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NUTRITIONAL ECOLOGY
OF THE DENALI CARIBOU HERD

A

THESIS

Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

Rodney D. Boertje, B.S.

Fairbanks, Alaska

May 1981

NUTRITIONAL ECOLOGY

OF THE DENALI CARIBOU HERD

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ABSTRACT

The Denali (McKinley) caribou herd was studied to assess the influence of forage selection and activity on the nutrition and energetics of this extremely reduced population. Activity budgets and comparisons of environmental conditions with other herds were used as a basis for documenting a high nutritional status of the herd. An energetics model based on activity budgets, and a nutritional model derived from estimates of forage quality and seasonal energy requirements (expressed on a dry matter basis) were developed for adult female caribou. Snow conditions, insect harassment, and other factors influencing energy expenditure and the extent of non-foraging activities, exclusive of range quality or productivity, were the main determinants of annual energy balance and nutrition. Negative nitrogen and phosphorus balances were predicted in winter, but caribou apparently are largely adapted to this phenomenon. The energetic and nutritional models enable assessment of dietary, behavioral, and environmental changes on caribou condition and population welfare.

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INTRODUCTION

This thesis is the first segment of a two-part study initiated to assess the influence of range-related factors on the status of caribou (*Rangifer tarandus granti*) in the Denali caribou herd, formerly referred to as the McKinley caribou herd. Interest in the herd was stimulated by a dramatic decline in the herd's number. My emphasis has involved modeling the factors controlling the energetic and nutritional status of the herd on a year-round basis. The energetic and nutritional models allow one to assess what effects varying dietary, behavioral, and/or environmental interactions could have on the nutritional status of caribou. The relationships between nutrition and caribou population ecology are also discussed, and comparisons are made with other caribou/reindeer (*Rangifer tarandus*) populations.

A companion study has focused on range productivity (Schultz in prep.). Together, the two theses will contribute to an understanding of the nutritional carrying capacity of the Denali herd's range. Moen (1973) outlined the concept for the estimation of carrying capacity based on energy and protein requirements, and Robbins (1973) discussed in detail the biological basis for the determination of nutritional carrying capacities. Wallmo et al. (1977) demonstrated the applicability of this concept in a study of a migratory mule deer (*Odocoileus hemionus*) population in north-central Colorado. Mautz (1978) and Swift et al. (1976) also described this concept and demonstrate its applications in regard to wild ruminants and elk (*Cervus canadensis*), respectively.

Objectives

1. To determine the dietary composition of the Denali caribou herd on a seasonal basis.
2. To determine seasonal activity budgets of the herd for use in modeling annual energy requirements and in assessing nutritional status.
3. To assess the nutritional quality of plant parts selected by caribou on their seasonal ranges.
4. To relate the diet selected to the nutritional requirements of adult female caribou, with emphasis on protein and energy requirements.

Emphasis has been placed on cow and calf groups in all phases of field work because of the importance of cow/calf nutrition to the population dynamics of the herd (see Chapter 3) and due to the sexual segregation that occurred among adults during most of the year.

Study Herd: History and Status

A change in the herd's name from the "McKinley" caribou herd to the "Denali" caribou herd was prompted by a recent change in the official name of "McKinley National Park" to "Denali National Park." Since the caribou herd remains within the park's boundaries most of the year, it seems appropriate that the herd's name be referenced to the park's official name. Sheldon (1930), Haber (1977), and Troyer (1980) have previously referred to this herd as the Denali caribou herd.

Prior to 1976, studies on the Denali caribou herd were limited almost entirely to intermittent investigations of seasonal movements and population statistics which are summarized by Murie (1944), Skoog (1968), Buskirk (1976a), and Haber (1977). More recently, from 1976 to 1979, the National Park Service has monitored the herd's seasonal movements and population statistics using radio-collared caribou (Troyer 1976, 1977, 1978; Grosnick 1979). Briefly, the Denali herd numbered 20,000 to 30,000 animals from the early 1900's to the early 1940's (Murie 1944) and declined to about 7000 to 9000 animals by the late 1940's or early 1950's (Murie's observations cited from Haber 1977; Murie 1961). The total population numbers apparently remained at about 7000 to 9000 animals from the early 1950's until 1967 (see Haber 1977), although numbers may have exceeded 14,000 animals in 1964 (Skoog 1968). From 1968 to 1972, the herd exhibited a rather steady decline from about 8000 to about 1500 animals (Haber 1977). Using radio-collared caribou, Troyer (1976, 1977, 1978, 1980; Grosnick 1979) estimated that the herd had a stable population of about 1200 to 1500 animals from 1976 to 1980.

Thus, it appears that the herd has undergone at least two declines, one in the 1940's from about 25,000 to 7000 animals and another during the late 1960's and early 1970's from at least 8000 to about 1500 animals. The most recent decline may have occurred due to the high frequency of extremely heavy snowfall years (see Study Area) during and immediately prior to the decline. J. Bryant (pers. comm.) frequently observed caribou carcasses in the western wintering area of the herd during the particularly heavy snowfall season of 1970-71. However, biologists do not necessarily agree that this decline resulted from extreme snow conditions (J. Davis pers. comm.), although a generally accepted alternative explanation does not prevail.

Emigration or a shift in distribution has consistently been implicated in the major decline of the herd during the 1940's (Murie 1946; Skoog 1968; Shepherd 1975; Haber 1977), but this conclusion is not universally accepted (see Bergerud 1980). Murie (1946) suggested that much of the decline may have occurred between 1941, when he counted 21,000 animals (Murie 1944), and 1946, but no census was made until 1952 when only about 7000 animals were observed (park reports cited from Haber 1977). Murie (1946) suggested that a portion of the herd had shifted its movements westward or outside the park boundaries. Skoog (1968) reviewed the subject of caribou/reindeer "shifts in distribution", and suggested that these shifts were historically "commonplace" among caribou at high densities (2 to 4 caribou • km^{-2} over the entire range). The Denali caribou herd probably reached these extremely high densities (about 2 caribou • km^{-2} maximum) prior to the decline. Most contemporary Alaskan and Canadian herds, including the Denali herd, are at densities of less than half this figure (about 0.3 to 0.8 caribou • km^{-2}), with the exception of one small Canadian herd (Bergerud 1980). This small herd may provide contemporary evidence that caribou emigrations occur at high densities.

Additional factors that might be implicated in the dramatic decline of the herd in the 1940's include fires on the winter range, heavy snowfall, overhunting, high predation rates, low reproduction, and overgrazed range conditions. From an historical review of wildfires in and near Denali National Park (Buskirk 1976b), it is evident that fire had a minimal effect on the herd's traditional or present range. It is also doubtful that heavy snowfall could have been a major factor affecting this decline, since only one heavy snowfall year occurred in the 1940's (see Study Area). This snowfall occurred in 1948, apparently after the decline was well underway (Murie 1946). Also, no severe decline in the herd was noted after the heavy snowfall years of 1935 and 1937. Overhunting was also not likely a major factor related to the decline, as Murie (1946, 1961) did not implicate hunting as a cause of the decline. Also, access to this herd was poor during the 1940's, except when the herd was within the park's boundaries where hunting was not allowed. Buskirk (1976a) summarized harvest reports on the Denali herd from 1967 to 1975 (from Alaska Department of Fish and Game harvest tickets) and indicated that human harvest in recent years has been fairly light, averaging less than 50 animals annually. It is also doubtful that predation was a major factor in this decline as predator control programs were carried out on wolves (the main predator of caribou) in Denali National Park from 1917 to 1952, particularly in the late 1930's and mid-1940's (Haber 1977). Also trapping activity, outside the north boundary of the park, was probably most important from the late 1930's to 1946, which coincided with the timing of the caribou's decline in numbers (Haber 1977). According to observations by Murie (cited from Haber 1977), a decline in the number of wolves in the park coincided with the caribou's decline in numbers. Of course, a number of these and other factors, together with a shift in the distribution of the herd, could have accounted for this decline. The associations between nutritional status, predation, reproduction, and range characteristics are discussed in relation to caribou population ecology in Chapters 2 and 3, particularly in regard to the stability of the population from 1972 to 1980 (Haber 1977; Troyer 1980).

Further historical accounts of the Denali caribou herd indicate that prior to 1932 a majority of the herd consistently wintered south of the Alaska Range, rather than north of the range as reported since 1933 (Murie 1944). This observation lends credence to the theory that shifts in caribou movements may be responsible for the historical decline in the Denali caribou herd in the 1940's. Changes in range use that have occurred since 1933 include the abandonment of the expansive traditional wintering areas of the herd (Buskirk 1976a). However, this restriction in range use commonly occurs as caribou populations decline and occurs in association with reductions in seasonal migratory distances (Skoog 1968). Use of summering areas and, to a lesser extent, calving areas has remained quite consistent since 1933 (Murie 1944; Haber 1977; Troyer 1976, 1977, 1978, 1980; Grosnick 1979). Recent exceptions to the traditional use of the Cantwell calving area as the major calving area occurred particularly in 1971 and 1977 when caribou calved primarily north of the Alaska Range and postponed their early spring movement south across the range. These postponements were thought to have occurred as a result of deep, lingering snow on the south side of the range (Haber 1977; Troyer 1977). Skoog (1968) also described the postponement of caribou movements to traditional calving areas due to deep, lingering snow.

Study Area

The present range of the Denali caribou herd is centered at 63° 30'N latitude and about 150° 30'W longitude. The total area utilized by the caribou, primarily adult females and calves, is about 4770 km^2, including migration routes (Figure 1). In addition, adult bulls utilize much of the area along the park road in spring and summer (about 450 km^2). Since the total caribou population presently numbers about 1200 to 1500 animals (Troyer 1980), the density of caribou is about 0.2 to 0.3 caribou $\cdot$ km^{-2}. Elevations of this study area are mostly between 430 to 1220 m, although caribou migrating to and from the Cantwell calving ground cross over the Alaska Range and reach elevations as high as 1646 m. Wahrhaftig (1958) and Reed (1961) discuss the geography and geology of Denali National Park and surrounding areas.

A detailed description of the plant communities of Denali National Park and adjacent areas is given by Heebner (in prep.). Dean (in prep.) provides a map of these plant communities in the park area. Briefly, treeline occurs at about 760 m, and trees (primarily spruce, *Picea* spp.) are common along the river drainages at this elevation. The caribou, however, are usually at higher elevations, except on the western wintering area. At mid-elevations (760 to 1220 m) on the Cantwell calving ground and summering range, mosaics of sedge tundra (*Carex* spp.) and shrub tundra (*Salix* spp. and *Betula nana*) dominate. At mid-elevations on the rutting ground and the eastern wintering range, tussock tundra (*Eriophorum vaginatum*) dominates the landscape,

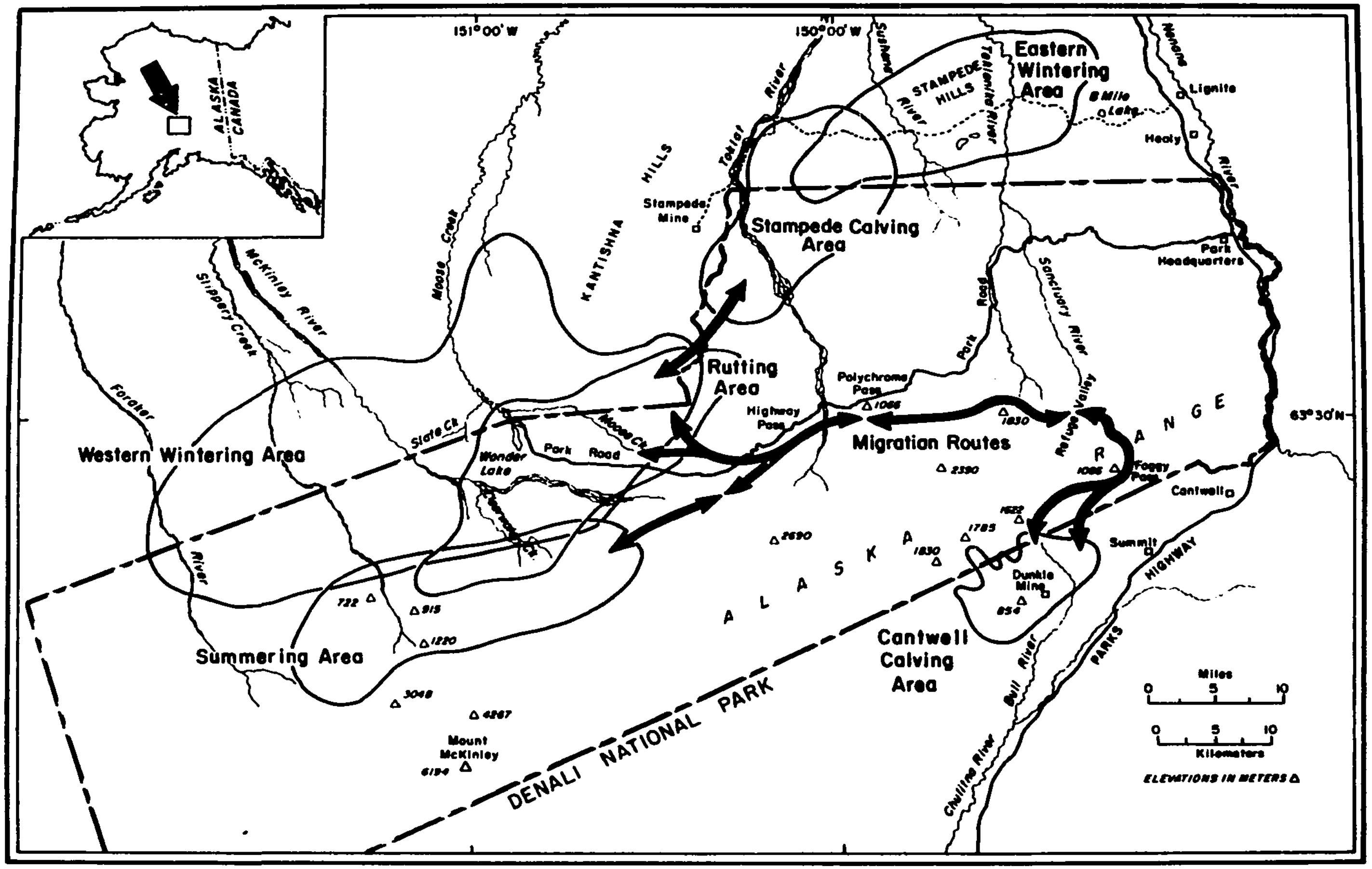

Figure 1. Seasonal caribou ranges in Denali National Park, 1978-1980.

although small ponds and drainages frequently are surrounded by _Carex_ spp., grasses, and shrubs (mostly _Salix_ spp.). The western wintering ground is largely a spruce forest with tussock, sedge, and shrub tundra occurring in the eastern portion of this area on the Kantishna Hills. Lichen stands are best developed on the summering range and western wintering area.

A continental montaine climate predominates in Denali National Park. However, it is important to recognize that the Alaska Range acts as a partial barrier for storms moving north from the Gulf of Alaska. As a result, precipitation rates are much higher south of the crest of the Alaska Range, which includes the Cantwell calving ground. For instance, annual snowfall at Summit, Alaska, just east of the Cantwell calving ground, averaged 307 ± 100 cm (s.d.) from 1943 to 1960. In contrast, the annual snowfall during the same period at Denali National Park headquarters, just north of the Alaska Range, averaged 178 ± 72 cm. It is also significant that average winter temperatures in the park are relatively mild compared to average winter temperatures over much of interior Alaska.

Weather data at Denali National Park headquarters from 1978 to 1979 is summarized in Table 1 from U.S. National Weather Bureau records. Mean annual temperatures were about normal (compared to the prior 53 years), but February temperatures in 1979 were much colder than usual. Annual precipitation rates were below normal for both years. However, precipitation rates at park headquarters (located at at the extreme east end of the park) are not necessarily indicative of

Table 1. Weather data for 1978 and 1979, Denali National Park headquarters. Values are from U.S. Weather Bureau records. "Normal" values are from 53 years of temperature data and 49 years of precipitation data.

	Temperature (°C)				Precipitation (cm)			
							Snow	
Month	Max	Min	Mean	Departure from Normal	Total	Departure from Normal	Total	Max on Ground
Jan., 1978	5.6	-31.7	- 9.6	7.7	0.64	-1.14	11.7	43.2
Feb.	4.4	-33.9	-11.9	1.9	2.79	1.27	67.3	94,0
Mar.	6.7	-27.2	- 9.7	0.5	0.81	-0.76	14.0	63.5
Apr.	11.7	-25.6	- 2.8	0.3	0.28	-1.19	2.5	58.4
May	18.3	- 8.3	6.4	1.3	1.98	-0.10	0	0
June	25.0	- 2.8	9.3	-1.9	3.61	-2.18	0	0
July	26.7	1.1	12.6	0	5.28	-2.21	0	0
Aug.	28.3	- 2.8	11.9	1.7	8.61	2.26	0	0
Sept.	24.4	- 6.1	5.9	0.8	2.24	-1.34	7.1	5.1
Oct.	12.2	-23.3	- 4.5	-0.4	1.35	-1.01	21.1	10.2
Nov.	5.6	-26.7	- 9.8	2.6	1.35	-0.89	27.9	17.8
Dec.	2.8	-29.4	-12.1	5.2	2.82	0.66	36.6	35.6
Annual, 1978			- 1.2	1.6	31.75	-6.65	188.2	
Jan., 1979	2.8	-27.8	-12.2	5.1	2.57	0.79	36.1	58.4
Feb.	-5.6	-42.2	-26.7	-12.9	1.07	-0.46	25.9	81.3
Mar.	5.6	-30.0	- 9.8	0.4	1.88	0.30	31.0	61.0
Apr.	14.4	-26.1	- 2.4	0.7	0.53	-0.94	12.7	55.9
May	21.1	- 6.1	6.7	1.6	1.27	-0.81	0	0
June	21.1	- 2.8	10.2	- 1.0	6.27	0.48	0	0
July	26.1	1.7	12.3	- 0.3	8.05	0.56	0	0
Aug.	27.2	1.1	12.6	2.4	2.97	-3.38	0	0
Sept.	21.1	- 6.1	6.1	1.0	1.98	-1.60	6.4	7.6
Oct.	14.4	-14.4	- 0.2	3.9	1.80	-0.56	T[a]	2.5
Nov.	7.2	-19.3	- 5.0	7.4	3.28	1.04	66.0	30.5
Dec.	- 1.7	-37.2	-21.4	- 4.1	0.86	-1.30	16.8	30.5
Annual, 1979			- 2.5	0.3	32.54	-5.88	194.9	

[a] T = trace

rainfall levels elsewhere in the park. Local residents and park employees considered 1978 and 1979 to be very heavy rainfall years in the park. Total annual snowfall was about average in both 1978 (188 cm) and 1979 (195 cm) compared to the mean annual snowfall from 1925 to 1979 (190 ± 74 cm (s.d.)). Total annual snowfall at park headquarters has exceeded the extreme depth of 250 cm only in the following years since 1925: 1935, 1937, 1948, 1957, 1962, 1966, 1967, 1968, 1970, and 1971. Haber (1977) illustrated the total annual snowfall levels for Denali National Park headquarters from 1925 to 1973. The high frequency of heavy snowfall years during the late 1960's and early 1970's are particularly important.

Caribou co-exist with a variety of other animals in the park, including moose (Alces alces), dall sheep (Ovis dalli dalli), brown bears (Ursus arctos), black bears (Ursus americanus), wolves (Canis lupus), coyotes (Canis latrans), red fox (Vulpes fulva), wolverine (Gulo luscus), lynx (Lynx canadensis canadensis), and a variety of small herbivores. Murie (1944, 1961) discussed the ecological relationships between many of these species in Denali National Park. More recently, Haber (1977) reported on a socio-ecological study of wolves in Denali National Park, and included discussions of the interactions between wolves, caribou, dall sheep, and moose.

Haber (1977) indicated that approximately 45 to 55 wolves (in at least 4 different packs) inhabited the range of the Denali caribou herd (Figure 1) as of 1974. However, Haber did not indicate whether any wolves may have occurred on the Cantwell calving ground, on the south side of the Alaska Range.

Monitoring of predator densities on caribou calving areas are particularly important in regard to the vulnerability of newborn caribou calves to predators. I observed that the main predators, wolves and brown bears, were at much lower densities on the Cantwell calving area compared to densities on the Stampede calving area and other minor calving areas (on the migration route between the Stampede and Cantwell calving areas) north of the Alaska Range. This is substantiated by my observations of only 1 wolf and 6 different brown bears on the Cantwell calving area during about 58 days of field observations. In contrast, during only a 4-day visit to the Stampede calving area, M. Grosnick (pers. comm.) and I observed 2 different wolves and at least 15 different brown bears. F. Dean (1976, pers. comm.) also suggested that densities of brown bears were much higher on the north side of the range in the park (about 1 bear • 28 km^{-2}) than on the Cantwell calving area (about 1 bear • 56 km^{-2}), in part because the Cantwell area has been hunted for bears.

These estimates indicate that about 30 to 35 brown bears occupy the Stampede and Cantwell calving areas and the migration area between these two areas. Other potential predators observed on the Cantwell calving area included 1 coyote, 1 wolverine, and 3 immature golden eagles (*Aquila chrysaetos*).

Field Study Periods and Logistics

Field work for this study was begun in June, 1978 and was completed in April, 1980. The duration of individual field trips varied from 4- to 46-day periods and were undertaken on a year-round basis. Table 2 lists the dates and locations that field studies were active during this study.

It was often necessary to identify specific locations of caribou, prior to and during ground observations, through aerial reconnaissance. This work often necessitated cooperative efforts with National Park Service personnel who were conducting a 4-year (1976 to 1979) radio-telemetry study of Denali caribou movements (Troyer 1976, 1977, 1978; Grosnick 1979). Transportation to study areas was achieved on foot or by using fixed-wing aircraft (usually a PA-18 Super Cub), snowmobile, or dog sled. Once in a particular study area, all work was completed on foot or on skiis, usually using lightweight mobile field camps.

Table 2. Periods of field work and associated study areas in and near Denali National Park, 1978 - 1980. See Figure 1 for locations of study areas.

