

COMPARATIVE PATTERNS OF WINTER HABITAT
USE BY MUSKOXEN AND CARIBOU
IN NORTHERN ALASKA

A

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By

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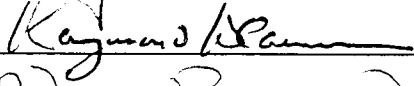
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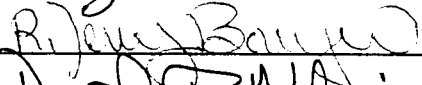
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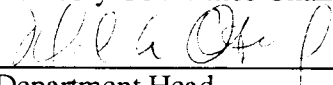
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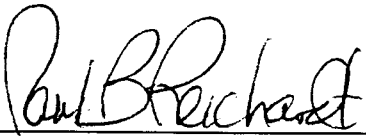


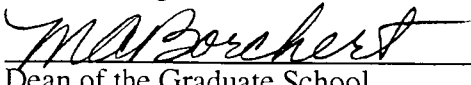


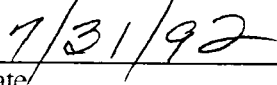
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ABSTRACT

Snow depth and hardness strongly influenced selection of feeding zones, (i.e., those areas used for foraging), in late winter by both muskoxen (*Ovibos moschatus*) and caribou (*Rangifer tarandus granti*) in northern Alaska. Snow in feeding zones was shallower and softer than in surrounding zones. Depth of feeding craters was less than the average snow depth in feeding zones. Moist sedge tundra types were used most often by muskoxen, and their diet, based on microhistological analysis of feces, was dominated by graminoids. Moist sedge and *Dryas* tundra types were most often used by caribou; lichens and evergreen shrubs were the major constituents of their diet. Despite selection of moist sedge tundra types by both muskoxen and caribou in late winter, dietary and spatial overlap was minimal.

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INTRODUCTION

Forage intake and diet composition is affected by one or more of the following: ingestion and digestion rates; toxin and nutrient intake; and time spent feeding (Stephens and Krebs, 1986). These constraints are intrinsic, as they relate to the morphological and physiological limits of the animal; or extrinsic, as determined by climatic or other environmental variables. Intrinsic and extrinsic constraints are not mutually exclusive; both influence the ability of a herbivore to acquire forage (Stephens and Krebs, 1986).

In winter, the ability to travel over and forage through snow is an extremely important determinant of foraging success by arctic ungulates. In late winter, snow on tundra ranges can reduce forage available to barren-ground caribou (*Rangifer tarandus granti* and *R. t. groenlandicus*) by $\geq 97\%$ (Adamczewski et al., 1988). Snow conditions, rather than forage per se, have been cited as possible limiting factors on populations of arctic ungulates (Henshaw, 1968; Miller et al., 1977; Bergerud, 1980). Roby (1980) suggested that snow is one of three dominant variables influencing the winter ecology of caribou. Similarly, Gunn et al. (1991) postulated that winter temperature and snow conditions may be the most important long-term ecological factors influencing muskoxen (*Ovibos moschatus*) populations on Banks Island.

Because of variable snow cover, tundra forage available to caribou is patchy and clumped (Tyler and Øritsland, 1989). Skogland (1984) reported that, in Norway, niche-breadth of wild reindeer in

winter was substantially narrower than in summer. Henshaw (1968) and Miller et al. (1982) noted that late winter snow made most vegetation unavailable to caribou in northwestern Alaska and in the Canadian Archipelago, respectively. Similarly, Adamczewski et al. (1988) reported that only 1-3% of meadow vegetation was available to caribou on Coats Island in mid to late winter. Patchy distribution of snow may concentrate reindeer in some areas, promoting localized overgrazing (Collins and Smith, 1991). Brooks and Collins (1984) concluded that limitations imposed by snow on forage availability to reindeer must be considered in determining carrying capacity of winter range.

Foraging by muskoxen and caribou reflects a balance between associated costs and benefits. Costs include time spent searching for suitable foraging areas (i.e., those areas with nutritious, high quality plant species and snow conditions that permit cratering), time spent cratering, and time spent eating (Thing, 1977; Skogland, 1984; Fancy and White, 1985; Klein, 1986). Thing (1977) noted that, because of harder snow in late winter, caribou walk more while foraging and cratering is 50% more "expensive" than during early winter. Similar differences can be assumed for muskoxen, at least for cratering (Klein, 1986). These costs must be balanced against the nutritional benefits derived from the forage obtained, as well as the ability of the animal to draw on body reserves (Skogland, 1984; Klein, 1990; Adamczewski et al., unpub. obs.).

Although muskoxen and caribou occur in many of the same arctic areas, they have evolved different morphological and physiological

characteristics (Klein, 1986). Caribou are classified as intermediate feeders, selecting for both quality and quantity of forage (Leader-Williams, 1988; Skogland, 1984), whereas muskoxen more closely resemble bulk and roughage feeders (Klein, 1986). This distinction may be associated with differences in mouth morphology and the rumen volume:body volume ratio. Hofman (1983) noted that a wide mouth and large rumen were typical of bulk feeders, whereas the reverse was characteristic of selective feeders. Muskoxen have a larger rumen and greater retention time than caribou allowing greater forage intake and digestion of fibrous plant parts (White et al., 1987; Staal and Thing, 1991). Because caribou are intermediate feeders, they spend more time searching and foraging than do muskoxen (Jingfors, 1980). Winter forages of caribou are highly digestible, particularly where lichens are abundant (Boertje, 1981; Skogland, 1984; Klein, 1990).

Snow may be a factor in reducing the overlap in resource use between muskoxen and caribou. In northern Alaska, both species are constrained by snow in the selection of winter habitat and forage, though to varying degrees. Smith (1989a) suggested, however, that muskoxen are not as well adapted as caribou for traveling or foraging through snow. Muskoxen have greater foot loading and lower chest height than caribou and therefore may be constrained to foraging and traveling in areas of shallower snow than caribou (Fancy and White, 1985; Klein, 1986).

Caribou may forage in areas that, due to snow depth, are unavailable to muskoxen. Barren-ground caribou are thought to crater

in snow to depths of 75 cm (Henshaw, 1968; Lent and Knutson, 1971; Thing, 1977), while craters of woodland caribou may exceed 100 cm (Vandal and Barrette, 1985; Brown and Theberge, 1990). In contrast, feeding craters of muskox generally do not exceed 30 cm in depth (Lent and Knutson, 1971; Rapota, 1984; Smith, 1984; Gray, 1987), although Thomas and Edmonds (1984) reported crater depths of 50 cm in the Canadian High Arctic, and Wilson (1992) reported crater depths > 45 cm in northeastern Alaska. In addition, caribou appear to be less constrained by snow hardness and crater in snow that is three times harder than the maximum occurring in muskox feeding zones (Lent and Knutson, 1971). Others have reported snow hardness values similar to those of Lent and Knutson (1971) for caribou (LaPerriere and Lent, 1977; Skogland, 1978; Duquette, 1988). Thus, if caribou select habitats or forage species in areas where snow characteristics exclude or discourage muskoxen, overlap in resource use will be low.

Comparative studies of habitat and forage selection by muskoxen and caribou have not been done in northern Alaska. Many such studies, however, have been conducted in other arctic regions. In the Northwest Territories (NWT) of Canada, little or no overlap in resource use between these ungulates was reported during summer (Kevan, 1974; Parker and Ross, 1976; Wilkinson et al., 1976; Ferguson, 1987) or winter (Parker et al., 1975; Miller et al., 1977; Parker, 1978; Vincent and Gunn, 1981; Thomas and Edmonds, 1984), except when snow conditions were particularly severe (Parker, 1978; Vincent and Gunn, 1981; Thomas and Edmonds, 1984). Gunn et al. (1991), however,

concluded that such overlap is of little consequence to either species because competition for forage and habitats in Canada is unlikely.

In arctic areas other than the NWT, however, there is considerable overlap in resource use between muskoxen and *Rangifer*. Alendal (1974) suggested that overlap in forage use with reindeer led to the decline of muskoxen on Svalbard, although direct evidence for a causal relationship was lacking. Klein and Staaland (1984) documented dietary overlap between muskoxen and caribou on Svalbard and suggested that direct competition for forage led to the demise of muskoxen. Likewise, Olesen (1991) observed a nearly 100% overlap in the winter diets of muskoxen and caribou in the Søndre Strømfjord area of West Greenland; both species made heavy use of graminoids and selected similar habitat types. Caribou numbers in this area are currently declining, and Lent (1989) suggested that this may be a result of competition with muskoxen.

The degree of overlap in resource use between muskoxen and caribou may vary greatly between regions. Thomas and Edmonds (1984:93) stated that "...patterns of habitat use will vary regionally and inferences about possible competition between caribou and muskoxen from studies in one area cannot be applied universally." Likewise, Rominger and Oldemeyer (1990) noted that forage selection by caribou should not be generalized across geographical regions due to the diversity of habitats in which the species occurs.

