HABITAT RELATIONSHIPS AND ACTIVITY PATTERNS OF A REINTRODUCED MUSKOX POPULATION

A

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ABSTRACT

A reintroduced muskox herd in arctic Alaska was studied over a 2-year period to assess seasonal changes in activity patterns and feeding behavior. This large herd showed high calving rates and early breeding in females, characteristic of a rapidly expanding population. Age- and sex-specific differences in activity budgets reflect seasonal energy demands of the different cohorts. Comparison with high arctic muskoxen shows that characteristics of suckling behavior provide a more sensitive indicator of differences in range quality than does variation in summer activity patterns. In summer, muskoxen appear to select vegetation types on the basis of abundance and phenological stage of preferred forage species; snow characteristics strongly influence habitat selection in winter. The herd remained within a limited home range with overlapping seasonal ranges and a distinct calving area. The restricted movements and conservative activity budgets permit minimization of energy expenditure and forage requirements, allowing for a year-long existence in areas of low primary productivity.

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INTRODUCTION

Muskoxen (*Ovibos moschatus*) have recently been reintroduced to several areas on the mainland of Alaska in attempts to reestablish them within their historical range. The source of these introductions was Nunivak Island, where muskoxen, originally derived from northeast Greenland, were released in 1935 and 1936. Live-capture and removal of animals from Nunivak Island were made to reduce population pressure and overgrazing of winter range on the island (Lent 1978). With the possible exception of transplants to Seward Peninsula and Nelson Island, all of these newly established population groups are within areas of the Alaskan Arctic known or presumed to be the original range of muskoxen prior to their extirpation before the turn of the last century (D. R. Klein, pers. comm.).

The traditional belief that muskoxen are characterized by low productivity has been questioned by Lent (1978). Increasing evidence suggests that females often produce calves in successive years. During favorable environmental conditions, cows may give birth to calves at 2 years of age (Alendal 1971a; pers. obs.). However, severe winters with deep snow and extensive icing formation have led to drastic fluctuations in high arctic muskox populations, including periods with complete absence of calf crops (Vibe 1958, 1967; Tener 1965; Gray 1973, 1977; Parker *et al.* 1975; Miller *et al.* 1977).

The muskox is the only ruminant species whose natural distribution is limited to arctic tundra regions. Tener (1965) described several adaptations of muskoxen to their arctic environment. Unlike caribou

(*Rangifer tarandus*), muskoxen are relatively sedentary with limited seasonal movements. Little is known about daily rates of group movement or the use of preferred areas during different phases of their annual life-cycle. In winter, muskoxen show a preference for snow-free areas or sites with relatively shallow snow depth (Lent and Knutson 1971). In summer, a general preference for moist habitats is apparent with willows (*Salix* spp.), sedges (*Carex* spp. and *Eriophorum* spp.) and grasses constituting important food items (Tener 1965; Hubert 1974; Wilkinson *et al.* 1976; Parker 1978). The pattern of forage selection for plants in early growth stages with high nutrient quality, which has been demonstrated for caribou and other arctic and alpine ungulates (Klein 1970a,b), has also been noted in muskoxen (Tener 1965; Bos 1967; Alendal 1971a). However, the non-migratory foraging characteristics of muskoxen may partially restrict opportunities for forage selection.

The muskox exhibits a characteristic activity pattern with regular alternations of feeding and resting periods. The duration of such periods in other ruminants has been related to the quality and availability of forage (Arnold 1964, 1970; Campbell *et al.* 1969; Cammell and Osbourn 1972) and the periodicity has been used for comparing summer ranges of muskoxen (Parker and Ross 1976; Wilkinson *et al.* 1976). Activity budgets, measuring the proportion of time spent in a number of distinct activities (i.e. lying, feeding, walking, standing, etc.), recently have been used in *Rangifer* research to evaluate animal condition and range quality (Segal 1962; Gaare *et al.* 1975; Roby 1978, in press; Reimers in press; White *et al.* in press) and to construct energetics models (White *et al.* 1975). The activity budgets of free-ranging muskoxen have received little attention. Smith (1976) described the influence of rutting behavior on muskox activity and Miller and Gunn (1979) recorded group activities in response to helicopter harassment.

This study was initiated to provide information on the patterns of establishment, feeding behavior and current welfare of a reintroduced muskox population in arctic Alaska. The original objectives were:

1. to obtain observations on the feeding behavior of a reintroduced muskox population as a basis for estimating the energetics of forage selection seasonally and as influenced by population characteristics, intraspecific social interactions and physical welfare;

2. to assess the relationship of the study herd to the qualitative aspects of forage present and to other ecological conditions of the habitat. (This secondary objective was carried out in conjunction with a separate study on muskox habitat use by M. A. Robus [in prep.]);

3. to compare activity patterns and feeding behavior of the reintroduced group with data collected from a muskox population in the Canadian High Arctic.

I made the comparison with a high arctic population to determine the influence of range condition on muskox activity patterns, feeding behavior and productivity. On the assumption that range condition is an important determinant of muskox activity, I expected to find significant differences between the two populations as a result of differences in range productivity and diversity. The comparison will be made in a later section (Section VI) following the description of the reintroduced Alaskan muskox population that was the focus of this study.

STUDY AREA

The study area is located along the Sadlerochit River drainage (69°40'-70°00'N, 144°25'W) which is within the William O. Douglas Arctic National Wildlife Range in northeastern Alaska (Fig. 1). A major portion of the study area lies within the coastal plain adjacent to the Beaufort Sea. The plain is flat to gently undulating, rising to a maximum elevation of 150 m. It is characterized by dry to moist tundra and patterned ground underlain by permafrost. Except for the river gravels of more recent origin, the entire coastal plain is made up of Pleistocene gravels, silts and clays (Hartman 1973).

About 40 km from the coast, foothills of the Sadlerochit Mountains begin to dominate the study area with elevations of up to 1500 m. Major unconsolidated deposits of glacial origin predominate in the foothills and overlie Cretaceous sedimentary rocks, deformed into long folds (Hartman 1973). The foothills in the southern portion of the study area are characterized by exposed bedrock with extensive talus and scree slopes. The Sadlerochit Springs originate from the base of the easternmost extention of the Sadlerochit Mountains to form a stream that is open year-round. The stream empties into an area of winter "aufeis" (overflow ice) formation about 6 km north of the springs.

The Sadlerochit River consists of a multitude of braided channels with gravel to cobble substrates. After it leaves the foothills it drains several smaller creeks on the coastal plain before emptying into the Beaufort Sea. Extensive gravel bars with a diversity of forbs, willows and other shrub species are typical of the riparian habitat.

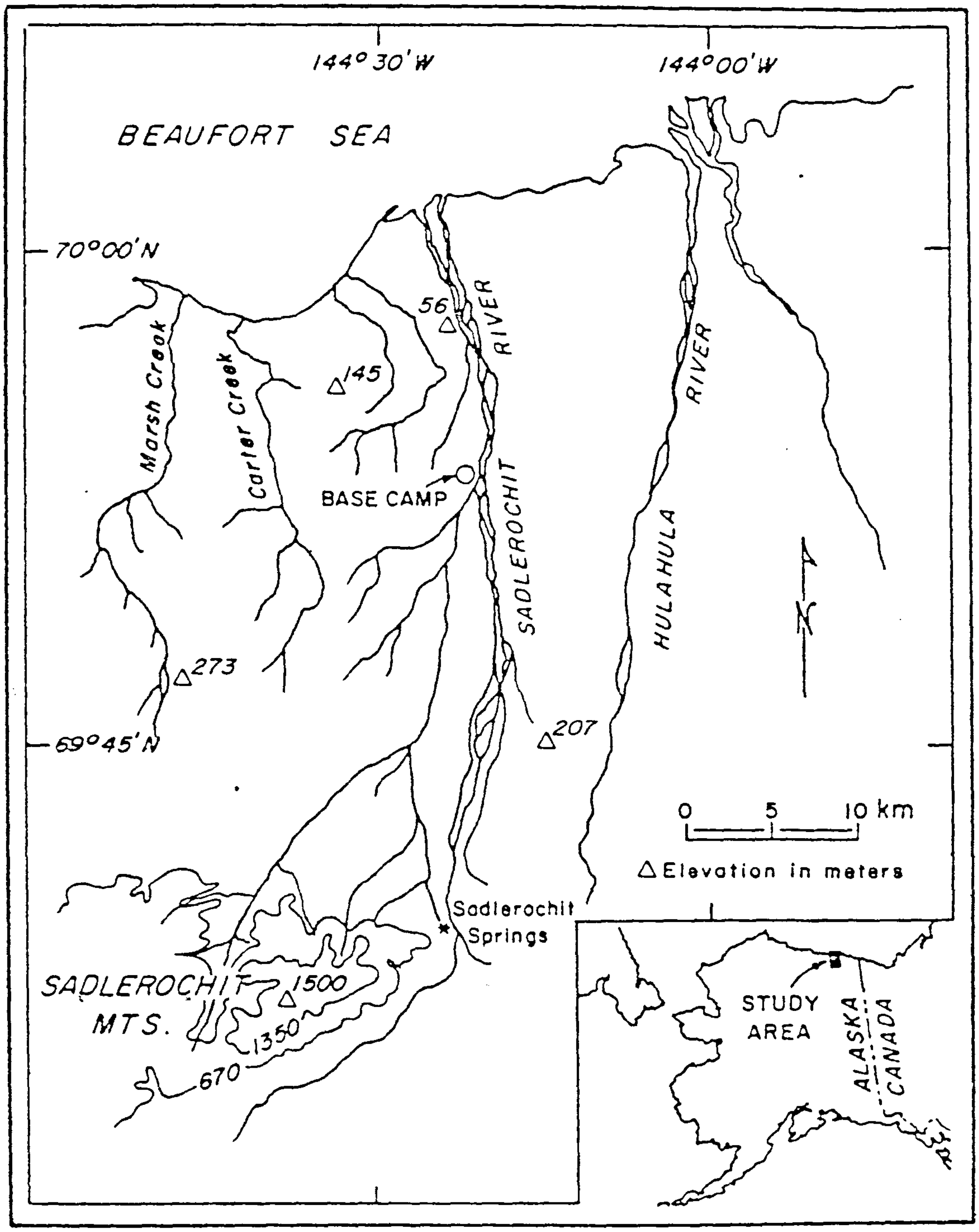

Figure 1. Map of the Sadlerochit River study area with inset showing its relative location.

Willow shrubs are particularly evident in the southern part of the study area where *Salix alaxensis* grows to over 2 m in height. The adjacent coastal plain is dominated by *Eriophorum*-tussock tundra interspersed with smaller areas of hydric sedge meadows and polygonized (patterned) tundra. A description of vegetation types is given in Table 1. For a detailed range description, the reader is referred to Robus (in prep.).

The climate of the coastal plain is characterized by cold winters and cool summers with low annual precipitation and strong surface winds. In winter, when the Beaufort Sea and Arctic Ocean are ice-covered, temperature patterns indicate some modifying effect along the coast due to the marine influence (Searby and Hunter 1971) and the mixing of air masses by wind action. However, persistent surface winds are capable of creating extremely low windchill factors in mid-winter. The coastal plain remains covered with dry, wind-packed snow for almost 9 months of the year (Benson 1969).

Table 1. Description of vegetation types, Sadlerochit River. Based on Robus (In prep.).

Vegetation Type	Site Description	Dominant Plant Species
Riparian Gravel Bar	Perturbed river gravel with clumps of pioneering plant species; often less than 50% vegetated.	*Astragalus alpinus*, *Epilobium latifolium*, *Artemisia arctica*, *Oxytropis Maydelliana*.
Riparian Willow Thicket	River gravel with more continuous vegetation cover than the gravel bar type. The site is less affected by changing water levels and contains several species associated with secondary seral stages.	*Salix alaxensis*, *S. glauca*, *O. borealis*, *Hedysarum Mackenzii*, *Lupinus arcticus*.
Riparian *Dryas* Terrace	Dry, flat vegetated ground with an underlying layer of gravel. Found along the banks of river channels.	*Dryas integrifolia*, *Carex* spp., *S. reticulata*, *Equisetum variegatum*, *Arctostaphylos rubra*.
Wet Sedge Meadow	Poorly drained ground especially in association with pond margins. Standing water is common to this type.	*C. aquatilis*, *Dupontia Fischeri*, *Eriophorum angustifolium*, *Potentilla palustris*.
Heath-Polygon Tundra	Elevated areas of polygon formation on organic and peaty soils near the river. The type has an abundance of Ericaceous plants.	*Betula nana*, *Vaccinium vitis-idaea*, *C. Bigelowii*, *Rubus chamaemorus*, *S. pulchra*, moss spp.
Tussock Meadow	Well-drained ground on the undulating coastal plain adjacent to the river. This is the most extensive vegetation type in the area.	*Eriophorum vaginatum*, *S. pulchra*, *C. Bigelowii*, *Betula nana*, moss spp.
Dry Ridge	Dry, well-drained ground restricted to ridge tops or talus screes. Most common in the southern foothills of the study area.	*Dryas integrifolia*, *S. phlebophylla*, *Luzula tundricola*.
Creek Willow Thicket	Sheltered areas along creek tributaries with dense willow growth on a soil substrate.	*S. lanata*, *S. pulchra*.

METHODS

I. OBSERVATION TECHNIQUES

A base camp was set up along the Sadlerochit River, ca. 15 km from the coast, and smaller spike camps were used as I followed the muskox herd on foot or skis for periods of up to 10 days at a time. Observation distances varied depending on the terrain but were generally kept between 800-1000 m. I found it considerably easier to watch the entire herd from an elevated vantage point over a period of time than trying to approach the animals and risk disturbing their normal daily activities. I made observations with the aid of 8x binoculars and 15x-60x zoom spotting scopes.

I classified muskoxen according to age/sex categories on the basis of horn development, relative size and prominence of the forehead patch (Allen 1913; Smith 1976). When recording activities of individual muskoxen, I used the following five age/sex classes: calves, yearlings, subadults (2 and 3-yr olds), adult bulls and adult females (4 yrs and older). It became apparent that some "subadult" females could be sexually mature and producing calves; therefore, the term is not strictly correct. However, in order to use activity data recorded prior to calving, I maintained the original classification.

I obtained quantitative information on activity patterns by timing the duration of activity and resting periods. Timing was initiated when half of the study herd either started or terminated a cycle of activity/resting. I recorded data on activity budgets using the instantaneous scan sampling method described by Altmann (1974). The herd was scanned at 15-min intervals for a continuous 12 or 24-h period by at least two observers. In early winter (Oct.-Nov.), continuous observations over a long time period were difficult to obtain due to the short day length. Attempts to use a Star-tron light-intensifier night scope were limited by cold temperatures and the short range of the instrument. To avoid observer bias related to the length of observation periods during winter, I made scans for at least one complete cycle of activity/resting. At each 15-min interval scan, I classified the activity of individual muskoxen as one of five possible activities:

1. Lying - resting, includes rumination.
2. Feeding - includes suckling by calves and feeding-related activities, such as olfactory search for forage and cratering in snow.
3. Walking - head elevated.
4. Standing - stationary with head elevated, includes urination.
5. Other - covers a variety of activities not included in the above, such as running, "playing" and sexual/agonistic behavior patterns. The latter were identified based on descriptions by Gray (1973) and Smith (1976).

I noted vegetation type preferences by recording the type used by a majority of the herd during each activity scan. Since "preference" for a vegetation type implies that the type is used in greater proportion than its availability (Petrides 1975), I delineated the total area used by the herd based on observed movements. Availability was then obtained by measuring the area occupied by individual vegetation types from NASA infrared aerial photographs (scale 1:63 500). I combined the Riparian Willow Thicket and *Dryas* Terrace (Table 1) due to the difficulty in separating these types from the photographs.

I recorded insect harassment levels at regular 15-min intervals as "none", "moderate" or "severe" based on subjective discomfort level of the observers. I timed suckling bouts with a stopwatch whenever possible and estimated the age of the calf based on its relative size. Timing was initiated at the first sign of bunting (striking of the udder) by the calf and terminated as the cow broke away from the calf. This represents a minimal estimate of the duration of a suckling bout since milk let-down may occur prior to bunting.

To provide an indicator of actual forage intake in observed muskoxen, I estimated the proportion of time spent ingesting forage ("eating rate", Skogland 1975) during a 5-min period of "feeding", as defined above, for bulls, cows and calves. I only measured eating rates when the muskoxen moved close enough to enable a clear view of the head region. During winter, I assumed a muskox was eating when it held its head low in a feeding crater and was not pushing snow aside with its muzzle.

I measured group movement rates in two ways. During each activity scan, I made a visual estimate of the distance over which the center of the herd had moved during the previous 15 min. To avoid the bias involved in visual estimates of distances, I also mapped movements on copies of aerial photographs. By measuring the straight-line map distance between bedding locations over a 24-h period, I estimated minimal daily group movement rates.

Temperature and wind speed and direction were recorded at half-hour intervals, between activity scans. I measured snow characteristics (depth, density and hardness) at 10-m intervals along transects through feeding sites. Using a spring penetrometer, described by Klein *et al.* (1957) and modified by Eriksson (1976), I recorded an average hardness value for each snow profile by repeated, vertical measurements. The maximum resistance or snow hardness measured in early and late winter was 5.0 kg $\cdot$ cm^{-2} and 20.0 kg $\cdot$ cm^{-2}, respectively. I measured density with a 0.250 dm^3 cylinder developed by Eriksson (1976).

II. DATA ANALYSIS

I divided my observations into the following periods of the musk-ox annual cycle:

1. Late winter (21 March - 4 April)
2. Calving (20 April - 31 May)
3. Post-calving (1 June - 30 June)
4. Mid-summer (1 July - 31 July)
5. Rut (1 August - 31 August)
6. Early winter (27 October - 12 November)

No data were collected during the periods 5 April- 19 April, 1 September - 26 October and 13 November - 20 March.

The instantaneous scan sampling method is useful when the primary objective is to provide estimates of the proportion of time spent in various activities (Dunbar 1975). I recorded observations as the number of muskoxen of different age/sex classes engaged in each activity during a given scan. The resulting frequencies were pooled for each season to arrive at a weighted estimate of the time (expressed as a percentage) devoted to various activities on a seasonal basis. Individual muskoxen, that could not be directly identified as to age/sex class during an activity scan, were lumped into an "unknown" category and later classified on the basis of known herd composition and the predominant herd activity. Subadults, particularly 3-year old females, were most likely to be in this category as a result of their similarity to older muskoxen. Since the "unknown" category usually represented less than 10 percent of the total number of muskoxen observed at any scan, I do not believe the bias seriously affected the accuracy of the estimates.

Statistical analyses of activity scans, beyond simple frequency descriptions, are limited by the degree of serial correlation between subsequent 15-min observations. By increasing the time interval between observations, each scan represented a random sample of activities for the different age/sex classes and could then be used for further analysis. I found the appropriate time interval by testing data sets for individual muskox classes over a continuous 12 or 24-h period using runs tests for randomness (Sokal and Rohlf 1969). The shortest interval, between observations that were statistically independent, was 90 min which is equivalent to scans made six 15-min periods apart. Using only observations taken at 90-min intervals, I described the relationship between activity, age/sex class and season by testing a set of hierarchial models for goodness of fit in a 3-way contingency table (Fienberg 1970; Bishop *et al.* 1975). Most statistical analyses were made with programs in the Statistical Package for the Social Sciences (Nie *et al.* 1975); I used an updated version (Nie and Hull 1977) for non-parametric analyses.

III. COMPARATIVE ASPECTS

In 1978, I had an opportunity to collect data from muskoxen at Polar Bear Pass, Bathurst Island, N.W.T. (75°44'N, 98°30'W). Field work extended from 5 May to 15 August. I obtained additional information on muskox distribution from J. P. Morgan (pers. comm.) between 16-29 August. Several different herds were observed and I used methods similar to those described earlier for the Sadlerochit River area. In addition, I collected fecal samples which were analyzed for plant epidermal fragments at the Composition Analysis Laboratory, Colorado State University. The quantification of fecal analyses can be biased by differential digestibility between plant species, vegetation classes and phenological stages (Pulliam and Nelson 1979). I also collected two important forage species used by muskoxen, *Salix arctica* and *Carex stans*, every 10 days throughout the summer and had them analyzed for nutrient content at the Agricultural Research Station, Palmer, Alaska. A vegetation map of Polar Bear Pass, prepared by Geale (1980), was used to estimate the availability of existing vegetation types.

For data analysis, I used the following seasons: calving (5 May-31 May), post-calving (1 June-30 June), mid-summer (1 July-31 July) and rut (1 August-29 August). Although signs of rutting were evident in late July on Bathurst Island, I maintained the chronological designation of seasons used at Sadlerochit River to facilitate comparison between areas. Quantitative comparisons of muskox activity budgets, movements and feeding behavior between the two populations will be made in Section VI.

RESULTS

I. POPULATION CHARACTERISTICS

A. Establishment and Productivity

In April-May 1969, a month after the release on Barter Island of 51 muskoxen that had been captured on Nunivak Island, less than 40 animals were thought to be alive (Lent 1971). Autopsies of five dead muskoxen found after the release indicated that three had died from a respiratory disorder, one from a broken pelvis and one for reasons unknown (Jennings 1970). Additional mortality was associated with erratic dispersal over the coastal plain. An adult bull and a yearling moved ca. 290 km east before they were shot in the MacKenzie River Delta the following August. Another subadult bull was shot near Arctic Village after moving ca. 250 km south, across the Brooks Range (Lent 1971). Shortly after the release, a group of five muskoxen (1 adult cow, 1 subadult cow and 3 yearlings) was seen near the Sadlerochit Springs, 60 km southwest of Barter Island (Lent 1971). Lent felt this group formed the nucleus of a herd that was regularly seen along the Sadlerochit River drainage during the following years.