Season	Dates	Study Area
Spring		
	June 3-10, 1978	Park road - caribou migration route
	June 17-27, 1978	Cantwell calving area
	May 12-15, 1979	Stampede calving area
	May 21-July 6, 1979	Cantwell calving area
Summer		
	July 6-August 11, 1978	Park road - caribou migration route
	August 12-19, 1978	Summer area (Slippery Creek)
	July 10-24, 1979	Park road - caribou migration route
	July 27-August 23, 1979	Summer area (Slippery Creek)
Autumn		
	August 23-24, 1978	Park road - reindeer feeding trials
	Sept. 28-Oct. 1, 1978	Rutting area (Moose Creek)
	Sept. 12-Oct. 9, 1979	Rutting area (Moose Creek)
Winter		
	Nov. 16-23, 1978	Western winter area (Slate Creek)
	Jan. 4-8, 1979	Eastern winter area
	March 7-16, 1979	Eastern winter area
	Nov. 28-Dec. 7, 1979	Eastern winter area
	Jan. 8-15, 1980	Eastern winter area
	March 28-April 4, 1980	Eastern winter area

CHAPTER 1: COMPOSITION OF SEASONAL DIETS

Introduction

Several authors have reported on the food habits of *Rangifer*, including Murie (1935), Edwards and Ritcey (1959), Sablina (1960), Karaev (1968), Skoog (1968), Bergerud (1972), Gaare and Skogland (1975), Wright (1979), and others. Courtright (1959), Bergerud (1977), and Luick (1977) summarize the results of several studies on caribou and reindeer food habits. It is readily apparent from these studies that the food habits of *Rangifer* vary greatly between herds, depending on the availability of palatable species. The only previous report on the food habits of the Denali caribou herd was by Murie (1944), but his investigations were of a very brief nature. A more intensive study was deemed necessary to provide comprehensive estimates of the proportions of food species in the diet on a seasonal basis.

Methods

Field Observation Techniques

Field observations were used to describe food habits on a qualitative basis, and emphasis was placed on determining forage selection of adult female caribou. Field observations were most useful in spring and summer when significant quantities of forbs were consumed but did not appear in the fecal analyses. Qualitative ranking of plant groups in the diets allowed approximation of the proportions of species in the diet. However, fecal analyses helped provide a numerical basis for many of these approximations, particularly in winter. The primary methods through which field observations helped document forage selection included: (1) searching for grazed plants in areas intensively grazed by caribou, and (2) observing caribou at close range with binoculars (10X) or a zoom spotting scope (20X - 60X). Botanical nomenclature followed Hultén (1968) for vascular species, Dahl and Krog (1972) for lichens, Crum (1976) for mosses, and Guild (1977) for mushrooms.

Investigations of grazed areas involved estimating percent cover of individual plant species and recording plant species found grazed and the relative amounts of each species selected. Thus an indication of which plant species were palatable to caribou became readily apparent. Palatability, in this paper, is defined as plant characteristics or conditions which stimulate a selective response by animals (Young 1948; Heady 1964). An indication of the caribou's relative preference for particular species could also be noted. Preference denotes that plant species are selected in greater proportions than they are available in the environment (Petrides 1975). For instance, certain species of forbs on the Cantwell calving ground were found grazed on almost every occasion observed, particularly in areas known to be grazed by caribou. Once I established that a particular plant was palatable to caribou, I took care in investigating plants of that species for signs of grazing during all field observations, particularly if signs of grazing were apparent in the area. After about 190 days of field observations in areas where caribou were abundant (Table 2), I developed sufficient knowledge to ascertain, for example, that certain forb species were highly palatable to caribou and constituted significant proportions of the diet even though these species did not appear in the fecal analysis.

This method of searching grazed areas is efficient and also necessary if one is to detect dietary species that are not satisfactorily estimated through fecal analysis. However, determination of diets based solely on this method is impractical as accurate knowledge of the duration of time spent in each vegetation type and the availability of each of these vegetation types is needed to complete the data base for this scheme. These parameters are extremely difficult to measure in Denali National Park considering the large variations in topographic relief and the many associated vegetation types. Also, the caribou move long distances annually, and therefore availability of vegetation types changes frequently. Perhaps the largest problem to consider is the vast range area in combination with the use, by caribou, of an exceedingly large variety of vegetation types. Many of these vegetation types and mosaics of vegetation types are visible from the ground, for example small patches of herbaceous tundra (Viereck and Dyrness 1980) that receive consistent use by caribou, but can not be accurately mapped using contemporary Landsat imagery techniques (F. Dean pers. comm.).

Observations of grazing animals at close range served to substantiate that species found in grazed areas were definitely grazed by caribou and not other animal species. Continuous observations usually lasted for short periods, often for less than 2 or 3 minutes, as the caribou either became aware of my presence and ceased feeding or fed on vegetation too close to the ground's surface to allow observation of particular plant species being consumed. The intake of shrubs, particularly non-prostrate willows, could be detected from distances of a few hundred meters and for long time periods because of distinct head motions involved in this feeding. However, these observation periods, too, were often interrupted by short feeding bouts during which the lips of the animals were submerged in the overstory vegetation. This prevented the observer from maintaining continuous observations of forage selection. Thus recording of quantitative data on meaningful, lengthy feeding bouts is lacking. However, this technique did help me acknowledge caribou use of a few species that I had not previously recognized as food species. It also enabled me to better define which areas were grazed so that intensive searches could be made for grazed plants. Several hours were spent solely on this activity in spring, summer, and autumn.

It should also be mentioned that feeding trials were attempted with a tame 2.5-year-old reindeer in August, 1979 in and near Denali National Park. However, results of these trials were not felt to be directly comparable to caribou feeding selectivity. For instance, transportation of the reindeer to vegetation types similar to those used by caribou in August was impractical in the time allotted. Also, there was not sufficient time to allow the reindeer to adapt to the availability of plants in a particular vegetation type (J. Wright pers. comm.). Observation of the reindeer was most useful in allowing me to view, at very close range, the feeding behavior involved in eating lichens, berries, and mushrooms. Also, the reindeer's feces were collected 30 to 48 hours after feeding trials to allow assessment of the accuracy of fecal analyses in determining diet composition.

Collection and Use of Fecal Samples

Caribou fecal samples were collected following procedures outlined by Hansen and Gold (1977). Each composite sample contained 25 fecal pellets from 25 different fresh defecations. To aid in preservation, salt was added to each fecal sample in quantities greater than or equal to the weight of the fecal sample. Analysis of fecal samples was conducted at the Composition Analysis Laboratory at Colorado State University, Fort Collins. I prepared a reference collection and plant species list for use in identifying plant fragments. Microscope slides for the fecal analysis were prepared as described by Sparks and Malechek (1968), Ward (1970), and Flinders and Hansen (1972). The percent relative density of plant fragments in fecal samples was based on 100 fields per sample.

To estimate actual dietary composition, results of fecal analyses were modified based on field observations of forage selection and the differential detectability and estimated digestibility (Chapter 3) of plants identified in the feces. The shortcomings of the fecal-analysis technique in estimating true dietary composition are discussed in the following section. Field observations were particularly important in regard to gaining information concerning the diversity and relative proportional intake of forbs, graminoids, and mushrooms. Using results of the fecal analyses as a starting point, increases in the dietary proportions of forbs, including Equisetum spp., were made in all seasons from values averaging about 1 percent to values between 7 percent and 16 percent of the seasonal diets. Likewise, the proportions of graminoids were increased from between 4 and 7 percent of the fecal analysis to between 10 and 14 percent of the seasonal diets. Also, mushroom values were increased about 6 percent from values given for summer and autumn fecal samples. Values for Salix and lichens from the fecal analyses had to be decreased in most seasons to allow for increases in dietary components that failed to appear in the fecal analyses. For example, in both spring and summer, Salix and lichen values from the fecal analyses were decreased about 9 percent and 12 percent, respectively. An 8 percent decrease was made in the proportion of mosses found in the fecal analyses of autumn and winter samples. This decrease in moss values in autumn and winter fecal samples allowed for increases in other forage classes that were underrepresented in the fecal analyses. As such, no compensating systematic decreases in the Salix and lichen values were necessary in the autumn and winter, as they were in the spring and summer.

Student t-tests (Zar 1974) were used to compare differences between adult male and female caribou fecal samples and between fecal samples collected on the eastern versus the western wintering grounds.

Results and Discussion

Fecal Analysis

The results of analysis of 27 fecal samples, from primarily adult female caribou, are listed in Appendix A and summarized in Table 3. Analyses of fecal samples from bulls, calves, and the tame reindeer are given in Appendix B. Spring and summer samples from primarily adult female caribou contained mostly fragments of *Salix* (50 to 56 percent) and lichens (28 to 38 percent), with very little moss (2 to 3 percent). In contrast, autumn and winter samples contained about twice as much lichen (67 percent) and substantial moss fragments (13 to 18 percent). Fragments of *Equisetum* (the only "forb" consistently identified), graminoids, and evergreen shrubs were minor proportions of the total fragments observed (1, 4 to 7, and 1 to 8 percent, respectively) in all seasons. Mushroom fragments averaged about 5 percent of the summer and autumn samples.

A high variability was noted in the results of fecal samples collected within a season (Table 3). At present, it can not be determined whether most of this variability can be attributed to the variability in the caribou's diet within a season or to the variability inherent in the analysis of fecal samples.

There is substantial evidence that fecal analyses alone are inadequate estimates of actual dietary composition. My observations of the diet composition of a tame reindeer under natural grazing conditions and subsequent fecal analyses (Appendix B) also substantiated this conclusion. For instance, the fecal analysis failed to estimate

Table 3. Average percentages (± s.d.) of discerned plant fragments in fecal samples collected primarily from adult female caribou, Denali caribou herd, 1978-1979. Results are summarized from Appendix A.

Plant Genus[a]	Spring (5/16 - 6/30) n=8	Summer (7/1 - 8/15) n=5	Autumn (8/16 - 10/15) n=4	Winter (10/16 - 5/15) n=10
Forbs				
Equisetum	1 ± 1.3	<1	2 ± 1.3	1 ± 1.0
Graminoids				
Carex	6 ± 4.1	4 ± 2.5	2 ± 0.6	2 ± 1.7
Festuca	1 ± 0.5	1 ± 0.9	1 ± 0.8	<1
Hierochloe	<1	<1	1 ± 0.9	1 ± 0.6
Deciduous Shrubs				
Salix	50 ± 22.0	56 ± 23.6	8 ± 7.0	<1
Vaccinium	1 ± 1.3	1 ± 1.3	2 ± 1.7	0
Evergreen Shrubs				
Dryas	0	1 ± 0.8	1 ± 0.1	<1
Ledum	<1	0	<1	1 ± 1.3
Vaccinium	1 ± 0.4	0	0	8 ± 2.5
Nonvasculars				
Lichens	38 ± 21.0	28 ± 17.5	68 ± 12.0	66 ± 13.4
Mosses	3 ± 2.1	2 ± 1.2	13 ± 8.2	18 ± 10.1
Mushrooms	0	6 ± 9.7	4 ± 1.9	1 ± 1.7
Total	101	99	102	98

[a] Eight additional plant species, averaging less than 1% on a seasonal basis, are presented in Appendix A, where the raw data is listed.

the actual proportion or species composition of forbs in the diet. *Mertensia*, *Epilobium*, *Equisetum*, *Rubus*, *Hedysarum*, *Boykinia*, *Lupinus*, *Pedicularis*, *Saussurea*, *Stellaria*, and *Polygonum* were some of the forbs selected and constituted about 10 percent of the diet. The fecal analysis also did not detect any mushrooms in the diet, yet mushrooms made up roughly 3 to 5 percent of the diet. Major genera and relative proportions of graminoids, lichens, and shrubs were identified correctly in the fecal analysis.

Several studies have shown that fecal analyses are biased by differential digestibilities between species and within a species (Croker 1959; Stewart 1967; Vavra et al. 1978). The digestibility within a species is influenced by the phenological stage of the plant and the plant part used. The digestibility of a forage is also directly related to the nutrient quality of the diet (Maynard and Loosli 1969). Other factors which may affect the detectability of forages in the feces, besides their digestibilities, include the quantity of cutin deposition on the cell wall, the persistence of identifiable cell features, the degree of fragmentation of the forages. For instance, values for mosses from fecal analyses are highly inflated over their actual composition in the diet due to their high degree of fragmentation, their extremely low estimated digestibility (Appendix C), and the ease with which minute moss fragments can be identified (Dearden et al. 1975).

Slater and Jones (1971) also warn against assuming that the relative proportions of plant fragments in the feces adequately estimate the relative amounts of plant species consumed. They found that white clover (Trifolium repens) could not be identified in the feces using the fecal-analysis techniques proposed by Sparks and Malechek (1968), even when the composition of the known diet was 37 percent clover. Similar relationships in regard to the consumption of forbs can be deduced in this study since analysis of fecal samples followed the same laboratory procedures (see Methods). McInnis (1976) and Free et al. (1970), working with sheep, and Anthony and Smith (1974), working with deer, also confirmed that the proportions of forbs can not be detected accurately in the diet using fecal analysis.

Zynar and Urness (1969) concluded that the fecal-analysis technique may have limited applicability in quantifying the diet of free-ranging deer because of the occurrence of small amounts of many forage species in the diet. These results agree with my findings, in that caribou consume small quantities of many species, particularly forbs, that can not be detected reliably through fecal analysis.

A method for modifying results from fecal analyses to approximate actual diets in elk (Cervus canadensis nelsoni) was presented by Pulliam and Nelson (1979). This method is based on the relative digestibilities of dietary components. By using a digestibility-based correction factor, Pulliam and Nelson (1979) were able to adjust the proportion of alfalfa (Medicago sativa) in the fecal analysis to within 3 percent of the actual dietary composition; whereas the fecal analysis alone underestimated the proportion of alfalfa in the diet by 91 percent. It is necessary to know the precise proportions of food species in the diet and proportions of plant fragments by species in the feces to develop these correction terms. To date, no such digestibility-based correction terms have been developed for caribou/reindeer forages. Dearden et al. (1975) formulated correction terms for a mixture of non-digested caribou/reindeer forages but these figures have limited applicability for use with fecal analyses, particularly in regard to the absence of figures for mosses, mushrooms, and forbs. Correction terms, of course, can only be applied to plants or plant parts that are distinguished in the feces. Since certain food items, particularly highly digestible forbs, are apparently not distinguishable in the feces, extrapolation of results from fecal analyses to an actual diet will always depend on field observations or other methods of determining food habits, particularly when estimating spring and summer diets.

Although I have stressed several shortcomings in using fecal analyses to estimate actual diets of caribou, I believe the analyses are useful in assessing seasonal trends of certain major food items, including shrubs, graminoids, lichens, and mosses. Results from fecal analyses could play a future role in comparing the relative proportions of major foods of caribou on different ranges, particularly in the winter. For instance, baseline information on winter range condition could be gained by comparing the composition of mosses in the winter feces of several herds. Most authors have agreed that mosses are likely consumed incidentally by caribou (Palmer 1926; Murie 1935; Skoog 1968; Bergerud and Nolan 1970), except possibly in the High Arctic where lichens are extremely scarce (Parker et al. 1975; Punsvik et al. 1980). Analysis of winter fecal samples collected in this study, in areas where lichens were extremely scarce, showed an unusually high proportion of mosses, as discussed later. I suggest that this intake of mosses was largely incidental to the intake of lichens, as mosses are not preferred food species and provide little known nutritive values due to their low estimated digestibilities (see Chapter 3). Mosses may serve as mineral supplements but energy is likely the most compelling requirement of caribou in winter, and lichens contain substantially more digestible energy than mosses (see Chapter 3). An unusually high proportion of mosses in the winter feces of a herd, relative to other herds, would provide an easily accessible index to the availability of lichens or preferred graminoids on the winter range. Speculation could then be made concerning the quality of the winter range and the winter nutrition of the herd. Of course, these comparisons might not be reliable indicators of nutritional status in High Arctic animals, for example Svalbard reindeer, that apparently have adapted to the scarcity of lichens in the winter diet (Reimers 1980). As discussed later, a relatively high level of evergreen shrub fragments in the feces may also indicate poor winter range condition.

Table 4. Approximate percentages of major foods[a] in the seasonal diets of adult female caribou, Denali caribou herd, 1978-1979. Estimates are based primarily on field observations and fecal analyses (Table 2), as explained in the Methods.

	Season			
	Spring	Summer	Autumn	Winter
Plant Species	(mid-May to July)	(July to mid-Aug)	(mid-Aug to mid-Oct)	(mid-Oct to mid-May)
Berries[b]	2	2	3	
Deciduous shrubs				
Arctostaphylos spp.	1			
Betula nana	2	2	2	
Salix spp.[c]	41	46	12	1
Vaccinium uliginosum	1			
	45	48	14	1
Evergreen shrubs				
Dryas octopetala		1	1	1
Vaccinium vitis-idaea			1	6
	0	1	2	7
Forbs				
Artemesia arctica		2		
Boykinia richardsonii		2	1	
Dodecatheon frigidum		1		
Epilobium angustifolium	3			
Epilobium latifolium	1	2		
Equisetum arvense	1	2	2	3
Equisetum variegatum	1	1	2	3
Sanguisorba stipulata	3		2	
Stellaria longipes				1
Other forbs[d]	7		2	
	16	10	9	7

Diet Composition

Composition of the seasonal diets of adult female caribou of the Denali caribou herd (Table 4) are discussed on a seasonal basis in the following sections. Emphasis is placed on factors affecting changes in the diets, including the phenological progression of food species and changes in the availability of food species associated with seasonal movements. Comparisons with other studies on *Rangifer* food habits are also documented.

Spring (mid-May to July)

Estimation of the spring diet is confounded to a certain extent by variability in the use of calving grounds. However, the major calving area is usually the Cantwell calving ground on the south side of the Alaska Range. This area is also the only significant post-calving area, and, therefore, the majority of adult females and calves are in this area from the last week in May until the first days in July. Compared to the Stampede and Wonder Lake calving areas, north of the range, the Cantwell calving area is characterized by late snow melt, more abundant lichen stands, lack of early flowering *Eriophorum vaginatum* tussock communities, lower predator densities (see Study Area), and higher plant productivity and an abundance of forbs (associated with the higher rainfall on the south slopes). Caribou also frequently use a mineral lick on the Cantwell calving ground (see Sodium section, Chapter 3). In contrast, the Stampede

Table 4. (Continued)

Graminoids				
Carex spp.[e]	7	6	9	7
Eriophorum spp.[f]	4		1	
Festuca altaica	1	2	2	2
Hierochloe alpina		2	2	2
	12	10	14	11
Lichens[g]	25	17	43	62
Mosses[h]			5	10
Mushrooms[i]		12	10	2

[a] Plant parts selected are given in Appendix C.

[b] Species of berries selected included primarily *Vaccinium uliginosum* and *V. vitis-idaea* with less use of *Empetrum nigrum*.

[c] Species of *Salix* selected included primarily *S. pulchra* with moderate use of *S. arctica*, *S. reticulata*, and *S. rotundifolia* and less use of *S. alaxensis*, *S. commutata*, *S. glauca*, and *S. fuscescens*. Frequency and timing of the collection of forage samples of these species (Appendix C) gives a better indication of their comparative uses.

[d] In spring, the term "other forbs" refers to *Anemone* spp., *Mertensia paniculata*, *Pedicularis* spp., *Petasites frigidus*, *Potentilla palustris*, *Streptopus amplexifolius*, and *Valeriana capitata*. In autumn, the term refers to *Petasites frigidus* and *Hedysarum alpinum*.

[e] Species of *Carex* selected included primarily *C. aquatilis*, *C. bigelowii*, and *C. podocarpa* (see Appendix C for their comparative uses).

[f] Species of *Eriophorum* selected included primarily *E. vaginatum* and *E. angustifolium*.

[g] Lichens species selected included primarily *Cladonia* spp. and *Cetraria cucullata*, with comparatively little use of *Stereocaulon* spp. and *Peltigera* spp.

[h] Species of mosses consumed were not identified to genera.

[i] Mushrooms consumed included primarily *Boletus* spp., although several other genera were selected (see Appendix C).

and Wonder Lake calving areas are characterized by widespread *Eriophorum vaginatum* tussock communities and early snow melt. During the pre-calving migration in late April to mid-May, the *Eriophorum* floral parts in these areas provide the caribou with the earliest green vegetation of the season. When the caribou do not migrate south of the range during calving, due to excessive snow cover, these floral parts would constitute a major food source.

The early spring diet on the Cantwell calving ground was dominated by lichens and, to a lesser extent, overwintering berries, *Salix* catkins and buds, and partially green *Carex* spp. The caribou made intensive use of areas of early phenological development in the last week of May. In particular, well-drained sites were eagerly sought such as the steep banks and upper bluffs of drainages. South-facing slopes were also preferred during early spring. By choosing these sites, caribou were able to select a substantial quantity of fast-growing, green vegetation a week prior to bud-break in most areas. A striking feature of this early phenological period was the high species diversity of deciduous shrubs in the diet. Intensive feeding on the new leaves of *Vaccinium uliginosum*, *Betula nana*, *Arctostaphylos* spp., and *Salix* spp., particularly *Salix pulchra*, was observed during the last week of May and the first week of June. By the second week of June, however, only *Salix* spp. continued to be grazed intensively. This temporary intensive use of new leaves from an unusually wide variety of species appears to be the combined consequence of their relatively high nutrient content (Chapin et al. 1980) and their low content of plant defensive compounds, which normally protect the leaves from overgrazing (Rhoades and Cates 1976).

Several species of forbs were also sought during early phenological stages, with young shoots of Epilobium angustifolium and Sanguisorba stipulata being most important. An estimation of 16 percent forbs in the spring diet (Table 4) is comparable to other work on spring diets of caribou in Newfoundland (Bergerud and Nolan 1970; Bergerud 1972). Also, this figure seemed reasonable since forbs were highly palatable abundant, and heavily grazed in many sites. Graminoids were also grazed heavily at times, particularly the young, fast-growing leaf tips of Carex podocarpa in alpine herb meadows.

About June 21 in 1979 the caribou moved from elevations of about 830 m ± 40 (s.d.) to 1080 m ± 20 in the southern foothills of the Alaska Range. The caribou usually remained at these elevations, except to visit the mineral lick, until they migrated north across the range in early July. Prostrate willows, primarily Salix rotundifolia, dominated the diet at these higher elevations. Alexandrova (1940) also found that S. rotundifolia was a palatable forage of reindeer. The movement toward higher elevations appeared disadvantageous from a foraging viewpoint, since the vegetative biomass at higher elevations is relatively low. However, this movement coincided well with the initiation of oestrid fly harassment, as discussed in Chapter 2.

Food habits of adult bulls (see Summer section) and calves appeared to differ significantly from the food habits of adult females. Caribou calves began eating forage a few days after birth, and their fecal pellets were easily distinguished by their small size (about 7 x 3 mm). Results of fecal analyses from two calf samples collected in spring and summer (Appendix B) contained about 50 to 100 percent more lichen fragments than samples collected from adult females on the same date and from the same group of caribou. Compensatory decreases in the Salix component of calf fecal samples occurred. Through analysis of rumen samples, Bergerud (1972) found that young caribou calves consumed large proportions of lichens and mosses and that intake of deciduous shrubs was significantly lower ($p < 0.001$) in calf diets compared to diets of adult females. Contrary to Bergerud's findings, I found no increased use of mosses by calves. This discrepancy might be due to differences in the accessibility of lichens on the two ranges, since increased incidental intake of mosses would likely coincide with increased lichen intake on a range where lichens are extremely scarce.

