 \pm 0.01	0.22 \pm 0.01

¹TNC = total nonstructural carbohydrate

Table 11. (continued)

Site description and species analyzed	Date	Nitrogen	Protein (Nx6.25)	TNC	Magnesium	Calcium	Phosphorus
2. Southwest-facing <i>Dryas</i> mat. 1275 m.							
<i>Carex microchaeta</i>	8 Jun 1977	3.57 ± 0.00	22.31 ± 0.00	--	0.18 ± 0.00	0.30 ± 0.03	0.38 ± 0.00
	12 Jul 1977	2.55 ± 0.01	15.91 ± 0.04	--	0.16 ± 0.00	0.54 ± 0.01	0.23 ± 0.00
	19 Aug 1977	1.80 ± 0.04	11.22 ± 0.22	--	0.21 ± 0.00	0.98 ± 0.04	0.13 ± 0.00
3. Southwest-facing <i>Festuca-Dryas</i> meadow. 1100 m.							
<i>Festuca altaica</i>	10 Jun 1977	2.33 ± 0.21	14.53 ± 1.28	11.7	0.10 ± 0.00	0.32 ± 0.01	0.24 ± 0.00
	12 Jul 1977	1.65 ± 0.12	10.28 ± 0.75	14.2	0.08 ± 0.00	0.30 ± 0.01	0.17 ± 0.01
	19 Aug 1977	1.12 ± 0.01	7.00 ± 0.09	10.0	0.07 ± 0.00	0.38 ± 0.01	0.10 ± 0.01
	15 Oct 1977	0.31 ± 0.01	1.94 ± 0.09	4.3	0.07 ± 0.01	0.44 ± 0.01	0.03 ± 0.00
4. South-facing willow-alder area. 1075 m.							
<i>Alnus crispa</i>	13 Jun 1977	4.76 ± 0.05	29.72 ± 0.31	--	0.24 ± 0.00	0.56 ± 0.01	0.54 ± 0.00
	13 Jul 1977	3.30 ± 0.01	20.63 ± 0.09	--	0.25 ± 0.07	0.80 ± 0.02	0.24 ± 0.00
	20 Aug 1977	3.35 ± 0.01	20.91 ± 0.04	--	0.27 ± 0.01	1.02 ± 0.02	0.21 ± 0.00
<i>Mertensia paniculata</i>	13 Jun 1977	4.80 ± 0.05	29.97 ± 0.31	--	0.26 ± 0.01	0.81 ± 0.03	0.50 ± 0.00
	13 Jul 1977	3.15 ± 0.04	19.66 ± 0.22	--	0.20 ± 0.01	1.53 ± 0.02	0.25 ± 0.00
	20 Aug 1977	2.12 ± 0.06	13.22 ± 0.40	--	0.22 ± 0.00	2.35 ± 0.03	0.20 ± 0.00
<i>Salix alaxensis</i>	13 Jul 1977	4.25 ± 0.01	26.53 ± 0.04	--	0.28 ± 0.01	1.44 ± 0.01	0.28 ± 0.00
	20 Aug 1977	3.32 ± 0.08	20.75 ± 0.53	--	0.26 ± 0.01	1.68 ± 0.06	0.18 ± 0.00
<i>Salix barclayi</i>	13 Jun 1977	5.39 ± 0.01	33.66 ± 0.04	10.3	0.38 ± 0.01	0.97 ± 0.03	0.75 ± 0.02
	13 Jul 1977	3.76 ± 0.00	23.50 ± 0.00	11.9	0.31 ± 0.00	1.40 ± 0.00	0.26 ± 0.00
	20 Aug 1977	3.48 ± 0.39	21.72 ± 2.43	12.0	0.31 ± 0.00	1.35 ± 0.07	0.17 ± 0.01
<i>Salix planifolia</i> ssp. <i>pulehra</i>	13 Jun 1977	4.90 ± 0.04	30.59 ± 0.22	3.7	0.25 ± 0.01	0.44 ± 0.01	0.57 ± 0.01
	13 Jul 1977	2.73 ± 0.01	17.06 ± 0.09	4.7	0.17 ± 0.00	0.66 ± 0.00	0.28 ± 0.01
	20 Aug 1977	2.89 ± 0.06	18.06 ± 0.35	4.8	0.20 ± 0.00	0.97 ± 0.02	0.21 ± 0.01

Table 11. (continued)

Site description and species analyzed	Date	Nitrogen	Protein (Nx6.25)	TNC	Magnesium	Calcium	Phosphorus
5. South-facing low shrub area. 1125 m.							
<i>Betula glandulosa</i>	14 Jun 1977	3.73 ± 0.06	23.31 ± 0.35	--	0.24 ± 0.01	0.39 ± 0.01	0.44 ± 0.00
	13 Jul 1977	2.71 ± 0.01	16.91 ± 0.04	--	0.22 ± 0.00	0.41 ± 0.01	0.24 ± 0.00
	20 Aug 1977	2.07 ± 0.04	12.94 ± 0.27	--	0.30 ± 0.00	0.54 ± 0.01	0.25 ± 0.00
<i>Vaccinium uliginosum</i>	14 Jun 1977	2.87 ± 0.01	17.91 ± 0.04	5.6	0.16 ± 0.01	0.30 ± 0.01	0.30 ± 0.00
	13 Jul 1977	1.94 ± 0.06	12.09 ± 0.40	5.8	0.16 ± 0.01	0.39 ± 0.01	0.18 ± 0.00
	20 Aug 1977	1.85 ± 0.00	11.56 ± 0.00	7.6	0.19 ± 0.01	0.59 ± 0.01	0.13 ± 0.00
6. North-facing willow thicket. 1100 m.							
<i>Boehmeria richardsonii</i>	26 Jun 1977	3.68 ± 0.03	23.00 ± 0.18	--	0.22 ± 0.00	1.15 ± 0.05	0.59 ± 0.00
	13 Jul 1977	2.81 ± 0.01	17.56 ± 0.09	--	0.81 ± 0.00	1.76 ± 0.04	0.34 ± 0.01
	20 Aug 1977	1.73 ± 0.07	10.81 ± 0.44	--	1.36 ± 0.04	3.64 ± 0.06	0.19 ± 0.00
	26 Jun 1978	3.05 ± 0.03	19.06 ± 0.18	--	0.73 ± 0.00	1.57 ± 0.01	0.50 ± 0.00
<i>Salix alaxensis</i>	26 Jun 1977	4.34 ± 0.02	27.09 ± 0.13	--	0.48 ± 0.03	0.71 ± 0.01	0.60 ± 0.00
	13 Jul 1977	4.08 ± 0.07	25.41 ± 0.49	--	0.63 ± 0.01	0.98 ± 0.01	0.36 ± 0.00
	20 Aug 1977	3.08 ± 0.06	19.25 ± 0.35	--	0.58 ± 0.03	1.58 ± 0.04	0.18 ± 0.00
	26 Jun 1978	3.97 ± 0.03	24.81 ± 0.18	--	0.51 ± 0.03	1.07 ± 0.02	0.48 ± 0.01
7. North-facing <i>Dryas</i> -moss- <i>Cassiope</i> mat. 1200 m.							
<i>Dryas octopetala</i>	30 Jun 1977	2.04 ± 0.02	12.72 ± 0.13	11.4	0.14 ± 0.00	1.14 ± 0.02	0.19 ± 0.00
	23 Jul 1977	1.99 ± 0.01	12.41 ± 0.04	10.3	0.17 ± 0.00	1.15 ± 0.03	0.18 ± 0.01
	20 Aug 1977	1.40 ± 0.04	8.75 ± 0.07	7.7	0.20 ± 0.02	1.41 ± 0.09	0.16 ± 0.01
<i>Cassiope tetragona</i>	30 Jun 1977	0.86 ± 0.01	5.34 ± 0.04	--	0.15 ± 0.02	0.52 ± 0.01	0.09 ± 0.00
	23 Jul 1977	0.83 ± 0.01	5.19 ± 0.09	--	0.15 ± 0.00	0.65 ± 0.01	0.09 ± 0.00
	20 Aug 1977	0.77 ± 0.01	4.78 ± 0.04	--	0.16 ± 0.00	0.60 ± 0.01	0.08 ± 0.01

Table 11. (continued)

Site description and species analyzed	Date	Nitrogen	Protein (Nx6.25)	TNC	Magnesium	Calcium	Phosphorus
8. Northeast-facing <i>Dryas</i> mat. 1375 m.							
<i>Anemone parviflora</i>	8 Jul 1977	2.69 ± 0.00	16.81 ± 0.00	--	0.15 ± 0.00	1.34 ± 0.03	0.27 ± 0.01
	17 Aug 1977	1.92 ± 0.01	12.00 ± 0.09	--	0.11 ± 0.00	2.26 ± 0.11	0.16 ± 0.00
<i>Astragalus umbellatus</i>	8 Jul 1977	5.42 ± 0.10	33.88 ± 0.62	--	0.26 ± 0.01	0.75 ± 0.01	0.62 ± 0.02
	17 Aug 1977	3.87 ± 0.03	24.19 ± 0.18	--	0.24 ± 0.00	2.19 ± 0.04	0.30 ± 0.00
<i>Dodecatheon frigidum</i>	8 Jul 1977	2.91 ± 0.06	18.16 ± 0.40	--	0.18 ± 0.00	1.11 ± 0.00	0.32 ± 0.01
	17 Aug 1977	2.31 ± 0.01	14.41 ± 0.04	--	0.24 ± 0.01	2.09 ± 0.08	0.16 ± 0.01
<i>Geum rossii</i>	8 Jul 1977	2.69 ± 0.13	16.78 ± 0.84	--	0.34 ± 0.01	1.13 ± 0.01	0.29 ± 0.01
	17 Aug 1977	1.72 ± 0.01	10.75 ± 0.09	--	0.30 ± 0.01	2.50 ± 0.04	0.15 ± 0.00
9. Northeast-facing small-rock scree slope. 1375 m.							
<i>Epilobium latifolium</i>	8 Jul 1977	2.43 ± 0.04	15.16 ± 0.22	--	0.71 ± 0.02	2.92 ± 0.03	0.26 ± 0.00
	17 Aug 1977	1.34 ± 0.04	8.34 ± 0.22	--	1.27 ± 0.01	6.11 ± 0.00	0.16 ± 0.00
<i>Oxyria digyna</i>	8 Jul 1977	2.17 ± 0.01	13.56 ± 0.09	--	1.21 ± 0.01	4.73 ± 0.03	0.23 ± 0.00
	17 Aug 1977	1.81 ± 0.01	11.28 ± 0.04	--	1.91 ± 0.01	6.39 ± 0.07	0.16 ± 0.01
10. South-facing large-rock scree slope. 1425 m.							
<i>Arnica alpina</i>	9 Jul 1977	2.04 ± 0.01	12.75 ± 0.09	--	0.27 ± 0.00	1.41 ± 0.07	0.20 ± 0.00
	16 Aug 1977	1.54 ± 0.02	9.59 ± 0.13	--	0.26 ± 0.00	1.90 ± 0.02	0.13 ± 0.00
<i>Hierochloa alpina</i>	9 Jul 1977	1.52 ± 0.05	9.47 ± 0.31	11.9	0.07 ± 0.00	0.16 ± 0.00	0.17 ± 0.00
	16 Aug 1977	1.30 ± 0.11	8.09 ± 0.66	14.3	0.06 ± 0.06	0.34 ± 0.02	0.10 ± 0.00
11. North-facing large-rock scree slope. 1425 m.							
<i>Papaver macounii</i>	9 Jul 1977	1.93 ± 0.01	12.03 ± 0.04	--	0.20 ± 0.00	2.94 ± 0.02	0.27 ± 0.01
	16 Aug 1977	0.80 ± 0.07	5.00 ± 0.44	--	0.21 ± 0.01	6.38 ± 0.09	0.19 ± 0.00

Table 11. (continued)

Site description and species analyzed	Date	Nitrogen	Protein (Nx6.25)	TNC	Magnesium	Calcium	Phosphorus
12. Northeast-facing small-rock scree slope. 1375 m.							
<i>Epilobium latifolium</i>	8 Jul 1978	3.07 ± 0.01	19.19 ± 0.09	6.5	0.43 ± 0.03	2.48 ± 0.21	0.31 ± 0.00
	17 Aug 1978	2.17 ± 0.01	13.53 ± 0.04	6.4	0.55 ± 0.02	5.13 ± 0.11	0.25 ± 0.00
<i>Oxyria digyna</i>	8 Jul 1978	3.50 ± 0.08	21.84 ± 0.49	7.9	0.68 ± 0.03	3.16 ± 0.04	0.32 ± 0.00
	17 Aug 1978	2.64 ± 0.01	16.47 ± 0.04	5.4	0.96 ± 0.03	4.54 ± 0.01	0.22 ± 0.00
13. Northeast-facing <i>Dryas</i> mat. 1400 m.							
<i>Anemone parviflora</i>	8 Jul 1978	2.67 ± 0.01	16.66 ± 0.04	--	0.15 ± 0.01	1.66 ± 0.01	0.26 ± 0.00
	17 Aug 1978	2.04 ± 0.01	12.72 ± 0.04	--	0.14 ± 0.00	2.36 ± 0.06	0.19 ± 0.01
<i>Geum rossii</i>	8 Jul 1978	2.47 ± 0.02	15.41 ± 0.13	10.6	0.23 ± 0.00	1.28 ± 0.02	0.23 ± 0.00
	17 Aug 1978	1.51 ± 0.06	9.44 ± 0.35	5.4	0.25 ± 0.01	2.95 ± 0.06	0.14 ± 0.00
14. South-facing large-rock scree slope. 1425 m.							
<i>Microchloa alpina</i>	9 Jul 1978	1.65 ± 0.01	10.31 ± 0.09	--	0.08 ± 0.00	0.29 ± 0.01	0.16 ± 0.00
15. South-facing large-rock scree slope. 1425 m.							
<i>Arnica alpina</i>	10 Jul 1978	1.86 ± 0.01	11.63 ± 0.09	--	0.34 ± 0.00	0.91 ± 0.04	0.19 ± 0.00
	16 Aug 1978	1.50 ± 0.05	9.34 ± 0.35	--	0.36 ± 0.01	1.71 ± 0.01	0.14 ± 0.01
<i>Microchloa alpina</i>	10 Jul 1978	1.68 ± 0.00	10.50 ± 0.00	20.3	0.06 ± 0.00	0.27 ± 0.01	0.14 ± 0.00
	16 Aug 1978	1.27 ± 0.01	7.94 ± 0.09	22.9	0.09 ± 0.01	0.43 ± 0.01	0.10 ± 0.00
16. West-facing <i>Dryas</i> mat. 1250 m.							
<i>Carex microchaeta</i>	12 Jul 1978	2.16 ± 0.03	13.50 ± 0.18	--	0.11 ± 0.00	0.84 ± 0.01	0.15 ± 0.00
	19 Aug 1978	1.57 ± 0.03	9.81 ± 0.18	--	0.18 ± 0.00	1.31 ± 0.01	0.12 ± 0.00
<i>Dryas octopetala</i>	12 Jul 1978	1.80 ± 0.00	11.25 ± 0.00	--	0.16 ± 0.01	1.21 ± 0.01	0.15 ± 0.00
	19 Aug 1978	1.32 ± 0.00	8.25 ± 0.00	--	0.10 ± 0.00	1.51 ± 0.01	0.10 ± 0.00

Table 11. (continued)

