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FACTORS AFFECTING GRAZING PATTERNS OF REINDEER ON SUMMER TUNDRA
RANGES

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FACTORS AFFECTING GRAZING PATTERNS

OF REINDEER ON SUMMER TUNDRA RANGES

A

THESIS

Presented to the Faculty of the University of Alaska

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Jeanette Trudell Moore, B.S.

Fairbanks, Alaska

May 1982

FACTORS AFFECTING GRAZING PATTERNS

OF REINDEER ON SUMMER TUNDRA RANGES

RECOMMENDED:

Chairman, Advisory Committee

Department Head

Director, Division of Life
Sciences

APPROVED:

Vice Chancellor for Research and Advanced Study

May 7, 1982.
Date

ABSTRACT

Factors influencing forage intake and selection by reindeer (Rangifer tarandus tarandus) were studied using esophageal and rumen fistulated animals tethered on arctic tundra. Eating rates and prehension patterns varied with plant species and growth forms eaten. Food intake increased linearly with plant biomass for all growth forms. Daily grazing time decreased while searching increased with increasing plant biomass. Bite rate was high and bite size small compared with those of sheep and cattle, reflecting the more selective foraging pattern of reindeer. Preference shown for forages was established on the basis of availability of preferred species and parts, plant biomass and phenology. Use of microhabitats depended on plant biomass, diversity and preferred forages present. Theoretically, selective compared with random use of forages and microhabitats resulted in biologically important increases in food intake, diet digestibility and net energy retention.

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INTRODUCTION

Large herbivores are distributed widely through climatic and
vegetational zones characteristic of tropical, temperate and
arctic regions of the world and possess special adaptations
enabling them to meet the demands of the environment. Hofmann
(1973) categorized large herbivores, according to the type of
diet selected, as grass and roughage feeders (grazers), interme-
diate feeders (adaptable mixed feeders), and concentrate selectors
(browsers). According to Van Dyne et al. (1980) and Kay et al.
(1980), grazers generally depend on grasses and other forages of
high fiber and low protein content so that a long rumen fermen-
tation time is necessary. Browsers on the other hand generally
select diets high in nutritive value, low in fiber and high in
protein, allowing for a faster rate of passage of digesta through
the rumen than grazers (Kay et al. 1980). However, classification
of ruminants to this scheme is difficult because no account is
taken of seasonal changes in the extent to which animals graze
and browse. For instance, large northern herbivores (moose, musk
oxen, reindeer and caribou) select diets which vary markedly on a
seasonal basis so that fiber content of the diet is also variable.

Reindeer are considered adaptable mixed feeders as they
combine characteristics of the grazer and the browser, selecting
a diet that varies in growth form, fiber structure and nutrient
content. This strategy should result in flexible use of forages

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in the diet in response to seasonal and site-specific variations in plant availability and quality. Making use of the most available forage may allow reindeer to meet daily energy requirements while more selective grazing may allow them to meet daily nutrient requirements. On the other hand, many high energy plants also contain secondary chemicals as a defense against herbivory (Longhurst et al. 1968; Rhoades & Cates 1976; Jung et al. 1979; Chapin 1980; Kuropat & Bryant 1980). By mixing several forages in the diet, concentrations of secondary compounds ingested should be diluted. Selection for forages offering highest nutrient and digestible energy content while reducing concentrations of secondary defense compounds requires that the reindeer devote some grazing time to searching. Therefore benefits of selective grazing must be weighed against the expense of harvesting so that adequate intake levels are also maintained.

This study documents the selective grazing patterns of reindeer to determine how these patterns are modified in response to the quantity and quality of forages available on the range. The quality of the range is correlated with the progression in plant phenology, and large ungulates which utilize the range on a seasonal or year-round basis tend to follow this phenological progression through selective grazing (Klein 1970; Skogland 1975; White et al. 1981). Although selective grazing may result in a high quality intake, productivity of the individual herbivore

(i.e., growth rate, reproduction, lactation) may still be limited by the quantity of food consumed. Control of food intake may be confounded, since in laboratory experiments the quantity of forage ingested is interrelated with its quality (Blaxter 1962; Baumgardt 1970).

Forage quantity can be defined as the amount of forage "available" to the grazing reindeer. Forage "availability" is influenced by many factors including biomass abundance, growth form presentation and preferred plant part distribution (i.e., green leaves and inflorescences) within the spectrum of herbages present. It is the general hypothesis of Chapter 1 that reindeer optimize intake in response to varying levels of forage availability by adopting patterns of grazing behavior which allow for the most effective use cf preferred forage species and their parts. These behavior patterns include methods of prehension (chewing, pulling, or lip harvesting), rate of biting and size of bite, and daily grazing time and intensity.

Selection for forage quality may indirectly assist in maximizing daily intake levels. Certainly, high nutrient intake should result from ingestion of immature over mature (Klein 1970; Skogland 1975; Thing 1980), and live over dead plant parts (Church 1979; Chapin 1980; Chapin et al. 1980). Selective use of habitats, vegetation types and plant species or parts should contribute toward maximizing digestibility of the diet (Van Dyne & Heady

1965; Leigh & Mulham 1966; Longhurst et al. 1968; Drozdz 1979). High diet digestibility may in turn influence levels of intake by minimizing rumen retention time (Blaxter et al. 1961; Blaxter 1962; Thornton & Minson 1972; Drozdz 1979; White et al. 1981).

Chapter 2 examines use of microhabitat and forage types by reindeer grazing on arctic tundra in relation to availability of herbage on the range. Although the content of nutrients and secondary compounds may influence use of vegetation, this project focused only on dry matter digestibility as an index of forage quality. Predictions are then made to determine whether a selected diet is more digestible than one chosen randomly from the vegetation available. Theoretical estimates of summer productivity (i.e., metabolizable energy intake, net energy available for fattening and daily weight gain) are also derived.

This research was conducted in conjunction with the RATE project (Research on Arctic Tundra Environments) which characterized processes of herbivory in arctic tundra systems (Batzli et al. 1980).

STUDY AREAS

Three areas - Atqasuk, Prudhoe Bay and Cantwell - were used
to document characteristic eating rates of reindeer on a variety
of forages (Chapter 1). The principal area was located near the
village of Atqasuk (70° 28'N, 157° 26'W), Alaska, on the Meade
River (Figure 1). This area is representative of upland shrub-
tussock tundra traditionally grazed by the Western Arctic caribou
herd in late summer and fall and by small resident bands in
winter and spring. Observations were made during June, July and
August over three consecutive years (1975-1977).

Within the Atqasuk study area, measurements of biting rate,
bite size and daily grazing activity were made in conjunction
with intake studies on major plant species and growth forms
(Chapter 1). Important forages on these sites included deciduous
shrubs (Salix pulchra, Salix glauca, ssp. acutifolia and Betula
nana ssp. exilis), graminoids (Carex aquatilis ssp. stans and
Eriophorum vaginatum ssp. spissum), lichens (Cetraria cucullata,
Alectoria nigricans, Dactylina arctica and Cladonia stellaris,
and forbs (Pedicularis langsdorfii ssp. arctica, Petasites
frigidus, Polygonum bistorta ssp. plumosum and Rubus chamaemorus).

For more intensive studies of selective grazing and digesti-
bility of forages (Chapter 2), two principal landforms were
chosen within the Atqasuk study area (Figure 12). These sites

-5-
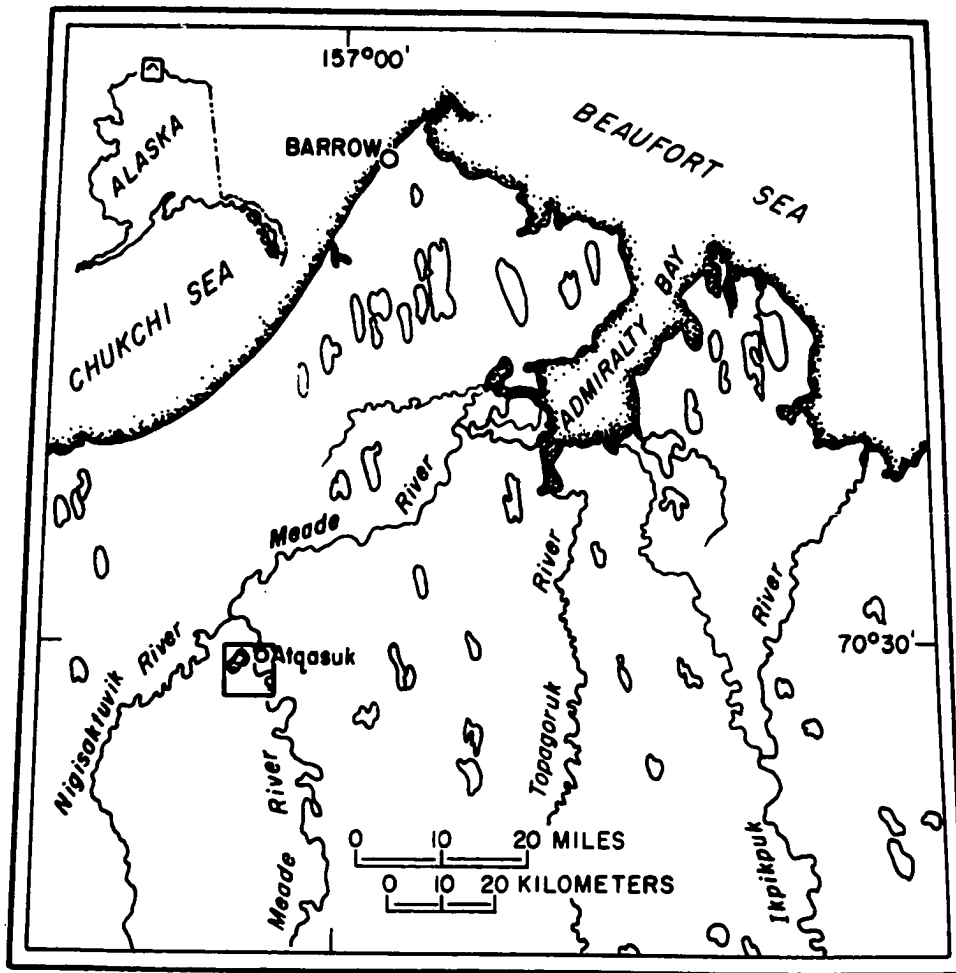
Figure 1. Location of Atqasuk, Alaska, on the Meade River.

were classified according to vegetation type as categorized by Komárková & Webber (1980) as follows:

(i) high-centered polygonized tundra (tussock graminoids and lichen species) interspersed with wet-trough tundra (deciduous shrubs and forbs) and semi-emergent tundra (seasonal single-stemmed graminoids);

(ii) lake-margin strangmoor (a complex of seasonal single-stemmed graminoids and deciduous shrubs) with a lowland border of deciduous shrub savanna (deciduous shrub and lichen species).

A complete listing of microhabitat types, growth forms and plant species available within these landforms is presented in Table 1. Nomenclature follows Hultén (1968). Lichen species were identified by M. Lechowicz (pers. commun.).

The second site, at Prudhoe Bay (70° 15'N, 148° 20'W) on the northern coastal plain of Alaska, is used during summer by caribou from the Central Arctic herd and occasionally by caribou from either the Western Arctic or Porcupine herds. Plant species used in eating rate trials included the shrub Salix ovalifolia and graminoids Carex aquatilis, Carex scirpoidea and Eriophorum angustifolium ssp. subarcticum. A complete report of use of this area has been made by White et al. (1975).

Additional measurements of food intake were made in central Alaska at the University of Alaska Reindeer Research Station,

Table 1. Summary of microhabitat types, plant growth forms, and plant species available within the two vegetation types studied in grazing experiments at Atqasuk. Superscript numbers indicate microhabitat types in which the growth forms are found (parentheses indicate occasional occurrence).

Vegetation Type	Microhabitat Types	Plant Growth Forms	Plant Species
Upland Tundra (Grazing plots P1-4; P6-8; ER1-2)	1. Intertussock tundra 2. Tussocks 3. Wet trough tundra 4. Semi-emergent _Carex_ marsh	Evergreen Shrubs$^{1-3}$ Deciduous Shrubs$^{3(1)}$ Tussock Graminoids^{2} Single-stemmed Graminoids$^{3-4}$ Herbaceous Forbs^{3} Lichens$^{1(3)}$ Mosses$^{1-2-3-4}$	<u>Cassiope tetragona</u> <u>Ledum palustre</u> <u>Vaccinium vitis-idaea</u> <u>Betula nana</u> <u>Salix pulchra</u> <u>Eriophorum vaginatum</u> <u>Carex aquatilis</u> <u>Rubus chamaemorus</u> <u>Alectoria nigricans</u> <u>Cetraria cucullata</u> <u>Cladina arbuscula</u> <u>Dactylina arctica</u> <u>Stereocaulon</u> sp. (see Table 10) (see Table 10)
Lake Margin (Grazing plots LM1-5)	5. Lichen ridge 6. _Salix_ strangmoor 7. Semi-emergent _Carex_ marsh	Evergreen Shrubs$^{5(6)}$ Deciduous Shrubs$^{5-6}$ Tussock Graminoids^{5} Single-stemmed Graminoids$^{6-7}$ Herbaceous Forbs^{7} Lichens$^{5(6)}$ Mosses^{5-6-7}	<u>Cassiope tetragona</u> <u>Ledum palustre</u> <u>Vaccinium vitis-idaea</u> <u>Salix pulchra</u> <u>Eriophorum vaginatum</u> <u>Carex aquatilis</u> <u>Pedicularis langsdorfii</u> (see above and Table 10) (see Table 10)

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Cantwell (63° 21'N, 149° 08'W). This area provided plant growth

forms characteristic of the northern boreal forest and included

the tall shrub _Betula glandulosa_, the sedge _Carex bigelowii_ and a

variety of lichens.

CHAPTER 1.

THE EFFECT OF FORAGE STRUCTURE AND AVAILABILITY ON FOOD

INTAKE, BITING RATE, BITE SIZE AND DAILY EATING TIME OF REINDEER

I.   INTRODUCTION

Recent studies have focused on factors that control food

intake by grazing ruminants (Allden 1962; Allden & Whittaker

1970; Arnold 1964, 1970, 1975; Arnold & Dudzinski 1967a, b;

Stobbs 1973a, b; White 1975; White et al. 1975). In these studies

food intake was either measured over a period of minutes to hours

(Allden & Whittaker 1970; White et al. 1975; Chacon & Stobbs

1976), or food intake was estimated on a daily basis (Arnold

1964, 1970, 1975; Arnold & Dudzinski 1967a, b; Langlands & Bennett

1973). Control of food intake on a short-term basis appears to

be related to the eating behavior of the animal which includes

such factors as the time spent searching in a grazing period, the

biting rate, and the size of bite. Daily food intake is strongly

influenced by the time devoted to grazing each day as well as the

former factors.

This first chapter examines the control of food intake by

components of grazing behavior and range characteristics in a

northern grazer-browser for comparison with domestic grazers that

have been studied.   ⁻10⁻

II. MATERIALS AND METHODS

A. Description of Reindeer

Reindeer used in intake and biting rate experiments were nonproductive adults (four nonpregnant, nonlactating females; one nonrutting male) in which the esophagus had been fistulated at least three months prior to experimentation. These animals ranged in age from 2 to 5 years and averaged 70 kg in body weight during peak season. Individual reindeer were used for each trial with trials distributed evenly between them. The reindeer were trained to be easily led and handled so that grazing activity could proceed normally during the study periods. A 10 m rope was routinely used to tether each animal.

B. Esophageal Fistula Collections

Food intake was estimated by collecting esophageal fistula extrusa over short time intervals (described in detail by White et al. 1975). In brief, esophageal egesta were collected over three grazing intervals of 1 to 5 min duration separated by 5 to 15 min. intervals throughout a grazing period free of insect harassment following a fasting period of 3 to 4 h. During this time the esophageal cannula was removed and a sponge was placed distally to the fistula to ensure complete collection of extrusa. Samples were collected in a mesh bag suspended inside a canvas collection bag fitted with a plastic liner. The collection bag

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was tied to the animal's neck with four canvas straps. To express food intake as $g \cdot (\text{min spent eating})^{-1}$, the grazing intensity was measured. Grazing intensity was defined as the percent of time in which the reindeer was observed to be ingesting food (i.e., the eating time) during a collection or grazing period and was measured with a stopwatch. In most studies the period not devoted to eating was used by the reindeer in searching activity. All activity related to the food searching and ingesting process comprised the grazing period.

For the intermediate feeders such as reindeer, varying rates of forage ingestion (3.7 to 48.0 g fresh $\text{wt} \cdot \text{min}^{-1}$, Gaare et al. 1970; 2.4 to 5.3 g dry $\text{wt} \cdot \text{min}^{-1}$, White et al. 1975) have been shown. Gaare et al. (1970) suggested that these variations could be attributed to the type of plant eaten, the time of day, the time of year, and weather conditions. In the present study, effects of the time of day and time of year were overcome by fasting the reindeer for 3 to 4 h before intake measurements were made and by conducting all trials in summer. Effects of weather conditions were also minimal. Because harassment of reindeer by insects could lead to complete cessation of feeding, all trials were conducted during periods of little or no insect activity.

C. Determination of Rumination Patterns

To characterize rumination activity, a reindeer was allowed to establish and continue a regular pattern of rumination following a long grazing bout. The cycle was timed to determine the duration of regurgitation, chewing, and swallowing of a bolus during a typical rumination bout. Bolus size was determined by removing the esophageal cannula, blocking the esophagus proximally to the fistula opening, and collecting the bolus as it was regurgitated. The cannula was then replaced loosely and the animal was allowed to continue rumination bouts for at least 5 min. To estimate the amount and rate of reswallowing of rumen contents, the loosely fitted cannula was removed immediately after a bolus had been regurgitated. The esophagus was blocked distally to the fistula to effect a complete recovery of the bolus as it was being reswallowed and egesta were collected in hand held plastic bags. Rumination behavior by the animal did not appear to be altered during collection bouts.

D. Determination of Biting-Chewing Rate

During grazing-browsing and rumination bouts, biting and chewing rates were estimated with equipment similar to that described by Law & Sudweeks (1975). Biting movements were recorded as pressure changes in a pneumatic bellows tube that encircled the jaw of the reindeer and was attached to a halter. The pneumatic

tube was adjusted so that it did not interfere with normal eating behavior. Pressure changes associated with jaw movement were monitored relative to atmospheric pressure by allowing a controlled air leakage into one end of the bellows. A pressure-sensitive transducer was fitted into the other end of the pneumatic tube and signals from the transducer were transmitted by electric leads to a telemetry transmitter attached to a small saddle on the reindeer's back. The transmitter unit was a modified ECG transmitter (Parks 27-1 model) used for routine human experimentation. An FM transistor radio received the transmitted signal, allowing the transmitting system to function independently from the recording system. The signal was transferred via a frequency/voltage converter (Parks 311 model) to a portable revolving chart recorder. By this instrumentation, instantaneous recordings could be made up to 30 m from the reindeer so that observer interference with the grazing event was minimized.

Biting rate was defined as the number of pressure-response events per min. The pressure waves moved in response to either jaw or lip movements and were recorded on the chart while the animal was actively engaged in eating. For lichens, recorded pressure fluctuations were assumed to provide accurate representations of jaw and lip movements as these could not be recorded visually. Other jaw or lip movements recorded during non-eating activity (i.e., while searching or drinking) were not considered

in the measurement of biting rate. Chewing rate, defined as jaw
movements observed during rumination, was estimated during rest
periods. Mean chewing rate was calculated over repeated rumination
cycles. The duration of the rumination cycle and the time
between each rumination event was estimated from the recorder
trace and from observations timed with a stopwatch. Bite size
($mg \cdot bite^{-1}$) was calculated as the eating rate ($g \cdot min^{-1}$) divided
by the biting rate ($bites \cdot min^{-1}$) estimated concurrently from the
amount of esophageal egesta collected.

E. Description of Vegetation Use

Vegetation type and plant species selected were recorded at
30-second intervals as the reindeer grazed mixed vegetation
types. Thus, prehension patterns could be related to species
ingested. Estimates of eating rate were also made on monospecific
stands of vegetation or on mixed stands in which only one species
or growth form was eaten. Estimates of biting rate and eating
rate could then be related to the above-ground live biomass of
the plants eaten as well as to the total standing crop.

F. Estimation of Plant Biomass

Plant biomass in experimental areas was measured by clipping
all vegetation above the moss layer in six to nine replicate
quadrats (30 x 30 cm). The samples were sorted by plant species

and parts. Dry matter content of the biomass samples and esopha-
geal fistula egesta from grazing and rumination studies were
determined by weighing subsamples dried at 110°C for 12 hours.
Total live biomass was defined as the combined biomass of vascular
plant and lichen material and did not include mosses and stems of
deciduous shrubs of diameter greater than 5 mm. Selected live
biomass refers to biomass of the specific plant part eaten during
a feeding experiment.

G.   Documentation of Daily Grazing Activity

Daily grazing activity was measured with vibracorders*
attached to a saddle (Allden 1962). These clocks recorded activity
of the animal through pendulum motion of a needle which inscribed
etching on a revolving time chart. Percent of the day actually
spent eating (i.e., during food ingestion) was then estimated as
the product of the daily grazing time (total time spent searching
for and ingesting food) and the grazing intensity (time spent
eating/time spent grazing).

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*Kienzle Apparate G.m.b.H., Villingen in Schwarzwald, W. Germany.
Supplied by Argo Instruments Corp., Long Island City, New York.

III. RESULTS

A. Intake and Prehension of Forages.

1. Food ingestion in relation to plant growth form and species

Mean eating rates estimated from esophageal egesta collections during the grazing trials at Atqasuk, Prudhoe Bay, and Cantwell are summarized according to plant growth form and species in Table 2. Single-stemmed graminoids and carpet shrubs were ingested at relatively low rates (2.4 to 3.6 $g \cdot min^{-1}$). Intake of shrubs and tussock graminoids was higher (5.3 to 6.9 $g \cdot min^{-1}$) while the intake of forbs and lichens was highest (5.9 to 12.7 $g \cdot min^{-1}$). When reindeer were offered an excess of fresh hand-picked lichens over a 5 min feeding bout, intake was extremely high (26.6 $g \cdot min^{-1}$).

2. Food ingestion in relation to plant biomass

The standing crop biomass differed among the various plant species and growth forms (Table 2 and Figure 2). Significant differences ($P<0.05$) are denoted in Table 2. Availability of the single-stemmed graminoids (10 to 70 $g \cdot m^{-2}$), tussock graminoids (10 to 80 $g \cdot m^{-2}$), carpet shrubs (30 to 90 $g \cdot m^{-2}$), and low shrubs (10 to 150 $g \cdot m^{-2}$) was comparatively low and overlapping (Figure 2). Availability of high shrubs (60 to 200 $g \cdot m^{-2}$) and lichens (60 to 400 $g \cdot m^{-2}$) was higher and could have accounted for higher eating

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Table 2. Estimates of mean ($\pm$ S.E.) dry matter intake and mean biomass of
representative plant species at Atqasuk, Prudhoe Bay and Cantwell, Alaska.

Life form and species	Number of observations	Eating rate (g dry wt·min⁻¹)	Biomass of species or growth form (g dry wt·m⁻¹)
Carpet shrubs			
Betula nana	9	3.6 $\pm$ 0.4	55.8 $\pm$ 7.7[a]
Salix reticulata	1	3.2	
Low shrubs (<1 m high)			
Salix glauca	6	9.6 $\pm$ 0.8	107.5 $\pm$ 1.4[a,b]
Salix ovalifolia[1]	2	5.3 $\pm$ 1.8	31.4 $\pm$ 7.6[c]
Salix pulchra	31	5.8 $\pm$ 0.6	51.9 $\pm$ 8.0[b,d]
High shrubs (> 1 m high)			
Betula glandulosa[2]	5	6.9 $\pm$ 1.4	
Salix lanata			
(catkins only)	5	3.3 $\pm$ 0.6	117.9 $\pm$ 43.4[e]
Salix pulchra	9	5.2 $\pm$ 0.7	71.7 $\pm$ 2.6[b,d,f]
Single-stemmed Graminoids			
Carex aquatilis	22	3.3 $\pm$ 0.3	31.2 $\pm$ 4.1[a,b,d,f,g]
Carex aquatilis[1]	2	2.4 $\pm$ 1.3	25.9 $\pm$ 3.2[b,f,h]
Carex Bigelowii[2]	6	3.2 $\pm$ 0.6	
Carex scirpoidea[1]	4	3.2 $\pm$ 0.9	35.3 $\pm$ 4.8[b,f,i]
Eriophorum angustifolium[1]	7	2.5 $\pm$ 0.4	34.1 $\pm$ 6.5[b,f,j]
Tussock graminoids			
Eriophorum vaginatum	9	5.7 $\pm$ 0.5	34.9 $\pm$ 8.6[b,f,k]
Lichen spp.			
Tussock tundra	50	8.8 $\pm$ 0.7	263.1 $\pm$ 13.7[a-1]
Lichen ridge[2]	4	10.9 $\pm$ 3.1	
Maximum intake ad lib[2,3]	3	26.6 $\pm$ 1.7	15900
Forbs			
Pedicularis langsdorfii	3	12.7 $\pm$ 1.8	21.5[a,b,d,f,g,1]
Petasites frigidus	1	8.5	
Polygonum bistoria	1	9.7	47.4
Rubus chamaemorus	2	5.9 $\pm$ 2.2	11.1 $\pm$ 7.1[b,1]

[1]Prudhoe Bay, Alaska.
[2]Cantwell, Alaska.
[3]Maximum intake of lichens was estimated by offering reindeer an excess amount
of fresh hand-picked lichens.

Biomass values with a common letter[(a-1)] are significantly different (P<0.05).
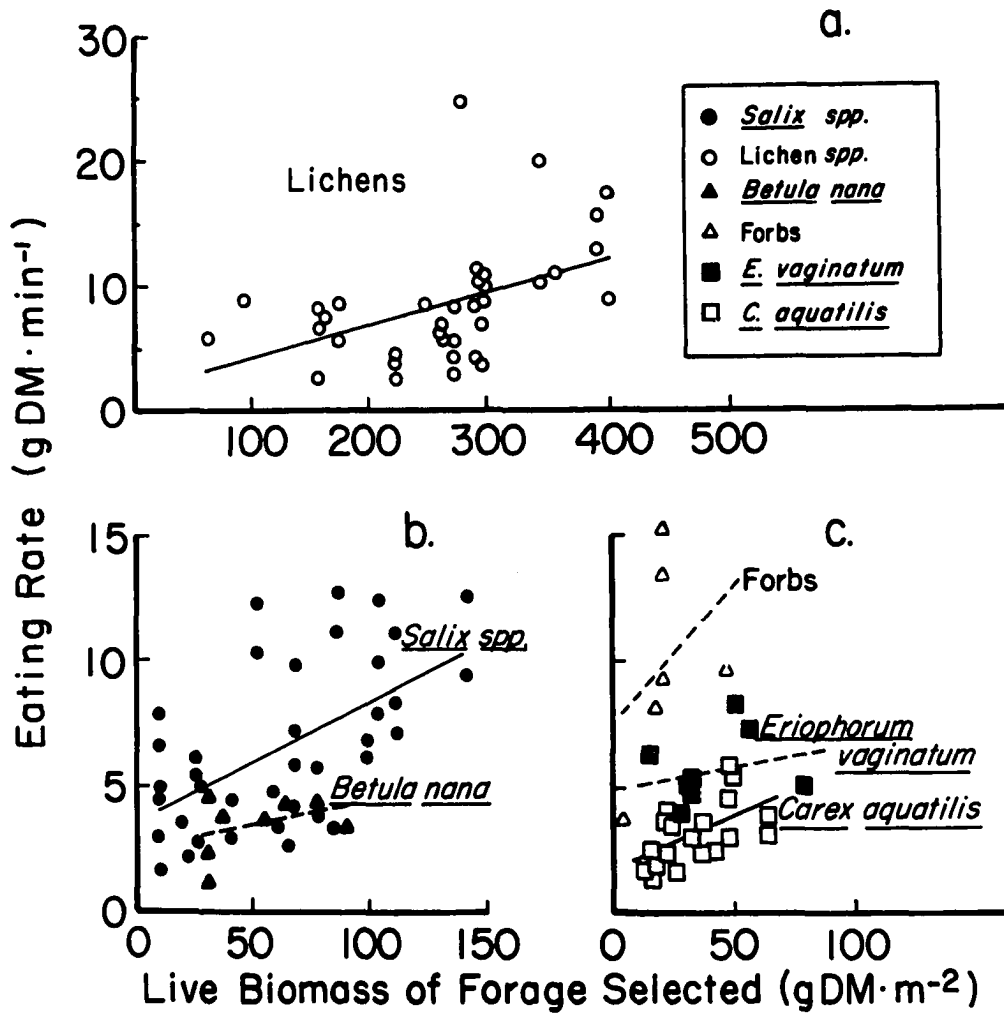
Figure 2. Relations between eating rate, as estimated by esophageal
egesta collections, and available live biomass of
monospecific stands.

rates shown in Table 2. However, intake of forbs was high even when the biomass of forbs was low (4 to 47 $g \cdot m^{-2}$).