In conclusion, a combination of factors can act to change the proportions of food species in the spring diet. Some of the major factors include the timing of snow melt, the timing and extent of migratory movements, the timing and degree of insect harassment, and plant phenology. All of these factors are associated to some extent with annual differences in weather patterns. The availability and quality of the food resources, including the availability of a mineral lick, appeared to strongly influence both the migratory and local movements of the caribou in spring. This is in agreement with findings by Klein (1970a) and Skogland (1975). The migratory movement across the range to an area of high plant productivity and forb abundance (associated with the higher rainfall on the south slopes), as well as the use of topographic variation in obtaining early green forage strongly suggests an optimal foraging stategy. This migratory movement prior to calving may also be associated with the survival benefits of moving to a calving ground with relatively few predators (see Study Area), as suggested by Whitten and Cameron (1980) for the Central Arctic herd. Another factor contributing to the caribou's strategy for optimizing the quality of the spring diet includes the selection of specific plant species, parts, and phenological stages that are high in available nutrients and low in plant secondary or defensive compounds (see Chapin et al. 1980; Kuropat and Bryant 1980). The mid-June movement of caribou to higher elevations, with relatively low plant productivity, likely involves optimizing trade-offs between nutrient intake and the energy expenditure associated with insect harassment (Roby 1980).

Summer (July to mid-August)

Movement north across the range to the summering grounds usually occurs in the first week of July and is likely precipitated by increasing oestrid fly harassment (see Chapter 2). The daily, summer foraging strategy of the caribou was controlled to a large extent by local weather patterns in conjunction with oestrid fly harassment. During calm days of reduced cloud cover, caribou were often restricted to high elevations of about 1900 m, particularly snow banks, or gravel bars where grazing seldom occurred. At other times, caribou moved to lower elevations (about 900 m) where shrub tundra, with relatively abundant lichen stands and mushrooms, was grazed intensively.

An abundance of lichens on the summer ranges of Alaskan caribou is rare according to Skoog (1968). However, lichens were more abundant on the summering range of the Denali herd than on any other seasonal range except the western portion of the wintering range. It is well known that lichens are a highly preferred food throughout the year, in spite of their low N and mineral contents. Therefore, an estimated proportion of 17 percent lichens in the summer diet (Table 4) does not seem unreasonable. Also, this figure is comparable to Palmer's (1926) estimate of 15 percent lichens in the summer diet of reindeer along the Alaskan coast of the Bering Sea, and Bergerud's (1972) finding of 22 percent lichens in summer rumen samples of caribou in Newfoundland. Likewise, Bergerud and Nolan (1970) found about 15 percent lichens in the summer diet of hand-reared caribou in Newfoundland. However, if lichens are very scarce on the summering range it is likely that considerably less lichen will be consumed. For example, White et al. (1975) found that caribou rumen samples collected near Prudhoe Bay, Alaska, where lichens are scarce, contained only 3 percent lichens in July, 1972.

The intake of forbs decreased somewhat from the spring to the summer diet. I have estimated that the forb component contributed about 10 percent to the total summer diet (Table 4). The decrease in use of forbs was due primarily to the decrease in availability of forbs on the summering range. Many of the forbs available on the Cantwell calving grounds were too discontinuous in distribution on the summering range or only available a short time in the spring before fruiting and senescing. Also, the young growth stages of forbs in spring were more palatable than mature, summer growth. Bergerud and Nolan (1970) and Bergerud (1972) noted a comparable decrease in caribou use of forbs in July and August in Newfoundland. Also, White et al. (1975) found that caribou rumen samples collected near Prudhoe Bay, Alaska contained 10 percent forbs in July.

Deciduous shrubs continued to be of great significance in the summer diet, contributing about 50 percent to the total summer's intake. Prostrate willows, including *Salix arctica*, *S. rotundifolia*, and *S. reticulata*, contributed significantly to the *Salix* component of the diet, particularly when the caribou retreated to higher elevations and wind-exposed ridgetops due to fly harassment. Murie (1944) also noted the use of these dietary components. *Salix pulchra* and *S. alaxensis* remain the most palatable willows throughout the summer, as they are in the spring, but these species predominate at lower elevations than the prostrate willows and *S. alaxensis* is particularly abundant along drainages. Skoog (1968) also found that *S. pulchra* and *S. alaxensis* were the most palatable willows in the diet of the Fortymile and Nelchina caribou herds in interior Alaska. Although *S. alaxensis* is palatable to caribou, adult females and particularly females with calves avoid the tall willow thickets characteristic of this species. When forced to move through these thickets on a migration route, the caribou were often alarmed and were observed to trot through the taller willows (Henshaw 1968;

Curatolo 1975). This behavior is likely related to the decreased visibility and, therefore, decreased likelihood of avoiding predators (Roby 1978). Bull caribou were observed to be much less apprehensive of grazing in tall willow thickets (Roby 1978).

Graminoids continue to be important in the diet in the summer, as they are throughout the year (Table 4). *Carex podocarpa*, *C. bigelowii*, *Festuca altaica*, and *Hierochloe alpina* predominate in the summer diet. These observations are in agreement with Skoog's (1968) observations of the Fortymile and Nelchina caribou herds in interior Alaska. Upland *Carex* spp. and *Hierochloe alpina* can be particularly important when caribou are restricted to ridgetops and upper slopes on days of moderate to severe insect harassment.

Mushrooms constitute a highly preferred food of *Rangifer*. Skoog (1968) reviews the comments of several authors who emphasized the strong craving that caribou/reindeer have for mushrooms. Luick (1977) noted that mushrooms are also highly prized by semi-domesticated reindeer herds and that the reindeer's intensive search for mushrooms often leads to straying and even stampeding. Even in winter, I observed caribou eating old, frozen mushrooms, and in late autumn caribou ate mushrooms that were decomposing. Mushroom fragments were identified in all late summer and autumn fecal samples collected after the first of August, and were also identified periodically in samples collected throughout the winter until early May (Appendix A).

A noteworthy change in the foraging behavior of caribou occurred in the summer. This was associated with a high degree of walking or searching during the undisturbed, summer grazing period. I found this activity to be due primarily to the caribou's search for mushrooms. For example, caribou were often seen to visually detect light-colored objects (mushrooms or rocks) from several meters and to, subsequently, walk rapidly to the object for scenting. Most genera of mushrooms were eaten without hesitation. However, one rather abundant genera, *Amanita*, seemed to be avoided. This genus is generally considered highly toxic to man (Guild 1977). Karaev (1968) stated that *Amanita* produces signs of poisoning in reindeer, but he did not consider it fatal. Large mushrooms of the genus *Boletus* contributed most importantly to the caribou's diet, followed closely by the genera *Lactarius* and *Russula*. On one occasion, the tame reindeer consumed 16 large *Boletus* mushrooms consecutively, under natural grazing conditions, before altering his search image to green plant material. This event occurred on the second day of natural grazing, and it was under these trials that the reindeer was thought to be first introduced to mushrooms (J. Wright pers. comm.). Several other genera of mushrooms were observed to be eaten by caribou and are listed in Appendix C.

Estimating the percentages of mushrooms in the caribou diets is difficult. Mushrooms seemed unusually plentiful on the summering grounds in both 1979 and 1980 and were frequently encountered along alpine ridges, although they were most abundant in lower shrub communities on flood plains and near timberline. Of course, the abundance of mushrooms can vary greatly on an annual basis. The yield of mushrooms is promoted by warm, wet weather, and growth is inhibited by early freezing (Karaev 1968). Skoog (1968) found that fungi comprised about 45 percent ± 23 (s.d.) of the total food volume in 19 rumen samples from caribou killed in late August, 1954, from the Fortymile caribou herd in interior Alaska. He felt that a substantial increase in the use of mushrooms occurred in mid-August, after the peak of the fly season, when caribou ventured near or below timberline. Bergerud (1972) found that fungi comprised about 25 percent of the volume in 14 caribou rumen samples in summer in Newfoundland. Therefore, my estimate of 12 percent mushrooms in the summer diet (Table 4) may be low; however, mushrooms were relatively scarce during the initial two-thirds of the summer (July to early August).

Application of the results of the fecal analyses to an estimation of the true dietary component of mushrooms is not possible at this time, since it is not known for certain whether mushrooms are overestimated or underestimated in the feces. The extremely high estimated digestibility of mushrooms (Appendix C) suggests that the fecal analyses underestimate the true proportion of mushrooms in the diet. However, mushrooms fragment readily and are easily identified in the feces, particularly the spores (T. Foppe pers. comm.). In tabulating the approximate seasonal diets, I have assumed that mushrooms were underestimated in the fecal analysis. I base this hypothesis on the extremely high digestibility of mushrooms and the fact that the tame reindeer consumed moderately high quantities of mushrooms during feeding trials under natural grazing conditions, yet mushrooms were not detected in his feces (Appendix B).

Various authors have noted the ingestion of berries by caribou, particularly from the following plant species: *Arctostaphylos alpina*, *A. uva-ursi*, *Empetrum nigrum*, *Rubus* spp., *Vaccinium uliginosum*, and *V. vitis-idaea* (Skoog 1968). I have observed use of berries from *V. uliginosum* and *V. vitis-idaea*. Also, the increase in fragments of *Vaccinium* in late summer and autumn fecal samples (Appendix A) is undoubtedly an indication of the berry component of the diet. This was substantiated through analysis of the tame reindeer's feces (Appendix B) collected after feeding trials in which the reindeer showed a strong preference for berries of *V. uliginosum*. Due to the high palatability of berries, it is possible that they can become an important component of the diet at times (Sablina 1960; Skoog 1968).

The food habits of bull caribou were studied only briefly due to the almost complete segregation of bulls from adult females in spring and the partial segregation during the summer. Two fecal samples were collected from bulls in the summer and early autumn of 1978 in the vicinity of the park road, where a large number of bulls spend the summer. These two fecal samples (Appendix B) had significantly greater ($p < 0.01$) *Salix* fragments than samples from female caribou for the same period. The proportion of *Salix* fragments in samples collected from bulls averaged 92 percent, whereas *Salix* fragments averaged only 56 percent in fecal samples from adult females. Also, based on field observations of bulls in the spring, summer, and autumn, it is likely that bulls consume proportionately more *Salix* than females as long as green *Salix* leaves are present.

In summary, the proportion of forbs in the summer diet decreased somewhat compared to the spring diet, due primarily to the decline in the availability of forbs on the summering range and to the later phenology of the forbs. *Salix* spp. dominate the summer diet, but graminoids, forbs, lichens, and mushrooms are also important. Variations in the summer diet could result most readily from weather patterns favoring fly harassment which acts to restrict caribou to windswept ridgetops and high elevations, resulting in decreased intake of food and a decrease in the proportion of *Salix* in the diet. Weather patterns also control the availability of preferred food species, particularly forbs and mushrooms. Therefore, the influence of weather patterns on the nutritional regime of the summer and fall diet should not be underestimated.

Autumn (mid-August to mid-October)

The autumn season is characterized by a gradual reduction in the quantity of green forage and the lack of a persistent snow cover. The first frosts in the west-central section of the park and the subsequent change in colors of the vegetation coincide with the initiation of the autumn migration of caribou to the rutting grounds. Forbs and mushrooms are the first affected by the frosts, followed by the deciduous shrubs, and, finally, the grasses and sedges. As the palatability of summer forage decreases, particularly the palatability of deciduous shrubs, an increase in the proportions of winter foods occurs in the diet, specifically lichens and the remaining green stems of *Carex* spp. (Table 4).

Skoog (1969) found that caribou distribution in the autumn was affected by changes in palatability of forages, and, specifically, that caribou tended to move to lower elevations or to wetter sites, where the vegetation remained green longer. This is in agreement with my findings in that the rutting grounds of the Denali herd is comparatively wetter than the summering grounds, and the caribou generally remain at lower elevations than on the summering grounds. The autumn movement, however, is away from the abundant lichen stands and mushroom growth of the summering grounds, and both lichens and mushrooms are highly palatable throughout the fall. Nevertheless, the caribou movements may be associated with the need to prolong the use of succulent, green vegetation in the diet, thus prolonging the period of high nutrition. Murie (1935) believed that seasonal changes in food supply strongly influenced the movements and distribution of caribou.

A gradual decrease in the presence of *Salix* fragments was noted in the autumn fecal samples (Appendix A), until *Salix* failed to be detected in the October 11 sample. *Salix pulchra* was the principal willow taken, and caribou were observed grazing the brown, persistent leaves for brief intervals throughout late autumn and winter.

An interesting increase in *Vaccinium* occurred in the autumn, and, as previously mentioned, was probably related to the intake of *V. uliginosum* berries, which were extremely abundant in the area at this time. The fecal sample collected from bulls in Polychrome Flats on September 9, 1978, showed an unusually high proportion (19 percent) of *Vaccinium* (Appendix B), and the bulls were observed grazing berries of *V. uliginosum* and *V. vitis-idaea* at the time of collection of the fecal sample.

Mushrooms were detected in all autumn fecal samples and were observed to be grazed on several occasions. However, since mushrooms were less prevalent on the rutting grounds than on the summering grounds in the years studied, an increase in intake of mushrooms from the summer to autumn diets seemed unlikely. Also, many mushrooms were decomposing in the early autumn. Lichens were also highly preferred as the presence of succulent, green vegetation became restricted.

Graminoids, particularly *Carex aquatilis* and to a lesser extent *Festuca altaica* and *Hierochloe alpina*, remained partially green and were grazed with greater intensity than in spring and summer. Skoog (1968) discussed caribou use of *Carex aquatilis* at length. Also, through analysis of rumen samples, Skoog (1968) documented that an in-increase in use of graminoids by the Fortymile caribou herd coincided with the progression of the autumn season. The decrease in *Carex* fragments in autumn fecal samples, as compared to spring and summer samples (Table 3), may be due in part to the low autumn sample size (n = 4) and the increase in less digestible food items in the diet (for example, mosses) that are easily identified in the feces. Appendix C gives the relative in vitro digestibilities of these plant groups. Equisetum arvense and evergreen E. variegatum are also important in the autumn diet, as they are throughout the year (Table 4).

Bull caribou reduce their intake during the autumn and intermingle with females making it difficult to segregate their feces. However, it is likely that bull caribou have diets similar to females during the autumn due to the low diversity of palatable species available at this time. Calf pellets could not be readily distinguished from adult pellets in the autumn, so no speculation can be made on possible differences in the autumn diets of different age classes.

In conclusion, lichens dominated the autumn diet, whereas willows decreased in importance and graminoids increased slightly compared to values obtained in the summer and spring. Mushrooms were also important in the autumn. Again, weather patterns are important in influencing the relative abundance of green plants and mushrooms on a caribou range, particularly in autumn. Hard freezes with continuing cold temperatures have the greatest positive influence on maintaining plants in their green condition. Skoog (1968) stated that mild temperatures can extend the period of availability of high quality green forage into late October in interior Alaska.

Winter (mid-October to mid-May)

Subsequent to the rutting season, the caribou begin moving to wintering grounds (Figure 1). Troyer (1976, 1977, 1978, 1980) documented that the Denali caribou herd had two distinct wintering grounds, although the caribou coalesce on the eastern area in April. Both wintering areas are on the northern boundaries of the park and adjacent areas to the north but are separated in part by the Kantishna Hills. The western wintering ground is much more expansive than the eastern area and less accessible. As a result, my investigations of the eastern area were more intensive (Table 2). The eastern wintering ground is characterized by a series of windswept hills, the Stampede Hills, extending west from Lignite with spruce stands and tussock meadows at lower elevations. These windswept hills provided some areas of snow-free vegetation throughout the winters of my study. This entire area, in general, is extremely windswept, thus curtailing the need for extensive cratering by foraging caribou. The western wintering area also has some windswept hills west and northwest of Wonder Lake, but a majority of the area is comprised of extensive spruce stands.

Murie (1944) noted that the presence of lichens seemed to be a requirement of a wintering ground for caribou, although lichens are definitely not the exclusive diet. Skoog (1968) mentioned some exceptions to the use of lichen-rich areas for caribou wintering grounds in Alaska. Caribou diets in these areas (the Alaska Peninsula and the North Slope) reportedly consist mostly of sedges during the winter. Nevertheless, lichens are highly preferred by caribou in winter, and the availability of lichens is generally considered of great significance (Baskin 1970). Lichen availability on the eastern wintering ground was variable but appeared to be much less favorable than on the western wintering area. Species composition of lichens was favorable in both areas, with *Cladonia* spp. and *Cetraria cucullata* predominating.

Differences in the proportion of lichen fragments in the feces collected on the eastern versus the western wintering area also indicated that lichen availability on the eastern area was less favorable. For example, three fecal samples were collected from the western wintering ground in late November of 1978 (Appendix A). These samples had significantly greater lichen fragments ($p < 0.01$) and significantly less moss fragments ($p < 0.01$) than the remaining winter fecal samples, which were collected on the eastern wintering area. This limited data shows a higher lichen availability and intake on the western area, particularly since less moss intake was noted. As previously suggested the intake of mosses inevitably increases on poorer lichen ranges. In regard to this trend, I feel that with more comparative data fecal analyses can be instrumental in assessing the relative value of lichen winter ranges.

Approximate proportions of foods in the winter diet is presented in Table 4. Lichens comprised the major component of the winter diet, due to the high palatability of lichens. My estimate of about 62 percent lichen in the winter diet is comparable with findings in other studies. Skoog (1968) found that lichens seldom constitute greater than 75 percent of the diet at any one time and felt that a more common estimate would be 50 percent or less when graminoids are readily available. Gaare and Skogland (1975) found that fruticose lichens comprised about 85 percent of 18 esophageal fistula samples collected in January and October from reindeer in Hardangervidda, Norway. Thirty-five rumen samples collected from wild reindeer over the same period averaged 47 percent lichens (Gaare and Skogland 1975). Skjenneberg et al. (1975) also used esophageal-fistulated reindeer and found that esophageal samples contained 79 percent lichen when lichens constituted about 6 percent of the vegetative cover. Karaev (1968) stated that lichens constitute close to 66 percent of the entire reindeer's food supply during the year in most arctic regions. Scotter (1967) found that caribou rumen samples collected from several areas in northern Canada contained from 52 percent to 73 percent lichens in winter. Caribou have excellent capabilities for detecting lichens beneath the snow (Pruitt 1960; Bergerud and Nolan 1970).

Several authors have investigated species preferences of lichens by *Rangifer*, including Palmer (1926), Karaev (1968), Pegau (1968) Des Meules and Heyland (1969), and Holleman and Luick (1977). In accordance with these studies, I found that *Cladonia* spp. were preferred, particularly *Cladonia alpestris*, *C. mitis*, *C. arbuscula*, and *C. rangiferina*. Another species of high palatability was *Cetraria cucullata*. According to the Composition Analysis Laboratory, the fecal analyses showed a high dietary preference for the genera *Cladonia* and *Thamnolia*, and a much more reduced intake of the genera *Dactylina*, *Cetraria*, *Alectoria*, and *Peltigera* (Appendix A). Results from analysis of the tame reindeer's feces indicate that the fecal analysis is generally reliable in regard to the identification of lichen genera.

Although the winter diet was dominated by fruticose lichens, graminoids and Equisetum spp. continued to be important (Table 4). Evergreen E. variegatum was grazed repeatedly in wet sedge meadows, while E. arvense, a non-evergreen species, was frequently sought by caribou in shrub commuities. Green stems of Carex aquatilus and other Carex spp. were also sought repeatedly in wet sedge meadows in winter. Green tissue is normally prevalent only among moist Carex meadows, although Festuca altaica, Hierochloe alpina, and Stellaria longipes may also retain some green tissue in the winter. Skoog (1968) stated that Russian reindeer specialists considered green vegetation to be an essential component of the reindeer's winter diet. Karaev (1968) summarized the current ideas relating to the importance of green winter foliage and mentioned several species of significance, including Carex aquatilus, Festuca, and E. variegatum.

Mushrooms also appeared sporadically in winter fecal samples (Appendix A). Karaev (1968) reported that reindeer eagerly searched for mushrooms in winter, as have other authors as reviewed by Luick (1977).

Evergreen shrubs were used significantly by caribou only during the winter, and Vaccinium vitis-idaea was the only species consistently identified in the winter feces (Appendix A). Karaev (1968) stated that evergreen browse species, including V. vitis-idaea, Ledum palustre, and Empetrum nigrum, were used by reindeer only during "lean" years. Alexandrova (1940), Steen (1968), and Klein (1968) agree that these species are definitely not preferred foods. Skoog (1968) also concluded from his own observations and a review of the literature that evergreen browse species do not comprise a major constituent of the winter diet, particularly when lichens and graminoids are available. The limited use of these abundant species likely originates from their relatively low palatability and digestibility. Nagy and Regelin (1977) documented that volatile oils from evergreen shrubs had a negative influence on food palatibility in mule deer. Relatively high use of certain evergreen shrubs by caribou likely indicates poor range condition, similar to the high intake of mosses as discussed previously. However, Scotter (1964) commented on unpublished Scandinavian work that indicated that the ingestion of *Vaccinium vitis-idaea* in combination with lichens could increase the digestibility of lichens. Also, *V. vitis-idaea* appears to be more palatable than many other evergreen shrubs (e.g. *Ledum* and *Empetrum*), and *V. vitis-idaea* also had relatively high estimated digestibilities (Appendix C).

More work is needed to substantiate this interaction and to evaluate its importance. At present, it seems likely that a relatively high intake of evergreen shrubs (e.g. 15 to 25 percent) is disadvantageous and would indicate poor range condition. Fecal analyses could provide easily accessible indices to the comparative use of evergreen shrubs by caribou under different range conditions. With such comparative data the fecal-analysis technique could eventually be used as a tool to compare winter range conditions of different caribou herds, both in respect to the increased intake of evergreen shrubs and increased intake of mosses on poor winter ranges. On good winter ranges, lichens and/or graminoids should predominate in the diet (Skoog 1968), but more comparative data are needed to specify the relative proportions of lichens, mosses, graminoids, and evergreen shrubs that would provide adequate nutritional qualities. Of course, a variety of other environmental conditions, particularly a crusted snow cover might occasionally exert a relatively greater influence on the winter nutritional status of a particular caribou herd than dietary composition. However, factors acting to decrease food intake may also be found to influence the proportion of dietary components through decreased selectivity; thereby giving the fecal analyses broader applications for indicating poor nutritional status. Caution would have to be applied in comparing different herds, particularly in respect to herds experiencing winter seasons of different duration.

In conclusion, lichens dominated the winter diet, whereas Equisetum spp., Vaccinium vitis-idaea, mosses and graminoids, particularly green tissue of graminoids, were taken in far less, but significant quantities. The intake of mosses was considered incidental to the selection of lichens, as discussed in previous sections. The rather high estimated proportional intake of mosses (10 percent) may suggest a sub-optimal winter range condition, at least on the eastern wintering area. However, to confirm this hypothesis, more comparative data are needed covering aspects of both fecal analyses and the availability of dietary components.