Information on composition and productivity of the Sadlerochit group is summarized in Table 2. Following 1974, the herd increased rapidly and doubled in numbers between 1976-79. Early sexual maturity was evident in 1979 when at least two 2-year old cows had calves indicating that the cows were bred as yearlings. Calf production in 1979 was equivalent to 0.89 calves per cow, 2 years and older. Lone bulls or bull groups are not included in Table 2. During summer 1979, I

Table 2. Sex and age composition of the Sadlerochit muskox herd, 1972-80.

Year	Season*	Herd Size	Age and Sex Group: Adult Male	Adult Female	3-yr old Male	3-yr old Female	2-yr old Male	2-yr old Female	Yearling	Calf	% Calves of Total Herd	Reference
1972	Spring	12	(			nd**		)	1	-	-	Roseneau and Stern (1974)
1972	Summer	14	(			nd			)	3	21.4	Roseneau and Stern (1974)
1973	Summer	12	(			nd			)	3	25.0	RRCS, *in* Bente (1977)
1974	Summer	12	(			nd			)	3	25.0	Bente (1977)
1976	Summer	27	(			nd			)	8	29.6	Bente (1977)
1977	Summer	35	6	10	(		4	)	7	8	22.9	Bente (1977)
1978	Spring	33†	3	6	3	4	6	1	7	-	-	Ross (1979)
1978	Summer	46	(			nd			)	13	28.3	Robus (pers. comm.)
1979	Spring	42	5	13	3	2	(7	)	12	-	-	This study
1979	Summer	58	6	12	2	3	2	4	12	17	29.3	This study
1980	Calving	64	6	15	0	4	6	6	17	10‡	-	This study

* Spring counts were made prior to calving.
** nd = no data available; parentheses indicate groups that were not classified as to age or sex.
† Includes 3 unclassified animals.
‡ Calving not yet complete.

observed at least three lone bulls in the Sadlerochit River area. A group of seven adult and subadult bulls was seen 15 km southwest of the Sadlerochit Springs on 3 May 1980 (Ross 1980).

No calf mortality was apparent from the composition counts made during this study. Assuming the muskoxen in earlier counts were correctly classified, three calves were missing between 1976-79 (Table 2). This represents about 10 percent of the total number of calves born during that period. Mortality in other cohorts was low and appears to have been limited to the adult bull segment. I found a skull from a bull muskox near the Sadlerochit Springs. One bull, which may not necessarily have been part of the Sadlerochit group, was shot near Barter Island in February 1978 "in defense of life and property" (Melchior 1979). A bull carcass was also found along the Sadlerochit River in May 1978 (Klein, pers. comm.).

Potential predators in the area include the wolf (*Canis lupus*) and the brown bear (*Ursus arctos*). I saw no signs of wolves during this study although wolves are known to use the Sadlerochit River drainage, particularly in winter (A. Thayer, pers. comm.). Brown bears were seen regularly in early summer. On 9 June 1979, a bear passed part of the herd at a distance of 75 m without approaching the muskoxen. In the summer of 1978, a bear was observed following a lone bull muskox that eventually turned and chased the bear away (Robus, pers. comm.).

B. Seasonal Herd Dynamics

Seasonal changes in the structure of the Sadlerochit herd are shown graphically in Figure 2. During 1979, the majority of calves were born during the first 3 weeks of May. Two calves were added between 12-16 June. During 1980, the first two calves were born on 4 May. Break-up conditions made it necessary to discontinue observations on 13 May when a total of 10 calves was present in the herd; four of these were born on 12 May. There was no indication that cows separated from the rest of the herd during parturition.

In 1979, prior to the rut, fracturing of the herd occurred twice while the muskoxen were feeding in tussock tundra. In both cases, the two groups rejoined in less than a week. Seasonal fluctuations in group size were particularly evident during the rut when fracturing of the herd into smaller groups was accompanied by an egress of adult bulls. In late July, a large bull easily recognized by a broken, right horn tip, joined the herd and assumed dominance over it. During August, after the herd had split into three groups, this bull remained dominant in the group of 33 muskoxen that included an additional three adult bulls. By early winter all three groups had rejoined but the previously dominant bull was no longer present.

C. Discussion - Population Characteristics

The Sadlerochit muskox herd, which became established following the release of muskoxen on Barter Island in 1969, is currently in a state of rapid increase. Calf production of 29.3 percent in 1979 was

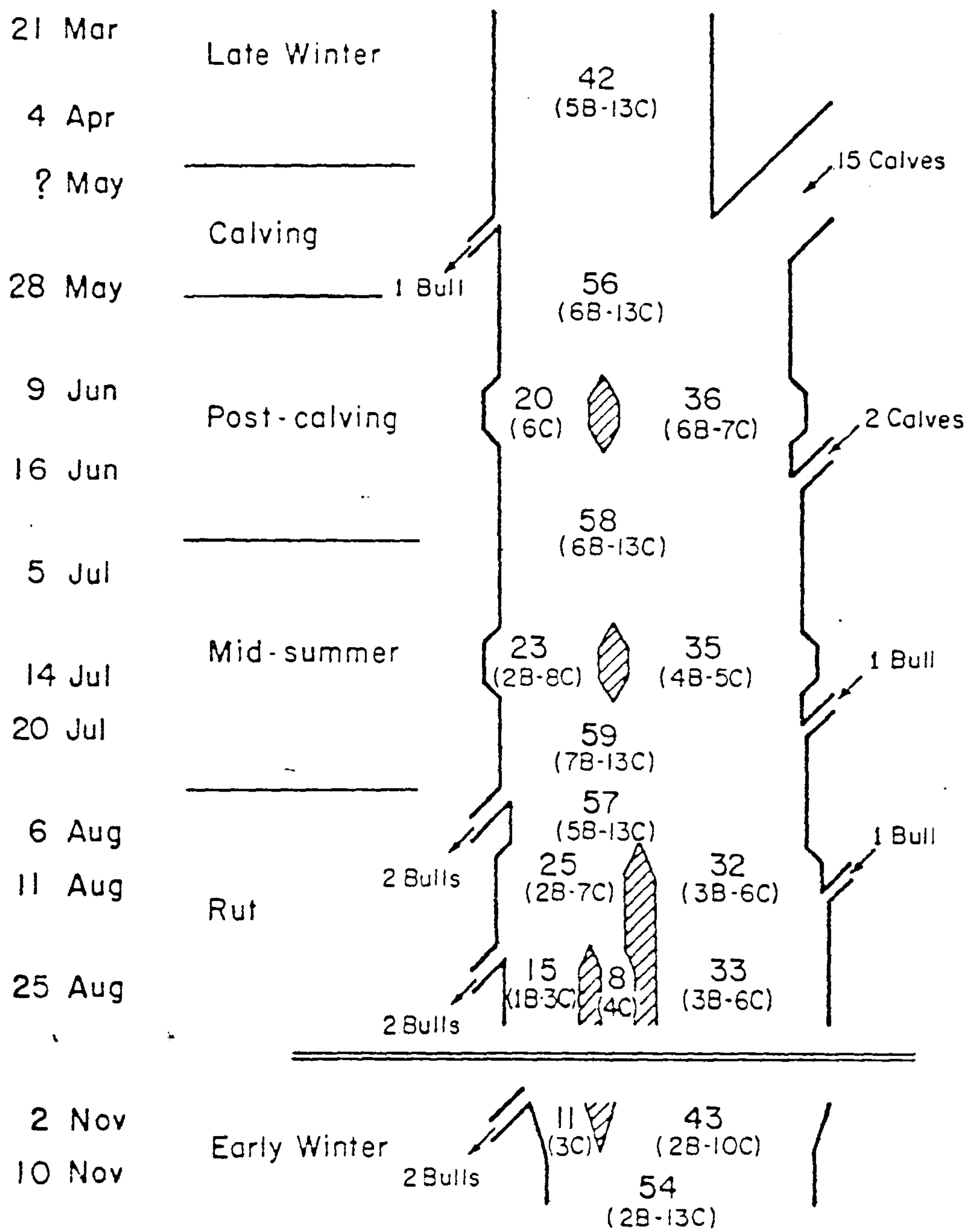

Figure 2. Seasonal herd dynamics of the Sadlerochit muskox group, 1979. Numbers refer to group totals with adult bulls (B) and cows (C) in parentheses. Shaded areas indicate fracturing of the herd.

higher than has been reported from other muskox populations (see Smith 1976). In the case of Nunivak Island, where the transplant originated, Spencer and Lensink (1970) estimated an average calf crop of 19 percent between 1947-68. The production of calves in the Sadlerochit group is also considerably higher than Leslie predicted (Appendix 2, *in* Tener 1965). Leslie assumed that muskox cows start breeding in their third year, that breeding occurs in alternate years and that the sex ratio is equal. With less than 50 percent calf mortality, the predicted calf crop would be 15-23 percent. A calf crop greater than 23 percent would, according to Leslie, indicate that cows were breeding at a younger age or that some cows were breeding annually, or both. In this study, the high productivity is thus a reflection of early sexual maturity, breeding in successive years as well as an imbalanced sex ratio in favor of cows. Should the present productivity levels continue, the population will double in less than 3 years.

A total of 148 muskoxen was observed within the William O. Douglas Arctic National Wildlife Range during a pre-calving survey by the U.S. Fish and Wildlife Service in 1980 (Ross 1980). The "Canning-herd" (48 muskoxen) was located 38 km southwest of the Sadlerochit group and the "Jago-herd" (27 muskoxen) 65 km to the east. An additional 19 bulls were observed in four groups.

Information from other areas, where muskoxen have recently been introduced, suggests a similar pattern of rapid expansion following an initial period of establishment with slow population growth. The group of 27 muskoxen introduced to West Greenland in 1962 and 1965 remained stable during the first 5 years following the release. Currently, the population is increasing rapidly; calves represented 25.8 percent of the population (N = 151) in 1977 and short-yearlings (10 months old) accounted for 25.0 percent (N = 220) in March 1980 (Holthe, Roby and Thing, unpubl. obs. - Thing, pers. comm.). From a transplant to the Seward Peninsula in 1970, a herd has regularly been seen in the Black Mountain area, 20 km northwest of Brevig Mission, for the past 7 years (Grauvogel 1980). In 1979, the herd consisted of 34 muskoxen, including two lone bulls (Klein, pers. comm.). Twelve calves were seen, representing 35.3 percent of the population. In a ground survey of the herd on 26 June 1980, I saw a total of 44 muskoxen including 11 calves and 12 yearlings. The calf to cow ratio, including cows 2 years and older, was 0.79. I observed one 2-year old cow nursing a calf indicating early sexual maturity comparable to that recorded for the Sadlerochit herd during 1979.

Early breeding in wild muskox populations has previously been confirmed only from a small, introduced herd in the Dovre Mountains of Norway (Alendal 1971a). In a group transplanted from Nunivak Island to nearby Nelson Island, all cows gave birth at 3 years of age and possibly one as a 2-year old (Lent 1978).

Since complete composition counts are not available for the Sadlerochit herd prior to 1977, it is not possible to assess herd dynamics during the slow initial increase in group numbers. Bente (1977) felt the population remained stable between 1972-74 as a result of poor calf survival. However, observations in the summer and fall of 1972 (Roseneau and Stern 1974) suggest that 3-4 muskoxen left the herd which may explain the apparent lack of increase in absolute herd numbers. Extensive dispersal, primarily by bulls, seems more important than natural mortality factors in restricting initial population growth. Experience with introductions suggests, however, that once a group of sexually mature muskoxen has localized into an area of favorable habitat, expansion is likely to follow.

The mean size of the Sadlerochit herd during this study (55.7) is considerably larger than herd sizes reported elsewhere. Spencer and Lensink (1970) found average group sizes of 14.5 in winter and 7.8 in summer on Nunivak Island. Corresponding herd sizes in the Thelon Game Sanctuary, N.W.T., were 19.7 and 11.3, respectively (Tener 1965). The large segment of young age classes in the Sadlerochit herd, in combination with its recent establishment, may have enhanced group cohesion. Should present productivity levels continue, it seems inevitable that the herd will split into smaller groups, perhaps making use of additional areas adjacent to the Sadlerochit River drainage. The fracturing of the herd observed during the rut is presumably related to increasing levels of aggressive behavior among the bulls. The importance to herd productivity of normally solitary bulls is evidenced by the case of the dominant bull that was present in the group of 33 muskoxen only during the rut.

Thus, after an initial period of establishment with slow population growth, the Sadlerochit herd is currently in a state of rapid increase characterized by excellent calf productivity, early sexual maturity and a large segment of young age classes.

II. ACTIVITY PATTERNS

A. Duration and Periodicity of Activity Periods

I timed a total of 228 activity and resting periods on a seasonal basis (Table 3). An analysis of variance indicated significant differences between seasonal mean durations of both activity ($F = 12.4$, df = 5 and 104, $p < 0.001$) and resting ($F = 28.7$, df = 5 and 112, $p < 0.001$) bouts. A multiple comparison between the means was made using the Student-Newman-Keuls procedure for homogeneous subsets (Sokal and Rohlf 1969). Activity and resting periods were both shortest in mid-summer. Resting bouts during early winter, late winter and calving were significantly longer than during other seasons. Assuming this periodicity was maintained during the night, the extended periods would result in 3-4 complete cycles of activity/resting during a 24-h period as compared with 6-7 cycles in mid-summer (Fig. 3).

To test whether the observed pattern of activity was linked to a 24-h cycle, I combined data from the period of continuous daylight (post-calving and mid-summer) in a Friedman's 2-way ANOVA test (Conover 1971). The proportion of the herd feeding during any specific 1-h interval was not significantly different from other times of the day ($\chi^2 = 23.8$, df = 23, $p > 0.05$). The same result was obtained when testing the proportion of muskoxen resting ($\chi^2 = 17.4$, df = 23, $p > 0.05$)

Table 3. Seasonal variation in the duration (min) of muskox activity and resting periods, Sadlerochit River, 1979-80. Mean, standard deviation and sample size (in parenthesis) are shown. Periods with the same letter are not significantly different.

Period	Season: Late Winter	Calving	Post-calving	Mid-summer	Rut	Early Winter
Activity	140 ± 23.6 (4) a,b	185 ± 64.8 (10) b	143 ± 51.1 (31) b	85 ± 39.1 (39) a	129 ± 46.2 (21) a,b	190 ± 27.6 (5) b
Resting	208 ± 37.7 (5) c	252 ± 75.5 (10) c	128 ± 47.5 (31) d	98 ± 40.9 (40) e	110 ± 28.4 (26) d,e	222 ± 41.3 (6) c

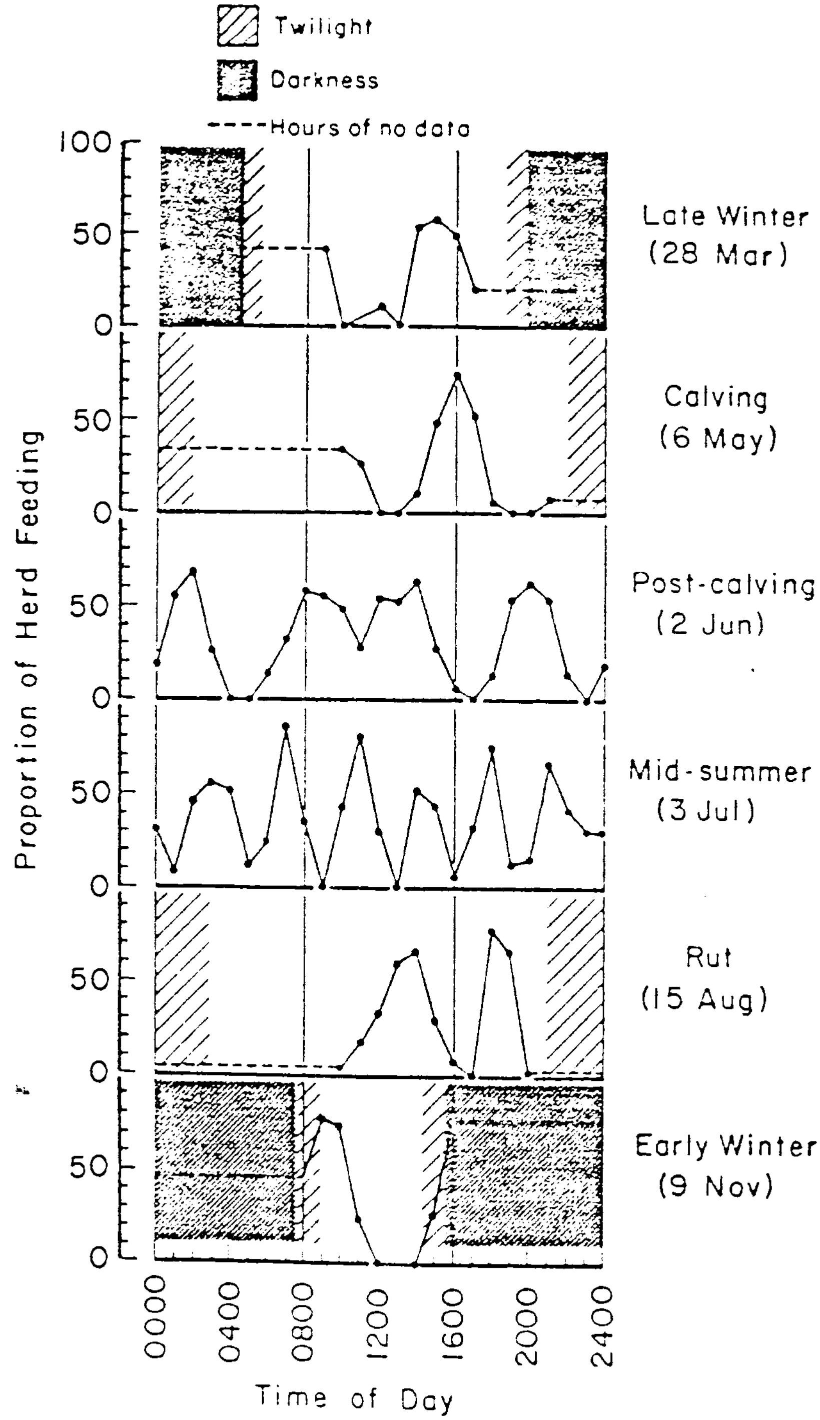

Figure 3. Periodicity of muskox feeding cycles, Sadlerochit River, 1979-80. Graphs indicate representative dates for each observation period. Extensive movements during mid-summer (see Fig. 12) are not reflected in the figure.

indicating that the observed activity pattern was not linked to a 24-h cycle during post-calving and mid-summer.

In early winter, a pattern with an active period in the morning and afternoon and a 3-4 h resting period around noon appeared to exist (Fig. 3). The observations in early winter were limited by the short period of daylight. Regular feeding activities appeared to continue through the night as evidenced by signs of cratered areas and limited observations using a night scope.

The degree of synchrony within the herd varied considerably between seasons. The turnover time from "all-feeding" to "all-lying" averaged about 85 min while the turnover time from "all-lying" to "all-feeding" was shorter (ca. 70 min). Individual muskoxen often remained active or resting longer than others resulting in a lack of synchrony with the main herd.

B. Sex and Age Differences in Activity Budgets

To describe the relationship between activity budgets, age/sex category and season, I tested a series of hierarchial models for goodness of fit. Since the tests were based on observations at 90-min intervals to meet the assumption of independence between activity scans, I did not include data from the winter and calving seasons due to small sample sizes. None of the possible models for two-variable interactions provided a satisfactory fit to the observed frequencies; this indicates that activity budgets were dependent on age/sex category and that this relationship varied on a seasonal basis (Table 4). The observed

Table 4. Chi square goodness of fit tests for models describing various interactions between muskox activity budgets [A], age/sex class [B], and season [C], Sadlerochit River, 1979. The occurrence of two variables within brackets indicates an assumption of dependence between those variables.

Model	χ^2	df	p
1. [A] [B] [C]	332.2	64	<0.001
2. [AB] [C]	137.4	48	<0.001
3. [AC] [B]	281.5	56	<0.001
4. [BC] [A]	322.8	56	<0.001
5. [AB] [AC]	86.6	40	<0.001
6. [AB] [BC]	128.1	48	<0.001
7. [AC] [BC]	269.9	40	<0.001
8. [AB] [AC] [BC]	76.2	32	<0.001

frequencies in the multidimensional contingency table are listed in Appendix A together with the standardized cell residuals that show which cells contributed most of the variation from the expected values. The largest chi-square contributions resulted during the rut when calves were feeding more than expected and bulls were more frequently involved in rutting-related activities.

Seasonal differences in activity budgets between age/sex categories are shown in Figure 4. Activity budgets for the yearling and subadult cohorts were similar, while differences were more pronounced between bulls, cows and calves. More time was devoted to lying than any other activity during all seasons, except post-calving. During late winter and calving, most muskoxen spent up to 60 percent, or more, of their time lying. The incidence of feeding increased during calving while less time was spent walking. Yearlings spent more time feeding (38%) than other age classes.

The post-calving period was characterized by a general increase in feeding, as well as walking, primarily at the expense of lying. Muskoxen typically spent 41-44 percent of their time feeding and slightly less time lying. In comparison, calves rested more than half of their time (51%) and spent more time walking, standing or playing (included in "other" category) than feeding (29 and 20%, respectively). This pattern was even more pronounced during the preceding calving period. The newborn calves, which were less than 1 week old when activity budgets were recorded, spent 78 percent of their time lying while feeding made up only 7 percent of their daily activity budget.