To test the effect of plant availability on food intake, relations between eating rates and available biomass of selected live plant material were determined (Figure 2). Significant correlations (P<0.01) were noted for lichens, the combined <u>Salix</u> species and <u>Carex</u> <u>aquatilis</u>. For each 100 $g \cdot m^{-2}$ increment in biomass, the intake of lichens increased at 2.6 ± 0.1 $g \cdot min^{-1}$, of <u>Salix</u> species by 4.9 ± 0.2 $g \cdot min^{-1}$, and of <u>C. aquatilis</u> by 4.3 ± 0.3 $g \cdot min^{-1}$. Although not significant, the trends for the forbs, <u>Eriophorum</u> <u>vaginatum</u>, and <u>Betula</u> <u>nana</u> were similar to those for the other groups.

A summary of the relations between eating rate and plant biomass is shown in Figure 3. An analysis of covariance performed for significant relations of eating rate and biomass (i.e., for lichens, <u>C. aquatilis</u> and <u>Salix</u> species) showed no significant difference between the slopes of these regression lines (P>0.05). Significant differences were found between the elevations of the following regression lines as shown in Figure 3: forbs and <u>Salix</u> species (P<0.01), forbs and <u>E. vaginatum</u> (P<0.05), forbs and <u>C. aquatilis</u> (P<0.01), forbs and <u>B. nana</u> (P<0.01), forbs and lichen species (P<0.05), <u>Salix</u> species and <u>C. aquatilis</u> (P<0.01), <u>Salix</u> species and <u>B. nana</u> (P<0.01), <u>Salix</u> species and lichens (P<0.05), <u>E. vaginatum</u> and <u>C. aquatilis</u> (P<0.01), <u>E. vaginatum</u> and <u>B.</u>
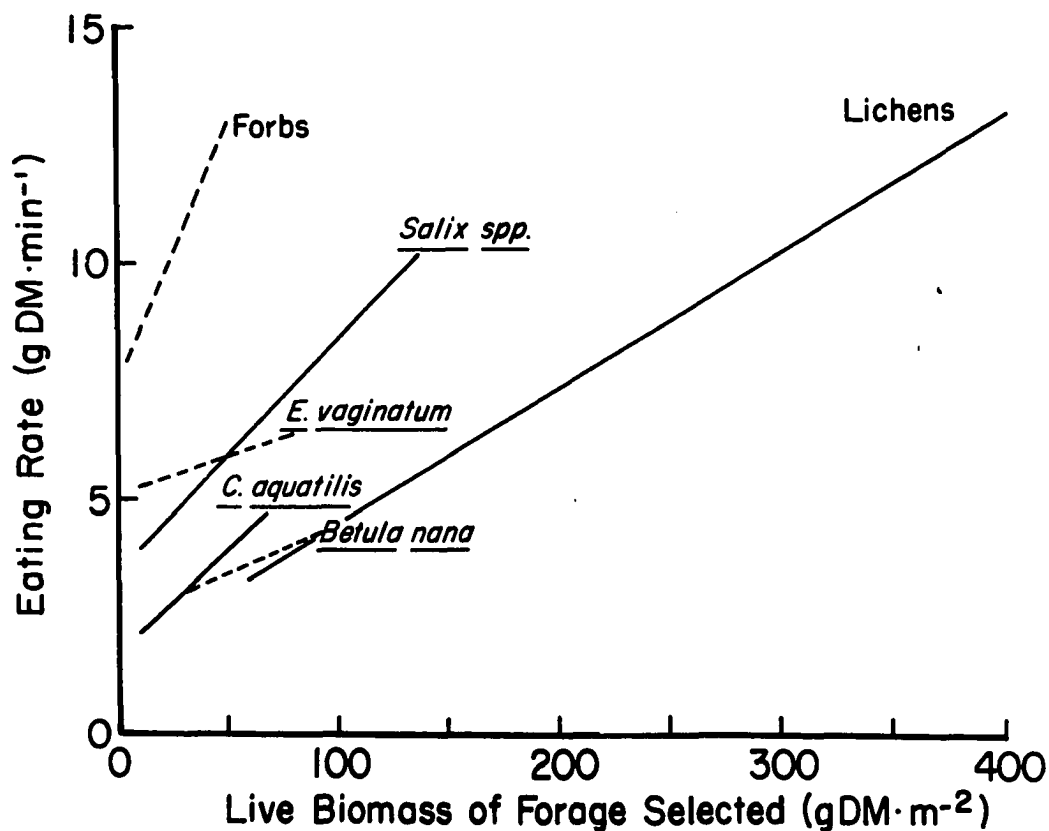
Figure 3. Comparison of plant growth form in the relation of eating
rate (I, $g \cdot min^{-1}$) and available selected live biomass (S,
$g \cdot m^2$) summarized from Figure 2. Solid lines indicate
significant relationships.

Lichen species	$I = 1.72 + 0.026S$	$r = .448$	$P < 0.01$	$n = 36$
Salix species	$I = 3.45 + 0.039S$	$r = .575$	$P < 0.01$	$n = 38$
Betula nana	$I = 2.38 + 0.021S$	$r = .437$	NS	$n = 9$
Carex aquatilis	$I = 1.72 + 0.043S$	$r = .577$	$P < 0.01$	$n = 20$
Eriophorum vaginatum	$I = 5.08 + 0.016S$	$r = .225$	NS	$n = 9$
Forb species	$I = 7.46 + 0.112S$	$r = .381$	NS	$n = 6$

nana (P<0.01). The following regression lines were not significantly different (P>0.05) in elevation: Salix species and E. vaginatum, E. vaginatum and lichens, C. aquatilis and B. nana, C. aquatilis and lichens, B. nana and lichens. The relative elevations of the regression lines indicate the importance of plant growth form in affecting intake. Highest eating rates per unit biomass were those noted for the forb species with E. vaginatum and Salix species intermediate, and C. aquatilis, B. nana, and lichen species lowest. This ranking in intake is similar to that in Table 2 except for lichens which are highly ranked in Table 2 due to the higher biomass.

3.   Food prehension patterns

Prehension patterns of reindeer eating the various plant growth forms are shown in Figure 4. Shrub willows were eaten using a combination of biting and pulling motions (Figure 4[a]), the latter serving to strip leaves, new stem growth, and some bark from branches. When lichens were ingested, lip movements were used to tease the lichens from the moss layer, producing a distinctive even wave motion of low amplitude (Figure 4[b]). Prehension patterns for shrubs of carpet growth form (i.e., Salix reticulata and Betula nana) were even but showed a more pronounced jaw movement (Figure 4 [c]). Pronounced, uniform jaw movements characterized prehension of graminoids. The most distinctive biting motion was noted for the single-stemmed sedge Carex
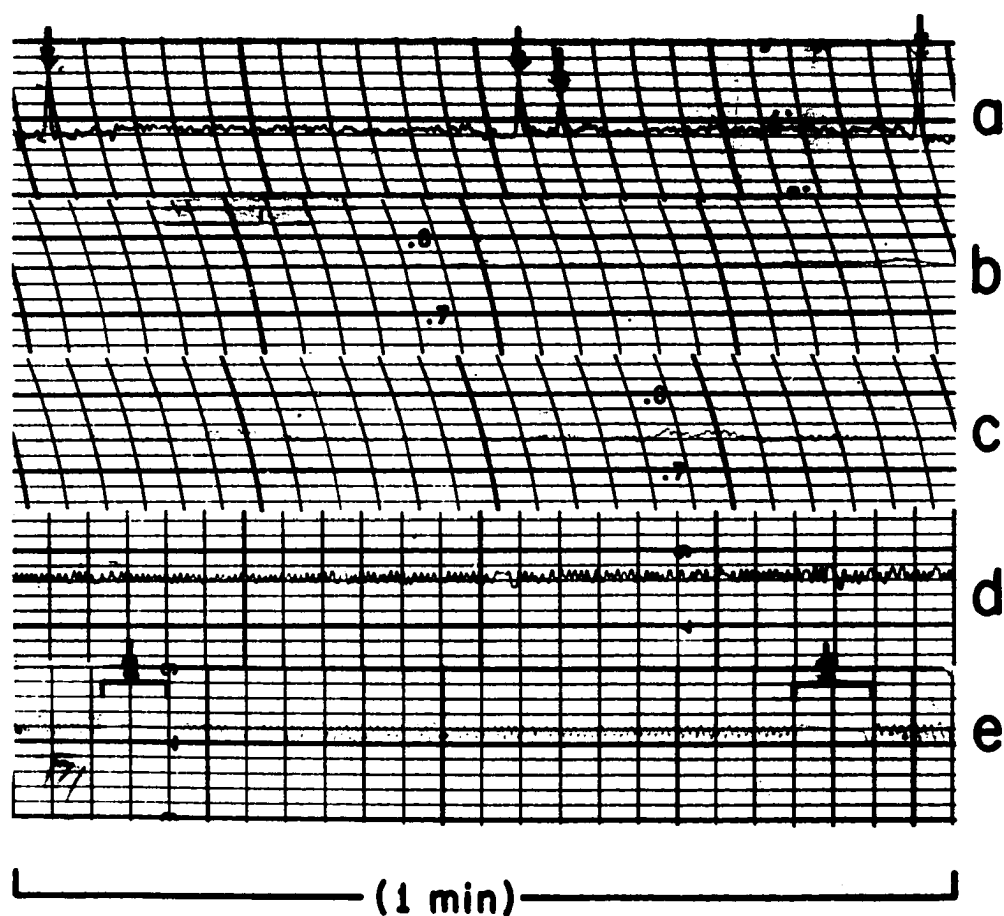
Figure 4. Prehension patterns for the major plant growth forms at
Atqasuk, Alaska. (a) tall shrub Salix pulchra (arrows
denote stripping of leaves); (b) lichen species; (c) shrubs
of carpet growth form (Salix reticulata; also seen for
Betula nana); (d) dense sedge stand (Carex aquatilis);
(e) rumination bout (arrows in brackets indicate
regurgitations).

aquatilis (Figure 4 [d]). Chewing motions following rumination were consistent in amplitude and rate (Figure 4 [e]) and were similar to those recorded when the reindeer was eating C. aquatilis. A distinctive pause was noted between each rumination event (see bracket and arrow, Figure 4 [e]).

4. Rumination and chewing behavior

Rumination data collected in four vegetation types are presented in Table 3. Regurgitation occurred approximately once each minute with each bolus weighing 96 to 155 g fresh wt (10 to 17 g dry wt). Chewing rate following regurgitation was 117 ± 3 chews·min^{-1} and was associated with swallowing of the bolus at a rate of 10 to 16 g dry wt·min^{-1} during the rumination bout. This was up to three times greater than food ingestion rates shown in Table 2. The amount of regurgitate swallowed per chewing movement was 79 to 161 mg dry wt.

5. Discussion - Forage intake in relation to plant availability

To date, most intensive studies of the components of the grazing process have been limited to domestic sheep (grazers or mixed feeders; Van Dyne et al. 1980) and cattle (grazers; Van Dyne et al. 1980) which were grazing temperate and tropical pastures. These studies indicate that instantaneous food intake

Table 3. Summary of mean rumination data in relation to vegetation type in reindeer grazing summer range.

| Vegetation type | Number of observation periods | Duration of rumination bout (min) | Regurgitation rate | | Chewing rate (chews· min^{-1}) | Chewing movements per bolus | Regurgitate swallowed per chewing movement (mg dry wt) |
			(g fresh wt· min^{-1})	(g dry wt· min^{-1})			
Wet polygonized tundra[1]	8	1.05	96.3	10.3	110	116	93
Upland tundra[1]	1	0.65	155.5	16.7	104	67	161
Lake margin[2]	7	0.94	107.5	11.5	124	108	106
Troughs of high centered polygons[3]	3	1.04	97.2	10.1	129	132	79

[1]Diet dominated by lichens, some Carex aquatilis, some Salix pulchra.
[2]Diet dominated by Salix pulchra and Carex aquatilis.
[3]Diet dominated by Carex aquatilis and lichens.

is dependent upon a number of factors related to the food resource.
Chacon & Stobbs (1976) found that leaf density of the pasture was
a major factor influencing intake by Jersey cows grazing tropical
grass swards. Allden & Whittaker (1970) observed that food
intake of sheep was correlated with tiller length in grass swards
but that there was little relation between herbage yield and
intake. On a daily basis, Arnold (1970) noted that for sheep
grazing grass and clover swards, 20 to 80% of the variability in
food intake was accounted for by the green and dry pasture yield
per unit area (plant biomass), pasture size, number of leaves per
unit area, and digestibility of the diet.

In the present studies instantaneous eating rate within each
plant growth form was influenced by the availability of vegetation.
The general trend presented in Figures 2 and 3 is that forage
intake decreases with decreasing availability of plant biomass,
confirming preliminary findings that, when available biomass is
less than 100 $g \cdot m^{-2}$, eating rate by reindeer grazing tundra
ranges may be limited by food abundance (White et al. 1975). No
maximal eating rate was documented, which is in contrast to
findings with sheep where a maximum intake is reached at a standing
biomass of grasses greater than 224 $g \cdot m^{-2}$ (Allden 1962). The
inability to define a maximal eating rate for vascular plants may
have resulted from the characteristically low biomass of tundra
ranges where only dwarf shrub leaf plus stem exceeds 200 $g \cdot m^{-2}$.

The mechanism by which rate of intake varies for different

plant growth forms may be related to the grazer and browser

feeding processes as shown by variations in the prehension patterns

in Figure 4. The mode of prehension undoubtedly represents a

balance of intake and selection. Rapid mouth and lip movements

as used in the ingestion of lichens may be important in selecting

and sorting lichens from the moss layer. Biting and pulling

movements used to eat shrubs are useful in removing leaves from

branches (browsing). Graminoids were eaten with motions which

resemble chewing during rumination, possibly aiding in reduction

of the leaf size before it is swallowed. The amount of regurgitate

swallowed per chewing movement during rumination was approximately

five times greater than the average bite size while eating (Table

4), indicating that the ability to swallow ingested food does not

limit eating rate. Clearly, selection for plant species or

growth form and for standing crop within a growth form is facil-

itated by prehension behavior and should serve to maximize food

intake of a reindeer during a grazing bout.

B. Biting Rate and Bite Size

1. Biting rate and bite size in relation to plant growth form

A summary of mean biting rate and bite size in relation to food intake for the various plant species is shown in Table 4. An analysis of variance performed on individual trials between plant species and groups indicated that there was no significant difference (P>0.05) in biting rate or bite size between the different vascular plant species. Highly significant differences (P<0.001) were noted between vascular and lichen groups in both biting rate and bite size. The overall mean ($\pm$ 1 S.E.) biting rate for vascular plants was 177 $\pm$ 3 bites·min^{-1} and was 205 $\pm$ 5 bites·min^{-1} for lichens. Mean bite sizes for vascular plants and lichens were respectively 21 $\pm$ 1 and 32 $\pm$ 4 mg dry wt.

2. Biting rate in relation to food intake

Comparisons of biting rate with food intake estimated by esophageal collection are shown in Figure 5. A significant positive relationship between bite rate (B, bites·min^{-1}) and eating rate (I, g·min^{-1}) was noted for the combined graminoids (Carex aquatilis and Eriophorum vaginatum) when intake was expressed both on a dry wt (eqn 1) and on a fresh wt basis (eqn 2).

$$B = 148 + 6.2 \ I \qquad r = 0.82, \ P<0.05, \ n = 8 \qquad (1)$$

$$B = 145 + 2.5 \ I \qquad r = 0.85, \ P<0.01, \ n = 8 \qquad (2)$$

Table 4. Comparison of eating behavior in relation to plant growth form in reindeer grazing representative stands of tundra vegetation.

Plant group and representative species	Number of observation periods	Intake rate (g dry wt · min^{-1})	Biting rate[3] (bites · min^{-1})	Intake per bite (mg dry wt)
Vascular plants				
Shrubs:				
Salix pulchra	13	4.1 ± 0.3	177 ± 6	23 ± 2
Betula nana	6	4.0 ± 0.2	186 ± 3	22 ± 1
Graminoids:				
Carex aquatilis	5	3.5 ± 0.5	173 ± 5	20 ± 2
Mixed[1]	3	3.6 ± 1.7	164 ± 15	20 ± 9
Lichens:				
Mixed[2]	11	6.5 ± 0.7	205 ± 5	32 ± 4

[1]Mainly Carex aquatilis and Eriophorum vaginatum.

[2]Mainly Cetraria cucullata. Biting rate was estimated as lip movements rather than jaw movements for lichen intake.

[3]Analysis of variance between vascular and lichen groups gives an F-ratio = 23.2 > $F_{0.01}$ = 7.39 for d.f. = 1, 36.
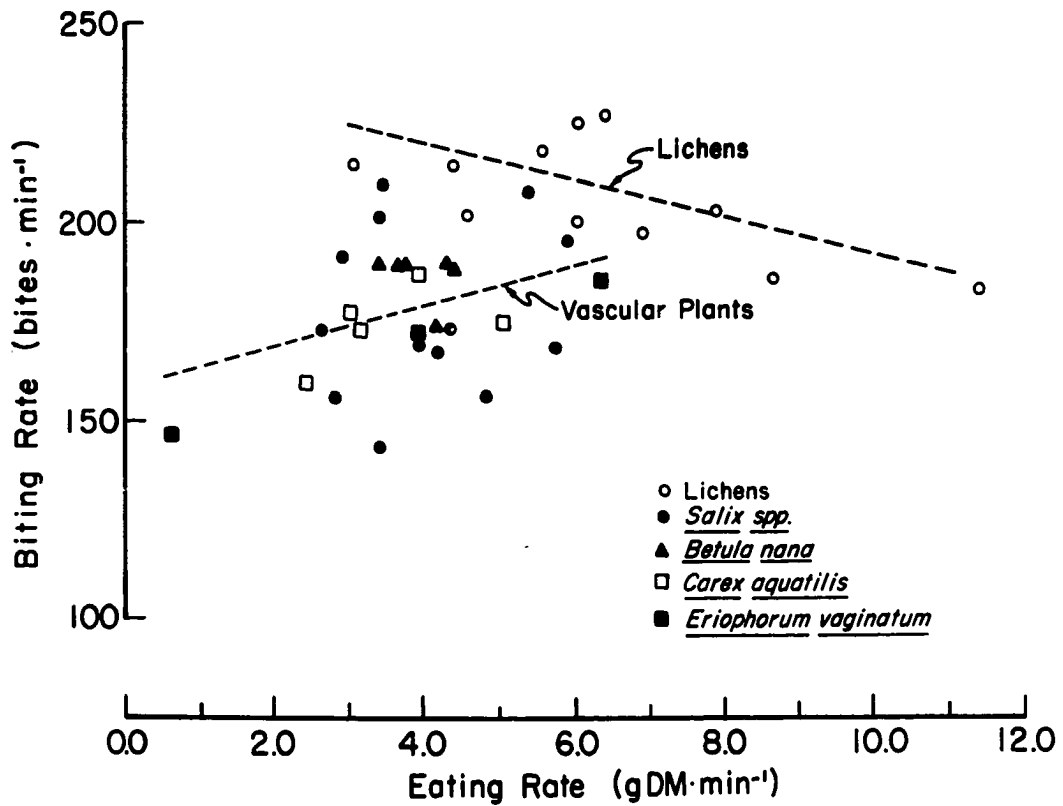
Figure 5. Comparison of vascular plants and lichens in the relation of biting rate (B, bites·min^{-1}) to eating rate (I, g dry wt·min^{-1}). For vascular plants combined, b = 157.6 + 4.97I ($\underline{r}$ = .355, P<0.10, n = 28); for lichen species, B = 237.33 - 4.69I ($\underline{r}$ = .587, P<0.10, $\underline{n}$ = 11). See also equations 1 and 2.

A similar trend was noted when all vascular plants were combined but the relationship was not significant (r = 0.35, P>0.05).

In contrast, biting rate for lichen species declined as the rate of food intake increased (Figure 5) indicating that bite size must have increased markedly to account for the increase in food intake shown in Figure 2. This relationship for lichens was not significant when food intake was expressed on a dry wt basis (r = 0.58, P>0.05) but was significant when intake was expressed on a fresh wt basis (eqn 3).

$$B = 231 - 2.3I \qquad r = -0.62, P<0.05, n = 11 \qquad (3)$$

3. Biting rate in relation to plant biomass

The relation between biting rate and total live plant biomass is presented by Figure 6 [a]. Regression analysis with respect to intake of single species was limited by the restricted ranges of biomass available so that no significant correlations were found for individual species. Regression analysis of the combined data for vascular plants indicated a significant positive relationship between biting rate (B, bites$\cdot$min^{-1}) and total live biomass (T, g dry wt$\cdot$m^{-2}) (eqn 4).

$$B = 167 + 0.046T \qquad r = 0.40, P<0.05, n = 25 \qquad (4)$$

The slope indicates that biting rate increased by 4.6 $\pm$ 2.1 bites$\cdot$min^{-1} for each 100 g$\cdot$m^{-2} increase in total biomass over the range of biomass studied. For lichens the relationship between
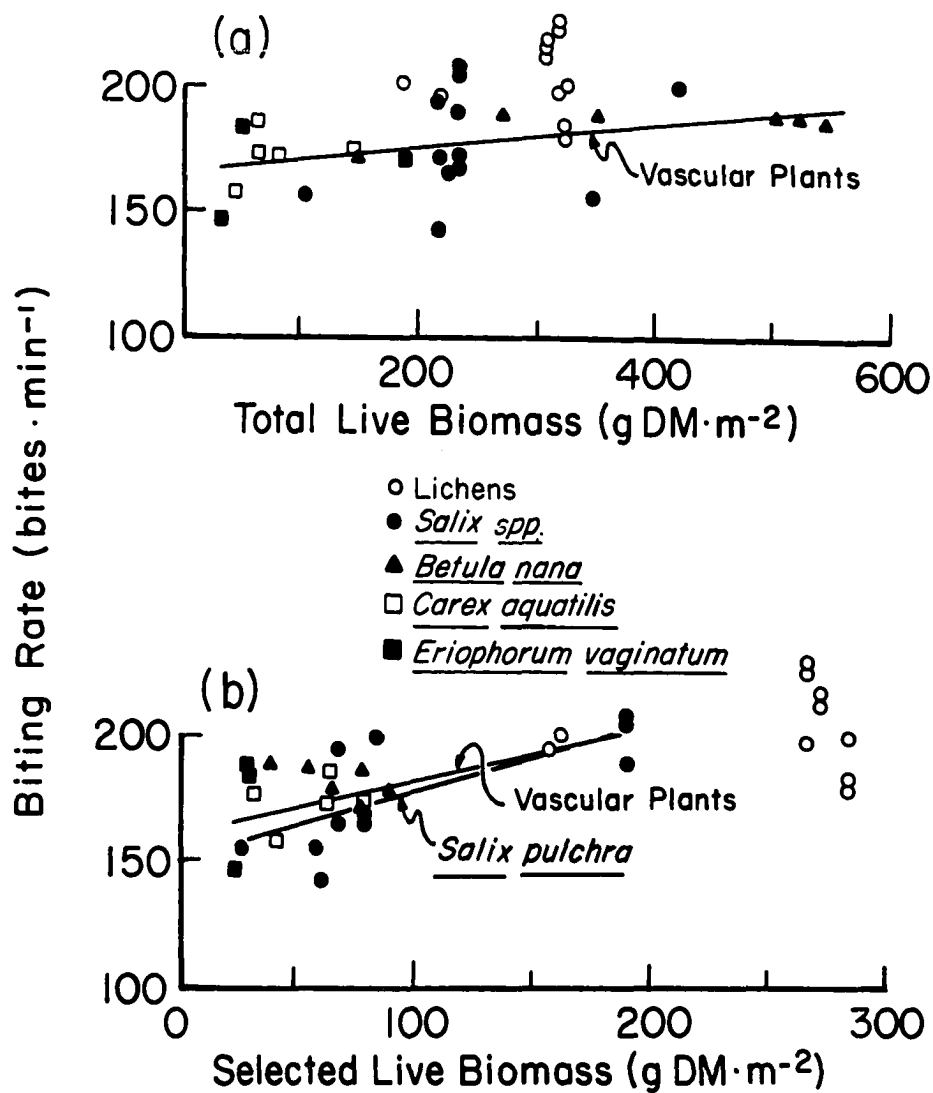
Figure 6. Relation between biting rate and total live biomass
(vascular plants + lichens) (a) or selected live biomass (b).

biting rate and total live biomass was not significant ($\underline{r}$ = .12, P>0.05).

Figure 6 [b] shows the relation between biting rate and the biomass of plant species and parts eaten. Biting rate (B, bites·min^{-1}) was significantly correlated with the selected vascular plant biomass (S, g dry wt·m^{-2}) (eqn 5) but no significant relationship was noted for lichens ($\underline{r}$ = 0.028, P>0.05).

$$B = 162 + 0.21S \qquad \underline{r} = .58, P<0.01, \underline{n} = 27 \qquad (5)$$

On an individual species basis, a significant relationship was noted between biting rate and live biomass of <u>Salix pulchra</u> (eqn 6).

$$B = 150 + 0.28S \qquad \underline{r} = .75, P<0.01, \underline{n} = 13 \qquad (6)$$

The slopes for equations 5 and 6 indicate biting rate increased at 21 $\pm$ 0.1 and 28 $\pm$ 2.1 bites·min^{-1} for each 100 g·m^{-2} increase in live biomass of the vascular plants and <u>S. pulchra</u> selected for, respectively.