Finally, variations in snow cover could influence the composition of the winter diet to a large degree, specifically in regard to restricting foraging caribou to windswept areas or areas having snow parameters favorable to cratering. As previously discussed, the eastern wintering ground of the Denali caribou herd was particularly windswept during the winters of this study. The precise influence of snow cover on the diet is however unknown and undoubtedly variable. Late autumn and winter weather favoring the prevalence of green vascular tissue could also influence the winter diet by favoring the intake of graminoids.

Summary and Conclusion

Caribou have been described as cursory grazers with fastidious feeding habits (Skoog 1968) and are sometimes considered generalist or opportunistic herbivores (Skoog 1968; Bergerud 1972) due to the large number of species in the diet. In general, the relative availability of palatable food species determines the diet of caribou on a particular range (Skoog 1968; Bergerud 1977; Luick 1977). Certain species of lichens, mushrooms, willows, horsetails, and green forbs are often considered to have high preference values. Consumption of large proportions of evergreen shrubs and bryophytes is generally avoided except under poor range conditions (Karaev 1968). With the exception of lichens, caribou generally select the most nutritious forage available to them throughout the year. Of course the digestibility of the forages is a major factor influencing their relative nutritional value. Aspects of forage quality and its influence on caribou nutrition are discussed in Chapter 3.

Seasonal phenomena that have been discussed in relation to their influence on food availability include plant phenology, snow cover, and weather patterns. Seasonal movements and range use patterns have also been considered in tabulating seasonal diets. Possible causative factors for the Denali caribou herd's seasonal movements have also been discussed. Skoog (1968) discussed in detail the various factors controlling caribou movements, including the influence that the quality of food resources has on seasonal movements. This subject is discussed further by Murie (1935), Klein (1970a), Skogland (1975), and Whitten and Cameron (1980).

CHAPTER 2: SEASONAL ACTIVITY AND ESTIMATED ENERGETICS

Introduction

This chapter focuses on aspects of the seasonal activity of female and young caribou of the Denali herd with three major emphases, as follows:

1) description and explanation of seasonal changes in activities,
2) documentation of comparisons with other caribou/reindeer activity-studies to provide an assessment of comparative range condition and nutritional status of the Denali herd, and
3) development of a model of seasonal energy requirements.

Calculations of energy requirements are useful as a basis for making comparisons between populations. These calculations also allow estimation of a population's daily food requirements (Chapter 3) which, together with estimates of food availability, allow approximation of the range's nutritional carrying capacity. Calculation of energy requirements also allows one to test the effect of any energy related variable on the total animal-range relationship. Some factors that can exert significant influences on a population's energy expenditure include insect-harassment levels, migratory distances, and characteristics of snow cover.

Study of caribou/reindeer activity has received emphasis by several authors. The first activity-studies were addressed primarily to estimating energy requirements of reindeer in the Soviet Union (Makarova and Segal 1958; Segal 1962). Thomson (1973, 1977) initiated intensive investigation of the activity and behavior of Rangifer in a study of wild reindeer in Norway. Gaare et al. (1975) summarized investigations of wild reindeer activity in Norway. Curatolo (1975) emphasized the influence that weather and insects have on local movements, activity, and behavior of caribou in east-central Alaska. White et al. (1975) discussed several aspects of the ecology and activity of caribou near Prudhoe Bay, Alaska, and included discussions of the effects of insects on caribou activity. White et al. (1975) also estimated the summer energy balance and energy flow through the Prudhoe Bay caribou population. Roby (1978) reported on a comprehensive study of year-round activity budgets and behavior of the Central Arctic caribou herd in Alaska. Wright (1979) studied the interactions between reindeer and birds on the Seward Peninsula in Alaska.

The most recent activity studies have concerned comparisons of the activity of nutritionally-stressed caribou in Greenland with the activity of caribou in north-central Alaska (Roby 1980), and comparisons of the activity of Svalbard reindeer with the activity of reindeer in Norway (Reimers 1980). Several of these studies have emphasized the usefulness of activity studies in judging the relative nutritional status of caribou/reindeer and/or range condition of a herd (Segal 1962; Gaare et al. 1975; Roby 1979, 1980; Reimers 1980).

As a basis for discussion of caribou/reindeer activity, it should be recognized that the synchrony of activity between animals in a group has been recognized by Segal (1962), Thomson (1973), Curatolo (1975), Roby (1978), and J. Wright (pers. comm.). These authors also mentioned the regular alternation between active and rest periods in the daily activity of Rangifer. The influences that circadian rhythms have on these active-rest periods has been stressed by Thomson (1973) and Roby (1978).

Methods

Documentation of Caribou Activity

Groups of caribou were observed with the aid of a zoom spotting scope (15x - 60x) and binoculars (10 x 50). Observations were made during all daylight hours and usually continued until dark or until the group moved out of view and could not be relocated. Observations were also discontinued if the caribou became aware of my presence. Caribou activity was documented by scanning each group at 10-minute intervals throughout an observation period and recording the number of individuals that were engaged in each of six categories of activity, as listed below. Each scan was completed as quickly as possible, often with the use of a tally counter.

Clarification of the six basic activities follows:

1) feeding - includes only the time when the caribou's lips were on or immersed in vegetation or snow while in a standing or walking posture. Much of the searching activity prevalent while grazing is excluded from the definition, thereby attaining a better estimate of the percent of time spent actually ingesting food (an extremely important parameter in nutrition studies). An exception to this definition occurs when caribou are under varying degrees of insect harassment and are standing with heads lowered not ingesting food, but often with their lips immersed in vegetation. Feeding animals were distinguished from animals in the insect-harassment stance by

the more frequent movement of feeding animals. If an animal moved forward over about a 7- to 10-second period, it was considered a feeding animal.

2) lying - self-explanatory.
3) standing - animal was stationary in a standing posture with its lips above the vegetation or snow; or, in the case of the insect-harassment stance, the animal was stationary, often for several minutes or longer usually with its lips on or immersed in vegetation. The standing posture includes activites such as urination, bush-thrashing, sparring, and nursing.
4) walking - animal was in a walking posture and not ingesting.
5) trotting/galloping - self-explanatory.
6) cratering in snow - animal was pawing in snow.

The method of using instantaneous scans to collect quantitative activity data has been described by Altmann (1974), and has been used in several studies of caribou/reindeer activity (Thomson 1973; Curatolo 1975; Gaare et al. 1975; White et al. 1975; Roby 1978, 1980; Wright 1979). Due to the synchrony of activity between animals in a group and the regular alternation of active and rest periods (Segal 1962; Thomson 1973; Curatolo 1975; Roby 1978; J. Wright pers. comm.), the instantaneous scan method should provide good estimates of the activity budgets of <u>Rangifer</u>.

The term "activity budget" refers to the tabulation of the percent of time that an animal spends in various activities. The "activity pattern", in contrast, is the short-term alternation between the two basic activites, grazing and resting (Thomson 1973; Roby 1978). I have defined the total time spent in a grazing period and adjacent rest period as an active-rest cycle. The point in time when a majority of the animals in a group ceased lying or resting and began grazing or walking marked the initiation of an active period and termination of a rest period. Likewise, when a majority of animals in a group ceased grazing or walking and began to rest, a rest period was initiated and the active period terminated.

Only observations made during complete active-rest cycles were used in the calculation of activity budgets, except during the insect season when cyclic activity was not apparent. The use of complete active-rest cycles in the calculation of activity budgets was necessary, for example, to prevent overestimation of time spent lying, as lying animals were the easiest to observe on consecutive scans. Also, if one observed a complete active-rest cycle and a portion of the succeeding active period, one would inevitably overestimate the proportion of time spent active. It is particularly important to adhere to this method when analyzing winter activity budgets, as distinct circadian rhythms occur in the caribou's activity patterns in winter (Thomson 1973; Gaare et al. 1975; Roby 1978). For instance, observations taken around mid-day (peak lying time) in early and mid-winter would greatly overestimate the proportion of time spent lying during the 24-hour period.

Segal (1962) found that reindeer exhibit cyclic activity patterns over 24-hour periods throughout the year, and he could not distinguish any differences in the duration of active-rest cycles between day and night. Segal also emphasized the constancy of these cycles within a season. Thus, observations made over complete, active-rest cycles should closely estimate the proportion of time spent in various activities throughout the day or the particular season. Unfortunately, no other study on caribou/reindeer activity has considered the use of active-rest cycles in calculating activity budgets, although essentially all authors have reported observing distinct active-rest cycles in the daily activity of caribou/reindeer.

The usual method for calculating activity budgets throughout a particular season has been to simply sum the number of caribou/reindeer that were observed in particular activites. Observation periods were of varying lengths, but were not restricted to graze-rest cycles. Subsequently, calculations were made of the proportion of animals observed in each activity. In contrast, I enumerated the number of caribou participating in each activity throughout individual active-rest cycles to attain estimates of the proportion of time caribou spent in each activity throughout a day or season. It was necessary to sustain a constant or nearly constant group size throughout the active-rest cycle, so that all segments of the cycle were represented by an equal number of caribou. Besides offering good estimates of daily and seasonal activity budgets, this method offers the further advantage of allowing one to calculate a measure of variability. The measure of variability compares the percentage of time spent in various activities between individual active-rest cycles.

Because my method of calculating activity budgets differs from methods in other caribou/reindeer studies, the results presented in this paper are not necessarily directly comparable with results of other studies, and the reader should consider this difference when comparisons are made with other studies.

Disadvantages of my method include the large amount of observation time required to attain an adequate sample of active-rest cycles, particularly under circumstances where the caribou may readily move out of view. Also, this method of calculating activity budgets may underestimate slightly the amount of time spent trotting/galloping and possibly the amount of time spent walking, but these activities occupy considerably less time than grazing and lying except during periods of moderate to severe insect harassment (Thomson 1973; Curatolo 1975; Gaare et al. 1975; White et al. 1975; Roby 1978; Wright 1979). I believe my estimates of the incidence of trotting/galloping and walking are quite accurate, although considerable variability in the time caribou spent in these activities was noted between active-rest cycles.

I used a different method for analyzing activity data collected during the insect season. This difference was mandatory because cyclic activity data was not observed during the insect season. As such, I calculated activity budgets for the insect season from all groups of caribou observed for periods longer than 2.5 hours. That is, the proportions of time spent in the various activities were calculated for each observation period lasting 2.5 hours or more without the bounds of cyclic activity previously described. Thus the measure of variability compares activity budgets between total observation periods rather than graze-rest cycles. An overestimation of the time spent walking and trotting/galloping may have occurred using this method. For example, since normal lying periods were never observed during daylight hours of the insect season, these periods likely occurred during the 4 to 8 hours of darkness each day when, for instance, insect harassment was lower than during daylight hours. As such, estimations of the proportions of time spent active (e.g. walking and trotting/galloping) are likely applicable only to the daylight hours, and are probably overestimations in regard to the true seasonal and daily activity budget.

The following supplemental observations were recorded at 15-minute intervals for each group observed:

1) observation number
2) time
3) date
4) location (from U.S.G.S., 1:250,000 topographic maps)
5) group size (where distances between individuals did not exceed 300m)
6) group composition (number of calves, yearlings, cows, and bulls)
7) slope aspect
8) slope shape (lower, mid-, or upper slope; or ridgetop, valley, or plateau)
9) elevation (from U.S.G.S., 1:250,000 topographic maps - 30.5 m contour lines)
10) approximate horizontal and vertical distance moved over previous 15 minutes
11) direction of movement

Supplemental observations (cont'd)

12) wind speed and direction
13) temperature
14) percent cloud cover
15) occurrence and rate of precipitation
16) insect-harassment descriptions
17) description of disturbances

Measurements of snow depth (cm), hardness ($g \cdot cm^{-2}$), and density ($g \cdot cm^{-3}$) were taken at caribou feeding sites if the snow cover was complete. Two spring penetrometers were used to measure snow hardness; one was calibrated from 10 to 500 $g \cdot cm^{-2}$ and the other from 100 to 10,000 $g \cdot cm^{-2}$. Both penetrometers were equipped with terminal discs of 1 cm^2 and could be fitted with detachable discs of 10 cm^2 and 100 cm^2. Density was calculated using a 250 cm^3 snow sampler and a 1000 g spring scale. All the above equipment followed standards described by Klein et al. (1950) and Thing (1977).

Contingency tables (Conover 1971) were used: (1) to compare activity budgets between the five seasons, and (2) to compare activity budgets between adult females and calves in the calving and post-calving season. Differences in the duration of active and rest periods between seasons were analyzed using the F-test and, subsequently, the Newman-Keuls test (Zar 1974). The t-test (Zar 1974) was used to analyze differences in elevations of grazing areas.

The caribou annual cycle (Miller 1972; Bergerud 1974a; Roby 1978) was divided into six periods for the purposes of analyzing seasonal activity. The six periods included: the calving and post-calving season (May 22 - June 30), the insect season (July 16 - August 31), the pre-rut and rutting season (September 16 - October 31), the early winter season (November 16 - December 31), the mid-winter season (January 1 - February 29), and the late winter season (March 1 - April 15). Activity budgets were not calculated for the mid-winter season because of the low number of observation periods. Also, observations during migratory periods were excluded from the calculation of seasonal activity budgets. Migratory periods served to divide each of the seasons, except the winter periods.

Calculation of Energy Requirements

Estimates of energy costs from the literature were applied to seasonal caribou activity budgets, movements, and productive processes to assess year-round energy requirements of adult female caribou. Observations of activity budgets and movements during daylight hours were extrapolated over 24-hour periods to calculate daily energy expenditure. This step seems well-founded as activity budgets (except those calculated over the insect season) were based on cyclic activity patterns, and Segal (1962) found no differences between day and night cyclic activity patterns of reindeer within individual seasons.

Methods for calculating daily energy requirements of ruminants are described by Blaxter (1962), Agricultural Research Council (1965), Moen (1973), Robbins (1973), Weiner (1975), and others. Generally, the following formula is given:

$$\text{Total daily energy requirement} = \text{Basal metabolic energy expenditure} + \text{Activity expenditure} + \text{Production costs considering associated efficiencies} + \text{Additional cost to maintain homeothermy}$$

Several assumptions were made in consideration of this formula. For instance I have assumed that there would be no additional costs to maintain homeothermy among adult caribou. This assumption is based on a study by Hart et al. (1961) that found that a 9-month-old caribou exhibited no increase in metabolism (measured using a face mask) when ambient room temperatures ranged from 25°C to -55°C. No shivering was observed in temperatures as low as -55°C, although panting and an increase in breathing rate was observed at a temperature of 25°C. No other data are available on metabolic rates of caribou at temperatures as low as -55°C, but it appears likely from the study by Hart et al. (1961) that any added costs of maintaining homeothermy among caribou in the Denali herd would be minimal. Temperatures as low as -55°C are extremely rare on the wintering grounds of the Denali caribou herd (see Study Area). In cases where windchill could be detrimental to energy balance, caribou have ready access to sheltered hillsides and/or stands of spruce.

I have also assumed in the energetic model that production costs included only the estimated energy costs of pregnancy, lactation, fattening, and hair growth. The energy costs of growing antlers was not considered due to the lack of values for estimating this cost. However, the energy cost of growing antlers can likely be considered of minor importance to adult female caribou compared to other production costs.

A further deviation from the use of the previously given formula for calculating daily energy requirements has been my use of resting metabolic rates (RMR), rather than basal metabolic rate (BMR) or fasting metabolic rate (FMR), as a maintenance metabolic level and as a basis for calculating daily energy requirements. Values of RMR given in this paper include the heat produced from digestive processes, often called the calorigenic effect of food. In contrast, measurement of BMR or FMR assumes standard conditions of fasting for 48 hours or more (post-absorptive state) and thus does not include the calorigenic effect of food. The heat produced from the calorigenic effect of food is not utilized by a ruminant experiencing warm ambient temperatures, but may be very important in winter, particularly when caribou are consuming snow. Even in summer however, the heat from the calorigenic effect of food is produced from food energy and therefore increases food requirements. Weiner (1977) reported that the added costs of the calorigenic effect of food increased daily heat production 25 to 30 percent over fasting heat production in roe deer (Capreolus capreolus) under thermoneutral conditions. Therefore, inclusion in the model of estimates of the calorigenic effect of food can be of considerable importance when estimating food requirements needed to meet the costs of daily metabolism. Addition of the calorigenic effect of food to the energy model gives estimates of "metabolizable energy requirements". I have dealt with estimates of metabolizable energy requirements throughout this chapter. By definition, metabolizable energy requirements are total food energy requirements less the energy contained in the feces, urine, and methane.

The method described above for estimating metabolizable energy requirements differs somewhat from the method described by the Agricultural Research Council (1965). For instance, the Agricultural Research Council (1965) used an average value of FMR divided by the efficiency of the utilization of metabolizable energy for maintenance (about 68 to 75 percent) as an estimate of maintenance metabolizable energy requirements of cattle and sheep. This method gives values essentially equal to the method I described above. My use of RMR was necessitated by the almost complete lack of values for FMR of reindeer/caribou (n=1), while values of RMR (nonfasted) are abundant.

Although BMR was not used in calculating energy requirements of caribou in this paper, an estimate of BMR was needed so that daily energy requirements could be expressed as multiples of BMR. Expression of energy requirements as multiples of BMR is useful in analyzing the variation in energy requirements between species. However, estimation of BMR is difficult and, in the case of reindeer/caribou, only one measurement has been made that approximates BMR. Measurement of BMR assumes standard conditions of thermoneutrality, post-absorptive digestive state, a lying posture, and a calm psychological state (Brody 1945). McEwan (1966) approximated these conditions in an experiment with a single adult female caribou that was fasted for a 21-day period in February. I have used this single value of 381 $kJ \cdot kg^{-0.75} \cdot day^{-1}$ as an estimate of winter BMR. A summer BMR was estimated as 482 $kJ \cdot kg^{-0.75} \cdot day^{-1}$. I estimated this value by assuming that a 21-percent reduction occurs in metabolic rates from summer to winter. This assumption was based on estimates in the literature (see Results and Discussion) that show that a 21-percent reduction in RMR occurs from summer to winter in adult female reindeer/caribou.

Winter reductions in metabolic rates were assumed to begin in November (McEwan and Whitehead 1970) and continue through May (McEwan 1970). Thus, "winter" in this section is defined as lasting from

November to calving and, conversely, "summer" lasts from calving to November.

Some of the methods I used to calculate energy expenditure are evident from the various tables. However, certain values require further explanation, including estimates of the energy costs of traveling in snow, cratering in snow, trotting/galloping, fattening, lactation, pregnancy, and hair growth.

Energy costs of walking in snow (sinking depth of 23 cm) were measured by Mattfield (1973) for white-tailed deer and found to be about 40 percent greater than walking without snow. I have estimated the energy costs of walking in snow as only 15 percent greater than summer values, taking into account: (1) the larger hoof-foot area of caribou (lower foot loading) compared to white-tailed deer, (2) the single-file strategy that caribou frequently exhibit when walking in deep, soft snow (personal observation), and (3) the wind-swept snow conditions observed during this study. Energy costs of trotting/galloping in snow were also assumed to be 15 percent greater than summer values.

Energy costs of cratering in snow were estimated from Makarova and Segal's (1958) measurements (n=27) of metabolic rates of reindeer cratering for periods lasting from 2 to 90 minutes. It should be noted, however, that snow conditions during these measurements were rather extreme (80 to 90 cm deep, soft snow or compact, crusted snow about 30 to 35 cm in depth). Thing (1977) made theoretical calculations of the energy costs of cratering, but assumed a 100 percent efficiency of converting chemical energy to mechanical energy. Thing's daily late winter values were only about 30 percent as great as measurements by Makarova and Segal (1958), but snow conditions were less severe in Thing's study. Due to the wind-swept condition of the Denali herd's eastern wintering grounds (with virtually no snow remaining in most foraging areas), I have calculated winter foraging costs with and without the costs of cratering.

The energy cost of trotting/galloping at a mean speed of 12 $km \cdot hr^{-1}$ (Thomson 1977) was estimated as 30 $kJ \cdot kg^{-1} \cdot hr^{-1}$. I chose this value because it is an average value from metabolic measurements made in three different studies. Mautz and Fair (1980) measured the energy cost of running for a white-tailed deer as 25 $kJ \cdot kg^{-1} \cdot hr^{-1}$. From measurements on reindeer, White and Yousef (1978) developed equations for predicting the energy cost of walking for various speeds and terrains. The equation for walking on dry tundra predicts an energy cost of 36 $kJ \cdot kg^{-1} \cdot hr^{-1}$ at a speed of 12 $km \cdot hr^{-1}$. Finally, measurements made by Hammel et al. (1961), on a reindeer running and pulling a sled, averaged 29 $kJ \cdot kg^{-1} \cdot hr^{-1}$. Thus, at present, it appears the energy cost of running for reindeer/caribou may average about 30 $kJ \cdot kg^{-1} \cdot hr^{-1}$.

In calculating energy costs of fattening, I have assumed that the total body weight of adult female caribou in the Denali herd fluctuates 10 kg annually, from 110 kg in autumn to 100 kg in spring (a 9 percent decrease from prime autumn weights). Data recorded by Skoog (1968) for 3- to 5-year-old female caribou in interior Alaska supports these figures. Also, the annual fluctuation in total body weight is substantiated by several other studies. Druri (1970) reported that the total live weight of semi-domesticated reindeer in the Soviet Union seldom drops more than 10 percent during winter. In a study of the Kaminuriak caribou herd in central Canada, Dauphiné (1976) found that both young and adult females lost between 6 and 11 percent of their prime autumn weights in winter. Adult females (over 2.5-years-old) declined about 10 kg in body weight over this period from 92 to 82 kg. Also, Steen (1968) reported that a decline in body weight of 10 kg or more is a characteristic feature in young and adult semi-domestic reindeer in winter in Scandinavia. Of course, much larger weight declines of 17 to 24 percent of total body weight in adult female reindeer have been noted during severe winter conditions (Preobrazhenskii 1968).

To determine the energetic cost of this weight gain and the subsequent energy available from this loss in body weight, an estimate must be made of the composition of the substance being metabolized. This is pertinent due to the high variability in the calorific values of body substances. I derived from studies on water metabolism in reindeer (Cameron and Luick 1972) that a 10-kg decline in total body weight throughout the winter corresponds to a decline of about 14 kg in total "body solids", due to the replacement of about 4 kg of body solids by water. The term "body solids" includes, for instance, the moisture in the animal's pelt, since moisture was measured using the tritiated water dilution method. Measurements of changes in in vivo body water in reindeer were made by Cameron and Luick (1972) from May 1969 to June 1970 in interior Alaska on 3 to 6 adult female reindeer grazing native forage under penned conditions (with some supplemental feeding in April and May). Mean body weight (about 79 kg) and total body solids (about 16 kg) were very similar prior to and at the termination of these measurements (May 1969 and June 1970). These reindeer fluctuated, on the average, 22 kg in total body weight and 30 kg in total body solids over the year. Only measurements on reindeer that were pregnant in 1970 were used in these calculations. I assumed a simple proportional relationship in calculating the 14-kg, annual fluctuation in total "body solids" for female caribou of the Denali herd.