Site description and species analyzed	Date	Nitrogen	Protein (Nx6.25)	TNC	Magnesium	Calcium	Phosphorus
17. Southwest-facing <i>Festuca-Dryas</i> strip. 1125 m.							
<i>Festuca altaica</i>	12 Jul 1978	1.39 ± 0.04	8.69 ± 0.27	--	0.08 ± 0.00	0.33 ± 0.01	0.12 ± 0.00
	19 Aug 1978	1.43 ± 0.01	8.91 ± 0.04	--	0.09 ± 0.00	0.51 ± 0.00	0.10 ± 0.00
18. South-facing low shrub area. 1150 m.							
<i>Betula glandulosa</i>	13 Jul 1978	2.65 ± 0.06	16.53 ± 0.40	--	0.26 ± 0.00	0.66 ± 0.00	0.24 ± 0.00
	20 Aug 1978	2.03 ± 0.01	12.66 ± 0.04	--	0.26 ± 0.00	0.79 ± 0.01	0.24 ± 0.00
<i>Vaccinium uliginosum</i>	13 Jul 1978	1.65 ± 0.01	10.31 ± 0.09	--	0.17 ± 0.00	0.40 ± 0.01	0.16 ± 0.00
	20 Aug 1978	1.60 ± 0.01	9.97 ± 0.04	--	0.22 ± 0.01	0.68 ± 0.02	0.14 ± 0.00
19. North-facing willow thicket. 1075 m.							
<i>Boyerkinia richardsonii</i>	13 Jul 1978	2.00 ± 0.01	12.50 ± 0.09	--	0.35 ± 0.01	3.14 ± 0.13	0.27 ± 0.01
	20 Aug 1978	1.10 ± 0.02	6.84 ± 0.13	--	0.31 ± 0.01	4.54 ± 0.16	0.17 ± 0.00
<i>Salix alaxensis</i>	13 Jul 1978	2.73 ± 0.04	17.03 ± 0.22	8.3	0.28 ± 0.00	1.66 ± 0.04	0.25 ± 0.00
	20 Aug 1978	1.91 ± 0.03	11.94 ± 0.18	11.4	0.29 ± 0.01	2.37 ± 0.02	0.14 ± 0.00
20. South-facing willow-alder thicket. 1075 m.							
<i>Alnus crispa</i>	13 Jul 1978	3.25 ± 0.08	20.28 ± 0.49	--	0.23 ± 0.00	0.69 ± 0.01	0.25 ± 0.00
	20 Aug 1978	2.98 ± 0.01	18.60 ± 0.04	--	0.21 ± 0.00	1.05 ± 0.01	0.21 ± 0.01
<i>Mertensia paniculata</i>	13 Jul 1978	2.12 ± 0.06	13.22 ± 0.40	--	0.22 ± 0.01	1.57 ± 0.04	0.18 ± 0.00
	20 Aug 1978	1.65 ± 0.02	10.28 ± 0.13	--	0.23 ± 0.01	2.64 ± 0.10	0.16 ± 0.00
<i>Salix alaxensis</i>	13 Jul 1978	3.17 ± 0.02	19.78 ± 0.13	9.4	0.22 ± 0.00	1.42 ± 0.01	0.27 ± 0.01
	20 Aug 1978	2.47 ± 0.00	15.44 ± 0.00	12.8	0.45 ± 0.01	1.70 ± 0.00	0.17 ± 0.00
<i>Salix borelayi</i>	13 Jul 1978	3.12 ± 0.05	19.47 ± 0.31	--	0.42 ± 0.02	1.96 ± 0.08	0.23 ± 0.00
	20 Aug 1978	2.33 ± 0.02	14.53 ± 0.13	--	0.48 ± 0.01	2.65 ± 0.00	0.16 ± 0.00
<i>Salix planifolia</i> ssp. <i>pulehva</i>	13 Jul 1978	2.78 ± 0.04	17.34 ± 0.22	6.9	0.27 ± 0.00	0.77 ± 0.01	0.28 ± 0.00
	20 Aug 1978	2.03 ± 0.00	12.69 ± 0.00	6.7	0.32 ± 0.01	1.31 ± 0.01	0.21 ± 0.00

Table 11. (continued)

Site description and species analyzed	Date	Nitrogen	Protein (Nx6.25)	TNC	Magnesium	Calcium	Phosphorus
21. West-facing, rocky <i>Dryas</i> mat. 1625 m.							
<i>Carex microchaeta</i>	28 Jul 1978	2.81 ± 0.01	17.53 ± 0.04	14.8	0.12 ± 0.01	0.52 ± 0.01	0.24 ± 0.00
	17 Aug 1978	2.12 ± 0.01	13.25 ± 0.09	16.9	0.11 ± 0.00	0.80 ± 0.02	0.18 ± 0.00
22. South-facing <i>Dryas</i> mat. 1825 m.							
<i>Dryas octopetala</i>	30 Jul 1978	1.65 ± 0.23	10.30 ± 1.41	14.0	0.07 ± 0.00	0.27 ± 0.01	0.21 ± 0.00
	19 Aug 1978	1.29 ± 0.00	8.06 ± 0.00	14.9	0.06 ± 0.00	1.46 ± 0.00	0.20 ± 0.00
23. Southwest-facing large-rock scree slope. 1825 m.							
<i>Papaver alboroseum</i>	30 Jul 1978	2.10 ± 0.01	13.13 ± 0.09	14.4	0.32 ± 0.01	3.95 ± 0.01	0.27 ± 0.01
<i>Senecio atropurpureus</i>	30 Jul 1978	2.02 ± 0.04	12.62 ± 0.27	11.3	0.26 ± 0.01	1.33 ± 0.00	0.28 ± 0.00

Table 12. Fiber analysis of selected plant species from the Sheep Creek study area, 1977 and 1978.
(mean values, n=2, in percent of total weight on a dry matter basis)

Site	Species	Date	Cell Wall Contents ¹	Hemi- Cellulose ²	ADF ³	Lignin	Cellulose	Ash	Presumptive Silica ⁴
1	<i>Carex scirpoidea</i>	25 May 1977	58.0	30.6	27.4	2.9	22.7	1.8	1.2
		23 Jun 1977	57.7	27.9	29.8	4.2	23.4	2.2	2.1
		21 Jul 1977	55.5	25.0	30.5	4.4	23.1	3.0	2.9
		15 Aug 1977	53.9	23.2	30.7	4.0	23.0	3.7	3.7
		14 Oct 1977	68.2	23.7	44.5	8.2	31.0	5.4	5.3
		4 Mar 1978	66.5	22.4	44.1	8.6	28.9	6.6	6.2
4	<i>Salix planifolia</i> ssp. <i>pulchra</i>	13 Jun 1977	15.1	1.0	14.1	5.4	8.7	0.0	0.0
		13 Jul 1977	20.8	1.5	19.3	7.4	10.7	1.2	0.8
		20 Aug 1977	33.5	8.2	25.3	11.8	12.6	0.9	0.4
21	<i>Carex microchaeta</i>	30 Jul 1978	54.1	33.7	20.4	2.6	16.8	0.9	0.9
		18 Aug 1978	53.3	31.5	21.8	2.7	17.4	1.7	1.4
22	<i>Dryas octopetala</i>	28 Jul 1978	24.5	5.2	19.3	5.4	12.7	1.2	0.3
		18 Aug 1978	24.4	5.8	18.6	5.3	13.0	0.4	0.2

¹Cell wall contents = total fiber or neutral detergent fiber

²Hemicellulose = cell wall contents - ADF

³ADF = acid detergent fiber = lignin + cellulose + ash

⁴Silica contained within ash

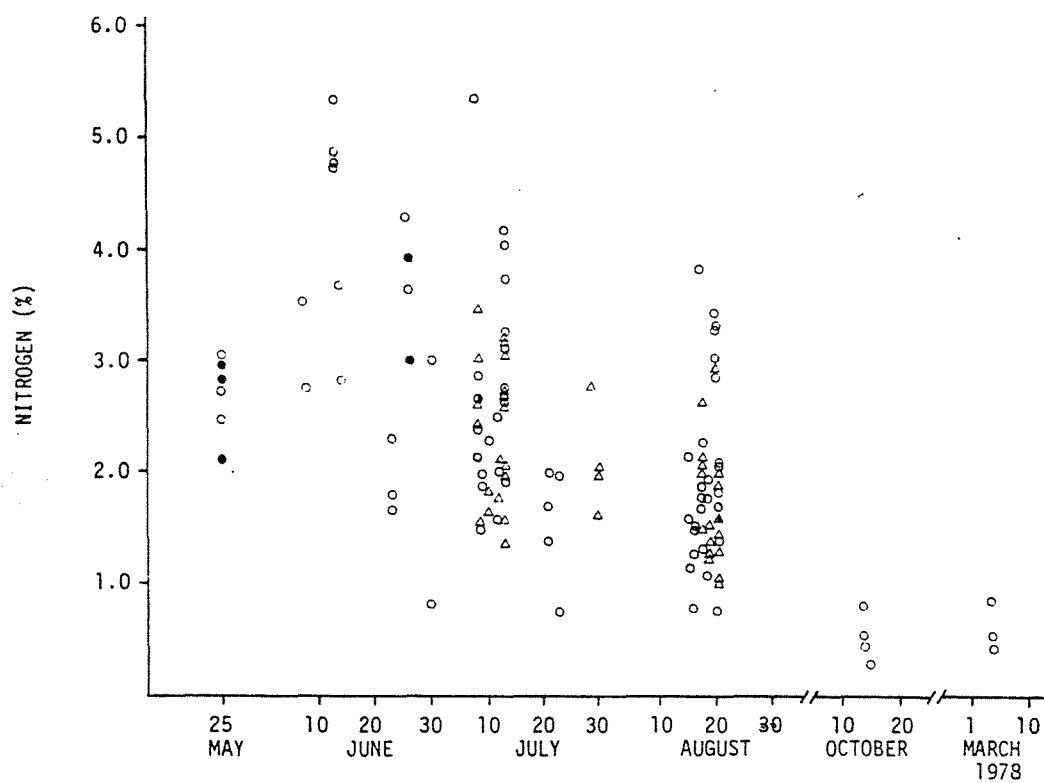


Figure 4. Nitrogen content of forage plants from the Sheep Creek study area, 1977 and 1978. ° = 1977 Tanana drainage value; Δ = 1978 Robertson drainage value; ● = plants re-collected in 1978; °, Δ = 2 identical data points. Values are from all species listed in Table 11.

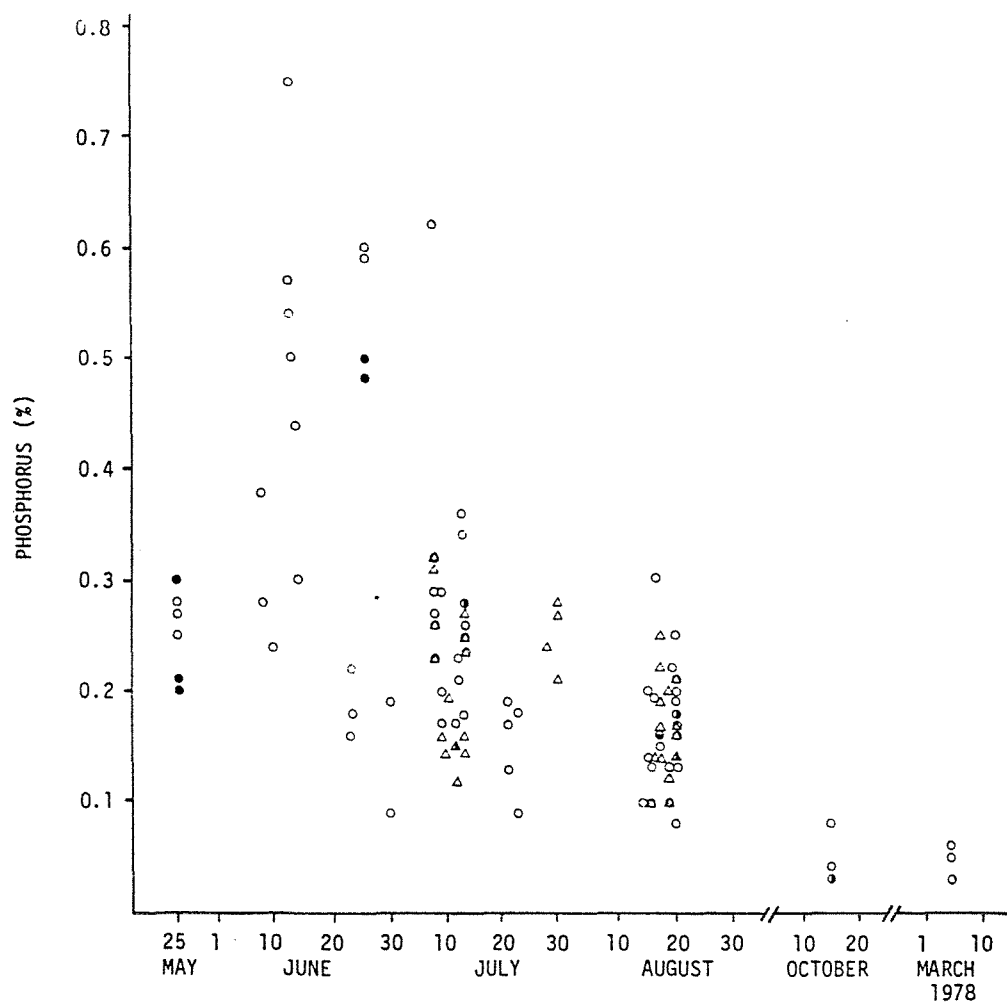


Figure 5. Phosphorus content of forage plants from the Sheep Creek study area, 1977 and 1978. ○ = 1977 Tanana drainage value; △ = 1978 Robertson drainage value; ● = plants re-collected in 1978; ◐, ◑, ◒ = 2 identical data points; ◓ = 4 identical data points. Values are from all species listed in Table 11.

levels of nitrogen and phosphorus. Although sample sizes were small during the winter months, it appears that nitrogen and phosphorus reached their lowest levels before mid-October and remained at low levels until growth resumed the following spring.

Calcium levels (Figure 6) changed in a manner opposite that of nitrogen and phosphorus. Low levels were present in early plant growth stages, but by late summer, calcium content had increased considerably. Relatively high levels remained throughout the winter, with March levels considerably higher than those the following May. Leaching during snowmelt in early spring may have reduced the winter calcium levels to those values found in May.

Magnesium values (Figure 7) showed a slight trend towards increasing concentration as plants matured. This trend was not as apparent as the trends of the other nutrients due to the lack of regularity in changes of magnesium content with plant maturity (Table 11).

Total nonstructural carbohydrate content (Table 11 and Figure 8) generally increased through August and in most cases decreased sometime thereafter; in some species this decrease began by mid-July. Although winter data were few, it can be seen that nonstructural carbohydrate levels decreased before the onset of winter, probably due to the translocation of carbohydrates to below ground storage structures. By March, nonstructural carbohydrate levels had decreased even further, possibly through leaching.

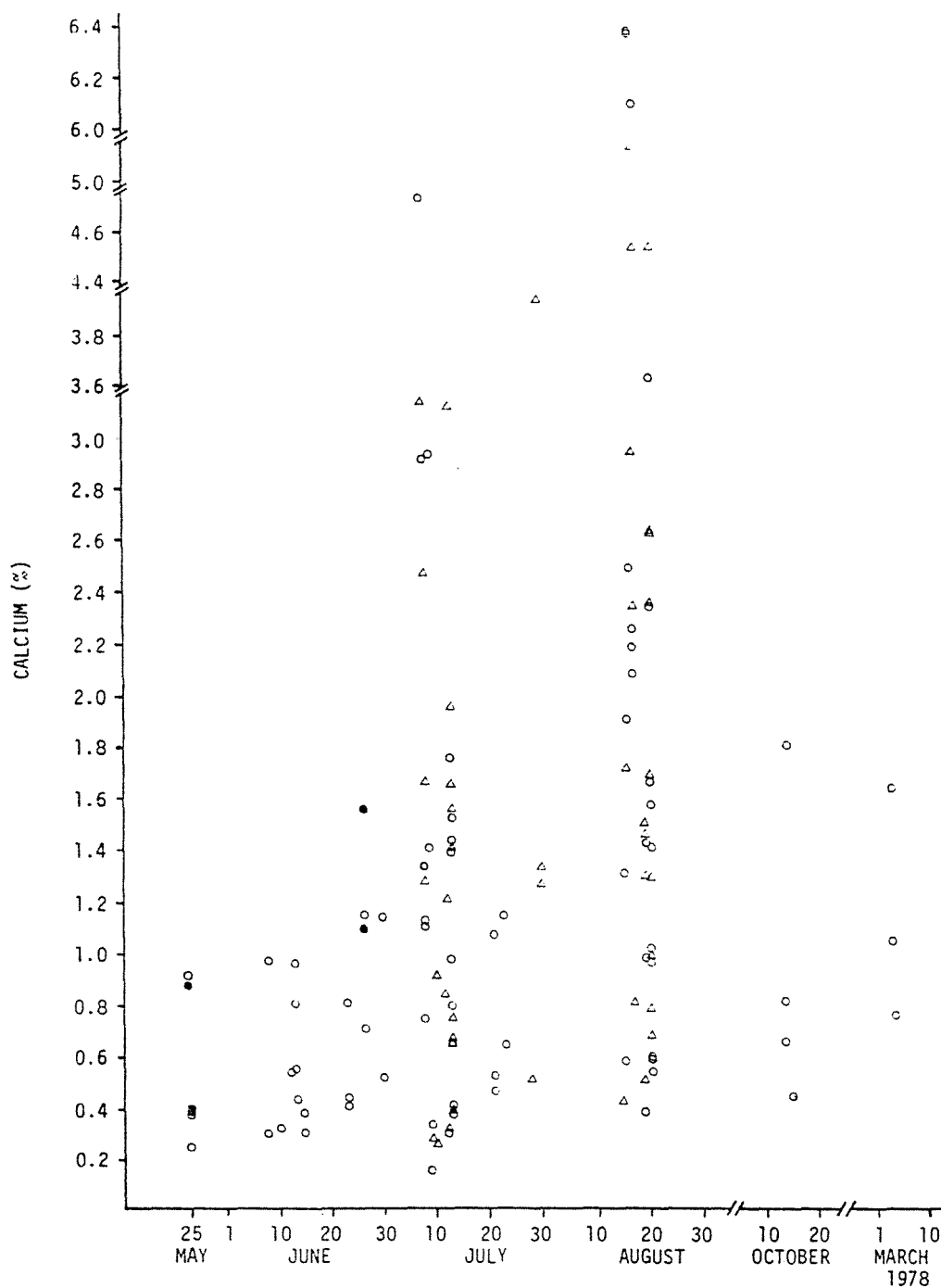


Figure 6. Calcium content of forage plants from the Sheep Creek study area, 1977 and 1978. o = 1977 Tanana drainage value; Δ = 1978 Robertson drainage value; • = plants re-collected in 1978. Values are from all species listed in Table 11.