4. Bite size in relation to plant biomass

Figures 7 (a) and 7 (b) show bite size in relation to total available live biomass and to the live biomass of selected plants, respectively. Bite size was not correlated with total live biomass or selected live biomass of individual species, of combined vascular species, or of lichens. Mean bite size for vascular plants (21 $\pm$ 1 mg) was significantly (P<0.001) less than for lichens (32 $\pm$ 1 mg).
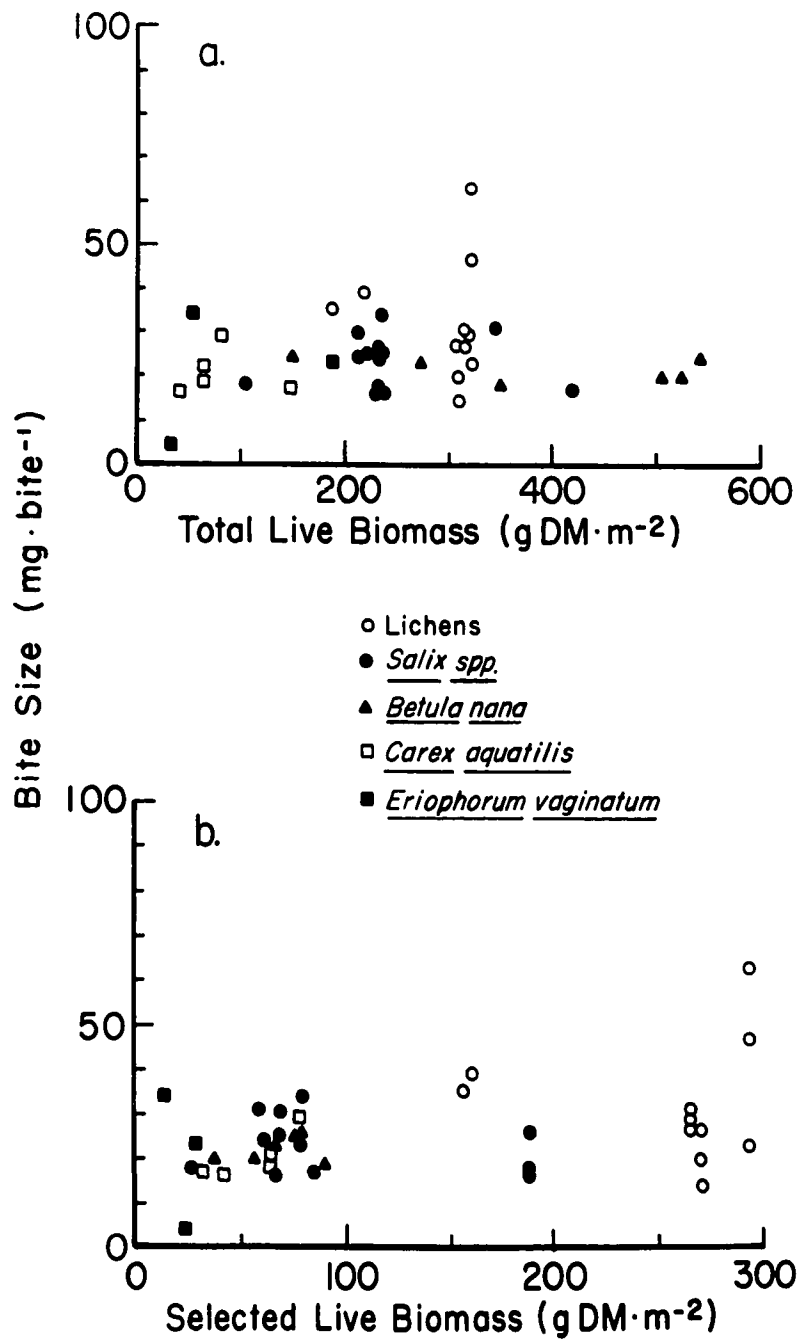
Figure 7. Variations in bite size over the range of total live biomass
(vascular plants + lichens) (a) or selected live biomass (b).

5. Discussion - Control of food intake and comparative behavior
    of other ruminants.

Components of the food prehension process which control
eating rate include biting rate and size of bite. Previous
studies with grazing animals have shown that the relative impor-
tance of biting rate and bite size to the control of food intake
is variable depending on plant species and/or vegetation stand.
For sheep on grass swards, Allden & Whittaker (1970) determined
through instantaneous visual observation of biting activity that
both biting rate and bite size were important in accounting for a
constant food intake with changing food availability at high
plant biomass. At lower biomass, biting rate decreased while
bite size increased as the length of the grass tiller increased.
For Jersey cows on tropical grass pastures, Chacon & Stobbs
(1976) recorded daily biting activity during grazing periods with
an electronic apparatus and also found that bite size increased
while biting rate decreased as the quantity of leaf material in
the sward increased. An increase in food intake was primarily
attributed to bite size. In comparison, bite size remained
constant irrespective of vascular plant biomass for reindeer
(Figures 7[a] and 7[b]) while biting rate increased in relation
to the biomass of selectively eaten grasslike and browse species
(Figure 6[b]; eqn 5) such that biting rate was correlated with
eating rate (Figure 5).

When reindeer were grazing on lichens, biting rate decreased
(bite size increased) with increasing eating rate which is inverse
to that noted for vascular plants (Figure 5) but similar to that
noted for sheep and cattle. To account for observed changes in
eating rate and lichen biomass (Figures 2 and 3), one would
expect that biting rate would decrease while bite size would
increase with increasing lichen biomass. In fact, no relationship
was noted between bite size or biting rate and lichen biomass
(Figures 6 and 7). No adequate explanation can be given except
that the physical properties of lichens may be important in
influencing intake. For instance, dry lichens are unpalatable
presumably because they cause lip abrasion, and they may require
an increase in chewing time to be moistened with saliva before
being swallowed. Also, some lichen species may be selected over
others during grazing since lichens vary markedly in digestibility
and preference rankings (Person et al. 1979; Holleman & Luick
1979). Some of the variance in biting rate may be due to this
sorting or selective feeding. When lichen biomass is low, its
separation from the moss layer may become more difficult while
sorting of preferred from non-preferred lichen species may take
place during prehension with unpalatable species and moss being
dropped from the corners of the mouth during eating (White et al.
1975). Therefore, bite size would not show a relationship to
biomass. In spite of these sorting processes, the bite size for

reindeer eating lichens is slightly greater than when eating

vascular plants (Table 4).

Comparative data on biting rate and bite size in other wild

grazer species are limited. Most studies of eating behavior of

wild species are limited to food selection by browsers (Wallmo et

al. 1973; Willms & MacLean 1978). There is one quantitative

measurement of bite size in white-tailed deer (Odocoileus

virginianus; Crawford & Whelan 1973). The feeding behavior of

reindeer is compared with that of domestic sheep, cattle, and

white-tailed deer in Figure 8. Reindeer (adaptable mixed feeders)

use a biting rate that is three times that of sheep while grazing

and a bite size that is approximately 25% that of sheep. The

bite size of white-tailed deer while browsing (8 mg dry wt·bite^{-1})

more closely resembles bite size in reindeer than sheep (Crawford

& Whelan 1973).

C. Daily Grazing Activity and Intake

1. Daily grazing time and intensity.

Through visual observations and vibracorder recordings of

reindeer grazing mixed vegetation during the summer (June through

August), it was found that the reindeer spent an average of

53 ± 3% of the day grazing. This value is in agreement with

previous estimates for adult caribou (53% of day, White et al.

1975) and wild reindeer (49% of day, Thomson 1971) during insect
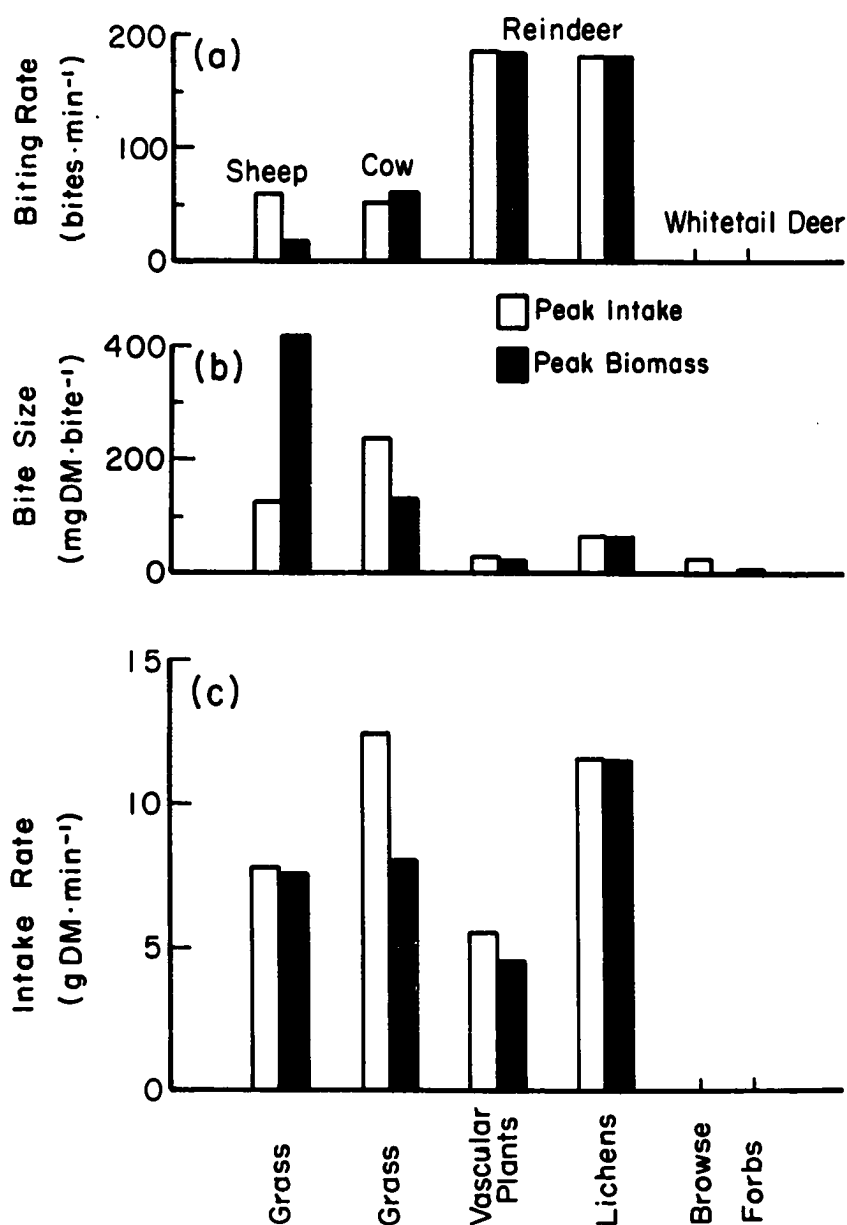
Figure 8. Comparison of food intake and eating behavior for sheep
(Allden and Whittaker 1970), Jersey cows (Chacon and Stobbs
1976), white-tailed deer (Crawford and Whelan 1973), and
reindeer. Light bars represent eating behavior values
when peak intake was reached; dark bars represent eating
behavior values at peak biomass levels.

free periods in the summer. The amount of time actually spent

eating was 26 $\pm$ 2% of the day (i.e., 374 min·day^{-1}), or approximately

50% of the grazing period. Daily grazing time (G, min·day^{-1}) and

eating time (E, min·day^{-1}) decreased significantly as total live

biomass (T, g dry wt·m^{-2}) increased (Figure 9; eqns 7 and 8).

$$G = 950.0 - 0.986T, \quad \underline{r} = -0.43, P<0.05, \underline{n} = 21 \quad (7)$$

$$E = 521.7 - 0.785T, \quad \underline{r} = -0.52, P<0.02, \underline{n} = 21 \quad (8)$$

Daily grazing time decreased by 1.6 $\pm$ .05 h (6.8 $\pm$ 0.2% of day)

and daily eating time by 1.3 $\pm$ 0.1 h (5.5 $\pm$ 0.5% of day) for each

100 g·m^{-2} increase in total available live biomass. Grazing

intensity (daily eating time/daily grazing time) decreased as the

total available biomass increased (Figure 9), indicating that the

fraction of time devoted to searching activity (i.e., the searching

intensity) during a grazing bout increased as biomass increased.

2.   Daily food intake.

Although daily food intake was not measured in the present

study, a theoretical estimate can be derived as the product of

the time spent eating (E, min·day^{-1}) and the eating rate (I,

g dry wt·min^{-1});

$$I' = E \times I \quad (9)$$
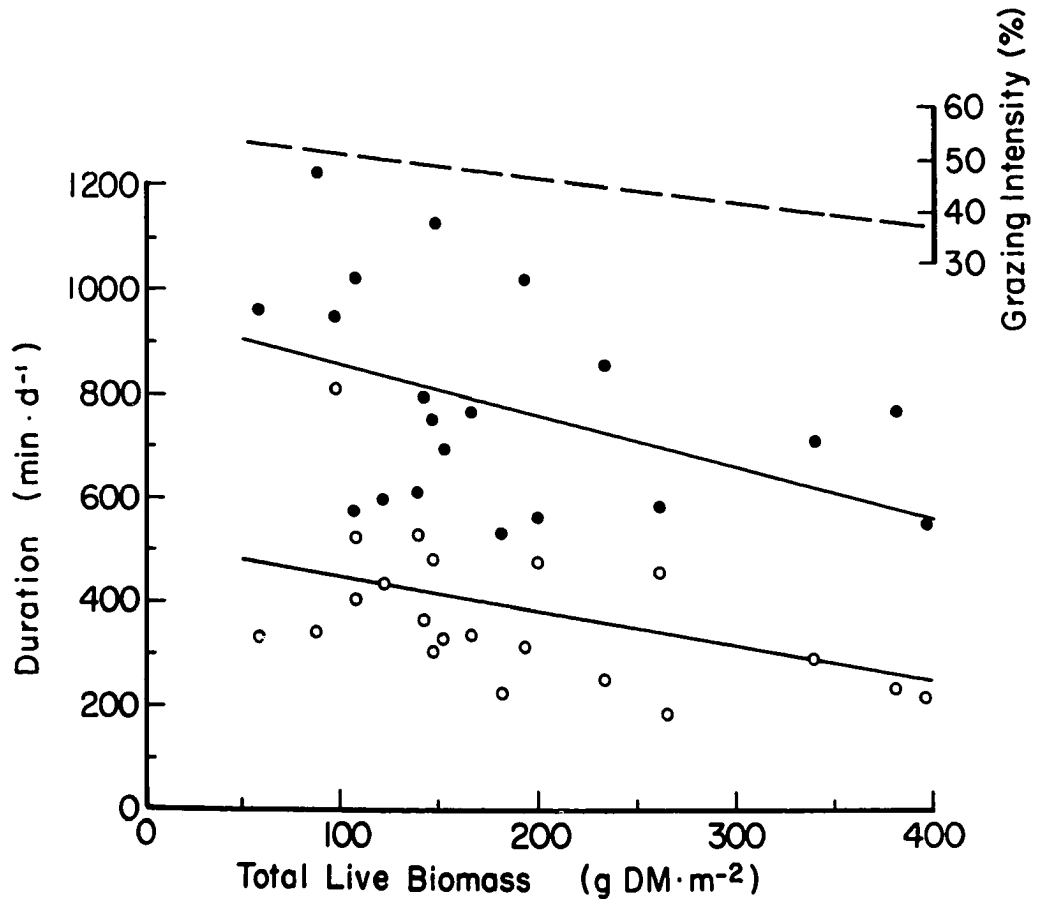
Figure 9. Daily grazing time (●) and daily eating time (0) in relation to total biomass (vascular plants + lichens) for reindeer tethered on tundra vegetation types throughout the summer.

where I' is daily food intake in g dry wt·day^{-1}. Since both E

and I are simple functions of food abundance expressed as live

biomass (see eqn 8 and Figure 3), the equation relating daily

food intake (I') to food availability is a second order polynomial.

The shapes of the predicted curve for the daily intake of <u>Salix</u>

species (eqn 10) and lichens (eqn 11) are shown in Figure 10.

$$I' = 1799 + 22.86T - 0.04T^2 \qquad (10)$$

$$I' = 897 + 12.21T - 0.02T^2 \qquad (11)$$

where T is the total aboveground live (vascular plants + lichens)

biomass (g dry wt·m^{-2}). Peak intake of <u>Salix</u> species and lichens

should occur at a live biomass of approximately 300 g·m^{-2}.

These relationships are theoretical in that during the summer

reindeer do not eat only one group of plants. Hence the instan-

taneous intake would vary with biomass and with the botanical

composition of the diet. Also, the time spent eating was estimated

for reindeer grazing mixed vegetation rather than only <u>Salix</u>

species or lichens so that the relationship of daily eating time

to the biomass of these species individually is not known.

3.   Discussion - Daily food intake in relation to plant avail-

      ability.

The theoretical responses in daily food intake with increasing

plant biomass shown in Figure 10 resemble empirically determined

relationships for sheep grazing mediterranean pastures (Arnold
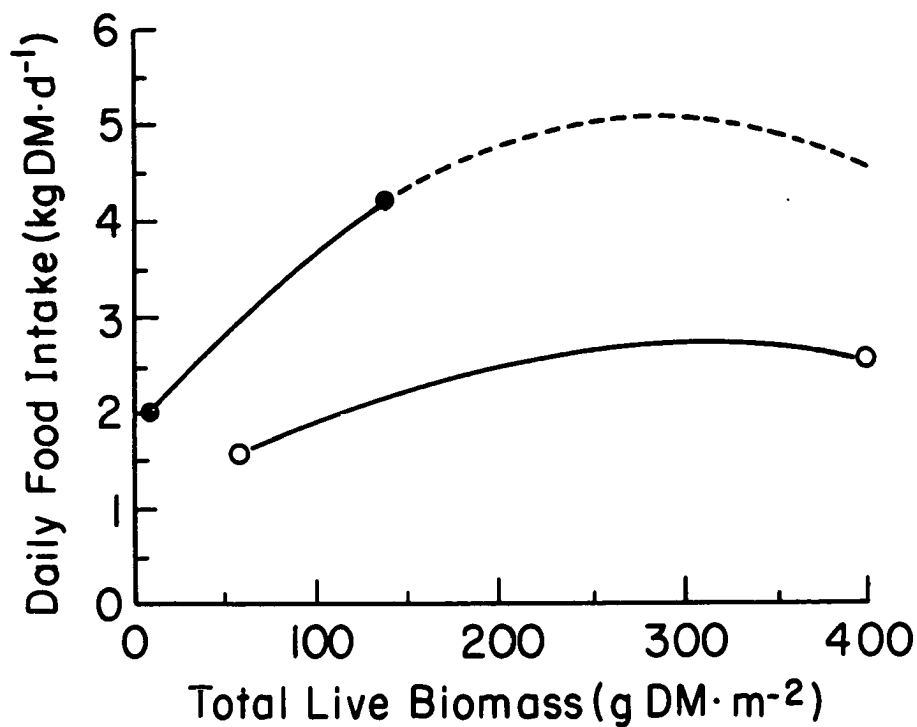
Figure 10. Predicted daily food intake for reindeer grazing Salix species (●) and lichen species (0) in relation to available live biomass. Dashed line indicates the theoretical relationship for biomass levels outside those found on study sites. Daily food intake was estimated as the product of eating rate (g·min^{-1}) and daily time spent eating (min·day^{-1}) and daily time spent eating (min·day^{-1}), eqn. 9.

1963, 1964; Arnold & Dudzinski 1966; Langlands & Bennett 1973).

To this extent, reindeer as adaptable mixed feeders resemble grazers. However, comparisons should be made with caution as similar studies have not been made for a typical browser species. Also, domestic sheep may not show the most extreme grazer responses as they too are adaptable mixed feeders when given highly variable ranges (Van Dyne et al. 1980).

The decline in the projected theoretical rate of increase in daily food intake with increasing plant biomass (Figure 10) results from differential responses of duration of eating (Figure 9) compared with rate of eating (Figures 2 and 3) in relation to plant biomass. In reindeer the time spent eating declined significantly with increasing biomass (Figure 9), however, only 27% of the variance in eating time was accounted for by the relationship (eqn 8). The equivalent relationship for sheep on grass pastures (Figure 11) is less variable. An important response occurs with sheep at plant biomass less than 50-70 $g \cdot m^{-2}$. We have too few observations at these low biomasses to determine if the marked increase in daily eating or grazing time found for sheep also occurs in reindeer. The lower elevation of the relationship of daily time spent eating for reindeer compared with the daily grazing time for sheep probably reflects the effect of search time as this was not reported in the sheep studies. The amount of time sheep spent searching was probably small, however, as the
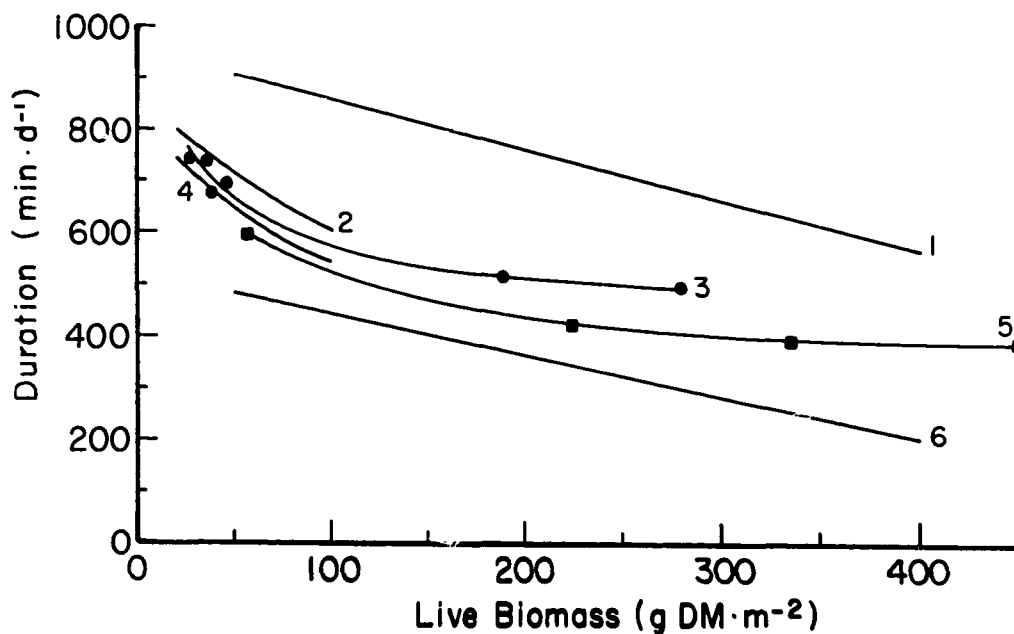
Figure 11. Between-species comparison of daily grazing or eating
times in relation to plant biomass. 1, Reindeer grazing
(this study); 2, nonlactating female reindeer eating
(White et al. 1975); 3, nonlactating female sheep grazing
(●; Young and Corbett 1972); 4, male reindeer eating (White
et al. 1975); 5, nonlactating female sheep grazing (■; Allden
1962); 6, reindeer eating (this study).

pastures were of low species diversity. After correcting for

search time it is clear that on these vastly different ranges

domestic sheep and reindeer spend a similar proportion of the day

eating. In contrast, the time spent foraging (eating and searching

for food) is very high in reindeer compared with sheep.

IV. CONCLUSIONS - Forage Availability and Food Intake

The higher diet quality ingested by large herbivores which adopt a concentrate selection (browsing) strategy versus a roughage selection (grazing) strategy should allow more time for searching because of a lower food residence time in the alimentary tract. A corollary to this hypothesis is that relationships between daily foraging time (eating and searching time) and forage availability under these browsing conditions may be extremely variable or even nonexistent except at extremely low plant biomass. At high biomass levels, the distribution of high quality food within the sward would presumably become more important than the biomass per se in controlling foraging time.

Reindeer, as adaptable mixed feeders, possess characteristics of both the grazer and the browser. As preferred plant species become more available, reindeer appear to graze and browse more selectively (i.e., searching intensity increases). Data from this study show that prehension patterns and biting rate are the primary components used in selective feeding and would therefore control food intake. When plant quality, diversity, and biomass are lower, daily searching intensity decreases and bite size and daily eating time are the primary determinants of food intake. Therefore, the balance of qualitative (i.e., plant species and growth forms) and quantitative (i.e., plant biomass) characteristics determine which strategy predominates during feeding.

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CHAPTER 2.

DIGESTIBILITY OF THE DIET AS INFLUENCED BY

FORAGE SELECTION PATTERNS OF REINDEER GRAZING TUNDRA

VEGETATION

I. INTRODUCTION

Studies of foraging behavior of reindeer discussed in Chapter

1 show that prehension patterns varied in response to plant

growth form and that highest eating rates were associated with

the more preferred plant parts (e.g., leaves of forbs and deciduous

shrubs, preferred species of lichens). These patterns provide

qualitative evidence for selective grazing. It was also shown

that daily searching time increased while daily eating time

decreased with increasing total live plant biomass. Presumably,

an increase in search time during grazing allows for more selective

use of the forages available. However, the actual extent to

which selectivity operates in the grazing of reindeer and caribou

on arctic tundra vegetation has not been documented.

The importance of forage availability to habitat and forage

selection in the genus Rangifer has been discussed in several

studies (Curatolo 1975; Skogland 1975; White et al. 1975; Roby

1978; Wright 1978). Klein (1970) suggested that caribou follow a

phenological progression of plant development on summer ranges so

that highly digestible, immature stages of plant growth are

selected (Loughrey 1957; Skogland 1975). White (1979) suggested that reindeer and caribou select for the available biomass as well as the phenological development of forage so that a high individual level of intake is maintained and the proportion of the year that energy intake exceeds requirements is maximized. Selection may be influenced as well by the physiological condition of the animal (i.e., age or reproductive state) and by social facilitation (Arnold 1970; Baumgardt 1970; Thomson 1971).

Church (1979) hypothesized that selectivity by the grazing animal changes relative to forage availability, defined as the abundance of biomass of forage plants. When forage is abundant, preference is expressed freely and results in the maximum use of the most highly nutritious forages (Swift 1948; Weir & Torell 1959; Bergerud 1972). When the forage supply is decreased, less preferred forages are eaten, although a large proportion of the total grazing time may still be spent on favored species of low accessibility (Arnold 1970; Westoby 1974). The relative selection of plant species may also depend on the spectrum of plants found in association with each species (Heady 1964; Freeland & Janzen 1974; Westoby 1974).

The objective of this study was to document feeding patterns of reindeer as forage and microhabitat use in relation to availability on two defined habitat types at Atqasuk, and to derive values of diet digestibility using the observed selection patterns.

Because digestibility can control food intake in ruminants (Blaxter 1962; Thornton & Minson 1972; Drozdz 1979), the extent to which the selection process influences the metabolizable energy intake is also discussed.

II. MATERIALS AND METHODS

A. Description of Animals

Reindeer used in studies of forage selection and digestibility were non-productive adults (i.e., four non-pregnant females; one non-rutting male) that were 2 to 5 years of age and averaged 70 kg in weight. Reindeer used in digestibility studies were rumen fistulated. For observations of grazing patterns in conjunction with other studies, esophageal fistulated reindeer were used as well. All animals had been fistulated at least 2 months prior to experimentation. Because degree of dietary adaptation has been found to influence digestibility values obtained for reindeer and caribou (Person 1975; Person et al. 1980; Trudell et al. 1980), reindeer were maintained on areas with plant species composition and stage of maturation similar to study sites for periods of at least 7 days prior to trials to facilitate ruminal adaptation. A 10 m rope was used to tether animals on the study sites.

B. Determination of Forage Use and Selection Patterns

Circular plots of 10 m radius were established within each of the two landform types (upland tundra and lake margin) to monitor grazing patterns of reindeer (Figure 12). Microhabitats defined according to plant species composition and sub-landform structure were mapped on each plot (see representative mappings

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Figure 12. Vegetation map of grazing sites. Circled numbers
representing location of study plots are grouped from top
to bottom - upland tundra plots ER (1-2), lake margin
plots LM (1-5), and upland tundra plots P (1-8). Map
is by V. Komárková and P.J. Webber. PL (low centered
polygons), PM (mixed polygons), PH (high centered polygons),
PF (flat polygons), Ut (upland tundra), Wt (wet tundra),
Lt (lichen tundra), Af (Arctophila fulva), Sp (Salix
pulchra), Ca (Carex aquatilis), Ev (Eriophorum vaginatum),
D (disturbed area), S (snowpatch), W (water).
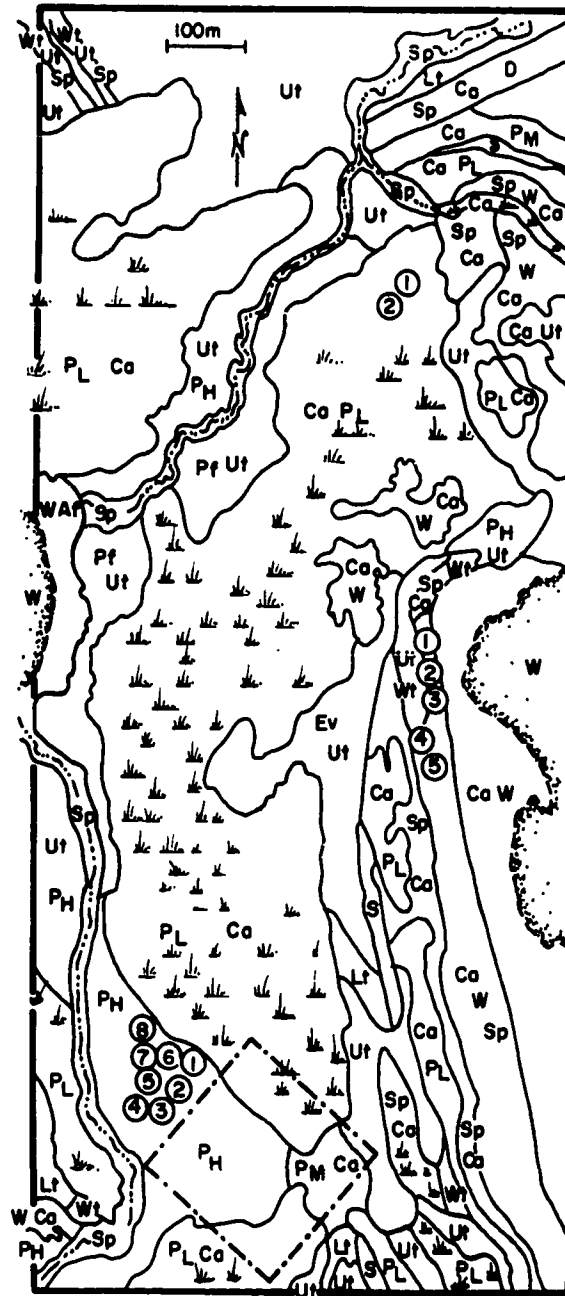
in Figures 18-24). Microhabitat cover was determined on each
plot as a percent of the total area and was used as an index of
availability.