Dauphiné (1976) stated that fluctuations in seasonal body weights of adult caribou are largely due to the deposition and mobilization of fat reserves. Measurements of chemical body composition of adult, female reindeer in March (n=1) and August (n=1) in Svalbard (Ringberg et al. 1980) indicated that about 90 percent of the change in the solids of ingesta-free body weights was accounted for by changes in fat reserves. Changes in the empty body weights of cattle (Reid and Robb 1971) and sheep (Kellaway 1973) have also been estimated to be 90 percent or more fat, although this figure varies considerably.

For the purposes of this paper, I have assumed that 4 kg of the total 14-kg, annual fluctuation in total "body solids" can be accounted for by the annual fluctuation in the weight of the pelt, antlers, and body ash from early spring to late autumn. Hyvärinen et al. (1977) suggested that mineral reserves (ash) are stored in the skeleton for use in the winter in reindeer. Energetic cost of growth of the pelt is considered later, and the fluctuations in weight of antlers and body ash have been assumed to have negligible energetic costs. Of the remaining 10 kg in body solids, I have estimated that 90 percent or 9 kg is fat and the remaining 10 percent is protein. Calorific values of fat and protein were considered to be 39.3 kJ • g^{-1} and 22.6 kJ • g^{-1}, respectively, as summarized by Robbins (1973) for several ruminants. As suggested above, a storage of about 90 percent of body solids as fat appears reasonable. Also, a storage of 9 kg of chemical fat by caribou for winter use appears reasonable. For instance, Wallmo et al. (1977) discussed some estimates of the storage of fat by mule and white-tailed deer and give a value of about 9 kg for deer weighing about 65 to 70 kg. The only measurements published to date on total autumn fat content in reindeer/caribou indicate that about 20 to 25 kg of dissectable fat is stored for winter use by adult Svalbard reindeer (n=2) weighing 80 to 110 kg (Ringberg et al. 1980). However, deposition of fat in Svalbard reindeer (about latitude 79° N) is undoubtedly much higher than in more southern populations (Reimers 1980).

The next step is to determine the time period during which deposition and mobilization of fat stores occur. This would undoubtedly vary regionally as well as locally, depending on variations in snow melt, plant phenology, insect harassment levels, and winter foraging conditions. I have assumed that deposition of fat stores occurred from mid-July to November 1 (107 days). Alternatively, utilization of reserves occurred from December 1 to mid-June (198 days). This is consistent with seasonal trends in the variation of back fat, kidney fat, abdominal fat, and femoral marrow fat in female caribou, over 3 years old, in the Kaminuriak herd in central Canada (about 63° N latitude, the same as the Denali herd) (Dauphiné 1976).

A gain of 10 kg of fat and protein in the above proportions has an energy content of about 376.3 MJ, using calorific values given above. The efficiency of the utilization of metabolizable energy for fattening was estimated to be 65 percent during lactation. This value is about 14 percentage units higher than that predicted (see Agricultural Research Council 1965) based solely on estimates of the metabolizable energy of the diet (10.0 MJ • g^{-1}) during fattening given in Chapter 3. However, I have taken into consideration the discussion and measurements by Moe et al. (1971) which suggest that the efficiency of the utilization of metabolizable energy is much higher for lactating than for non-lactating animals. Thus, the fattening costs apply only to lactating animals, which undoubtedly would be more nutritionally stressed than non-lactating animals. Metabolizable energy requirements for the deposition of 10 kg of fat and protein is, therefore, about 578.9 MJ (376.3 MJ ÷ 0.65) or 5.41 MJ • day^{-1} when gaining weight at a rate of 93 g • day^{-1}. The mobilization of the 10 kg of fat and protein (51 g • day^{-1}) was assumed to be 97 percent efficient, which denotes a utilization of 365.0 MJ or 1.84 MJ • day^{-1} of metabolizable energy from body reserves during the winter (198 days). Energy requirements for fattening calculated here for caribou are intermediate between those given for sheep and cattle by the Agricultural Research Council (1965).

The effect of lactation on the energy requirements of female caribou was calculated by combining measurements on milk production and the energy content of this milk in reindeer (Luick and White 1971; Luick et al. 1974). The efficiency of the utilization of metabolizable energy for lactation is discussed by Blaxter (1962), the Agricultural Research Council (1965), and Robbins (1973). An efficiency coefficient of 70 percent appears to be a good average value considering the high metabolizable energy content (11 MJ • g^{-1}) of the spring and summer diets of the Denali caribou herd (Chapter 3). This value was used after July 1, when fat reserves would no longer be used for milk production. Prior to this date, I used an efficiency coefficient of 76 percent taking into account the higher efficiency associated with producing milk partially from the energy in fat reserves rather than solely from dietary energy (Moe et al. 1971). In calculating average daily energy costs of lactation for each season, I considered the gradual reduction in milk production reported by Luick and White (1971) for reindeer.

The energy requirements of pregnancy were calculated by assuming that a proportional relationship exists between the energy costs of pregnancy in cattle (Agricultural Research Council 1965) and caribou, based on the weights of the fetus of each species at birth. For example, the metabolizable energy requirement for pregnancy in cattle is about 36.8 MJ • day^{-1} during the last 2 weeks of pregnancy. This estimate is for a dairy cow giving birth to a calf weighing about 38 kg (Agricultural Research Council 1965). This estimate assumes that the cow's diet contains about 9 MJ • day^{-1} of metabolizable energy, which is comparable to the metabolizable energy content of the Denali caribou's winter diet (Chapter 3). By assuming a proportional relationship between energy requirements of pregnancy in cattle versus caribou (based on weights of the fetus at term), a caribou giving birth to a 6-kg calf (Skoog 1968) would require about 5.8 MJ • day^{-1} of metabolizable energy during the last 2 weeks of pregnancy. This value represents nearly a peak daily value and is the basis for the computation of a relationship that predicts the energy requirements of pregnancy during particular segments of the gestation period. Thus, to determine the energy requirements for pregnancy during particular segments of the gestation period, I modified an equation by Jakobsen (1961) to allow calculation of the total metabolizable energy requirements of pregnancy in MJ (y) up to any particular day of the gestation period (t):

$$y = (7.24\ e^{0.0174t}) - 7.367$$

The gestation period of caribou was assumed to be 227 days, as summarized by Skoog (1968) and McEwan and Whitehead (1972). Thus by assuming "t" is equal to 227 in the above equation, the total metabolizable energy requirements of pregnancy (y) is 368.57 MJ. To calculate the requirements on a daily basis over the last two weeks of pregnancy, one simply has to solve for "y" using a "t" value of 213 and subsequently subtract this value from the above total requirement and divide by 14 days. It is important to be able to solve for the energy requirements of pregnancy for any time period, because these requirements increase dramatically during the last one-third of the gestation period. This relationship was derived by Jakobsen (1961) (reviewed by Blaxter 1962) from analysis of the energy content of the uterus and its contents during different stages of pregnancy in cattle.

The energy retained in growth of the pelt in white-tailed deer was determined by Robbins (1973). Robbins gave the following equation for predicting the energy retained in hair growth after a 100-day autumn molt, where Y = energy retained in the pelt in kcal • day^{-1} (kcal x 4.184 = kJ), and X = ingesta-free body weight (kg):

$$Y = 151.97 + 58.60 \text{ Log}_e X$$

The ingesta-free body weight was calculated from the following equation, where Y = ingesta-free body weight (kg) and X = live weight (kg):

$$\text{Log}_e\ Y = -0.0771 + 0.9928 \text{ Log}_e\ X$$

These equations were developed by Robbins (1973) from measurements made on 16 white-tailed deer sacrificed in late October. I assumed the efficiency of the utilization of metabolizable energy for hair production was 70 percent, based principally on the low fat content of hair (10 percent) (Robbins 1973). Thus, a 110-kg white-tailed deer can be assumed to require about 70 MJ of metabolizable energy during a 100-day autumn molt. To account for the increased length and density of fibers in the winter pelage of reindeer/caribou compared to white-tailed deer (Skoog 1968; personal observation), I have increased the metabolizable energy requirements of hair growth in caribou about 40 percent above those derived for white-tailed deer. Since caribou annually grow a short, dark summer coat followed by an autumn growth of white guard-hairs through the summer coat (Skoog 1968), I have assumed the energy cost of growing the winter pelt in caribou was distributed evenly over the 122 day period from June 1 to October at a rate of 0.82 MJ • day^{-1}.

Results and Discussion

Environmental conditions during the collection of activity data have been summarized on a seasonal basis (Table 5). Curatolo (1975) studied the interrelationships between weather and caribou activity in summer and stressed that caribou have a wide range of tolerance to changes in weather. He found that weather in summer acted most significantly as an indirect factor on caribou behavior by regulating the influence of disturbing insects. Thomson (1973), White et al. (1975), and Roby (1978) also discuss this interaction at length. In winter, severe windchill can affect caribou activity by directly stimulating short bursts of running or extended lying periods (Henshaw 1968; Thomson 1973; Roby 1978). My only observations of caribou during severe winter weather occurred in mid-winter at low temperatures (-38 to -48°C) with no wind. Caribou did not exhibit unusual active or rest periods during these conditions, as discussed later. Weather patterns and climate conditions are also important in controlling the chronology of seasonal migratory behavior and activity within the caribou's annual cycle, particularly in respect to influences on snow melt, plant phenology, emergence of insects, and snow cover conditions (Skoog 1968; Roby 1978).

Because this chapter deals primarily with discussions of caribou activities observed on each seasonal range, little is reported on the migrations between ranges (see Figure 1). These migrations can contribute significantly to the annual energy expenditure of particular

Table 5. Seasonal distribution of environmental conditions during the collection of scan-data used for computing activity budgets of the Denali caribou herd, 1978-1980. Number of 15-minute scans (n) for each season is given in parentheses.

	Season					
	Calving and Post-calving (5/22-6/30) (395)	Insect (7/16-8/31) (316)	Pre-rut and Rut (9/16-10/31) (238)	Early Winter (11/16-12/31) (211)	Mid-Winter (1/1-2/29) (36)^c	Late Winter (3/1-4/15) (105)
Cloud Cover (mean percent ± s.d.)	70 ± 30	80 ± 25	55 ± 35	55 ± 40	30 ± 40	70 ± 30
Precipitation (percent of scans)	14	16	4	13	0	1
Temperature (°C)						
mean ± s.d.	10 ± 4	13 ± 3	9 ± 5	-6 ± 5	-42 ± 7	-5 ± 5
minimum	2	7	0	-14	-48	-9
maximum	21	21	21	1	-38	6
Wind Speed ($m \cdot sec^{-1}$)						
mean ± s.d.	2.5 ± 2.3	1.0 ± 0.7	2.0 ± 2.5	1.4 ± 0.8	0 ± 0	2.8 ± 1.9
minimum	0	0	0	0	0	0
maximum	6.7	5.4	8.9	3.6	0	6.8

Table 5. (Continued)

Elevation (m)						
mean ± s.d.	940 ± 140	1040 ± 250	790 ± 60	730 ± 150	610 ± 0	960 ± 200
minimum	840	780	700	580	610	520
maximum	1280	1740	940	1040	610	1100
Slope shape[a]						
(mean ± s.d.)	3.2 ± 1.3	1.6 ± 1.2	1.6 ± 1.3	2.6 ± 1.5	1.0 ± 0	4.3 ± 0.8
Slope aspect[b]						
(mean ± s.d.)	3.6 ± 0.9	2.1 ± 0.3	4.7 ± 1.8	3.8 ± 0.8	5.0 ± 0	4.3 ± 2.1
Snow cover (percent of ground covered)						
mean ± s.d.				30 ± 20	100 ± 0	25 ± 15
minimum				20		10
maximum				80		50
Snow depth (cm)						
mean ± s.d.				N.A.[d]	34 ± 2	N.A.[d]
Snow hardness (kg · cm^{-2})						
mean ± s.d.				N.A.[d]	.065 ± .017	N.A.[d]

[a] Recorded on a scale of 1 to 5: 1 = plateau or valley bottom, 5 = top of ridge or hill.

[b] Recorded on a scale of 1 to 5: 1 = N, 2 = NE or NW, 3 = E or W, 4 = SE or SW, 5 = S.

[c] Low variability in mid-winter was due to the small number of obervations (Table 8).

[d] N.A. refers to "not applicable" due to low percentage of snow cover.

herds. Therefore it should be recognized that the present annual migratory distances of the Denali herd are relatively short (about 450 km) compared to the present migratory distances of the much larger Porcupine caribou herd (about 1600 km) and Western Arctic herd (about 1200 km). Annual migratory distances have decreased in the Denali herd in direct relation to the decline in numbers (see Study Herd: History and Status). This is in agreement with Skoog's finding that a positive correlation exists between herd size and length of migratory distances.

Effect of Human and Predator Disturbance

The effect that human disturbance had on the energy expenditure of the female and young caribou of the Denali herd was negligible, due to the relative inaccessibility of these cohorts from hikers and to the present regulations against hunting and low-flying aircraft. A majority of individual female and young caribou appeared to be susceptible to human harassment almost exclusively during a 1- to 3-day period, usually occurring in early July, when these animals were migrating adjacent to and within a few kilometers of the park road. Low levels of harassment of these cohorts was also observed on the rutting grounds. In contrast, a large part of the adult and immature male cohort was susceptible to harassment from photographers, hikers, and traffic along the park road for most of the summer. Many of these animals became accustomed to human activity, as opposed to the extremely wary and usually easy excitability of adult females and particularly females with neonatal calves. Roby (1978) studied caribou along the Trans-Alaska Oil Pipeline, and also reported that female caribou with calves avoided human activity much more strongly than adult bulls. Tracy (1977) reported on some reactions of wildlife, including caribou, to human activity along the Denali Park road, but these observations were essentially limited to male caribou and a few females that did not participate in the post-calving migration. Tracy found that calves reacted most strongly to human activity, whereas adult bulls were the least wary. My observations along the park road were very limited, since I remained with the majority of the females and calves most of the year.

The effect of predators on the energy expenditure of adult female and calf caribou was also observed to be of minor consequence to the animal's annual energy expenditure. However, predator densities in the study area were high (F. Dean pers. comm.; Haber 1977), though probably somewhat reduced on the Cantwell calving ground (see Study Area). In considering the apparent discrepancy between high predator densities and the few number of predator/caribou interactions, one should consider that my observations were made only during daylight or crepuscular hours, and wolves do most of their hunting at night in summer (Murie 1944). Also, I observed, on the average, only about 30 caribou per hour of observations. A summary of caribou interactions with predators/scavengers and the total number of hours I observed caribou of the Denali herd is given in Table 6. Murie (1944), Skoog (1968), Curatolo (1975), and Roby (1978) discussed at length the relative effect of these predators/scavengers on caribou. Generally, only interactions with brown bears, wolves, and coyotes caused a high degree of alarm associated with trotting/galloping within a group of caribou. Exceptions included one interaction with a red fox and one occasion when a golden eagle landed next to a group of females with young calves.

It should be recognized that of the several caribou interactions with large predators, wolves only chased the caribou 50 percent of the time while bears gave chase only about 35 percent of the time and coyotes gave chase 100 percent of the time. By far the longest

Table 6. Seasonal incidence of sightings of disturbances of female and young caribou by predators/scavengers and humans during 1978 and 1979, Denali caribou herd. Approximations of the number of caribou in view each hour are given in Table 10.

	Spring Observations (May 12-June 30)	Summer Observations (July 1-August 30)	Autumn Observations (Sept 1-Oct. 31)	Winter Observations (Nov. 1-May 1)
No. hours caribou were observed	237	120	112	131
Predator/Scavenger				
Brown bears	6	5	0	0
Coyotes	3	5	0	0
Golden eagles	4	0	0	0
Long-tailed jaegers	1	0	0	0
Raven	1	0	0	2
Red fox	1	0	1	0
Wolves	3	0	6	1
Humans	0	3	3	0

pursuit was by a coyote, and this pursuit exceeded a distance of 4.5 km. The only successsful pursuits were observed during the first 2 weeks following calving, during which a brown bear and a wolf were each observed to kill a calf. Troyer (1976, 1977, 1978) and Grosnick (1979) also reported observing low predation rates on the Denali herd in recent years. However, when the Denali herd calved north of the Alaska Range and numbered 20 to 30 times the present numbers, Murie (1944) reported that wolves preyed extensively on young calves. Bergerud (1980) discussed the mortality factors acting on young caribou calves and suggested that wolf and brown bear predation is of primary significance when these predators are present in high numbers.

Seasonal Variations in Activity

Comparison of activity data from the five seasons (Table 7) showed a significant difference between the proportion of time caribou allocated to the five basic activites ($X^2 = 13,223$, df = 16, $p < 0.001$). The following activities and their respective seasons were the major factors contributing to this high level of significance:

1) the high proportion of time spent lying during the calving and post-calving season,
2) the low proportion of time spent lying during the insect season,
3) the high proportion of time spent walking and standing during the insect season, and
4) the low proportion of time spent standing during the late winter and calving and post-calving seasons.

These anomalies are discussed in the following sections.

Calving and Post-calving Season (May 22 - June 30)

The calving and post-calving season began with the peak of calving, which occurred from May 19 to 25 in 1976 to 1978 (Troyer 1978). Initiation of this season was also marked by bud break among shrubs in areas of early phenological development (May 23 in 1979 on the Cantwell calving ground). Termination of the calving and post-calving season was marked by the departure of caribou from the Cantwell calving ground. This departure was likely due to increasing harassment by oestrid flies. Oestrid fly harassment was first observed on June

Table 7. Seasonal changes in the percentage of time caribou (primarily adult females) allocated to various activities within active-rest cycles, Denali caribou herd, 1978-1980. Standard deviations (s.d.) show the variability in the percentages of each activity between individual active-rest cycles.[a]

						Mean Percentage ± s.d.[d]					
Season	Major age/sex component	No. of animals in all scans	No. of 10-min. scans	No. of groups	No. of graze-rest cycles	Feeding	Lying	Walking	Standing	Trotting/ Galloping	Cratering
Calving and Post-Calving (5/22-6/30)	cows[b]	19,793	589	14	17	37 ± 5	52 ± 8	7 ± 4	3 ± 4	0.9 ± 2.0	
Insect (7/16-8/31)	cows and calves	14,680	472	14	0	33 ± 17[a]	19 ± 19	21 ± 12	25 ± 23	1.7 ± 2.1	
Pre-rut and Rut (9/16-10/31)	cows and calves[c]	7,118	355	13	16	40 ± 4	39 ± 5	7 ± 3	12 ± 7	1.2 ± 2.0	
Early Winter (11/16-12/31)	cows and calves	7,286	316	7	7	48 ± 5	32 ± 3	11 ± 5	8 ± 2	0.4 ± 1.0	0.5 ± 1.0
Late Winter (3/1-4/15)	cows and calves	21,206	157	7	7	53 ± 5	42 ± 7	4 ± 2	2 ± 1	0.1 ± 0.3	0.4 ± 0.7

[a] No active-rest cycles were observed during the insect season, so standard deviations in this season show the variability in the percentages of each activity between groups of caribou observed over 2.5 hours.

[b] Data on calves during the calving and post-calving season were excluded from these calculations (see Table 9).

[c] Data on mature bulls during the pre-rut and rutting season were excluded from these calculations.

[d] A significant seasonal difference was found in the proportion of time caribou allocated to the five major activities ($X^2 = 13{,}323$, df = 16, $p<0.001$).

21 in 1979. This date also corresponded to the movement of caribou to higher elevations from 830 m ± 40(s.d.) to 1080 m ± 20 ($p < 0.001$), which was likely related to oestrid fly avoidance. Lying and, particularly, standing animals were often observed on lingering snowbanks during warm weather following oestrid fly emergence. Snowbanks are apparently sought due to the prevailing low ambient temperatures which inhibit insect attack (Skoog 1968). Thermoregulatory stress may also be partially responsible for this movement to snowbanks, since caribou were observed consuming snow. Insect-caribou interrelationships are discussed at length in the following section.

Curatolo (1975), Roby (1978), and Wright (1979) delineated a separate post-calving or early summer period in the caribou/reindeer annual cycle, during which mosquitoes exerted a dominant influence on caribou activity. However, mosquitoes (Cuculidae) were not abundant enough to affect caribou activity during any of my observations of the Denali herd, as discussed in the following section.

The proportion of time adult caribou spent lying was notably high during the calving and post-calving season (52 percent) compared to other seasons (19 percent to 42 percent) (Table 7). Table 8 clearly shows that the high incidence of lying was due to the unusually brief active periods (averaging 74 minutes, compared to 105 minutes for rest periods). Short spring and summer active periods, relative to winter values (Table 8), are presumably a result of increased forage quality and availability in the spring and summer, which increases the efficiency of filling the rumen, resulting in the

Table 8. Seasonal variation in activity patterns (mean ± s.d.) of primarily adult female caribou, Denali caribou herd, 1978-1980. In comparisons between rest periods or between active periods, means with identical numerical superscripts are not significantly different ($p<0.05$, Newman-Keuls test).

Season	Dates	Average Rest Period[c] (minutes)	n	Average Active Period[d] (minutes)	n	Average Active-Rest Period[e] (minutes)
Calving and Post-calving	May 22-June 30	105 ± 29^{1}	22	74 ± 29^{1}	17	179
Insect[a]	July 16-August 31					
Pre-rut and Rut	September 16-October 31	78 ± 25^{2}	18	88 ± 45^{1}	16	166
Early Winter	November 16-December 31	112 ± 12^{1}	9	210 ± 37^{2}	7	322
Mid-Winter[b]	January 1-February 29	100 ± 11[b]	2	150[b]	1	250
Late Winter	March 1-April 15	110 ± 17^{1}	7	145 ± 21^{3}	7	255

[a] A pattern of alternating active and rest periods was not discernable during the insect season.

[b] Insufficient sample size during mid-winter did not allow statistical comparisons with the remaining four seasons.

[c] Length of rest periods was significantly different between the four seasons (mid-winter excluded) ($p<0.001$, F test).

[d] Length of active periods was significantly different between the four seasons (mid-winter excluded) ($p<0.001$, F test).

[e] Sum of the average rest period and active period.

stimulation to initiate a rest period (Bell 1961; Blaxter et al. 1961; Comline and Titchen 1961; Arnold 1970). Segal (1962) and Gaare et al. (1975) reported slightly higher values than I observed in the duration of summer active periods (about 105 minutes and 120 minutes, respectively). However, Segal's value for the mean duration of undisturbed summer lying periods is identical to mine (105 minutes). Therefore, Segal's animals presumably had more difficulty in reaching satiety, as they were active for about 30 minutes longer than the Denali caribou before they apparently were able to fill their rumens. In this comparison at least, it appears that the availability of forage on the Denali herd's range is relatively high, compared with the availability of forage in Segal's study. No further comparisons could be made with the literature due to the lack of spring or summer values that reflect the length of undisturbed active/rest periods. Disturbances such as mosquitoes, oestrid flies, and rutting behavior often greatly influence the length of these periods in summer and autumn.