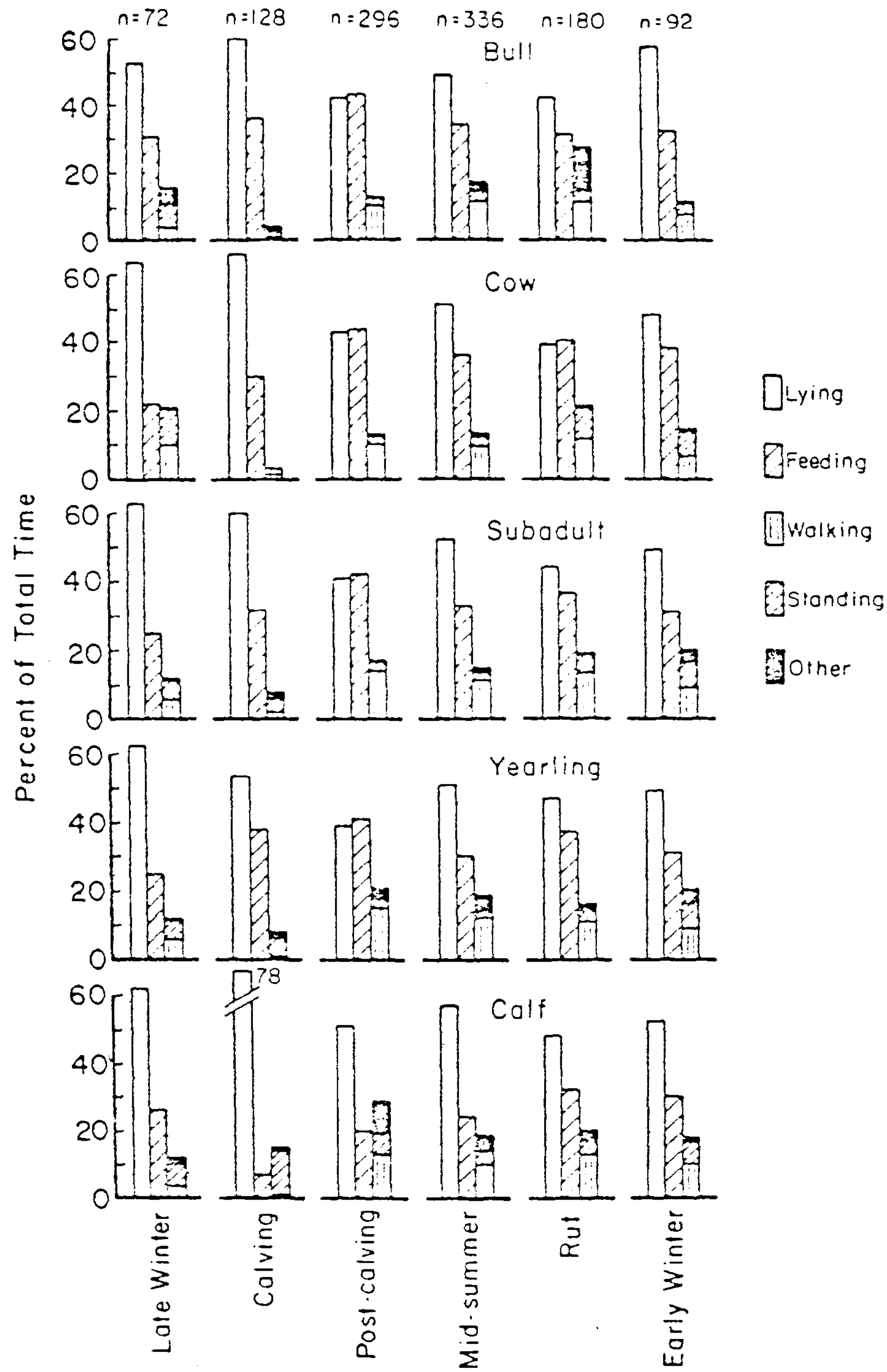

Figure 4. Seasonal activity budgets for a reintroduced muskox population, Sadlerochit River, 1979-80. Sample sizes refer to the number of 15-min interval scans.

A trend of increasing proportion of time spent lying was evident for all age/sex categories in mid-summer. During the following rut, the activity budget of calves resembled that of other age groups. The bulls were involved in rutting-related activities, on the average, 15 percent of the time. However, the bull that joined the herd in late July and assumed dominance in the group spent up to 50 percent of the time in sexual or agonistic pursuit of other muskoxen (Fig. 5). In early winter, the incidence of feeding was higher among cows (38%) than other groups while bulls spent 57 percent of their total time lying. Signs of rutting were still evident among subadults and yearlings (4% each).

C. Discussion - Activity Patterns

In a ruminant herbivore, the period of inactivity is not only required for rest but also for rumination of the forage ingested during the active period. Thus, a regular pattern of alternating activity and resting periods is typical of most ruminants. The extended periods of rest and activity in early and late winter have also been observed among wild reindeer in Russia (Segal 1962) and Norway (Thomson 1973; Gaare *et al.* 1975), and among caribou in Alaska (Roby 1978). The seasonal differences in the duration of activity and resting bouts appear to be a response to changing availability and quality of forage (Arnold 1964, 1970; Campbell *et al.* 1969; Cammell and Osbourn 1972). Thus, the duration of resting periods in winter could be related to a lower quality of food (less digestible) which results in longer rumination time (Cammell and Osbourn 1972; Reid *et al.* 1979). Forage digestibilities,

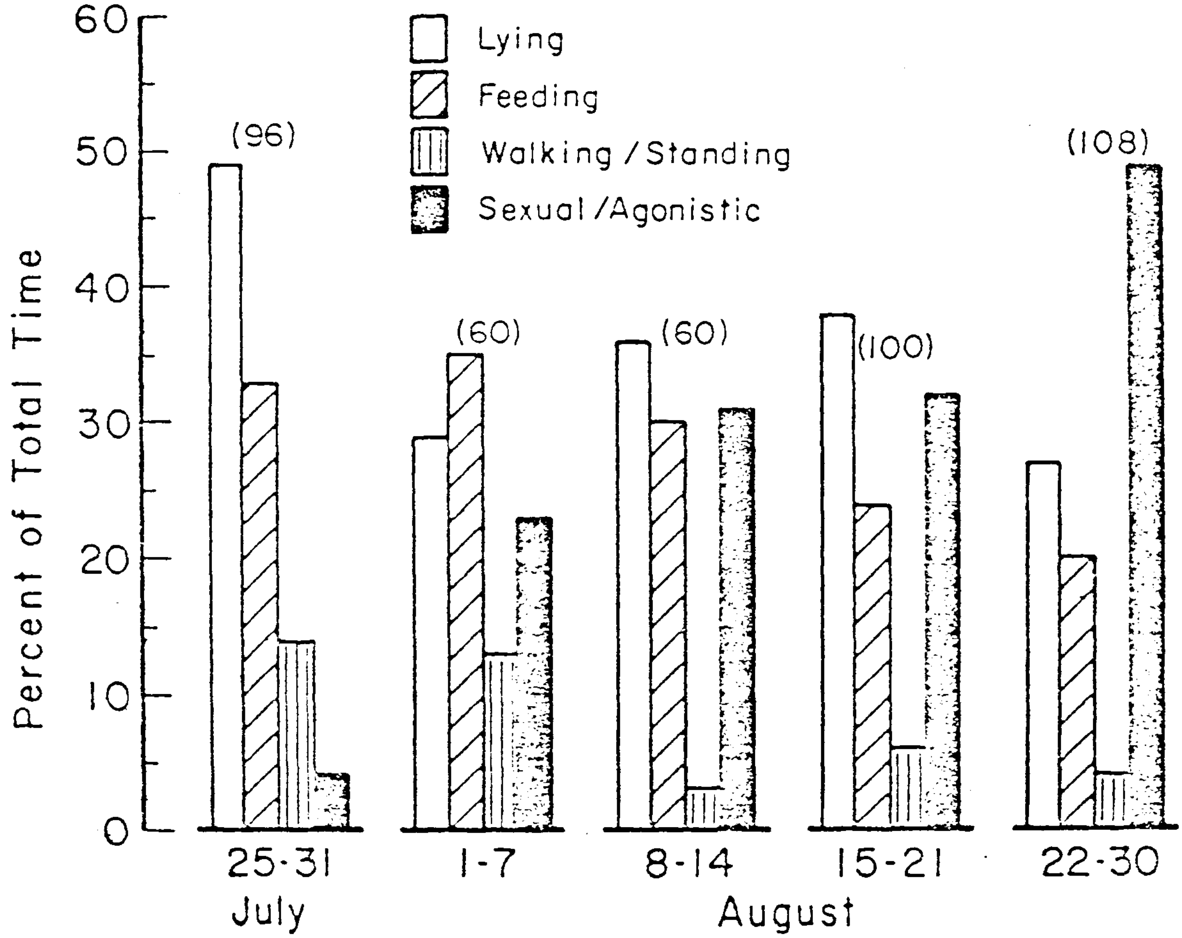

Figure 5. Activity budgets of a dominant bull muskox during the rut, Sadlerochit River, 1979. The number of 15-min interval scans are shown in parenthesis for each period.

however, are quite variable and will depend on the diet, the ratio of live and dead material eaten, as well as the particular plant part used (White *et al.* 1975; Trudell *et al.* in press). If the digestibility of muskox winter forage at Sadlerochit River is lower in winter than summer, an increased rumen turnover time would be expected resulting in longer periods of resting (for rumination). Similarly, low forage availability requires longer active periods for cratering and searching through the snow cover. Since the snow on the coastal plain is more dense and heavily crusted in late winter, one would expect muskoxen to spend more time active in trying to obtain their forage. However, the active periods are short in late winter and they probably reflect the selection of exposed, windswept areas for feeding. A large proportion of time spent resting, leaving less for activity, can also be seen as a means of conserving energy and reducing forage requirements. A similar strategy has been observed among white-tailed deer (*Odocoileus virginianus*) in the winter (Moen 1976). The short bouts of both resting and activity in summer suggest that muskox forage may be of higher quality than in winter and also more readily available, resulting in shorter rumen turnover times and less time required to fill the rumen.

The alternating pattern of activity and resting shows that feeding is a synchronized group activity. The synchronization of activity is thought to be a result of social facilitation (Thomson 1973). The degree of synchrony depends on the season and probably also on the size of the group. Gray (1973) found turnover times from feeding to resting and vice versa in a "medium-sized" muskox herd (n = 10) to be about 45 and 30 min, respectively, or approximately half the length of time observed in this study. During late winter and calving, subadults and yearlings often remained feeding in already cratered areas long after the main group had bedded down. During early summer, calves were often the first to lie down and rested considerably longer than other age classes. The lack of synchrony observed during the rut was primarily a result of the persistent courtship behavior of the dominant bull.

Thomson (1973) described the activity pattern of wild reindeer as consisting of two rhythms: a short-term polycyclic rhythm of alternating activity/resting periods and a long-term, 24-h rhythm controlled by photoperiod, which set the activity to the time of day. The latter was most obvious in the winter. It is possible that a long-term rhythm is present in muskoxen, at least in early winter; however, more information on the periodicity of muskox activity patterns in winter is needed. The absence of a circadian rhythm during summer is not surprising due to the continuous daylight. Miller and Gunn (1979) found no distinct daily rhythm of activity during the summer from their study of muskoxen on Prince of Wales and Russell Islands in the Canadian Arctic.

Activity budgets for muskoxen are "typical" only for a particular age/sex category during a particular season. Although seasonal trends are apparent, primarily as a result of changes in forage availability and quality, variations between age/sex categories indicate differences in individual energy demands for processes such as growth, lactation and breeding.

The low incidence of grazing observed among calves indicates the importance of milk as a source of energy during the calving and post-calving periods. As part of the natural weaning process, the calves gradually acquire an activity pattern similar to other cohorts. The energy demands of lactation are reflected in the large proportion of time spent feeding by cows during post-calving. During late winter and early calving, the pregnant cows were considerably less active than other age/sex classes which would reduce their energy loss prior to parturition. Measurements of energy requirements for gestation among domestic ruminants indicate a significant increase in maternal metabolism during the last one-third of pregnancy (Flatt *et al.* 1969; Moe and Tyrrell 1972). Assuming a gestation period of 35-36 weeks for muskoxen (Palmer and Rouse 1936; Alendal 1971b) and that the majority of calves are born during the first half of May, a marked increase in energy requirements for fetal development could be expected in late February.

The time spent by bulls in sexual and agonistic activities is apparently related to the dominance status of the bull. In the group of 33 muskoxen, 3-4 bulls were present throughout August. Observations elsewhere, where average herd sizes are considerably smaller, suggest that a single bull takes possession of a group during the rut, deterring ingress of other bulls and egress of cows (Smith 1976). In this study, the dominant bull spent an increasing amount of time in courtship behavior at the expense of non-rutting (maintenance) activities. The weight losses observed among rutting bulls in the Canadian Arctic

(Hubert 1974) are presumably a function of the change in activity budgets. A large proportion of the bull's time was devoted to active herding of one or more cows that drifted away from the main group while feeding. The frequent anogenital inspections by the bull are reflected in the increased incidence of standing among cows. The other bulls spent more time in maintenance activities which explains the observed average of 15 percent of the total time used by bulls for courtship behavior. Smith (1976) found that dominant bulls on Nunivak Island spent over 50 percent of their time in rutting-related activities during early August and early September. The latter period coincided with the peak of the rut as the cows came into estrus. The results are in agreement with the observed activity budget of the dominant bull in this study.

The small proportion of time spent feeding, relative to lying, in late winter is consistent with observations of voluntary weight loss among captive muskoxen despite the *ad. lib.* availability of good quality feed (Tener 1965; Hubert 1974; Wilkinson 1974; McEwan 1975). In recent feeding trials with captive muskoxen, R. G. White (unpubl. obs.) found the dry matter intake to decrease from 102 g $\cdot$ d^{-1} $(kg^{0.75})^{-1}$ in August to 38 g $\cdot$ d^{-1} $(kg^{0.75})^{-1}$ in February. Hubert (1974) felt, that a reduction in metabolic rate thereby reducing weight loss, may have a definite survival value during the late winter period of low energy and nutrient availability.

The increase in the incidence of feeding during late summer among all categories of muskoxen, except bulls, has also been reported for caribou in Alaska (Curatolo 1975; Roby 1978). The decreasing forage quality, due to maturation of the vegetation, was thought to result in longer feeding times required to obtain the necessary nutrients.

Environmental influences, other than forage quantity and quality, are also important in determining activity budgets. The time spent in "other" activities during mid-summer, was primarily a response to mosquito harassment as a result of high temperatures and low wind speeds. This response was particularly evident among yearlings and calves. The influence of weather parameters and insect harassment on activity budgets will be discussed in Sections III and V, respectively.

Although movement rates increased markedly during mid-summer (Section IV), this is not apparent from the incidence of walking as determined by the 15-min interval scan observations of the herd. The reason is the difficulty in following a rapidly moving herd for a continuous period of time while accurately recording individual activities. Thus, the activity budgets in mid-summer are biased towards observations taken of the herd when it remained fairly stationary.

In summary, the seasonal variation in the duration of activity and resting periods appears to be related to changes in forage availability and quality. Muskox activity budgets are "conservative" with more time spent lying than any other activity. Differences in individual activity budgets reflect age and sex-specific energy demands during the annual life cycle.

III. FEEDING BEHAVIOR

A. Suckling

A majority of the suckling bouts (78%, N = 442) were recorded within 30 min of either the initiation or termination of an activity period. Often, calves attempted to suckle immediately after the cows rose from a resting period.

Due to the obvious difference in body size between the calves born in mid-June and those born a month earlier, I was able to compare the duration of suckling bouts between the two calf cohorts (Fig. 6). The two late born calves consistently suckled longer than the other calves, at the same age. The duration of suckling bouts for the early born calves declined rapidly during the first 5 weeks and then at a decreased rate during the remainder of the summer, *viz.*

$$Y = 180\ e^{-0.722X} + 55e^{-0.046X}$$

where Y = duration of suckling bout (sec) and X = age of calf (weeks). I saw no suckling attempts in late winter but observed cows nursing yearlings twice during the following calving period.

In the first 2 weeks, 20.3 percent of all suckling bouts were terminated as the calf lowered its head and backed up from the inguinal region of the cow. During the remainder of the summer, all nursings were terminated by the cow, walking or running away from the calf.

I observed "multiple sucklings" (two calves suckling from the same cow) twice. An additional six nursings were interrupted as a second calf attempted to suckle from a cow that was in the process of nursing

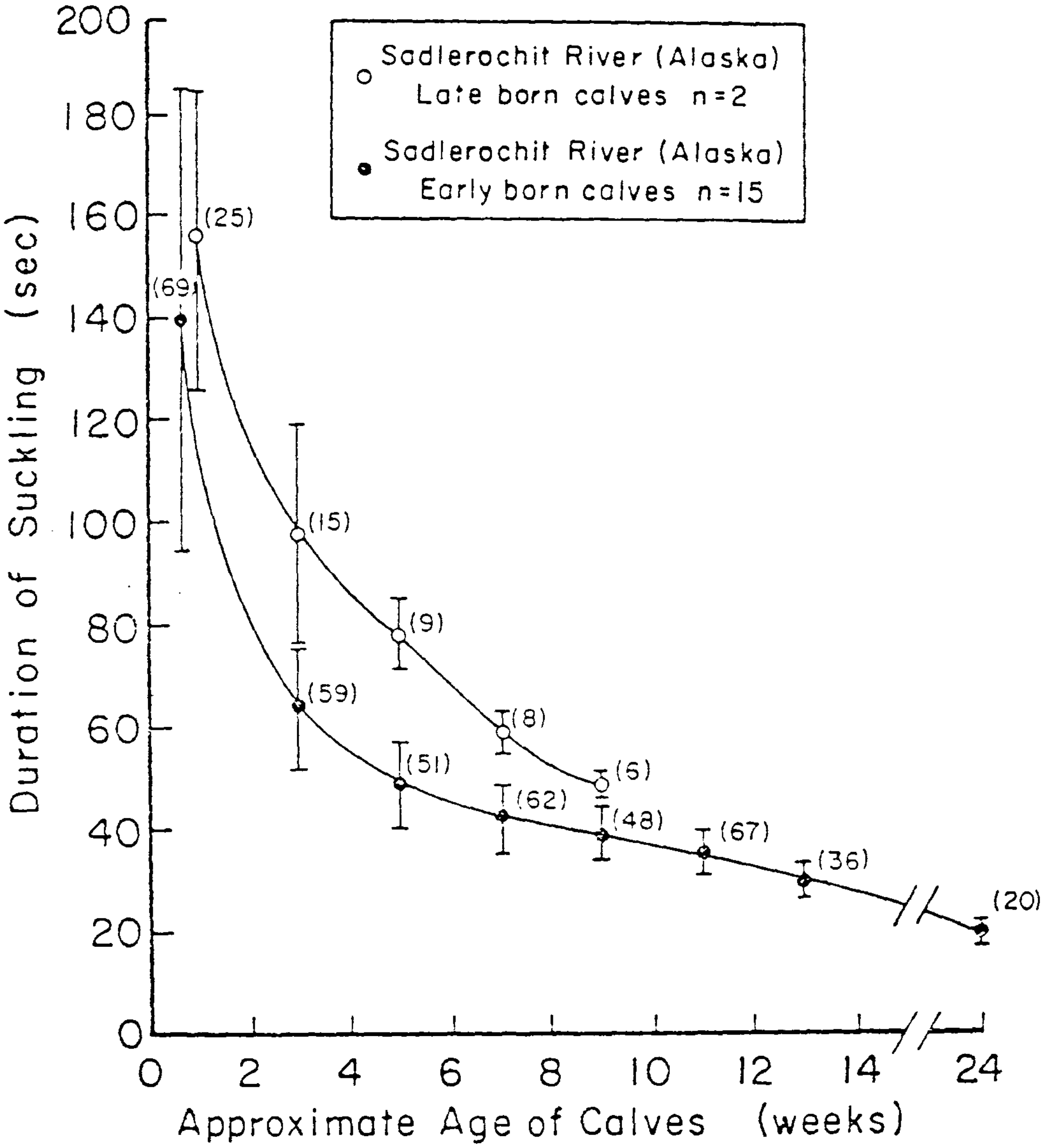

Figure 6. Comparison of the ontogeny of suckling behavior in two muskox calf cohorts, Sadlerochit River, 1979.

another calf. I made two observations of calves suckling from the rear of the cow; all other sucklings were made from the side.

B. Daily Eating Time

I recorded the proportion of time actually spent eating ("eating rate") during 5-min feeding periods for bulls, cows and calves on a seasonal basis. The results are shown in Table 5 where the corresponding proportion of time spent feeding (eating + searching), based on observed activity budgets, is included. The difference in eating rates between cows and calves was significant during post-calving ($U_s = 40.0$, $\rho < 0.01$) and mid-summer ($U_s = 60.5$, $\rho < 0.01$). Eating rates for cows and bulls were not significantly different during any season. I recorded the lowest eating rates for adult muskoxen in late winter and the highest during post-calving.

When combined with feeding time, the eating rates can be used to estimate the actual time (min) that the animal spends eating per day ("daily eating time" - Fig. 7). Cows fed more intensively than bulls during all periods except in late winter and during calving. During post-calving, cows spent 44 percent of their total time eating which was significantly more ($U_s = 46.0$, $\rho < 0.01$) than the corresponding eating time for bulls. Differences between the sexes were particularly evident during the rut. Calves spent an increasing proportion of their time grazing, and during the rut their eating times were higher than those of bulls (29 and 27%, respectively).

Table 5. Seasonal variation in mean eating rates among muskox groups, Sadlerochit River, 1979-80. Plus or minus (±) values are standard deviations.

Season	Group	Feeding Time* (%)	Eating Rate** (%)	N
Late Winter	Bull	31	75 ± 6.3	6
	Cow	22	77 ± 4.7	5
	Calf	26	67 ± 7.1	6
Calving	Bull	36	79 ± 4.0	5
	Cow	30	78 ± 3.6	5
	Calf	7	nd†	0
Post-calving	Bull	43	92 ± 3.8	7
	Cow	46	95 ± 3.0	8
	Calf	20	53 ± 14.2	5
Mid-summer	Bull	34	88 ± 6.1	7
	Cow	37	89 ± 4.9	9
	Calf	24	74 ± 7.4	7
Rut	Bull	29	91 ± 3.6	8
	Cow	40	93 ± 3.6	10
	Calf	34	87 ± 6.7	7
Early Winter	Bull	32	86 ± 5.1	3
	Cow	38	84 ± 4.8	5
	Calf	30	79 ± 5.6	5

* Proportion of total time spent feeding (eating + searching). Based on Fig. 4.