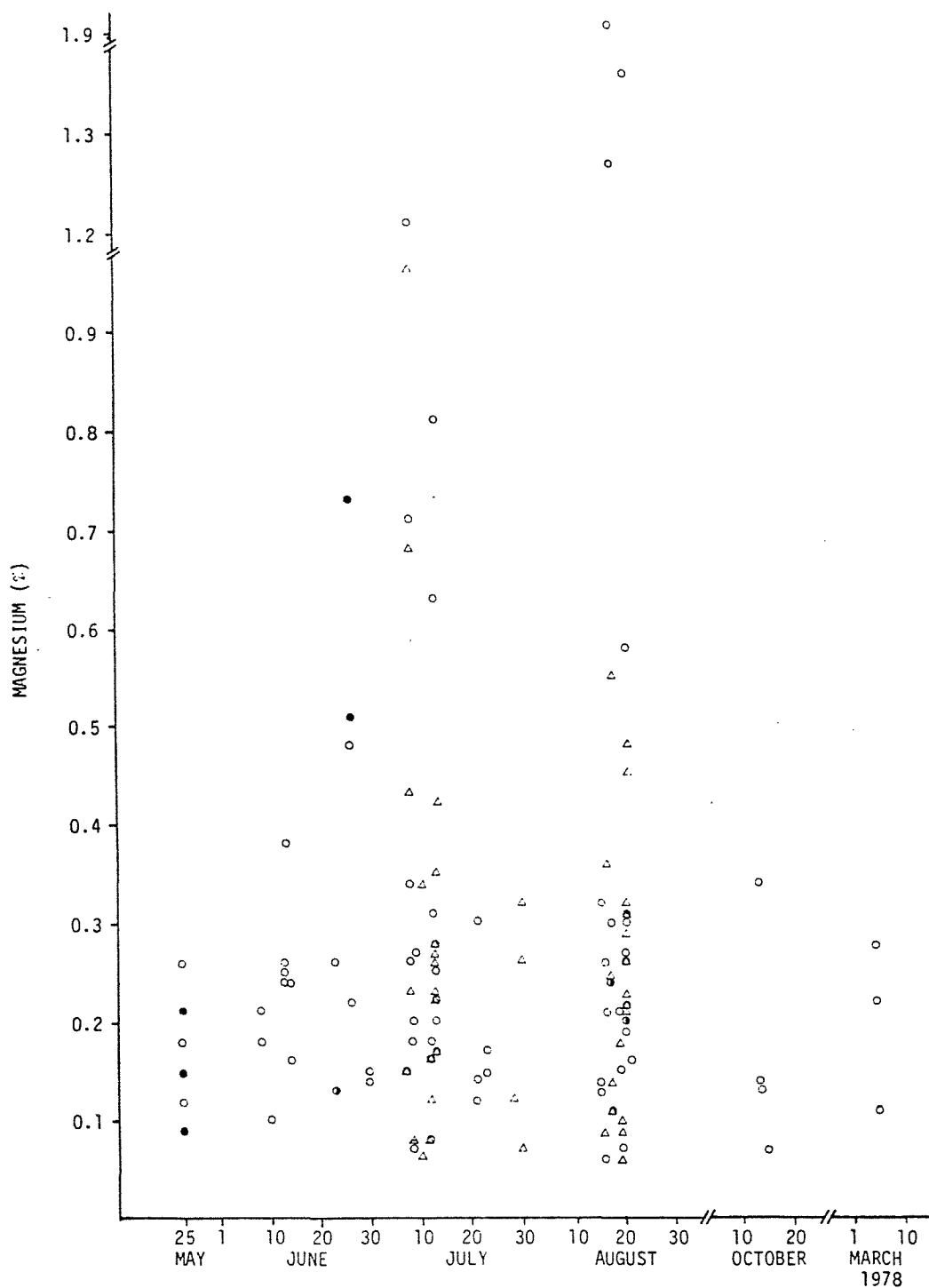


Figure 7. Magnesium content of forage plants from the Sheep Creek study area, 1977 and 1978. \circ = 1977 Tanana drainage value; Δ = 1978 Robertson drainage value; \bullet = plants re-collected in 1978; \circ = 2 identical data points. Values are from all species listed in Table 11.

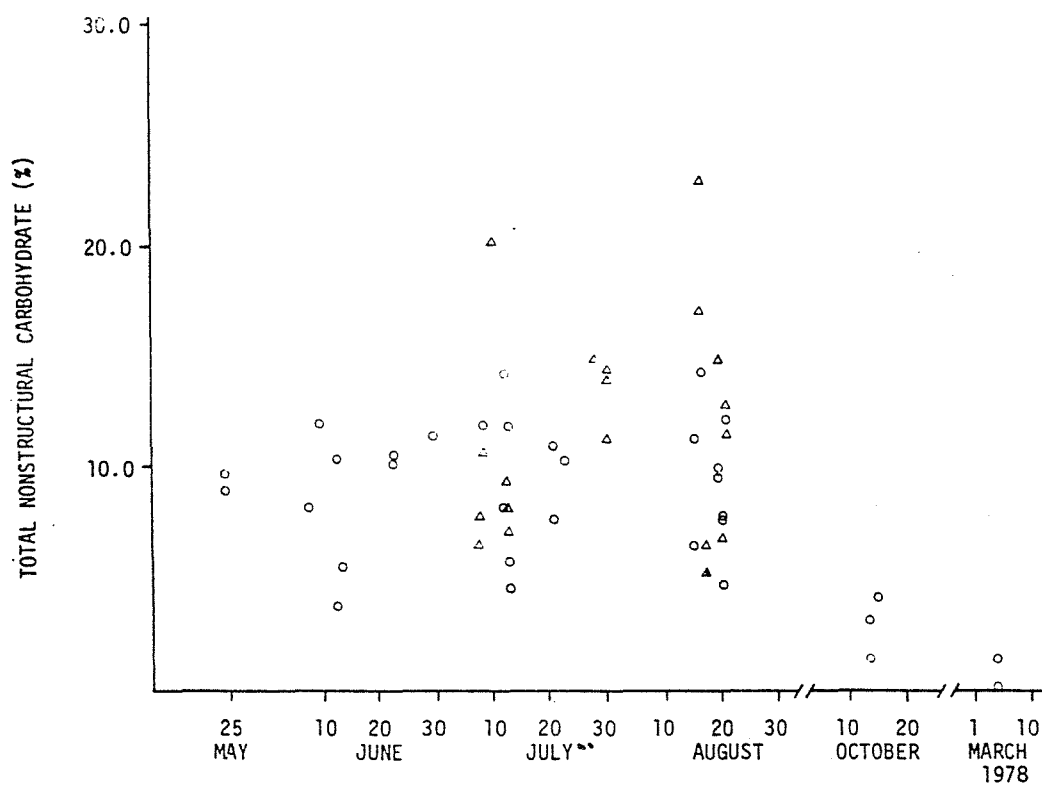


Figure 8. Total nonstructural carbohydrate content of selected plants from the Sheep Creek study area, 1977 and 1978. o = 1977 Tanana drainage value; Δ = 1978 Robertson drainage value; Δ = 2 identical data points. Values are from Table 11.

The results of the fiber analyses (Table 12) showed that of the four species examined, virtually all exhibited increases in fiber components, except hemicellulose, as the growing season progressed. Hemicellulose increased for two species and decreased for the other two.

Comparison of Plant Nutrient Values from McKinley Park and Sheep Creek

Plant nutrient values from sheep ranges in McKinley Park, Alaska (Whitten 1975) were compared with nutrient values obtained in this study. Comparisons of plant nutrient values were made between species collected from similar sites as discerned from site descriptions (Table 13).

To correct for differences in nutrient content caused by different collection dates and different lengths of growing seasons prior to collection, an average daily correction factor was devised. The difference in values for each nutrient from a particular plant species collected on two different dates was divided by the number of days between the two sampling dates. This produced an average daily change for the time interval for that species which was then multiplied by the number of days by which the McKinley Park and Sheep Creek sample collection dates differed. The resulting value was then added to or subtracted from the Sheep Creek nutrient value, depending on the specific nutrient and the direction of the collection date difference. The correction factor produced in this manner was used to compare

Table 13. Plant species compared between McKinley Park and the Sheep Creek area.

Whitten (1975) (1973 data)				This Study (1977 data)			
Site	Species	Elevation	Date Collected	Site	Species	Elevation	Date Collected
1	<i>Vaccinium uliginosum</i>	1200 m	10 Jun 10 Jul	5	<i>Vaccinium uliginosum</i>	1125 m	14 Jun 13 Jul
2	<i>Vaccinium uliginosum</i>	1150 m	16 Jun 10 Jul 19 Aug	5	<i>Vaccinium uliginosum</i>	1125 m	14 Jun 13 Jul 20 Aug
2	<i>Salix planifolia</i> ssp. <i>pulchra</i>	1150 m	16 Jun 10 Jul 19 Aug	4	<i>Salix planifolia</i> ssp. <i>pulchra</i>	1075 m	14 Jun 13 Jul 20 Aug
3	<i>Cassiope tetragona</i>	1100 m	27 Jun	7	<i>Cassiope tetragona</i>	1200 m	30 Jun
4	<i>Arnica alpina</i>	1250 m	15 Jul 19 Aug	10	<i>Arnica alpina</i>	1425 m	9 Jul 19 Aug
5	<i>Geum rossii</i>	1350 m	11 Jul	8	<i>Geum rossii</i>	1375 m	8 Jul
5	<i>Dodecatheon frigidum</i>	1350 m	11 Jul	8	<i>Dodecatheon frigidum</i>	1375 m	8 Jul
7	Grass	1350 m	28 Jul	10	<i>Hierochloa alpina</i>	1425 m	9 Jul
8	<i>Boykinia richardsonii</i>	1075 m	21 Jun	6	<i>Boykinia richardsonii</i>	1100 m	26 Jun
9	<i>Dryas octopetala</i>	1275 m	26 Jun	2	<i>Dryas octopetala</i>	1275 m	12 Jul
10	Grass	1125 m	8 Jul	3	<i>Festuca altaica</i>	1100 m	12 Jul
10	<i>Carex</i> spp.	1125 m	8 Jul	2	<i>Carex microcheta</i>	1275 m	12 Jul

nutrient values for plant samples which were collected either within the first or last third of an approximate two month interval for a particular species with three or more approximately equally spaced sampling dates within that interval. This correction factor was also used to compare samples collected within an approximate one month interval with only two sampling dates forming that interval. For instances in which samples were taken near the midpoint of an approximate two month interval with three approximately equally spaced sampling dates forming that interval, the mean value of the two mean monthly intervals (June-July and July-August) was used as the daily correction factor. This was done to more accurately correct the nutrient value, since the rate of change of nutrient content varies considerably with plant growth stage.

The dates for the emergence of shrub leaves were chosen to correct for differences between the onset of the growing seasons from Sheep Creek and McKinley Park. Leaf emergence in shrubs was chosen because data on flowering phenology were limited in Sheep Creek in 1977 and, for McKinley Park, data on altitude and exposure were inadequate for evaluating flowering phenology. Thus, six days, the difference between leaf emergence of shrubs at Sheep Creek and McKinley Park, were multiplied by the average daily change and that product was, depending on the particular nutrient involved, added to or subtracted from each 1977 Sheep Creek nutrient value.

A correction factor of one day for each 25 m of altitudinal

difference between the compared samples was used, following the observations reported by Hopkins (1920) and Costello and Price (1939). The number of altitude-equivalent days was multiplied by the average daily change for the growth interval nearest the date of collection. This value was then added to or subtracted from the original Sheep Creek nutrient value, depending on the direction of the elevation difference and the specific nutrient involved.

The 1977 Sheep Creek area nutrient values were standardized to the 1973 values of Whitten (1975) to eliminate altitudinal and growth stage differences. The values from the two areas were then statistically compared by the Mann-Whitney test (Conover 1971). No significant differences ($\alpha = 0.05$) between the two areas were found for the four nutrients tested, plant nitrogen, phosphorus, calcium, or magnesium.

Comparison of Plant Nutrient Values from the Kenai Peninsula and Sheep Creek

Nichols (1973) reported nitrogen and total available carbohydrate values for 10 plant species collected from sheep winter range sites, during late July and early August, on the Kenai Peninsula, Alaska. Nitrogen values from the Kenai Peninsula appeared to be approximately equal to or slightly less than Sheep Creek values for the same period, but due to a lack of information concerning site parameters and plant growth phenology, this comparison could not be statistically tested.

Total available carbohydrate values from the Kenai Peninsula were somewhat higher than those from Sheep Creek, possibly the result of an advanced growing season at the lower latitude of the Kenai Peninsula.

Comparison of Nutrient Values Between the Robertson and Tanana Drainages

Plants were collected for nutrient analysis from physiographically and floristically similar sites in the Tanana and Robertson drainages to determine if the nutrient composition of plants in the two areas differed. Differences in nutrient composition might explain why the two drainages supported different densities of sheep during summer.

The same plant species were collected from the Tanana drainage in 1977 and from the Robertson drainage in 1978, on the same calendar date when possible. To correct for differences in nutrient composition caused by an earlier spring in 1978, five plant species were re-collected in 1978 at two locations in Sheep Creek. *Carex scirpoidea*, *Dryas octopetala*, and *Elymus innovatus* at nutrient site 1 were re-collected 25 May 1978. *Salix alaxensis* and *Boykinia richardsonii* were re-collected 26 June 1978 at site 6. The 1977 nutrient value was divided by the 1978 value for each nutrient for each of these five re-collected species. The resulting values for each nutrient were then summed for the five species and the mean value of the ratio for each nutrient was multiplied by each tested 1978 value from the

Robertson drainage. These corrected values were then used in statistical comparisons of the Robertson and Tanana nutrient values. The direction of change between the two years indicated that in the Tanana drainage, the 1978 growing season was advanced over that of 1977.

The paired nutrient sites 2 and 16, 3 and 17, 4 and 20, 5 and 18, 6 and 19, 8 and 13, and 10 and 15 were compared to determine whether differences in plant nutrient composition exist between the Robertson and Tanana drainages. Corrected nutrient values were used for the Robertson drainage. Thirty-two paired values for 15 species from the Tanana and Robertson drainages were then compared statistically with the Mann-Whitney test (Conover 1971). No significant differences ($\alpha = 0.05$) between the two areas were found for values of plant nitrogen, phosphorus, calcium, and magnesium.

Comparison of the Robertson and Tanana Drainages within the Study Area

Vegetation differences - The two drainages were compared to determine if differences existed in the relative amounts or characteristics of the vegetation types. Differences might explain why the two drainages supported different densities of sheep during summer.

One of the most obvious differences was the higher treeline of the Robertson drainage which averaged approximately 200 m higher than that in the Tanana drainage. Spruce were present in continuous stands in the Robertson drainage to 1060 m on south-facing slopes and to

1000 m on north-facing slopes. Scattered spruce reach elevations of 1300 m on south-facing slopes and 1125 m on north-facing slopes. Cottonwoods 3 to 6 m tall reached an altitude of 1100 m along creek banks. In the Tanana drainage, cottonwoods 3 to 6 m tall reached an altitude of 925 m. The limit of spruce growth averaged about 820 m, with projections of spruce found up to 950 m. Most of the conifers in the Tanana drainage were on north-facing slopes, due to the topographic properties of that portion of the study area. Although south-facing slopes of the same elevation as those that supported tree growth in the Robertson drainage were present, no trees grew on these slopes. This indicated factors other than aspect were influencing the altitudinal limits of tree growth.

Other vegetation types were also present at higher elevations in the Robertson drainage. Willow-alder in the Robertson drainage was present in relatively continuous stands to 1370 m, while in the Tanana drainage stands reached elevations of only 1125 m. Continuous low shrub stands reached approximately 1150 m in the Tanana drainage. Scattered low shrubs or small, isolated stands of such shrubs were found up to 100 m higher than the continuous low shrub stands. Within the Robertson drainage, most *Festuca-Dryas* areas were found at elevations between 1300 and 1430 m, with occasional extensions from the main areas reaching 1500 m. *Festuca-Dryas* areas in the Tanana drainage ranged from 1075 to 1300 m in elevation.