The reported regional differences in diets of muskoxen and caribou and the lack of comparative studies in northern Alaska

emphasized the need to compare habitat and forage selection in an area where both species were present. The purpose of this study was to describe and evaluate habitats, snow characteristics and forage species selected by caribou of the Central Arctic Herd (CAH) and muskoxen present during late winter. Hypotheses to be tested were as follows: 1) muskoxen and caribou select winter feeding zones, (i.e. those areas where feeding craters occur), based on differences in snow depth and snow hardness; 2) caribou select winter feeding zones with a higher lichen abundance than zones selected by muskoxen; and 3) muskoxen select feeding zones with higher willow (*Salix* spp.) and graminoid abundance than zones selected by caribou. Two predictions arise from hypothesis 1: a) muskoxen and caribou will crater in shallower and softer snow than that characterizing the general feeding zone, and b) muskoxen will select feeding zones having shallower and softer snow than those of caribou.

Testing of these hypotheses required examination of patterns of resource partitioning between muskoxen and caribou. The extent of potential resource overlap is important, particularly in light of the current expansion of muskoxen to areas previously occupied by caribou only. If the extent of overlap is minor, it may be inferred that increases in muskox numbers and areas occupied will have little or no adverse impact on caribou of the CAH.

Study Area

The study area is near the confluence of the Sagavanirktok and Ivishak rivers, approximately 100 km south of Prudhoe Bay and 50 km west of the Kavik River (Fig. 1). This location was chosen because muskoxen and caribou are known to overwinter in this area. Muskoxen occurring in the study area originated from animals translocated to or near the Arctic National Wildlife Refuge (ANWR) (then the Arctic National Wildlife Range) in 1969 and 1970 (Smith, 1989b).

Translocated muskoxen initially dispersed into a few localized areas within ANWR, thereafter the population increased rapidly (Jingfors and Klein, 1982). In the late 1970's muskoxen were sighted west of the Canning River (R.Cameron, pers. comm.) and in 1982 began an accelerated dispersal to areas east and west of ANWR, including the present study area (Reynolds, 1989). Initially, only bulls inhabited the study site, but in 1986 mixed-sex groups began overwintering in this general area as well (Reynolds, 1989).

As numbers of muskoxen dispersing to the west increased, with the associated establishment and expansion of local populations, the likelihood of overlap in use of forage and habitat with CAH caribou also increased. The CAH has been increasing over the past few years, and as of 1991 the herd numbers about 20,000 animals (D. Reed, ADF&G, unpubl. data). The annual range of these caribou lies approximately

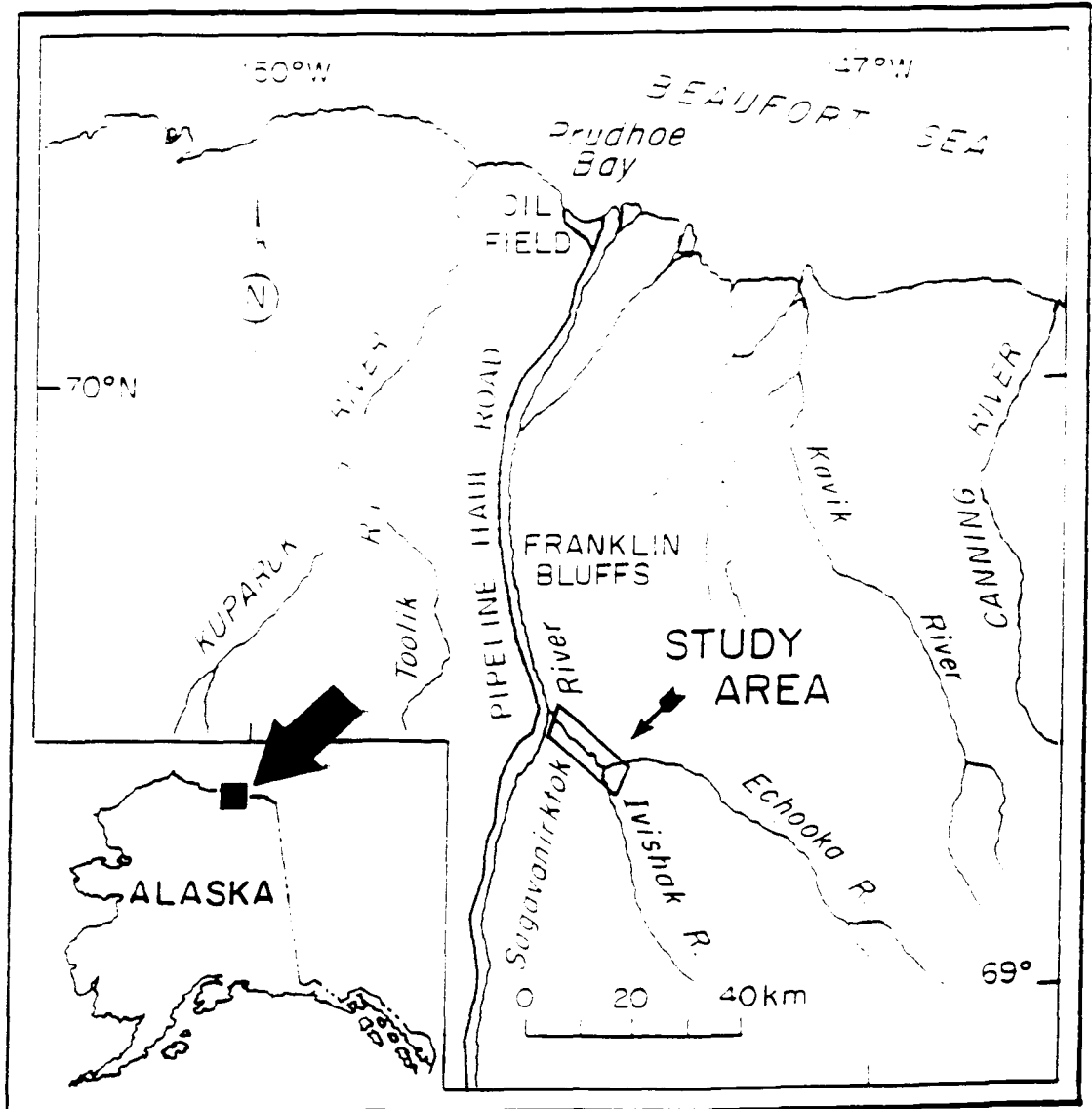


Fig. 1. The study area within northern Alaska.

between the Canning and Colville rivers. Winter range is primarily in the northern foothills of the Brooks Range, and summer range is on the Arctic Coastal Plain (Cameron and Whitten, 1979). Beginning in late spring there is a general northward migration towards the coastal plain, and by early autumn caribou begin moving back toward the foothills (Fancy et al., 1989). The study area is within typical winter range of the CAH (Cameron and Whitten, 1979).

Muskoxen in the study area, much like CAH caribou, move north in summer and south in winter, though on a much more limited scale. Muskoxen remain in the study area throughout the winter. In June, most muskoxen move north, summering between Franklin Bluffs and the Kavik River (Fig. 1) (P. Reynolds, pers. comm.), although solitary bulls remain in the study area. Muskoxen are found in the vicinity of the study area by late October or early November (P. Reynolds, pers. comm.).

The two major terrain types in the study area are gently rolling foothills and flat river floodplains. Numerous small ponds and several creeks occur throughout the area. Vegetation is typical arctic tundra. Near rivers, xeric terraces similar to the *Dryas* tundra described by Walker (1983) are present with a high occurrence of *Dryas* spp., lichens, forbs and small or prostrate shrubs. Partially vegetated gravel bars are common, as are stands of riparian willows (primarily *Salix lanata*, *S. alaxensis* and *S. glauca*). These willows are the tallest vegetation in the area, some growing to a height of 2 m. Mesic areas similar to the moist sedge types described by Walker (1983), with

sedges, forbs, mosses, *Equisetum* spp. and small or prostrate shrubs are abundant in low-lying areas adjacent to rivers. Hillsides are characterized by moist, tussock sedge tundra (Walker, 1983) with *Eriophorum* spp., mosses and small evergreen and deciduous shrubs. Mesic areas similar to those near rivers occur in the hills adjacent to ponds and along small creeks. A complete list of plant species encountered in the study area is included in Appendix I. Plant nomenclature is according to Hultén (1968). Robus (1981) provided a description of fauna occurring on the north slope of Alaska.

During late winter (late March and April) of my 1990 and 1991 field seasons, the weather was characterized by cold, sunny days with frequent breezes. Temperatures ranged from -40°C to slightly above 0°C . There also were occasional storms with strong winds and blowing snow. Snow on the tundra of northern Alaska is generally <40 cm deep (Hall, et al., 1991) and is often wind-blown and hard, depending upon the underlying vegetation and terrain (Evans et al., 1989).