Two types of experiments were conducted to evaluate forage
selection by grazing reindeer in relation to plant availability.
For the first experiment (3-day grazing), eight plots were estab-
lished within the upland tundra site (plots P1-P8; Figure 12) and
four plots within the lake margin site (plots LM1-LM4; Figure 12).
Following a fasting period of 3 to 4 hours, reindeer were tethered
individually on a plot for a period of 3 days. Mappings of
grazing events were made initially when the animal was first
tethered on the plot, three times daily during the course of the
trial, and again just before the animal was removed from the
plot. Biomass measurements were made at initial and final grazings
so that corresponding plant species availabilities could be
related to use patterns. Use would then presumably reflect
changing available biomass over a short period due to intensive
grazing.

The second experiment (seasonal grazing) was performed on
two upland tundra plots (ER1, 2; Figure 12) and two lake margin
plots (LM4, 5; Figure 12). Reindeer were tethered on these plots
for single grazing periods (approximately 1 hour duration) at 2-
week intervals during the summer of 1976. Animals again were
fasted for 3 to 4 hours prior to tethering, and mappings were

done as in the 3-day grazing experiment. Biomass measurements were made at the time of the mappings so that use could be determined relative to changing plant species availabilities. Because these mappings were made at 2-week intervals from June to August, changing use patterns in response to growth and maturation of plants through the peak growing season could be studied.

In both experiments, mappings were made by observing animals over entire grazing periods. During the grazing period, defined as one continuous period of eating and searching for food, the location and activity of the animal was noted on the microhabitat map at 30-second intervals. Because level of insect harassment has been shown to influence grazing behavior (White et al. 1975), percent of the total grazing period spent in insect avoidance (i.e., shaking or running) was recorded (Appendix A). Temperature, wind speed and precipitation at the time of each grazing period were also recorded. If the animal was eating at a given 30-second interval, plant species and parts being ingested were recorded. Microhabitat use was defined as the number of observations of a reindeer in a given microhabitat divided by the total number of observations during the grazing period. Vegetation use was quantified as the percent of the total observations of eating that a reindeer spent eating a given plant species or part.

For each grazing event observed, a preference index was determined for microhabitat type and plant species. The preference index for a microhabitat type was calculated as the percent use of the microhabitat during the grazing event divided by the percent availability of that microhabitat type on the grazing plot as determined by cover estimates. The preference index for a plant species was calculated in a similar fashion as use divided by availability of the selected plant parts obtained through biomass measurements. Microhabitat type or plant species were considered to be selected for when the preference index values exceeded 1.00.

C.   Collection and Preparation of Vegetation Samples

For determining available plant biomass on each of the grazing plots, triplicate quadrats (30 x 30 cm) were clipped at random from each microhabitat type concurrent with mapping of the grazing event. All plant material excluding the moss layer and stems of diameter greater than 5 mm was removed and notes were made as to stage of development (i.e., growth and maturation of leaf, stem and flowering parts). Biomass samples were separated by plant species and major plant parts (i.e., living or dead material; leaf, stem or flowering parts) and subsamples were dried in a forced-air oven at 110°C for 12 hours to determine dry matter content. Biomass of each plant part, plant species,

and/or plant growth form on a given grazing plot was calculated

as the dry matter composition ($g \cdot m^{-2}$) of each microhabitat type

multiplied by the percent availability of that microhabitat type

on that plot summed over all microhabitat types for the plot.

This yielded dry matter biomass as $g \cdot m^{-2}$ over the entire plot.

Availability of each plant part, plant species and/or plant

growth form was then calculated as a percent of the total plant

biomass on the entire plot.

For studies of forage digestibility, representative plant

species were collected from areas adjacent to those being grazed

to ensure complimentarity to the diet. Samples were separated by

plant part and dried under the same conditions as the biomass

samples. The samples were then ground in a Wiley Mill (20-mesh,

1 mm screen) and stored in air-tight bags in a cool place.

D.   Determination of Nylon Bag Digestibility

Apparent digestibility values for representative plant

species were determined with the use of nylon bags incubated

within the rumen (Van Keuren & Heinemann 1962) during the 3-day

grazing trials. Ground dried forage samples (0.5 to 1.0 g dry

wt) were placed into nylon bags (4 X 7 cm) which were tied in

triplicate onto a 35 cm piece of flexible plastic tubing. Glass

marbles were included in a few bags to aid in suspension of the

bags within the rumen. The tubing with bags attached (approximately 30 bags) was placed into the rumen through a 4 cm fistula. After 10 or 48 hours, tubing and bags were removed, rinsed of particles clinging to the exterior and dried at 110°C for 12 hours. Dry matter disappearance was calculated as the percent weight loss of forage from the bag. The forage which disappeared was assumed to have been "apparently" digested.

E. Determination of In Vitro Digestibility

Potential digestibility was measured with the first stage digestion technique of the in vitro system described by Tilley & Terry (1963) using rumen liquor from reindeer that had been grazing for at least 7 days on vegetation similar to forage samples being analyzed for digestibility. First stage digestion in vitro was performed to approximate rumen digestion for comparison with nylon bag values. Rumen contents obtained from rumen fistulated reindeer were collected into a prewarmed thermos (38°C) using a plastic tube and were immediately transported to the laboratory. The liquor was strained from the rumen contents through 3 layers of nylon netting and was added to a prewarmed phosphate buffer solution (McDougall 1948) that previously had been bubbled with CO_2 for 2 hours. Liquor was added in the ratio of 5 ml to every 20 ml buffer. Previous studies by Person et al. (1975) indicate that substrate nitrogen could be limiting when

lichens are digested by the in vitro method so that artificially
low estimates of digestibility are obtained. To alleviate any
problems of N-limitation, urea was added to the buffer solution
(1%).

Dried ground forage samples (.25 g dry wt) were incubated in
triplicate in 25 ml of the liquor-buffer solution at 38°C for 48
hours. Contents were shaken every 6 hours and pH was checked
initially and at 24 hours with adjustments being made to a range
of pH 6.7 to 6.9 with the addition of NaOH or HCl.

At the end of the incubation period, digestion was terminated
with the addition of 1 ml of 5% $HgCl_2$. Samples were centrifuged,
filtered through sintered-glass crucibles, and oven-dried at
110°C for 12 hours. Dry matter disappearance was calculated as
the percent weight loss of the forage sample incubated. Control
tubes containing no substrate were used for correction of dry
weight in samples due to rumen liquor. The resultant digestibility
values represented "potential" digestion in a controlled environ-
ment and may differ from values realized in vivo.

F.   Estimation of Diet and Vegetation Digestibility

Preliminary studies by Person (1975) and Person et al.
(1980a) indicated that a theoretical estimate of digestibility
can be obtained for a mixed stand of vegetation by summing the
products of the digestibility of the individual plant components

with their percent occurrence. This method was used to estimate

values of diet digestibility and of available vegetation digesti-

bility at initial and final grazings of the 3-day experiments.

G. Discussion of Methodology

Selective grazing is defined as the process by which some

forages are chosen in preference to others so that the relative

proportions of botanical components in the diet may not match

their availabilities on the range (Van Dyne et al. 1980). Selec-

tion operates in response to many factors (Arnold 1970; Arnold &

Hill 1972; Church 1979) which are combined by the concepts of

palatability and preference as defined by Heady (1964). Palat-

ability refers to stimulation of the animal feeding response by

plant characteristics and is often measured as the amount of the

food consumed in a no-choice situation. Forage characteristics

which influence palatability include growth form, chemical consti-

tuents and nutrient content of the forage. Because palatability

is assessed as the amount of food consumed, its value may be

reflected by forage use in the present study. Preference reflects

the relative use of forages which is modified in response to

herbage availability on the range. Both palatability and prefer-

ence are influenced by seasonal and site-specific variations in

vegetation as well as by inherent phagic behь̣ ˙ꞩr of the grazing

animal. In the present study, analyses were l   .ted to grazing

preferences because trials were conducted to determine relative use of the available forages on a diverse range and palatabilities for individual forage plants were not determined.

Selective grazing was assessed through comparisons of forage use in relation to vegetation availability (i.e., the preference index). Since this study was made, Wright (1980) reported that observations of forage use made at 30-second intervals closely approximate dietary use estimated by recording number of bites of each plant species. Therefore the method used in the present study should accurately reflect dietary composition.

The method of calculating preference assumes that selection for or against a forage occurs when its frequency in the diet differs from its frequency on the plot (Chesson 1978). Although this index of preference has been used in other studies to reflect the relative importance of forage types in the diet of reindeer (White & Trudell 1980a,b; Wright 1980), Johnson (1980) has cautioned that the actual "availability" of forages to the animal may be difficult to assess and that biases which result may preclude an absolute value for the preference index. In the present study, for example, a potential bias resulted from the assumption that mosses and stems greater than 5 mm diameter were "unavailable" to the grazing reindeer. The "availability" of green blades of the tussock graminoid, Eriophorum vaginatum, appears to be strongly influenced by a high proportion of standing

dead blades which makes green blades difficult to harvest (White

et al. 1975; Batzli et al. 1980; White & Trudell 1980b). Yet the

ratio of live to dead blades was not used to calculate availability

in this study. Avoidance of some evergreen shrubs (e.g., Vaccinium

vitis-idaea) and mosses could be attributed to low accessibility

as these plants may be undetectable or difficult to harvest due

to their growth form. Preference values in this study therefore

were compared by ranking their relative value in the selected

diet while variability in preference was accounted for through

relationships between use and availability.

III. RESULTS

A. Forage Use and Selection

1. Available biomass of forage types on grazing sites

Average available plant biomass as g dry wt·m^{-2} and as a
percent of the total available biomass at initial and final
grazings are summarized in Table 5 for the upland tundra site and
Table 6 for the lake margin site. Deciduous shrubs, graminoids
and forbs are treated on a species and plant part basis. Because
use of evergreen shrubs, lichens and mosses by grazing reindeer
was not observable to species, these plants are treated on a
growth form basis. Biomass of stems of deciduous shrubs of
diameter greater than 5 mm are excluded. Estimates of the avail-
able biomass of mosses were recorded by Komárková & Webber
(1980).

On the upland site, lichens constituted the greatest propor-
tion of the initial total biomass (39%), while mosses (29%) and
living vascular material (23%) also comprised a major proportion.
Of the vascular plant species, major components included live
portions of the evergreen shrubs (9.9%), Carex aquatilis (5.7%),
Eriophorum vaginatum (1.9%), and stem portions of Betula nana
(1.9%) and Salix pulchra (1.4%). Live plant material was more
available on an average than was dead material except in the case
of the tussock graminoid, E. vaginatum. Stem parts were more

-61-

Table 5. Mean ± 1 SE availability of plant biomass over eleven 3-day trials on upland grazing plots. Biomass on each plot was calculated as $g \cdot m^{-2}$ for each growth form, species, or part on each microhabitat summed over all microhabitats on the plot. Reductions in biomass were calculated as (mean initial biomass-mean final biomass) ÷ mean initial biomass. Significance in reduction was determined through comparisons of mean initial and mean final biomass.

Plant Growth Form/Species/Part		Initial Grazing Biomass $(g \cdot m^{-2})$	(% total)	Final Grazing Biomass $(g \cdot m^{-2})$	(% total)	Reduction (%)
Evergreen shrubs/	live	60±7	9.9	41±6	8.9	33
	dead	7±4	1.2	5±2	1.2	26
Deciduous shrubs/Salix pulchra/leaf		5±2	0.8	0.3±0.1	0.1	94
	new stem	0	0	0	0	–
	stem	8±5	1.4	7±5	1.5	18
	catkin	0.2±0.2	0.1	0	0	100
	dead leaf	0.4±0.2	0.1	0.2±0.1	0.1	50
/Betula nana/leaf		4±2	0.6	0.3±0.2	0.1	92
	stem	12±5	1.9	4±3	1.0	63
Tussock Graminoid/Eriophorum vaginatum/	live	11±2	1.9	9±1	1.9	24
	dead	31±5	5.0	21±3	4.6	32
Single-stemmed Graminoid/ Carex aquatilis/	live	35±9	5.7	22±6	4.8	37
	dead	14±3	2.3	16±5	3.5	–
Forb/Rubus chamaemorus/	live	2.2±0.9	0.4	1.4±0.6	0.3	36
	dead	0.2±0.1	0.1	0	0	100
Lichens		238±36	39.3	151±26	33.1	36
Mosses		179	29.4	179	39.1	–
Subtotal Vascular /	live	141±20	23.3	87±12	19.0	38*
	dead	52±7	8.6	43±4	9.3	18
Total	live	558±36	92.0	417±24	91.2	25**
	dead	52±7	8.0	43±4	8.8	18
TOTAL		610±35	100.0	459±21	100.0	25**

*$P<0.05$

**$P<0.01$

Table 6. Mean ± 1 SE availability of plant biomass over six 3-day trials on lake margin plots. For calculations, see Table 5.

Plant Growth Form/Species/Part	Initial Grazing Biomass ($g \cdot m^{-2}$)	(% Total)	Final Grazing Biomass ($g \cdot m^{-2}$)	(% Total)	Reduction (%)
Evergreen shrubs/ live	39+13	8.9	48+5	14.6	–
dead	1.0+1.0	0.2	0.4+0.4	0.1	60
Deciduous shrubs/Salix pulchra/leaf	34+7	7.7	4+1	1.1	90**
new stem	5.2+0.8	1.2	2+1	0.6	62*
stem	47+15	10.7	38+20	11.6	18
catkin	0.2+0.2	0.1	0	0	100
dead leaf	11+5	2.5	2.3+0.8	0.7	79
Tussock Graminoid/Eriophorum vaginatum/ live	2.9+1.5	0.7	2.1+0.9	0.6	28
dead	0	0	0	0	–
Single-stemmed Graminoid/Carex aquatilis/ live	15+2	3.4	14+3	4.3	5
dead	19+4	4.3	22+1	6.6	–
Forb/Pedicularis langsdorfii/ live	1.8+0.6	0.4	0.5+0.4	0.2	72
dead	0	0	0	0	–
Lichens	132+137	30.2	67+12	20.3	49
Mosses	129	29.7	129	39.3	–
Subtotal Vascular/live	146+30	33.5	110+34	33.5	25
dead	31+5	7.0	24+2	7.4	20
Total/ live	407+41	93.4	307+39	93.1	25
dead	31+5	6.6	24+2	6.9	20
TOTAL	437+42	100	331+39	100	24

*$P<0.05$

**$P<0.01$

available than leaf or other parts of deciduous shrubs. Forb
biomass was low.

Comparisons between the biomass available at initial and
final grazing trials indicate a significant reduction (P<0.01)
of the overall total (by 25%) and total live portions (by 25%) of
the biomass. A significant reduction is shown for living vascular
plant material (by 38%; P<0.05). Reductions were also noted for
individual plant species except current year stem of S. pulchra,
dead blades of C. aquatilis, and mosses. All reductions could
have been due to a combination of grazing, clipping and trampling.

Biomass estimates for the lake margin site (Table 6) showed
that the initial biomass was primarily composed of living vascular
plant materials (34%), lichens (30%), and mosses (30%). S.
pulchra stems also comprised a large portion (11%). Other impor-
tant vascular plant parts included live portions of the evergreen
shrubs (8.9%), S. pulchra leaf (7.7%), and live C. aquatilis
(3.4%). Live plant biomass was more available than was dead
biomass except for C. aquatilis. Forb biomass was again low.

Final biomass estimates showed that significant reductions
occurred in the biomass of S. pulchra leaf (by 90%; P<0.01) and
new stem portions (by 62%; P<0.05). Total live and total biomass
were reduced by 25% and 24%, respectively. Reductions were also
noted for individual plant species except live evergreen shrubs,
dead blades of E. vaginatum and C. aquatilis, dead forbs, and
mosses.

Seasonal availability of plant species is presented for a plot upland tundra plot (ER 1) and a lake margin plot (LM 4) in Figure 13. Representative plots only are presented here because all trials for seasonal grazing were conducted on plots of dissimilar biomass composition and on different days throughout the season. On the upland tundra site, lichens and evergreen shrubs predominated during the early season (>95%) and made up more than 50% of the total biomass throughout the growing season in spite of slow growth rates. The relative availability of C. aquatilis increased during mid-season as blade growth and maturation progressed. Relative availabilities of E. vaginatum, the deciduous shrubs, and the forbs tended to increase from mid-season (July 15).

On the lake margin site, the relative availability of both deciduous and evergreen shrubs increased mid-season while that of lichens decreased. The relative availability of the graminoids, C. aquatilis and E. vaginatum, remained constant throughout the season. Forb availability increased late in the season.

2. Foraging patterns under 3-day and seasonal grazing

Mean use and availability of forage species or growth forms as a percent of the total grazing observations under 3-day grazing of the upland tundra and lake margin sites are presented in Figure 14. Lichens made up an average of 52% as the principal
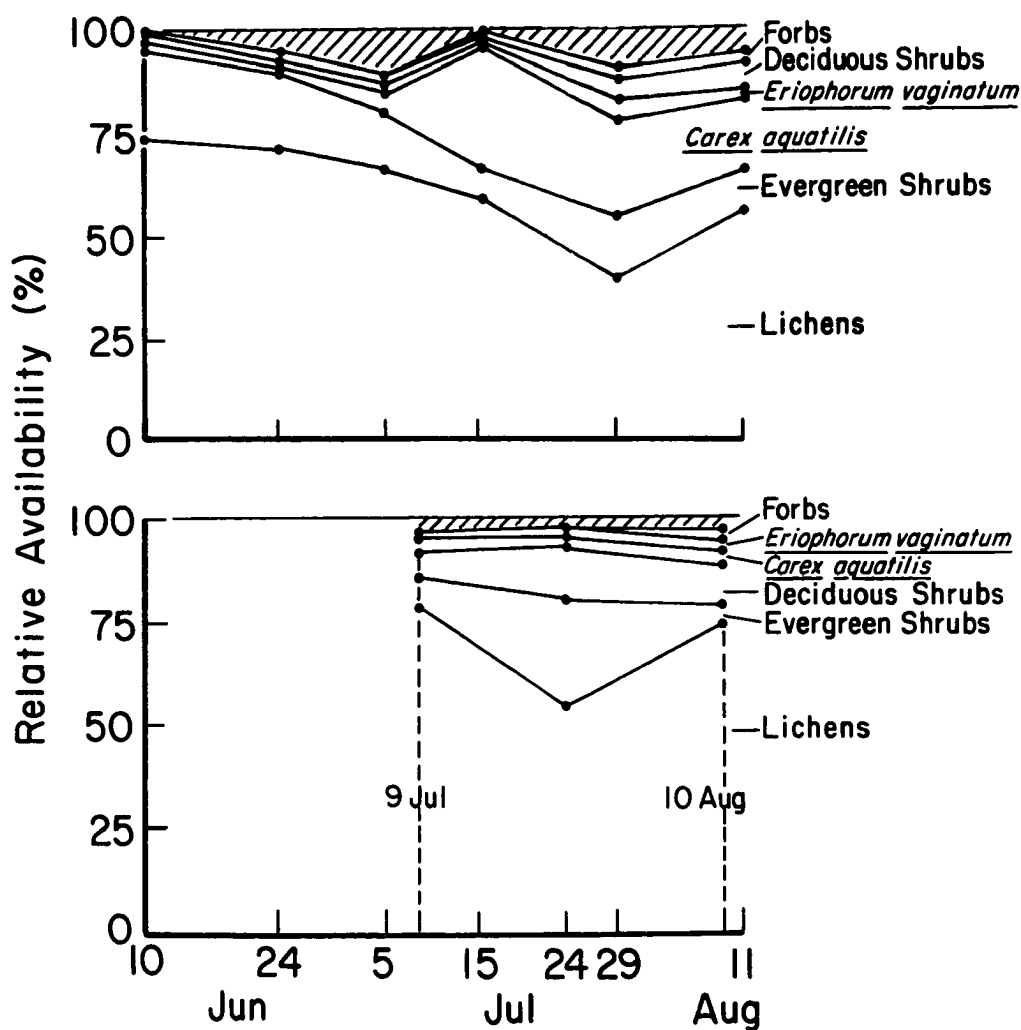
Figure 13. Relative availability (%) of forage species on the upland
           tundra site (plot ER1) from 10 June to 11 August 1976 and
           the lake margin site (plot LM4) from 9 July to 10 August
           1976. Shaded area represents unidentified dead plant
           debris.
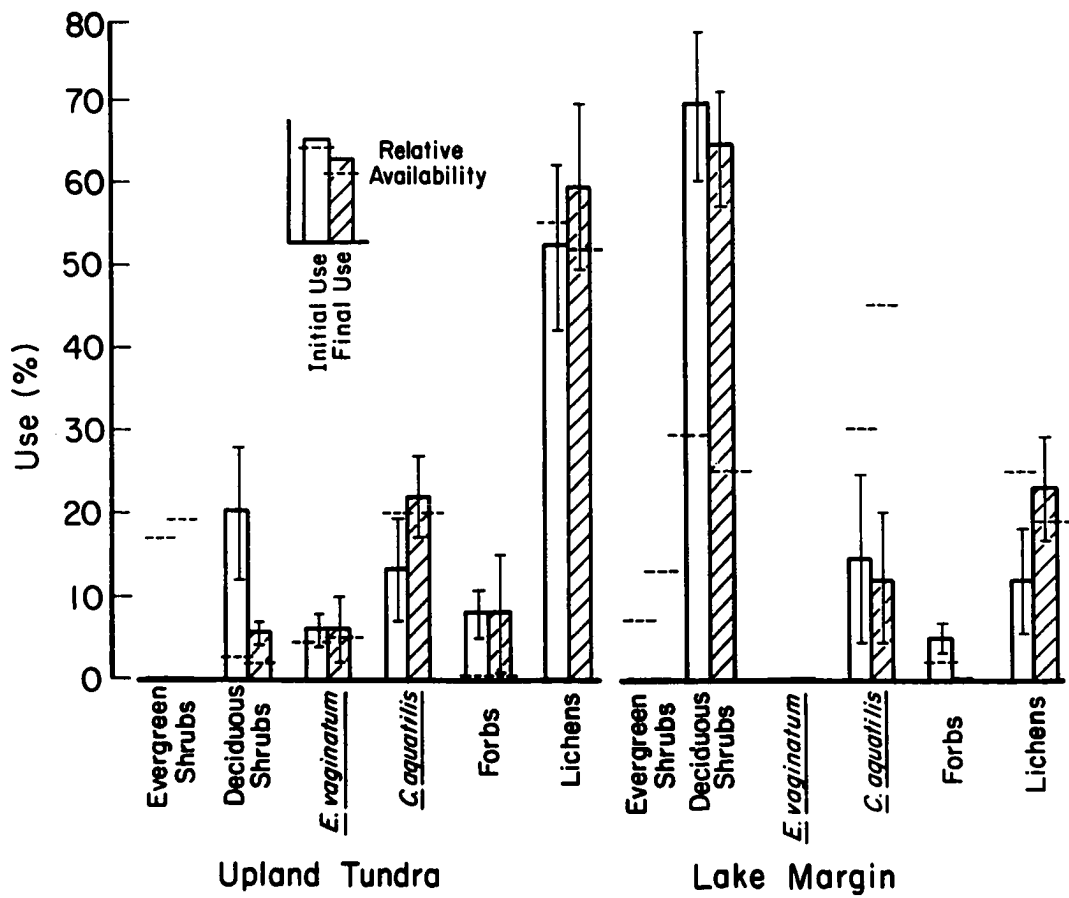
Figure 14. Mean +/- 1 SE use of forages as a percent of total grazing
use on sites grazed in 3-day trials over three summers
(1975, 1976 and 1977). Mean availabilities as a percent
of total plant biomass are shown as dashed lines.

component of the initial diet on the upland tundra site. The
remainder of the diet was composed of deciduous shrub leaves and
current-year stems (21%), green blades of Carex aquatilis (13%),
forbs (8%), and green blades of Eriophorum vaginatum (6%). Use
of evergreen shrubs and mosses was not observed. Mean use of
forage in final grazings showed an increase in lichens (to 59%)
and C. aquatilis (to 22%) and a decrease in deciduous shrubs (to
6%) in the diet. Use of other forages in final grazings was
similar to initial use.

Deciduous shrubs (mainly Salix pulchra) were the principal
component of the initial diet (69%) on the lake margin site. Use
was also made of green blades of C. aquatilis (14%), lichens
(12%), and forbs (5%). Use of E. vaginatum, evergreen shrubs,
and mosses was not observed. Mean use of forages during final
grazings showed continued predominant use of deciduous shrubs
(64%), an increase in the use of lichens (to 23%), and a slight
increase in the use of E. vaginatum (to 0.3%). Mean use of C.
aquatilis and the forbs decreased (to 12% and 0.2%, respectively).
Use of evergreen shrubs and mosses was not observed during initial
or final grazings.

Forage use throughout the summer season in 1976 is summarized
in Figure 15. In mid-June, more than 90% of the diet of reindeer
grazing on the upland tundra site was composed of lichens.
Lichens were used less as the season progressed but averaged more
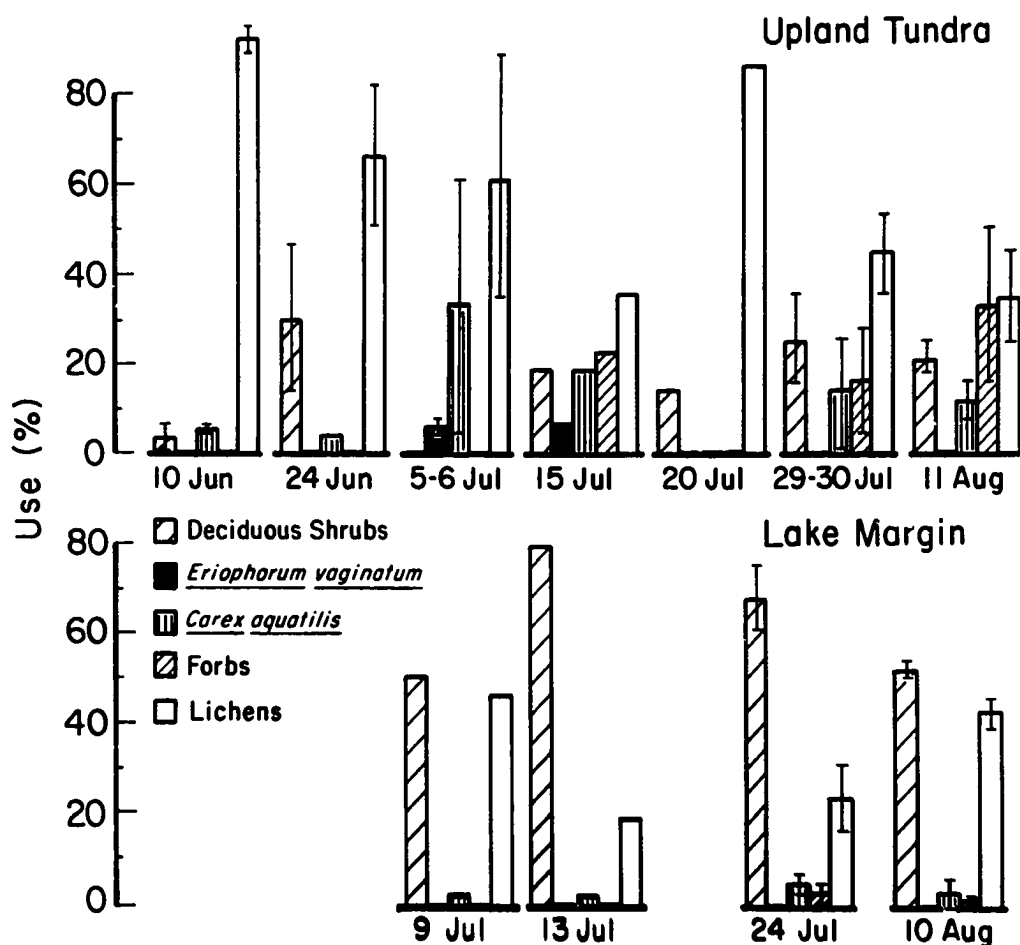
Figure 15. Seasonal use of forages as a percent of total grazing use
on the upland tundra and lake margin sites in 1976.
Variances represent differences between animals and plots.
Use of evergreen shrubs and mosses was negligible
throughout the season.

than 60% of the diet overall. Use of deciduous shrubs increased in late June as leaf material became available and averaged 16% throughout the season. Green blades of C. aquatilis and E. vaginatum were used primarily in early July, averaging 13% and 1.6% of the diet, respectively. From mid-July, use of E. vaginatum decreased while use of forbs increased in the diet to an average of 20% in late season and an average of 10% overall. From mid-July to the end of the season, use was more evenly distributed between the deciduous shrubs, C. aquatilis, forbs, and lichens than earlier in the season.