Visual estimates of the percentage of each vegetation type within

each subdrainage of the Robertson and Tanana drainage were made. The area of each subdrainage was determined from a topographic map of the study area. Percentage values of each vegetation type were then converted to map area by multiplying the percentage for each vegetation type by the total area of the subdrainage. These map area values were then summed for the subdrainages and the map area values converted back to percentages of the total area by dividing the summed map area values by the summed area of the subdrainages of each of the Robertson and Tanana drainages. The results are presented in Table 14.

For the majority of vegetation types, the percentage of the total area covered by a particular vegetation type was virtually the same within both Robertson and Tanana drainages. Exceptions were the *Dryas-moss-Cassiope*, wet sedge, and grass-sedge vegetation types. *Dryas-moss-Cassiope* and wet sedge each formed less than one percent of the total area within the Robertson drainage portion of the study area. Grass-sedge meadows were not found in the Robertson drainage portion of the study area.

Area above 1370 m - There appeared to be more area occupied by the more densely vegetated vegetation types (e.g., *Dryas*, wet low-*Salix*, *Festuca-Dryas*) in the alpine zone of the Robertson drainage than in the Tanana drainage. The 1370 m level was chosen to represent the lower limit for this comparison, as this level represented the approximate lower limit of sheep altitudinal distribution for July and August, the period during which both portions of the study area

Table 14. Percentage of the total area occupied by each vegetation type within the Tanana and Robertson drainages within the Sheep Creek study area, 1977 and 1978.

Vegetation Type	Tanana Drainage		Robertson Drainage	
	Area (%)	Area Above 1370 m (%)	Area (%)	Area Above 1370 m (%)
<i>Dryas</i> mat	20.4	21.7	19.7	23.6
<i>Dryas</i> -moss- <i>Cassiope</i>	6.6	1.1	< 1.0	< 1.0
Willow-alder	9.0	0.0	9.0	0.5
Low shrub	16.3	0.0	16.0	2.5
Large-rock scree	36.4	49.9	36.9	48.0
Small-rock scree	6.1	8.9	7.0	9.4
Cliff	7.8	17.0	9.1	12.7
Grass-sedge	< 1.0	0.0	0.0	0.0
<i>Festuca</i> - <i>Dryas</i>	0.7	0.0	1.3	2.2
Wet sedge	0.4	1.4	< 1.0	< 1.0
Wet low- <i>Salix</i>	0.2	< 1.0	0.5	0.5
Total Area	47.2 km ²	23.9 km ²	31.5 km ²	21.3 km ²

were examined.

The area above 1370 m in the Robertson drainage (21.3 km^2) was almost equal to that above 1370 m in the Tanana drainage (23.9 km^2) even though the total area of the Tanana drainage (47.2 km^2) was almost one-third larger than that of the Robertson drainage (31.5 km^2). Consequently, the Robertson drainage had a greater proportion of its area (68 percent) above 1370 m than did the Tanana drainage (51 percent).

Similar proportions of the vegetation types were found in both portions of the study area (Table 14), although the Robertson drainage contained approximately 1 km^2 (5 percent) more area above 1370 m, composed of *Dryas*, *Festuca-Dryas*, and wet low-*Salix* vegetation types, than did the Tanana drainage. This additional area conceivably could have provided nutritional advantages to the sheep by increasing the total number of plants available for forage selection in late summer feeding areas.

FEEDING ECOLOGY

Summer Forage Species

Dall's sheep fed on many plant species during the summer months. Table 15 presents a list of those species which sheep ingested as determined by direct observation or by inspecting rumen samples and sheep feeding sites during the summer of 1978. Since it was often difficult to determine if inconspicuous, rare, or isolated plants were eaten, this list is undoubtedly incomplete.

Although many plants were eaten by sheep during the summer, a relatively small number of species formed the major part of the diet. *Dryas octopetala*, several grasses, notably *Festuca altaica* and *Hierochloe alpine*, the sedge *Carex microchaeta*, the low-growing willows *Salix polaris* ssp. *pseudopolaris* and *Salix reticulata*, and the forbs *Epilobium latifolium*, *Oxyria digyna*, and *Geum rossii* were eaten throughout the summer and constituted a major portion of the sheep's diet. Other species contributed substantially, but only during certain periods of the summer. Four willow species, *Salix alaxensis*, *S. barclayi*, *S. glauca*, and *S. planifolia* ssp. *pulchra* were the most notable in this regard, having been eaten commonly in May, extensively in June, and only occasionally in July. Several forbs also incurred time-specific grazing.

Forbs did not form a large portion of the diet during all parts of the summer, although at times an individual sheep's diet may be composed almost entirely of forbs. Forbs were an important food group,

Table 15. Plant species eaten and the relative frequency each species was grazed during summer 1978 in the Sheep Creek study area. (Species are listed in order of observation. A = abundantly grazed; C = commonly grazed; O = occasionally grazed; R = rarely grazed; I = incidentally grazed)

Species	Relative Frequency of Grazing			
	May	June	July	August
<i>Elymus innovatus</i>	A	O	--	--
<i>Festuca altaica</i>	A	A	A	A
<i>Calamagrostis purpurascens</i>	A	A	--	--
<i>Carex scirpoidea</i>	C	C	O	--
<i>Artemisia alaskana</i>	A	--	--	--
<i>Pulsatilla patens</i>	C	--	--	--
<i>Anemone parviflora</i>	A	A	O	--
<i>Salix alaxensis</i>	A	A	O	--
<i>Epilobium angustifolium</i>	A	A	--	--
<i>Artemisia boreale</i>	C	--	--	--
<i>Dryas octopetala</i>	A	A	A	A
<i>Artemisia tilesii</i>	O	--	--	--
<i>Calamagrostis canadensis</i>	C	C	--	--
<i>Populus balsamifera</i>	R	--	--	--
<i>Androsace chamaejasme</i>	I	--	--	--
<i>Zygadenus elegans</i>	C	O	--	--
<i>Diapensia lapponica</i>	O	O	--	--
<i>Betula glandulosa</i>	O	R	--	--
<i>Vaccinium uliginosum</i>	C	A	O	--
<i>Salix planifolia</i> ssp. <i>pulchra</i>	A	A	O	--
<i>Poa arctica</i>	O	O	O	C
<i>Hierochloe alpina</i>	O	A	A	A
<i>Salix glauca</i>	--	C	O	--
<i>Salix barclayi</i>	--	A	O	--
<i>Mertensia paniculata</i>	--	C	--	--
<i>Epilobium latifolium</i>	--	A	A	A
<i>Carex podocarpa</i>	--	C	C	--
<i>Delphinium glaucum</i>	--	O	--	--
<i>Cassiope tetragona</i>	--	R	R	--
<i>Arctostaphylos alpina</i>	--	O	--	--
<i>Boykinia richardsonii</i>	--	A	A	--
<i>Ranunculus nivalis</i>	--	C	--	--
<i>Dodecatheon frigidum</i>	--	O	--	C

Table 15. (continued)

Species	Relative Frequency of Grazing			
	May	June	July	August
<i>Artemisia arctica</i>	--	O	O	O
<i>Salix reticulata</i>	--	A	A	A
<i>Oxyria digyna</i>	--	C	A	A
<i>Astragalus umbellatus</i>	--	C	--	--
<i>Geum rossii</i>	--	O	A	A
<i>Minuartia arctica</i>	--	O	O	--
<i>Alnus crispa</i>	--	R	--	--
<i>Polemonium acutiflorum</i>	--	O	--	--
<i>Pyrola grandiflora</i>	--	O	--	--
<i>Salix polaris</i> ssp. <i>pseudopolaris</i>	--	C	A	A
<i>Carex microchaeta</i>	--	A	A	A
<i>Salix phlebophylla</i>	--	O	C	C
<i>Silene acaulis</i>	--	--	C	--
<i>Arnica alpina</i>	--	--	O	O
<i>Senecio atropurpureus</i>	--	--	A	C
<i>Saxifraga oppositifolia</i>	--	--	O	O
<i>Papaver alboroseum</i>	--	--	A	C
<i>Salix arctica</i>	--	--	C	--
<i>Trisetum spicatum</i>	--	--	O	O
<i>Pedicularis capitata</i>	--	--	O	--
<i>Pedicularis lanata</i>	--	--	O	--
<i>Cardamine purpurea</i>	--	--	O	--
<i>Loiseleuria procumbens</i> ¹	--	O	O	--
<i>Equisetum scirpoides</i> ¹	--	I	I	--
<i>Vaccinium vitis-idaea</i> ¹	--	R	R	--
Lichens ¹	--	I	I	--
Mosses ¹	--	I	I	--

¹from rumen samples

particularly during late July and early to mid-August; however, the bulk of the forb portion of the diet was composed of relatively few species.

Some species, *Cassiope tetragona* and *Alnus crispa* for example, were abundant on sheep range but were rarely eaten. Some species also appeared to be eaten incidentally with preferred species due to their close association with these species. *Androsace chamaejasme*, *Equisetum sciropoides*, moss, and lichen fit into this category. Lichens, however, are not always taken incidentally with other forage, particularly in winter (Nichols 1974; Heimer 1978), when up to 16 percent of late winter ewe rumen contents consisted of lichens.

Rumen Sample Analysis

Two rumen samples from ewes killed at the Sheep Creek mineral lick 22 June and 7 July 1978 supported my observations of plant species eaten (Table 16). Most of the identifiable species in the rumen contents of the yearling female were *Dryas octopetala* and grasses and/or sedges. The 4 year old ewe also had a large percentage of grasses and/or sedges and *Dryas octopetala* in her rumen. In addition, *Epilobium latifolium*, *Geum rossii*, and the low willows *Salix reticulata*, *S. polaris* ssp. *pseudopolaris*, and *S. phlebophylla* contributed substantially to the identifiable contents of the 4 year old ewe's rumen. Based on the rumen contents, it appears that this ewe had fed in several vegetation types shortly before her death,

Table 16. Analysis of rumen contents from ewes killed in Sheep Creek in 1978.

Species	Percent of Contents	
	A ¹	B ²
Grass-sedge	14.4	20.0
<i>Dryas octopetala</i>	7.0	12.6
<i>Salix polaris</i> ssp. <i>pseudopolaris</i> or <i>Salix phlebophylla</i>	0.5	4.9
Lichens	0.3	0.1
Mosses	0.2	< 0.1
<i>Salix polaris</i> ssp. <i>pseudopolaris</i>	--	1.8
<i>Geum rossii</i>	< 0.1	2.2
<i>Epilobium latifolium</i>	< 0.1	3.0
<i>Salix reticulata</i>	0.1	1.8
<i>Loiseleuria procumbens</i>	< 0.1	1.0
<i>Vaccinium uliginosum</i>	< 0.1	0.8
<i>Boykinia richardsonii</i>	--	0.4
<i>Vaccinium vitis-idaea</i>	< 0.1	0.1
<i>Minuartia arctica</i>	--	< 0.1
<i>Cassiope tetragona</i>	< 0.1	< 0.1
<i>Equisetum scirpoides</i>	< 0.1	< 0.1
<i>Hierochloe alpina</i>	0.1	< 0.1
<i>Betula glandulosa</i>	< 0.1	--
Rock	0.1	--
Unidentified woody twigs	1.0	2.2
Unidentified material	76.3	49.1

¹obtained from a yearling female which died between 15 June and 22 June 1978; sample removed 23 June

²obtained from a 4 year old female which died 7 July 1978

most likely *Dryas*, *Dryas-moss-Cassiope*, wet low-*Salix*, large-rock scree, or *Festuca-Dryas*.

Other researchers have described similar summer forage use by Dall's sheep, with data from direct observation (Murie 1944; Jones 1963b; Viereck 1963; Hoefs 1975; Whitten 1975), from rumen samples (Murie 1944; Heimer 1973, 1978; Hoefs 1975) and from fecal samples (Nichols 1974). Most studies indicated that grasses, sedges, willows, and *Dryas* comprise the bulk of the summer diet, with the remainder contributed by forbs.

Hoefs (1975) reported that forbs comprised over 50 percent of the July and August diet of Dall's sheep in the Kluane Game Sanctuary, Yukon Territory, Canada. It should be noted that Hoefs included *Dryas integrifolia* and the low growing willows in the forb category. If these species are excluded, forbs comprised approximately 35 percent of the July and August forage. Hoefs (1975) reported relatively low use of *Dryas*, less than 6 percent, during the summer months. Rumen sample data from Murie (1944) and Heimer (1973) and my observations indicate that *Dryas* is a much more important forage species for Alaskan sheep populations. The fact that different *Dryas* species exist in the two areas may account for the use differences. *Dryas integrifolia* is found on the Kluane sheep range (Hoefs 1975), but *Dryas octopetala* is the abundant species on Alaskan sheep ranges.

Feeding Behavior

Dall's sheep fed on leaves, flowers, buds, and non-woody stems during the summer months. When feeding on woody plants in summer, sheep ate predominately leaves and flowers and not woody stems; however, when stripping leaves and catkins from branches, sheep often scraped bark from the branch ends. In the case of *Vaccinium uliginosum*, sheep also ate young stems of the current growing season, usually less than 1 mm in diameter and soft and succulent.

New leaves and flowers were eaten most frequently; however, all growth stages of certain species, particularly the grasses and sedges, were eaten. By changing forage species, sheep were able to use early plant growth stages throughout most of the summer, stages which, as shown in other studies, are more palatable, most easily digested, and more nutritious than plants in advanced growth stages (Oelberg 1956).

Sheep generally fed with their heads close to the ground, except in low shrub or willow-alder when they often kept their heads raised as they moved from willow to willow. Sheep generally moved slowly forward, without raising their heads while feeding, although when feeding on tall shrubs, they moved more rapidly, often taking a few bites from one plant and then moving to the next.

Table 17 presents the species and amounts of those species eaten by sheep in the feeding sites. In feeding sites d and 21, no plants were found that had been grazed by sheep. Coverage values for

Table 17. Plant species and amount of each species eaten in each feeding site in the Sheep Creek study area in 1978¹.

Site	Species	Coverage (%)	Frequency of Occurrence (%)	Coverage Eaten ² (%)	Frequency Eaten ³ (%)	Plant Tissue Eaten (%)	Plant Parts Eaten
a	<i>Carex scirpoidea</i>	26.5	100	1.8	60	30	leaves
	<i>Elymus innovatus</i>	11.2	80	0.9	60	30	leaves
	<i>Calamagrostis purpurascens</i>	5.5	50	1.6	40	35	leaves
	<i>Artemisia alaskana</i>	6.8	50	10.5	30	33	new leaves + old stems
	<i>Zygadenus elegans</i>	0.1	10	5.0	10	50	leaves
	<i>Androsace chamaejasme</i>	0.7	40	< 0.1	10	25	flowers
b	<i>Dryas octopetala</i>	56.1	100	< 0.1	50	10	leaves, flowers
	<i>Diapensia lapponica</i>	8.1	60	0.1	10	10	leaves, flowers
	<i>Calamagrostis purpurascens</i>	2.1	50	4.0	20	40	leaves
c	<i>Arctostaphylos alpina</i>	3.0	30	< 0.1	10	75	leaves
	<i>Vaccinium uliginosum</i>	9.5	90	1.0	20	10	leaves, small stems < 1 mm in diameter
e	<i>Dryas octopetala</i>	7.5	40	0.5	10	25	leaves, flowers
	<i>Carex microchaeta</i>	6.5	90	0.5	10	10	leaves
	<i>Festuca altaica</i>	15.5	100	5.0	10	50	leaves
f	<i>Salix alaxensis</i>	22.0	80	1.1	20	5	leaves, flowers
	<i>Dryas octopetala</i>	24.0	90	1.0	30	25	leaves, flowers
	<i>Anemone parviflora</i>	4.0	80	< 0.1	10	5	leaves, flowers
	<i>Carex microchaeta</i>	5.7	80	< 0.1	30	10	leaves, flowers
	<i>Festuca altaica</i>	19.0	100	< 0.1	50	10	leaves
	<i>Vaccinium uliginosum</i>	4.0	30	0.5	10	20	leaves, flowers
g	<i>Carex scirpoidea</i>	10.5	90	1.0	30	20	leaves
	<i>Elymus innovatus</i>	9.3	60	< 0.1	10	33	leaves
	<i>Anemone parviflora</i>	2.8	100	1.0	20	50	leaves, flowers
	<i>Artemisia arctica</i>	0.6	70	1.0	20	10	leaves

¹In sites d and 21, no plants were eaten

²In percent of total coverage present for each species

³Based on 10 sample plots

Table 17. (continued)

Site	Species	Coverage (%)	Frequency of Occurrence (%)	Coverage Eaten (%)	Frequency Eaten (%)	Plant Tissue Eaten (%)	Plant Parts Eaten
g	<i>Carex microchaeta</i>	4.0	50	< 0.1	10	25	leaves, flowers
	<i>Boykinia richardsonii</i>	< 0.1	10	2.5	10	25	leaves
	<i>Ranunculus nivalis</i>	0.7	50	4.0	30	85	leaves, flowers
h	<i>Polemonium acutiflorum</i>	0.2	30	1.0	10	25	leaves
	<i>Salix bavelayi</i>	1.0	10	5.0	10	25	leaves
	<i>Boykinia richardsonii</i>	8.5	50	9.5	10	95	leaves, flowers
i	<i>Dryas octopetala</i>	27.0	100	< 0.1	30	20	leaves
	<i>Vaccinium uliginosum</i>	7.0	60	1.0	20	20	leaves
	<i>Salix reticulata</i>	3.0	50	< 0.1	10	50	leaves
j	<i>Dryas octopetala</i>	23.5	100	0.1	40	20	leaves, flowers
	<i>Vaccinium uliginosum</i>	14.5	100	3.1	80	25	leaves
	<i>Salix reticulata</i>	4.0	70	< 0.1	10	25	leaves
	<i>Carex microchaeta</i>	5.0	80	3.0	20	25	leaves
	<i>Pyrola grandiflora</i>	0.9	60	1.0	10	25	leaves, flowers
	<i>Astragalus umbellatus</i>	0.8	50	2.5	10	25	leaves, flowers
	<i>Festuca altaica</i>	5.5	40	0.5	10	10	leaves

species not eaten and that formed the remainder of the vegetation of the feeding site may be found in Tables 4 through 8, in which coverage values for all plants in the feeding and nutrient sites are included.