METHODS

Access to animals was via snowmobile. Once located, we remained about 1-2 km away to avoid disturbing them. Transects in feeding zones (i.e., areas where feeding craters occurred) and nonuse zones were marked, and measurements were made only after the animals had moved away. Animals were located daily and feeding zones were generally sampled <2 days after they were made.

Randomly-oriented transects were established through the center point of each feeding zone. Each transect extended in opposite directions from the center of the feeding zone into adjacent nonuse zones and through a 100 m transition zone into far nonuse zones (Fig. 2). Transects were marked by pounding 0.5 m sections of steel pipe into the frozen ground at the center and both ends of the transect. A 1.5-m fiberglass rod with nylon flagging was inserted into the pipe. Transect length varied according to the number of measurements taken in the feeding zone; this number was matched in adjacent and far nonuse zones and was dependent upon the size of the feeding zone (i.e., if 5 measurements were taken in the feeding zone, 5 were taken in the adjacent and far nonuse zones). This sampling design is similar to that used by Wilson (1992) in a study of muskox habitat selection in ANWR.

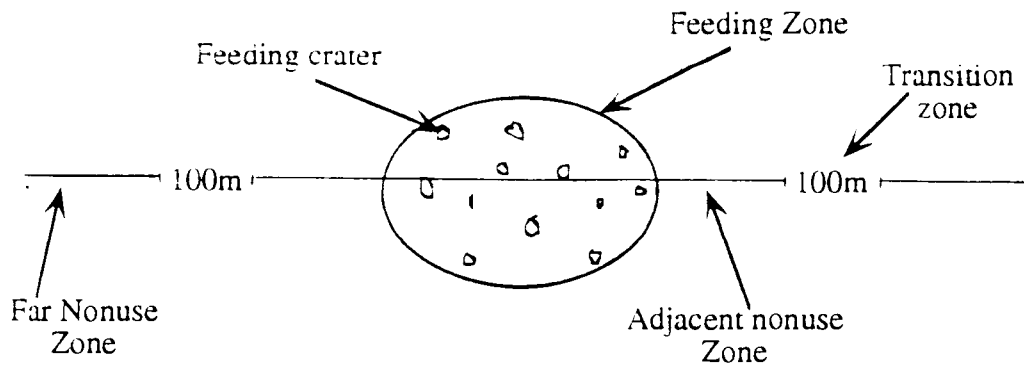


Fig. 2. Schematic of zones for sampling snow and vegetation in northern Alaska 1990-91.

Snow depth and hardness measurements were taken every 5 m in each zone. Snow depth was measured to the nearest 1 cm, and snow hardness was determined using a Rammsonde penetrometer (Lent and Knutson, 1971). Data were combined to provide a mean depth and hardness for each of the 3 zones.

Depth of the 10 craters closest to the transect was measured to the nearest 1 cm at the least disturbed edge (i.e., the point at which the animal ceased cratering). Vegetation in each crater was recorded as graminoid, lichen, moss, forb, *Dryas* spp., *Equisetum* spp., *Cassiope* spp., and *Salix* spp. or other shrubs. In sites with <10 craters, all craters present were sampled. Frequency of occurrence of each vegetation type within each site was calculated as the number of craters with each type divided by the number of craters sampled at that site.

Samples of 15-20 fresh fecal pellets (generally <2 days old) were collected in each feeding zone. While in the field, samples were kept frozen. Fecal samples were kept separate by ungulate species but were pooled within a species (in 1990 n=20 and 16, and in 1991 n= 19 and 22 for muskoxen and caribou, respectively) into two equal composite samples for each ungulate based on feeding zone location: upland (i.e. foothills) and lowland-riparian (i.e. in or adjacent to riparian areas). Samples were sent to the Wildlife Habitat Laboratory of Washington State University for microhistological analysis of plant tissues (Todd and Hansen, 1973). One hundred fifty fields were examined for each sample. To adjust for differential digestion of plant species (Dearden et al., 1975; Boertje et al., 1984), correction factors were derived from

digestibilities reported by Boertje (1981). Lacking specific digestibility values for muskoxen, the same correction factors were used for both ungulates (Appendix II).

During late June and July 1990 and 1991, transects established the previous winter were relocated and the vegetation was sampled.

Vegetation present was assumed to be reasonably representative of that occurring in winter (Appendix II). Percent relative cover of vegetation was estimated every 5 m using a ten-pin sample frame (Hays et al., 1981). Individual plant species (Appendix I) were grouped into vegetation categories as follows: *Salix* spp., mosses, graminoids, lichens, evergreen shrubs, deciduous shrubs, forbs and *Equisetum* spp. Other categories were litter (sample frame pin hit dead plant material as well as live plant material), litter alone (sample frame pin hit dead plant material only) and unvegetated (rock, gravel, soil). Additionally, plant communities as described by Walker (1983) were assigned to each feeding zone based on the dominant plant taxa and moisture regime. For statistical purposes, sample sites were categorized as either upland or lowland-riparian habitats. Aspect of each feeding zone also was recorded.

Data on feeding zones and feeding craters were considered separately. Each data set was analyzed by year and ranked (Zar, 1984), due to non-normality, prior to all analyses. All statistical analyses were conducted using SAS (1989) and SPSS (1986).

For both data sets, stepwise discriminant analysis by forward selection and backward elimination (SAS, 1989) was used to choose all

variables for analyses, except for lichens which were not chosen by forward stepwise selection from the 1991 feeding zone variables. Regardless, lichens were used in the analysis because of their reported importance to CAH caribou (Roby, 1978). Selected variables were then entered into a discriminant function analysis (DFA) and classified according to species (muskoxen or caribou) and zone type. Multivariate analysis of variance (MANOVA) was applied to each data set. In 1990, three independent variables were used in analysis of zones: species, zone type, and habitat. In 1991, however, habitat could not be used due to redundancies in the design matrix (muskoxen occurred exclusively in lowland-riparian habitat). Therefore, an analysis of variance (ANOVA) was used for the habitat effect. A Mann-Whitney U-test was used to test for differences between mean depths of muskox craters and caribou craters and to test for differences between mean depths of feeding zones and feeding craters within each species.

RESULTS

Feeding Craters

In 1990, mean depth of feeding craters of muskoxen and caribou were not significantly different (Fig. 3). In 1991, however, the mean depth of muskox feeding craters was significantly greater than that of caribou feeding craters (Fig. 3).

Variables used for analysis were chosen from those listed in Table 1. For 1990, lichen, *Salix* spp. and shrubs were selected, and for 1991, *Salix* spp., forb and lichens were used. DFA correctly classified 90.0% and 100.0% of the 1990 crater data for caribou and muskoxen, respectively. For 1991 data, DFA classified 95.5% and 94.7% of the crater data correctly for caribou and muskoxen, respectively.

For 1990, vegetation occurring in craters was significantly different for muskoxen and caribou (MANOVA, Hotelling-Lawley Trace $F=19.62$, d.f.=3,31, $p<0.0001$). The relative contribution to the MANOVA was highest for lichens ($F=37.92$), followed by shrubs ($F=7.38$) and *Salix* spp. ($F=1.54$). For 1991, the overall model also was significant (MANOVA, Hotelling-Lawley Trace, $F=24.85$, d.f. = 3,37, $p<0.0001$). Again, lichens ($F=41.69$) made the greatest relative contribution, followed by *Salix* spp. ($F=15.19$) and forbs ($F=4.28$). Occurrence of lichens was far greater in caribou than in muskox

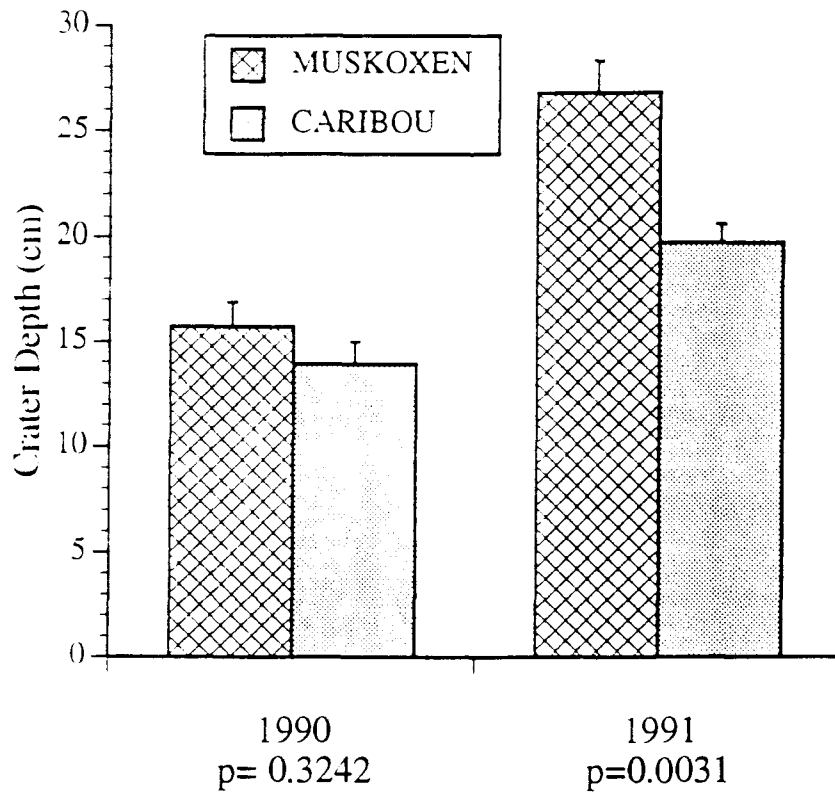


Fig. 3. Comparison of mean depth (+S.E.) of muskox and caribou feeding craters in northern Alaska, 1990 and 1991. P-values obtained from Mann-Whitney U-test.