On the lake margin site, deciduous shrubs became increasingly important in the diet from early to mid-July and averaged 62% throughout the season. C. aquatilis and forb species made up a small proportion of the diet overall (averaging 3% and 1.2%, respectively) but showed a slight increase in use in late July. Use of lichens was more pronounced in early and late summer (averaging 44%) than during mid-summer (averaging 22%).

Mean preferences of reindeer for forage on the upland tundra and lake margin sites during 3-day and seasonal grazings are presented in Table 7. Initially, deciduous shrubs and forbs were highly selected for on the upland tundra site. E. vaginatum was also selected for but to a lesser extent. Lichens were selected roughly in relation to their availability while C. aquatilis was

Table 7. Mean ± 1 SE preference of reindeer for forages on the upland tundra and lake margin sites under 3-day and seasonal grazing. The index of preference was calculated as use/availability.

Forage Type	Upland Tundra			Lake Margin		
	(n=11) Initial Grazing	(n=11) Final Grazing	(n=12) Seasonal Grazing	(n=6) Initial Grazing	(n=6) Final Grazing	(n=6) Seasonal Grazing
Evergreen shrubs	0	0	0	0	0	0
Deciduous shrubs	12.2 ± 3.4	3.7 ± 2.0	10.2 ± 3.7	2.6 ± 0.5	3.2 ± 0.8	10.0 ± 2.6
Eriophorum vaginatum	2.0 ± 0.7	1.4 ± 0.6	1.1 ± 0.5	0	0.02 ± 0.02	0
Carex aquatilis	0.6 ± 0.2	1.1 ± 0.2	3.0 ± 1.3	0.9 ± 0.7	0.3 ± 0.2	1.4 ± 0.6
Forbs	6.9 ± 3.2	4.0 ± 3.5	6.6 ± 2.8	2.2 ± 1.0	0.2 ± 0.2	1.2 ± 0.8
Lichens	1.0 ± 0.2	1.4 ± 0.5	1.0 ± 0.1	0.7 ± 0.3	1.4 ± 0.3	0.5 ± 0.1
Mosses	0	0	0	0	0	0

not selected for. Final grazings showed decreased but still selective use of the forbs, deciduous shrubs and E. vaginatum. Preference for lichens and C. aquatilis was increased so that selection was made for these forages slightly above their availabilities. Evergreen shrubs and mosses were selected against.

Seasonal grazing on the upland tundra site showed that deciduous shrubs and forbs were highly selected for overall, although forbs were primarily selected for later in the season. C. aquatilis was also selected for but to a lesser extent and earlier in the season. E. vaginatum was preferred mostly during mid-summer and along with lichens was selected roughly in relation to availability overall. Again, evergreen shrubs and mosses were selected against.

On the lake margin site, initial selection during the 3-day grazing trials was made for the deciduous shrubs and forbs. C. aquatilis and lichens were used but not selected for. E. vaginatum, evergreen shrubs and mosses were not preferred. In final grazings, selection was made for the deciduous shrubs and to a lesser extent for lichens as well. Very little use was made of C. aquatilis, the forbs, and E. vaginatum so that these forages along with the evergreen shrubs and mosses were not preferred.

Deciduous shrubs were highly selected for throughout the season on the lake margin site. C. aquatilis and the forbs were also selected for but to a lesser extent and mostly in mid- to

late summer. Lichens were not selected for. E. vaginatum, the

evergreen shrubs and mosses were selected against.

Regression analyses of forage use versus availability per-

formed to determine the significance of the variability in the

preference index for all grazing trials are presented in Figure

16. Intercepts of all regression lines except that for E. vaginatum

were significantly different from zero (P<0.05; Figure 16). This

indicated that preference of reindeer for the deciduous shrubs,

C. aquatilis, forbs and lichens varied depending upon their

availabilities on the grazing site (Figure 17). E. vaginatum was

preferred independent of its availability (Figure 17). Significant

positive relationships of use versus availability (P<0.01) were

noted for the deciduous shrubs, lichens and E. vaginatum. All

relationships confirm patterns of preference and selection noted

for mean values of preference for forages. When available,

deciduous shrubs and forbs were always selected for. E. vaginatum

was selected roughly in relation to its availability. Lichens

and C. aquatilis were selected for only when their availabilities

were less than 33% and 10%, respectively.

3. Discussion - A comparison of reindeer and caribou diet

    selectivity.

Several studies of the foraging patterns of reindeer and

caribou have shown that these animals are highly flexible in

Upland Tundra & Lake Margin
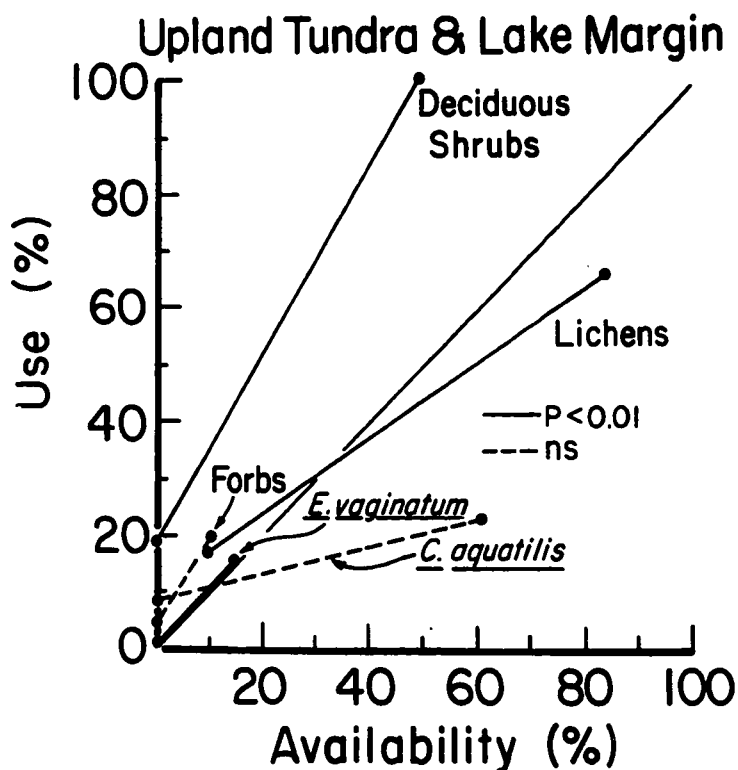
Figure 16. Regression of use versus availability of forage plants on the upland tundra and lake margin sites under 3-day and seasonal grazing. Relationships are:

Deciduous shrubs	y = 18.85 + 1.65x
	n = 48, r = .671, P<0.01
Eriophorum vaginatum	y = -0.11 + 1.06x
	n = 48, r = .467, P<0.01
Carex aquatilis	y = 7.58 + 0.26x
	n = 48, r = .232, P>0.05
Forbs	y = 4.79 + 1.34x
	n = 48, r = .170, P>0.05
Lichens	y = 10.93 + 0.67x
	n = 48, r = .495, P<0.01

Selection was made for forages when regression lines passed above the equivalence line (x=y).
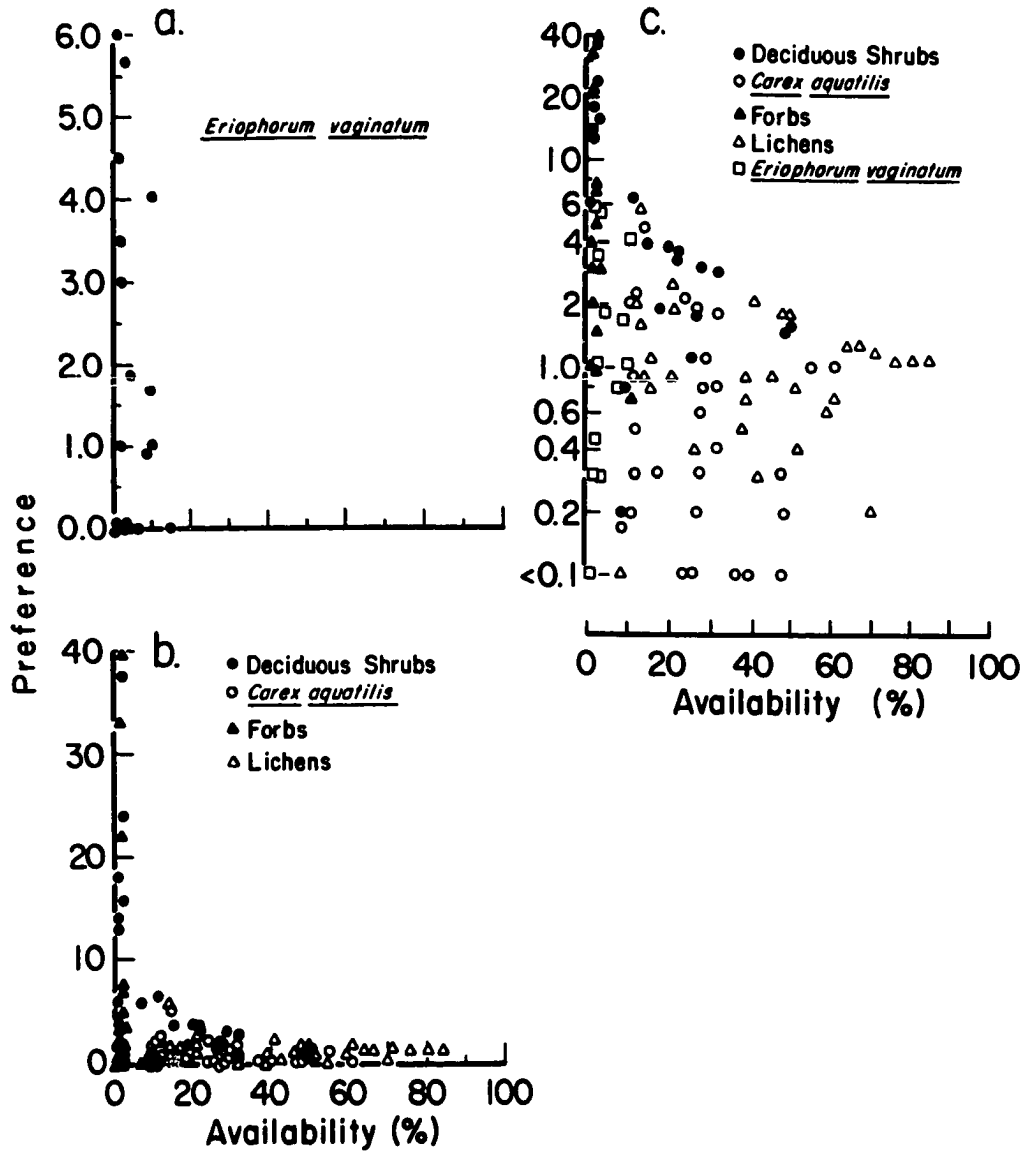
Figure 17. Preference of reindeer for forage on the upland tundra and
lake margin sites on linear (a,b) and $\log_{10}$ transformed (c)
scales in relation to forage availability.

their selection comparisons between diets from different regions may not be meaningful, discussion of these studies can be viewed in terms of selective use of forages in relation to their availabilities.

During April and early May in Norway (Gaare & Skogland 1975; Skogland 1975), Greenland (Thing 1980), Canada (Kelsall 1968; Bergerud & Nolan 1970; Bergerud 1972; Bloomfield 1980), and Alaska (Lent 1966; Skoog 1966; Wright 1978; Kuropat & Bryant 1980; Boertje 1981), reindeer and caribou use lichens primarily in areas where they are abundant. With the onset of spring snowmelt and subsequent development of new plant growth, heavy use is made of green blades and inflorescences of the graminoids _Eriophorum_ _vaginatum_ (Lent 1966; Skoog 1966; Roby 1978; Wright 1978; Kuropat & Bryant 1980), _Poa_ spp., _Festuca_ _brachyphylla_ (Thing 1980), _Scirpus_ _cespitosus_, and species of _Carex_ (Bergerud & Nolan 1970; Bergerud 1972; Skogland 1975; Bloomfield 1980; Boertje 1981), and evergreen shrubs including _Empetrum_ _nigrum_, _Kalmia_ _polifolia_, _Vaccinium_ _angustifolium_ and _V._ _vitis-idaea_ (Bergerud & Nolan 1970; Bergerud 1972; Wright 1978; Boertje 1981).

At Atqasuk, lichens predominated in the diet of reindeer from mid-May through early June (White & Trudell 1980a,b; Trudell & White 1981) and also comprised a major portion of the diet of caribou sighted in the area (White & Trudell 1980b). Caribou

also used sedges (Carex spp.) and berries of Vaccinium vitis-idaea in early May. Although the inflorescences of E. vaginatum are an important forage for caribou throughout May and June in the western arctic region (Lent 1966; Roby 1978; Kuropat & Bryant 1980), selection by reindeer for E. vaginatum was not observed until late June in the present study. This could be attributed to a combination of a low density of E. vaginatum inflorescences, a high density of dead blades of E. vaginatum, and a high density of highly acceptable lichens (moist, preferred species).

Evergreen shrubs were not preferred nor used by reindeer in the present study. This observation contrasts with other studies which showed that evergreen shrubs constitute an important part of the spring and early summer diets (Bergerud & Nolan 1970; Bergerud 1972; Wright 1978). This could be attributed to the abundance of Ledum palustre and Cassiope tetragona on the grazing sites (Jung et al. 1979; Komárkova & Webber 1980) which have been found to be highly unpalatable to reindeer and caribou (Palmer & Rouse 1945; Banfield 1954; Kelsall 1968; White & Trudell 1980a,b) and to be of low digestibility in the present study (Table 10). E. nigrum, P. mariana, and K. polifolia were selected for by reindeer and caribou in other studies but were not present on the Atqasuk study site. While V. vitis-idaea was also shown to be selected for in other studies (Wright 1978; White & Trudell 1980b), its low abundance and prostrate growth form could have

made it less "available" in the present study when found among forages of higher biomass.

Lichens, some evergreen shrubs, and graminoids continue to constitute an important part of the early and mid-summer diets of reindeer and caribou in Norway (Gaare & Skogland 1975; Skogland 1975), Greenland (Thing 1980), Canada (Banfield 1954; Kelsall 1968; Bergerud & Nolan 1970; Bergerud 1972; Bloomfield 1980), and Alaska (Lent 1966; Klein 1968; Curatolo 1975; White et al. 1975; Roby 1978; Wright 1978; White & Trudell 1980a,b). During mid-summer, other forage species begin to show increasing importance in the diet. The rapid development of new growth by deciduous shrubs (species of Salix and Betula) may account for a shift to predominant use of these forages in the present and other studies (Banfield 1954; Lent 1966; Skoog 1966; Kelsall 1968; Klein 1968; Bergerud & Nolan 1970; Bergerud 1972; Curatolo 1975; Gaare & Skogland 1975; Skogland 1975; White et al. 1975; Roby 1978; Wright 1978; Thing 1980; White & Trudell 1980a,b; Boertje 1981). Use of forb species and fungi (mushrooms) also occurs during June, July and August, although the importance of these latter species in the diet may be limited by their availabilities on the range.

In the present study, use of forages throughout the summer responded to increasing biomass (e.g., leaves of deciduous shrubs and forbs) and stage of maturity of the preferred plant parts on

the grazing sites (e.g., green blades of E. vaginatum and C. aquatilis). Preference for some forage was high in spite of low or reduced biomass. For example, selection for deciduous shrub leaves remained high in final grazings of the lake margin site even though leaf biomass was significantly reduced (Table 6). Selection for forbs on both the upland tundra and lake margin sites was very high in spite of low biomass (Tables 5, 6 and 7). In contrast lichens were selected against at high biomass (Figure 16). Considering the relative importance of lichens in the diet, however (averaging more than 60% throughout the summer), lack of preference shown for lichens in some grazing studies does not reflect their actual importance in the summer diet.

Forage use by reindeer in the present study was evenly distributed between deciduous shrubs, sedges, forbs and lichens later in the summer (August) which agrees with observations of forage use by reindeer and caribou in other studies (Kelsall 1968; Bergerud & Nolan 1970; Bergerud 1972; Gaare & Skogland 1975; White et al. 1975; Roby 1978; Wright 1978; Bloomfield 1980). Use at this time of year appears generally to be governed by the availability and maturity of forages on the grazing site with preference being exhibited when possible. Lichens continue to show an increasing importance in the diet of reindeer and caribou in late summer and early fall (August and September) as other forages show signs of senescence (Bergerud & Nolan 1970;

Bergerud 1972; Gaare & Skogland 1975; Roby 1978; White & Trudell
1980a,b; Boertje 1981).

B.   Microhabitat Use and Selection

1.   Cover and available biomass of microhabitats on grazing

      sites

      Microhabitat cover and average biomass available on the

upland tundra and lake margin study sites are summarized in

Table 8. The intertussock area provided the most cover and

biomass on the upland tundra grazing site although it offered a

low diversity of plant species. Lichens dominated the cover.

Tussocks and the Carex marsh provided the next most available

cover while offering lowest biomass and plant diversity (Table

1). Wet tundra offered the highest plant species diversity

(Table 1) and second highest biomass. Similar cover and biomass

were provided by microhabitats on the seasonal upland tundra

grazing site.

      On the lake margin grazing site, the Carex marsh provided

the most cover but the least biomass of the three available

microhabitats (Table 8). The Salix strangmoor provided the

second most available cover and biomass. The least cover was

provided by the lichen ridge. Plant diversity on the lake margin

site was more evenly distributed among microhabitats than on the

upland tundra site (Table 1).

Table 8. Mean ± 1 SE cover and plant biomass available on 3-day and
seasonal grazing plots over the three summer study periods (1975,
1976 and 1977).

Vegetation Type/ Microhabitat Type	Cover (% plot Area)		Biomass $(gDM \cdot m^{-2})$	
	Short-term grazing	Seasonal grazing	Short-term grazing	Seasonal grazing
Upland Tundra	(n=7)	(n=2)	(n=11)	(n=6)
Tussock	25+6	33	12+2	5+1
Intertussock	43+5	37	330+42	349+35
Wet trough	11+3	11	139+26	209+25
Carex marsh	21+4	18	45+7	36+14
Lake Margin	(n=4)	(n=2)	(n=6)	(n=3)
Lichen ridge	25+3	16	217+32	444+94
Carex marsh	44+4	54	31+9	6+4
Salix strangmoor	31+2	29	75+17	92+21

2.   Use and selection of microhabitats during grazing

Patterns of microhabitat use expressed as a percent of the total grazing use by reindeer during the 3-day grazing trials are summarized in Figure 18. Because initial and final grazings were relatively free of insect harassment, use patterns reflected grazing activities. On the upland tundra plots, initial grazing use of intertussock tundra was high (55%) as was use of the wet troughs (29%). Less use was made of the Carex marsh (12%) and tussocks (4%). After 3 days of grazing, even heavier use was made of the intertussock areas (to 62%) with a decline in the use of the wet troughs (to 13%). Increases in use of the Carex marsh (to 19%) and tussocks (to 6%) were noted. However, differences between initial and final grazing use of microhabitats were not significant due to large variations between trials.

These patterns of microhabitat use of upland tundra are also shown by representative initial and final grazing maps for 1975 (Figure 19), 1976 (Figure 20) and 1977 (Figure 21). Initial grazing was concentrated on the intertussock polygon rims and wet troughs while final grazing was expanded into polygon centers and the Carex marsh.

On the lake margin plots, heaviest initial use during day one of the 3-day grazing period was made of the Salix strangmoor areas (59%) while the rest of the grazing time was distributed evenly between the lichen ridge (22%) and the Carex marsh (19%).
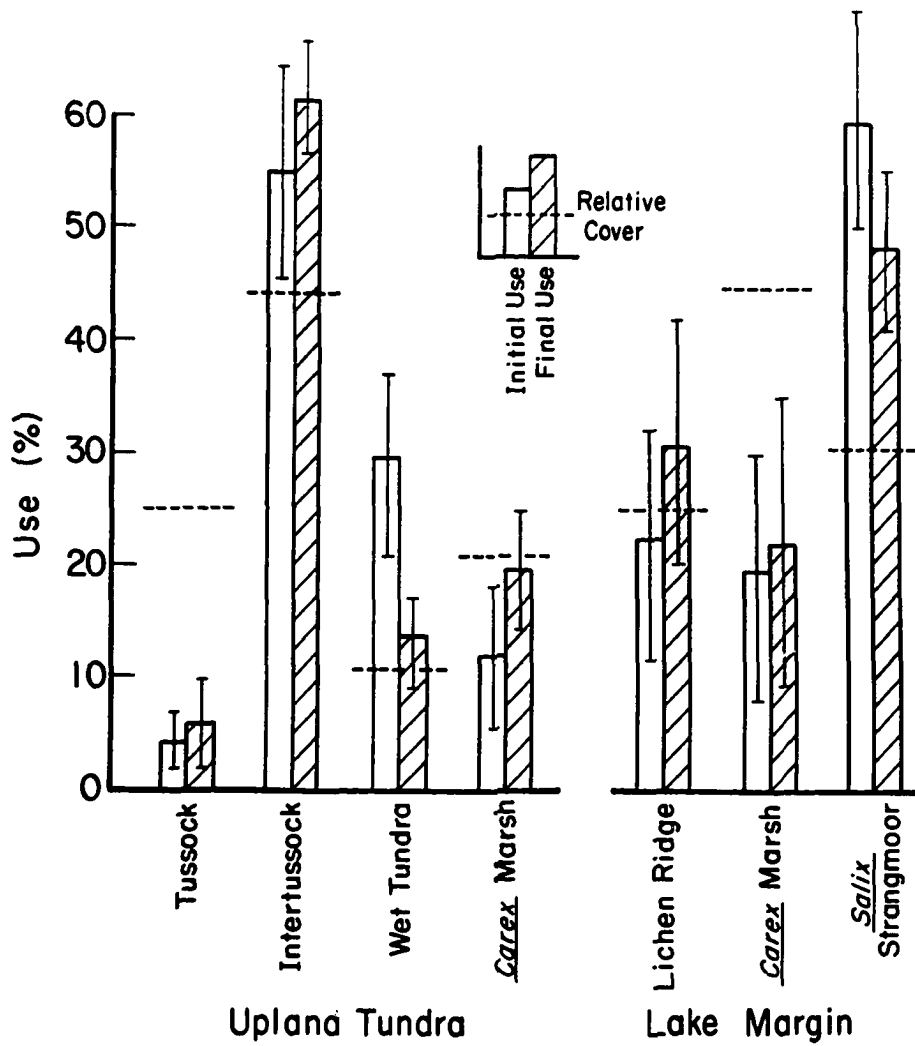
Figure 18. Mean +/- 1 SE use of microhabitats as a percent of total
grazing use and relative cover on plots grazed in 3-day
trials over three summers (1975, 1976 and 1977).
Differences between mean initial use and mean final
use were not significant.
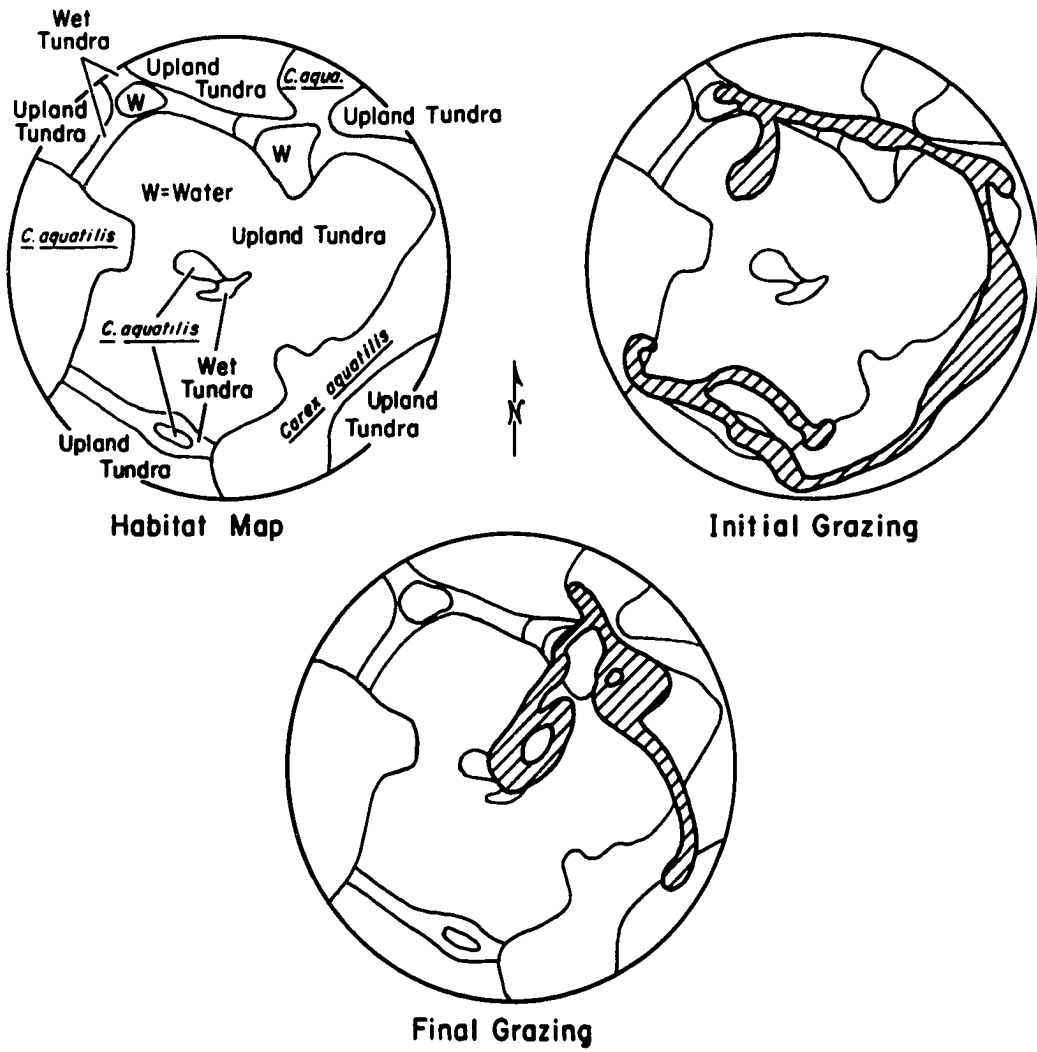
Figure 19. Maps of initial and final grazing events on upland
tundra plot P3 in 1975.