Generally, less than 40 percent of the above ground portion of a plant was observed eaten, although up to 99 percent of a plant was observed eaten. In the later case, the plants were small, solitary forbs such as *Anemone parviflora* or *Ranunculus nivalis*. An individual plant is defined here as the foliage developing from a single stem emerging from the ground or a discreet clump of grass-like plant.

In all feeding sites examined, less than 1.5 percent of the total plant coverage was removed. Similarly, Hjeljord (1971) reported that mountain goats (*Oreamnos americanus*) rarely removed as much as one percent of the above ground biomass on summer range feeding sites.

Daily Feeding Patterns

During the summer months, sheep were observed feeding during most times of the day. Feeding alternated with rest and rumination periods during the day, with a generally longer period of rest during midday; the most intense feeding periods were during early morning and late evening. Sheep were judged to be ruminating if they were bedded and if nearly continuous chewing was observed.

There appeared to be no distinct pattern of site selection for resting or rumination between feeding periods. Sheep would often bed in the general area where they had been feeding, often in the midst of other feeding sheep. Some individuals sought small outcrops or other areas slightly higher than the surrounding terrain for resting and ruminating. Ridge tops and rock outcroppings were used for extended rest periods during the night and occasionally for a long midday rest.

Feeding and rumination periods are presented in Table 18. Summer feeding and rumination periods average 1.0 hours and 0.9 hours, respectively. Average summer feeding periods of 1.6 hours and average rumination periods of 1.3 hours were reported by Whitten (1975) for sheep in Mt. McKinley National Park, Alaska.

Lamb Nutrition

Lambs began feeding on solid matter about two to three weeks after birth. While dependent on the ewe's milk, lambs would occasionally sample plant species that the ewe had fed on. As the lambs grew older, they began to feed more on vegetation. Lambs seemed to be particularly fond of flowers and often would feed exclusively on flowers, notably those of *Dryas octopetala*. Duration and frequency of suckling also decreased as the lambs grew and switched to plants. Some suckle durations are shown in Table 19.

Table 18. Duration of summer feeding and rumination periods for sheep in the Sheep Creek study area during 1978.
 (Dashes indicate the exact time was not recorded.
 Each feeding time is immediately followed by the
 the rumination time listed.)

Date	Age, Sex, and Number of Sheep	Feeding Time (minutes)	Rumination Time (minutes)
6 May	yearling ram	67	23
	2 1/4 curl rams	67	23
	7/8 curl ram	--	95
8 May	3/4 curl ram	--; 25	20; 35
	3/4 curl ram	--; 143	49; --
14 May	1/2 curl ram	--	52
10 Jun	ewe	72	59
	ewe	72	64
	ewe	77	59
12 Jun	ewe	135	49
	ewe	135	67
	2 ewes	127	34
	ewe	135; 50; 23	37; 28; --
	ewe	--; 60;	45; --
	1/2 curl ram	--; 6; 28; 21	25; 6; 6; --
13 Jun	ewe	86	44
29 Jun	ewe	61	24
	ewe	--	118
	ewe	--	136
	ewe	--	137
	2 ewes	--	95
	ewe	--	97
	ewe	--	109
	yearling	--	112
30 Jun	2 ewes	--	9
	3 ewes	--	29
	ewe	--	33
	yearling	--	33

Table 18. (continued)

Date	Age, Sex, and Number of Sheep	Feeding Time (minutes)	Rumination Time (minutes)
6 Jul	ewe	--	29
	ewe	25	40
26 Jul	yearling ram	--	58
	yearling ram	--	74
	yearling ram	--	84
28 Jul	ewe	--	26
	ewe, yearling	90	46
	2 ewes	--	95
	ewe	--; 9; 45	25; 67; --
	yearling ram	25; 24; 19	18; 42; --
	ewe	120	36
30 Jul	ewe	45	84
	ewe	52	67
9 Aug	ewe	59	8
16 Aug	ewe	23	--
	ewe	25	--
	ewe	58	--
18 Aug	ewe	--	66
	ewe	--; 53	68; 13
Average		60.7 minutes (1.0 hours)	53.3 minutes (0.9 hours)

Table 19. Durations of suckling by lambs in the Sheep Creek study area during 1977 and 1978.

Date	Duration of Suckling (sec)
26 May 1978	26
27 May 1978	10
31 May 1978	10;13
5 Jun 1977	5
26 Jun 1977	9
30 Jun 1978	8
18 Aug 1978	4; 6

Forage Selection

Krueger et al. (1974) reported taste to be the most important sense used by domestic sheep for forage selection. The other senses supplemented taste, although for certain plant species, sight and smell were important. Leuthold (1970) concluded that smell was the most important sense used in forage selection by the gerenuk (*Litocranius walleri*). Longhurst and Kepner (1968, cited by Krueger et al. 1974) determined that initial selection of forage by deer (*Odocoileus* spp.) is based on smell. Longhurst et al. (1968) found that taste served as a secondary means of selection for deer. Various volatile compounds within the plants are believed to be the indicators by which the animals discern palatability.

Dall's sheep appeared to use several senses to select forage. Sight was important, particularly when feeding on sparsely vegetated scree slopes. On these areas, sheep moved about the slopes, selecting primarily highly visible species such as *Senecio atropurpureus* and *Papaver alboroseum*, particularly when those species were in flower. At certain times, scattered tall willows on *Dryas* or *Dryas*-moss-*Cassiope* mats appeared to be chosen by sight. Smell, taste, touch, and sight were all probably involved in forage selection to some degree in those densely vegetated areas where sheep fed with their muzzles close to the surface. Species such as *Alnus crispa* and *Betula glandulosa* are generally not eaten by Dall's sheep, yet are relatively high in nutritive value when compared with other common

forage plants. Therefore, nutrient content alone does not account for differences in palatability.

Longhurst et al. (1968) believed that deer could not smell differences in nutritive quality in plants. They believed that deer were responding to differences in concentrations of volatile oils or other "indicator" compounds. Certain volatile substances have been found to inhibit and kill rumen microorganisms (Nagy et al. 1964; Oh et al. 1967; Longhurst et al. 1968; Nagy and Tengerdy 1968). In low concentrations, volatile compounds have very little impact on rumen microorganisms, but the inhibitory action increases with increasing concentration (Nagy and Tengerdy 1968). Plant species containing volatile substances with the most effective antimicrobial action or those with the highest volatile oil concentration have been shown to be the least palatable to deer (Longhurst et al. 1968; Nagy and Regelin 1977).

The concentration of various volatile substances has been found to vary with plant growth stage. Longhurst et al. (1968) found certain volatile substances present in mature needles of Douglas fir (*Pseudotsuga menziesii*), to be absent in new growth needles. Deer fed on new growth needles, but as the needles matured, the deer shifted their browsing to other plant species.

It therefore seems likely that selection of forage by Dall's sheep is also being influenced by plant volatile oils. The apparent low palatability of *Alnus crispa* and *Betula glandulosa* may be explained

by the presence of volatile resins that are found in the leaves and twigs (Viereck and Little 1972). Since these species are eaten to a very limited extent by sheep, it appears that if any substantial inhibitory effect on rumen function occurs, it does so only when substantial quantities of these plants are eaten. By eating small amounts of these species, sheep probably are able to benefit from the high nutritive value with little interference to normal rumen function. This situation has been described for mule deer (*Odocoileus hemionus*) feeding on sagebrush (*Artemisia* spp.) (Nagy and Tengerdy 1968).

Forage species become less palatable and digestible with maturity, as lignin and cellulose content increase (McLean and Tisdale 1960; Van Soest 1965; Dietz 1970; Mueggler 1970). Sheep tend to select new growth during the course of the summer by feeding in different vegetation types and at different elevations. Whether sheep are able to detect increased fiber content in forage by taste, texture, succulence, or smell is uncertain. Sinclair and Gwynne (1972), working with African buffalo (*Syncerus caffer*), concluded the tensile strength of grass leaves appeared to be an important factor in selection. They found that grass leaves with a high protein level broke more readily due to their lower fiber content, making them easier to eat. Field (1976) concluded that the amount of crude fiber does not influence the dietary preferences of African buffalo, but that a high silica content (5 to 6 percent) may reduce palatability. If sheep are able to detect increased fiber levels, selection could then be influenced

by that factor.

Although palatability and subsequently forage selection may be related to forage nutrient levels, which in turn are related to stage of plant growth, volatile compounds, silica, and fiber can play roles in forage selection. Therefore, it seems likely that sheep, as with deer, may not be selecting the nutrients necessary for maintenance and growth, but selecting against components which adversely affect the metabolizing of necessary nutrients.

Forage Quality

Nutrient levels of summer forage in the Sheep Creek area appear to be adequate for growth and maintenance of Dall's sheep, if the nutrient requirements of Dall's sheep are comparable to those of domestic sheep. Among domestic sheep, early-weaned lambs and/or ewes during the first eight weeks of lactation have the highest nutrient requirements (National Research Council 1975). Early-weaned lambs require the highest energy content and the highest protein content. Calcium and phosphorus requirements are highest for lactating ewes.

Protein levels of Sheep Creek area forage plants in early growth generally exceeded the levels required by early-weaned domestic lambs. By mid to late summer, average plant protein levels had dropped and no longer met the minimum requirements for lambs. Plant protein levels throughout the summer generally met the requirements of

lactating ewes. By selecting species with high protein content (e.g., willows) and feeding on early growth stage plants as the summer progressed, Dall's sheep were able to consume a sufficient amount of protein to meet their dietary requirements.

Magnesium content of Sheep Creek area forage plants met or generally exceeded the National Research Council requirements for domestic sheep (0.04 to 0.08 percent). All forages from the Sheep Creek area were within or surpassed these levels.

Calcium levels of 0.21 to 0.52 percent of the diet are recommended for domestic sheep by the National Research Council (1975). All forages from the Sheep Creek area equalled or exceeded the general recommendations, except for the grass *Hierochloe alpina*. However, several of the forage species did not contain the high calcium levels (0.52 percent) required by lactating domestic ewes, particularly in June, but also during July. *Dryas octopetala* and willows, major food items of Dall's sheep during June, had calcium levels well above the requirements for lactating domestic ewes.

Phosphorus requirements for domestic ewes range from 0.16 to 0.37 percent of the diet, with the greatest levels required by lactating ewes (National Research Council 1975). Sheep Creek area forage plant phosphorus levels generally were well within that range from late May through July. By mid-August, many of the species contained phosphorus in amounts below the minimum level, although several forbs and willows still contained adequate amounts. As in the case

of calcium, the phosphorus content of many plants did not meet the requirements of lactating domestic ewes.

Forage quality during winter is radically different than that during summer. The few winter samples from Sheep Creek indicate that crude protein and phosphorus levels are below the maintenance requirements of domestic sheep. Similar results have been found on other Dall's sheep winter range (Nichols 1974; Whitten 1975), and on bighorn sheep range (Demarchi 1968). Calcium and magnesium levels remained above the minimum requirements for domestic sheep.

Sheep Creek area forage is very high in nutrients during early summer and provides a high plane of nutrition for lactation, growth, and development. Quality declines as plants mature, and by late summer some nutrients may not meet optimum growth requirements for sheep in specific age, sex, and body condition classes. By winter, quality has declined to the point where some nutrient levels are below body maintenance requirements.

HABITAT UTILIZATION

Sheep Distribution and Movements

Mineral licks are used by sheep upon leaving their winter ranges and prior to occupying summer range (Jones 1963b; Geist 1971; Heimer 1973; Summerfield 1974). Consequently, mineral licks are thought to have a major influence on sheep distribution and movements (Jones 1963a,b; Erickson 1970; Pitzman 1970; Heimer 1973).

Within the Sheep Creek study area there are two major, heavily used and several small, scattered, occasionally used mineral licks. The largest mineral lick is located approximately at the 1400 m level of the ridgeline separating the two forks of Sheep Creek. The other heavily used mineral lick, which I have called the Robertson mineral lick, is located approximately 5.5 km southeast of the Sheep Creek mineral lick and slightly below the summit of one of the passes leading from Sheep Creek to the Robertson drainage portion of the study area.

Sheep began to use the Sheep Creek mineral lick by early June. The period of heaviest use was late June to mid-July. By late July, use of the Sheep Creek mineral lick had decreased to levels similar to those found in early June. During late July and during August, activity at the Sheep Creek mineral lick was limited to less than 30 sheep.

Sheep activity at the Robertson mineral lick increased during late July and use of this mineral lick continued until observations

in this area ended 20 August. Up to 54 sheep were seen at this mineral lick. Prior to 20 July, little activity was noted at this mineral lick.

Daily observations of sheep were usually restricted to either fork of Sheep Creek or to one drainage within the Robertson portion of the study area. All portions of Sheep Creek, the remainder of the Tanana drainage, or the entire Robertson drainage could not be viewed completely within a short time; therefore an accurate count of the total number of sheep in the area was not possible.

Numbers of sheep in Sheep Creek and the remainder of the Tanana drainage portion of the study area varied considerably from season to season. The Tanana drainage was used by some sheep as winter range, although exact number or age and sex composition data are not available. On 28 March 1978, three ewes, one lamb (short yearling), and three rams were observed on snow-free slopes of Sheep Creek. On 29 March 1978, two ewes, one lamb, and five rams, some of which were probably sighted the previous day, were observed in the same general area. Undoubtedly, more sheep were present within the Tanana drainage portion of the study area since all areas were not seen and some sheep may have been overlooked on snow-covered slopes.

Numbers of sheep increased in Sheep Creek during May, usually ranging from 20 to 50 animals. Most were rams, occurring singly or in small groups of two to six rams, although bands composed of as many as 20 rams were seen. Ewes and yearlings were also present

during May; their numbers slowly increased as June approached. Small rams (yearlings to three quarter curl rams) were often associated with the ewe-juvenile bands throughout the summer. Lambs were first sighted on 17 May 1977 and 25 May 1978.

By the first week of June, most large rams (three quarter curl and larger) had left Sheep Creek, although occasional bands of three to six rams were still seen in the area. Whether the rams moved to other portions of the Tanana or Robertson drainages, or to areas within the Robertson River drainage outside the limits of the study area was unknown.

Numbers of sheep continued to increase in Sheep Creek during June. Daily observations revealed that numbers of sheep ranged from 2 to 88 sheep, with the average number approximately 40 sheep, in either of the forks of Sheep Creek. Much of the area of both forks of Sheep Creek could be seen from a ridgeline between the two forks and on one occasion, 27 June 1977, 232 sheep (73 lambs and 159 non-lambs) were seen, 40 lambs and 83 non-lambs within the main fork and 33 lambs and 76 non-lambs within the west fork. This was the largest number of sheep seen within Sheep Creek and numbers of sheep remained at this level for only about two weeks.

During July and August 1978, approximately every other week was spent observing sheep in the Robertson drainage portion of the study area. During these periods, numbers of sheep in the Robertson portion of the study area ranged from 60 to 100 animals, with few large rams

present.