Table 1. Mean frequency of occurrence (\pm SE) of vegetation in feeding craters and mean depth (\pm SE) of feeding craters within muskox and caribou feeding zones in northern Alaska, 1990 and 1991.

Variable	1990		1991	
	Muskox	Caribou	Muskox	Caribou
Snow Depth (cm)	15.73 \pm 1.17	13.92 \pm 1.07	26.75 \pm 1.53	19.70 \pm 0.92
Graminoid	0.85 \pm 0.06	0.89 \pm 0.07	0.74 \pm 0.07	0.85 \pm 0.05
<i>Salix</i> spp. ^{1,2}	0.47 \pm 0.05	0.35 \pm 0.04	0.56 \pm 0.07	0.24 \pm 0.05
Shrub ¹	0.21 \pm 0.06	0.50 \pm 0.09	0.12 \pm 0.04	0.27 \pm 0.06
Forb ²	0.28 \pm 0.04	0.33 \pm 0.04	0.09 \pm 0.04	0.22 \pm 0.06
Lichen ^{1,2}	0.32 \pm 0.07	0.84 \pm 0.05	0.27 \pm 0.06	0.85 \pm 0.05
Moss	0.64 \pm 0.06	0.70 \pm 0.04	0.54 \pm 0.08	0.77 \pm 0.05
<i>Cassiope</i> spp.	0.03 \pm 0.02	0.06 \pm 0.03	0.08 \pm 0.03	0.49 \pm 0.07
<i>Dryas</i> spp.	0.03 \pm 0.01	0.09 \pm 0.05	0.33 \pm 0.06	0.53 \pm 0.06
<i>Equisetum</i> spp.	0.09 \pm 0.04	0.03 \pm 0.02	0.22 \pm 0.06	0.17 \pm 0.06

¹Used in 1990 analysis.

²Used in 1991 analysis.

craters whereas *Salix* spp. was more abundant in muskox craters (Table 1). Occurrence of graminoids was high in the feeding craters of both ungulates (Table 1). Crater depth, although significantly greater for muskoxen than for caribou in 1991, was not selected from either data set, reflecting the small overall differences in the depth of muskox and caribou craters.

Feeding and Nonuse Zones

For 1990 data on feeding and nonuse zones, snow depth, snow hardness, moss, forb, lichen, *Equisetum* spp., evergreen shrub and *Salix pulchra* were chosen by forward stepwise discriminant analysis from all variables measured (Table 2). *Salix pulchra* was not included in the *Salix* spp. category because it was consistently chosen as a separate variable both before and after category variables were created.

Using the selected variables, DFA correctly classified 80.0% and 87.5% of the feeding zone data for muskoxen and caribou, respectively. For zone type, 88.9% of the feeding zones, 44.4% of the adjacent nonuse zones, and 63.9% of the far nonuse zones were correctly classified. High error rates for nonuse types result from misclassification of one nonuse type into the other, not misclassification of nonuse into feeding type.

The MANOVA for 1990 zone data was significant for all three effects ($p < 0.0001$), indicating differences in use between muskoxen and caribou. The interaction of species by type, however, was not significant

Table 2. Mean snow depth and hardness and mean relative plant cover occurring within zone types for muskoxen and caribou in northern Alaska, 1990.

Variable	Zone					
	Feeding		Adjacent nonuse		Far nonuse	
	Muskox	Caribou	Muskox	Caribou	Muskox	Caribou
Depth (cm) ¹	20.67	21.73	32.51	37.16	32.48	36.06
Hardness (kg) ¹	4.45	4.66	5.40	7.01	6.25	8.25
LITA ²	0.07	0.06	0.05	0.07	0.07	0.06
Litter ³	0.57	0.53	0.58	0.55	0.57	0.51
Moss ¹	0.67	0.70	0.71	0.69	0.64	0.67
<i>Salix</i> spp.	0.13	0.07	0.25	0.07	0.17	0.06
Graminoid	0.20	0.25	0.21	0.27	0.20	0.24
Lichen ¹	0.13	0.19	0.08	0.10	0.09	0.12
E. shrub ^{1,4}	0.26	0.32	0.22	0.24	0.22	0.23
D. shrub ⁵	0.09	0.11	0.11	0.10	0.08	0.08
Forb ¹	0.08	0.04	0.06	0.04	0.04	0.05
<i>Equisetum</i> spp. ¹	0.11	0.01	0.09	0.02	0.10	0.03
Unvegetated ⁶	0.02	0.02	0.04	0.03	0.05	0.07
<i>Salix pulchra</i> ¹	0.006	0.04	0.004	0.05	0.008	0.03

¹Selected for analysis.

²Litter alone (i.e., pin hit only dead plant material).

³Pin hit live and dead plant material.

⁴Evergreen shrubs.

⁵Deciduous shrubs (excluding *Salix* spp.).

⁶Includes rock, gravel, soil.

Table 3. Results (F -values) of MANOVA applied to zone data collected in northern Alaska, 1990. Variables were selected by stepwise discriminant analysis.

Variable	Species ^a	Zone Type ^b	Habitat ^c
Depth	0.20	44.95***	8.78**
Hardness	5.80*	17.81***	2.64
<i>Salix pulchra</i>	17.62***	1.83	19.18***
Moss	0.23	0.43	1.55
Forb	0.45	0.84	0.004
Lichen	1.78	3.22*	4.12*
<i>Equisetum</i> spp.	10.80**	0.65	2.81
Evergreen shrub	0.001	5.08**	3.98*

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.0001$.

^aMuskoxen or caribou.

^bFeeding, adjacent nonuse, and far nonuse.

^cUpland or lowland-riparian.

($p \geq 0.726$), indicating no difference between the two ungulates in selection of feeding zones.

Salix pulchra and *Equisetum* spp. contributed most to the species effect (Table 3). *Salix pulchra* cover was higher in caribou feeding zones, whereas *Equisetum* spp. were more common in muskox feeding zones (Table 2). *Salix pulchra* also made the greatest relative contribution to the habitat effect (Table 3). Snow depth and snow hardness made the greatest relative contributions to the type effect (Table 3), indicating that selection of feeding zones by muskoxen and caribou is based primarily on snow characteristics.

For 1991 data on feeding and nonuse zones, stepwise discriminant analysis chose snow depth, snow hardness, *Salix* spp., other deciduous shrubs, graminoids, *Equisetum* spp. and unvegetated from all variables measured (Table 4). In addition, lichens were entered in all analyses. *Salix pulchra* was included in the *Salix* spp. category because it was not selected before category variables were created (as happened in 1990).

Using the selected variables, DFA correctly classified 80.0% and 81.8% of feeding zone data for muskoxen and caribou, respectively. For zone type, 90.5% of the feeding zones, 54.8% of the adjacent nonuse zones, and 78.6% of the far nonuse zones were correctly classified. High error rates in nonuse types were the result of misclassification of one nonuse zone into the other, although error rates were not as high as in 1990.

Only two independent variables were used in 1991: species

Table 4. Mean snow depth and hardness and mean relative plant cover occurring within zone types for muskoxen and caribou in northern Alaska, 1991.

Variable	Zone					
	Feeding		Adjacent nonuse		Far nonuse	
	Muskox	Caribou	Muskox	Caribou	Muskox	Caribou
Depth (cm) ¹	30.50	23.09	45.09	37.53	46.75	47.95
Hardness (Kg) ¹	7.50	8.90	11.22	15.82	9.74	13.99
Lita ²	0.06	0.08	0.03	0.08	0.03	0.06
Litter ³	0.56	0.61	0.49	0.53	0.51	0.56
Moss	0.65	0.60	0.68	0.67	0.76	0.66
<i>Salix</i> spp. ¹	0.09	0.04	0.11	0.05	0.17	0.52
Graminoid ¹	0.13	0.09	0.12	0.11	0.10	0.10
Lichen ¹	0.05	0.24	0.04	0.13	0.02	0.11
E. shrub ⁴	0.16	0.26	0.12	0.22	0.12	0.17
D. shrub ^{1,5}	0.08	0.07	0.06	0.06	0.06	0.04
Forb	0.06	0.08	0.04	0.05	0.04	0.04
<i>Equisetum</i> spp. ¹	0.08	0.03	0.07	0.07	0.08	0.07
Unvegetated ^{1,6}	0.11	0.03	0.15	0.07	0.12	0.10

¹Selected for analysis.