Values in Table 8 indicate that most of the seasonal variability in the proportions of time spent active versus resting is due to the length of active periods. In fact, rest periods under undisturbed conditions are not significantly different ($p < 0.05$) between seasons (Table 8). Thus, if the duration of rest periods under undisturbed spring or summer periods is found to be relatively constant between herds, then the length of active periods could be used as a tool to indicate the accessibility of food species, and thus range condition. This relationship could also be used in comparing winter range condition between herds if snow conditions are comparable.

Calculations of caribou/reindeer activity budgets have seldom been accompanied by the duration of active and rest periods (Segal 1962; Gaare et al. 1975) and never with accompanying figures on statistical variability. However, the duration of active and rest periods, and particularly the seasonal variability in the length of undisturbed active periods, obviously contribute much to the understanding of why activity budgets differ significantly between seasons. This relationship has not been previously described in studies of caribou/reindeer activity.

Similarity in the duration of undisturbed rest periods in summer and winter (Table 8) can be explained in part by the reduction in rumen size occurring in the winter in reindeer (Staaland et al. 1979). In a healthy ruminant, the rest period (including rumination) is generally considered to last until gut distension declines (Blaxter et al. 1961; Comline and Titchen 1961) and is presumably dependent largely on the digestibility of the diet, amount of food consumed, and rumen size. Estimates of the digestibility of components of the seasonal diets (Chapter 3) indicates that digestibility of the winter diet is slightly lower than estimates in the spring and summer, which predicts slightly longer rest periods in the winter. However, to rationalize the similarity in the duration of rest periods in summer and winter, it is suggested that animals in winter versus summer would empty their rumens during similar time periods because of the compensating factors of the smaller rumen in winter and the more digestible diet in summer.

Gaare et al. (1975) reported that adult female reindeer from two populations in Norway exhibited considerable differences in the percent of time spent feeding during the first 10 days following calving. Gaare et al. indicated these differences were due to variations in the reindeer's winter range conditions and nutritional status. A low percentage of time spent grazing (36 percent) was observed in the healthy population, whereas this proportion was considerably increased (54 percent) in the nutritionally stressed population. Gaare et al. also indicated a significantly greater proportion of time spent in activities other than feeding and lying (22 percent) in the healthy population, compared to a value of 8 percent in the stressed population. Activity budgets of the Denali herd during the calving and post-calving season indicate a similarity to feeding values given for the healthy population (37 percent of the time spent feeding in the Denali herd compared to 36 percent). However, the Denali herd spent only 11 percent of its time in activities other than feeding and lying, and therefore was not as active as the healthy population reported on by Gaare et al. Nevertheless, this comparison suggests moderate to good nutritional status among animals of the Denali herd. Roby (1978) reported values for the Central Arctic caribou herd that are nearly identical to mine during the calving period; whereas Curatolo (1975), in studies of the Steese-Fortymile caribou herd, and Wright (1979) in a study of reindeer on the Seward Peninsula, reported values nearly identical to Gaare's values for the nutritionally-stressed population.

Table 9. Differences in the proportion of time cow and calf caribou allocated to various activities within active-rest cycles in the calving and post-calving season (May 22-June 30), Denali caribou herd, 1978-1980. Standard deviations (s.d.) are given for percentages of activities between individual active-rest cycles.

					Mean Percentage ± s.d.[a]				
Caribou Classification	No. of caribou in all scans	No. of 10-minute scans	No. of groups	No. of graze-rest cycles	Feeding	Lying	Walking	Standing	Trotting/ Galloping
Cows	19,793	589	14	17	37 ± 5	52 ± 8	7 ± 4	3 ± 4	0.9 ± 3.0
Calves	8,482	589	14	17	12 ± 3	70 ± 8	10 ± 5	6 ± 3	2.0 ± 2.0

[a] A significant difference was found in the proportion of time cows and calves allocated to the various activites ($X^2 = 1855$, df = 4, $p<0.001$).

Gaare et al. (1975) also described differences in the nursing behavior between the healthy versus the nutritionally-stressed population. Again his descriptions of the healthy population more closely fit the description of activites observed in the Denali herd. For instance, calves nursed from a side position rather than between the hind legs of cows. Also, calves, not their dams, usually terminated nursing bouts during the first month following calving, and dams were attentive of calves during nursing bouts.

A final note of importance involves the significant difference between activity budgets of cows versus calves during the calving and post-calving period ($X^2 = 1855$, df = 4, $p < 0.001$) (Table 9). The relatively low percent of time calves spent grazing (12 percent) and relatively high percent of time calves spent lying (70 percent) were the major factors contributing to this high level of significance. Gaare et al. (1975) and White et al. (1975) reported comparable figures for activity budgets of calves less than a month old.

Insect Season (July 16 - August 31)

The insect season was denoted by the occupation of the summering range (see Study Area) by a majority of the herd's female and young caribou; and although this season encompasses the peak of activity among oestrid flies, significant harassment by flies was also observed during post-calving and rutting activities. Two species of parasitic oestrid flies are responsible for this harassment, the warble fly (*Oedemagena tarandi*) and the nasal bot fly (*Cephenomyia trompe*). "Insect" as used in the context of "insect season" refers only to the presence of these flies, or other large flies and bees that would stimulate oestrid fly defense reactions. The term "insect season" is not necessarily related to the presence of mosquitoes or black flies (Simuliidae), as these insects were virtually absent during observations of the Denali caribou. An active searching for mushrooms by caribou also characterized the entire insect season, particularly throughout August.

Although I have referred to the summer period as the "insect season", this period has frequently been termed "August dispersal" (Kelsall 1960, 1968; Curatolo 1975; Roby 1978). The term "August dispersal" is meant to describe the distinct scattering of caribou into small groups. This dispersal presumably results from caribou avoidance of oestrid flies and is associated with panic running (Curatolo 1975; Roby 1978). My observations of the Denali herd did not reveal any tendencies toward reduced group size during the insect period (Table 10), although harassment of caribou by oestrid flies was obvious. The lack of dispersal among the Denali caribou was likely related to the relative accessibility of insect-relief sites on the Denali herd's summering range, which could effectively reduce the need for panic running. This is discussed later in a comparison with other Alaskan caribou herds.

The only obvious change in group size that I observed in the summer was an increase in group size which occurred from June 21 to about July 20 just prior to and during the post-calving migration (Table 10). This increase in group size is described by Skoog (1968)

Table 10. Seasonal variation in mean group size of caribou, Denali caribou herd, 1978-1980.

Season	Dates	No. of Groups Observed (n)	Group size (mean ± s.d.)
Calving and Post-calving	May 22- June 20	28	31 ± 24
Migratory Massing	June 21- July 1	8	125 ± 69
Insect	July 16- August 31	56	27 ± 28
Pre-rut and Rut	September 16- October 31	51	18 ± 12
Early Winter	November 16- December 31	45	22 ± 15
Late Winter	March 1- April 15	14	41 ± 34

as a common regrouping behavior among caribou which occurs soon after calving and in preparation for the usually large-scale post-calving migration. Post-calving migrations are commonly noted for their impressive aggregations of moving caribou. The stimulus for this post-calving migration has never been clearly defined and is probably dependent to some extent on the particular situation. Also, this stimulus may be related to a combination of factors, some of which may no longer be operating. However, the similarity in the timing of the initiation of oestrid fly emergence with the timing of the pre-migratory massing of caribou suggests that the emergence of oestrid flies may be an important stimulus for the post-calving migrations. This hypothesis is obviously somewhat contrary to findings that oestrid flies cause a dispersal among caribou, and that these flies emerge after the post-calving migration (Curatolo 1975; Roby 1978). However, I suggest in the following paragraphs that oestrid flies emerge earlier than previously expected.

Oestrid fly harassment was first observed on June 21 in 1979 on the Denali herd's Cantwell calving ground, and this date coincided precisely with the initiation of the pre-migratory massing. The caribou were also observed to move to significantly higher elevations ($p < 0.001$) in the Alaska Range following this date. Observations of adult oestrid flies on or immediately adjacent to Alaska's north coast in late June and early July also suggest that oestrid flies stimulate post-calving migrations of the arctic herds. For instance, during the very late spring of 1980, J. Wright (pers. comm.) captured two adult warble flies on June 30 within a kilometer of Alaska's northern coastline. He also observed a group of about 500 caribou of the Central Arctic herd on this date, which indicates a similarity between the timing of oestrid fly emergence and the pre-migratory summer massing of caribou in the arctic. This date also corresponded well with my observations in 1980 of the pre-migratory massing of the adjacent Porcupine caribou herd. An adult oestrid fly was also captured on July 4 in 1979 on the north coast of Alaska adjacent to the Porcupine caribou herd (G. Calef pers. comm.). From these observations, it is likely that oestrid flies begin to emerge from about June 15 to 20 in interior Alaska and June 25 to 30 in arctic Alaska.

Roby (1978) reported observing oestrid fly harassment beginning July 29 in the Central Arctic herd in 1975, and Curatolo (1975) did not observe oestrid fly harassment until July 11 in the Steese-Fortymile herd in 1973 in interior Alaska. However, observations described above indicate that oestrid flies emerge earlier in the summer than previously expected. Roby (1978) speculated that the pre-migratory/ post-calving aggregation of caribou was a response to mosquito harassment and also discussed the influence that predators have on increasing group size and movements in caribou. Davis et al. (1979) suggested that predation and/or socialization are the ultimate causes for the formation of post-calving aggregations, whereas the maintenance of these aggregations was thought to be related to prevailing insect levels. Skoog (1968) suggested that the post-calving aggregations resulted primarily from social instincts and secondarily from harassment by mosquitoes and black flies. It should be recognized, however, that harassment of caribou by mosquitoes or black flies is not necessary to stimulate the post-calving aggregations at least in the case of the Denali herd.

Kelsall (1975) compared warble fly infestation rates from several Canadian caribou herds and reported that caribou that move away from calving areas (where adult flies are emerging from pupae) will benefit by avoiding severe harassment and infestation rates. He also noted that male caribou had significantly higher numbers of infestation rates compared to females, because males often remained in areas where flies emerged from pupae. Therefore, caribou participating in post-calving migrations may have distinct survival advantages in relation to the avoidance of oestrid flies. In conclusion, the factors presumably stimulating the pre-migratory/post-calving aggregations include predation, socialization, and/or insect harassment, whereas the stimulus for the subsequent migrations may be most strongly related to the avoidance of oestrid flies.

Thomson (1973), Curatolo (1975), Kelsall (1975), White et al. (1975), and Roby (1978) have discussed at length the weather factors influencing mosquito and/or oestrid fly harassment levels. Basically, negative correlations with wind speed and cloud cover and a positive correlation with temperature have been observed in respect to insect harassment.

Under weather conditions favoring severe oestrid fly harassment, the Denali caribou moved to higher elevations (about 1700 m), often less than 3 or 4 km from grazing areas. This movement often occurred at a fast walking pace, and animals usually regrouped upon reaching suitable insect-relief terrain (usually lingering snowbanks, glaciers, or barren ridgetops). These sites were usually in areas void of vegetative growth which precluded any sporadic grazing. Under mild harassment, gravel bars were often selected. Groups as large as 300 animals (25 to 30 percent of the entire herd) were observed on a single snowbank during July and early August. Upward movement to insect-relief terrain commonly occurred in the morning prior to the warmer portion of the day when oestrid flies appeared more bothersome (Nikolaevskii 1968; Roby 1978). Downward movement to grazing areas usually began by 1600 to 1700 hours.

Banfield (1954), Espmark (1968), Kelsall (1968), and others have described the defense reactions of caribou/reindeer to harassment by oestrid flies. My findings agreed closely with the results of these studies. Briefly, when preparing for attack, caribou remained in a standing posture with head lowered. Occasionally, caribou remained in this stance continuously for several hours. Periods of standing were interrupted at times by lying periods or short bursts of running.

The relatively high availability of insect-relief sites on the Denali herd's summering range deserves special attention. Roby (1978) stated that there is little effective oestrid fly escape terrain on the arctic coastal plain, where the majority of female and young caribou of the Central Arctic herd spend the summer. Reindeer studied by Wright (1979) on the Seward Peninsula spent the summer in similar coastal topography. Roby (1978) frequently observed solitary caribou on unvegetated gravel bars or on the few bare ridges, and emphasized the "panicked running [of caribou] at top speed". This running frequently resulted in the breakdown of social bonds and dispersal of groups. Curatolo (1975) also emphasized the panicked running of caribou and dispersal of groups on the summering range of the Steese-Fortymile herd. This range has a much more irregular terrain than the arctic coastal plain, and animals have access to lingering snowbanks and a higher number of bare, windy ridgetops. However, insect-relief sites are comparatively few in number relative to the numbers present on the cool, glaciated terrain of the Denali herd's summering range. The differences in the availability of insect-relief sites between summering ranges are reflected in the low percent of time spent trotting/galloping in the Denali herd (1.7 percent) during the oestrid fly season, relative to comparable values for the Central Arctic herd (3.1 percent) (Roby 1978), the Steese-Fortymile herd (10 percent) (Curatolo 1975), and Seward Peninsula reindeer (8 percent) (Wright (1979). As previously suggested, the relatively high availability of insect-relief sites on the Denali herd's range and resulting low proportion of time caribou spent trotting/galloping are likely associated with the maintainance of group cohesion in the Denali herd (Table 10), in contrast to the "August dispersal" observed by Curatolo (1975) and Roby (1978).

Several authors have documented that harassment by oestrid flies increased the proportion of time caribou spent standing and walking, with corresponding decreases in the proportion of time spent grazing and particularly lying (Thomson 1973; White et al. 1975; Curatolo 1975; Roby 1978; Wright 1979). However, none of these studies reported the striking increases in the proportion of time spent standing and walking as proposed for the Denali herd (Table 7). In fact, the proportion of time spent in "non-productive" activities (e.g. walking, running, and standing) during mid- to late summer was higher in the Denali herd (48 percent) than in the Central Arctic herd (14 percent) (Roby 1978), the Steese-Fortymile herd (37 percent) (Curatolo 1975), or the reindeer studied by Wright (1979) on the Seward Peninsula (35 percent). This high value for the Denali caribou was due in part to the extremely high proportion of time spent "walking" during mushroom-searching activities which, as discussed later, were not observed in these other studies. Also, "searching" activities were included as "grazing" in these other studies. Much of the running activities observed in these other studies was replaced in the case of the Denali herd, by walking to higher elevations and, subsequently, standing in insect-relief sites. The high incidence of standing in the Denali herd (25 percent) is comparable only to that given by Curatolo (1975) (24 percent) while values given by Roby (1978) and Wright (1979) are less than half this value. This high incidence of standing indicates the significant influence that oestrid flies have on the energy balance of the Denali herd, as this standing precluded any foraging activities.

Kelsall (1975) indicated that infestation rates of warble fly larvae were greater on sub-arctic caribou ranges than on more northerly ranges, due in part to the latitudinal differences in the duration of warble fly activity. Based on latitudinal variations in daily mean maximum temperatures, Kelsall reported that the season of activity of warble flies in the most northerly Canadian populations (about 78°N) would likely be restricted to July, while at latitudes comparable to that of Denali National Park (about 63°N) the season would likely last from June through September. This agrees with my observations of oestrid fly defense reactions from June 21 to October 7 on the Denali herd's range. Roby (1978) reported that no insect harassment was observed after September 2 on the Central Arctic herd's range (latitude 70°N). From previous estimates that oestrid flies emerge about 10 days earlier in Denali National Park than in arctic Alaska, it appears that the Denali caribou could be affected by oestrid fly harassment for 30 to 40 days longer than Alaska's arctic herds.

Nikolaevskii (1968) indicated the adverse effect that insect harassment could have on growth and fattening of reindeer and pointed out that greater than 60 percent of the reindeer's day is spent in avoiding insects and running during prolonged hot periods. Steen (1968) also reported that reindeer were in relatively poor condition after warm summers compared to cool summers. Prolonged warm periods of severe harassment presumably can have adverse effects on productivity and winter survival as a consequence of interference with feeding during summers and a resulting poor autumn body condition. Apparently, it is to the caribou's advantage to react to oestrid fly attack, as the physiological stress imposed by heavy loads of infestation is likely of great significance. Nikolaevskii (1968) stated that a single warble fly can lay 500 to 700 eggs.

The relative scarcity of mosquitoes on the spring and summer ranges of the Denali herd (even during the extremely wet spring and summer seasons of 1978 and 1979) represents a significant distinction from the densities observed on many other Alaskan caribou ranges (D. Klein pers. comm.). My observations of mosquito densities on the Porcupine caribou herd's range in 1980 indicated that, comparatively, mosquitoes were virtually absent on the Denali herd's range. The lack of mosquito harassment among the Denali caribou is, undoubtedly, of significance when making comparisons between the energy balance and the resulting nutritional status of different herds. However, it is difficult to differentiate the influences that mosquitoes versus oestrid flies have on caribou activity, particularly in regard to the distinct possibility that oestrid flies emerge earlier in the summer than previously expected. However, it appears that, compared to humans, caribou can withstand relatively high levels of mosquito harassment, and that even a single oestrid fly can exert a greater influence on caribou activity than extreme densities of mosquitoes (Curatolo 1975; Roby 1978).

During cool, windy, and/or rainy days, in the absence of insect attack, caribou on the summering range exhibited a feeding behavior unique to the insect season, and likely due to the abundance of mushrooms (see Chapter 1). The result of this feeding behavior was the replacement of normal active-rest periods (Table 8) by long graze-search (feeding) periods lasting up to 4 or 5 hours continuously. These feeding periods were only observed to terminate due to changes in weather that caused the caribou to exhibit insect-avoidance behavior. Also, the long feeding periods were associated with an extremely high degree of walking/searching activity and the temporary straying of animals from groups. This searching activity contributed significantly to the high proportion of "walking" during the insect season (Table 7) and the high daily movement rates (Table 11). Makhaeva (1963), Skoog (1968), and Luick (1977) have also indicated that caribou/reindeer exhibit intensive searching for mushrooms. The searching for mushrooms was also likely related to the relatively few rest periods during the insect season. For example, rest periods and the accompanying rumination bouts were never observed in entirety in the absence of insect attack, and presumably occurred almost solely during the 4 to 8 hours of darkness or during foggy or hard rainy periods which precluded observations. Active-rest cycles therefore were never observed during the insect season. It is significant that the marked absence of active-rest cycles over an entire season has only been documented in detail once previously for caribou under natural conditions. This event occurred in a winter study of starving caribou, where extremely long lying periods and short, sporadic active periods were observed (Roby 1980). In my study, the combination of mushroom-searching activities and insect avoidance appeared to completely dominate the caribou's daily activities throughout the insect period with the resulting elimination of active-rest cycles of normal duration (Table 8).

Table 11. Seasonal variation in daily movement rates of primarily adult female caribou, Denali caribou herd, 1978-1980. Means and standard deviations are given.

Season	Dates	Grazing Distance[a] (km • day^{-1})	Walking Distance[b] (km • day^{-1})	Trotting/ Galloping Distance[c] (km • day^{-1})	Estimated Total Daily Movement[d] (km)
Calving and Post-calving	May 22- June 30	1.1 ± 0.2	5.4 ± 3.1	2.6 ± 5.8	9.1
Insect	July 16- August 31	1.0 ± 0.5	16.2 ± 9.2	4.9 ± 6.0	22.1
Pre-rut and Rut	September 16- October 31	1.2 ± 0.1	5.4 ± 2.3	3.5 ± 5.8	10.1
Early Winter	November 16- December 31	1.5 ± 0.2	8.5 ± 3.9	1.1 ± 2.9	11.1
Late Winter	March 1- April 15	1.7 ± 0.2	3.1 ± 5.4	0.3 ± 0.9	5.1

[a] Calculated as (percent of daily time budget spent grazing in a particular season (Table 7)) X (average grazing speed = 0.13 km • h^{-1}). Average grazing speed was estimated from 15-minute scans on grazing animals as 0.13 km • h^{-1} ± 0.08 (s.d.) (n = 380).

[b] Calculated as (percent of daily time budget spent walking in a particular season (Table 7)) X(average walking speed = 3.22 km • h^{-1}, from Thomson (1977)).

[c] Calculated as (percent of daily time budget spent trotting/galloping in a particular season (Table 7)) X (average trotting/galloping speeds = 12 km • h^{-1}, from Thomson (1977)).

[d] Sum of a, b, and c above.

In comparable studies, where mushrooms were very scarce, caribou/reindeer continued to exhibit active-rest cycles between periods of moderate to severe insect harassment (J. Curatolo pers. comm., D. Roby pers. comm.; J. Wright pers. comm.). Thus it appears that the presence of mushrooms stimulates a greater degree of walking/searching in caribou, and this activity largely replaces active-rest cycles of normal duration (Table 8). It may also be possible that caribou eating significant quantities of mushrooms may not have to ruminate/rest as often, due to the low cell wall content and presumably high digestibility of mushrooms (Appendix C). The effect that searching activity has on the energy balance and nutritional status of caribou is difficult to ascertain. However, this searching activity undoubtedly increases seasonal energy expediture (Table 7).

Pre-rut and Rutting Season (September 16 - October 31)

The pre-rut and rutting season began with the arrival of caribou groups of mixed sexes on the rutting grounds, and extended throughout the period when adult bulls were sexually active and were herding cows. Termination of the rutting season was marked by the movement of caribou to the wintering grounds. Copulation was observed on October 7 and 8 in 1979. Non-evergreen vegetative tissue was almost completely senescent during this period, except in wet areas where some grasses and sedges remained green.

Relatively short rest periods were observed during the pre-rut and rutting season. Also, a high variability was noted in the duration of active periods (Table 8), due partly to the disruption of rhythmic activity patterns by sexually active bulls. Reduction in forage availability, resulting from the senescence of non-evergreen tissue, was associated with an increase in the duration of active periods compared to active periods during the calving and post-calving season.

The high proportion of time female and young caribou spent standing (12 percent ± 7) (Table 7) during the pre-rut and rutting season was due partly to the aggressive behavior of bulls. Also, caribou exhibited behavior indicative of oestrid fly avoidance throughout September and early October during weather favoring oestrid fly harassment. Characteristic of this behavior was the caribou's substitution of the lying posture for a standing posture during rest periods. Also, female caribou often stood with their heads lowered, which is indicative of insect harassment. Clumping together and body-shaking were observed infrequently during these periods but are further indicators of insect harassment. Bursts of running were not observed. Conditions favoring these reactions included direct sunshine, temperatures greater than 13°C (measured in the sun), and low wind speeds (0 to 2.2 $m \cdot sec^{-1}$). According to Brejew (1956) as summarized by Kelsall (1975), these environmental conditions are favorable to oestrid fly activity. However, oestrid flies were not observed during these periods, and neither were other large flies that may have prompted the caribou's behavioral responses. The fact that several hard freezes and periods of temporary snow cover preceded these late-September observations lends some credence to the suggestion that the caribou may simply have been conditioned to insect-avoidance behavior during periods of late autumn weather favorable to insect activity. However, adult oestrid flies have been observed to withstand periods of snow cover in the arctic (D. Klein pers. comm.). Kelsall (1975) suggested that the critical environmental parameter inhibiting warble fly activity is mean daily maximum temperature, apparently regardless of freezing temperatures during prior summer or autumn periods. Kelsall (1975) further reported that mean daily maximum temperatures would permit oestrid fly activity from June through September in the southern Yukon at latitudes similar to that of Denali National Park (62° to 63°N). This discussion should reveal the need for more systematic studies of the interrelationships between caribou/reindeer and oestrid flies.