Twelve neck-collared ewes and one ear-tagged yearling ram and one lamb, marked by the Alaska Department of Fish and Game at the Sheep Creek mineral lick during 1977 and 1978 (a total of 40 sheep were tagged during 1977 and 1978, Wayne Heimer, Alaska Department of Fish and Game, pers. comm.), were seen during July and August in the Robertson drainage. Ten collared ewes were sighted in the Robertson drainage on more than one occasion. This indicated that some of the sheep which occupied summer range in the Robertson drainage used the Sheep Creek mineral lick and the surrounding area.

After 20 July 1978, sheep activity in the Sheep Creek mineral lick and drainage decreased considerably. After this date, no more than 30 sheep were seen in the area. Sheep activity was primarily confined to the mineral lick and to the main fork of Sheep Creek, the major route leading from the Sheep Creek mineral lick to summer range in the Robertson drainage. Sheep activity in the west fork of Sheep Creek and in the other drainages in the Tanana portion of the study area was minimal during this period.

Use of Vegetation Types

Dall's sheep used a variety of different vegetation types during the spring and summer months, although not all vegetation types were used equally. Figure 9 presents the observations of patterns of use of vegetation types by sheep for all activities during summer 1978.

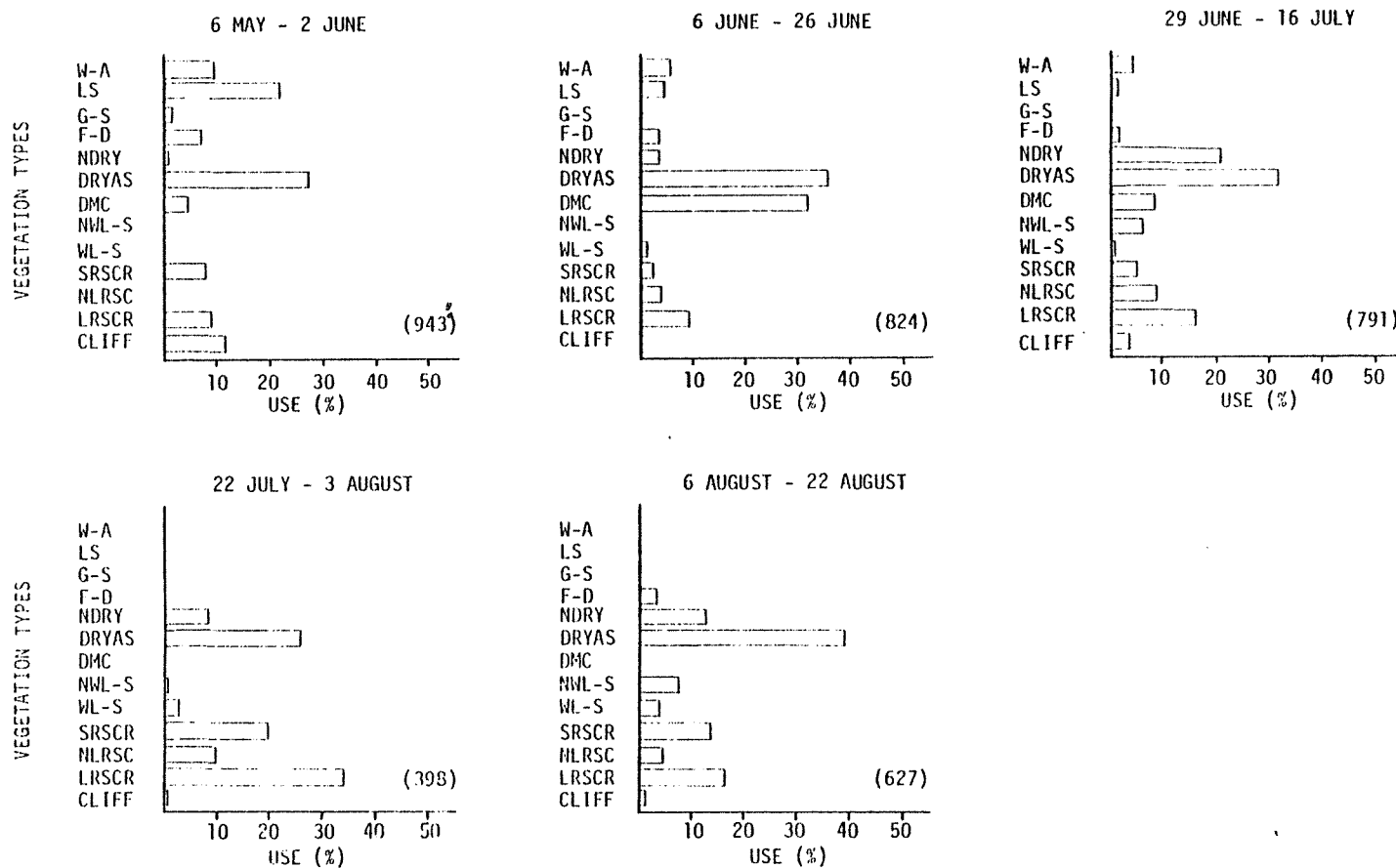


Figure 9. Patterns of use of vegetation types by sheep for all activities during summer 1978 in the Sheep Creek study area. (The number in parentheses indicates the total number of observations, excluding lambs. W-A = willow-alder; LS = low shrub; G-S = grass-sedge; F-D = *Festuca-dryas*; NDRY = north-facing *Dryas*; DRYAS = *Dryas*; DMC = *Dryas-moss-Cassiope*; NWL-S = north-facing wet low-*Salix*; WL-S = wet low-*Salix*; SRSCR = small-rock scree; NLRSC = north-facing large-rock scree; LRSCR = large-rock scree; CLIFF = cliff)

Observations of use of the same vegetation type, but in different locations, were combined for each date. Observations of use of vegetation types for the Robertson and Tanana drainages were combined for the July and August intervals. These observations were divided into five time intervals, delineated by my short absences from the study area. Vegetation types were not observed equally during the summer nor were rams and ewes observed proportionately to their presence in the study area. These factors and the changing patterns of use of vegetation types during the summer prevented an estimation of total use. Lambs have been excluded from the observations because they are always associated with ewes, and their presence in a vegetation type does not therefore denote selection (Whitten 1975).

Use of vegetation types by sheep for all activities changed during the course of the summer (Figure 9). In May, most of the sheep activity was concentrated in willow-alder, low shrub, cliff, and *Dryas* vegetation types. These areas occurred primarily on south-facing slopes that were essentially snow-free and where new plant growth was present. During June, use shifted to primarily *Dryas* and *Dryas*-moss-*Cassiope* slopes. These areas were heavily used by sheep leaving the Sheep Creek mineral lick. During the first half of July, use of *Dryas* and north-facing *Dryas* essentially replaced that of *Dryas*-moss-*Cassiope*, which had been heavily used during June. Use of large-rock scree and north-facing large-rock scree also increased during this period. During the last half of July, sheep used the sparsely

vegetated scree slopes to a great extent, with the remainder of vegetation type use contributed by *Dryas* and north-facing *Dryas*. During this interval and for the remainder of the summer, willow-alder and low shrub, both low altitude vegetation types, were not used. Use of scree slopes in August decreased somewhat in favor of the more densely vegetated *Dryas*, north-facing *Dryas*, *Festuca-Dryas*, and the north-facing wet low-*Salix* vegetation types.

The pattern of use of vegetation types by feeding sheep (Figure 10) was similar to that for all activities. Use of small-rock scree for feeding in late July was less than half that for the total use of small-rock scree, and during August feeding in small-rock scree was not observed. The areas of small-rock scree were primarily the two mineral licks and the preferred bedding sites, areas where little feeding occurred.

Jones (1963b), working with low quality Dall's sheep populations in the Dry Creek area of the central Alaska Range, recorded use of vegetation types during June and July 1962. He found little use of *Dryas*-moss-*Cassiope* or scree slopes in Dry Creek, two heavily used vegetation types in the Sheep Creek area, during either June or July. *Dryas* mat vegetation was more important to the Dry Creek sheep than to the Sheep Creek sheep during June, particularly in the last half of June. The *Dryas*/sedge vegetation type in Dry Creek was greatly used during July, especially in late July. This vegetation type was not found in the Sheep Creek area.

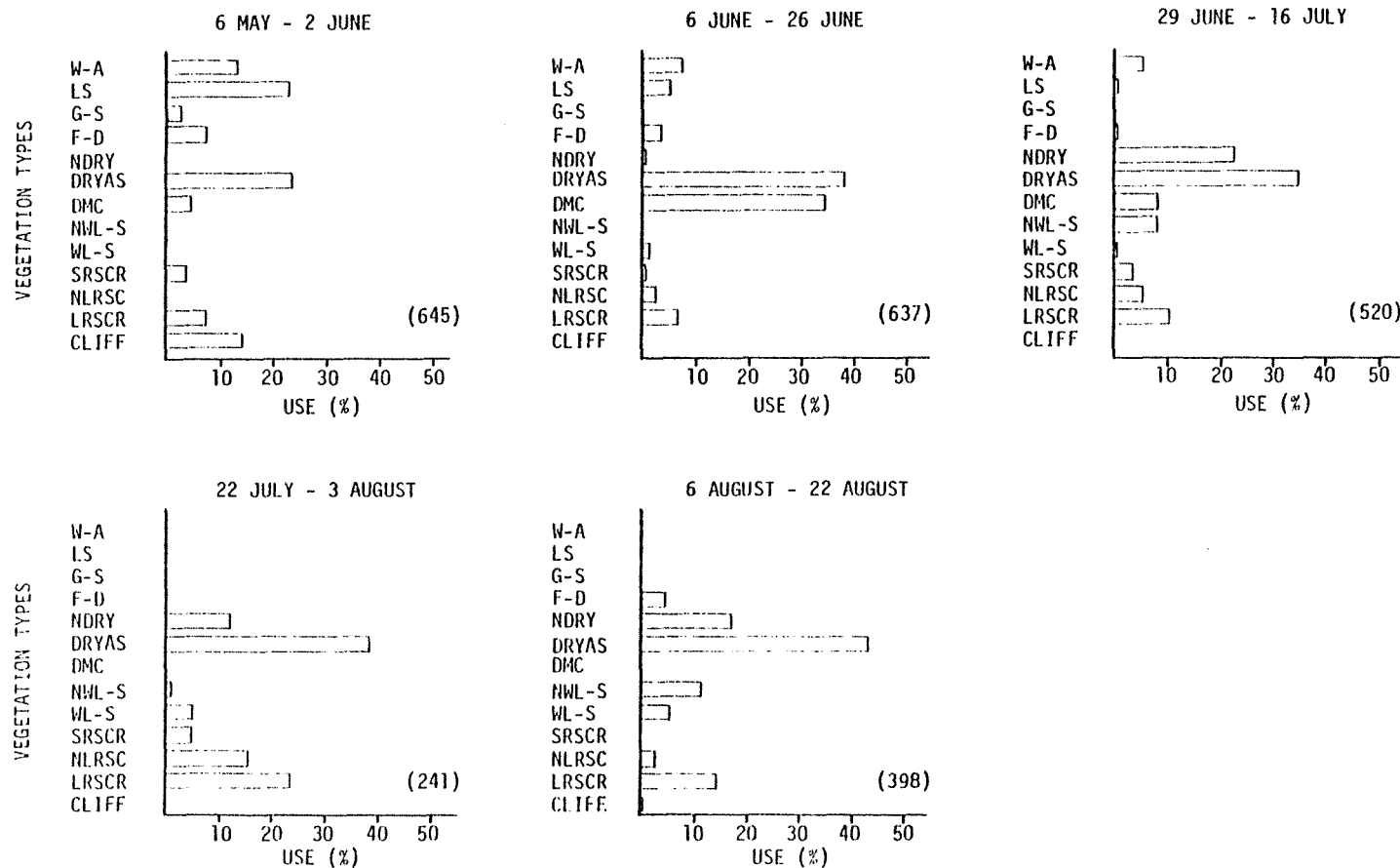


Figure 10. Patterns of use of vegetation types by sheep for feeding during summer 1978 in the Sheep Creek study area. (The number in parentheses indicates the total number of observations, excluding lambs. W-A = willow-alder; LS = low shrub; G-S = grass-sedge; F-D = *Pentstemon-Dryas*; NDRY = north-facing *Dryas*; DRYAS = *Drumstick*; DMC = *Dryas-moss-Cassiope*; NWL-S = north-facing wet low-*Galix*; WL-S = wet low-*Galix*; SRSCR = small-rock scree; NLRSC = north-facing large-rock scree; LRSCR = large-rock scree; CLIFF = cliff)

Whitten (1975) found that willow-alder and shrub tundra accounted for over 75 percent of the use of vegetation types during late May-early June in McKinley Park, a considerably higher use of these types than that by sheep in the Sheep Creek area or at Dry Creek. Use of south-facing *Dryas* in McKinley Park during this period was considerably less than that in the Sheep Creek area. Use of willow-alder and shrub tundra in McKinley Park dropped to levels comparable to those from the Sheep Creek area during mid-June to mid-July. Small-rock scree and south-facing *Dryas* were used more in McKinley Park than in Sheep Creek during mid-June to mid-July. Use of vegetation types from mid-July through August in McKinley Park and the Sheep Creek area were quite similar.

Generally, use of vegetation types by sheep in the Sheep Creek area follows that reported for sheep in other areas in Alaska, with some differences arising from the physiography and vegetation specific to each area.

Altitudinal Migration

Concurrent with shifting patterns of use of vegetation types, altitudinal migration was a major component of summer habitat use. Altitudinal distributions of sheep were combined for all vegetation types and are presented for 1978 in Figure 11. Observations of altitudinal distributions of sheep are divided into the same time intervals as was use of vegetation types.

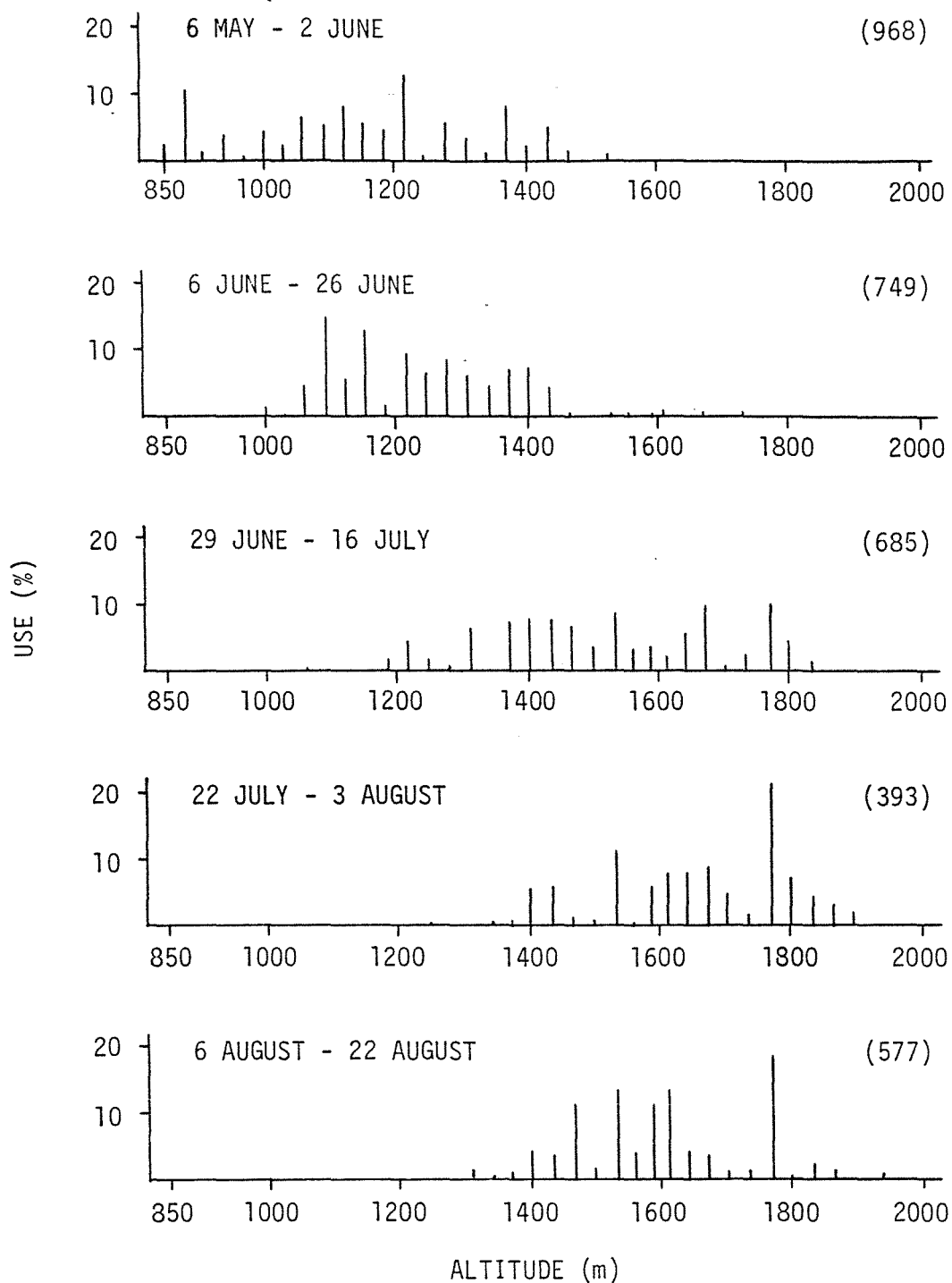


Figure 11. Altitudes of summer habitat used by sheep in the Sheep Creek study area during summer 1978. (The number in parentheses indicates the total number of observations, excluding lambs.)