Habitat Map

Initial Grazing
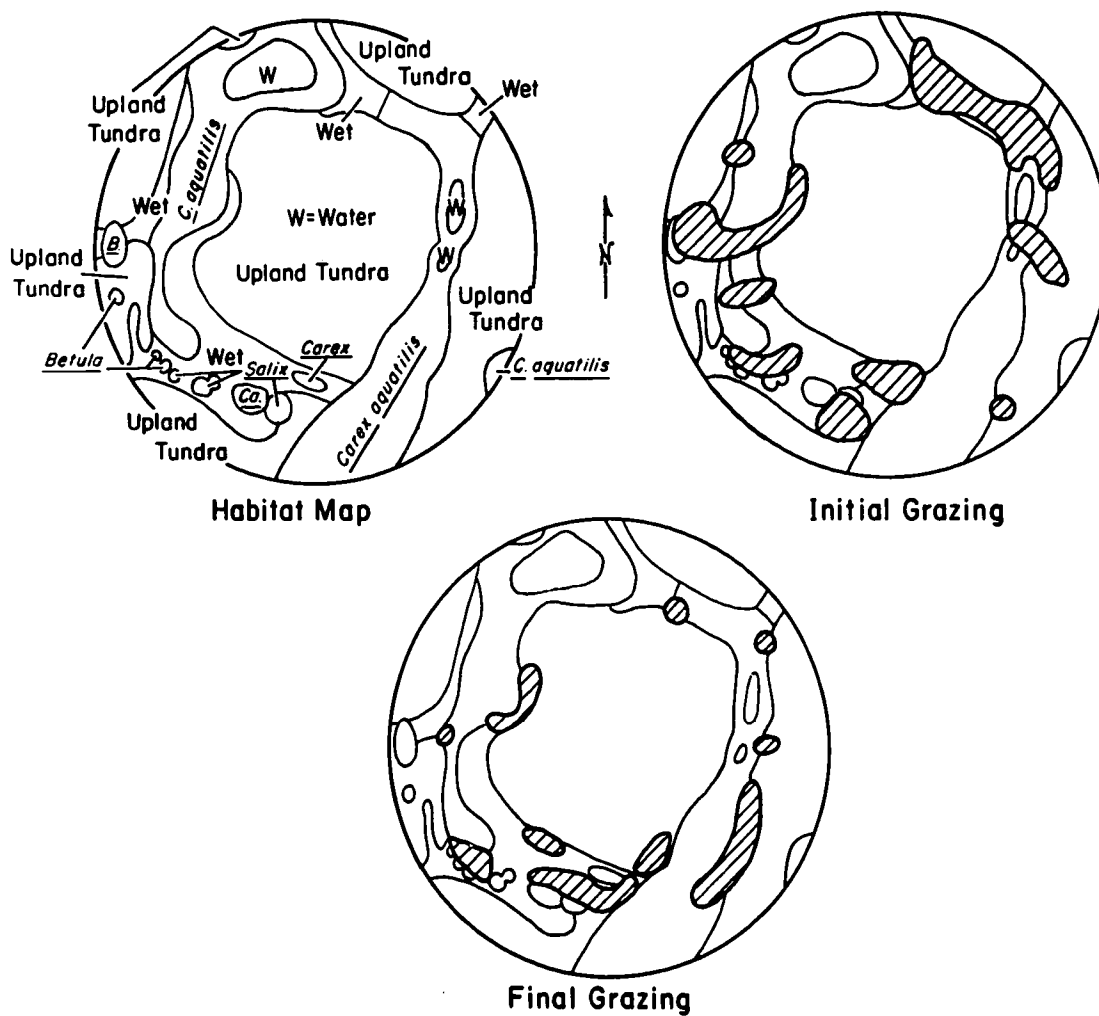
Final Grazing

Figure 20. Maps of initial and final grazing events on upland tundra plot P6 in 1976.

Habitat Map

Initial Grazing
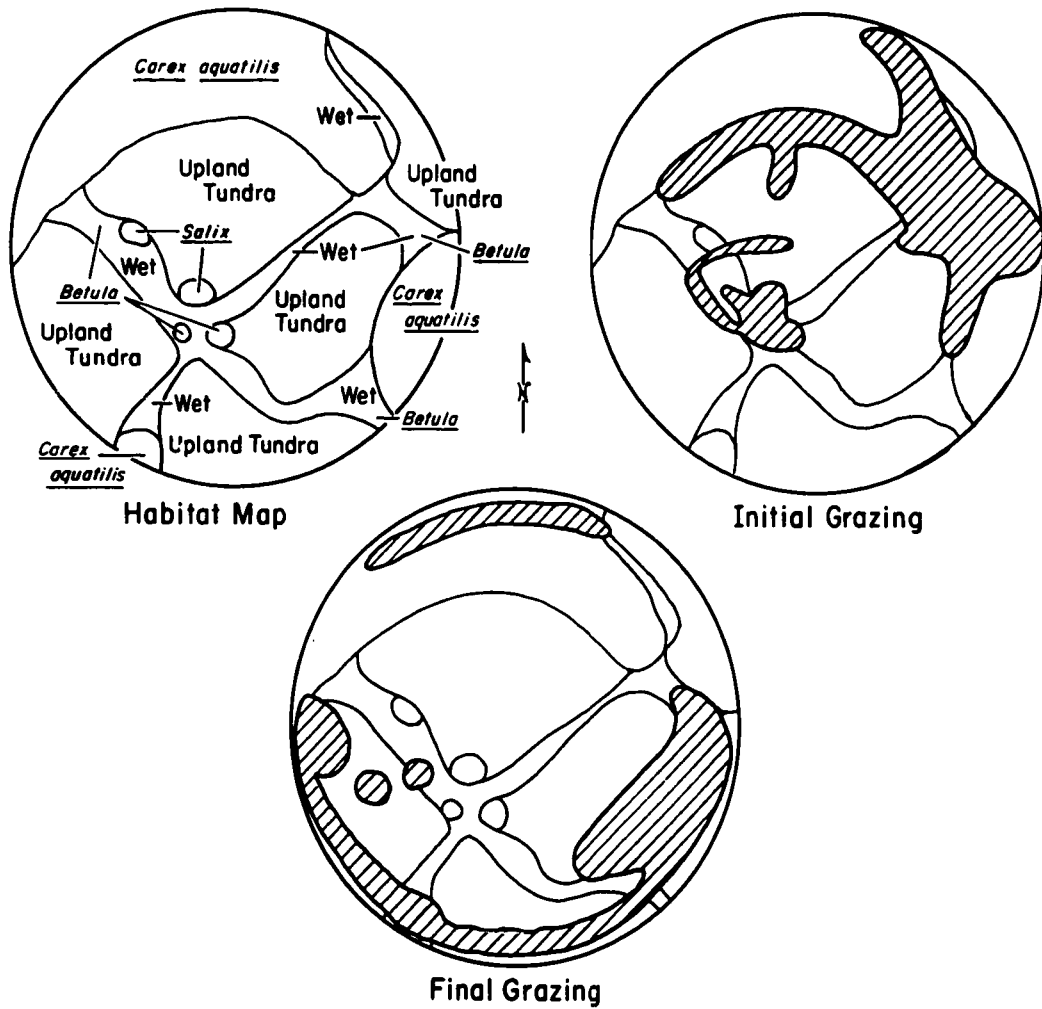
Final Grazing

Figure 21. Maps of initial and final grazing events on upland
tundra plot P8 in 1977.

Final grazings after 3 days indicated a tendency toward decreased use of the Salix strangmoor (to 48%) with a slight increase in use of the Carex marsh (to 22%) and a larger increase in use of the lichen ridge (to 31%). Again, however, differences between initial and final grazing use of microhabitats were not significant. Representative grazing maps for the lake margin 3-day grazing site for 1975 (Figure 22), 1976 (Figure 23) and 1977 (Figure 24) support these observed patterns of microhabitat use.

Total use of two representative plots (P3 and LM1) over all observed grazings during a 3-day period in 1975 is shown as the shaded areas in Figure 25. On the upland tundra plot (P3), 57% of the plot was grazed during the 8 grazing periods observed. Use was heaviest on wet trough areas, polygon rims and the Carex marsh. The ungrazed portion was primarily in the tussock and intertussock areas. For the lake margin plot (LM 1), 66% of the entire plot was grazed over the 5 grazing periods observed. Most of the plot was covered during grazing with only sporadic portions of the Carex marsh not being used for grazing.

Microhabitat use by reindeer grazing the upland tundra and lake margin sites at 2-week intervals is shown in Figure 26. On the upland tundra site, use of the intertussock and wet trough areas averaged more than 80% of all grazing use. No clear pattern of changing use through the peak season was noted although there was a tendency towards an increase in use of the wet trough areas
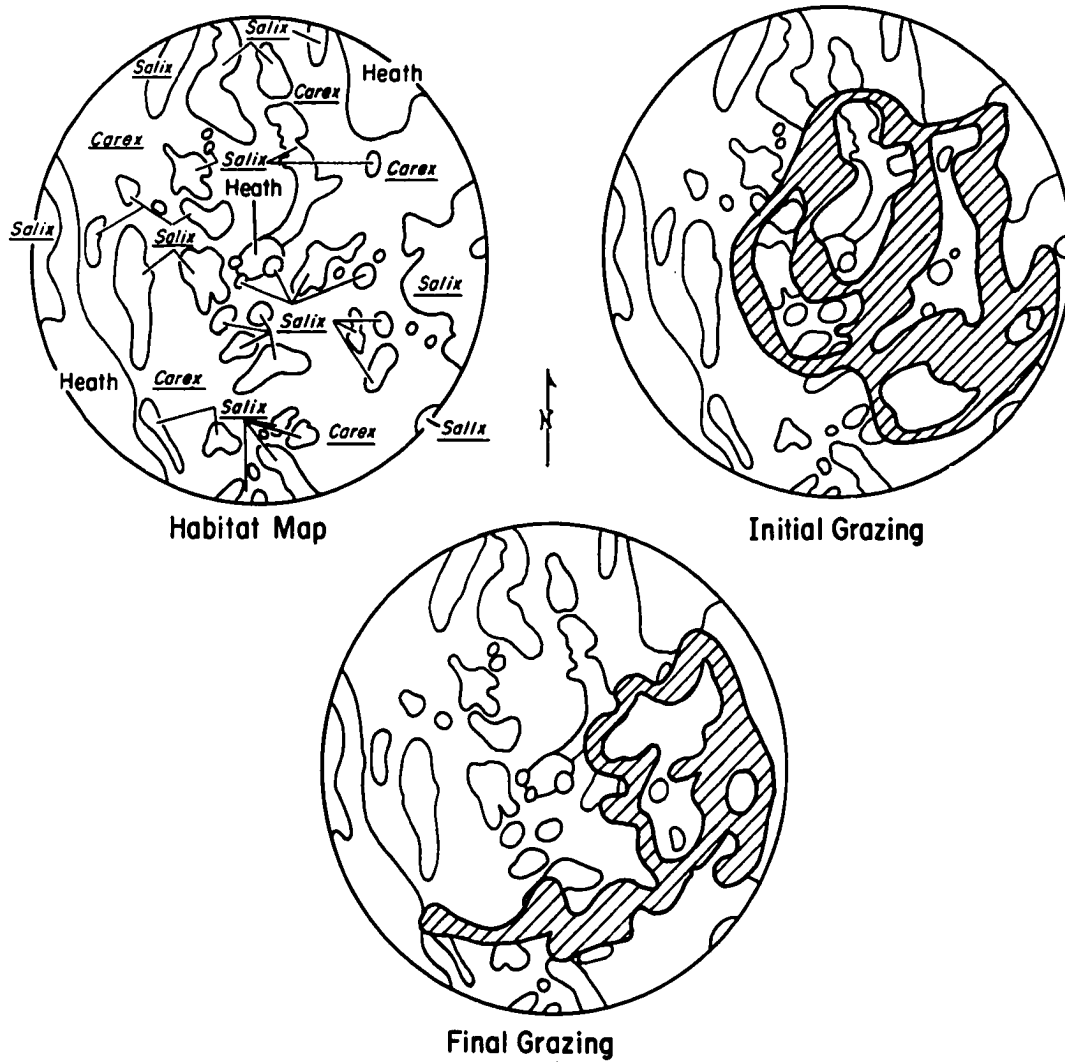
Figure 22. Maps of initial and final grazing events on lake margin plot LM1 in 1975.
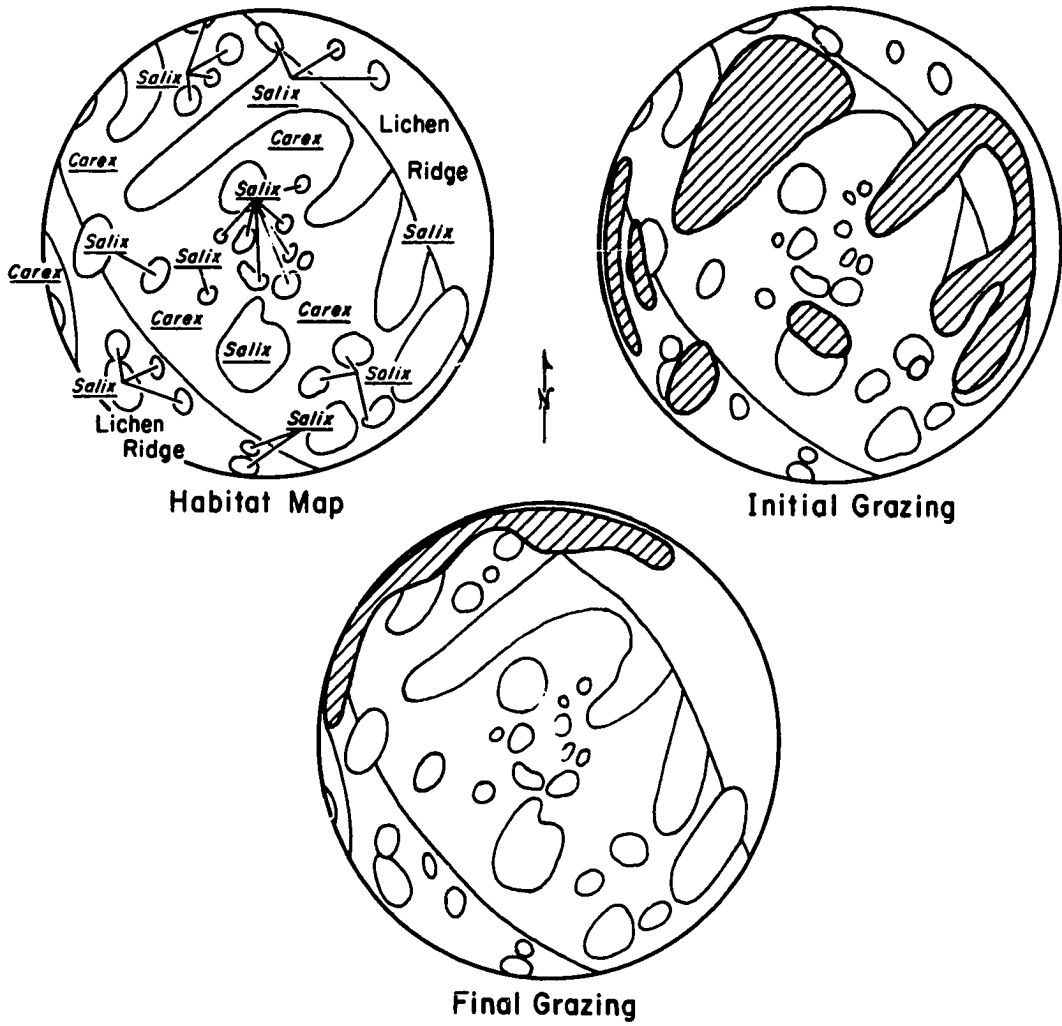
Figure 23. Maps of initial and final grazing events on lake margin
plot LM3 in 1976.

Habitat Map

Initial Grazing
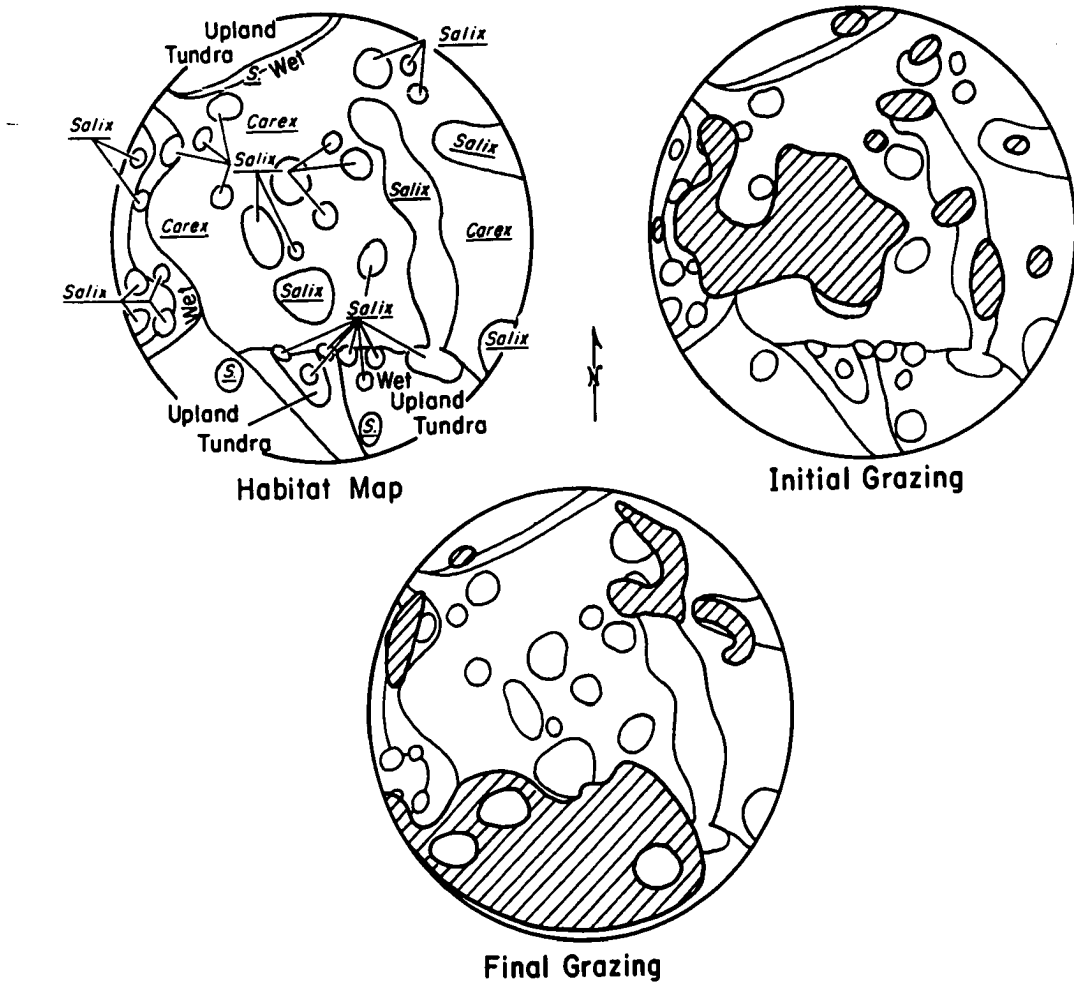
Final Grazing

Figure 24. Maps of initial and final grazing events on lake margin plot LM4 in 1977.
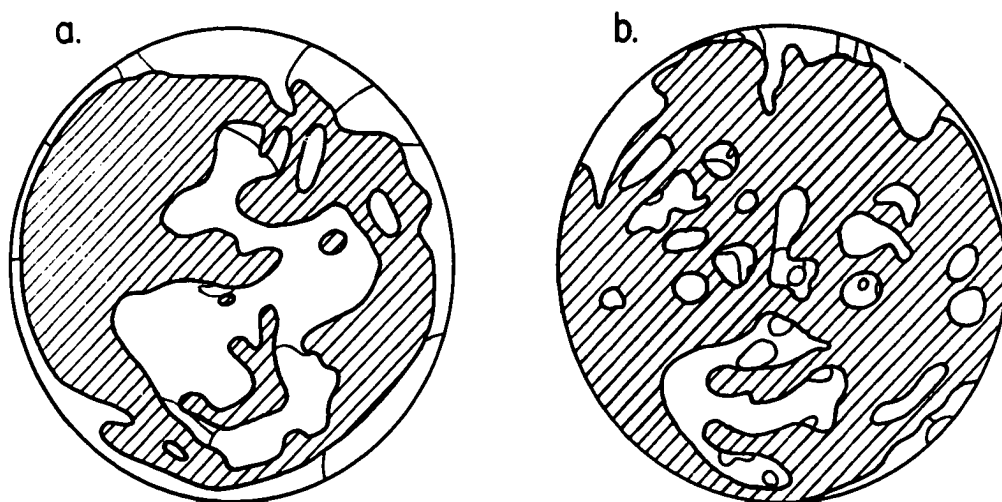
Figure 25. Total observed grazing use of representative plots in the
3-day grazing trials on (a) an upland tundra site (plot P3)
and (b) a lake margin site (plot LM1) in 1975. Shading
represents areas used in grazing events. Refer to figures
19 and 22 for corresponding microhabitat maps.
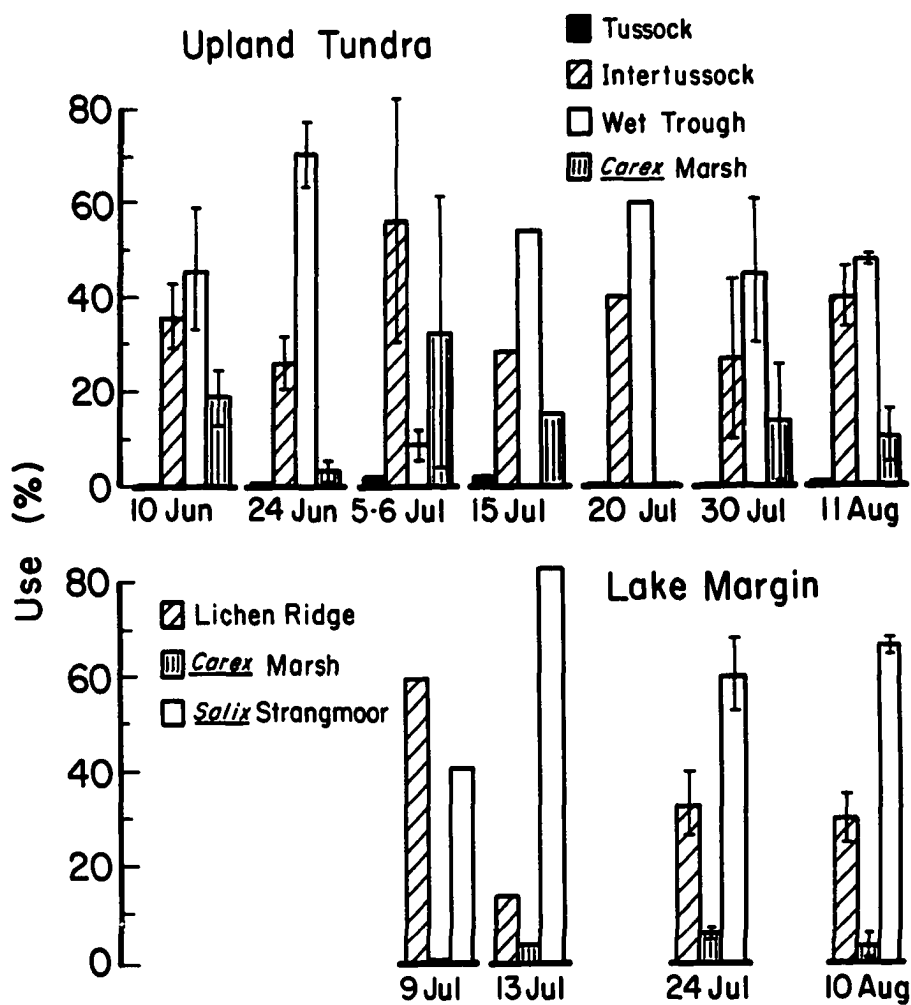
Figure 26. Seasonal grazing use (%) of microhabitats on the upland tundra and lake margin sites in 1976. Variances represent differences between animals and plots.

in late June and an increase in use of the tussocks and <u>Carex</u>

marsh in early July. On the lake margin site, there was a tendency

towards increased use of the <u>Salix</u> strangmoor with a sharp rise

occurring in mid-July. Use of the <u>Salix</u> strangmoor averaged more

than 60% of all peak season grazing use. Use of the lichen ridge

predominated in early July prior to leaf development on the <u>Salix</u>

strangmoor and averaged more than 30% throughout the peak season.

Use of the <u>Carex</u> marsh remained low with a slight increase

occurring in late July.

Mean preferences for microhabitat types based upon use

versus availability are summarized for the upland tundra and lake

margin sites in Table 9. On the upland tundra site, preference

was in the order wet tundra>intertussock tundra><u>Carex</u> marsh>tussock

tundra for both initial and final grazings. Wet troughs and

intertussock tundra were selected for initially while tussock

tundra and to a lesser extent <u>Carex</u> marsh were selected against.

In final grazing trials, selection was extended to include the

<u>Carex</u> marsh areas while tussock tundra was again selected against.

These rankings were maintained throughout the summer with only

the wet trough areas selected for. Other microhabitats were used

in relation to availability except for the tussock areas which

were selected against throughout the summer.

Order of mean preference for microhabitats on the lake

margin site also remained the same from initial to final grazings

Table 9. Mean ± 1 SE preference of reindeer for microhabitats under 3-day and seasonal grazing regimes. The index of preference was calculated as an average of use/availability for each grazing trial.

Vegetation Type/ Microhabitat Type	3-day Grazing		Seasonal Grazing
	Initial Grazing	Final Grazing	
Upland Tundra	(n=11)	(n=11)	(n=8)
Tussock	0.15+0.06	0.30+0.17	0.01+0.005
Intertussock	1.29+0.18	1.56+0.23	0.86+0.11
Wet trough	3.29+1.03	1.76+0.74	4.96+0.70
Carex marsh	0.84+0.45	1.28+0.31	0.67+0.21
Lake Margin	(n=6)	(n=6)	(n=6)
Lichen ridge	0.76+0.34	1.23+0.42	2.02+0.33
Carex marsh	0.46+0.26	0.56+0.35	0.06+0.02
Salix strangmoor	1.95+0.25	1.64+0.27	2.17+0.19

(Table 9): <u>Salix</u> strangmoor>lichen ridge><u>Carex</u> marsh. Selection was extended from <u>Salix</u> strangmoor initially to include lichen ridges in final grazings. Mean seasonal preferences were ranked similarly with selection being made for both the <u>Salix</u> strangmoor and lichen ridges at all times.

To test the hypothesis that preference is dependent on the availability of the microhabitat, regression analyses of use versus availability were performed (Figure 27). Significant relationships were shown only for the wet trough areas on the upland tundra site (P<0.01) and the <u>Carex</u> marsh on the lake margin site (P<0.02). Regression equations were also tested for intercept and slope. For the tussock and <u>Carex</u> marsh microhabitats on the upland tundra site, the intercepts did not differ significantly from zero (P>0.05), indicating that preference for these microhabitats was independent of availability (Figure 28). For all other microhabitats on the upland tundra and lake margin sites, the intercepts differed significantly from zero (P<0.05, Figures 27 and 28). This indicated that preferences for these microhabitats differed depending upon their relative availabilities on particular grazing sites. Figure 28 also shows a peak preference (PR=11) occurs for microhabitats at an availability of about 10%.