A further contributing factor to the high proportion of standing during the pre-rut and rutting season was the predominance of short periods of standing prior to and immediately following lying periods. This was important during this season due to the short, frequent rest periods.

Finally, in view of a report that the Denali caribou herd had a low proportion of bulls (about 25 bulls per 100 cows) in 1979 (Grosnick 1979), it is noteworthy that all cows I observed during the rutting period in 1979 (up to 300 different cows in one day) were accompanied by mature, sexually active bulls. Also rutting activity appeared to peak about October 8 in 1979 as one would expect if calving peaks about May 22. These dates indicate a gestation period of 227 days which is precisely that given by Bergerud (1961) and McEwan and Whitehead (1972) for wild caribou/reindeer.

Winter Periods (November 16 - April 15)

The early winter period (November 16 - December 31) was distinguished from other winter periods on the basis of a higher incidence of sparring, bush-thrashing, and playing among female, calf, and young bull caribou. These activities were virtually absent by late winter (March 1 - April 15). The result was a notably higher proportion of time spent standing (includes sparring and bush-thrashing) and walking in early winter compared to late winter (Table 7), and significantly longer active periods in early versus late winter ($p < 0.05$) (Table 8). Any seasonal differences in caribou activity that may occur during mid-winter (January 1 - February 29) are difficult to ascertain due to the small number of observations (Table 8). However, sparring, bush-thrashing, and play activities appeared to have been curtailed prior to observations in January, although this reduction may have been due to the severe weather conditions during mid-winter observations (Table 5). Thomson (1977) reported that sparring and bush-thrashing occurred throughout January among wild reindeer in Norway, and Roby (1978) reported that caribou in the Central Arctic herd sparred throughout winter.

Roby (1978, 1980) also divided the winter season into early, mid-, and late winter periods, but he based this division primarily on changing snow conditions and how they appeared to affect caribou distribution and feeding behavior. Snow conditions, however, did not differ significantly between early and late winter in this study (Table 5), due primarily to the wind-swept character of foraging areas and sublimation.

The wind-swept condition of foraging areas obviously contributed significantly to the low percent of time caribou spent cratering (Table 7). Comparative measurements on the percent of time spent cratering by other caribou/reindeer populations are lacking in the literature. This is unfortunate as measurements on the time spent on cratering activities is of importance when estimating annual energy requirements of Rangifer populations.

It should be recognized that caribou will not always crater for forage when a complete snow cover exists. For instance, foraging caribou will often respond to a snow cover of soft, powdery snow up to several centimeters in depth by pushing their mouths through the snow to reach vegetation (personal observation). This foraging procedure is likely more efficient energetically than digging feeding-craters. The desired snow conditions for this procedure often prevail in foraging areas between windy periods. Another characteristic feature of snow in windy areas was the presence of a very thin hard crust of snow. Caribou were observed to shatter this crust with a single pawing motion and to subsequently enlarge the feeding-crater considerably solely with the use of their muzzles. LaPerriere and Lent (1977) also noted that caribou will feed in areas of shallow, extremely hard snow, where the snow can be fractured into slab-like pieces for relatively easy access to forage. Davydov (1963) concluded that cratering through shallow, hard, dense snow is accompanied by less fatigue than cratering through deep, soft snow.

Cratering in deep snow in and near Denali National Park was usually associated with the seeking of Equisetum spp. which grow in small drainages or low areas where wind-blown snow often accumulates.

Characteristics of snow cover have often been acknowledged as a critical factor influencing the survival and well-being of arctic and sub-arctic Rangifer populations (Pruitt 1959; Henshaw 1968; Parker et al. 1975). Relative to snow conditions in caribou foraging-areas in northern Alaska (LaPerriere and Lent 1977; Thing 1977; Roby 1978), the Denali herd has relatively easy access to forage during the winter, at least on most of the eastern wintering area and part of the western area. As previously stated, this is due to the high winds and to the early emergence of snow-free areas due to sublimation on the Denali herd's wintering areas. Wind-swept foraging areas were particularly prevalent in the Stampede Hills and in portions of the Kantishna Hills. However, snow conditions will obviously vary between years and between areas. For instance, snowfall south of the Alaska Range, on the Cantwell calving ground, is extremely heavy compared to snowfall north of the range (see Study Area), and this heavy accumulation has exerted a significant influence on early spring movements of caribou in some years (see Study Herd: History and Status).

Thomson (1977) found very little variation in the activity budgets of wild reindeer in winter. However, he admitted that a bias existed in his data, as field observations were clustered around the middle of the day (peak lying time). In contrast to Thomson's work, Roby (1978,

1980) and I observed an increase in the proportion of time caribou spent lying in late versus early winter (Table 7). However, the duration of lying or rest periods appeared to remain constant (about 100 to 120 minutes) throughout winter (Table 8). A constancy in the length of rest periods was also observed by Segal (1962) in mid- and late winter (90 to 135 minutes with a mean of 112 minutes). Roby (1978) reported similar values for mid- and late winter lying periods (120 minutes (n = 12), and 103 minutes (n = 13), respectively). Therefore, it follows that the increase in the proportion of time caribou spent lying in late versus early winter is due to an increase in the duration of active periods (Table 8). In fact, the variability in activity budgets throughout winter can be attributed largely to the duration of active periods, since the length of rest periods is presumably constant. The decrease in the length of active periods as winter progressed was due to a substantial decrease in the proportion of time caribou spent walking and standing (includes sparring and bush-thrashing) (Table 7; Roby 1978). A result was the reduction in mean daily movement rates by more than 50 percent from early to late winter (Table 11).

Thus caribou respond to long winters by reducing energy expenditure, specifically by increasing the proportion of time spent lying and feeding, and reducing the incidence of standing and walking. The relationships between the proportions of time spent feeding versus lying presumably will depend on snow conditions and range condition, but rest periods appear to be nearly constant throughout winter. An exception to this constancy occurs during severe winter foraging conditions (Roby 1980).

Roby (1980) reported on an extreme case of winter activity budgets among starving caribou in west Greenland. These animals, too, reacted to the progression of winter by reducing the amount of time spent walking and standing, but in a much more emphatic manner as lying time increased to over 50 percent of the time budget, and activities other than feeding and lying were reduced to only 2 percent of the time budget. Movement rates decreased to less than 1 km • day^{-1}. Length of lying periods was not given, but lying periods were described as being longer than the active periods. Normal active-rest cycles were no longer apparent due to the environmental stress of malnutrition. In such a case, the reduction in overall energy expenditure is quite dramatic.

Roby (1980) reported that the above listed conditions could be used as tools to assess caribou nutritional stress in mid- and late winter. I suggest that frequency distributions of the duration of rest periods and active periods would provide more relevant information concerning the degree of rumen fill and nutritional status. This information is also more reliable compared to estimates of the proportion of time spent lying, unless one calculates the proportion of time spent lying in complete active-rest cycles. Nevertheless, from comparisons with Roby's (1980) late-winter descriptions of a nutritionally-stressed caribou population, it is possible to state, again, that the Denali caribou herd does not appear to be under nutritional stress.

The extremely low proportion of time spent cratering in snow (Table 7) likely contributed significantly to the apparently good nutritional status in late winter. An increase in the proportion of lying time and reduction in energy expenditure as winter progresses may occur as a normal event in the caribou's annual cycle, and may not necessarily indicate an unusually poor nutritional state.

Synopsis and Conclusion

With the exception of periods when oestrid flies, mushroom-searching activities, or sexually aggressive bulls acted to disrupt activity patterns, the dominant factor influencing seasonal differences in the activity budgets of female and young caribou was the duration of active periods in the active-rest cycle. Duration of active periods is presumably most strongly related to rumen fill and thus availability of forage. Therefore, the variability in the duration of active periods could be important in assessing relative seasonal range condition between herds. Unfortunately, comparative data on this aspect of feeding activity is virtually absent in the literature and has not received prior emphasis in caribou/reindeer studies. Therefore, assessment of the herd's relative nutritional status from data on activity patterns is difficult at present.

However, from former reports on the activity budgets of caribou/reindeer experiencing poor nutritional condition, it was substantiated, in two instances, that adult females of the Denali caribou herd are not experiencing unusual nutritional stress. This was indicated by the low proportion of time spent lying in late winter and the low proportion of time spent grazing in spring. Spring nursing behavior among caribou of the Denali herd also indicated that adult females were not nutritionally stressed.

Several other indicators also suggest that the Denali herd is not energetically stressed, compared to other Alaskan herds. For instance, on most of the eastern wintering ground and on at least a portion of the western wintering area, caribou spent a minimum of time (less than 1 percent) cratering through snow to reach forage. This was due to the extreme wind-swept character of foraging areas, with virtually no snow remaining, and to sublimation, resulting in early availability of snow-free areas. Obviously, snow conditions will vary between years and between areas. For instance, heavy snowfall on the Cantwell calving ground often remains until mid-May or later.

Due to the longer insect period experienced by the Denali herd, compared to more northerly populations, it might be predicted that the Denali caribou are harassed and energetically stressed by insects to a larger extent than other herds. However, the influence that insects have on the energetic status of the Denali caribou is likely of relatively moderate proportions due to the virtual absence of mosquito and black fly harassment (at least in 1978 and 1979), the high availability of insect-relief sites (snowbanks and glaciers) on the summering range, and the movement of females and calves away from areas where oestrid flies emerge from pupae. The relatively short, annual migratory distances of the Denali herd (compared with migratory distances of larger Alaskan herds) also suggests that this herd is not energetically stressed. It is also obvious that the Denali area experiences a longer growing season than more northerly areas, allowing Denali caribou to store larger quantities of fat for winter use than is the case among caribou in the larger arctic herds.

The reduction in activity that was observed as winter progressed may have occurred as a normal event in the caribou's annual cycle and may not necessarily indicate an unusual nutritional stress. Skoog (1968) described the annual fat cycle in caribou and indicated that early spring green growth was a vital factor in caribou nutrition. Dauphiné (1976) also reported that fat reserves of caribou are very low by late winter. Reduced activity and energy expenditure in late winter acts to conserve fat and is likely a common behavioral response among Rangifer to the stress of long arctic and sub-arctic winters. An important negative influence on fattening is harassment by insects, but caribou are presumably conditioned to a certain amount of insect harassment while still being able to store sufficient quantities of fat for winter use.

Estimated Energy Requirements

Estimates of the energy required for various activities and productive processes were summarized from the literature (Tables 12 and 13). Subsequently, total daily energy requirements of adult female caribou were calculated on a seasonal basis (Tables 14 and 15, and Figure 2), based on the proportion of time spent daily in various activities and the seasonal energy costs of lactation, pregnancy, fattening, and hair growth.

A 21-percent reduction in the resting metabolic rates of caribou/reindeer was calculated from summer to winter from values in the literature (Table 12). Several authors have reported similar reductions in metabolic rates of Rangifer. Kvitkin (1950), cited by Segal (1962), reported a 20- to 27-percent reduction in metabolic rates of reindeer from summer to winter, while Segal (1962) reported a value of 30 percent for reindeer fasted over 12 hours. This decline apparently occurs by mid-November, as McEwan and Whitehead (1970) reported that the resting metabolism, per unit of metabolic weight, was about 25 percent lower in mid-November than mid-August in a male reindeer. McEwan and Whitehead suggested further that this reduction may be less apparent in females. Therefore, at least until more measurements are made, a 21-percent reduction in resting metabolic rates from summer to winter is a reasonable estimate for adult female caribou.

Several other factors contribute significantly to seasonal differences in energy expediture (Figure 2) besides the 21-percent

Table 12. Summary of resting metabolic rates of adult female *Rangifer* in summer and winter and factors influencing these estimates.

Season	Subspecies	No. of animals	Average Body Weight (kg)	Air Temperature (°C)	No. of Observations	Time since Feeding (h)	Resting Metabolic Rate[a] (kJ · $kg^{-0.75}$ · day^{-1})	Reference
Summer								
	reindeer	4	92		34	4-6	523[b]	White and Yousef (1978)
	reindeer	2	96.5		8+	4-6	620	White and Yousef (1978)
	reindeer	2	96.5		8+	4-10	686-854[c]	White and Yousef (1978)
	reindeer	3	91		17	feeding	620	Luick and White (1971)
	reindeer	3	(assumed 95)	0° - 14°	63	feeding	736	Segal (1962)
	reindeer	1	115		10+	0-8	584	Young and McEwan (1975)
	caribou	1	97		10+	0-8	624	Young and McEwan (1975)
							640 ± 86 (s.d.)	

Table 12. (Continued)

Winter								
	reindeer	4[f]	(assumed 87)	-1° - -16°	7	feeding	503[d]	Makarova and Segal (1958)
	caribou	2	85	15°	32	4-13	507[e] 505 ± 3(s.d.)	McEwan (1970)

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[a] In all known cases, resting metabolic rates were measured on animals in a standing posture. Lying animals normally refuse a mask.

[b] Animals were under penned conditions (R. White pers. comm.)

[c] Animals were being used in walking experiments (R. White pers. comm.)

[d] Assumed a calorific value of O_2 of 20.0 $kJ \cdot l^{-1}$ from Segal (1962).

[e] Errors were found in McEwan's (1970) conversions of $kcal \cdot day^{-1}$ to $kcal \cdot kg^{-0.75} \cdot day^{-1}$.

[f] One animal was a bull.

Table 13. Estimated energy costs of activities and productive processes used in the calculation of seasonal energy expenditure in adult female caribou.

Activity	Season	Energetic cost	Reference
Standing	Summer	$640\ \mathrm{kJ} \cdot \mathrm{kg}^{-0.75} \cdot \mathrm{day}^{-1}$	Table 12 - reindeer/caribou
	Winter	$505\ \mathrm{kJ} \cdot \mathrm{kg}^{-0.75} \cdot \mathrm{day}^{-1}$	Table 12 - reindeer/caribou
Lying	Summer	$582\ \mathrm{kJ} \cdot \mathrm{kg}^{-0.75} \cdot \mathrm{day}^{-1}$	Standing costs are 10% greater, Brody (1945), White and Yousef (1978)-reindeer
	Winter	$459\ \mathrm{kJ} \cdot \mathrm{kg}^{-0.75} \cdot \mathrm{day}^{-1}$	Standing costs are 10% greater, Brody (1945), White and Yousef (1978)-reindeer
Lying to Standing and return		$0.10\ \mathrm{kJ} \cdot \mathrm{kg}^{-1}$	Blaxter (1962) - cattle
Rumination		$0.13\ \mathrm{kJ} \cdot \mathrm{kg}^{-1} \cdot \mathrm{h}^{-1}$	Osuji (1974) - sheep
Foraging/eating		$1.88\ \mathrm{kJ} \cdot \mathrm{kg}^{-1} \cdot \mathrm{h}^{-1}$	Osuji (1974) - sheep
Cratering costs	Winter	$0.94\ \mathrm{kJ} \cdot \mathrm{kg}^{-1} \cdot \mathrm{h}^{-1}$	see Methods[a]
Walking (horizontal)	Summer	$2.30\ \mathrm{kJ} \cdot \mathrm{kg}^{-1} \cdot \mathrm{km}^{-1}$	White and Yousef (1978)[b] - reindeer
Walking in snow	Winter	$2.64\ \mathrm{kJ} \cdot \mathrm{kg}^{-1} \cdot \mathrm{km}^{-1}$	see Methods[c]

Table 13. (Continued)

Climbing (vertical)			
+9% grade		31.0 kJ · kg^{-1} · vert.km^{-1}	White and Yousef (1978)[d] - reindeer
-9% grade		- 5.7 kJ · kg^{-1} · vert.km^{-1}	White and Yousef (1978)[d] - reindeer
Trotting/Galloping			
(mean 12 km · h^{-1})[e]	Summer	30 kJ · kg^{-1} · h^{-1}	see Methods[f]
	Winter	35 kJ · kg^{-1} · h^{-1}	see Methods[c]
Hair growth		100 MJ · year	see Methods
Lactation		560.26 MJ per calf	see Methods
Pregnancy		368.57 MJ per calf	see Methods
Fattening	Summer	578.9 MJ per summer	see Methods
	Winter	-365.0 MJ per winter	see Methods

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[a] Values include only additional costs of cratering.

[b] Value was taken from reindeer walking on dry tundra and includes only the added cost of walking.

[c] Costs of traveling through snow were assumed to be 15 percent greater than summer values (see Methods).

[d] Values include only additional costs of ascent or descent.

[e] Mean trotting/galloping speed is from Thomson (1977).

[f] Value includes total costs involved in trotting/galloping.

Table 14. Seasonal estimates of daily energy requirements (Qe) of adult female caribou in the Denali caribou herd, 1978-1980.[a] Energy costs of individual activities are given in Table 13.

	Season									
	Calving and Post-Calving (May 22-June 30)		Insect (July 16-August 31)		Pre-rut and Rut (Sept. 16-Oct. 31)		Early Winter (Nov. 16-Dec. 31)		Late Winter (March 1-April 15)	
Assumed Body Weight[b]	100 kg		105 kg		110 kg		110 kg		105 kg	
	% Time	Qe[c]	% Time	Qe	% Time	Qe	% Time	Qe	% Time	Qe
Activity										
Lying	52	9.57	19	3.63	39	7.71	32	4.99	42	6.32
Standing	3	0.61	25	5.25	12	2.61	8	1.37	2	0.33
Feeding[d]	37	9.42	33	8.74	40	11.00	48	11.05 (12.24)	53	11.75 (13.01)
Walking[e]	7	2.66	21	8.33	7	2.69	11	4.40	4	1.52
Trotting/ Galloping	0.9	0.65	1.7	1.29	1.2	0.95	0.4	0.37	0.1	0.09
Ruminating[f]	26	0.08	10	0.03	20	0.07	16	0.06	21	0.07
Lying to Standing and return	18	0.18	10	0.11	22	0.24	10	0.11	14	0.15
Ascent	0.10 vert.km • day^{-1} events	0.31	0.32 vert.km • day^{-1} events	1.04	0.08 vert.km • day^{-1} events	0.27	0.05 vert.km • day^{-1} events	0.17	0.03 vert.km • day^{-1} events	0.10

Table 14. (Continued)

Descent	0.10 vert.km • day^{-1}	-0.06	0.32 vert.km • day^{-1}	-0.19	0.08 vert.km • day^{-1}	-0.05	0.05 vert.km • day^{-1}	-0.03	0.03 vert.km • day^{-1}	-0.02
Lactation	mean daily rate	6.39	mean daily rate	3.69	mean daily rate	0.55	mean daily rate	0	mean daily rate	0
Pregnancy	mean daily rate	0	mean daily rate	0	mean daily rate	0.15	mean daily rate	0.38	mean daily rate	2.41
Fattening	mean daily rate	-1.15	mean daily rate	5.41	mean daily rate	5.41	mean daily rate	-1.24	mean daily rate	-1.84
Hair Growth	mean daily rate	0.62	mean daily rate	0.82	mean daily rate	0.29	mean daily rate	0	mean daily rate	0
Totals (MJ • day^{-1})		29.28		38.15		31.89		21.63		20.88
Totals (kJ • kg$^{-0.75}$ • day^{-1})		926		1163		939		637		637
Multiple of BMR[g]		1.92		2.41		1.95		1.67		1.67

[a] Migratory periods are excluded from this table.

[b] Basis for the seasonal weight changes is discussed in the Methods.

[c] Qe=MJ • day^{-1}.

[d] Feeding costs = standing costs + foraging costs + walking costs (at speed of 0.13 km • h^{-1} - Table 11). Values in parentheses include foraging/cratering costs in rather extreme snow conditions compared to no cratering costs (see Methods).

[e] Walking costs = standing costs + walking costs. Winter values include the cost of traveling through snow (see Methods).

[f] Rumination time assumed at 50 percent of lying time (Thomson 1977).

[g] Basal metabolic rate (BMR) was assumed to be 381 kJ • kg$^{-0.75}$ • day^{-1} in winter periods and 482 kJ • kg$^{-0.75}$ • day^{-1} from calving through the rut (see Methods).

Table 15. Estimated total seasonal and annual energy requirements of an adult female caribou in the Denali caribou herd, 1978-1980.[a]

Season	Dates	No. of Days	Daily Energy Requirement (MJ)	Multiples of BMR	Seasonal Energy Requirements (MJ)
Calving and Post-calving	(May 22 - June 30)	40	29.28	1.92	1171.2
Summer Migration	(July 1 - July 15)	15	36.66	2.32	549.9
Insect	(July 16 - August 31)	46	38.15	2.41	1754.9
Fall Migration	(Sept. 1 - Sept. 15)	15	34.25	2.09	513.8
Pre-rut and Rut	(Sept. 16 - October 31)	46	31.89	1.95	1466.9
Early Winter Migration	(Nov. 1 - Nov. 15)	15	23.69	1.83	355.4
Early Winter	(Nov. 16 - Dec. 31)	46	21.63	1.67	995.0
Mid-winter	(Jan. 1 - Feb. 29)	60	20.53	1.62	1231.8
Late Winter	(March 1 - April 15)	46	20.88	1.67	960.5
Late Winter Migration	(April 16 - May 21)	36	23.67	1.97	852.1
					Annual Requirement = 9851.5 MJ

[a]Includes cost of pregnancy and lactation, but not costs of cratering in snow (about 190 MJ • yr^{-1} maximum).

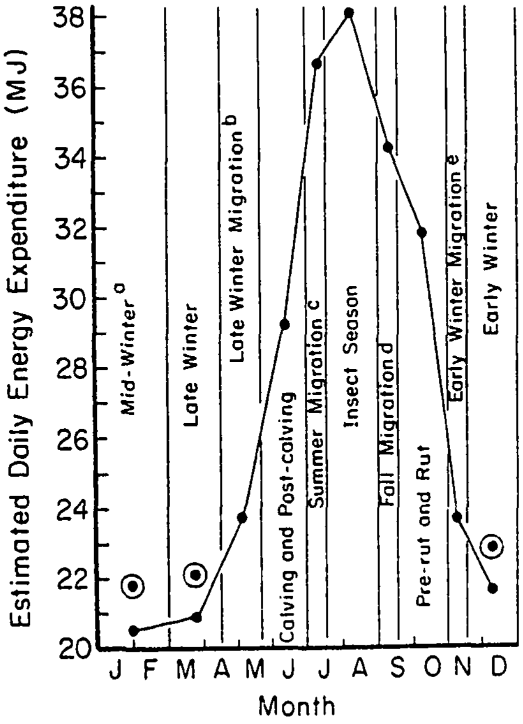

Figure 2. Year-round estimates of daily energy requirements of an adult female caribou with calf in the Denali caribou herd, 1978-1980. Circled values include foraging costs in extreme snow-cover conditions, compared to foraging in the absence of snow (see Methods).