²Litter alone (i.e., pin hit only dead plant materials).

³Pin hit live and dead plant material.

⁴Evergreen shrubs.

⁵Deciduous shrubs excluding *Salix* spp.

⁶Includes rock, gravel, soil.

(i.e. muskoxen and caribou) and zone type (i.e. feeding, adjacent nonuse and far nonuse). The MANOVA was significant for both effects ($p < 0.0001$), but the interaction of species by type was not ($p > 0.186$), again indicating a significant difference in use but not selection. Lichen contributed most to species effect, but *Salix* spp., snow depth and snow hardness also were relatively important (Table 5). Lichen cover was greater for caribou feeding zones, and willow cover was greater for muskox feeding zones (Table 4), consistent with the trend for the crater data (Table 1). Snow in muskox feeding zones, on average, was deeper than in caribou feeding zones (Table 4), which is consistent with the findings of crater depth analysis (Fig.3). Snow hardness, however, was greater in caribou feeding zones (Table 4). As in 1990, snow depth and snow hardness made the greatest contributions to zone type (Table 5).

In 1991, muskoxen selected lowland-riparian habitat exclusively, while caribou occurred in upland habitat 41% of the time ($n=9$). The ANOVA indicated a significant difference in habitats selected ($F=13.19$, $d.f.=1,40$, $p < 0.0008$).

Spatial Separation of Muskoxen and Caribou

Throughout both winters, muskoxen remained in the relatively flat terrain north and west of the Ivishak and Sagavanirktok rivers (Fig. 1). There were no obvious barriers to prevent muskoxen from crossing these rivers; snow was shallow on the river ice and probably did not restrict travel. Caribou, on the other hand, were predominately

Table 5. Results (F -values) of MANOVA applied to zone data collected in northern Alaska, 1991. Variables were selected by stepwise discriminant analysis.

Variable	Species ^a	Zone Type ^b
Depth	6.11*	50.28***
Hardness	17.53***	11.58***
Lichen	69.15***	5.35*
<i>Equisetum</i> spp.	0.04	2.57
Deciduous shrub	0.04	2.66
Graminoid	1.40	0.10
<i>Salix</i> spp.	10.75**	0.62
Unvegetated	0.03	1.40

* $p < 0.015$, ** $p < 0.001$, *** $p < 0.0001$.

^aMuskoxen or caribou.

^bFeeding, adjacent nonuse, and far nonuse.

south of the Ivishak river, which has more topographic relief than the north side, with elevations reaching 350 m.

Snow Depth in Feeding Zones vs. Crater Depth

The greatest differential in depth (mean snow depth of feeding zones - mean crater depth) was observed for caribou feeding areas sampled in 1990; depths of caribou craters were significantly less than snow depths in feeding zones in both years (Table 6). Muskoxen followed the same pattern of selection of cratering sites. Although the depth differential was smaller than that of caribou in 1990, it was significant (Table 6). Mean crater depths were less than feeding zone depths in 1991 as well (Table 6), although the difference was marginally non-significant ($p=0.10$).

Fecal Analysis

Microhistological analysis of plant fragments in muskox and caribou fecal samples show many of the same dietary trends in forage selection as data for craters and feeding zones. In 1990, lichens composed the largest proportion of plant tissue identified in caribou feces (Table 7). In 1991, the proportion of lichens in caribou feces declined considerably relative to 1990, while prevalence of evergreen shrubs doubled (Table 7). Despite high occurrence and cover values of graminoids in caribou craters and feeding zones, graminoids composed a small percentage of plant fragments in caribou feces in both

Table 6. Muskox and caribou depth differential^a (cm) occurring in feeding zones in northern Alaska, 1990-91, and results from Mann-Whitney U-test.

Year	Muskox	Caribou
1990	4.9**	7.8**
1991	3.8	3.4*

^aMean depth of feeding zones - mean depth of feeding craters.

* $p < 0.05$, ** $p < 0.009$

Table 7. Mean percent of discernible plant fragments in muskox and caribou fecal samples collected in northern Alaska in March and April, 1990-91.

Values are summarized from Appendix III.

Variable	Muskox ^a			Caribou			
	Lowland-Riparian 1990 n=2	Lowland-Riparian 1991 n=2	Upland 1990 n=2	Lowland-Riparian 1990 n=2	Lowland-Riparian 1991 n=2	Upland 1990 n=2	Upland 1991 n=2
Lichens	0.8 (1)	0.9 (2)	1.9 (3)	19.9 (34)	7.4 (12)	20.2 (34)	4.7 (8)
Mosses	20.4 (11)	31.8 (18)	40.0 (23)	45.4 (25)	28.6 (15)	41.6 (22)	42.6 (24)
Graminoids	41.6 (44)	31.3 (35)	25.8 (31)	6.7 (8)	3.8 (4)	7.1 (8)	10.1 (12)
Forbs	13.6 (12)	9.0 (9)	10.4 (11)	11.9 (11)	22.8 (20)	14.8 (14)	13.3 (13)
Deciduous shrubs ¹	8.5 (10)	12.8 (17)	7.2 (10)	1.8 (2)	4.8 (6)	2.3 (3)	2.5 (3)
Evergreen shrubs	15.3 (21)	14.2 (20)	14.7 (22)	14.5 (20)	32.1 (43)	14.1 (20)	26.6 (39)

() = Corrected estimate %.

^aMuskoxen occurred exclusively in lowland-riparian habitat in 1991.

¹Primarily *Salix* spp.

years (Table 7). Graminoids, however, made up the largest proportion of plant fragments in muskox feces in both 1990 and 1991 (Table 7). Forb fragments were nearly equal in prevalence in both muskox and caribou feces throughout the study period, and *Equisetum* composed $\geq 5\%$ of plant fragments identified in all but two samples (Appendix III).

Classification of Plant Communities in Feeding Zones

In 1990, muskoxen most often selected moist tussock sedge types (Table 8) which, together with moist nontussock sedge types, composed 75% of all muskox feeding zones sampled. Caribou followed a similar pattern, although moist low shrub-tussock sedge types were selected exclusively by caribou (Table 8).

In 1991, moist sedge types were once again most often selected by muskoxen; however, no tussock types occurred in the feeding zones sampled (Table 8). Caribou feeding zones, in contrast to 1990, were most commonly located in *Dryas* tundra, although moist sedge types were still used (Table 8). In both years, caribou did not select dry barren-low willow types (consisting primarily of willows), whereas muskoxen occasionally fed there (Table 8).

Table 8. Occurrence of plant community types at muskox and caribou feeding zones in northern Alaska, 1990 and 1991. Classification is based on Walker (1983), Level C.

Plant Community	Muskox		Caribou	
	1990 (n=20)	1991 (n=20)	1990 (n=16)	1991 (n=22)
Moist tussock sedge-low shrub	0.20	0	0.375	0.04
Moist tussock sedge-dwarf shrub	0.30	0	0.125	0.14
Moist low shrub-tussock sedge	0	0	0.250	0
Moist sedge-dwarf shrub	0.20	0.55	0.125	0.23
Moist sedge-dwarf shrub-wet graminoid	0.05	0.05	0	0
Dry barren-low willow forb	0.15	0.20	0	0
Dry barren-low willow complex	0	0.05	0	0
River gravels	0	0.05	0	0
<i>Dryas</i> tundra	0.10	0.10	0.125	0.59

DISCUSSION

Snow Characteristics of Feeding Zones

My first hypothesis, that muskoxen and caribou select feeding zones differentially in relation to snow depth and hardness, was not falsified. Based on analyses of zone data, snow depth and snow hardness largely determined where muskoxen and caribou foraged. These two ungulates consistently fed in areas with softer, shallower snow cover than in surrounding areas. Additionally, depth of feeding craters of both species was less than snow depth in the overall feeding zone, which was my first prediction for hypothesis 1. The second prediction, that muskoxen will feed in areas with shallower, softer snow than do caribou, was only partially correct. In 1990, there were no significant differences in snow depth of muskox and caribou feeding zones. Similarly, no significant difference was noted in depths of feeding craters of the two ungulates, in contrast to 1991 when both depths of muskox craters and snow depths in muskox feeding zones were greater than for caribou. This is inconsistent with the second prediction and with the findings of Lent and Knutson (1971). In both winters, however, snow hardness in caribou feeding zones was greater than in muskox feeding zones, as was predicted. Although differences in snow hardness were small, the MANOVAs indicate they were significant (Tables 3, 5), and I hypothesize that the similarities in snow characteristics in feeding zones of the two ungulates account for the small differences they exhibited in selection. Snow depth dominated the

analyses (Tables 3,5), and apparently prevented the model from detecting any differences between muskoxen and caribou in selection of feeding zones.