In May, sheep in Sheep Creek ranged between 850 and 1675 m, with the majority of sheep activity distributed between 850 and 1460 m. Most of the areas occupied by sheep were windblown, south-facing slopes supporting some new plant growth at altitudes from 850 to 1300 m. During May, sheep were observed at the lowest elevations of their summer altitudinal range.

In June, altitudinal distributions of sheep ranged from 1000 to 1735 m, although most of the sheep activity was between 1065 and 1430 m. The bulk of this activity occurred on *Dryas* and *Dryas*-moss-*Cassiope* slopes which sheep frequented after leaving the Sheep Creek mineral lick.

In the first half of July, the altitudinal distribution of sheep was between 1065 and 1830 m, with the majority of sheep activity between 1200 and 1800 m. As can be seen from Figure 11, sheep were more evenly distributed among the range of altitudes during this time interval than they were at any other time. During the second half of July, sheep reached their maximum altitudinal advance for the summer, and were primarily between 1525 and 1860 m. The peak of activity at 1765 m was caused by the presence of the Robertson mineral lick at this elevation and the extensive use of this mineral lick and its immediate surrounding area by sheep during mid and late summer.

During August, sheep began to descend slightly from their late July maximum altitudinal distribution. The major sheep activity at this time was confined to habitat between 1460 and 1765 m. Four sheep

were observed at 1920 m during this period, the highest altitude at which sheep were observed during this study.

Altitudinal distributions of feeding sheep (Figure 12) showed the same general pattern as did altitudinal distribution for all activities. In May, sheep were widely distributed altitudinally due to their feeding in a variety of snow-free vegetation types. Some of the lower altitude vegetation types were particularly heavily used, notably low shrub and to a lesser extent willow-alder, grass-sedge and *Festuca-Dryas*. Feeding activity in June was concentrated between 1000 and 1400 m, primarily on south-facing *Dryas* and north-facing *Dryas*-moss-*Cassiope* slopes. In early July, sheep continued their altitudinal advance, primarily feeding between 1300 and 1600 m on *Dryas* slopes. Increased feeding in large-rock scree and in moist, north-facing *Dryas*, and in wet low-*Salix* occurred at this time. In late July, feeding was concentrated above 1500 m, in sparsely vegetated scree and in *Dryas* characterized by small mats separated by scree. Sheep were descending to and feeding at altitudes from 1400 to 1600 m in August. They had abandoned much of the large-rock scree slopes for feeding and returned to the more densely vegetated *Dryas*, north-facing *Dryas*, *Festuca-Dryas*, and north-facing wet low-*Salix* vegetation types. This movement possibly reduced the energy cost to sheep of acquiring food by feeding in more densely vegetated areas, but at the expense of slightly lower quality food. This expense was probably partially offset by the sheep's increased feeding in moist north-facing *Dryas* and

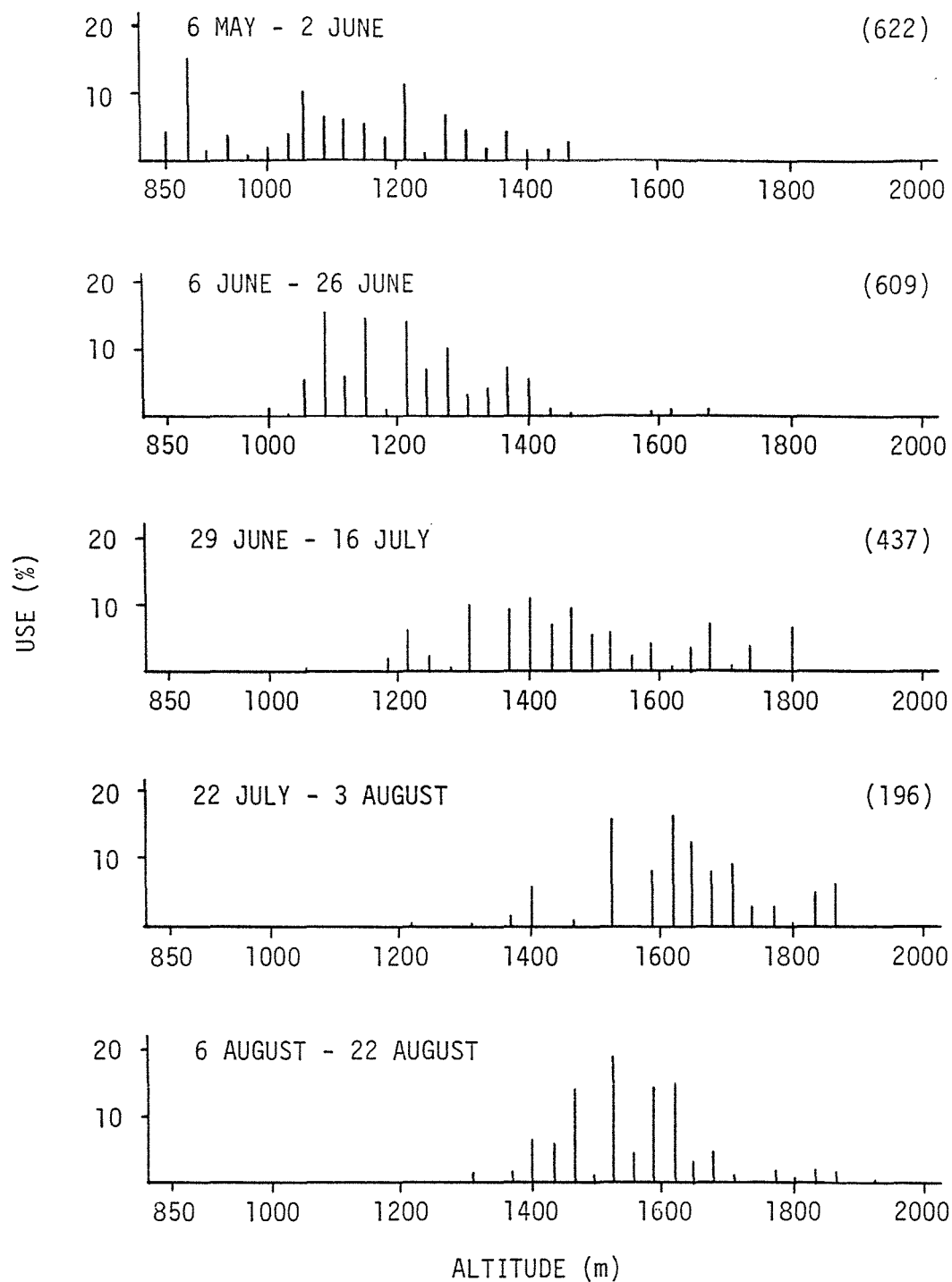


Figure 12. Altitudes of summer habitat used by sheep in the Sheep Creek study area for feeding during summer 1978. (The number in parentheses indicates the total number of observations, excluding lambs.)

north-facing wet low-*Salix*, areas where plants were at presumably slightly younger stages of growth and thus more nutritious.

Jones (1963b), working with Dall's sheep in the Dry Creek area, found a gradual upslope movement of sheep beginning in early June and continuing until early August when habitat at the maximum of the summer altitudinal distribution was used. In early June at Dry Creek, most sheep were found between 1065 and 1370 m. By late June, maximum concentrations of sheep were found at 1370 m. During the first half of July, the upslope movement continued, with sheep primarily concentrated between 1370 and 1675 m. Altitudinal advance continued during late July and the first week of August, with all sheep found between 1370 and 1830 m. As in early July, the majority of sheep were found at 1525 m. Subsequent movements were not observed, although a local guide reported that sheep usually began moving downward in altitude in mid-August.

Jones (1963b) recorded altitudinal distributions of sheep at approximately 150 m intervals beginning at approximately 760 m. If altitudinal distributions of sheep in the Sheep Creek area are described in a similar manner by combining altitudinal distributions for approximately 150 m intervals centered on the intervals selected by Jones (1963b), comparisons between the two areas reveal the following. In the Sheep Creek area from 22 July to 3 August, sheep were using habitat at altitudes higher than that used by the sheep in Dry Creek during the period of 16 July to 5 August. During the period from

6 August to 22 August, sheep in the Sheep Creek area were located in habitat at altitudes still slightly higher than the altitudes occupied by Dry Creek sheep for the period 16 July to 5 August. If only altitudinal distributions of feeding sheep from Sheep Creek are used, sheep were still found at higher altitudes from 6 August to 22 August when compared with altitudinal distributions of sheep in the Dry Creek area during 16 July to 5 August. Thus, it appears that sheep in the Sheep Creek area are using habitat at higher altitudes and for a longer period than do sheep in the Dry Creek area.

Whitten (1975) reported sheep in McKinley Park remained on lower slopes feeding on willow-alder and shrub tundra until mid-June when a general upslope movement began. Sheep moved progressively higher during the summer, using primarily *Dryas* slopes in early summer and then shifting their vegetation type use to scree slopes and ridgetops at higher altitudes during the latter part of the summer. Upper north-facing slopes were the last summer habitats reoccupied by sheep.

Dall's sheep in the Peters Creek area of the Chugach Mountains in southcentral Alaska moved to lower slopes at or just above the brushline following snowmelt in spring (Erickson 1969). Upward movement was thought to be influenced more by the greening of vegetation than by the melting of snow since the upper slopes were largely snow-free well before sheep returned to them.

Summerfield (1974) also found an upward drift in elevation for Dall's sheep in the Atigun Canyon area, Brooks Range, Alaska. Sheep

were seen at elevations ranging from 760 to 1525 m, with the highest elevations reached in mid-July, followed by a shift to habitat at lower elevations by early August.

Hoefs (1975) reported that Dall's sheep on Sheep Mountain in the Yukon Territory, Canada, began following the altitudinal advance of plant phenology during late May, with ewes using habitat at higher elevations sooner than rams. Rams reached their highest mean elevation during August, approximately 150 m higher than nursery bands. Descent of the nursery bands began in late August, with rams descending in mid-October.

It appears that all Dall's sheep populations migrate altitudinally to some degree. By doing so, they are able to benefit from foraging on highly nutritious plants in early stages of growth for a longer period of time and maintain a high plane of nutrition for a longer period of time than if no altitudinal migration occurred.

DISCUSSION

Among mountain sheep populations there exist differences in behavioral, demographic, and morphological characteristics. From observations of bighorn and Stone's sheep, Geist (1971) hypothesized that differences in such characteristics were the result of differences in the amount of energy available to each population.

Geist (1971) stated that high quality populations would be expected during colonization or expansion periods when abundant high quality forage is available; low quality populations would occur in stable or declining situations. High quality populations would be characterized by more fecund, large, early maturing, vigorous, short-lived individuals which grow large skulls and horns, interact socially more frequently and intensely, and have ewes which suckle lambs for longer durations and refuse suckling attempts less frequently. Conversely, low quality populations are characterized by individuals which grow slower, mature later and live longer, grow smaller bodies and horns, interact less frequently and intensely, are less fecund, and have ewes which suckle lambs for shorter periods and refuse suckling attempts more frequently.

Shackleton (1973), from observations of expanding and stable populations of bighorn sheep, supported some of the aspects of Geist's (1971) population quality hypothesis. He found larger skull dimensions, shorter life expectancy, advanced social maturity, faster

growth rates, and greater lamb suckle durations and play periods in the expanding population. The differences in the characteristics between the populations were attributed to differences, based on lamb nursing and play behavior, in the bioenergetic regimes of each population. The extent of the seasonal altitudinal migration was believed to be an important factor contributing to the amount of energy available to each population.

Seasonal altitudinal migration has been shown to be an important characteristic of ungulates. A number of factors have been proposed as the causative agents of altitudinal migration, among them are nutritional benefits accrued by following newly emergent plant growth (Blood 1963; Hebert 1973; Shackleton 1973), weather factors (Edwards 1956; Nichols 1972), insect harassment (Egorov 1967; Summerfield 1974), and combinations of forage and weather factors (Blood 1963; Hoefs 1975). Internal motivation synchronized by these and other external environmental factors have also been suggested as the cause of migrations (Geist 1971).

Sheep in the Sheep Creek area, by undertaking summer altitudinal migration, are able to maintain a high plane of nutrition, since plants growing at higher elevations are nutritionally superior to similar species growing at low elevations (Johnston et al. 1968; Hebert 1973) and are also more palatable and digestible (Dietz 1970; Hebert 1973). This increases the amount of nutrients and energy available for growth and replenishment of body stores for much of the plant growing season.

Concurrent with altitudinal migration, sheep altered their patterns of use of vegetation types and their patterns of use of the exposure of the terrain containing these vegetation types. North-facing slopes support younger growth stages of plants due to generally cooler temperatures arising from less direct insolation and often from abundant moisture from persistent snow patches. In addition, early drying of soil on the south-facing slopes makes plants mature earlier, which in turn, hastens the seasonal changes in chemical composition (Laycock and Price 1970). Plants inhabiting north-facing slopes maintain their nutrient contents at levels which effectively extend the availability of highly nutritious, easily digestible, early growth stages of forage into late summer, although moist sites are not entirely restricted to north-facing slopes during summer. The increased feeding by sheep in the north-facing wet low-*Salix* vegetation type during August undoubtedly provided a considerable nutritional advantage due to the presumed higher quality plants present in these moist areas.

Another means by which Dall's sheep increase the nutritional quality of their summer diet, concurrent with altitudinal migration and vegetation type use changes, is by changing the species composition of their diet during the course of the summer. Feeding primarily on newly emerging grasses and sedges in early spring, sheep then shift their foraging emphasis to emerging willow leaves and catkins, structures high both in nutritional quality and digestibility. As

summer progresses, more use of forbs at higher elevations occurs, continuing the progression of use of early stages of plant growth.

Differences in the extent of topographic relief found in the areas inhabited by populations of sheep could influence nutritional levels by limiting the extent of altitudinal migration and subsequent use of plants in early stages of growth. The Sheep Creek area is slightly higher than the Dry Creek area, with slightly more area above 1830 m. Also, based on width of map contour intervals, terrain in the Sheep Creek area appears to be steeper than the terrain in the Dry Creek area. The steeper slopes in the Sheep Creek area could provide a greater amount of plants in early stages of growth by restricting the amount of insolation reaching north-facing slopes, causing slower snow melt and delaying plant growth in these areas. Plants growing in these areas would then be more nutritious later in the plant growing season.

In McKinley Park, the sheep population studied by Whitten (1975) used primarily the "outer range" of the Alaska Range. Most of the relief in this area is below 1900 m, substantially lower than that of either the Dry Creek or Sheep Creek area. This lowered range of relief may express itself through smaller body and horn sizes, the result of a shorter duration of plants in early stages of growth available to sheep, which would limit the amount of energy and nutrients that could be channelled into growth and development.

The southeast portion of the Wrangell Mountains produce the

largest Dall's rams in Alaska, possibly the result of the greater relief found in the area and the slightly lower latitude, both factors which could contribute to a greater distribution in time and space of plants in early stages of growth.

Klein (1965, 1970) proposed that the crucial factors causing differences in growth and body size of deer (*Odocoileus hemionus*) in Alaska were the altitudinal range, slope, and exposure of the areas inhabited by deer. He argued that since plants in early growth stages are the most nutritious, deer populations inhabiting areas with greater topographical variation will have an increased period over which to feed on high quality vegetation compared to deer populations with a more restricted altitudinal range. Klein (1970) also suggested that mountain sheep and mountain goats were similarly affected by topographic variation.

Shackleton (1973) reported differences in lamb suckling behavior and growth rates and dimensions of horns and skulls between two populations of bighorn sheep in the Canadian Rocky Mountains. He speculated that these differences were due to a much greater altitudinal range used by one of the populations, allowing it much greater use of new vegetation growth.

Whitten (1975) similarly suggested that it is not the peak quality of forage itself, but rather the amount and duration of high quality forage that determines sheep growth. He further suggested that in areas where larger animals occurred, greater topographic variability

was likely to occur, providing a wide spread in both time and space.