Figure 27. Relation of microhabitat use (%) with availability (%) on
upland tundra and lake margin 3-day and seasonal grazing
sites in 1975, 1976 and 1977. Relationships are:

UPLAND TUNDRA

Tussock $y = 1.18 + 0.08x$
                        $n=30$, $r=.110$, $P>0.05$
Intertussock $y = 19.67 + 0.76x$
                        $n=30$, $r=.276$, $P>0.05$
Wet trough $y = 8.75 + 2.19x$
                        $n=30$, $r=.519$, $P<0.01$
Carex marsh $y = 2.32 + 0.62x$
                        $n=30$, $r=.345$, $P>0.05$

LAKE MARGIN

Lichen ridge $y = 30.21 + 0.06x$
                        $n=18$, $r=.019$, $P>0.05$
Carex marsh $y = 103.17 - 1.87x$
                        $n=18$, $r=.542$, $P<0.02$
Salix strangmoor $y = 50.8 + 0.20x$
                        $n=18$, $r=.032$, $P>0.05$

Microhabitats were selected for when the regression
lines were above the equivalence line ($x=y$).
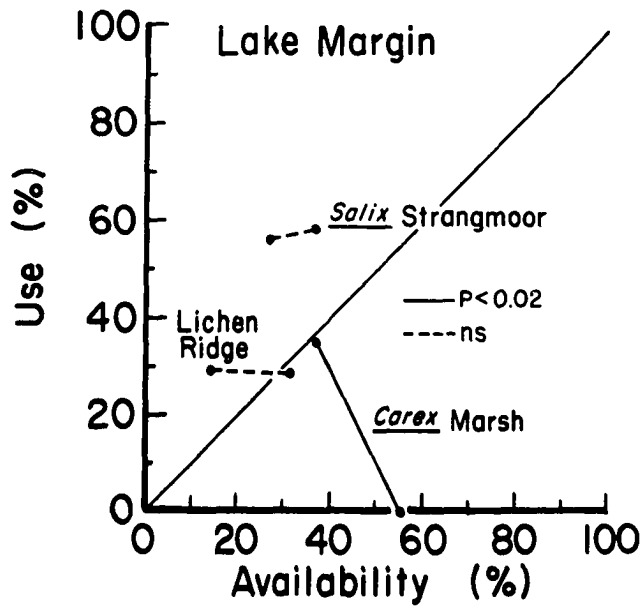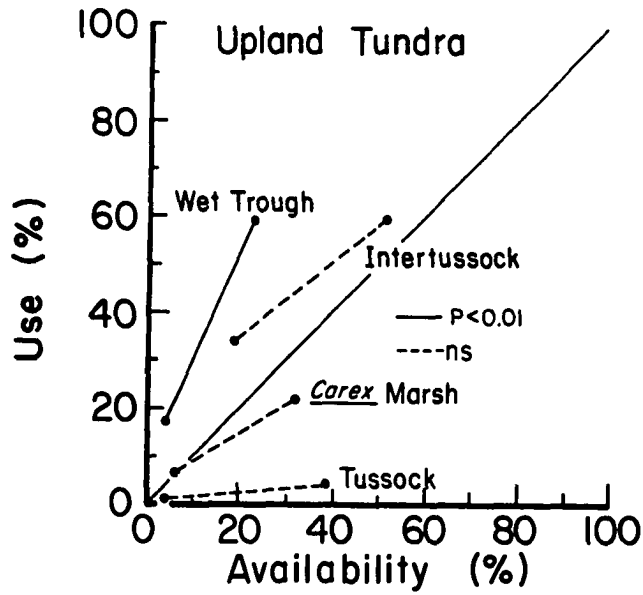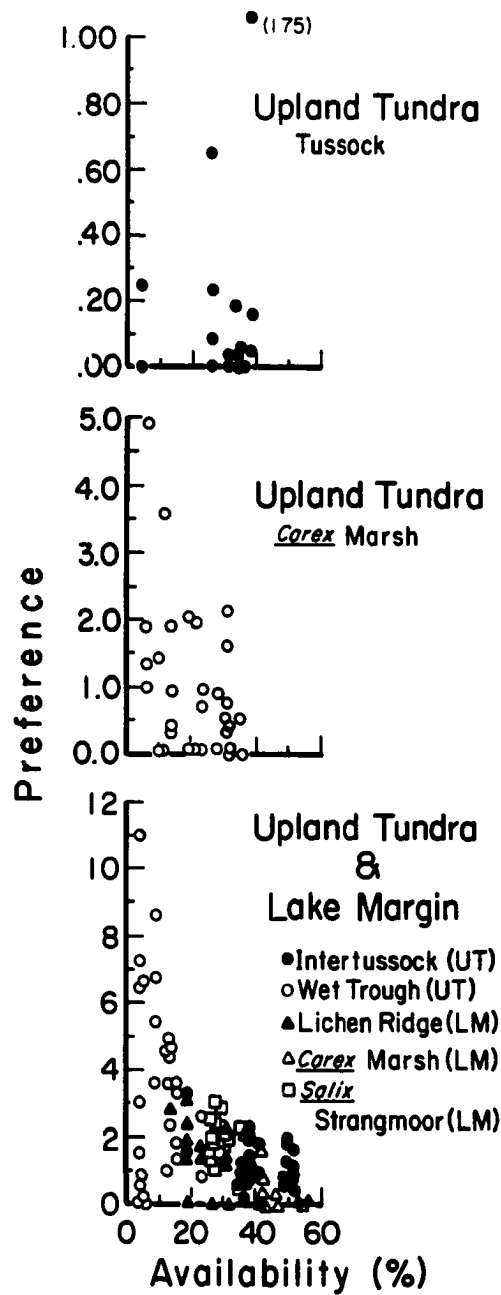
Figure 28. Relation of preference for microhabitats with availability (%) where preference is constant (tussock and Carex marsh areas on upland tundra) and preference changes with availability (intertussock and wet trough areas on upland tundra; lichen ridge, Carex marsh and Salix strangmoor on lake margin).

3.   Discussion - Use and selection of microhabitats.

Selection by reindeer and caribou during grazing can occur at many levels - for vegetation type, for microhabitat type within vegetation type, and for plant growth form, species and parts within microhabitats. In this study, use of vegetation types was not studied. Other studies show that choice of vegetation type by reindeer and caribou is influenced by several factors which include insect and predator avoidance (Skoog 1966; Bergerud 1972; Curatolo 1975; White et al. 1975; Roby 1978; Wright 1978; Boertje 1981), behavioral activities (migration, rut; Thomson 1971; Roby 1978; Boertje 1981), and local topographical and climatic conditions (slope, aspect; wind, snow; Pruitt 1959; Lent 1966; Gaare & Skogland 1975; LaPerriere & Lent 1977; Roby 1978; Bloomfield 1980; Boertje 1981). Vegetation types may also be selected because of their forage characteristics including phenological stage of development (Klein 1970; Skogland 1975; Bloomfield 1980; Kuropat & Bryant 1980; Thing 1980; Boertje 1981), biomass availability (White et al. 1975; Roby 1978; Wright 1978; White 1979; White & Trudell 1980a,b) and quality (Skogland 1975; Thing 1980; White & Trudell 1980a,b; Boertje 1981).

Selection for microhabitats has received little attention. In the present study, use of microhabitats was associated with forage characteristics such as high plant biomass and diversity

(intertussock tundra and wet troughs on the upland tundra site;
Salix strangmoor and lichen ridges on the lake margin site.
Proportional cover of microhabitats on the grazing sites was not
necessarily associated with feeding use of those areas (e.g.,
high use of wet troughs which provided low cover on the upland
tundra site; low use of the Carex marsh which provided the most
cover on the lake margin site). The availability of preferred
plant species and parts also influenced use of microhabitats such
as wet troughs on the upland tundra site and Salix strangmoor on
the lake margin site. In trials conducted at 2-week intervals
throughout the summer, highest use of microhabitats was noted
when preferred plant species were highly accessible. For ex-
ample, the graminoid-containing microhabitats on the upland
tundra site (tussocks and Carex marsh) were not used in late June
and early July when the proportion of immature, green blades was
high in relation to dead blades (also Kuropat & Bryant 1980;
Thing 1980). Growth of forbs and leaves of deciduous shrubs on
both the upland tundra and lake margin sites in mid-July was also
associated with higher use of and selection for microhabitats
containing these plants. Lichen-containing microhabitats were
most preferred when the moisture content of these plants was high
(also Kelsall 1968; Trudell & White 1981) or the availability of
other preferred forage species was low (early June and late
August).

Total observed use of the area on both grazing sites (57% of the upland tundra site; 66% of the lake margin site) indicated that grazing over a 3-day period may have required the reindeer to use the plots more intensively than free-roaming reindeer or caribou (1900 times an average density of 1.4 to 2.1 km^{-2} in arctic Alaska; White et al. 1981). Such intensive use of grazing sites, however, may approximate annual use of summer and winter ranges by large groups of caribou (26 $d \cdot km^{-2} \cdot y^{-1}$, White & Trudell 1980, compared to 60 to 190 $d \cdot km^{-2} \cdot y^{-1}$, White et al. 1981). Results obtained may also reflect limited ranges of available microhabitats (Table 8) and preferred plant biomass (Tables 5 and 6).

Ranking of preferences for microhabitats on both grazing sites was not influenced by changes due to intensive or seasonal grazing (Tables 9 and 13). Therefore, use of microhabitats was altered in response to changing biomass over 3 days of intensive grazing (Carex marsh on the upland tundra site; lichen ridge on the lake margin site). This suggests that, although preferences for forages are maintained by reindeer and caribou throughout their range, actual use is guided by biomass availability. Clearly, the large variabilities observed in use of and preference for microhabitats (Figures 27 and 28) indicate that the selective process involves many factors.

C.   Forage Digestibility

1.   Digestibility of forage plants on grazing sites

Estimates of dry matter disappearance (DMD) obtained through the 48-hour in vitro and the 10- and 48-hour nylon bag techniques are presented for a variety of tundra plant species in Table 10. Although digestibility values varied depending upon which technique was used, leaf material was generally found to be more digestible than stem material, leaf buds were more digestible than leaves (deciduous shrubs), current year stems were more digestible than older stems, and live plant material was more digestible than dead material (deciduous shrubs and graminoids). Based on DMD values obtained through the 10-hour nylon bag technique, grazed portions of plant growth forms occurring on the grazing sites rank by decreasing digestibility as follows:

forbs

deciduous shrub leaves and current year stems

evergreen shrubs

preferred lichens

non-preferred lichens

Carex aquatilis green blades

Eriophorum vaginatum green blades

mosses

Table 10. Mean ± 1 SE digestibility values (as % ary matter disappearance) for forage plants available at Atqasuk. Sample sizes (n) appear in parentheses. Plant species available on the upland tundra and lake margin study plots are indicated by an *.

Plant Growth Form/ Species/Parts		DMD 48-hour in vitro	DMD 48-hour Nylon Bag	DMD 10-hour Nylon Bag
Evergreen shrubs				
*Cassiope tetragona		21.2 ± 2.6 (3)	34.8 ± 6.2 (3)	
Dryas integrifolia		17.0 ± 1.4 (3)	37.0 ± 10.4 (3)	6.4 ± 1.5 (3)
*Ledum palustre		23.0 ± 1.3 (3)	31.1 ± 1.1 (3)	33.9 ± 1.0 (2)
*Vaccinium vitis-idaea		23.5 ± 6.0 (7)	72.0 ± 1.2 (19)	54.2 ± 3.2 (9)
Deciduous shrubs				
*Betula nana	leaf	25.9 ± 5.8 (3)	40.8 ± 0.8 (3)	
	stem	13.9 ± 4.5 (3)	25.0 ± 1.1 (3)	
Salix alaxensis	leaf bud	43.9 ± 0.9 (3)	84.6 ± 2.0 (6)	58.6 ± 5.6 (3)
	stem	22.9 ± 2.5 (3)	76.6 ± 6.7 (4)	39.8 ± 3.5 (3)
	catkin	46.8 ± 2.1 (3)	91.0 ± 2.0 (3)	74.2 ± 3.0 (5)
Salix glauca	leaf		75.3 ± 1.8 (3)	
	stem		58.6 ± 1.0 (3)	49.5 ± 3.7 (5)
	catkin		63.2 ± 4.1 (3)	61.6 ± 3.0 (3)
Salix lanata	leaf bud	41.1 ± 1.2 (3)	80.6 ± 1.3 (6)	61.0 ± 7.5 (5)
	stem	16.9 ± 0.4 (3)	53.6 ± 3.8 (6)	
	catkin	49.8 ± 1.0 (3)	88.0 ± 2.1 (3)	
Salix phlebophylla	leaf/stem		61.8 ± 0.3 (3)	53.6 ± 1.0 (3)
*Salix pulchra	leaf bud	45.9 ± 0.7 (8)		
	leaf	39.8 ± 1.0 (8)	81.7 ± 0.8 (72)	53.9 ± 2.1 (14)
	dead leaf	24.1 ± 2.0 (6)	44.3 ± 5.2 (9)	5.8 ± 3.7 (3)
	current year stem			47.9 ± 1.8 (3)
	stem	25.4 ± 0.8 (3)	49.4 ± 2.5 (9)	36.9 ± 0.5 (3)
	catkin	50.5 ± 1.6 (3)	75.5 ± 6.7 (6)	53.6 ± 3.0 (6)
Graminoids				
Arctagrostis latifolia				23.6 ± 1.8 (3)
Arctophila fulva				44.8 ± 5.9 (3)
Bromopsis pumpelliana		67.0 ± 1.9 (3)	79.7 ± 0.5 (3)	52.5 ± 1.1 (3)
	dead	31.9 ± 1.1 (3)	54.4 ± 19.5 (3)	
*Carex aquatilis		53.6 ± 1.2 (9)	65.0 ± 3.0 (15)	31.4 ± 1.8 (3)
	dead	29.0 ± 2.6 (5)	50.3 ± 3.8 (6)	7.5 ± 4.2 (2)
Carex bigelowii		36.5 ± 3.0 (3)	49.9 ± 12.9 (3)	29.3 ± 0.9 (3)
	dead	18.3 ± 2.2 (3)	44.2 ± 9.2 (3)	
Eriophorum angustifolium		51.6 ± 2.4 (3)	88.2 ± 2.5 (3)	26.0 ± 7.2 (6)
	dead	17.7 ± 1.5 (3)	48.9 ± 1.5 (3)	7.2 ± 0.9 (2)
Eriophorum Scheuchzeri		57.1 ± 1.0 (3)	86.3 ± 2.3 (3)	43.1 ± 1.5 (2)
*Eriophorum vaginatum		52.6 ± 1.9 (9)	78.7 ± 3.5 (9)	21.1 ± 1.9 (2)
	dead	23.4 ± 2.8 (3)	50.5 ± 7.8 (3)	
Equisetum arvensus				71.8 ± 0.9 (3)
Festuca brachyphylla				29.1 ± 2.2 (3)
Hierochloe alpina		50.1 ± 0.9 (3)	66.1 ± 1.1 (3)	35.3 ± 0.6 (2)
Juncus arcticus				17.2 ± 2.7 (3)
Leymus mollis v.				31.8 ± 2.8 (3)
Poa arctica		65.8 ± 2.7 (3)	79.8 ± 0.8 (3)	41.8 ± 1.9 (3)

Table 10. Cont.

Plant Growth Form/ Species/Parts	DMD 48-hour In vitro	DMD 48-hour Nylon Bag	DMD 10-hour Nylon Bag
Forbs			
Arctous alpina	48.0 ± 2.8 (3)	90.0 ± 1.4 (3)	79.5 ± 1.2 (3)
Astragalus alpinus			73.4 ± 1.6 (3)
Bistorta plumosa	43.7 ± 1.8 (3)	78.6 ± 0.3 (2)	65.3 ± 2.5 (3)
Boykinia richardsonii			56.3 ± 3.2 (3)
Lupinus arcticus	55.4 ± 2.1 (3)	81.3 ± 0.8 (2)	71.9 ± 0.9 (3)
Nardosmia frigida	59.5 ± 0.5 (3)	87.8 ± 1.1 (3)	76.3 ± 2.5 (2)
Oxytropis gorodkovii			34.1 ± 2.4 (3)
Pediculariopsis verticillata			77.6 ± 0.4 (3)
Pedicularis capitata	57.7 ± 4.8 (3)	78.5 ± 6.8 (3)	72.1 ± 1.9 (3)
Pedicularis lanata	59.5 ± 3.2 (2)	86.6 ± 1.8 (3)	64.2 ± 4.8 (3)
*Pedicularis langsdorfii	49.4 ± 3.3 (2)	88.1 ± 0.8 (3)	88.4 ± 0.3 (3)
Pedicularis lapponica			52.7 ± 0.7 (2)
Pedicularis sudetica	51.8 ± 1.6 (3)	71.2 ± 2.0 (3)	58.4 ± 0.8 (3)
*Rubus chamaemorus	36.1 ± 1.5 (3)	43.6 ± 3.4 (3)	37.0 ± 1.1 (3)
Lichens-preferred			
*Alectoria ochroleuca	28.5 ± 5.0 (6)	88.3 ± 2.5 (4)	
*Cetraria cucullata	24.4 ± 1.7 (6)	89.9 ± 1.6 (3)	50.1 ± 3.8 (9)
*Cetraria nivalis	71.7 ± 2.8 (4)	85.2 ± 2.5 (3)	49.2 ± 0.4 (2)
*Cladina arbuscula	26.2 ± 4.3 (6)	74.0 ± 1.5 (4)	31.7 ± 0.7 (2)
*Cladina rangiferina	27.3 ± 2.8 (6)	58.1 ± 4.7 (4)	20.0 ± 2.0 (3)
*Cladonia stellaris			26.7 ± 1.5 (3)
*Cornicularia divergens	26.5 ± 3.6 (3)	85.7 ± 1.4 (3)	
*Dactylina arctica	40.4 ± 12.3 (3)	94.7 ± 1.2 (3)	52.0 ± 1.5 (3)
*Stereocaulon sp.	18.0 ± 5.1 (3)	45.7 ± 2.1 (3)	29.6 ± 1.8 (3)
*Thamnolia sp.	17.6 ± 1.5 (3)	87.0 ± 0.6 (3)	48.2 (1)
Lichens-nonpreferred			
*Alectoria nigricans	2.7 ± 2.7 (3)	86.6 ± 2.2 (3)	43.9 ± 2.9 (3)
*Bryoria nitidula	17.7 ± 1.9 (3)	90.4 ± 0.9 (3)	31.8 ± 2.7 (3)
*Cetraria richardsonii			41.2 ± 0 (2)
*Nephroma arcticum	16.1 ± 3.8 (3)	36.5 ± 2.6 (3)	
*Parmelia sp.	19.0 ± 2.3 (3)	80.0 ± 0.2 (3)	24.2 ± 1.4 (3)
*Peltigera aphthosa	39.3 (1)		
*Siphula ceratites			17.0 ± 1.0 (2)
Mosses			
*Aulacomnium turgidum	12.9 ± 1.9 (2)	8.7 ± 5.7 (3)	
*Drepanoclaudis sp.	0.8 ± 0.8 (3)	6.8 ± 4.9 (3)	
*Tomenthipnum nitens	3.7 ± 3 7 (3)	25.8 ± 2.9 (3)	
Pelleted Ration			
PCS	59.6 ± 2.6 (2)	64.0 ± 1.3 (3)	
UBC-QT	69.0 ± 3.6 (12)	83.7 ± 0.8 (28)	74.6 ± 1.2 (7)

Based on DMD values obtained through the 48-hour in vitro and

nylon bag techniques, the graminoids (C. aquatilis and E.

vaginatum) rank at a higher digestibility than indicated above

while evergreen shrubs and non-preferred lichens rank lower.

Theoretical estimates of the mean DMD for vegetation offered

by microhabitats on the upland tundra and lake margin sites based

on 48-hour in vitro and 10- and 48-hour nylon bag techniques are

presented in Table 11. Significant declines in DMD of the micro-

habitat vegetation were noted following the 3-day grazing period

for the wet troughs (48-hour nylon bag) on the upland tundra site

and for the Carex marsh (10- and 48-hour nylon bag) and the Salix

strangmoor (48-hour in vitro and nylon bag) on the lake margin

site, indicating that highly digestible forage had been removed

from these areas. According to summed 10-hour nylon bag DMD,

microhabitats on the upland tundra site ranked by decreasing

digestibility as

     intertussock tundra

     wet troughs

     Carex marsh

     tussocks

and microhabitats on the lake margin site ranked by decreasing

digestibility as

     Salix strangmoor

Table 11. Mean ± 1 SE estimated digestibility of available vegetation within each microhabitat on the upland tundra and lake margin sites. DMD was estimated both before (initial) and after (final) 3-day grazing. Mosses are not included in these estimates.

Vegetation Type/ Microhabitat	48-hour in vitro DMD		48-hour Nylon Bag DMD		10-hour Nylon Bag DMD	
	Initial	Final	Initial	Final	Initial	Final
Upland Tundra (Initial n=12; Final n=11)						
Tussock	30.6 ± 0.9	30.4 ± 0.6	57.4 ± 0.8	57.1 ± 0.6	10.5 ± 0.4	10.4 ± 0.3
Intertussock	26.3 ± 0.6	25.8 ± 0.2	66.7 ± 2.7	69.4 ± 1.6	37.1 ± 0.6	37.8 ± 0.4
Wet trough	30.4 ± 2.8	27.7 ± 1.2	59.2 ± 2.1	53.1 ± 2.0***	33.7 ± 2.1	30.4 ± 2.2
Carex marsh	39.9 ± 1.1	38.0 ± 1.0	55.5 ± 1.6	55.6 ± 0.6	18.1 ± 1.1	15.9 ± 1.1
Lake Margin (Initial n=7; Final n=6)						
Lichen ridge	26.7 ± 0.5	26.2 ± 0.3	66.9 ± 1.9	64.2 ± 2.7	35.2 ± 0.6	35.2 ± 0.9
Carex marsh	37.0 ± 0.9	36.4 ± 0.6	60.0 ± 1.8	55.2 ± 0.5*	25.1 ± 2.8	16.1 ± 0.8**
Salix strangmoor	32.1 ± 0.6	29.5 ± 0.5***	59.9 ± 1.2	53.9 ± 0.7***	36.7 ± 1.5	33.7 ± 0.7

*   Differences between initial and final estimates are significant (P<0.05).
**   Differences between initial and final estimates are significant (P<0.02).
*** Differences between initial and final estimates are significant (P<0.01).

lichen ridges

<u>Carex</u> marsh

Rankings based on the 48-hour <u>in vitro</u> technique showed consistently higher placement of the graminoid-containing microhabitats (<u>Carex</u> marsh and tussocks on the upland tundra; <u>Carex</u> marsh on the lake margin).

To indicate the extent to which diet selection significantly affected the DMD, theoretical estimates of DMD based on the composition of the diet of grazing reindeer were compared with those based on the available vegetation (Table 12). Significant increases in DMD were noted for all comparisons with the largest estimated for 48-hour <u>in vitro</u> DMD on both the upland tundra (30%) and the lake margin (40%) sites. These increases were maintained during final grazing periods in spite of reductions in biomass of many of the preferred plant species (Tables 5 and 6).

2.   Summary of preference and DMD

Relationships of grazing preferences defined as use versus availability and forage digestibility which have been discussed were summarized by ranking mean values in decreasing order for 3-day and seasonal grazing experiments on the upland tundra and lake margin sites. These rankings are presented in Table 13 for microhabitat types and in Table 14 for forage types.

Table 12. Summary of mean ± 1 SE estimated available forage digestibility and estimated selected forage digestibility values (as % DMD) on 3-day grazing sites at initial and final grazings. The percent increase in DMD provided by selection was calculated as (selected DMD - available DMD) $\cdot$ (available DMD)$^{-1}$ $\cdot$ 100. Differences between initial and final grazing DMD were not significant.

	Estimated Available DMD	Estimated Selected DMD	% DMD Increase
Upland Tundra (n=11)			
Initial Grazing			
48-hr in vitro	28.8 ± 0.7	37.5 ± 1.5	30.2**
48-hr Nylon Bag	65.6 ± 1.5	74.8 ± 1.5	14.0**
10-hr Nylon Bag	32.9 ± 0.7	39.6 ± 1.4	20.4**
Final Grazing			
48-hr in vitro	28.8 ± 0.7	37.8 ± 1.4	31.3**
48-hr Nylon Bag	65.1 ± 1.6	73.3 ± 2.6	12.6*
10-hr Nylon Bag	31.0 ± 1.0	36.6 ± 0.7	18.1**
Lake Margin (n=6)			
Initial Grazing			
48-hr in vitro	29.4 ± 0.3	41.3 ± 1.8	40.5**
48-hr Nylon Bag	62.0 ± 4.0	79.3 ± 1.7	27.9**
10-hr Nylon Bag	38.0 ± 2.1	50.7 ± 2.4	33.4**
Final Grazing			
48-hr in vitro	28.4 ± 0.8	39.5 ± 1.5	39.1**
48-hr Nylon Bag	57.3 ± 3.0	79.0 ± 1.3	37.9**
10-hr Nylon Bag	33.8 ± 1.3	46.2 ± 1.9	36.7**

* $P < 0.05$
** $P < 0.01$

Table 13. Rankings of microhabitats of the upland tundra and lake margin sites under 3-day and seasonal grazing regimes (1 = highest preference). Preference rankings marked by * were selected for during grazing.

Vegetation Type Microhabitat	3-day Grazing							Seasonal Grazing			
	Cover	Initial Biomass	Use Initial	Final	Preference Initial	Final	DMD 10-hour Nylon Bag	Cover	Mean Biomass	Use	Preference
Upland Tundra											
Wet trough	4	2	2	3	1*	1*	2	4	2	1	1*
Intertussock	1	1	1	1	2*	2*	1	1	1	2	2
Carex marsh	3	3	3	2	3	3*	3	3	3	3	3
Tussock	2	4	4	4	4	4	4	2	4	4	4
Lake Margin											
Salix strangmoor	2	2	1	1	1*	1*	1	2	2	1	1*
Lichen ridge	3	1	2	2	2	2*	2	3	1	2	2*
Carex marsh	1	3	3	3	3	3	3	1	3	3	3

Table 14. Rankings of forage types according to preference by reindeer grazing on upland tundra and lake margin sites; (1) plants preferentially grazed when available; (2) plants grazed when preferred species are less available; (3) plants minimally used regardless of availability; (a) plants preferred early season; (b) plants preferred mid-season; (c) plants preferred late season; (d) plants not preferred; (parentheses indicate preference is secondary).

Relative 3-day Preference

Plant species/ growth forms	Upland Tundra				Lake Margin				Relative Seasonal Preference	
	Relative Preference	48-hour in vitro	DMD 48-hour Nylon Bag	10-hour Nylon Bag	Relative Preference	48-hour in vitro	DMD 48-hour Nylon Bag	10-hour Nylon Bag	Upland Tundra	Lake Margin
Deciduous Shrubs	1	3	3	1	1	4	4	2	a,b,c	a,b,c
Forbs	1	4	6	3	1	3	1	1	b,c	b,c
Eriophorum vaginatum	(1)	2	2	6	2	2	3	6	(b)	d
Carex aquatilis	2	1	4	5	(1)	1	5	5	a,b,(c)	(a,b,c)
Lichens	2	5	1	4	2	5	2	4	a(b,c)	(a,b,c)
Evergreen Shrubs	3	6	5	2	3	6	6	3	d	d
Mosses	3	7	7	7	3	7	7	7	d	d

Initial use, biomass and 10-h nylon bag DMD of microhabitats

on the upland tundra site were ranked identically (Table 13).

Intertussock areas showed highest ranking of both forage quantity

(biomass) and overall quality (10-h nylon bag DMD) which could

account for highest use of this microhabitat. Cover rankings of

microhabitats differed from those for use and preference, indi-

cating that microhabitat area was less important than forage

quantity and quality in determining grazing use. Slight differ-

ences were noted between rankings of initial, final and seasonal

use patterns and can be attributed to variations in the avail-

ability of preferred plant species in relation to the overall

biomass. For example, the wet trough areas were most highly

preferred in all trials because they offered highly preferred

forbs and leaves of deciduous shrubs (Table 14). Use of wet

troughs ranked lower when sites were grazed more intensively (3-

day trials), owing to limited availabilities of preferred plant

species on this microhabitat in combination with larger quantities

of biomass offered by other microhabitats. Preference rankings

for microhabitats on the upland tundra site support the hypothesis

that preferences are pronounced even when forage availabilities

are low (Figures 17 and 28). When biomass quantity is limiting,

however, selective use of more microhabitats is also necessitated.