Selection of shallower, softer snow by muskoxen and caribou may be driven by an effort to reduce energetic costs of cratering (Fancy and White, 1985) or to increase of forage intake (Miller et al., 1977; Smith, 1987; Adamczewski et al., 1988). Smith (1987) demonstrated that a three-fold decrease in integrated snow hardness caused a four-fold increase in forage availability to caribou and concluded that selection of feeding sites is primarily influenced by forage availability. Fancy (1986), however, demonstrated that a 10% increase in daily activity costs resulted in only a 5% decrease in daily energy balance and suggested that efficiency of locomotion allows caribou to move from areas with snow conditions unfavorable for cratering to areas more suitable for cratering. Both reduction of costs and greater forage availability, however, are likely to be important in the selection of feeding areas.

Snow conditions during this study did not approach the restrictive limits noted by previous investigators for either muskoxen (Lent and Knutson, 1971; Rapota, 1984; Smith, 1984; Thomas and Edmonds, 1984; Gray, 1987; Wilson, 1992) or caribou (Henshaw, 1968; Lent and Knutson, 1971; LaPerriere and Lent, 1977; Thing, 1977; Skogland, 1978; Duquette, 1988). Furthermore, snow depths measured previously in nearby areas by Roby (1978) and Hall et al. (1991) indicate the winters of 1990 and 1991 were relatively “normal.” Therefore, snow

conditions in the study area are not often likely to exceed muskox or caribou tolerances.

Caribou, compared to muskoxen, are less constrained by snow in initial selection of wintering grounds (Smith, 1989). Additionally, caribou are able to travel through deeper snow (Klein, 1986) and, therefore, may be able to move with greater ease from one area to another. During this study, caribou moved in and out of the study area on nearly a daily basis. Conversely, muskoxen arrived in the study area in late autumn and did not leave until late spring (P. Reynolds, pers. comm.). The restricted movements of muskoxen may result from their limited ability to travel through deeper snows surrounding the study area, similar to the “snow fence” hypothesis developed by Pruitt (1959) for caribou. I hypothesize that the combination of the sedentary nature of muskoxen (Klein, 1986), snow conditions of mid to late winter and constraints on the ability of muskoxen to travel through it, make initial selection of overwintering areas crucial to muskox survival in severe winters.

Vegetative Characteristics of Caribou Feeding Zones

Lichens appear to be relatively important to CAH caribou. Occurrence of lichens in craters of caribou exceeded 80% in both field seasons (Table 1), and in 1990, lichens composed 30% of the plant fragments in caribou fecal samples (Table 7). This is about the same proportion as reported by Boertje et al. (1985) for Western Arctic Herd caribou but is much less than reported for Alaskan caribou in areas of

high lichen abundance (Boertje, 1990; Fleischman, 1990). Crater and fecal analysis indicate strong selection for lichens by caribou in 1990. The lichen F -value relative to species effect in the 1990 MANOVA, however, is relatively small. This indicates no significant difference in lichen cover in muskox and caribou feeding zones, contrary to hypothesis 2, in which a higher lichen abundance in caribou feeding zones was expected.

In 1991, based on fecal analysis, lichens were largely replaced by evergreen shrubs in the caribou diet (Table 7). This is due, in part, to the large proportion of feeding zones located in *Dryas* tundra in 1991 (Table 8). *Dryas* tundra was characterized by *Dryas* spp., *Cassiope tetragona* and *Salix reticulata*. Lichens, primarily *Cetraria* spp., also occurred in this plant community, although the standing crop of lichens tends to be low in *Dryas* tundra (Roby, 1978). Despite this, occurrence of lichens in feeding craters remained high (Table 1). Bergerud (1974) reported caribou to locate lichens by scent, particularly in areas where vegetation was above the snow surface; this may account for the high occurrence of lichens in craters. Nonetheless, the proportion of lichens in the diet was much reduced (Table 7) in 1991. Crater and fecal analyses both indicate intake of *Dryas* spp. and *Cassiope* spp. was greater in 1991 than in 1990, and the proportion of evergreen shrubs in 1991 fecal samples was double that in 1990 fecal samples (Table 7).

Equisetum also was relatively common in the diet of caribou, particularly in 1991 (Appendix III), despite relatively low cover of *Equisetum* in feeding zones. This is in agreement with Roby (1978),

who suggested that *Equisetum variegatum* is utilized by caribou of the CAH as a protein supplement in their diet.

Intake of mosses by caribou was relatively high (Table 7) although when compared to the high percent relative cover occurring in feeding zones (Tables 2, 4), the importance of, and preference for, moss is questionable. Indeed, the contribution of moss to the 1990 MANOVA is low (Table 3), indicating minimal importance to caribou. Mosses were not chosen by stepwise discriminant analysis in 1991, implying even less importance in that year. Mosses are low in digestibility (Boertje, 1981; Person et al., 1980), and intake may be largely incidental to feeding on lichens (Klein, 1986). Parker (1978) reported mean relative densities of mosses in rumen samples of caribou in the Canadian High Arctic to be 20 to 85%. This is substantially higher than fecal estimates in this study (Table 7). Conversely, fecal estimates of moss abundance are higher in this study than those reported by Boertje (1981) for the Denali Caribou Herd. This pattern of increased moss intake with latitude follows the trend reported by Klein (1986).

Salix pulchra made a large contribution relative to both species and habitat effects in the 1990 analysis of zone data, due primarily to higher cover of *Salix pulchra* in upland areas where caribou were located. Based on crater and fecal analysis, however, caribou were not utilizing willows as a primary food source.

Vegetative Characteristics of Muskox Feeding Zones

Graminoids composed the bulk of the muskox diet in both winter field seasons, in support of most comparable studies. Occurrence of graminoids in muskox craters was high in both years (Table 1), and fecal analysis indicates that graminoids composed 31-44% of the winter diet (Table 7). O'Brien (1988) and Wilson (1992) reported graminoids to be the dominant component in the late winter diet of muskoxen overwintering on the coastal plain of the ANWR. On the other hand, Robus (1981) noted sedges and grasses to be used little in late winter in relation to their abundance, although no winter feces were analyzed. Graminoids also are prominent in the diet of muskoxen in Greenland (Thing, et al., 1987; Klein and Bay, 1990; Klein and Bay, 1991; Olesen, 1991) and Canada (Parker, 1978). Graminoid cover in caribou feeding zones and occurrence in caribou craters are equal to or exceed cover and occurrence values for muskoxen, primarily because graminoid cover (and therefore occurrence) is high throughout the study area. This is contrary to hypothesis 3, in which graminoid abundance was expected to be greater in muskox feeding zones than in caribou feeding zones. Cover values are similar within and between species and between zone types (Tables 2, 4), and F -values for graminoid in the 1991 MANOVA (Table 5) are small.

As was hypothesized, *Salix* spp. cover and occurrence were higher for muskoxen than for caribou, and willows were selected for all analyses. According to the fecal results, *Salix* spp. composed 10% of the muskox winter diet in 1990 and 17% in 1991 (Table 7). The greater

intake of willows in 1991 reflects the fact that all muskox feeding zones sampled were near the Ivishak River with its associated riparian willows. Willow tops often were browsed, although most tall (>50 cm) willow stands were inaccessible due to deep snow. Similarly, Wilson (1992) reported little use of riparian shrubs by muskoxen in ANWR due to deep snow. Restrictive snow depths in riparian areas in this study area may account for the lower proportion of willow fragments in muskox feces than that in winter-type fecal pellets collected by O'Brien (1988) in ANWR. O'Brien (1988) collected winter-type pellets in summer, however, and snow conditions occurring at the time feces were deposited is unknown. Robus (1981) also reported that willows were the main component of muskox winter diets in northeast Alaska. The intake of willows by muskoxen in this study, however, was comparable to willow intake by muskoxen in Peary Land, northern Greenland (Klein and Bay, 1990) and the High Arctic of Canada (Parker, 1978).

In 1991, "unvegetated" cover in muskox feeding zones was greater than in 1990 because of increased selection of riparian willow communities (Table 8). Willow communities tend to have little understory and often occur on river gravels. Unvegetated was selected for the 1991 MANOVA (Table 5) and was characteristic of some feeding zones of muskoxen.

Equisetum also is of some importance to muskoxen. The proportion of *Equisetum* fragments in muskox feces (Appendix III) is roughly equal to the percent cover in feeding zones of muskoxen (Tables 2, 4), indicating it was consumed in proportion to its abundance.

In addition, *Equisetum* spp. was selected for both feeding zone analyses and made a relatively large contribution to the species effect in 1990. *Equisetum* was utilized by caribou as well, and some dietary overlap may therefore occur in this forage class.

Evergreen shrubs, primarily *Dryas* spp. and *Vaccinium* spp., composed about 20% of the plant fragments of muskox feces in both years. These are higher than values reported by O'Brien (1988) and Robus (1981). Lent (1978), however, reported that muskoxen used *Vaccinium* spp. in upland sites on Nunivak Island. Similarly, Rapota (1984) reported that muskoxen on the Taimyr Peninsula utilized *Dryas* spp. in late winter when snow restricted access to more favorable forage species. Evergreen shrubs also were utilized by caribou in this study, indicating the possibility of dietary overlap with muskoxen.