The length of the plant growing season, particularly the time of the onset of plant growth in the spring, is an important parameter affecting the nutritional regime of sheep and other northern ungulates. New plant growth provides abundant energy and protein, which in spring is used to replenish body stores used for winter maintenance and for support of final fetal growth and subsequent lactation. If plants begin growing earlier in a particular area, depleted body reserves may be replenished earlier, allowing more nutrients to be available for body and horn growth. Thus, the earlier the onset of spring growth, the greater the nutritional advantages are to the individual sheep.

The plant growing season appears to start earlier in the Sheep Creek area than in McKinley Park. The emergence of new leaves on shrubs occurred about one week earlier in the Sheep Creek area than in McKinley Park. Weather records (U.S. Dept. of Commerce 1956-1978) indicated that for the growing seasons compared, McKinley Park was colder and had more snow than the Sheep Creek area. However, comparisons with long-term averages indicated that the mean air temperature at McKinley Park during April 1973 was 2.7°C warmer than average, whereas the mean air temperature at Tok in April 1977 was 1.0°C above average. Mean air temperature during May at both areas for both years departed from normal by -0.3°C. In June, the mean air temperature at Tok departed from normal 1.6°C more than did the mean air temperature at McKinley Park. Snow data for March and April indicated

that although McKinley Park had a greater amount of snow in March 1973 than did Tok in March 1977, maximum snow depths in both areas were approximately 25 percent below the long-term average. In April, maximum snow depths were equal in both areas, although snow depth was 41 percent below average in McKinley Park in 1973 whereas it was only 17 percent below average at Tok in 1977. These data suggest that the growing season at McKinley Park in 1973 probably started earlier than normal and that there is a difference in the start of the plant growing season between McKinley Park and the Sheep Creek area. However, since the weather recording stations in both areas are some distance from the sheep range and the McKinley Park weather recording station is approximately 135 m higher than the Tok station, precise comparisons cannot be made.

The latitudes of McKinley Park and the Sheep Creek area are approximately equal and thus latitude is not a factor influencing the start of the growing season in this situation, although it is an important factor when comparing some other sheep populations. Sheep populations in the Wrangell Mountains and at Sheep Mountain, Yukon Territory, both with similar horn growth characteristics (Hoefs 1975), and both approximately two degrees of latitude farther south than Sheep Creek, may have part of their large body and horn size differences due to the earlier availability of new growth forage. Hopkins (1920) states that each degree of latitude produces a four day change in plant growth phenology. Flowering data indicate that the difference

in plant growth phenology between Sheep Mountain and Sheep Creek may be slightly less than the predicted amount.

Differences in rumination times should reflect differences in forage quality. Passage of forage through the digestive system is inversely related to forage quality; this is, the higher the forage quality, the shorter the time required to digest the forage and eliminate any undigestible material (Tyler 1964). As a forage matures, fiber and lignin increase, requiring more effort on the part of the ruminant to mechanically break down the structural tissue of the plants. Digestibility of forages by rumen microorganisms also decreases as lignin and fiber content increases (Church 1976). The breakdown of plant tissue is thus of paramount importance since particle size largely determines the retention time of food residues within the digestive tract (Freer and Campling 1965). Consequently, ruminants feeding on a higher quality forage should have shorter rumination times than ruminants consuming poorer quality forage.

Sheep Creek and McKinley Park sheep may be consuming forage of differing quality. Average rumination periods of 0.9 and 1.3 hours were recorded for Sheep Creek and McKinley Park sheep, respectively. If the above precepts are correct, the sheep of the Sheep Creek area should be selecting forage of higher quality than the sheep in McKinley Park. Previously, it was shown that no significant differences existed in nutrient values between plants of Sheep Creek and McKinley Park and that species selected for food were generally the

same although differences did exist. These factors probably did not contribute substantially to the differences in average rumination times. It appears that the major factor that contributed to the differences in rumination times may be the extent of the altitudinal migration and the subsequent ability of the sheep to select higher quality, more easily digestible forage at the higher elevations in the Sheep Creek area during the course of the summer.

Since primarily ewe-juvenile groups were observed during this study, and these observations are being used to describe horn and body growth in both ewes and rams, the argument may be raised that these results may not be indicative of the actual situation in rams. The highest horn and body growth rates for rams occur during their first four years, with most of the maximum body weight attained near six years of age (Bunnell and Olsen 1976), and most horn growth by seven years of age (Heimler and Smith 1975). Young rams usually leave the ewe-juvenile bands when they reach two to four years of age (Geist 1971), join ram bands, and establish permanent home range patterns. Bunnell (1978) has suggested that the condition of the ewe during pregnancy and birth affects the horn growth of rams, perhaps for the succeeding five years. Cumulative horn growth is also depressed during years of low forage production (Bunnell 1978). Therefore, since nutritional conditions have the greatest influence on growth and development during the first few years of life, it would appear that observations of ewe-juvenile feeding ecology would be at least

indicative of the nutritional situation in rams.

While no data are available which describe forage species selection differences between ewes and rams, some observations of altitudinal distributions of sheep in early and late summer may indicate that rams are less selective foragers than ewes. Hoefs (1975) noted that during the early summer altitudinal migration rams followed the phenological advance of vegetation less closely than did ewes, while the ewe-juvenile bands appeared "to be in a hurry to reach alpine elevations." He suggested this difference in feeding behavior may be due to ewes with lambs desiring to be in proximity to escape terrain which is largely at alpine elevations. Vertical descent of ewe-juvenile groups on Sheep Mountain took place in late August (Hoefs 1975), while rams remained at alpine elevations for an additional four to six weeks. Ewe-juvenile bands in the Sheep Creek area began their descent to more densely vegetated slopes by mid-August. Since few rams were seen in the Sheep Creek area during August, statements concerning their altitudinal distribution at this time are limited. The few large rams observed during August were either at elevations higher than the ewe-juvenile bands or were using vegetation types (i.e., scree) different from those used by ewe-juvenile bands (i.e., *Dryas*, *Festuca-Dryas*, wet low-*Salix*). Rams were not seen feeding in areas supporting young plant growth during August, areas favored by ewe-juvenile bands.

This pattern of early altitudinal advance and subsequent descent of ewe-juvenile bands when compared with ram movements may indicate

that sheep in the ewe-juvenile bands change their altitudinal distribution to select higher quality forage more so than do rams. The increased nutritional demands of lactation over that of normal growth and development may be the factor inducing this proposed difference in forage selection. Lactating ewes, lambs, and juvenile sheep may have greater need than do rams for the higher nitrogen and digestible energy content found in the earliest plant growth stages for replenishing body stores, growth, and development. Since nitrogen levels of Sheep Creek forage plants generally exceed the nitrogen requirements of domestic sheep, it is probably the greater digestible energy content which the sheep in the ewe-juvenile bands are seeking.

Geist and Petocz (1977) proposed from winter range observations of bighorn sheep that rams segregate from ewes to minimize competition for resources between themselves and present and future offspring. Such may be the case for Dall's sheep on summer range, at least in the Sheep Creek area. By segregating from ewe-juvenile bands during summer, direct competition would be avoided, allowing maximum use by ewes and juveniles of the highest quality forage on the range. This would be particularly important during the late summer when areas of younger growth stage plants are less abundant and yet heavily used by the ewe-juvenile bands.

Variations in the pattern of horn growth in sheep has been shown to be associated with population quality (Shackleton 1973; Bunnell 1978), as predicted by Geist (1971), and has even been used to define

quality (Heimer and Smith 1975). Horn growth in sheep follows the pattern of rapid early growth, producing large annual increments in the first few years of life, followed by a decrease in the size of the annual increments during the remainder of the individual sheep's life. Generally, in high quality sheep populations, sheep have more rapidly growing and larger horns than do sheep in low quality populations. This pattern has been attributed to differences in the bioenergetic regime of the populations (Geist 1971; Shackleton 1973; Bunnell 1978).

Shackleton (1973) found increased horn growth in high quality populations only during the early years of life. In later years, however, annual horn growth was found to be equal to or less than that of similar aged sheep from poor quality populations. This difference in horn growth rate was attributed to the overall faster growth rate of sheep from the high quality population, resulting in these animals reaching adult size at an earlier age and then reducing or ceasing further growth. The slow growing sheep in the low quality populations had not yet reached adult proportions and were still physically immature and increasing in size when high quality sheep had reached adult size, thus producing annual horn increments in the low quality sheep equal to and often larger than increments from high quality sheep.

Rams from Dall's sheep populations in Alaska also exhibit variation in the rate and extent of horn growth (Table 20). The age of average maximum horn growth (see Heimer and Smith 1975) is five

Table 20. Ram horn growth characteristics of Alaskan Dall's sheep populations.
(Adapted from Heimer and Smith 1975)

Mountain Range/Area	Sample Size	Mean Volume at 7 Years (mm ³ in thousands)	Mean Maximum Sustained Growth Rate (mm ³ in thousands/year)	Maximum Growth (years)
Wrangell Mountains ¹ WMR III	14	1921 ± 381	426	5
Alaska Range East				
² ARE I	65	1282 ± 284	282	5
ARE II	37	1549 ± 410	351	5
³ ARE III	16	1796 ± 393	402	5
⁴ Mt. McKinley Park	16	1515 ± 338	316	5
Alaska Range West				
⁵ ARW I	8	1100 ± 256	303	5
Brooks Range				
⁶ BRR II	28	1316 ± 269	295	6
⁷ BRR III	40	1272 ± 315	332	7

¹denotes an area within the mountain range -- see Heimer and Smith (1975) for area description

²includes the Dry Creek area and the area immediately east of Mt. McKinley Park

³the Tok Management Area, including the Sheep Creek study area

⁴Mt. McKinley Park sheep horn values computed according to Heimer and Smith (1975)

⁵area southwest of Mt. McKinley Park

⁶central Brooks Range; includes the study area of Summerfield (1974)

⁷eastern Brooks Range

years for rams in most areas, although in portions of the Brooks Range the average maximum horn growth is reached at age six or seven. Mean horn volume at seven years of age is greatest for rams in the Wrangell Mountains and the Tok Management Area, while the lowest value is reported from rams in the Alaska Range west of McKinley Park. Values for McKinley Park rams are similar to ram horn values from low quality areas, although the mean seven year volume for rams from McKinley Park is considerably higher than that for rams from low quality areas located immediately east and west of McKinley Park.

Shackleton (1973) also noted differences in horn development between ewes of two populations. Ewes from the high quality population had greater horn development until their third year, after which the lower quality ewes had longer horn increments. Ewes from the high quality population also conceived at an earlier age than did the low quality ewes. The age of conceiving coincided with the change in the rate of horn development between the two populations, suggesting, Shackleton thought, that the increased nutritional demands of reproduction and lactation usurped energy that had been channelled to horn growth in pre-reproduction years.

Differences in body sizes also exist among populations of Dall's sheep. Heimer (1977) reported that ewes from the high quality Sheep Creek area are heavier than identical age ewes from the low quality Dry Creek area. Age corrected weights of ewes from Sheep Creek collected during autumn average 65.5 kg and those of sheep from Dry

Creek averaged 59.4 kg. The corrected average weights of ewes collected in spring were 50.3 kg for Sheep Creek ewes and 47.6 kg for Dry Creek ewes. Dall's ewes collected on the Kenai Peninsula averaged 57.8 kg in November and 50.4 kg in spring (Heimer 1973).

The fact that nutrition can play an important role in determining the weight of sheep can be seen from weights of captive wild sheep. A captive Dall's ram at the Yukon Game Farm, receiving supplemental feed, weighed approximately 31 kg more than rams in the population from which it was captured (Bunnell and Olsen 1976).

Variation in live weights of rams from a population are thought to be attributed to differences in horn mass more so than to weight losses associated with rut or body condition changes over winter (Bunnell and Olsen 1976). Less variation in horn size and a smaller portion of their total weight composed of horns produces less variation in total weight in females than in males (Bunnell and Olsen 1976). However, other researchers have shown that a substantial weight loss occurs over winter. Heimer (1973) reported an approximate 15 percent average weight loss for five and six year old ewes from mid-November to mid-June in Dry Creek. An overwinter weight loss of 13 percent was found for ewes on the Kenai Peninsula (Heimer 1973). It has also been found that a male Dall's lamb may lose 25 percent of its mid-November weight by spring (Nichols 1972).

Bunnell (1978) concluded that horn growth and body size are not correlated, although there is a general tendency for heavier rams to

have more horn growth. He argued that rams born during years of poor forage production, which would result in a small initial horn core and subsequently influence the size of horns grown, could be considered in later years to be of low quality, based on horn size.

Altitudinal migration, topographic variability, and the length of the growing season may affect horn growth in a manner similar to which horn growth may be affected by a year of poor forage production. These factors, separately or in combination, which determine the spatial and temporal availability of plants in early stages of growth, in part, determine the amount of energy that may be channelled into body and horn growth. Sheep in areas where the above factors create conditions which allow only limited amounts of nutrients to be used for horn and body growth should have correspondingly smaller horn and body sizes than sheep in areas where nutrients and energy are more abundant. Such is possibly the case between Dry Creek, McKinley Park, and Sheep Creek sheep. The earlier onset of spring plant growth, the greater topographic variability, and the greater altitudinal migration by the Sheep Creek sheep, permitting extended use of plants in early stages of growth, could enable more nutrients to be made available for horn and body growth. These factors could allow the greater horn and body growth found in Sheep Creek sheep than that found in Dry Creek or McKinley Park sheep.

The proposed effects of the length of the plant growing season on Dall's sheep can be seen by comparing horn growth rates of various

populations. Dall's rams in portions of the Brooks Range reach their average maximum sustained horn growth rate one to two years later than do sheep in other areas. This rate is also at the lower range of growth rates for Alaskan Dall's rams (Table 20). The shorter growing season of the Brooks Range, due to the two to six degree latitudinal difference between this area and the other areas containing Dall's sheep populations, restricts the temporal availability of new growth plants. This reduced availability of new growth forage in turn would provide reduced amounts of energy and nutrients beyond maintenance which could be used for horn growth. This reduced amount of energy could produce smaller horns in terms of volume, and could produce the overall slow horn growth rate of these sheep. The probable longer period of growth before complete adult size and maturation is reached would also delay the years during which maximum horn growth occurs.

SUMMARY

This study focused on summer habitat and food utilization by Dall's sheep in the eastern Alaska Range near Tok, Alaska. Sheep habitat was classified into several vegetation types, based on floristic composition or physiographic characteristics. Vegetation types were found to differ floristically.

Plant growth phenology was influenced by altitude, aspect, and soil moisture. Chemical analyses indicated that plant nutritional quality is highest in early plant growth stages and decreased with plant maturation. No significant differences in plant nutrient composition were found between portions of the study area or between Sheep Creek area and McKinley Park plants. Plant nutrient values were also similar to those found on sheep range on the Kenai Peninsula, Alaska.

Differences in the altitudinal limits of certain tree species and of several vegetation types were found between the two portions of the study area. Percentages of each vegetation type in the two portions of the study area were similar. The percentage of the total area above 1370 m was greatest in the Robertson drainage portion of the study area.

Food habits of sheep in the Sheep Creek area were comparable to those found in other studies of Dall's sheep. Grasses, sedges, willows, *Dryas octopetala*, and a few forbs formed the bulk of the sheep's summer diet. Sheep fed almost exclusively on non-woody plants. Less than 1.5 percent of the total plant cover in any of the

feeding sites was eaten by sheep. Plants in early stages of growth were most often eaten by sheep, although all stages of growth of many species were eaten. Selection of forage species and early stages of growth was possibly influenced by concentrations of volatile compounds, fiber, and silica present in the plants. Summer forage quality of Sheep Creek area plants met or exceeded the nutrient requirements of domestic sheep.

Sheep distribution and movements were influenced by use of mineral licks and by plant growth phenology. Patterns of use of vegetation types were influenced by apparent preference by sheep for feeding on plants in early stages of growth. Altitudinal migration was also closely tied to selection of plants in early stages of growth.

Differences in morphological characteristics among Alaskan Dall's sheep populations may be due in part to differences in the amount of energy available to each population. Summer altitudinal migration, dietary changes during the course of the summer, and topographic variability within feeding areas can allow for selection of early plant growth stages during much of the summer. The onset of the plant growing season may also be an important parameter which varies among areas inhabited by sheep.

The greater summer altitudinal migration by sheep, the earlier onset of the growing season, and the greater topographic variability of the Sheep Creek area than that found in other areas of Dall's sheep range, leading to increased availability and use of plants

in early stages of growth, are proposed to be the factors responsible for the large body and horn sizes of the Sheep Creek area sheep populations. These factors are also proposed to be responsible for the horn and body characteristics of Dall's sheep in other mountain ranges in Alaska.

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