Use, preference and 10-h nylon bag DMD of microhabitats on

the lake margin site were ranked identically for all trials

(Table 13). Rankings by biomass availability differed for those of use and preference. These patterns indicate that grazing was primarily controlled by the availability of the most highly preferred and digestible plant species (e.g., leaves of Salix pulchra). Because biomass of preferred plant species was generally high, total forage biomass was of secondary importance in determining grazing use of microhabitats. Cover rankings showed that area was not very important in influencing microhabitat use. Rankings in preference for lake margin microhabitats were identical for all trials (i.e., initial, final and 2-week grazings), indicating the availability of S. pulchra leaves dramatically influenced patterns of use and selection. Again when biomass quantity was limiting, more microhabitats were selected for.

Comparisons of preference and digestibility rankings of forages on the upland tundra and lake margin sites were more obscure (Table 14). Rankings of forages by DMD varied depending upon which technique was considered (i.e., 10- or 48-h nylon bag; 48-h in vitro). Highly preferred forbs and deciduous shrubs generally were highly digestible. DMD values of these forages ranked lower using the 48-h nylon bag and in vitro techniques, however. Studies by White & Trudell (1980a) have shown that cell soluble contents of forbs and deciduous shrubs are released within the first few hours of digestion which may account for the observed high preference and digestibility rankings. Lower

rankings in digestibility of these forages during the 48-h trials could be attributed to the presence of secondary compounds which inhibit rumen function or to more complete digestion of other forages over longer digestion times. Therefore, ingestion of forbs and deciduous shrubs may be most beneficial when rumen retention times are short and when these forages are mixed with other forages to enable dilution of secondary compounds. These forages may also be more important in the diet when they offer more digestible immature growth stages.

In contrast to forbs and deciduous shrubs, evergreen shrubs were consistently selected against yet showed a high digestibility ranking based on 10-h nylon bag values. In vitro and nylon bag 48-h DMD rankings of the evergreen shrubs were also much lower and more closely matched preference rankings. Toxic secondary compounds contained in these forages may require longer retention times within the rumen before they are released which could account for the rankings in digestibility observed. Because reindeer use sensory cues to determine preference while grazing, however, the nature of the avoidance cue may require that these forages always be selected against.

Graminoids, Eriophorum vaginatum and Carex aquatilis, were ranked moderately high in preference yet 10-h nylon bag DMD rankings were low. In vitro rankings of these forages were higher and more closely approximated rankings in preference.

Benefits of selecting these forages during the summer may depend
primarily upon use of immature growth stages which offer higher
digestibility values. Use of mature growth stages may be more
important during the winter months when rumen retention times are
longer and other forages are less available.

Preference rankings for lichens were closely approximated by
48-h nylon bag DMD rankings. Therefore, digestibility of lichens
is highest given longer retention times within the rumen. This
indicates that lichens will be most important in the diet when
other forages are less available. Preference for lichens should
be maintained secondary to preferred plant species.

Finally, mosses were the only forages which showed consis-
tently low rankings in preference and digestibility over all
grazing trials and digestibility techniques.

3.   Discussion - The advantages of selecting a mixed diet.

Diet diversity for both reindeer and caribou is high through
spring migration (Bloomfield 1980) and on summer ranges (Klein
1969; Skogland 1975; White et al. 1975) and has been stressed as
an important adaptation of the generalist herbivore (Longhurst et
al. 1968; Arnold & Hill 1972; Freeland & Janzen 1974; Westoby
1978; Van Dyne et al. 1980). The advantages of mixing forages in
the diet include minimizing cost in time and effort spent searching
(Westoby 1978). This would allow high levels of intake to be

maintained even along migration routes (White et al. 1981).

Selecting for variety in the diet may enable "sampling" activity

to continue so that new forages can be tested for palatability as

they become available. The rumen microbial system could then be

primed for any sudden shifts in diet composition (Freeland &

Janzen 1974; Westoby 1978). It has been hypothesized that

generalist herbivores have certain tolerance levels for the

toxins in any one plant species (Longhurst et al. 1968) and that

the levels of toxins which can be ingested and successfully

detoxified are established with previous experience (Freeland &

Janzen 1974). It may be advantageous to mix forages in the diet

in order to minimize "dosage effects" of secondary plant compounds

(Freeland & Janzen 1974; Oh et al. 1968) which may inhibit rumen

function and therefore decrease food intake (Oh et al. 1968).

Janis (1976) has suggested that the initial increase in fore-

stomach size of ruminants may have evolved to include plant

detoxifying bacteria within the digestive system. Different

forages may also synergistically combine to increase the available

nutrients to the animal while offsetting toxic doses of secondary

plant compounds (Westoby 1978). There are indications that the

ingestion of a small quantity of low palatability plants may

stimulate diet digestibility (Trudell et al. 1980) even though

synergistic effects of dietary constituents are generally not

found for reindeer (Person 1975; Person et al. 1980a).

The extent to which mixing forages is beneficial to the nutritional status of reindeer and caribou has yet to be shown. It is frequently speculated that selection for both forage species and habitat type is important in determining the nutrient value of the diet ingested (White & Trudell 1980b; Chapin 1980; Kuropat & Bryant 1980; Person et al. 1980b; Whitten & Cameron 1980). Use of deciduous shrubs, graminoids and forbs in particular may provide Rangifer with the richest available sources of N, P and K in the summer (Chapin et al. 1980; Boertje 1981). Lichens also constitute an important part of the diet throughout the summer although they contain low levels of N, P and K. They may be important in the diet for reasons other than supply of specific nutrients (i.e., as an energy source, for dilution of secondary plant compounds ingested or to maintain microbial adaptation to a lichen diet over the summer).

The ability of other ruminants to select a diet high in nutrient content and digestibility has been documented (Swift 1948; Weir & Torell 1959; Leigh & Mulham 1966; Oh et al. 1968). Selection for nutrients and DMD has been hypothesized for reindeer (White 1979; Person et al. 1980b; White & Trudell 1980a,b; White et al. 1981) and caribou (Klein 1970; Chapin et al. 1980; Kuropat & Bryant 1980; Whitten & Cameron 1980; White et al. 1981). Because selection primarily operates by sensory cues, however (i.e., smell, taste, sight, touch; Longhurst et al. 1968; Arnold

1970; Arnold & Hill 1972), reindeer and caribou may not be selecting

for specific nutrients per se but rather for characteristics

which are highly correlated with those nutrients. For example,

selection for sweetness may maximize ingestion of cell solubles

and therefore most of the available N, P and K as well as energy

metabolites within the plant (White 1979). Na detection is well

established and may maximize cation intake. Ease of harvest may

be negatively associated with crude fiber intake. Finally,

volatile oils may indicate the presence of plant toxins. Selection

for nutrients is probably a multidimensional process which is

influenced by the overall composition of the diet (Arnold & Hill

1972).

Selecting a diet which maximizes nutrient intake may also

result in ingestion of secondary defense chemicals, however,

which may be high in forage species such as deciduous shrubs

(Jung et al. 1979; Kuropat & Bryant 1980; Chapin 1980; Chapin et

al. 1980). These compounds may prove detrimental to rumen di-

gestion if ingested in sufficient quantities. Most major vascular

plant species present on the study sites (Table 1) contain both

alkaloids and tannins (Jung et al. 1979). Exceptions were Carex

aquatilis which contained only alkaloids and Eriophorum vaginatum

which did not show evidence for either alkaloids or tannins.

These graminoids are generally very tolerant to grazing (Chapin

et al. 1980). Evergreen shrubs more commonly contained tannins,

alkaloids, saponins and anthraquinones which could account for their observed low preference. In contrast, deciduous shrubs were highly preferred yet commonly contained both tannins and alkaloids. There is evidence that rumen retention time is increased when deciduous shrubs are the sole diet source (White & Trudell 1980b). No distinctions were made in the study by Jung et al. (1979) as to the composition of leaf versus stem or stage of maturation of the samples tested which could explain some apparent anomalies between preference rankings and secondary compound content.

In the present study, the preference index depended upon the relative availabilities of forages on the grazing site (Figures 17 and 28). For all forage species except E. vaginatum, the preference index was biomass dependent such that its value was high at low biomass and decreased as biomass increased. This scheme indicates that at higher forage biomass, reindeer tend to prefer a more diverse diet. Selecting a more diverse diet may in turn reduce levels of specific toxic substances ingested through dilution. Decreased preference for plants when they are highly available (e.g., Salix pulchra) may also reflect increased maturity of plant parts available.

D. Diet Selectivity and Implications For Dry Matter Digestibility.

Food intake by large ruminants is regulated primarily by

physical distention of the rumen and subsequent rate of digestion

(Montgomery & Baumgardt 1965; Baumgardt 1970; Thornton & Minson

1972; Westoby 1974; Drozdz 1979; White et al. 1981). Apparent

DMD of the summer diet estimated for reindeer (38-41%; Table 12)

and caribou (37-43%; White et al. 1975) on arctic ranges indicate

rumen distention probably signals the end of feeding for these

animals as well (White 1975; White et al. 1981). Digestibility

and fiber content of the diet influence intake by determining

retention time of food within the rumen (Blaxter et al. 1961;

Blaxter 1962; Thornton & Minson 1972; Drozdz 1979). Therefore,

daily intake levels theoretically increase when a high diet

quality is selected for (Van Dyne & Heady 1965; Longhurst et al.

1968; Thornton & Minson 1972; Person 1975; Person et al. 1975;

Drozdz 1979; Person et al. 1980a,b). For example, immature

growth stages generally contain large amounts of digestible

tissues, low concentrations of fibrous lignified components

(Butler & Bailey 1973), and low levels of secondary defense

compounds which may inhibit digestion or prove toxic to the

animal (Longhurst et al. 1968). Ingestion of immature plant

parts should result in decreased rumen retention time (RRT) and

increased digestible dry matter intake (DDMI). Selection for

immature over mature stages would thus be beneficial to reindeer

and caribou.

Although digestibility has been used as an indicator of diet quality, the actual value of DMD realized in vivo may be highly dependent on diet diversity and RRT (Table 14; Person et al. 1980a,b; White & Trudell 1980b). Lichens, for example, require longer RRT and adaptation of rumen microbes in order to achieve maximum levels of digestibility (Trudell et al. 1980). Relative preferences may also be influenced by RRT. White & Trudell (1980b) have reported RRTs of 11 hours for initial grazings and 23 hours for final grazings on the lake margin site. Deciduous shrubs and forbs are highly digestible when retention time is short (11 h) which occurs at initial grazings. Lichens and graminoids are more completely digested at final grazings when retention times are longer (23 h). Graminoids were grazed even when retention time was short so that their use may also depend upon the visibility of green blades among standing dead blades.

Selection just for digestibility would not necessarily maximize net energy and nutrient intake, however, and the cost in time and effort required to select a more digestible diet must be balanced against the advantages. For instance, intake of poor quality food be necessary for rumen "filling" because the most highly digestible forages may not be the most highly available on the range. In the present study, forbs were both highly preferred and highly digestible, yet intake of forbs was limited by extremely low availability on the grazing site. In contrast, less

digestible, less nutritious, and less preferred lichens were highly available and made up a large portion of the diet.

Increasing DDMI and decreasing RRT through selective grazing theoretically results in increased energy intake and retention and decreased residence time of secondary compounds in the rumen (White & Trudell 1980b; White et al. 1981). These relationships are used to best advantage when increasing energy intake above maintenance requirements. Studies by Blaxter et al. (1961) and Blaxter (1962) performed with sheep in stalls indicate a direct relationship between daily food or energy intake and DMD of the diet. For diet digestibility levels of less than 66 to 70%, gut distention signaled the end of feeding (Blaxter 1962). Above a diet digestibility of 70%, regulation of feeding was chemostatically controlled and resulted in the maintenance of a constant level of energy intake (Butler & Bailey 1973). For diet digestibilities between 40 and 60%, proportionately large increases in the level of energy intake were observed in relation to small increases in digestibility and it was suggested that the grazing animal may use this relationship to his advantage when the digestibility of forages on the grazing site falls within these levels. Thus, Blaxter et al. (1961) showed that by increasing the digestibility of the ingested forage by 10% (from 50 to 60%) which could come about through selective grazing, the energy intake was increased 32% and resulted in a 200% increase in energy retention above maintenance requirements.

In the present study, estimates were made of the metabolizable energy intake (MEI) and energy available for fattening of reindeer grazing on the upland tundra and lake margin sites. Calculations were based on those made by White et al. (1975) and are presented in Table 15. In order to show the advantage of selection, the diet used by reindeer was compared with a theoretical diet based on random use of vegetation on the range. Diet digestibility was calculated using average 10-hour DMD values from Table 12 for both available and selected forages. Intake values were calculated from those published by White & Trudell (1980b). Corrections of DMD to account for any post-ruminal digestion followed Hume and Purser (1975).

Selection provided for an 8% increase in DMD in the alimentary tract of forage on the upland tundra site and a 14% increase on the lake margin site (Table 15). MEI values obtained (6.2 Mcal/d selected on the upland tundra site; 8.2 Mcal/d selected on the lake margin site) agree with estimates obtained by Holleman et al. (1979) for esophageal fistulated reindeer on a lichen diet (5.6 Mcal/d) and caribou grazing on lichen range (9.1 Mcal/d), and with estimates obtained by White et al. (1975) for reindeer grazing on the coastal plains near Prudhoe Bay, Alaska (5.55-6.82 Mcal/d). MEI was increased 46% on upland tundra and 45% on lake margin when reindeer grazed selectively versus grazing randomly on these sites.

Table 15. Theoretical estimates of metabolizable energy intake and energy available for fattening of a 70 kg reindeer based on estimates of dry matter intake (White & Trudell 1980b) and digestibility (Table 12) of forage on the upland tundra and lake margin sites. Calculations follow White et al. (1975).

	Upland Tundra		Lake Margin	
	Available Diet	Selected Diet	Available Diet	Selected Diet
Daily Dry Matter Intake, DMI $[g \cdot (kg^{0.75}d)^{-1}]$	73	99	92	117
DMD (%, 10-hour nylon bag)	33	40	38	51
DMD_w (%, whole animal)	60	65	63	72
DMD Increase (%, whole animal)	8		14	
Digestible Dry Matter Intake, DDMI $[g \cdot (k^{0.75} \cdot d)^{-1}]$	44	64	58	84
Metabolizable Energy Intake, MEI^b $[kcal \cdot (kg^{0.75} \cdot d)^{-1}]$	176 (4.3 Mcal·d^{-1})	259 (6.2 Mcal·d^{-1})	233 (5.6 Mcal·d^{-1})	338 (8.2 Mcal·d^{-1})
MEI Increase (%)	46		45	
Energy Requirements, ER_m, at Maintenance^c $[kcal \cdot d^{-1} \cdot (kg^{0.75})^{-1}]$	194	194	194	194
$MEI \cdot ER_m^{-1}$	0.91	1.34	1.20	1.74
Energy Available for Fattening^d $[kcal \cdot d^{-1} \cdot (kg^{0.75})^{-1}]$	-18	65	39	144
Body weight gain^e (g·d^{-1})	-96.8	170	102	377

^{a}DDMI = DMI x DMD

^{b}MEI = DDMI x gross energy of food (4.9 kcal·g^{-1}) x metabolizability of digested energy (0.82)

^{c}ER$_m$ = 2 x fasting metabolic rate [97 kcal·d^{-1}·(kg $^{0.75}$)$^{-1}$]

^{d}Energy available for fattening = MEI - ER$_m$

^{e}Body weight gain = energy available for fattening x efficiency of fattening (0.39) x [energy content of new tissue (3.6 kcal·gFW^{-1})]$^{-1}$

MEI estimates were then compared with energy requirements for maintenance (from White et al. 1975) so that net energy available for production (fattening) and weight gains could be estimated. Selective grazing resulted in a theoretical weight gain of 170 $g \cdot d^{-1}$ when reindeer grazed on the upland tundra site and 377 $g \cdot d^{-1}$ on the lake margin site. This observation may be especially important from mid to late summer when insect harassment levels primarily control selection of habitat types (White et al. 1975; Roby 1978; Wright 1978; White & Trudell 1980b). Caribou in this region have been observed to make primary use of dry windblown lichen ridges during this time (White & Trudell 1980b) so that selective grazing or increased rumen retention time would be required for these animals to meet summer energy requirements.

IV. CONCLUSIONS - Chapter 2

Reindeer and caribou have adopted a mixed feeder strategy in which the botanical composition of the diet is altered on a seasonal and site-specific basis depending on forage availability. Studies of the diet of reindeer and caribou indicate that lichens, graminoids, deciduous shrubs, and forbs are each important components at different times of the year. Flexibility in seasonal use of these forages should allow for optimizing daily nutrient and energy intake through selective grazing although the animals may not be directly selecting for nutrients per se. Selective use of highly digestible forages enables reindeer to maximize energy intake, minimize rumen retention time, and avoid or buffer toxic effects of secondary plant compounds. In addition, the degree of selectivity used in grazing must strike a balance between dietary gain, avoidance of secondary plant compounds and minimization of grazing effort to be advantageous to the animal.

In this study, selective grazing by reindeer on arctic tundra range was evident through comparisons of forage use in relation to availability on the study sites. The quantity of forage available was a major factor determining forage use and preference. Lichens were readily available in the vegetation types studied and as such were important in the summer diet. However, selection for lichens occurred only when they made up a small proportion (< 33%) of the forage biomass.

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The availability of preferred plant parts (those chosen over all available plant parts on the grazing site) also influenced forage use and selection. Forbs and deciduous shrubs were selected for at all availabilities on both upland tundra and lake margin sites. For the graminoids, _Carex aquatilis_ and _Eriophorum vaginatum_, the relative availability of green blades and inflorescences determined by the phenological stage influenced their use and selection by grazing reindeer.

Use of and preference for specific microhabitats within tundra sites by reindeer also provided further evidence of selective grazing. Those microhabitats most highly used and preferred were those with highest species diversity (e.g., wet troughs) and available biomass (e.g., intertussock tundra and _Salix_ strangmoor).

In general, preferences for microhabitats were ranked similarly to the ranking of microhabitat DMD so that selective foraging at the microhabitat level results in selection for digestibility. It was beyond the scope of this study, however, to determine whether diet DMD was the basis for selective feeding by reindeer.

Theoretical estimates of diet DMD were higher by 12-41% than if reindeer had eaten all forage species in relation to their availability on the range. High diet DMD levels were maintained throughout a 3-day intensive grazing trial in spite of significant reductions in biomass of preferred plant species and parts, indicating that the overall range quality was high.

SUMMARY

Grazing behavior of reindeer on summer tundra ranges was

studied in order to identify factors controlling food intake and

digestive efficiency. Tame reindeer fitted with esophageal and

rumen fistulas were tethered on vegetation-landform units offering

a variety of plant species diversity and biomass. Effects of

ᴸ·tensive grazing on behavior were studied by tethering reindeer

on individual sites for 3 days. Investigations of plant use and

preference over the peak growing season (June through August)

were conducted by tethering reindeer on specific sites for single

grazing events at two-week intervals.

Food intake was estimated from 2 to 5 min collections of

esophageal fistula egesta; biting rate was measured concurrently

(Chapter 1). Rate of food intake depended on the plant species,

growth form, and available plant biomass (Table 2; Figure 3).

When corrected to a constant biomass (50 $g \cdot m^{-2}$), ranking of plant

types by eating rate was forbs (13 $g \cdot min^{-1}$) > Salix species and

Eriophorum vaginatum (6 $g \cdot min^{-1}$) > Carex species, Betula nana and

lichens (3-4 $g \cdot min^{-1}$). Food intake rate increased linearly with

biomass for all growth forms except forbs which were eaten rapidly

even when scarce. At peak standing crop, single-stemmed graminoids

and carpet shrubs were ingested at 2.4-3.6 $g \cdot min^{-1}$, tussock

graminoids and tall shrubs at 5.3-6.9 $g \cdot min^{-1}$ and forbs and

lichens at 5.9-12.7 g·min^{-1}. No maximal eating rate was observed and may have been due to the relatively low levels of biomass present on tundra ranges (< 200 g·m^{-2}).

Prehension patterns were found to differ by plant growth form and may serve to facilitate harvesting of forage by reindeer. For example, leaves of deciduous shrubs were stripped from the stems using a pulling motion, palatable lichens were teased from the moss layer using rapid lip movements, and carpet shrubs and graminoids were broken up and ingested using pronounced chewing motions (Figure 4).

A significant difference (P<0.001) was found in bite rate and bite size between vascular plants (177 bites·min^{-1}, 21 mg ·bite^{-1}) and lichens (205 bites·min^{-1}, 32 mg·bite^{-1}). For each 100 g·m^{-2} increase in biomass offered, bite rate increased by 5 bites·min^{-1} when eating vascular plants, by 21 bites·min^{-1} when eating selected parts of vascular plants, and by 28 bites ·min^{-1} when eating the highly preferred shrub Salix pulchra. No significant correlation was found between bite rate and biomass of lichens. This may have been due to the limited range of biomass present, to sorting out of unpalatable lichens in the mouth during ingestion, or to the requirement for moistening of lichens during intake.

For the graminoids Carex aquatilis and E. vaginatum, a significant positive correlation was found between bite rate and

food intake (P<0.05) and a similar trend was noted for all vascular

plants combined (Figure 5). In contrast, a negative trend was

noted between bite rate and food intake of lichens. The trend

observed for intake of lichens is similar to that observed for

sheep and cattle grazing tropical grass swards.

An average of 53% of the day was spent grazing (Figures 9, 11)

while 50% of that or 26% of the day was actual eating time. On a

daily basis, time spent grazing and eating decreased at the

respective rates of 1.6 h and 1.3 h for each 100 $g \cdot m^{-2}$ increase

in total plant (vascular + lichen) biomass. In contrast, daily

time available for searching during grazing increased with in-

creasing biomass.

Reindeer biting rates were considerably higher than those

for sheep and cattle (approximately 3-fold) while bite sizes were

proportionately smaller (approximately 25%). Bite size of reindeer

more closely approximates that of the white-tailed deer (a browser).

These results suggest that the high bite rate and small bite size

used by grazing reindeer favor forage selection.

At low biomass levels, foraging by the adaptable mixed

feeder tends to maximize the quantity of food ingested. Therefore,

patterns of daily eating time and bite size appear to control

intake. At higher biomass, more time is available for searching

so that the quality of forage consumed is maximized. This is

achieved through modification of prehension and biting rate

depending on growth form.

Forage selection patterns were documented from forage and microhabitat use in relation to availability on upland tundra and lake margin (Chapter 2). Grazing events were mapped over 3-day intervals, simulating intensive grazing. Single grazing events at 2-week intervals were conducted to identify grazing use and selection patterns over the peak growing season. Use versus availability ratios were ranked to determine the relative preference of reindeer for individual plant growth forms, species and microhabitats on defined vegetation types. To assess the effect of selection on digestive efficiency, the DMD of plant forages was determined using the nylon bag technique and the first stage of the in vitro digestion technique.

On upland shrub-tussock tundra sites, the average diet was composed of 52% lichens, 21% deciduous shrubs (S. pulchra and Betula nana), 13% C. aquatilis, 8% Rubus chamaemorus and 6% E. vaginatum (Figure 14). After 3 days of intensive grazing, significant reductions were noted in the biomass of the total above-ground plant material (25%) and in live vascular plant biomass (38%). Large though not significant reductions in biomass of deciduous shrub leaves and forbs also occurred (Table 5). The observed increase in use of lichens (to 59%) and C. aquatilis (to 22%) was accompanied by decreased use of deciduous shrubs and forbs in the final grazing bouts and was apparently in response to reductions in deciduous shrub biomass.

The average diet on the lake margin sites was composed of 69% S. pulchra, 14% C. aquatilis, 12% lichens and 5% Pedicularis langsdorfii (Figure 14). Biomass of S. pulchra leaves and current year stems, total live and total plant material were all signif- icantly reduced during 3 days of intensive grazing (by 90%, 62%, 25%, and 24% respectively; Table 6). In spite of removal of leaves during the intensive grazing period, S. pulchra was still heavily used (64%) along with lichens (23%) in final grazing bouts while use of other forages decreased (e.g., C. aquatilis, to 12%; forbs, to 0.2%).

In studies of the seasonal patterns of plant use, lichens were the most important dietary constituent throughout the summer on the upland tundra site (90% of diet mid-June; 60% overall; Figure 15). Use of other forages was in relation to availability of the preferred parts (i.e., leaves of deciduous shrubs, green blades of C. aquatilis and E. vaginatum, leaves and flowers of R. chamaemorus). The most important constituent of the diet on the lake margin site throughout the growing season was S. pulchra leaves (62% overall; Figure 15) with lichens also being important (44% overall).

When preferences were determined for all grazing bouts, the most consistent preferences were noted for the deciduous shrubs and the forbs (Table 7; Figure 16). Preferences for the grami- noids, C. aquatilis and E. vaginatum, were microhabitat-specific

and depended upon availability, association with other plant
groups, and phenology. Lichens were preferred only at lower
availabilities although their overall use was very high. Evergreen
shrubs and mosses were discriminated against and mostly were
absent from the diet. For all forages except E. vaginatum, the
degree of preference shown was dependent upon the availability of
the forages on the range (Figures 16, 17). High preference
ratios were found for forbs, deciduous shrubs, lichens and C.
aquatilis at low availability.

Use of and preference for microhabitat types on the grazing
sites were guided by the available biomass, diversity of forages,
and available preferred plant species offered by each (Tables
8, 9; Figures 18-27). On the upland tundra site, 84% of the 3-
day grazing periods and 80% of the seasonal grazings were spent
on the intertussock and wet trough areas. On the lake margin
site, the Salix strangmoor (59% over 3-day grazing, 60% over the
season) and the lichen ridges (22% over 3-day grazing, 30% over
the season) were the most used and preferred microhabitats.

Microhabitat ranking based on forage biomass and 10-h nylon
bag DMD (estimated for the herbage available) were similar to
rankings of use and preference (Tables 11, 13). At the species
level, rankings of DMD (Tables 10, 14) were also similar to
rankings of preference ratios.

Comparisons of range DMD with diet DMD based on observed grazing use (Table 12) showed that selective grazing increased the DMD by about 28%. Based on estimates of diet DMD on the upland tundra and lake margin grazing sites, selective grazing provided for an 8% increase in whole tract DMD for forages ingested on upland tundra and a 14% increase on lake margins (Table 15). MEI was estimated to increase by 46% when reindeer selectively grazed on upland tundra and by 45% when selectively grazing lake margins. Based on these estimated increases in MEI, it was shown that individual productivity of the grazing reindeer would also be increased on upland tundra and on lake margin sites through selective use of the forages available.

It is concluded that reindeer selectively graze subunits of vegetation of high biomass and forage species diversity. Selective use of range not only maximizes intake of dry matter but also maintains a high diet quality as shown by changes in DMD and MEI. Foraging behavior including bite rate, size, daily grazing time and search time are all modified to accomplish these ends.

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Appendix A. Climatic conditions and reindeer grazing/insect avoidance patterns observed during 3-day grazing trials.

Year	Plot	Temperature (°C)		Wind Speed (mph)		Initial Trial Activity			Final Trial Activity		
		Initial	Final	Initial	Final	Grazing (%)	Eating (%)	Insect Avoidance(%)	Grazing (%)	Eating (%)	Insect Avoidance (%)
1975	P1	6	7*	6-10	8-16	93	86	0	95	89	0
	P2	6*	6*	9-14	7-9	98	93	0	100	95	0
	P3	13	11	6-9	4-6	100	76	0	99	94	0
	LM1	16*	16	5-9	18-28	100	64	0	98	73	0
	LM2	7	3	9-12	10-16	89	79	0	76	73	0
1976	P1	-1	4	7-10	10-17	78	39	0	72	37	0
	P3	25*	0*	8-10	8-10	84	35	0	99	48	0
	P4	18	10	5-7	7-9	93	46	0	62	30	25
	P6	12	15	10-16	8-14	78	43	0	89	37	0
	LM1	10*	10*	3-5	5-7	89	47	0	94	46	0
	LM3	10	12	10-16	10-14	98	45	0	98	49	0
1977	P2	21	16	5-7	2-5	56	29	3	82	28	0
	P3	21	19	5-7	5	63	45	0	70	36	0
	P7	14	11	7-15	10-15	71	32	3	70	31	13
	P8	18	13	10-15	8-12	78	40	0	81	42	3
	LM1	16	13	0-2	10-18	88	40	0	70	30	2
	LM4	19	10	0-5	10-20	59	23	3	84	35	0

*Precipitation occurred prior to trial.