Mosses are thought to be unimportant to muskoxen (Klein, 1986) and composed a relatively small proportion of the plant fragments in their feces (Table 7). Similarly, lichens composed a small proportion of plant fragments in muskox feces (Table 7), indicating little dietary overlap with caribou for lichens.

Plant Community Selection

In 1990, most muskox and caribou feeding zones were in moist sedge types (Table 8). A major difference, however, is the location of feeding zones. Muskox feeding zones were most frequently present in lowlands near the Ivishak River (14 of 20). In contrast, most caribou feeding zones were in the surrounding foothills (13 of 16). This is the

general trend for other arctic areas as well. Miller et al. (1977) reported that muskoxen in Canada used lowland areas and caribou used upland ridges. They also noted little spatial overlap except in instances of extreme snow and icing conditions when muskoxen moved to upland ridges. Robus (1981) and Jingfors (1980) reported muskoxen in northeast Alaska to concentrate use in riparian areas. Similarly, Wilson (1992) noted that most winter feeding sites of muskoxen occur within 100 m of a creek or river. Roby (1978) reported *Eriophorum* tussock tundra was the habitat most frequently occupied by caribou of the CAH, although he noted riparian areas in early to mid winter also were used in response to the distribution and availability of *Equisetum variegatum* and lichens.

In 1991, muskoxen were located exclusively in lowland-riparian areas near the Ivishak and Sagavanirktok rivers. Again, moist-sedge types were the major plant communities used, although tussock-dominated types were not used. Tussock communities generally occur in upland sites, and non-use of this plant community type may be a consequence of predominant use of lowland areas. Caribou were located most often in lowland habitats (13 of 22), and an increase in the selection of *Dryas* tundra types also was observed. *Dryas* tundra, although often located in lowland areas, generally occurs on elevated river terraces and is characterized by relatively shallow snow. The reason for caribou shifting from upland sites in 1990 to lowland areas in 1991 is not clear, but it may have been a response to increased snow depths. Snow in muskox feeding zones was deeper in 1991 than in 1990.

Snow in caribou feeding zones, on the other hand, was similar in the 2 years. The shift from upland tussock tundra in 1990 to *Dryas* tundra in 1991 by caribou may account for the similar between-year snow depths in feeding zones of caribou.

Some muskox feeding zones, in contrast to those of caribou, were located in dry barren-low willow types (Table 8). These communities include a high proportion of riparian willows, which are favored by muskoxen in ANWR (Robus, 1981; O'Brien, 1988). Most riparian willows in this area, however, are covered by deep snow (>50 cm). Because muskoxen are constrained in forage selection by snow depths exceeding 50 cm (Lent and Knutson, 1971), most riparian areas were inaccessible, thus accounting for the small proportion of muskox feeding zones in riparian willows.

Spatial separation of muskoxen and caribou was observed. Muskoxen occurred exclusively on the northern side of the Ivishak River in both years. Caribou infrequently used the northern side, but were located predominantly south of the Ivishak. This may have been a response, particularly by muskoxen, to the topography of the area. The north side is predominately flat, with a few small hills reaching 250 m, whereas the south side is quite hilly with elevations reaching 350 m. Muskoxen, which generally avoided upland habitat, may have remained on the northern side to avoid the relatively hilly terrain found across the Ivishak. Although this difference may diminish as muskoxen numbers in the area increase, it effectively separated muskoxen and caribou at the time of this study.

CONCLUSIONS

Muskoxen and caribou select winter feeding zones differentially in relation to snow depth and snow hardness. Snow in feeding zones of both ungulates was consistently shallower and softer than in surrounding nonuse areas. Additionally, crater depths were significantly less than snow depths in the surrounding feeding zones. Selection of feeding areas, therefore, occurs at two levels: large scale and microsite. This selection pattern also was reported by LaPerriere and Lent (1974) for caribou in northeastern Alaska. Contrary to the results of other comparative studies, however, snow in this study could not be invoked as a significant factor in niche separation of muskoxen and caribou. Zone data analyses indicated no significant differences in selection by muskoxen and caribou because of similarities in snow characteristics in feeding zones. Snow depth was the dominant variable in both MANOVAs and was similar between the two ungulates. Therefore, even though differences in use of vegetation occurred, differences in selection were not detectable.

Snow in the study area is unlikely to exceed muskox or caribou tolerances. Only during severe winters is it likely that muskoxen would be excluded from feeding sites preferred by caribou. On a larger scale, however, muskoxen might be constrained in their movements to other locations by deep snows in the area surrounding the study area. If density of muskoxen increases this could create problems of spatial overlap with caribou feeding areas.

Despite the similar snow characteristics encountered by the two species, I conclude there is differential selection of feeding areas by muskoxen and caribou. Broadly, muskoxen occurred in lowland-riparian areas (although not exclusively in 1990), and caribou were most often located in upland areas. In addition, muskoxen used the flatter areas north of the Ivishak River, whereas caribou tended to use areas of greater topographic relief south of the Ivishak. Exceptions to both these generalizations occurred, but for the most part spatial separation between feeding zones of muskoxen and caribou was readily apparent.

Despite the high use of moist sedge plant communities, dietary overlap is low. Fecal analyses indicate graminoids composed an average of only 8% of the caribou diet, whereas graminoids averaged 37% of the muskox diet. Dietary separation also occurs with respect to the lichen forage class. Caribou made relatively heavy use of lichens, while the intake of lichens by muskox was very low. Deciduous shrubs, primarily *Salix* spp., are used by muskoxen 3 to 5 times as much as by caribou. *Dryas* spp., *Vaccinium* spp. and *Equisetum* spp., however, were utilized by both ungulates to about the same extent, indicating dietary overlap exists for these forage species.

Dietary overlap does not confirm the existence of competition (Gunn, 1990). Even though populations of both muskoxen and caribou are increasing, there is relatively low dietary and spatial overlap in winter, indicating little or no competition during a season of low forage availability.

Certainly, if numbers and densities of muskoxen and caribou continue to grow or if winter conditions become more severe, the degree of dietary overlap may increase. If caribou numbers exceed the range carrying capacity and lichens are depleted, caribou may become increasingly dependent on graminoids, as happened in Greenland (Olesen, 1991). If this occurs, dietary overlap with muskoxen would increase and competition may result. In addition, occasional severe winter snow conditions could force muskoxen out of lowland-riparian areas and into areas preferred by caribou, again increasing the probability of dietary overlap and competition. Under present conditions, however, interspecific conflicts between muskoxen and caribou is not likely to occur.

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APPENDIX I. List of plants encountered in northern Alaska in June and July, 1990-91.

FAMILY	SPECIES
Betulaceae	<i>Betula nana</i>
Caryophyllaceae	<i>Minuartia arctica</i>
	<i>Silene acualis</i>
	<i>Stellaria longipes</i>
	unidentified <i>S. spp.</i>
Compositae	<i>Artemisia arctica</i>
	<i>A. tilesii</i>
	unidentified <i>A. spp.</i>
	<i>Aster sibiricus</i>
	<i>Petasites frigidus</i>
	<i>Saussurea angustifolia</i>
Cruciferae	<i>Parrya nudicaulis</i>
Cyperaceae	<i>Carex aquatilis</i>
	<i>C. atrofusca</i>
	<i>C. Bigelowii</i>
	<i>C. capillaris</i>
	<i>C. capitata</i>
	<i>C. chordorrhiza</i>
	<i>C. holostoma</i>
	<i>C. membranacea</i>
	<i>C. podocarpa</i>
	<i>C. rariflora</i>
	<i>C. rotundata</i>
	<i>C. saxatilis</i>
	<i>C. scirpoidea</i>
	<i>C. vaginata</i>
	unidentified <i>C. spp.</i>
	<i>Eriophorum angustifolium</i>
	<i>E. russeolum</i>
	<i>E. vaginatum</i>
Empetraceae	<i>Trichophorum caespitosum</i>
Equisetaceae	<i>Empetrum nigrum</i>
	<i>Equisetum arvense</i>
	<i>E. variegatum</i>

APPENDIX I. (Continued)

FAMILY	SPECIES
Ericaceae	<i>Andromeda polifolia</i> <i>Arctostaphylos alpina</i> <i>A. rubra</i> <i>Cassiope tetragona</i> <i>Ledum palustre</i> <i>Rhododendron lapponicum</i> <i>Vaccinium uliginosum</i> <i>V. vitis-idaea</i>
Gramineae	<i>Arctogrostis latifolia</i> <i>Arctophila fulva</i> <i>Poa arctica</i> <i>unidentified grasses</i>
Leguminosae	<i>Astragalus alpinus</i> <i>A. umbellatus</i> <i>unidentified A. spp.</i> <i>Hedysarum alpinum</i> <i>H. Mackenzii</i> <i>Lupinus arcticus</i> <i>Oxytropis campestris</i> <i>O. Maydelliana</i> <i>O. nigrescens</i>
Liliaceae	<i>Tofieldia pusilla</i>
Lycopodiaceae	<i>Lycopodium spp.</i>
Onagraceae	<i>Epilobium latifolium</i>
Papaveraceae	<i>Papaver lapponicum</i>
Polemoniaceae	<i>Polemonium acutiflorum</i>
Polygonaceae	<i>Polygonum bistorta</i> <i>P. viviparum</i>
Primulaceae	<i>Androsace chamaejasme</i>
Pyrolaceae	<i>Pyrola grandiflora</i>
Ranunculaceae	<i>Ranunculus lapponicus</i>
Rosaceae	<i>Dryas Drummondi</i> <i>D. integrifolia</i> <i>D. octopetala</i> <i>Potentilla biflora</i> <i>Rubus chamaemorus</i>