** Proportion of feeding time spent eating. Based on 5-min feeding bouts.

† nd = no data available.

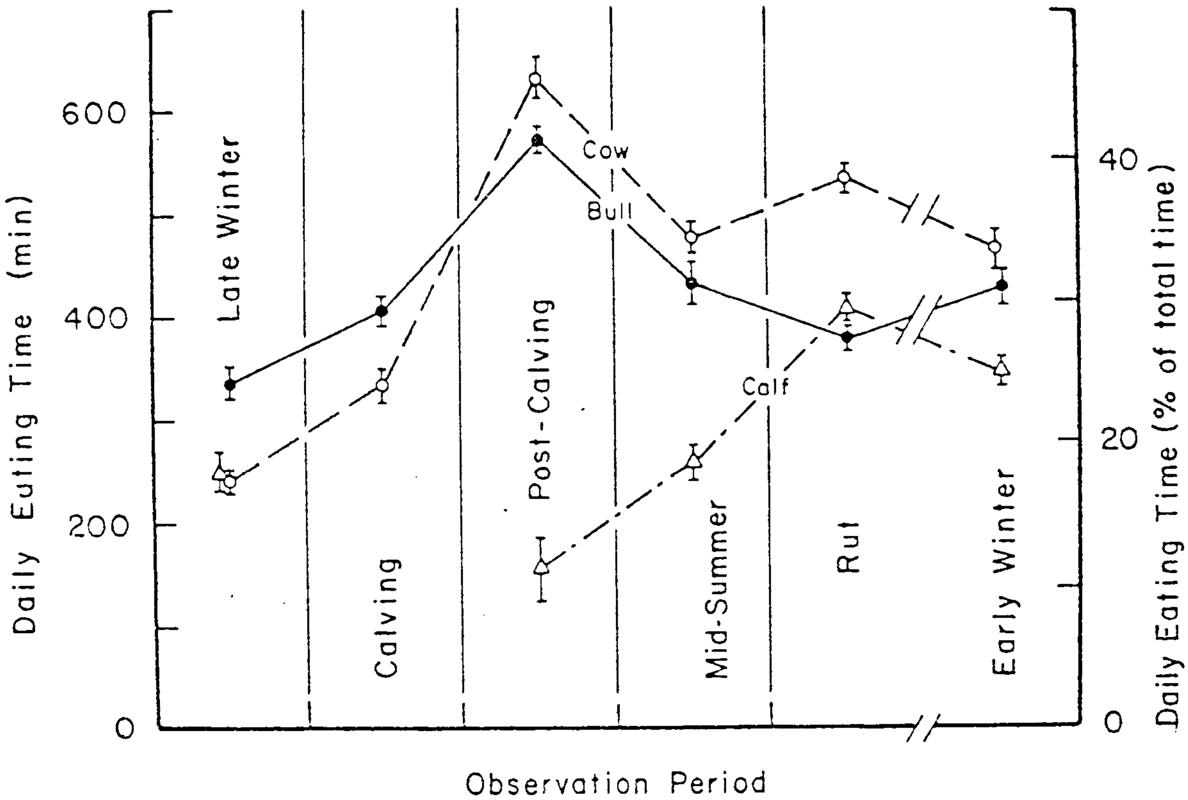

Figure 7. Seasonal variation in daily eating time among muskox groups during periods of observation, Sadlerochit River, 1979-80. Mean and standard deviation are shown.

C. Vegetation - Type Preferences

Observations made of feeding muskoxen in relation to vegetation types indicated exclusive use of the riparian habitat during early and late winter (Fig. 8). At this time muskoxen primarily browsed the senescent leaves and terminal twigs of *Salix pulchra* and *S. alaxensis*. Signs of feeding were also evident on the green stems of *Equisetum variegatum*, the winter-green leaves of *Oxyria digyna*, and the leaves and stems of *Lupinus arcticus, Stellaria longipes* and *Dryas integrifolia*. Prior to calving, the herd moved to the hills in the Carter Creek area, 8 km west of the Sadlerochit River. This area is largely made up of Tussock Meadows with small bands of Dry Ridge communities along the hill tops. The muskoxen made extensive use of south-facing slopes where sun and wind action had exposed individual tussocks. Signs of feeding were evident on *Carex bigelowii, Eriophorum vaginatum* (both standing dead and new leaves), *Salix pulchra* (terminal twigs and senescent leaves) and *S. phlebophylla*.

The herd remained on Tussock Meadows throughout the post-calving period. The use of forage species during summer is described by Robus (in prep.). Muskoxen continued to use the tussock community and the associated Creek Willow Thickets, along tributaries of the Sadlerochit River, during early parts of mid-summer. In mid-July, the animals moved to the riparian habitat and remained there until early rut when the herd split up and formed three separate groups. The largest group (33 muskoxen) returned to the Tussock Meadow community while the other groups continued to use the riparian areas. Over the entire study

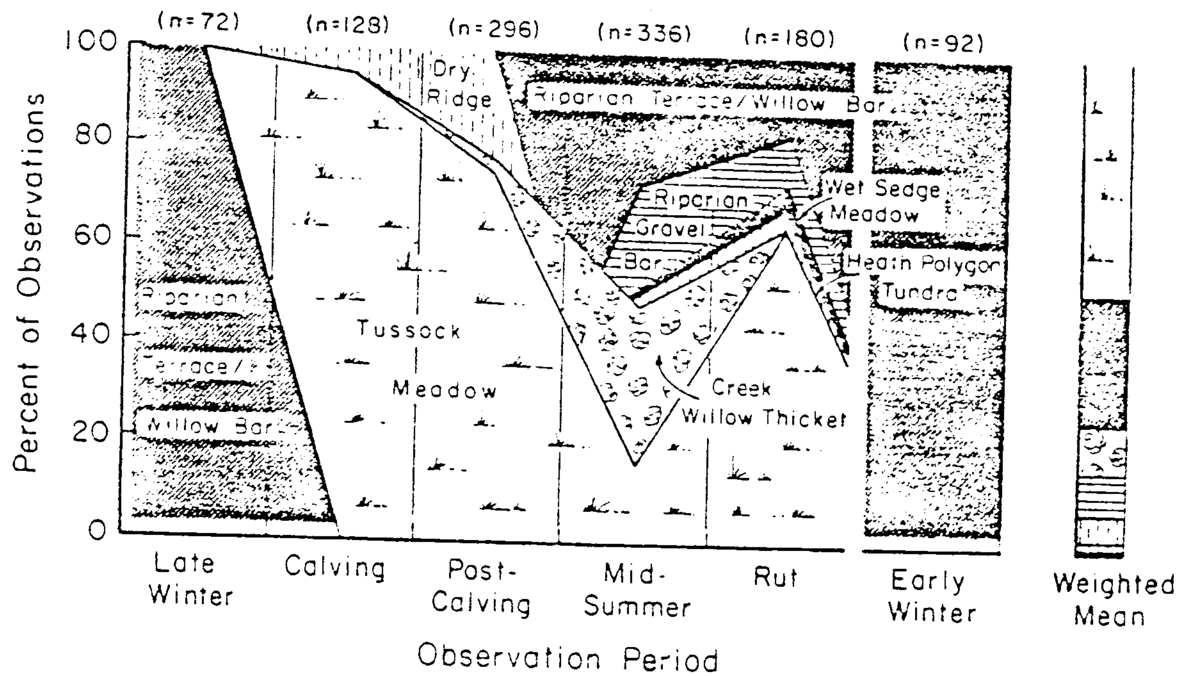

Figure 8. Seasonal use of vegetation types by muskoxen, Sadlerochit River, 1979-80. Sample sizes refer to the number of 15-min interval scans of feeding muskoxen during periods of observation.

period, most observations of feeding muskoxen were made in the Tussock Meadow and Riparian Terrace/Willow Bar communities (48 and 26%, respectively).

I combined information from the snow-free period (post-calving, mid-summer and rut) to determine overall summer use in relation to availability of existing vegetation types (Fig. 9). Availability is biased towards vegetation types present in this particular study area, which may not be representative of the entire coastal plain. Creek Willow Thickets were highly preferred both for feeding and lying (preference ratios of 4.57 and 3.66, respectively). Muskoxen selected the Dry Ridge type primarily for lying (PR = 3.42), while Tussock Meadows and riparian communities were used essentially in proportion to their availability. An apparent discrimination against the Wet Sedge Meadow and Heath Polygon types was noted.

D. Influence of Weather

Snow

The persistent winds on the coastal plain of Arctic Alaska create a hard, wind-packed snow surface which usually overlays a lower density layer of depth hoar. The wind may sweep large areas free of snow while creating deep, hard-packed drifts in topographic depressions.

Snow characteristics of muskox feeding sites were measured in early and late winter (Table 6). The snow was generally deeper, harder and more dense in late winter. Considerable differences in snow characteristics were evident between the 2 years of study. A

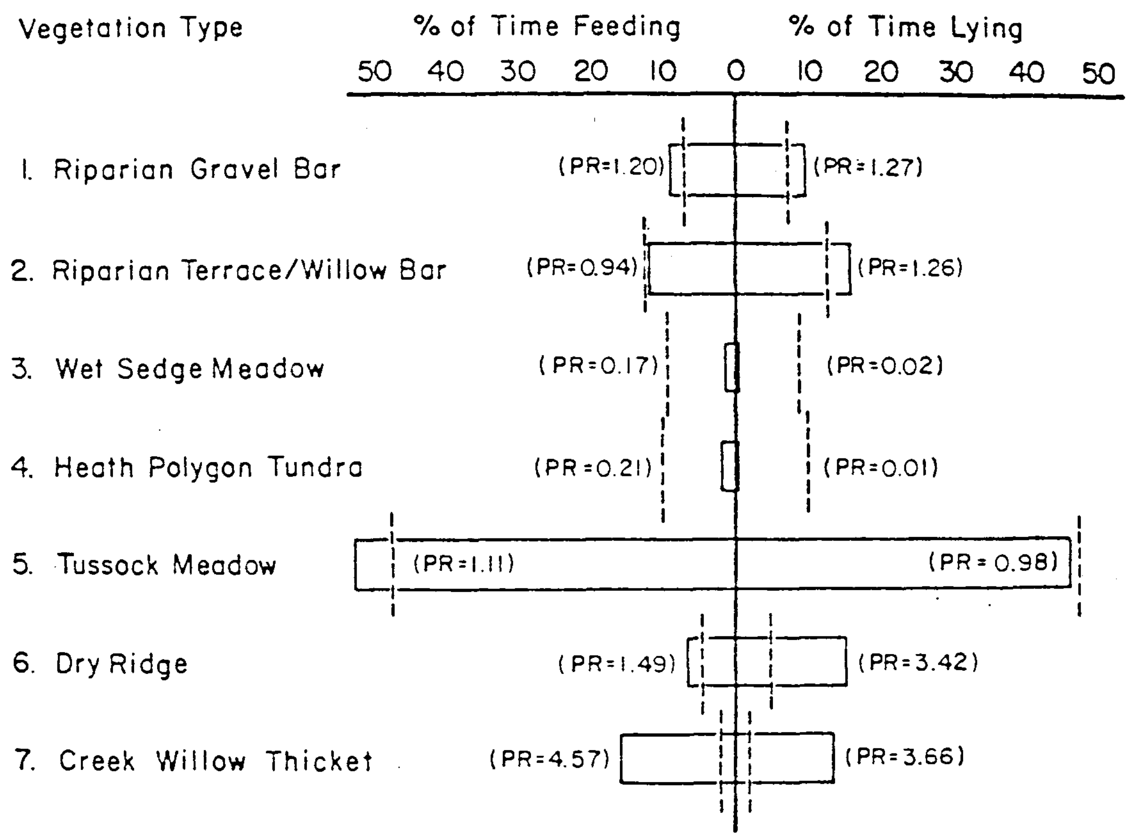

Figure 9. Summer use of vegetation types by muskoxen in relation to availability, Sadlerochit River, 1979. Availability (dotted line) is expressed as percent of study area covered by vegetation type. Preference ratio (PR) is calculated as the proportion of use to availability.

Table 6. Snow characteristics (mean ± SD) of muskox feeding areas during 1978-80, Sadlerochit River. Based on snow profiles taken at 10-m intervals along a 50-m transect.

Date	Depth (mm)	Density ($kg \cdot m^{-3}$)	Hardness ($kg \cdot cm^{-2}$)	Vegetation Type
29 Oct. 1978	150 ± 22	126 ± 20	0.02 ± 0.01	Riparian Terrace
2 April 1979	192 ± 76	298 ± 22	>5.0	Riparian Terrace
5 Nov. 1979	205 ± 45	202 ± 21	0.27 ± 0.10	Riparian Terrace (prior to freezing rain)
7 Nov 1979	224 ± 34	275 ± 30	3.73 ± 1.18	Riparian Willow Bar (after formation of hard crust)
29 April 1980	249 ± 53	350 ± 19	>20.0	Dry Ridge (not cratered)
1 May 1980	160 ± 44	328 ± 27	>20.0	Tussock Meadow (cratered)

period of thaw with freezing rain, followed by cold temperatures, resulted in a more than 10-fold increase in snow hardness between 5-7 November 1979. Subsequent measurements, in late April-early May, confirmed the presence of one or more, low-lying layers of ice (5-20 mm thick) in the snow profiles examined. In addition, a sun crust had developed in the top layer. The hardness of these profiles was beyond that which could be recorded by the spring penetrometer (> 20.0 kg $\cdot$ cm^{-2}). Hardness values were also high during the previous late winter period (> 5.0 kg $\cdot$ cm^{-2}); however, ice layers were not present and the snow cover consisted of hard wind slabs overlaying a ground layer of depth hoar.

In late April and early May, muskoxen restricted their feeding activities to south-facing Tussock Meadow slopes where snow depth and density were less than in adjacent areas. Snow profiles in the feeding areas had only one layer of ice (5-20 mm thick) as compared with two or three layers in the Dry Ridge area. During this time, large parts of the riparian habitat were covered by a layer of ground-fast ice (50-300 mm thick) probably as a result of extensive overflow earlier in the winter. Hard-packed drifts overlying the ice reached depths exceeding 2 m along the river banks.

The mode of foraging by muskoxen varied with the nature of the snow cover. In early winter, the soft snow was pushed aside with the nose ("nosing"). As snow density and hardness increased, digging became more frequent. In late winter, muskoxen were commonly seen "chinning", or breaking slabs of wind-packed snow by a downward sweep with their chin. The underlying, low-density depth hoar was then pushed aside by nosing. Muskoxen also frequently browsed shrubs (*Salix* spp.) protruding through the snow cover. The snow around the shrubs was softer and more easily penetrated than in areas of continuous snow surface and these areas were used extensively when muskoxen fed below the snow surface. In late April and May, muskoxen grazed exposed tussocks along south-facing slopes and cratering was less frequent.

Temperature and wind

Temperature and wind recordings are summarized in Appendix B. I analyzed the combined effect of low temperatures and strong winds on muskox activity budgets by calculating windchill equivalents ("atmospheric cooling values") from the formula derived by Siple and Passel (1945):

$$K_{-} = (\sqrt{v \cdot 100} + 10.45 - v)\ (33 - T_{-})$$

where K_o = wind $K_o = (\sqrt{v \cdot 100} + 10.45 - v)\ (33 - T_a)$

v = wind velocity ($m \cdot sec^{-1}$)

T_a = ambient temperature (°C)

The results showed a slight decrease in feeding with increasing windchill (Fig. 10). The resulting proportion of time spent lying increased up to windchill equivalents of 1300 and then declined. A median test indicated no significant differences in the proportion of

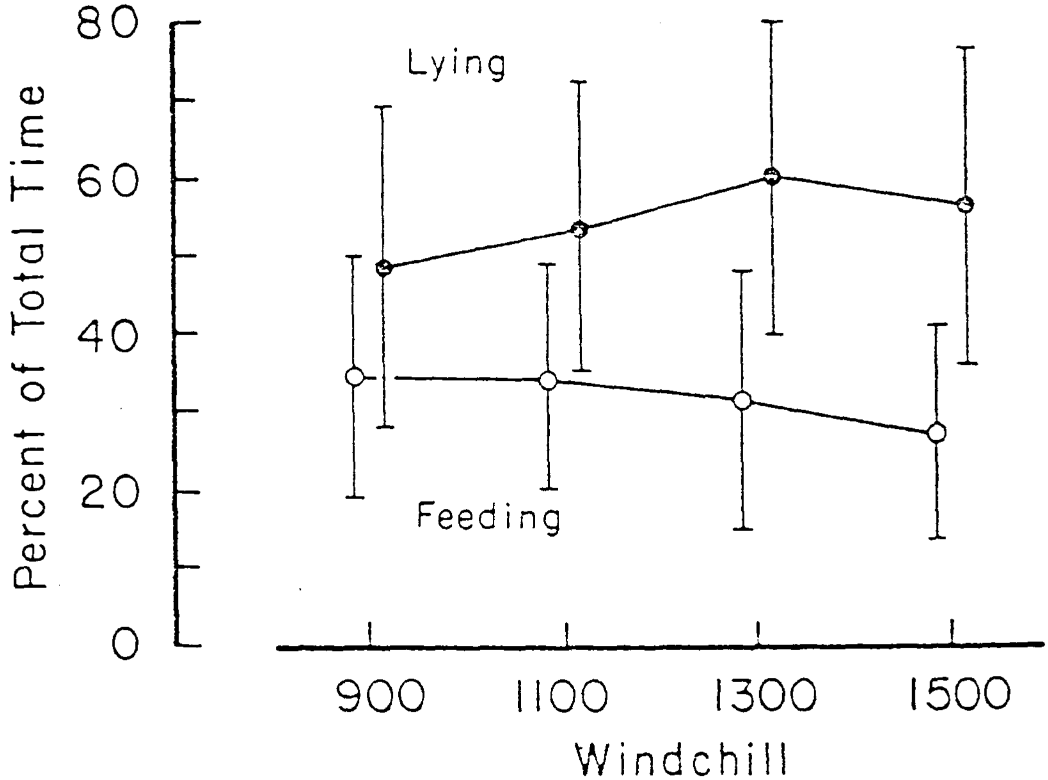

Figure 10. Influence of windchill on muskox winter activity budgets, Sadlerochit River, 1979-80. Mean and standard deviation are shown.

muskoxen lying ($\chi^2 = 0.774$, df = 3, $p > 0.05$) or feeding ($\chi^2 = 2.224$, df = 3, $p > 0.05$) over the different windchill values.

Muskoxen frequently faced away from the wind when bedded down during strong winds in combination with low temperatures (e.g. windchill equivalents over 1300). I noted a tendency among muskoxen to aggregate as visibility declined due to blowing snow or white-out conditions.

Observations on the bedding location of newborn calves in relation to wind direction and the position of the cow showed that calves rested close to their cows in 93 percent of all observations (Fig. 11). When the cows were bedded down broadside to the wind, the calves rested on the leeward side significantly more often ($\chi^2 = 4.76$, df = 1, $p < 0.05$) than would be expected from a random orientation based on the two possible locations.

In an attempt to simulate wind velocities encountered by a calf that is lying down (unsheltered) as opposed to standing, I measured wind speeds at 0.1 m and 0.5 m above the ground surface. Wind velocities at the latter height were, on the average, 1.66 times higher (SD ± 0.27, N = 24) than those recorded 0.1 m above the ground surface. At -10°C, this represents an increase in windchill equivalents of 125 units (e.g. from 1200 to 1325).

E. Discussion - Feeding Behavior

The longer suckling bouts, recorded for the two calves born in June, probably reflect changing range conditions. The greater

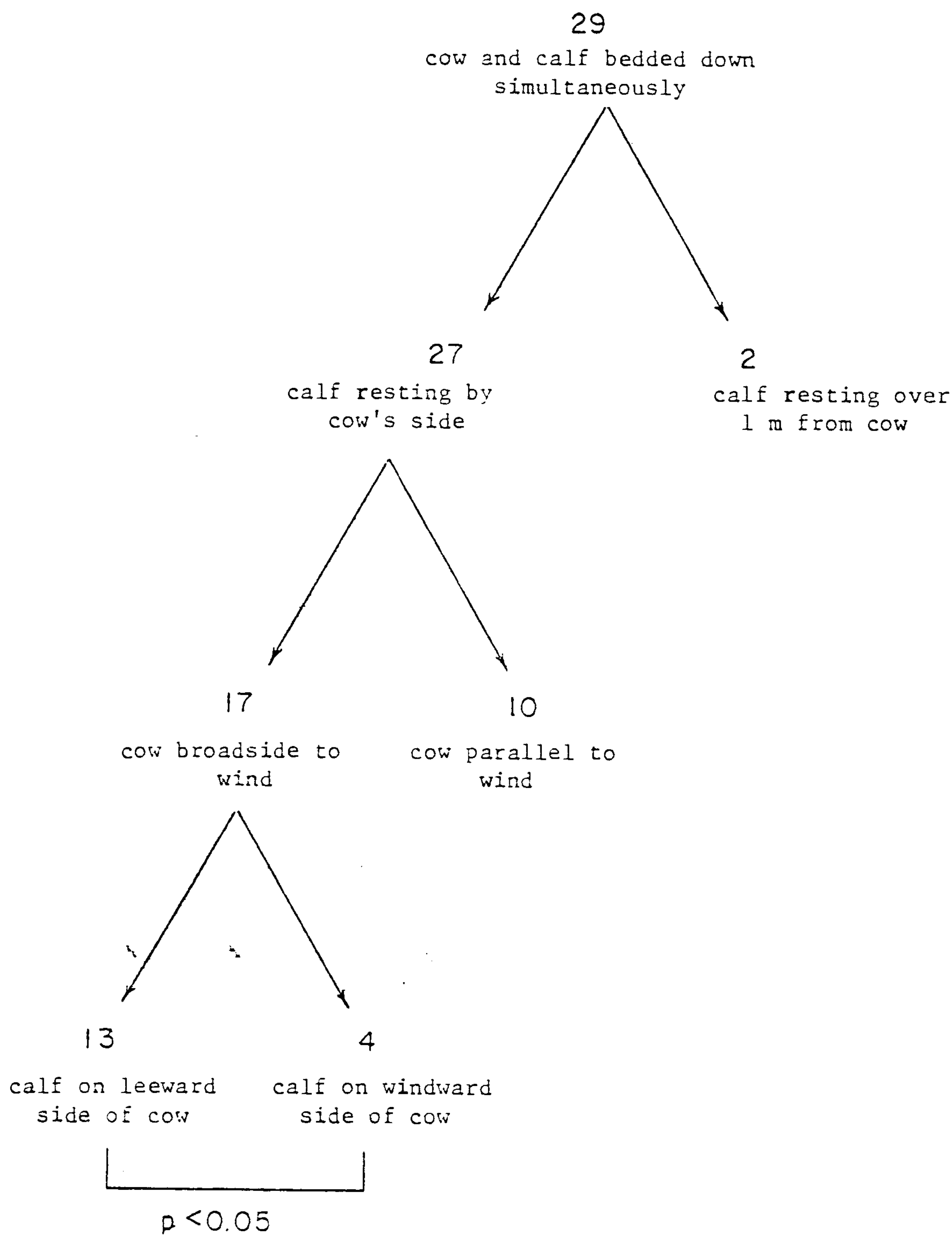

Figure 11. Bedding location of newborn muskox calves (less than 1 week old) in relation to wind direction, Sadlerochit River, 1980. All observations made in wind velocities over 5 m · sec^{-1}.

availability of forage in June may have stimulated an accelerated milk production in the two cows nursing the late born calves. Adequate milk production during early lactation is dependent upon sufficient pre-calving body reserves of the female, as well as on the current plane of nutrition (White *et al.*, in press). On the other hand, one would also expect the greater availability of forage suitable for calves to stimulate more grazing and less suckling by the late born calves. However, the data indicate that this was not the case; the two calves suckled consistently longer than the early born calves, throughout the summer. If a longer suckling bout is accompanied by increased milk intake, nutrient intake may be maximized during the remainder of the summer. The presence of all calves in the herd during the following calving season indicates that the longer suckling bouts enabled the late born calves to make some compensation for their late birth and reach an adequate body size prior to the onset of winter to enable their survival. There was no apparent difference in body size between the two calf cohorts at birth suggesting that the late born calves were a result of later conception rather than a prolonged gestation period.

The marked decrease in the duration of a suckling bout after the first weeks following parturition has also been noted in caribou (White *et al.* 1975), reindeer (Espmark 1971; Thomson 1973) and domestic sheep (Munro 1956; Ewbank 1967). In a study of the domestic muskox herd at College, Alaska (Lent 1970), the duration of nursing decreased markedly from the first to the fourth month (averaged 180 and 32 sec, respectively).

The duration of a suckling bout is not an absolute measure of milk intake. In experiments with reindeer calves, milk intake per suckling bout increased with age of the offspring until August. The development of physical features, such as the buccal cavity, apparently enables the older calf to drain the udder more efficiently (White, unpubl. obs.).

Bunting, which is thought to induce milk flow (Hafez *et al.* 1969), also became more frequent and vigorous with age of the muskox calf. Lent (1974) suggested that bunting by calves may be associated with the weaning process as discomfort to the cow results in aggression towards the calf and/or withdrawal with increasing regularity. The absence of nursing observations in late winter suggests that the majority of calves in the Sadlerochit group were weaned during mid-winter.

The low eating rates observed in late winter indicate a large proportion of searching time as a result of cratering for forage of low availability. Since forage at this time could also be of low digestibility, muskoxen spend more time ruminating, leaving less time for grazing. The resulting daily eating times reached their lowest values for adult muskoxen during late winter. The higher eating rates recorded during calving reflect a decrease in searching time as a result of feeding on exposed, south-facing slopes where cratering was less frequently required. Sex-specific differences in daily eating times during late winter and calving are primarily a result of differences in activity budgets; cows spent less time feeding and more time lying than the bulls during these periods.

During post-calving, a time of high nutritive demand on the lactating cows, the appearance of new growth, high-quality forage resulted in increased eating rates and a larger proportion of the active time spent feeding. An increase in food intake during lactation has also been reported for caribou (White *et al.* 1975), moose (Gasaway and Coady 1974) and domestic cows (Campling 1970). Expansion of the alimentary tract, presumably allowing for an increased food intake and rate of passage, has been observed in lactating sheep (Fell *et al.* 1964). Grazing by calves was less intensive and often interrupted by other activities, such as playing. Although calves were observed nibbling at vegetation within a week of birth, their main source of nutrition during the early summer is milk. Data from reindeer show that milk is the primary component in the dietary intake of calves for at least 50 days. After that time, milk production in the cow declines rapidly (White *et al.*, unpubl. obs.).

It has been shown that food intake for domestic sheep on pasture increases with increasing available plant biomass, while grazing time and the number of bites required decreases (Allden 1962; Arnold 1964, 1970; Young and Corbett 1972). Similar responses have been observed in elk (Collins *et al.* 1978) and also in caribou (White *et al.* 1975; Trudell and White in press) where available biomass was found to limit food intake on most plant communities. I did not measure food intake *per se* in muskoxen; however, the relatively low eating rates combined with the short feeding bouts during mid-summer, a period when live biomass peaked (Robus, in prep.), suggest that muskoxen respond in a similar way.

While eating rates were similar for cows and bulls during the rut, bulls spent a greater proportion of their time in rutting-related behavior. This difference in activity budgets is reflected in the daily eating times for adult muskoxen. The large increase in grazing by calves during this period coupled with the shorter duration of nursings suggests that the rut is a stimulation for accelerated weaning. The observation, that muskox calves "are too small and weak to forage for themselves in the first winter of life." (Wilkinson 1974) is not borne out in this or other studies and is apparently based on no substantive information.

Daily eating times for caribou are considerably higher than those observed for muskoxen in this study. White *et al.* (1975) found that unharassed female caribou spent up to 53 percent of the day eating; a similar value for lactating cow muskoxen during June (post-calving) was 44 percent (Fig. 7). The observed discrepancy is most likely a result of differences in energy balance and subsequent nutrient requirements between the two species. Muskox food intake has been described as "very conservative" (Wilkinson 1974) and proportionately less than that of reindeer per unit body weight (Palmer 1944). Based on fecal output, Hubert (1974) estimated the dry matter intake of adult bull muskoxen on Devon Island, N.W.T., to be about 90 $g \cdot d^{-1}$ $(kg^{0.75})^{-1}$ in late July. For comparison, White *et al.* (1975) found male caribou at Prudhoe Bay, Alaska, to have a higher intake per unit body weight [103 $g \cdot d^{-1}$

$(kg^{0.75})^{-1}$] during the same time of year in an area with similar forage availability. The "conservative" activity budgets of muskoxen, in combination with their localized foraging characteristics seem adaptive in reducing energy expenditure which helps to explain the relatively lower eating times and amount of forage intake. Preliminary evidence suggests that muskoxen are also more efficient in the uptake of energy; digestibility in captive muskoxen was higher than would be anticipated from a proximal analysis of the same feed (White, pers. comm.).

The preference for a particular vegetation type varied on a seasonal basis. Several factors influence this preference, including the quantity and quality of forage. Forage availability is affected by environmental parameters such as snow conditions and the duration of spring break-up. Other animals, primarily insects and caribou (Section V), also influenced the selection of habitats by muskoxen. Underlying the preference for a vegetation type is the selection of individual plant species and parts within that vegetation type. Certain species, such as *Salix pulchra*, were present in several different vegetation types but in varying amounts and were used extensively by muskoxen both in summer and winter.

In early and late winter, the elevated Riparian Terraces and Willow Bars provided windblown areas where muskoxen frequently browsed willows shrubs (*Salix* spp.) protruding through the shallow snow cover. The south-facing slopes used during calving were characterized by early snowmelt and exposed tussocks where forage was more accessible than in adjacent, low-lying areas. As a result of the windblown location and increasing levels of solar radiation, these Tussock Meadows were phenologically more advanced than other vegetation types and provided the muskoxen with the first available new growth of important forage species, such as *Eriophorum vaginatum* (flowering heads) and *S. pulchra* (leaves). Alendal (1971a) noted selective grazing by muskoxen for the most rapidly growing plant parts. Forage selection on a qualitative basis has been demonstrated for caribou and other arctic and alpine ungulates (Klein 1970a,b). The selection of an area where forage is both relatively available and also of high quality is of vital importance to muskoxen during a time when movements are restricted by flooding accompanying the spring thaw and the limited mobility of the young calves.

The strong preference for Creek Willow Thickets, particularly during mid-summer, is probably related to the abundance of *Salix* spp. in this community; willows continue to be a major component of the diet at this time. Muskoxen also used willow shrubs for head thrashing and rubbing during severe harassment from mosquitos (Section V). The switch to the riparian habitat in mid-July, while increasing the availability of willow leaves, was also accompanied by an increased use of new leaves and flowers of legumes and other forbs (Robus, in prep.). The dietary mixing of willows and nitrogen-rich legumes would enable the muskoxen to maintain a high intake of nutrients during the summer months. Since muskox use defined the boundaries of the study area, the relative prominence of the riparian habitat in the area is, in itself, an indication of habitat preference.

The apparent discrimination against Wet Sedge Meadows is surprising in light of other studies emphasizing the importance of lowland sedge meadows to muskoxen (Hubert 1974; Parker and Ross 1976; Wilkinson *et al.* 1976). However, the Wet Sedge Meadows in the Sadlerochit River area were flooded during most of June and early July and thus not available for grazing. Following break-up, this community provided prime mosquito habitat and their abundance there may have influenced use by muskoxen. In addition, the Sadlerochit River area provides a greater diversity and abundance of willow species and forbs (Robus, in prep.) than areas in the Canadian High Arctic where the above-mentioned studies were made.

In winter, muskoxen showed a strong preference for feeding in areas with relatively shallow snow cover where vegetation was partly exposed as a result of wind action and, by late winter, solar radiation. Similar observations were made by Lent and Knutson (1971) on Nunivak Island where muskoxen concentrated along a narrow coastal zone of shallow snow in the late winter months as snow depths in the interior of the island restricted forage availability.

Due to the maritime influence, heavy snowfall and icing conditions are common on Nunivak Island and have been implicated in causing heavy mortality among muskoxen (Spencer and Lensink 1970). Similar conditions have led to large-scale die-offs in East Greenland (Vibe 1958, 1967) and more recently, in the Canadian High Arctic (Parker *et al.* 1975; Miller *et al.* 1977). The winter of 1979-80 brought heavy snowfall to the coastal plain of northeastern Alaska with at least two thaw periods accompanied by freezing rain. Despite the resulting icing conditions and delayed spring break-up, I found no evidence of winter mortality in the yearling and subadult cohorts.

Little is known about nival thresholds for muskoxen. Snow hardness is difficult to measure on the coastal plain as a result of the shallow, wind-packed snow cover. Skogland (1978) found the spring penetrometer unreliable at resistances exceeding $10.0\ kg \cdot cm^{-2}$ and instead used a Rammsonde penetrometer for hardness measurements in late winter. Lent and Knutson (1971) suggested that measurements of snow depth alone would be adequate to predict where muskoxen will feed. The extent of icing in the snow profile is also an important parameter and should be considered together with snow depth. While muskoxen appear well adapted for breaking large slabs of wind-packed snow through chinning or digging with their short, strong forelimbs, extensive icing and particularly the formation of ground-fast ice is likely to make large areas unavailable for grazing.

By selecting habitats with exposed vegetation and shallow snow cover, muskoxen would reduce the energetic costs associated with cratering. Since movements are restricted during late winter and calving (Section IV), the energy cost of walking would be reduced; however, the intensive use of a small area would also limit the opportunity for forage selection. In winter, forage selection is less important and muskoxen use a strategy of localized foraging which is possible assuming muskoxen have a relatively high digestive efficiency for forage of high fiber content.

The effect of temperature and wind on muskox behavior may be largely indirect, through their influence on forage availability and quality and the degree of insect harassment. White *et al.* (1975) related ambient air temperatures and wind speeds to different levels of insect harassment. In winter, the direct effects of windchill on muskox activity budgets were small as evidenced by the large variability in the incidence of both feeding and lying within each interval of windchill equivalents. The results are different from those obtained by Roby (1978) on caribou of the Central Arctic Herd where feeding increased with increasing windchill equivalents. Muskoxen however, did spend the largest proportion of time lying (63% for the total herd) during late winter, a time when the highest windchill values were recorded. The effectiveness of bedding posture as a heat conservation mechanism is relatively greater at higher wind velocities and colder temperatures (Moen 1973). Heat loss in muskoxen is also reduced by their slow movements and insulative properties of their thick coat made up of long (450-620 mm in bulls, Tener 1965), outer guard hairs and short (50-70 mm), soft underwool.

Tener (1965) felt that cold, stormy weather could be directly lethal to newborn calves. Recent studies indicate that the healthy neonates are well prepared for such conditions through a combination of highly efficient insulation and a high thermogenic potential from large deposits of metabolically active brown fat (Blix *et al.* 1979). Further thermoregulatory benefits are apparently derived through the large amount of time spent lying (78%) during the first week of life.

This places the neonate in a favorable microclimate where wind velocity is reduced by surface friction. The reduction in wind speed is greater over a rough, vegetation-covered surface (such as Tussock Meadow) than over a smooth, snow surface (Moen 1973). Additional protection is received by bedding down on the leeward side of the cow. Exposed body surface area, especially that less well insulated, is also reduced when lying.

In summary, the duration of suckling bouts decreased with age of the calf and varied between calf cohorts. Correspondingly, calves spent a larger proportion of their time grazing in late summer. Daily eating times for muskoxen were lower than those reported for caribou which may reflect differences in animal energy balance and subsequent nutrient requirements. In summer, muskoxen selected feeding areas in relation to plant phenology and the abundance of preferred forage species; a strong preference was shown for Creek Willow Thickets. Winter feeding areas were selected primarily on the basis of snow characteristics. Windchill had little direct effect on muskox winter activity budgets.

IV. MOVEMENTS AND SEASONAL DISTRIBUTION

A. Group Movement Rates

The daily group movement rates, obtained by measuring the map distance between bedding locations over a 24-h period, showed a strong degree of seasonal variability (Fig. 12). An analysis of variance, following a logarithmic transformation of the data, confirmed significant

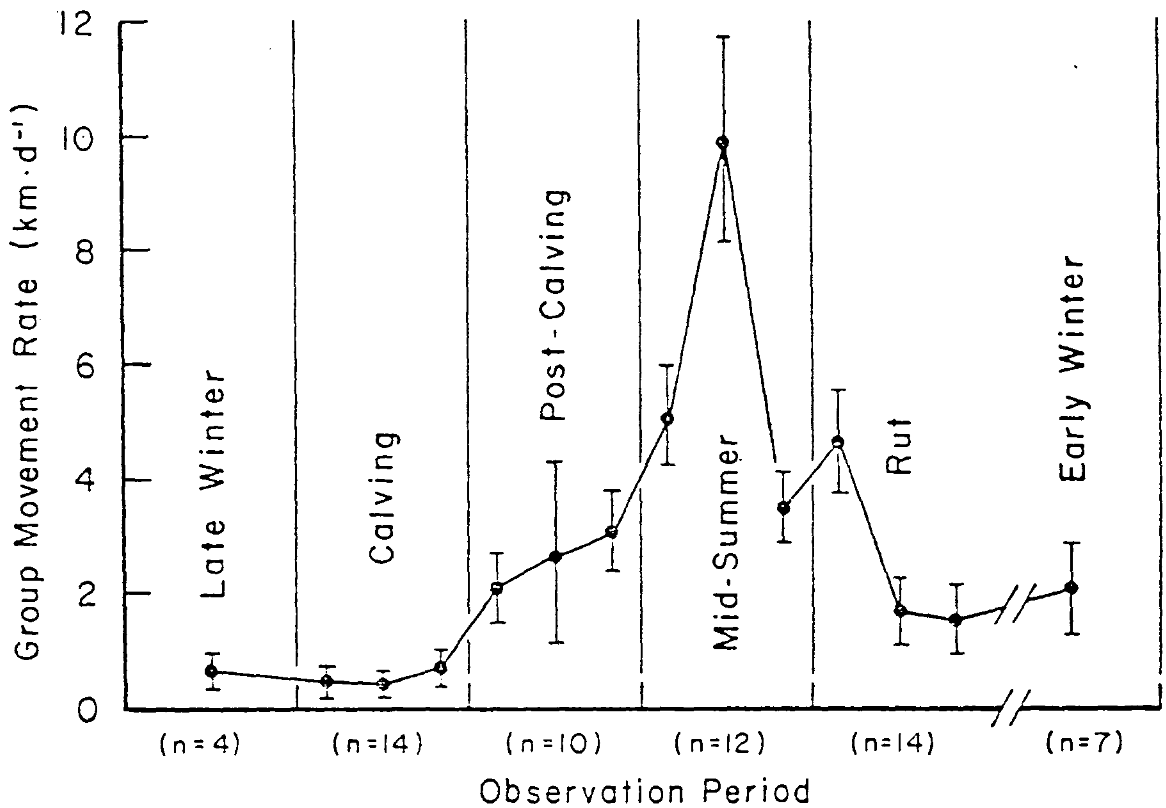

Figure 12. Seasonal variation in the mean rate of group movement (±SD) for a reintroduced muskox population during periods of observation, Sadlerochit River, 1979-80. Sample sizes refer to the number of 24-h periods for which movements were recorded.

differences in movement rates between periods of observation ($F = 18.2$, $df = 5$ and 55, $p < 0.001$). In late winter, movement was restricted as the herd remained feeding within a small area in the northern part of the Sadlerochit River drainage. The lowest daily rates of movement were recorded during calving when the herd moved, on the average, less than 0.5 $km \cdot d^{-1}$. Movement rates increased during post-calving to reach a peak in mid-summer when daily group movement rates were significantly higher than during other periods. Between 11-20 July, the four movements recorded averaged 9.9 $km \cdot d^{-1}$ (SD ± 3.6). Movement rates again declined during the rut and early winter. Of 27 directional herd movements observed, where leadership was obvious, 15 were led by adult cows and 12 by bulls. The few observations of isolated bulls, either as single or in groups of two or three, suggested that they moved more extensively than the large groups during summer. A group of two bulls covered 80 km during a period of 6 days in June, averaging 13.3 $km \cdot d^{-1}$.

B. Seasonal Distribution

I plotted range extremities of the Sadlerochit herd based on observed movements between 1978-80. By marking locations reported for the herd between 1972-77 (Roseneau and Stern 1974; Bente 1977) I found that 33 out of 39 observations made of groups with at least 10 muskoxen fell within the same area that was used during this study (Fig. 13). The area measures approximately 330 km^2. Assuming a muskox population of 60 animals, including lone bulls, the density in 1979 was 0.182 muskoxen km^{-2}.

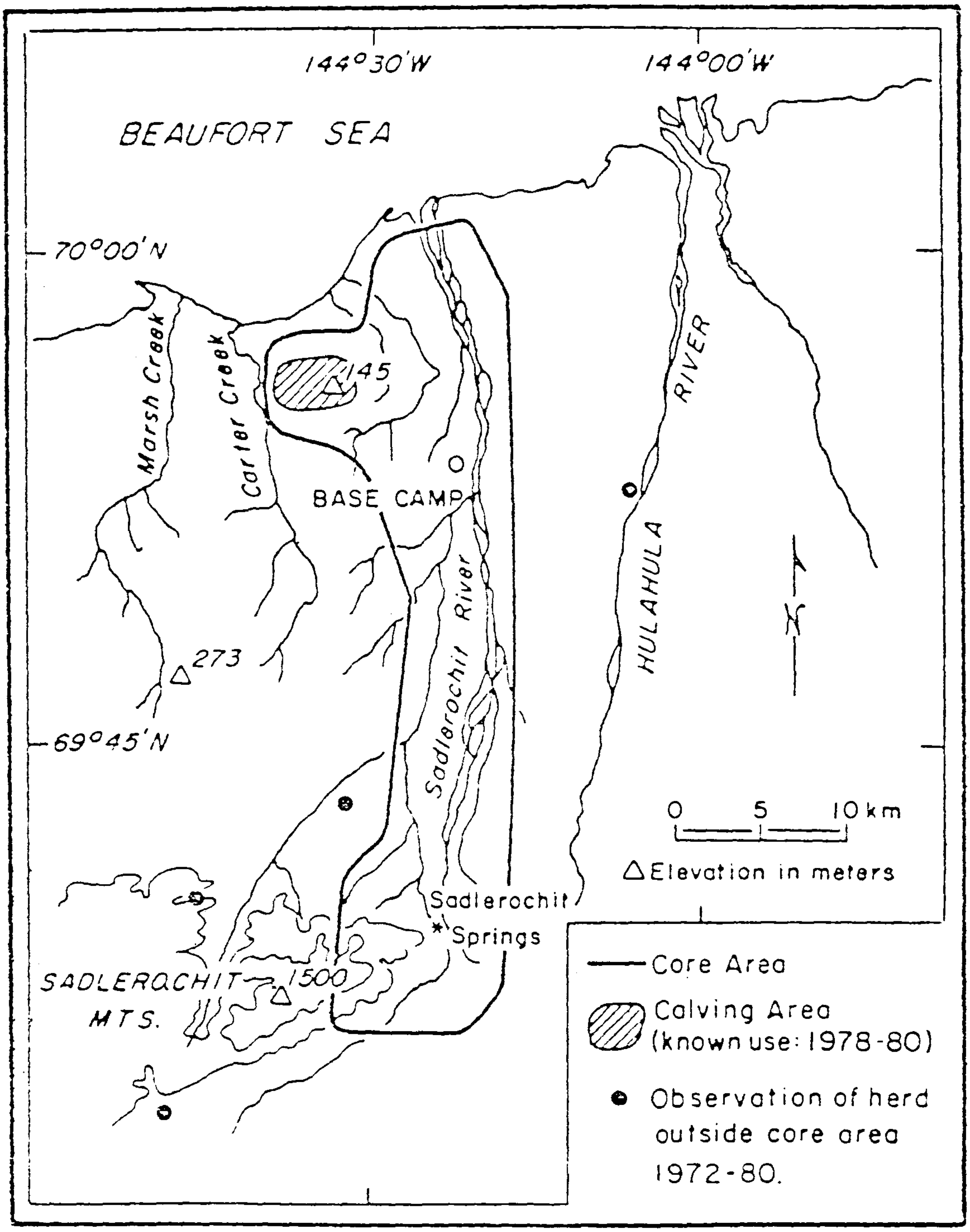

Figure 13. Map showing the core area used by the Sadlerochit muskox herd between 1972-80.