APPENDIX I. (Continued)

FAMILY	SPECIES
Salicaceae	<i>Salix alaxensis</i>
	<i>S. arctica</i>
	<i>S. brachycarpa</i>
	<i>S. chamissonis</i>
	<i>S. glauca</i>
	<i>S. hastata</i>
	<i>S. lanata</i>
	<i>S. planifolia pulchra</i>
	<i>S. phlebophylla</i>
	<i>S. polaris</i>
	<i>S. reticulata</i>
	<i>unidentified S. spp.</i>
	Saxifragaceae
<i>Saxifraga hieracifolia</i>	
<i>S. punctata</i>	
Scrophulariaceae	<i>unidentified S. spp.</i>
	<i>Pedicularis capitata</i>
	<i>P. Kanei</i>
	<i>P. sudetica</i>
	<i>P. verticillata</i>
Lichens	<i>unidentified P. spp.</i>
	<i>Cetraria cucullata</i>
	<i>C. islandica</i>
	<i>C. nivalis</i>
	<i>Cladina spp.</i>
	<i>Cladonia spp.</i>
	<i>Dactylina spp.</i>
	<i>Masonhalea spp.</i>
	<i>Nephroma spp.</i>
	<i>Peltigera spp.</i>
	<i>Stereocaulon spp.</i>
<i>Thamnolia spp.</i>	

Appendix II. Possible sources of error in fecal analysis and vegetative cover estimates, 1990-91.

A possible source of error exists in the results of fecal analysis reported for muskoxen. Due to an absence of specific forage digestibility values for muskoxen, digestibilities reported for caribou (Boertje, 1981) were used for both ungulates. This may have resulted in under-estimation of the amount of fibrous plant species (i.e., graminoids and shrubs) in the muskox diet because muskoxen are believed to be better able to digest fibrous plant parts than caribou (Staal and Thing, 1991). Lichens may be over-estimated in the muskox diet because muskoxen probably lack the rumen microbial population essential for efficient lichen digestion. I believe, however, that it was better to use the same correction factor for both ungulates than none at all. Serious over-estimation of the dietary contribution of indigestible plants, particularly mosses, results when fecal analysis are not adjusted for differential digestion.

A second possible source of error relates to the assumption that plant cover in summer is an accurate representation of that in winter. Although forb cover is definitely higher in summer than in winter, forbs did not enter most analyses and, when used, were relatively unimportant. Cover of the other forage types, particularly deciduous shrubs and graminoids, may be higher in summer as well. However, in

Appendix II. (Continued)

my judgement, it was a reasonable assumption that increases in cover were uniform between feeding zones of muskoxen and caribou as well as between feeding and nonuse zones. Therefore, comparisons between species and zone types are likely valid, even though actual winter cover values may be lower than reported.

APPENDIX III. Percent discernible plant fragments (uncorrected) in muskox and caribou fecal samples collected March and April, 1990 and 1991 in riparian (R) and upland (U) areas in northern Alaska.

YEAR = 1990

	Caribou R1	Caribou R2	Caribou U1	Caribou U2	Muskox R1	Muskox R2	Muskox U1	Muskox U2
Lichens								
<i>Stereocaulon</i> ,								
<i>Cladina, Cladonia</i>	9.1	15.0	19.1	9.2	0.2	0.2	0.6	0
<i>Peltigera</i>	8.3	2.9	4.8	5.7	0	0.7	0.6	1.0
<i>Nephroma</i>	1.9	0.6	0.4	0.5	0	0.1	1.2	0.3
<i>Cetraria, Dactylina</i>	0.3	0.4	0.2	0.5	0.3	0	0	0
other lichens	0.1	1.2	0	0	0	0	0	0
Mosses	47.7	43.0	40.8	42.3	18.9	21.9	40.5	39.4
Sedges & Grasses								
<i>Carex aquatilis</i>	0	0	0	0	8.8	5.8	4.1	1.9
<i>Carex Bigelowii</i>	0	0	0	0	12.2	11.8	9.7	6.5
<i>Carex</i> spp.	0	0	0	0	17.9	11.1	6.8	6.3
<i>Eriophorum</i> spp.	0	0	0	0	7.3	6.9	3.7	9.7
other sedges	6.1	6.3	5.8	7.4	0	0.3	0	0
grasses	0.6	0.4	0.3	0.7	0.7	0.3	2.0	0.9
Forbs	5.6	6.4	3.6	5.9	3.8	6.2	3.9	3.3
flower	0	0	0	0.4	0	0.5	0	0.5
<i>Equisetum</i> spp.	2.3	9.4	10.5	9.2	5.8	10.8	7.2	5.9
<i>Salix</i> spp.	1.1	1.5	1.5	1.3	5.4	7.7	4.9	6.9
<i>Dryas</i> spp.	8.1	1.4	4.3	6.4	5.2	7.7	5.7	2.4

APPENDIX III. (Continued)

YEAR = 1990

	Caribou R1	Caribou R2	Caribou U1	Caribou U2	Muskox R1	Muskox R2	Muskox U1	Muskox U2
<i>Cassiope</i> spp.	1.5	2.2	3.5	4.1	1.3	0.2	2.2	2.8
<i>Vaccinium</i> spp.	4.7	4.2	3.2	2.8	4.9	1.7	2.6	2.8
<i>Pyrola</i> spp.	0.7	1.0	1.0	0	0	0.3	0.2	0.5
<i>Ledum</i> spp.	0.6	0.4	0.1	0.4	0	0	0	4.1
<i>Andromeda</i> spp.	0	0	0	0	5.0	0	0	0
Other shrubs	1.3	3.7	0.9	3.2	2.3	5.8	4.1	4.8

YEAR = 1991

	Caribou R1	Caribou R2	Caribou U1	Caribou U2	Muskox R1	Muskox R2
Lichens						
<i>Stereocaulon</i> ,						
<i>Cladina</i> , <i>Cladonia</i>	3.4	2.1	3.1	2.1	0	0.3
<i>Peltigera</i>	6.9	2.0	1.5	1.9	0.1	1.1
<i>Nephroma</i>	0.1	0	0.1	0.1	0.2	0
<i>Cetraria</i> , <i>Dactylina</i>	0.1	0.1	0.6	0	0.1	0
other lichens	0	0	0	0	0	0

APPENDIX III. (Continued)

YEAR = 1991

	Caribou R1	Caribou R2	Caribou U1	Caribou U2	Muskox R1	Muskox R2
Mosses	32.0	25.2	41.9	43.2	27.5	36.1
Sedges and Grasses						
<i>Carex aquatilis</i>	0	0	0	0	4.7	3.7
<i>Carex Bigelowii</i>	0	0	0	0	6.0	12.0
<i>Carex</i> spp.	0	0	0	0	14.5	12.4
<i>Eriophorum</i> spp.	0	0	0	0	3.8	2.7
other sedges	3.6	3.6	9.9	9.2	0	0
grasses	0.1	0.3	0.2	0.9	1.7	1.1
Forbs	5.1	9.4	4.9	5.3	3.1	4.7
flower	0.4	0.3	0.1	0	0	0.2
<i>Equisetum</i> spp.	13.1	17.3	8.9	7.4	5.6	4.4
<i>Salix</i> spp.	3.4	2.2	2.3	1.9	15.0	7.1
<i>Dryas</i> spp.	12.8	17.5	16.4	16.2	9.7	7.0
<i>Cassiope</i> spp.	5.9	6.4	5.0	3.9	1.3	1.1
<i>Vaccinium</i> spp.	8.7	7.3	3.8	5.6	2.6	4.0
<i>Pyrola</i> spp.	0.2	0.1	0	0.1	0	0

APPENDIX III. (Continued)

YEAR = 1991

	Caribou R1	Caribou R2	Caribou U1	Caribou U2	Muskox R1	Muskox R2
<i>Ledum</i> spp.	0	0.4	0	0	0	0.1
<i>Andromeda</i> spp.	0	0	0	0	0	0
Other shrubs	3.1	5.8	1.1	1.9	4.0	2.0

**COMPARATIVE PATTERNS OF WINTER HABITAT
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**A
THESIS**

MASTER OF SCIENCE

**By
Mark Edward Biddlecomb, B.S.**

**Fairbanks, Alaska
September 1992**