The seasonal distribution of the herd indicated overlap between feeding areas used during parts of the summer and those used in early and late winter. Feeding movements in the riparian habitat were generally linear as the muskoxen moved along the river drainage. Calving in 1979 and 1980, and most likely also in 1978 (Robus, pers. comm.), occurred in the hills close to Carter Creek (Fig. 13). During post-calving, the muskoxen moved towards the Sadlerochit Springs area where the entire herd spent 10 days feeding on a Tussock Meadow plateau at an elevation of ca. 700 m. After moving north along the river in early mid-summer, the herd returned to the hills near the calving area where it remained until late July. Movements at this time were extensive although the muskoxen remained within the described core area. During the first week of rut, the herd moved south along the river and split up into two groups. The larger group left the river drainage and returned to the creeks immediately south of the calving area. In early winter 1979, the herd had rejoined and was located in the same riparian area, opposite base camp, where it was first observed in late October the previous year.

C. Discussion - Movement Rates and Seasonal Distribution

Two main types of movement have been described for muskoxen. Wilkinson *et al.* (1976) referred to movement as being either within or between feeding areas while Smith (1976) distinguished movements involving simple grazing patterns ("drift") from directional, "led" movements when steady movement of the herd was usually maintained.

Presumably, these authors are describing the same type of movement, using different terms. Observations of the Sadlerochit herd support the distinction of drift within feeding areas from the directional movements between such areas.

Since movements, particularly within feeding areas, are seldom linear, the observed movement rates generally underestimate the actual distances covered. However, the relative rates are useful when comparing seasonal differences in the extent of movement. During calving, movement rates were particularly low and the muskoxen often returned to the same bedding location more than once after being spread out during a feeding period. Cows with newborn calves moved less than other muskoxen and served as a focal point for the rest of the herd. The high movement rates in mid-summer coincided with the emergence of mosquitos, and the extensive movements at the time may have resulted from the search for insect-relief areas. Muskoxen remained more stationary during the rut as the dominant bull actively herded cows that diverged from the group back to it, thereby promoting herd stability. Similar observations were made on Nunivak Island (Smith 1976) where movement rates averaged 1.5 km $\cdot$ d^{-1} for three groups during the rut.

Movement rates of muskoxen are considerably lower than those observed for caribou. White *et al.* (1975) found undisturbed groups of caribou to move about 14 km $\cdot$ d^{-1} during the summer. Insect harassment increased movement rates up to 28 km $\cdot$ d^{-1}.

The wide-ranging movements of lone bulls, particularly during rut, have been mentioned by Tener (1965) and Smith (1976). An extensive movement was observed among the muskoxen recently introduced to the Seward Peninsula, Alaska, as a lone bull travelled about 48 km over a 24-h period (C. A. Grauvogel, pers. comm.). The observation was made after the muskoxen had localized in the area. Pederson (1931, *in* Hone 1934) and Tener (1965) have suggested that colonization of an area by muskoxen is preceded by the appearance of lone bulls.

The seasonal distribution of the Sadlerochit herd has already been shown to be related to snow conditions and forage availability and quality (Section III). The calving area is characterized by altitudinal relief providing south-facing slopes with exposed vegetation and early green-up. The extensive visibility from the ridge area may be important in detecting potential predators or disturbance during the critical calving period; predator density may also be lower away from the riparian habitat. The area is well-drained, providing a dry substrate for the neonates. The avoidance of the riparian habitat in early summer is probably related to the flooded conditions of the river drainage following break-up, which would present a hazard for the movement of calves as well as resulting in inundation of potential feeding areas.

The fidelity of the muskox herd to the Sadlerochit River drainage and adjacent coastal plain indicates the importance of tradition in directing movements and the subsequent use of feeding areas. Since directional movements are led by adult muskoxen (Gray 1973; Smith 1976; pers. obs.), the consistent use of the same areas observed in this study is influenced by the early experience of muskoxen that originally colonized the area about 10 years ago. It seems relevant to speak of a "home range" for the herd, a concept defined by Burt (1943) as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young." The concept is less useful for lone bulls due to their extensive wanderings.

The efficiency of range use is likely to decrease with increasing population levels and may act as a mechanism for herd fracturing when herd size exceeds the bounds of feeding efficiency. As the muskox population continues to grow, fracturing of the herd will probably result in extensions of the home range to include additional feeding areas and possibly the use of distinct seasonal home ranges. Presently, muskox density in the study area is comparatively low (0.182 km^{-2}) but similar to the overall density of 0.200 muskoxen km^{-2} on Nunivak Island (Spencer and Lensink 1970). Much higher densities are reported by Hubert (1974) who estimated 0.867 muskoxen km^{-2} on northeastern Devon Island, N.W.T., and by Wilkinson *et al.* (1976) from their study on north-central Banks Island, N.W.T., where muskox densities varied from 1.070 to 2.970 km^{-2}.

The concept of a home range for muskoxen is also apparent from a report by Lundh (1979) on the establishment of a herd in Sweden that originally wandered over from Norway in 1971. The population, 17 muskoxen in 1979 (Lundh, pers. comm.), has remained within a 150 km^2 area with distinct winter and summer ranges located 20 km apart. Calving has occurred in an area (2-5 km^2) at tree-line that is part of the winter range. This is the area that was first used for calving in 1973 and has since then been used every year.

The inheritance of social traditions has been described in wild sheep (Geist 1967, 1971) where seasonal areas of distribution are maintained by passing on patterns of home range use from generation to generation. Similarly, herd formation in muskoxen allows the passage of knowledge regarding feeding areas which would assist the survival of young animals (Tener 1965). Familiarity with a particular area undoubtedly results in a more efficient range use than would random movements.

In summary, the year-round fidelity of the Sadlerochit herd to a limited area made it possible to delineate a home range with overlapping seasonal ranges and a distinct calving area. Muskoxen were most stationary during the calving period; the highest movement rates were recorded during mid-summer which coincided with periods of severe insect harassment.

V. INTERSPECIFIC INTERACTIONS

A. Insects

Large numbers of mosquitos (*Aedes* spp.) were present in the study area throughout mid-summer, from 1 July to 31 July. The intensity of harassment varied on a daily basis and became severe during periods of high temperatures (generally above 15°C) in combination with low wind speeds. A cool period with frequent coastal fog in early August 1979 resulted in reduced numbers of mosquitos.

Behavioral responses by muskoxen to harassment from mosquitos were first observed on 2 July 1979. I frequently saw ear flicking and rubbing of face and sides against tussocks or other muskoxen. During resting periods, individual muskoxen often got up to shake their heads and bodies vigorously. During periods of severe harassment, it was common to see muskoxen head thrashing among shrub willows. The mosquitos appeared particularly bothersome around the facial regions of the muskoxen. In late July, two cows and at least one calf had puffy eyes, presumably as a result of irritation caused by mosquitos.

As described earlier, daily group movement rates reached a peak during mid-summer (Fig. 12) as a result of extensive movements between feeding areas. I also recorded movement rates within feeding areas during 15-min interval scan observations. During periods of severe harassment, the rate of movement was higher ($\bar{X}$ = 0.318 km $\cdot$ h^{-1}, SD ± 0.305) than when no harassment was experienced ($\bar{X}$ = 0.222 km $\cdot$ h^{-1}, SD ± 0.126). The difference was not statistically significant.

To determine whether the muskox herd tended to walk into the wind during mosquito harassment, I categorized movement as either into, away from or perpendicular to the wind. Movement direction was analyzed in relation to harassment level using the chi-square goodness of fit test. The direction of muskox movement did not differ significantly (χ^2 = 2.78, df = 2, $p > 0.05$) from a random orientation in regard to wind direction during severe insect harassment levels in mid-summer.

The influence of insect harassment on herd activity budgets is shown in Figure 14. During severe levels of harassment, muskoxen spent

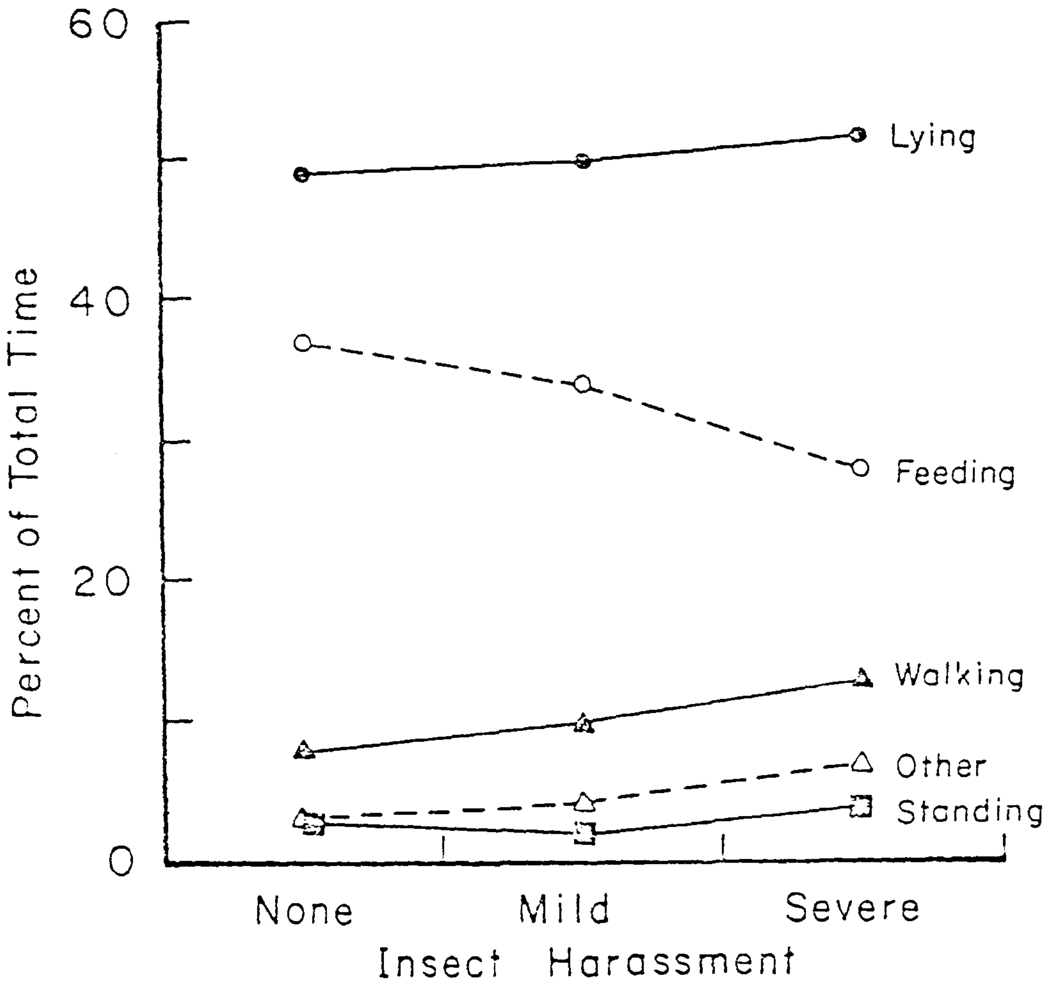

Figure 14. Effect of insect harassment on muskox summer activity budgets, Sadlerochit River, 1979.

less time feeding while "non-productive" activities, such as standing, walking and "other" increased in proportion. The latter category was primarily in response to mosquitos (e.g. rubbing, shaking and head thrashing). No playing behavior was seen among calves between 2-28 July, although it was common both before and after this period.

Some indication of habitat selection for insect relief was apparent. During periods of insect harassment the herd usually rested in higher-lying, drier areas where a breeze was common during mid-day. On three separate occasions during mid-summer, the herd used an isolated mud slope for resting and frequent rubbing. The slope was dry and devoid of vegetation. While mosquitos were abundant in the wind-protected Creek Willow Thickets, the tall shrubs were used extensively for rubbing and head-thrashing by the muskoxen.

B. Caribou

Part of the Porcupine caribou herd was present in the study area from 11 May to 21 June 1979. The largest concentrations were seen between 10-20 June, when an estimated 4-6000 caribou were slowly moving through the study area in a northeasterly direction.

After calving in the Carter Creek area, the muskoxen moved to the Sadlerochit Springs where large groups of caribou were present. Two days after arriving at the springs (15 June), the muskoxen moved up a steep talus slope to a Tussock Meadow plateau where relatively few caribou were seen. The herd moved down from the plateau 4 days after the last bands of bull caribou had left the area.

I observed a total of nine interactions between caribou and musk-oxen. In all interactions, one or more caribou approached the muskox herd. The reaction of the muskoxen varied in intensity depending upon the number of caribou approaching and the distance to the herd. Most frequently, the muskoxen bunched up and observed the passing caribou with raised heads. On 20 June, a band of 15 caribou passed 75 m to the side of the grazing muskoxen. After bunching up, the muskox herd started running away from the caribou and ran for 150 m while the caribou trotted alongside. As the muskoxen stopped, the caribou circled downwind of the herd and then left the area.

C. Discussion - Intraspecific Interactions

Little information is available on the response of muskoxen to insect harassment. This is partially explained by the relatively low densities of insects on muskox ranges in the Canadian High Arctic where the species has been studied in more detail than elsewhere. Clarke (1940) described muskoxen in the Thelon Game Sanctuary, on the Canadian mainland, as both "fly and predator proof". However, Tener (1965) found numerous "bites" on examination of the eyelids of five bull muskoxen collected in the same area during the insect season. The herd kept at College, Alaska, before being transported to Nunivak Island in 1935, suffered greatly from mosquitos (Hone 1934; Palmer and Rouse 1936). Muskoxen on Nunivak Island have been observed rubbing their heads in willows, lying on snowbanks and sitting in rivers to avoid insects (Bos 1967). Individuals in the Sadlerochit group were standing in water for up to 20 min at a time in mid-August during a period of exceptionally warm weather when insect harassment was less severe than in July. Here, the observed behavior may more likely be a means of dissipating heat than avoiding insects.

Rubbing and shaking is observed in muskoxen during various times of the year, particularly when the underwool is being shed. However, the increased frequency of these activities during mid-summer plus the fact that most muskoxen had already shed their wool during post-calving, suggests that rubbing and shaking are also a response to mosquitos.

Muskox responses to insect harassment appear less pronounced than those reported for caribou. During severe harassment, caribou show a strong tendency to aggregate and to drastically increase movement rates, directing their movements into the wind while actively seeking out insect-relief areas (Thomson 1973; White *et al.* 1975; Roby 1978). In addition to mosquitos, caribou also experience harassment from oestrid flies (the warble fly, *Oedamagena tarandi*, and the nasal bot fly, *Cephenomyia trompe*). The "aberrant running" (Curatolo 1975) characteristic of caribou in response to oestrid flies, was not observed among muskoxen. I noted few reactions of muskoxen to any insects in August when the oestrid flies are most common on the coastal plain. Tener (1965) found no evidence of larval scars from warble flies in the numerous muskox hides he examined.

The time spent lying and feeding decreased drastically during severe insect harassment in caribou (White *et al.* 1975) and wild reindeer (Thomson 1973). While muskoxen decreased their time feeding, the time spent lying increased slightly. Espmark and Langvatn (1979) suggested that inactivity could be an important part of the strategy used by red deer (*Cervus elaphus*) in response to head fly (*Hydrotae irritans*) harassment. In a site with low mosquito density, inactivity may result in fewer mosquitos harassing the muskoxen. The insignificant change in the total time spent lying over different harassment levels suggests that muskoxen are more tolerant to high mosquito densities than are caribou. This is supported by the lack of observations suggesting that muskoxen directed their movements into the wind during periods of severe harassment.

A review of the literature suggests that competition for forage between muskoxen and caribou is limited, or insignificant, as a result of differences in habitat selection (Tener 1965; Bos 1967; Spencer and Lensink 1970; Wilkinson *et al.* 1976; Miller *et al.* 1977; Parker 1978). Consequently, few direct encounters between the two species apparently occur. Wilkinson *et al.* (1976) observed only three interactions in over 450 h of observations; in two of those cases, the species ignored each other. Gray (1973) described interactions similar to those observed in the Sadlerochit River area. In addition, Gray often saw caribou and muskoxen grazing in close proximity to each other without any overt reactions.

The encounters observed in this study suggest a limited tolerance by muskoxen to approaching caribou. It appears, that the massive influx of caribou in June influenced the use of feeding areas by muskoxen. It is tempting to speculate that by moving to the elevated

Tussock Meadow plateau, the muskoxen avoided the large concentrations of caribou in the riparian habitat and on the adjacent coastal plain. By avoiding caribou, muskoxen are able to forage more efficiently and minimize disturbance caused by approaching caribou. Although caribou were observed using forage species similar to muskoxen (Robus, in prep.), the effects of potential competition, which assumes the active demand for a limiting resource (Miller 1967), are reduced during early summer when the food resource is abundant. Competition is further limited by the short period of the year that caribou use the Sadlerochit River area.

In summary, behavioral responses of muskoxen to mosquito harassment were observed in mid-summer. During severe harassment, muskoxen decreased the proportion of time spent feeding while increasing movement rates. Observations of direct interactions between muskoxen and caribou, following a temporary, massive influx of caribou to the study area, suggested a limited tolerance of caribou by muskoxen.

VI. COMPARISON WITH A HIGH ARCTIC MUSKOX POPULATION

A. Range Description

Bathurst Island (BI) is part of the Queen Elizabeth Islands in the Canadian Arctic Archipelago. The muskox range that will be compared to the Sadlerochit River (SR) area is centered around the broad valley between Bracebridge and Goodsir Inlets including an area of 160 km^2 (Fig. 15). The valley, better known as Polar Bear Pass is about 27 km long and 4 km wide, surrounded on either side by rolling hills.

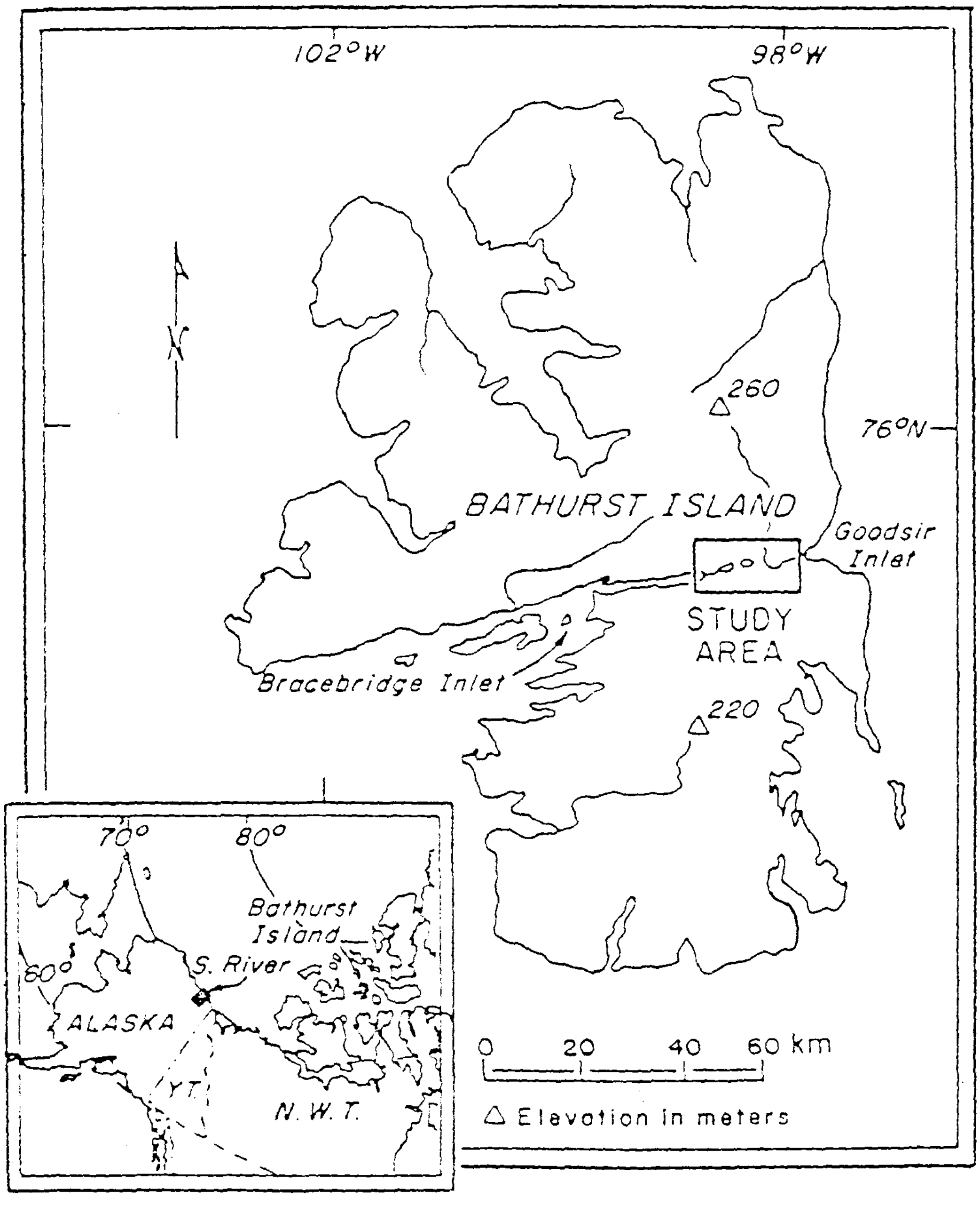

Figure 15. Map of the Polar Bear Pass study area, Bathurst Island, with inset showing its location relative to Sadlerochit River.

A description of vegetation types in Polar Bear Pass, based on work by Geale (1980), is given in Appendix C. When compared to the SR area, BI has less diversity of vascular plant species used by muskoxen. Legumes (Family Leguminosae) are not present and the only woody shrub is the prostrate willow (*Salix arctica*). Plant productivity values for the various vegetation types in Polar Bear Pass are shown in Appendix D. Although not directly comparable to the aboveground biomass values reported for individual species at SR (Robus, in prep.), it is apparent that plant productivity is considerably lower on BI. Peak biomass values for the current year's growth of *Salix alaxensis* and *S. pulchra* at SR were 54.17 and 36.25 $g \cdot m^{-2}$ respectively (Robus, in prep.); a similar value for *S. arctica* on Willow Meadow was 18.56 $g \cdot m^{-2}$ (Appendix D).

A comparison of weather data between the two areas (Appendix B) indicates considerably higher temperatures year round at SR. Break-up and the emergence of new vegetative growth occurred over a month later on BI. For a more detailed description of the climate, geology and fauna of Polar Bear Pass and BI, the reader is referred to Gray (1973).

B. Population Characteristics

A seasonal influx of muskoxen to Polar Bear Pass was apparent during post-calving and early rut. Densities varied from 0.156 to 0.356 muskoxen km^{-2}; in comparison, the muskox density at SR during summer 1979 was 0.132 km^{-2}.

Mean herd size on BI was 15.0 (SD ± 8.4, n = 10, range 2-29). I made composition counts from the ground twice during post-calving and once during the rut. The proportion of calves varied from 23.7 percent to 31.6 percent of the total number of muskoxen observed (Table 7). The number of calves per adult cow (4 yrs +) ranged from 0.68 to 0.86. While most cows with calves were 4 years and older, I observed one 3-year old cow with a calf. Productivity, as judged by the number of calves per reproductive age cow, was higher at SR where cows were also breeding at an earlier age with some 2-year old females producing calves. A comparison of the age distribution between the two populations indicated fewer subadults and more adult females in the herds observed on BI.

C. Activity Patterns

A comparison between BI and SR showed no significant differences in the duration of activity and resting bouts during post-calving, midsummer and rut (Table 8). There were significant differences in the length of both activity ($t = -3.08$, $df = 12.6$, $p < 0.05$) and resting ($t = -3.16$, $df = 21$, $p < 0.01$) bouts between the two areas during calving.

Activity budgets on BI were recorded as the proportion of time muskoxen spent "active" versus "lying". I was unable to record differences between age/sex classes. The incidence of lying during each season was compared to similar data from SR (Fig. 16) using the method described by Sokal and Rohlf (1969, p. 607) for testing the equality

Table 7. Sex and age composition of muskoxen at Polar Bear Pass, Bathurst Island, 1978, with similar information from Sadlerochit River, 1979.

Location	Age and Sex Group (%)					Calves per cow 4 yrs +	N
	Bull	Cow	Subadult*	Yearling	Calf		
Bathurst Island							
5 June	15.8	31.5	4.4	21.0	23.7	0.68	114
21 June	7.0	36.9	10.5	14.0	31.6	0.86	57
7 August	8.7	37.0	6.5	17.4	30.4	0.82	46
Combined**	12.0	35.9	6.5	18.4	27.2	0.76	217
Sadlerochit River	10.3	20.7	19.0	20.7	29.3	0.89†	58

* Two and 3-yr old animals.

** Combined total is likely to include individuals observed more than once.

† Represents number of calves per cow 2 yrs +.

Table 8. Duration (min) of muskox activity and resting periods at Bathurst Island (BI), 1978, and Sadlerochit River (SR), 1979-80. Mean, standard deviation and sample size (in parenthesis) are shown. NS = not significant.

		Season			
Period	Location	Calving	Post-calving	Mid-summer	Rut
Activity	BI	116 ± 32.1 (12)	142 ± 62.1 (18)	106 ± 69.8 (25)	113 ± 40.4 (13)
	SR	185 ± 64.8 (10)	143 ± 51.1 (31)	85 ± 39.1 (39)	129 ± 46.2 (21)
		$p < 0.005$	NS	NS	NS
Resting	BI	171 ± 46.4 (13)	123 ± 31.4 (20)	84 ± 29.8 (30)	114 ± 42.9 (13)
	SR	252 ± 75.5 (10)	128 ± 47.5 (31)	98 ± 40.9 (40)	110 ± 28.4 (26)
		$p < 0.01$	NS	NS	NS

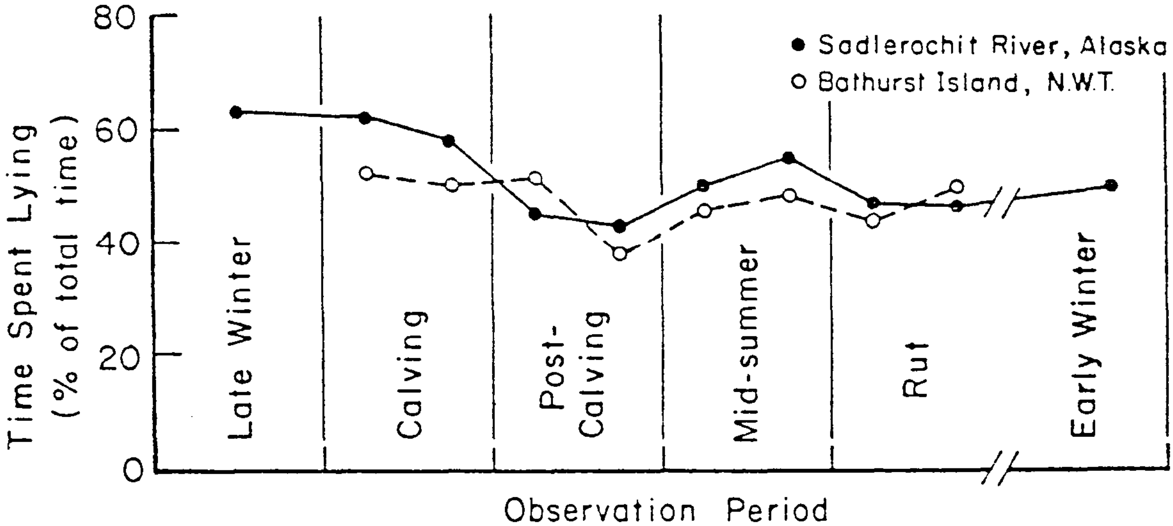

Figure 16. Seasonal comparison between two muskox populations in the proportion of time spent lying during periods of observation.

of two proportions. The percent of time spent lying was not significantly different between the two populations.

The time spent in rutting-related activities was calculated for an adult bull in a herd of 15 muskoxen. I observed the first copulation on 12 August. On the basis of 84 activity scans, the bull spent 34.6 percent of the total time in courtship behavior between 8 and 12 August 1978. No other adult bull was present in the vicinity of the herd during that time. In comparison, the dominant bull in the SR herd spent up to 50 percent of the time in rutting-related activities when two other adult bulls were present in the herd.

D. Feeding Behavior

Suckling bouts were consistently shorter on BI (Fig. 17). In mid- and late summer the average nursing lasted 25-30 sec. I observed cows nursing yearlings on 14 different occasions throughout the summer with a mean duration of 17.4 sec (SD ± 3.8). At SR, I never observed cows nursing yearlings during the summer; however, I did see two sucklings by yearlings during the preceding calving season.

The herds observed on BI showed marked seasonal preferences for specific vegetation types (Table 9). When analyzed over the entire study period, Willow and Mesic meadows were used at about three times their availability (preference ratios of 3.00 and 2.75, respectively). Similarly, muskoxen at SR showed a strong selection for feeding in Creek Willow Thickets during the summer (PR = 4.57).

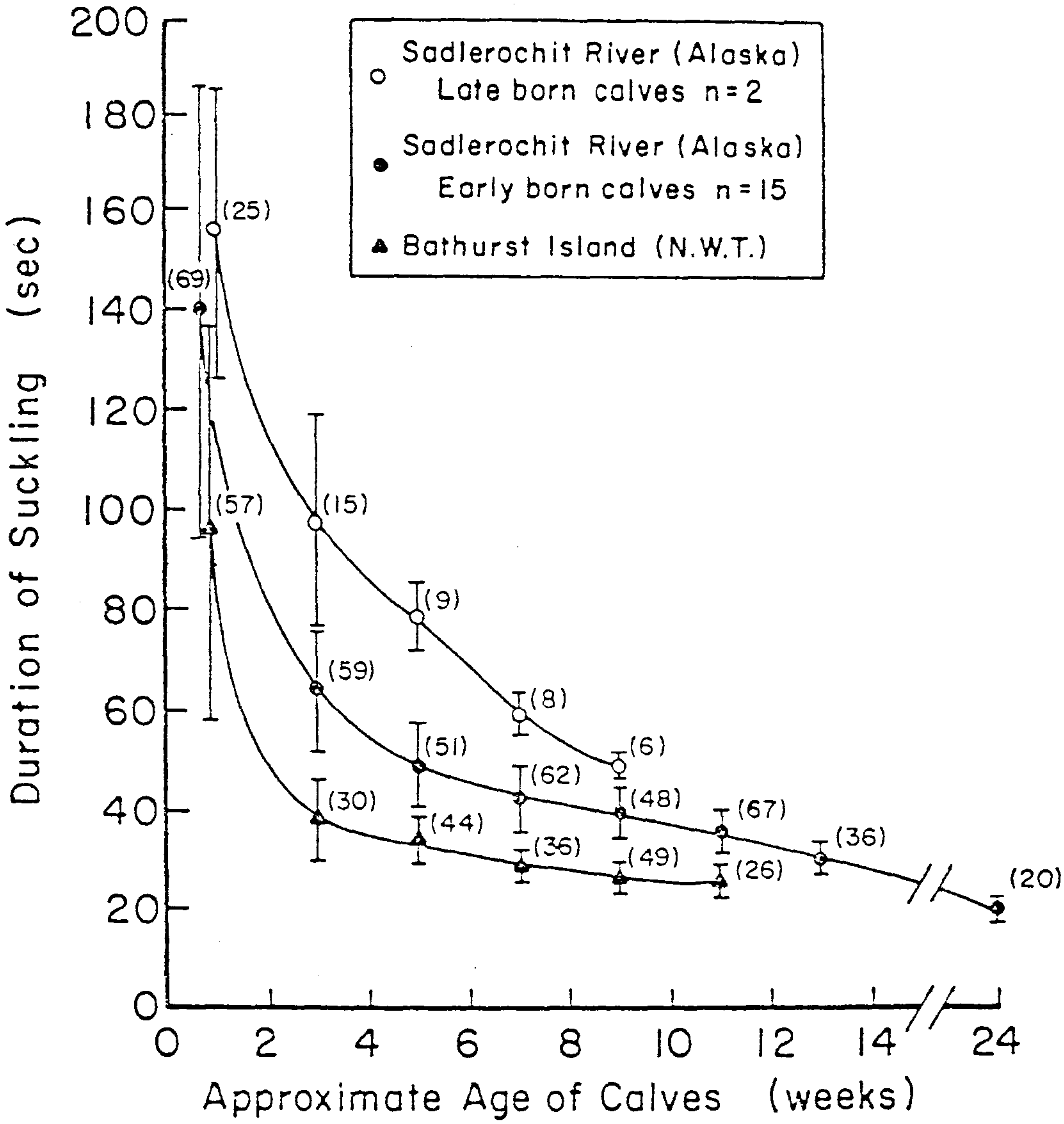

Figure 17. Comparison of the ontogeny of suckling behavior in muskox calves on a high arctic range (▲) with late born (○) and early born (●) calves from an Alaskan range.

Table 9. Seasonal selection of available vegetation types by muskoxen, Polar Bear Pass, Bathurst Island, 1978.

Season	Number of Observations	Percentage Observations in Vegetation Type							
		Ridge (13)*	Polar Desert (7)	Mesic Ridge (18)	Hummock/ Seepage Slope (9)	Mesic Meadow (4)	Hydric Meadow (20)	Willow Meadow (7)	Un-vegetated (13)
Calving	81	9	9	6	23	12	17	10	14
Post-calving	153	18	9	3	14	18	16	20	2
Mid-summer	200	13	9	4	23	6	15	30	1
Rut	224	8	2	12	11	10	39	19	0
Overall	658	12	7	7	17	11	23	21	2
Preference Ratio		0.92	1.00	0.39	1.89	2.75	1.15	3.00	0.15

* Availability expressed as the percentage of range covered by this vegetation type.

An analysis of plant epidermal fragments from fecal samples collected on BI indicated high proportions of willow (*Salix arctica*) throughout the summer and especially during mid-summer (Appendix E). Samples from adult and calf muskoxen had similar plant species composition except during post-calving when more willow and less sedges (*Carex* spp.) were present in calf feces. Visual examination of winter feeding areas showed browsing signs on willow twigs and heavy cropping of graminoids which is reflected in the large proportion of *Carex* spp. in the winter feces.

E. Movement Rates

Daily group movement rates were considerably lower on BI during mid-summer and early rut (Fig. 18). Movement rates were comparable during calving and post-calving. The limited movements during the rut were evidenced by a herd of 29 muskoxen that remained within a 5 km^2 area for 20 days (7-27 August). Similarly, a herd of 15 muskoxen used an area of 1.5 km^2 over a period of 10 days between 6-16 August. While daily movements within feeding areas were usually irregular, there appeared to be preferred grazing areas which served as focal points for directional movements. In agreement with observations from SR, lone bulls on BI appeared to travel more extensively than the herds, particularly prior to and during rut. A bull observed between 21-25 July moved a distance of 24 km, averaging 4.8 $km \cdot d^{-1}$.

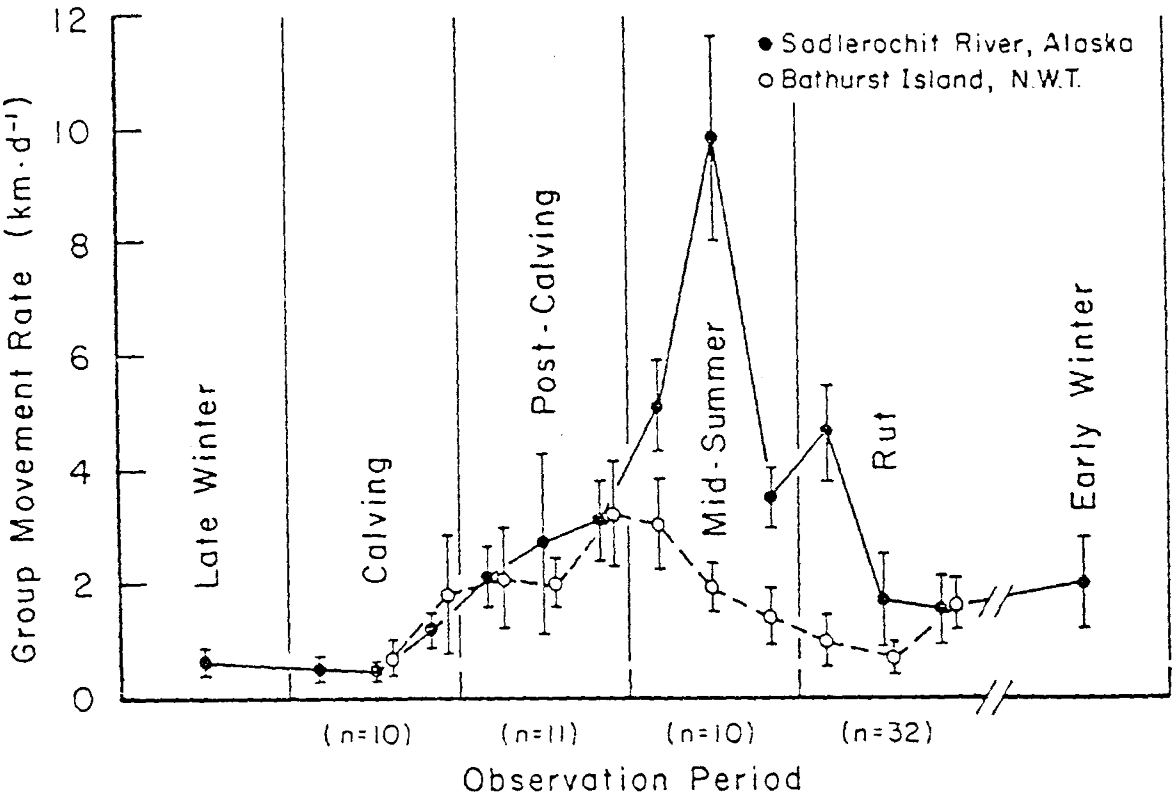

Figure 18. Seasonal variation in the mean rate of group movement (±SD) between two muskox populations during periods of observation. Sample sizes refer to the number of 24-h periods when movements were recorded for different herds on Bathurst Island.

F. Discussion - Comparative Aspects

The muskox population on BI has undergone a series of drastic fluctuations over the past 20 years, including periods of total reproductive failure (see Gray 1977 for a review). Based on a history of occasional increased mortality combined with fluctuating recruitment rates, Hubert (1974) suggested "boom-or-bust" rates of population change on Devon Island, N.W.T. This pattern agrees with the observations from BI. The large proportion of calves and yearlings observed in 1978 suggests that the muskox population was in a state of increase and that winter mortality during 1977-78 was low. Calf production was comparable to that found in the SR population which indicates that the potential for rapid increase is also present among muskoxen in the High Arctic during periods of favorable environmental conditions. I believe the earlier age of first reproduction among females in the SR herd reflects differences in range quality between the two areas. The higher productivity and diversity of the SR range, coupled with a longer growing season, presumably enables the muskoxen to maintain a higher nutritional plane during the time of conception. Alendal (1971a) attributed the early sexual maturity among muskoxen in Norway to the abundance of forage and the early onset of the vegetative growing season.

Differences in the duration of activity and resting periods between muskox populations have been related to differences in range quality. Parker and Ross (1976) compared activity patterns of muskoxen at Bailey Point, Melville Island and Mokka Fiord, Axel Heiberg Island, N.W.T. The shorter feeding and resting times observed at Bailey Point were related to the higher plant productivity of the area. Gray (1973) found muskoxen on BI to feed and rest at intervals of approximately 150 min each. In their study on Banks Island, N.W.T., Wilkinson *et al.* (1976) found feeding periods to be, on the average, one-half as long as those reported by Gray and suggested that the summer range of muskoxen on Banks Island was superior.

The similarity in the duration of activity/resting bouts and in the proportion of time spent lying between SR and BI, despite the differences in plant productivity and diversity, indicates that activity patterns are of limited use when making range comparisons. While total plant productivity at Bailey Point (Parker and Ross 1976) appears similar to that recorded at Polar Bear Pass, BI (Appendix D), the length of resting and feeding periods are shorter (summer mean: 75 and 98 min, respectively) than those observed on BI (summer mean: 120 and 104 min, respectively). It seems more useful to analyze activity patterns of muskoxen as a general, rather than a range-specific response to seasonal changes in the availability and quality of forage. Thus, the short resting periods observed at both SR and BI during July and early August are also apparent from the information provided by Gray (1973) and Parker and Ross (1976), presumably reflecting shorter rumination times as a result of increased forage digestibility.

When comparing observations on suckling behavior, the frequency as well as the duration of suckling bouts are important parameters. I was unable to record frequencies of suckling at SR due to the large number of calves in the study herd. However, the relatively fewer calves on BI made it possible to estimate both the frequency and intensity of suckling by recording all successful attempts during a given activity period. As with duration, the frequency of sucklings decreased with age of the calf (Table 10). By combining frequency with duration, I found the resulting time spent suckling to decrease from 20.5 min $\cdot$ d^{-1} during the first 2 weeks following parturition to 2.0 min $\cdot$ d^{-1} in mid- and late summer.

Assuming the frequency of suckling among calves at SR was similar to that observed on BI, it appears that the cows produced more milk at SR. I believe the earlier onset of the growing season in combination with a higher plant productivity enable the lactating females at SR to provide their calves with more milk. If growth rates in calves depend on milk production, one would expect calves on BI to be relatively smaller and to mature later. Lacking information on body weights, a visual comparison of horn development in yearling muskoxen (at 15 months) indicated relatively larger horn sizes in the SR population, where females also conceived as yearlings. While most calves at SR were weaned in mid-winter, the dependency on milk was longer on BI as evidenced by the more frequent observations of cows nursing yearlings. It appears that observation of suckling behavior in muskoxen provides a more sensitive indicator of differences in range quality than does variation in activity patterns.

The summer preference for vegetation types dominated by willow species was similar at both SR and BI. Tener (1965) suggested that

Table 10. Frequency and intensity of suckling by different muskox calf cohorts, Bathurst Island, 1978. Mean, standard deviation and sample size (in parenthesis) are shown.

Age of Calf (d)	Suckling Frequency (bouts · h^{-1})	Suckling Duration (sec)	Suckling Intensity (min · d^{-1})
1 - 15	1.06 ± 0.52 (15)	97.7 ± 78.6 (57)	20.5
16 - 44	0.45 ± 0.22 (13)	35.5 ± 12.3 (74)	3.2
45 - 84	0.37 ± 0.12 (14)	27.2 ± 5.5 (101)	2.0

willow is the most important summer food on Ellesmere Island, N.W.T., as well as in the Thelon Game Sanctuary on the Canadian mainland. Based on microscopic analysis of rumen and fecal samples, Parker (1978) concluded that muskoxen in the High Arctic consume near equal amounts of willow and sedges in summer.

I analyzed the use of Willow Meadows by muskoxen on BI in relation to the nitrogen (N) content of leaves and catkins from *Salix arctica* (Fig. 19a). A peak in N-content (4.6%) occurred immediately following the emergence of new, green leaves. This coincided with a period when muskoxen used the Willow Meadows most extensively; I calculated use for 10-day periods as a weighted proportion of the total number of observations. The reduced use of Willow Meadows was correlated with a gradual decrease in N-content ($r = 0.875$, $0.05 < \rho < 0.10$). In comparison, the seasonal change in N-content of *Carex stans* was less pronounced. A peak (2.6%) was apparent in early August, prior to the first snow fall. *Carex stans* was most common in Hydric Meadows which were used by muskoxen primarily during August (Table 9), a period when the N-content of *C. stans* was similar to, or higher than, that recorded for willow.

The N-content of related plant species (*S. pulchra* and *C. aquatilis*) from Alaska also shows a seasonal pattern (Fig. 19b) with most peaks early in the growing season. While the N-content is usually highest in young, green plant material, variations do exist as a result of environmental factors, including site variation and climate (Wielgolaski *et al.* 1975).

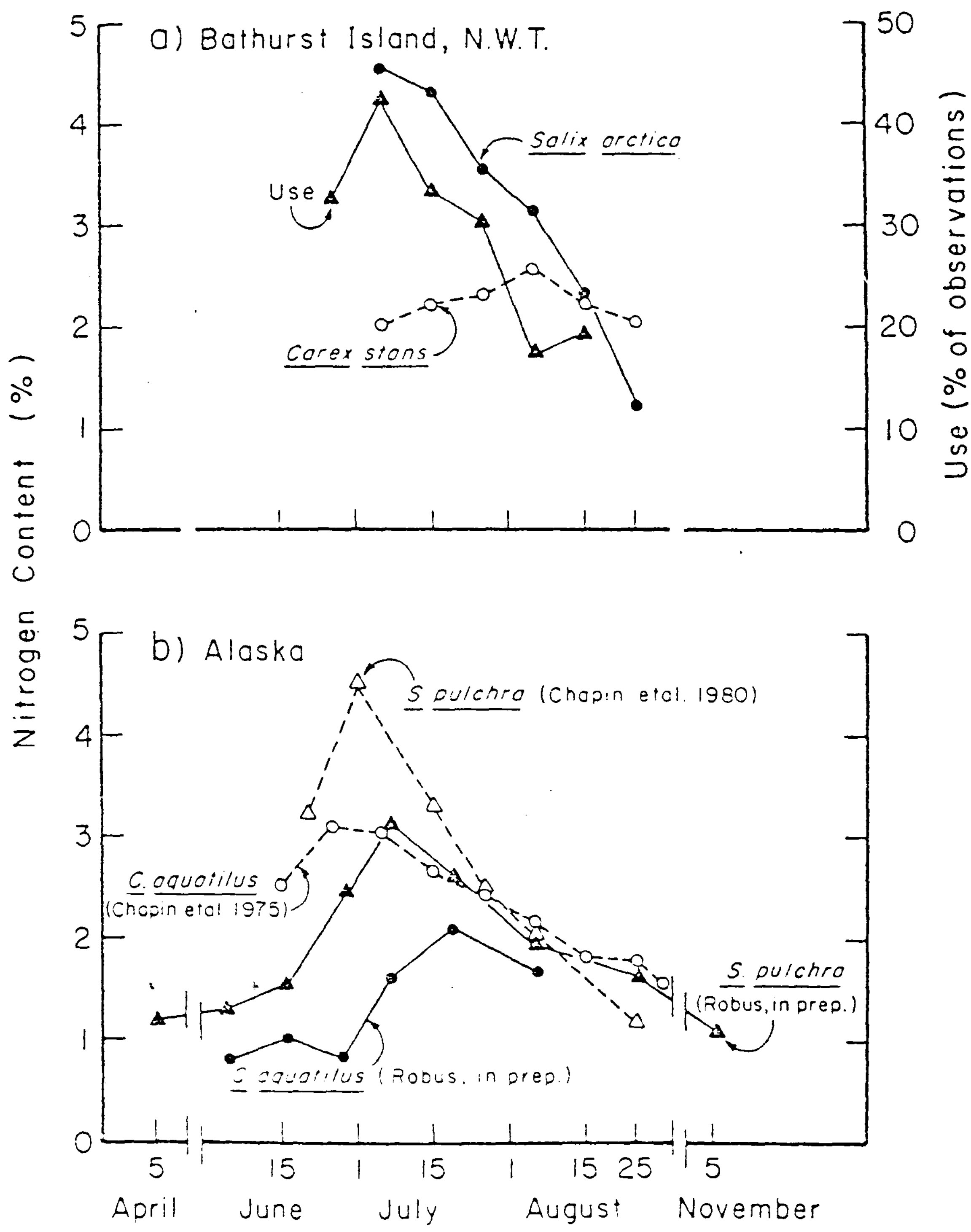

Figure 19. Seasonal pattern of nitrogen concentration in above ground, green parts of a) *Carex stans* and *Salix arctica* on Bathurst Island in relation to use of Willow Meadows by muskoxen; b) *C. aquatilis* and *S. pulchra* from Alaska, based on work by Robus (in prep.) and Chapin *et al.* (1975, 1980).

Based on the extensive summer use of sedge-producing meadows at Bailey Point, Melville Island, Parker and Ross (1976) suggested that the ability of an area to support muskoxen is dependent upon the abundance of lowland meadows. A comparison between study areas shows, that hydric meadows are more abundant but less productive on BI; willow production in both areas is similar. The observations of muskoxen at SR and BI indicate that the dependency on lowland meadows is not a general phenomena. The observed discrepancies in habitat use may reflect differences in feeding strategies which are likely to be influenced by specific range characteristics and animal energy balance. It is tempting to speculate that muskoxen at Bailey Point maximized biomass intake by selecting the most productive vegetation type, while the herds on BI selected summer habitats primarily on the basis of N-content of preferred forage species. An intermediate strategy was used at SR where muskoxen mixed N-rich legumes with abundant willow species.

The marked difference in movement rates between the Bathurst Island and Alaskan populations during mid-summer and early rut is probably related to the periods of severe insect harassment on the coastal plain of Alaska. In comparison, muskoxen on BI are not subject to harassment by mosquitos. The abundance of preferred feeding areas in Polar Bear Pass, relative to the rest of the island, is also likely to limit the extent of movement.

Based on aerial surveys, Miller *et al.* (1977) found concentrations of muskoxen along the coast of BI during spring and believed that muskoxen moved along water courses to the interior during summer. This agrees with the observations of a seasonal influx of muskoxen to Polar Bear Pass, which has also been described in detail by Gray (1973). Muskoxen on Nunivak Island moved inland during summer while using coastal areas for winter range (Bos 1967).

While winter and summer ranges on the Arctic islands may overlap, be adjacent to each other or even be up to 80 km apart (Tener 1965), it is difficult to delineate potential "home ranges" for muskoxen on BI without knowing more about individual or specific group movements. Resightings of marked muskoxen showed that individuals, whether alone or in herds, moved between Polar Bear Pass and other areas of muskox concentrations up to 50 km away (Gray 1979). Although the study area is traditionally used in spring, summer and fall, the absence of musk-oxen during mid-winter (Gray 1973, 1979) suggests that additional areas, such as the coast, are used at that time. The use of separate winter and summer ranges is probably a response to variable snow conditions affecting forage availability. In contrast, the fidelity to a fixed-sized range, shown by the Sadlerochit herd, suggests that the river drainage and adjacent tussock tundra provide sufficient forage to allow the muskoxen to remain within a restricted area throughout the year.

In summary, results from an Alaskan population were compared to similar data collected from Bathurst Island, a muskox range in the High Arctic with lower productivity and diversity of preferred forage spe-cies. Calf productivity was high in both areas during this study. It appeared that calves received more milk and were weaned earlier in the

Sadlerochit herd where females also produced calves at an earlier age. These differences could be related to differences in range quality between the two areas. Summer activity patterns were comparable and appear to be of limited use when making range comparisons between musk-ox populations. Both populations showed seasonal preferences for specific vegetation types; willows were used extensively in both areas. Movement rates were similar except during mid-summer when insect harassment resulted in increased movements by the Sadlerochit herd.

SYNOPSIS AND CONCLUSIONS

I. SADLEROCHIT RIVER STUDY

The muskox herd, that localized in the Sadlerochit River area following the transplant from Nunivak Island, is currently in a period of rapid increase. I believe that favorable range conditions, particularly the abundance of willow species and the diversity of forbs, many with nitrogen-fixing symbionts (Robus, in prep.), have enabled the muskoxen to breed in successive years with some females producing calves at 2 years of age.

The seasonal variations observed in activity patterns and feeding behavior reflect the marked seasonality of the arctic environment. Changes in forage quality and quantity appear to strongly influence the duration of activity and resting periods. While feeding may be considered a synchronized group activity, seasonal differences in age and sex-specific activity budgets are apparent. I believe these differences result from variations in specific energy and other nutrient demands during the annual life-cycle for processes such as lactation, breeding and growth. Windchill has little direct effect on muskox activity; however, the combined effect of temperature and wind leading to increased insect harassment levels resulted in a decrease in the active time spent feeding and an increase in daily movement rates. Winter feeding areas are selected primarily on the basis of snow characteristics. Muskoxen prefer windswept areas with shallow snow cover and exposed vegetation. The calving area was characterized by altitudinal relief and south-facing slopes, with exposed vegetation in early growth stages, good visibility and a dry substrate for the neonates. In summer, vegeta-tion types are selected in relation to plant phenology and abundance of preferred forage species.

Direct observations of interactions between muskoxen and caribou indicated a limited tolerance of caribou by muskoxen. Since caribou use of the study area is primarily restricted to early summer when food quality and availability are optimal, the effects of potential competi-tion for forage are presumably reduced. However, the availability of highest quality forage at growth initiation is generally limited [illegible] much less available than later in the summer (Klein, pers. comm. [illegible] Muskoxen showed a strong, year-round fidelity for the study area. [illegible] was possible to delineate a home range for the herd with overl[illegible] seasonal ranges and a distinct calving area. I believe tra[illegible] an important influence in directing movements and the subsequent [illegible] of feeding areas. The predominance of young age classes has ap[illegible] enhanced group cohesion and resulted in an unusually large her[illegible] Should present productivity levels continue, fracturing of the [illegible] herd will probably result in expansion of the range to includ[illegible] tional areas adjacent to the Sadlerochit River.

The prospect of oil exploratory and developmental acti[illegible] the William O. Douglas Arctic National Wildlife Range raises [illegible] the continued welfare of the reintroduced muskoxen. The [illegible] tat with its abundance of preferred forage species and [illegible] with its altitudinal relief and early snow melt are of [illegible] tance to the muskoxen. Disturbance to the riparian [illegible] gravel removal for drill pads, roads, etc., is likely to eliminate a portion of this habitat which is of limited availability in the Arctic National Wildlife Range. Range desertion and changes in daily activity patterns may occur as a result of harassment from low-flying aircraft or ground activity (including close encounters with photographers). This could lead to a reduced foraging efficiency which may influence the reproductive potential and ultimately the welfare of the muskoxen. In a study of the immediate behavioral responses by muskoxen to helicopter harassment, Miller and Gunn (1979) found an inverse relationship between the level of response and the altitude of the helicopter overflight. Observations during ground party activities suggested that muskoxen may respond more (by greater displacement from activity centers) to people than to a helicopter alone.

II. COMPARATIVE ASPECTS

The seasonal influx of muskoxen to the Polar Bear Pass area on Bathurst Island, in combination with the relative instability of the herds, made it difficult to delineate potential home ranges. While Polar Bear Pass is "lush" relative to the rest of the island, primary productivity and diversity of important forage species are considerably lower than in the Sadlerochit River area. In addition, large areas are completely devoid of vascular vegetation. The large proportion of calves and yearlings observed in Polar Bear Pass indicate that the Bathurst population was expanding in 1978, following a series of drastic fluctuations. The later age of breeding in females and the delayed weaning of calves probably reflect differences in range quality between the two areas. Observations on the duration of nursing bouts indicated that calves in the Sadlerochit herd received more milk throughout the summer. I believe this is related to the earlier onset of the growing season and the higher plant productivity of the area. Differences in range quality are not apparent from a comparison of activity patterns between the two populations. Daily group movement rates were similar except during mid-summer when extensive movements were observed among the Sadlerochit muskoxen presumably in response to insect harassment. A strong preference for *Salix* spp. was evident in both areas. Use of Willow Meadows on Bathurst Island was correlated with the nitrogen content of *S. arctica*, suggesting forage selection on the basis of nutrient content.

Unlike most caribou, muskoxen do not undertake large-scale migrations but remain in the tundra biome throughout the year in smaller, more stable groups. While their localized foraging characteristics may limit the phenological options available for a strong degree of forage selection, their slow movements and conservative activity budgets limit energy expenditure and reduce forage requirements. These characteristics may be important adaptations to a year-long existence in areas of low primary productivity.

Continued monitoring of the expanding, reintroduced populations in Alaska is desirable, particularly with reference to productivity and habitat selection. Range use by the Sadlerochit herd has been studied (Robus, in prep.) and the results will assist an understanding of muskox range potentials in the Alaskan Arctic. The use of specific areas for calving should be investigated in other areas of muskox distribution. Nutritional aspects of muskox biology, including metabolic rates, forage intake and digestive efficiencies, have not been adequately studied. Ongoing experiments at the Institute of Arctic Biology, University of Alaska, will hopefully provide information that, when combined with the observations of feeding behavior and activity budgets, may be used to further elucidate the relationship of muskoxen to their food base.

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Appendix A. Distribution of activities* relative to age/sex class and season based on observations at 90-min intervals of a reintroduced muskox population, Sadlerochit River, 1979. Each cell contains the observed frequency and the standardized residual.**

	Season														
	Post-calving					Mid-summer					Rut				
Age/Sex Class	L	F	W	S	O	L	F	W	S	O	L	F	W	S	O
Bull	85 0.48	78 0.07	31 -0.11	2 -0.62	2 -1.79	113 0.40	80 0.48	31 -0.66	5 0.44	5 -1.41	55 -1.07	55 -0.61	18 1.22	3 0.06	13 4.29
Cow	155 -0.45	177 0.73	38 -1.15	13 0.95	6 -0.08	240 0.33	174 -0.28	64 1.21	11 -0.92	9 -0.13	112 0.07	108 -0.51	16 -0.29	9 0.35	4 0.33
Subadult	115 -0.40	130 -0.90	47 0.12	5 -1.41	1 -1.73	176 -0.14	126 -0.34	57 0.07	18 1.10	12 1.64	113 0.61	99 -0.59	21 -0.28	10 0.09	3 0.27
Yearling	126 -0.82	139 0.21	57 0.52	3 -0.93	11 0.70	209 -0.44	162 0.37	74 0.53	8 0.07	15 0.08	120 1.48	96 -0.70	14 -1.76	7 1.12	3 0.38
Calf	243 0.97	90 -2.10	74 0.44	25 0.95	37 1.18	366 -0.10	130 0.11	83 -1.04	32 -0.23	51 -0.03	182 -1.01	118 2.43	39 1.10	18 -0.83	15 -1.37

* L = lying, F = feeding, W = walking, S = standing, O = other

** Standardized residuals (Z_{ijk}) were calculated from the formula

$$Z_{ijk} = \frac{X_{ijk} - \hat{m}_{ijk}}{\sqrt{\hat{m}_{ijk}}} \quad \text{(Bishop \textit{et al.} 1975, p. 136)}$$

where X_{ijk} = the observed frequency in the ith row, jth column and kth block, and
$\hat{m}_{ijk}$ = the expected value in the corresponding cell (based on Model No. 8, Table 4).

Appendix B. Temperature and wind recordings from Sadlerochit River (1979), and Bathurst Island (1978).

	Sadlerochit River (Alaska)				Bathurst Island (N.W.T.)			
	Temperature (°C)			Wind ($m \cdot sec^{-1}$)	Temperature (°C)			Wind ($m \cdot sec^{-1}$)
Season	Mean	Highest	Lowest	Mean Speed	Mean	Highest	Lowest	Mean Speed
Late Winter	-19.5	-12.0	-28.0	5.5	(		nd*	)
Calving**	- 9.0	+ 2.0	-23.0	6.2	-10.5	- 2.0	-22.0	6.5
Post-calving	+ 8.7	+18.0	- 3.0	4.2	- 2.4	+ 5.0	-13.0	5.0
Mid-summer	+12.8	+21.0	+ 8.0	1.4	+ 5.2	+13.0	- 1.0	6.2
Rut	+11.1	+22.0	± 0.0	2.4	+ 0.9	+ 0.7	- 4.0	5.7
Early Winter	- 7.4	+ 2.0	-20.0	1.9	(		nd	)

* nd () = no data available from Bathurst Island during this season.
** Weather data for SR collected during 1980.

Appendix C. Description of vegetation types, Polar Bear Pass, Bathurst Island. Based on work by Geale (1980).

Vegetation Type	Site Description	Characteristic Plants
Ridge	Xeric to mesic upland ridge vegetation	*Cerastium alpinum* *Saxifraga oppositifolia* *Papaver radicatum*
Polar Desert	Exposed gravel habitats	*Dryas integrifolia* *Draba bellii* *Saxifraga oppositifolia*
Mesic Ridge	In sites of more persistent snow cover and with finer grained substrate than the Ridge community.	*Puccinellia bruggemanni* *Arctagrostis latifolia* *Juncus biglumis*
Hummock-Seepage Slope	Along stream valleys, alluvial terraces and side slopes of ridges with typical snowbed communities.	*Papaver radicatum* *Festuca brachyphylla* *Oxyria digyna*
Mesic Meadow	In well-drained sites along the periphery of valley bottoms.	*Luzula nivalis* *Alopecurus alpinus* *Stellaria longipes*
Hydric Meadow	In wet valley bottoms	*Dupontia Fisheri* *Carex stans* *Eriophorum triste* *Eriophorum Scheuzeri* *Salix arctica*
Willow Meadow	On sandy, alluvial lowland deposits	*Salix arctica* *Alopecurus alpinus*

Appendix D. Above ground standing crop (dry wt in $g \cdot m^{-2}$; mean ± SD) for vegetation types in Polar Bear Pass, Bathurst Island. Based on data from Goale (1980). Quadrats were harvested during the period of maximum vegetative growth (early to mid-August), 1975.

Vegetation Type	Number of Quadrats	Plant Group							
		Litter*	Lichen	Rushes	Grasses	Sedges	Herbaceous Forbs	Woody Forbs	Willow
Ridge	4	6.40 ± 2.73	8.29 ± 3.03	0.34 ± 0.34	0.69 ± 0.57	-	15.05 ± 10.43	16.80 ± 10.57	0.12 ± 0.12
Polar Desert	5	8.05 ± 2.51	12.20 ± 6.88	0.12 ± 0.12	0.16 ± 0.11	-	17.53 ± 11.86	13.74 ± 6.30	0.34 ± 0.22
Mesic Ridge	nd**								
Hummock/Seepage Slope	34	13.29 ± 4.80	18.91 ± 4.77	0.99 ± 0.71	2.20 ± 0.71	-	10.98 ± 3.73	13.83 ± 4.79	0.44 ± 0.65
Mesic Meadow	5	31.38 ± 6.62	8.71 ± 6.79	1.14 ± 0.91	5.07 ± 1.67	3.68 ± 3.55	3.78 ± 3.55	4.45 ± 4.16	4.84 ± 1.63
Hydric Meadow	42	19.99 ± 4.51	1.07 ± 0.42	0.24 ± 0.16	8.97 ± 2.39	8.72 ± 2.45	0.64 ± 0.24	0.41 ± 0.27	2.66 ± 0.90
Willow Meadow	5	27.26 ± 4.26	4.09 ± 0.52	0.33 ± 0.17	0.51 ± 0.44	-	0.01 ± 0.01	0.52 ± 0.43	18.56 ± 3.40

* Includes standing dead material.
** nd = no data available.

Appendix E. Percent relative density of plant epidermal fragments from muskox fecal samples collected in Polar Bear Pass, Bathurst Island, 1978. Based on 100 fields per sample.

	Season							
	Winter	April/May	Post-calving		Mid-summer		Rut	
Plant Species			Adult	Calf	Adult	Calf	Adult	Calf
Carex spp.	89.23	60.16	23.30	5.33	-	-	18.12	11.49
Eriophorum spp.	1.57	0.88	-	-	0.14	-	1.44	1.48
Dupontia Fischeri	0.39	-	0.50	0.51	-	-	1.08	-
Luzula nivalis	0.39	0.88	0.50	-	-	-	-	-
Cerastium alpinum	0.78	4.57	5.77	7.05	-	-	-	-
Draba spp.	-	-	1.51	1.02	-	-	-	-
Papaver radicatum	-	0.88	0.50	0.51	-	-	-	-
Stellaria longipes	0.39	2.23	3.60	6.47	0.14	-	-	0.37
Saxifraga spp.	1.18	1.76	6.33	4.22	0.14	0.43	1.08	1.87
Salix arctica	4.08	25.95	56.48	74.38	99.58	99.57	78.28	84.05
moss spp.	1.99	2.69	1.51	0.51	-	-	-	-