[a] Mid-winter energy expenditure was assumed to be intermediate between early and late winter (Table 14). Mid-winter pregnancy costs (58.48 MJ total) were added, and utilization of 110.40 MJ of fat reserves was subtracted. Body weight was assumed to be 107 kg, and the period lasted 60 days.

[b] Late winter migration value includes the costs of a 200 km migration in snow (94.16 MJ), an ascent and descent of 2380 m (6.30 MJ), pregnancy (174.99), fattening (66.24 MJ), and late winter daily activity (69.34 MJ total) (Table 14). Body weight was assumed to be 100 kg, and the period lasted 36 days.

[c] Summer migration value includes the costs of a 140 km migration (71.8 MJ), an ascent 3600 m (11.72 MJ), a descent of 3290 m (2.00 MJ), lactation (83.68 MJ), hair growth (12.3 MJ), and daily activity equal to that during the insect period (423.45 MJ total). Body weight was assumed to be 105 kg, and the period lasted 15 days.

[d] Fall migration value includes the costs of a 50 km migration (26.71 MJ), ascent of 730 m (2.49 MJ), descent of 970 m (.62 MJ), fattening (81.15 MJ), lactation (25.94 MJ), hair growth (12.3 MJ), and daily activity equal to that during the prerut and rutting season (382.35 MJ total). Body weight was assumed to be 110 kg, and the period lasted 15 days.

[e] Early winter migration value includes the costs of a 60 km migration (30.74 MJ), ascent of 640 m (2.18 MJ), descent of 1100 m (-0.70 MJ), pregnancy (3.28 MJ), and early winter daily activity (314.34 MJ total). Body weight was assumed to be 110 kg, and the period lasted 15 days.

reduction in resting metabolic rates. For instance, the energy cost related to the deposition of fat reserves in summer and the yield of energy from the catabolization of stored fat and protein in winter (Tables 13 and 14) contribute significantly to the large differences in food energy requirements in late summer and autumn versus winter (Table 14). The high energy costs related to lactation are most important during the calving and post-calving season (Table 14), but the high incidence of lying during this season and the low fat reserves combine to give intermediate values between winter and later summer values. Energy costs of pregnancy are most important during the late winter season, and particularly during the late winter migration just prior to calving (Table 15). One might expect that the high energy costs of pregnancy in late winter would contribute to a significant increase in energy requirements from the mid-winter to late winter periods. However, the reduction in daily activity (particularly the incidence of walking) in late winter acted to give comparable values between the two periods (Figure 2). The highest daily energy requirements were exhibited during the insect season due to the high proportion of time spent active, the high energy costs of lactation, and the extremely high costs associated with the deposition of fat reserves. Summer migration values were also high due to the high costs of activity and lactation, but the deposition of fat reserves had not yet begun.

Changes in body weight also influenced seasonal differences in energy requirements. For instance, a caribou weighing 110 kg can be expected to spend about an additional 2 MJ • day^{-1} than a 100-kg caribou during the same season. In comparison, seasonal differences in activity budgets can affect changes in daily energy expenditure from about 2 MJ • day^{-1} (comparing early and late winter activity costs) to an extreme of about 6 MJ • day^{-1} (comparing activity costs between late winter and the insect season). Cratering costs, alone, can add about 1.2 MJ • day^{-1} to winter energy requirements if cratering is prolonged and snow conditions are severe (see Methods). Thus, cratering costs can be of great significance to the total energy expenditure in winter.

McEwan (1970) reported that the maintenance digestible energy intake (DEI) in two penned, adult female caribou averaged 665 ± 18 kJ • $kg^{-0.75}$ • day^{-1} from February to May. Converting to metabolizable energy intake (MEI = 0.82 x DEI, Agricultural Research Council 1965), a value of 545 kJ • $kg^{-0.75}$ • day^{-1} is obtained. This is about 1.43 times winter-BMR. My model gives a value of about 652 kJ • $kg^{-0.75}$ • day^{-1} (1.71 times winter-BMR) over the same period assuming the caribou is not pregnant and on a maintenance diet as in McEwan's study. My higher value can be associated primarily with the increased costs of activity in free-ranging versus penned caribou. In a separate study, McEwan and Whitehead (1971) estimated the mean DEI of 11 pregnant reindeer and caribou fed _ad libitum_ over the entire gestation period. These results indicated a MEI of 571 kJ • $kg^{-0.75}$ • day^{-1} (1.50 times winter-BMR) I have estimated a mean value of about 683 kJ • $kg^{-0.75}$ • day^{-1} (1.79 times winter-BMR) over the same period including pregnancy costs. Again, the difference (0.29 winter-BMR) is largely due to the sedentary nature of the penned animals. The differences in these two comparisons are comparable (0.28 and 0.29 winter-BMR), which lends credibility to the model.

These comparisons indicate that free-ranging caribou require about 20 percent more metabolizable energy in winter than penned reindeer/caribou. The costs of cratering were not considered. The next step is to calculate the activity costs of a penned reindeer/caribou to determine if the model can account for this 20 percent difference in metabolizable energy requirements. McEwan's animals were in very small pens during his experiments (R. White pers. comm.), therefore I have assumed an activity budget of 60 percent of the time spent lying, 30 percent standing, 7 percent feeding, and 3 percent walking. This activity budget would be associated with an energy requirement of about 16.8 MJ • day^{-1} for a 105-kg reindeer/caribou. The energy costs associated with the late winter activity budgets of caribou in the Denali herd were estimated to be about 20.3 MJ • day^{-1} (Table 15), which is almost exactly a 20 percent increase from the energy budget of the penned reindeer/caribou. This example exemplifies the apparent accuracy of the model in predicting actual food energy requirements.

It is difficult to make further comparisons with intake-studies. McEwan and Whitehead (1970) estimated maintenance MEI of two penned female and male caribou in winter as 25.94 MJ • day^{-1} and 27.20 MJ • day^{-1}, respectively, with body weights of approximately 70 kg. However, these estimates were extrapolated from measurements on young caribou on a high plane of nutrition. As such, the estimates are inherently excessive due to the high energy requirements of young animals and the high quality diet (Blaxter 1962). It is interesting that these values were slightly higher than those reported for reindeer (mean of 23.01 MJ · day^{-1}) under the same conditions. Steen (1968) reported slightly lower winter maintenance values for MEI of penned female reindeer (21.3 MJ · day^{-1}) but does not give body weights, diets, age of the animals, or methods used in this determination.

Thomson (1977) attempted to model the year-round energy expenditure of wild reindeer in Norway using estimates of energy expenditure from the literature. However, Thomson's applications of energy costs were entirely different from mine, making comparisons difficult. The most significant deviations encountered in Thomson's calculations included: (1) the exclusion of estimates for the heat of digestion or the calorigenic effect of food, and (2) the extremely high energy expenditure related to "trotting/running". Thomson's exclusion of the calorigenic effect of food accounts for the approximately 30 percent reduction in his values (exclusive of running costs) compared to mine (see Methods). However, when running costs are considered, Thomson's values are often much higher than mine. This was due to his much higher estimates of the proportion of time reindeer spent trotting/running in combination with his extremely high estimate for the energy cost of trotting/running. Thomson used a value of 61 kJ · kg^{-1} · hr^{-1} for trotting/running at a speed of 10 km · hr^{-1}, compared to my value of 30 kJ · kg^{-1} · hr^{-1} at a speed of 12 km • hr^{-1}. Thomson obtained his value from Blaxter (1962) by extrapolating from an equation that predicts the energy costs of walking (at various walking speeds) for sheep. However, this estimate appears to be in error compared to estimates elsewhere in the literature (see Methods).

Gaare et al. (1975) also estimated seasonal energy requirements of wild reindeer in Norway on a seasonal basis. However, their estimates are approximately 2000 to 8000 times greater than my estimates. Since they did not present energy-cost estimates of the various activities, it is impossible to account for the difference. White et al. (1975) estimated the summer energy requirements for caribou activity as simply 2 times BMR. However, they used a winter-BMR value, so their summer energy estimates are substantially lower than mine.

Future studies are needed to assess the contribution that physiological stresses have on caribou energy requirements. Physiological stresses from insect harassment, predators, humans, and heavy parasite loads (particularly infestations of oestrid fly larvae) may be of considerable importance. For instance, it has been noted that when harassment by insects, predators, and humans are absent as in Svalbard, reindeer are able to gain extremely high quantities of fat compared to more southern populations (Dauphiné 1976; Reimers 1980). A large portion of this fat is undoubtedly gained simply as a result of the decreased activity of Svalbard reindeer which is associated largely with the lack of harassment in summer (Reimers 1980).

However the lack of physiological stresses, such as nervousness, in Svalbard reindeer may also be of significance. For instance, Blaxter (1962) indicated that nervousness and increased muscular tension accounted for a 10-percent increase in fasted metabolic rates of untrained versus trained sheep. Thus, assuming an increase in energy expenditures of 2.5 MJ • day^{-1} due to physiological stress, caribou would require about 76 MJ more annually if experiencing stress for an average of 2 hr • day^{-1}. This level of disturbance may be associated with running for a maximum of about an hour per week, which has a cost of about 160 MJ throughout the year. This example illustrates the effect that predators, insects, and humans could have on the annual energy requirements of caribou/reindeer. However, estimates of the energy costs of physiological stresses require further study.

Conclusion

The energy model appears to predict the food energy requirements of caribou very well. Thus estimates of the energy costs associated with the various activities and productive processes can be used to test the effect of a single factor or combination of factors on the total animal-range relationship. Comparisons can also be made of energy budgets between populations to assess relative nutritional status. Total annual energy requirements for an adult female caribou, including costs of pregnancy (368.57 MJ) and lactation (560.26 MJ), was estimated at about 9850 MJ (without considering additional costs of physiological stresses or cratering activity). When compared to intake-studies of caribou energy requirements, the model appears to take into consideration energy requirements associated with physiological stresses. However, if cratering costs are added throughout the three winter periods, annual energy requirements could be increased to 10,032 MJ assuming extreme snow conditions. Cratering activities would presumably have a direct influence on activity budgets, specifically by increasing the proportion of time spent active (Bergerud 1974b). Thus there would be some added activity costs if caribou are required to crater extensively throughout the winter. However, the annual energy expenditure would still not likely exceed 10,300 MJ, as caribou would likely react to excessive energetic stress in late winter by reducing energy expenditure (Roby 1980).

CHAPTER 3: NUTRITIONAL ECOLOGY

Introduction

The nutritional regime of the adult female cohort of the Denali caribou herd is described on a seasonal basis in this chapter by combining previous estimates of dietary composition (Chapter 1) and energy requirements (Chapter 2) with data on the digestibility and nutrient quality of the forages. This data base also allowed estimation of the daily dry matter intake requirements of caribou on a seasonal basis. I have also discussed the role of nutrition in caribou population ecology.

The protein and mineral content of caribou/reindeer diets exhibit extreme annual variations (Steen 1968; Bergerud 1977; Luick 1977). Klein (1970a, 1970c), discussed the factors responsible for the high nutrient quality of spring and summer forage in arctic and alpine regions. Klein (1962, 1968) also found that spring and summer feeding behavior of feral reindeer results in the selection of the highest quality forage available on a given range. McEwan and Wood (1966), Klein (1968, 1970c) and Steen (1968) stressed the importance of high quality spring and summer forage in affecting growth and fattening in caribou/reindeer. The influence of qualitative characteristics of spring and summer forage on body size and reproductive success of North American cervids has also been discussed by Klein (1968, 1970c).

In contrast to the summer season, the winter season is usually considered a maintenance period at best for northern cervids (Klein

1968; Luick 1977). Steen (1968) suggested that the lichen-dominated winter diets of caribou were starvation diets on the basis of their low levels of protein and most minerals. As such, Steen suggested that protein and minerals were stored in the summer for use in the winter. The extremely low levels of protein and most minerals in fruticose lichens is well-documented (Scotter 1962; Hemming and Pegau 1970; Scotter and Miltimore 1973; and others). A lichen diet, however, is generally known to be high in digestible energy (Steen 1968; Klein 1970a; McEwan and Whitehead 1970). Kay et al. (1979) considered the need for energy the most compelling requirement determining the quality and quantity of food ingested by wild ruminants. Protein, however, is also considered of great importance in the diet. For instance, Moen (1973), in consideration of annual nutritional requirements, stated that "the energy and protein requirements of an animal are related to both its behavioral and its physiological characteristics since everything an animal does 'costs' something in terms of energy and protein." It should be recognized that energy-rich lichens are not the only forage consumed by caribou in winter (see Chapter 1), and that the relatively high protein content of non-lichen winter forage (compared to the protein content of lichens) is likely of great significance to the winter protein balance of the animals (Jacobsen and Skjenneberg 1975; Holleman et al. 1979; Klein 1980a).

In summary, the protein- and energy-rich spring and summer diets (diets are discussed in Chapter 1) and energy-rich winter diets are keys to the understanding of caribou nutrition, particularly in regard to the dramatic seasonal changes in protein and energy requirements of caribou/reindeer.

Methods

Forage Sampling and Determination of Forage Quality

Forage Sampling

Forage samples were collected for determinations of fiber and nutrient content and in vitro dry matter disapperance (IVDMD). Information recorded for each forage sample included date and location of sampling, plant phenological stage, plant part, plant species, and relative degree of use by caribou in the particular grazed area. Wet weights of forage samples were obtained immediately after collection using a 100-g Pesola spring scale. When it was necessary to collect samples during or soon after rain, wet weights were not recorded. Only plant parts selected by caribou were included in forage samples. For instance, only the upper portions of most forbs were collected to simulate use by caribou. Collections were normally made over an area of 25 to 150 m^2 and only in areas grazed by caribou. Sampling of a particular species was carried out, for the most part, only during periods of use by caribou. Frequency of sampling of a particular species was dependent on the degree of use by caribou and the phenological stage of the plant species. For instance, the frequency of sampling a particular species was increased during periods of high use by caribou and during early phenological stages, when forage quality varies considerably on a short-term basis. Sampling of lichens was kept to a minimum due to the availability of an abundance of data in the literature (Hemming and Pegau 1970; Bergerud 1977; Luick 1977) and the apparent lack of seasonal variation in the nutrient content of lichens.

Forage sample preparation

Samples were usually partially air-dried before delivery to the University of Alaska in Fairbanks, where they were promptly frozen in plastic bags until drying. All samples were freeze-dried in a Thermovac freeze-drier to constant weight and ground in a Wiley mill using a 20-mesh screen. Subsequently, samples were sent to the University of Alaska Agricultural Experimental Station, Palmer Research Center for fiber and nutrient analyses. Forage samples underwent in vitro digestibility analyses at the Institute of Arctic Biology, University of Alaska in Fairbanks. In all cases, discrete subsamples were dried at 100° to 110°C and results of analyses were corrected to a 100-percent dry weight basis.

Fiber and nutrient content

Forage samples were analyzed for fiber content at the Palmer Research Center using procedures outlined by Goering and Van Soest (1970). This included analysis for neutral-detergent fiber (NDF) or cell walls, acid-detergent fiber (ADF), lignin, cellulose, and ash. Hemicellulose was calculated as NDF-ADF, and cell solubles as 1-NDF. In preparation for nutrient analyses, forage samples underwent plant tissue digestion following the method described by Isaac and Johnson (1976). Nitrogen (N) and phosphorus (P) were subsequently measured with a Technicon Autoanalyzer. Potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na) were determined from the digesta by atomic absorption. All analyses, except the analysis for total nonstructural carbohydrate (TNC), were standardized against a National Bureau of Standards orchard leaf standard. Determination of TNC was made using the "Modified Weinmann Method of Removing Total Nonstructural Carbohydrates" (Smith 1969). However, the extract was analyzed for reducing power by the Technicon Autoanalyzer method for "Reducing Sugars in Tobacco Extracts" using ferricyanide reduction rather than copperiodometric titration.

In vitro dry matter disappearance (IVDMD).

Estimation of the IVDMD of forage samples was conducted by Karma Krelle, laboratory technician, and myself in 1980 under the auspices of Dr. Robert G. White, Institute of Arctic Biology, University of Alaska, Fairbanks. Laboratory methodology followed procedures outlined by Tilley and Terry (1963) with certain exceptions. Samples were contained in centrifuge tubes and weighed approximately 0.25 g, rather than 0.50 g. Thus, the volumetric prescriptions outlined by Tilley and Terry were reduced by 50 percent. Inoculum was contained in several centrifuge tubes and was spun in a centrifuge for 25 minutes at about 3500 $r \cdot min^{-1}$. Middle contents of the centrifuge tubes were used as inoculum. Incubation was carried out in centrifuge tubes. To ensure anaerobic conditions, centrifuge tubes were gassed with CO_2 before being fitted with pressure-release valves. Centrifuge tubes were shaken twice during the first 48-hour incubation period. Incubation temperature was maintained at 39°C, and toluene was not added at the completion of the initial 48-hour incubation. Each sample was tested in quadruplicate.

Rumen liquor was obtained from a fistulated adult female reindeer from January 7 to March 31 and from a fistulated, adult reindeer steer from April 28 to July 15. Daily rations for the reindeer usually contained about 0.5 kg *Epilobium angustifolium* and *Equisetum* spp. (fresh frozen weight), about 0.5 kg *Salix* leaves, about 0.5 kg *Carex* spp., 2 to 3 kg lichens (about 60 percent *Cladonia rangiferina* and 40 percent *Cladonia* and *Cetraria* spp.), and a Cattle Starter #1 (PCS, Ralston Purina Co.) ad libitum. This diet was fed to the reindeer for 2 weeks prior to beginning trials. Trials were run at about 2-week intervals. A mixture of four vascular plant species was used in all trials to allow for correction for between-animal and between-trial variation in IVDMD of non-lichen species. This mixture contained 25 percent (dry weight) *Eriophorum vaginatum*, 25 percent *Epilobium latifolium*, 25 percent *Betula nana*, and 25 percent *Carex bigelowii*. Two lichen species, *Cladonia rangiferina* and *Cetraria cucullata*, were used in all trials containing lichens to allow standardization of lichen analyses.

Fecal Sample Collection and Analysis

Collection of fecal samples were made at isolated field sites which necessitated that samples be allowed to air dry in paper bags. After transfer to the University of Alaska, samples were stored at -10°C, and later freeze-dried, ground in a Wiley mill (20-mesh screen), and sent to the Palmer Research Center where analysis for N, P, and fiber followed methods described for the analysis of forage samples. During winter collections, samples remained frozen until freeze-drying and were not air-dried.

Approximation of Apparent Dry Matter Digestibility (ADMD) of Forages

A direct relationship exists between the ADMD and digestible energy of a forage, therefore, estimates of the ADMD of forages were needed to complete the forage intake calculations in the following section. Actual in vivo measurements of the ADMD of caribou/reindeer forages are virtually absent in the literature, with the exception of ADMD-measurements for lichens. Determination of ADMD requires conventional feeding trials with animals and is calculated as follows:

$$\text{ADMD} = \frac{\text{Dry Matter Intake} - \overset{\text{Fecal Dry}}{\text{Matter Output}}}{\text{Dry Matter Intake}} \times 100$$

I have used three methods to estimate ADMD of forages, depending on the plant group under consideration. However, there is a clear need to substantiate these estimates using conventional digestibility trials. More significantly, measurements of the ADMD of actual seasonal dietary mixtures of <u>Rangifer</u> forages are needed, because the digestiblity of a mixture of components is not necessarily equal to the weighted sum of the apparent digestibilities of its components (Blaxter 1962).

For the purposes of this paper, the ADMD of plant species other than shrubs and lichens was estimated to be equivalent to determinations of IVDMD. According to Van Soest et al. (1966), the in vitro digestiblity technique reported by Tilley and Terry (1963) yields values essentially comparable to apparent in vivo dry matter digestibilities. However, it should be emphasized that this technique was developed for grass stands under domestic animal range conditions. Ruggiero and Whelan (1976) also found that in vitro determinations, measured using the Tilley and Terry technique, gave estimates closely approximating ADMD for a ration fed to two white-tailed deer. However, this relationship appears to vary depending on the digestibility of the forages and the animal species utilized (Scales et al. 1974; Urness et al. 1977), which points out the need for conventional digestibility trials with Rangifer forages.

Measurements of the IVDMD of shrubs and lichens were not used to estimate ADMD of these plant groups due to complications with the IVDMD estimates of these groups. These complications were discussed in detail by Person et al. (1980). Briefly, it was speculated that low IVDMD values compared to nylon-bag digestibilities (NBD) for shrubs and lichens may have resulted from the presence of chemical toxins and/or digestion inhibitors in both groups and from the limited nitrogen availability of lichens. In vitro estimates would likely be influenced by these factors to a larger extent than NBD or ADMD, since the in vitro analysis is a "closed system" as opposed to the "open flow" system of the nylon bags suspended in the rumen (Person et al. 1980).

Due to these complications, I have assumed that the NBD of shrubs reported by Person et al. are adequate estimates of the ADMD of shrubs. This assumption is tenuous. At present, correlations with NBD and ADMD vary considerably (Van Dyne and Weir 1964; Scales et al. 1974; Hall and Hennessy 1975). However, the two obvious shortcomings in assuming an equivalency between NBD and ADMD appear to counterbalance each other. For example, the actual retention time of summer forages in the rumen is between 8 and 12 hours (White and Trudell 1980), so the use of a 48-hour incubation period for the nylon bags would predict that NBD overestimates ADMD. In contrast, measurements of NBD do not include estimates of the dry matter digestion that occurs after the food leaves the rumen. Blaxter (1962) reported that 15 to 30 percent of total digestion occurs in parts of the intestinal tract posterior to the rumen.

The ADMD of lichens was assumed to be 70 percent in this paper. This value agrees well with the ADMD-value of 69 percent given by Syrjälä et al. (1980) using reindeer. Also, this figure agrees closely with values of 68 percent (McEwan and Whitehead 1970) and 67 percent (Wales et al. 1980) for the apparent digestible energy of lichens measured in vivo using reindeer and caribou. There is almost a 1:1 relationship between apparent digestible energy and ADMD of forages in ruminants, as discussed in the next section. An estimate of 70 percent ADMD for lichens also agrees closely with measurements by Jacobsen and Skjenneberg (1975) of a 75 percent apparent organic matter digestibility (AOMD), for a lichen diet (90 percent Cladonia alpestris) fed to 3 male reindeer calves in two trials. The AOMD of a ration is usually a few digestibility units higher than the ADMD, due to the influence of indigestible ash in lowering estimates of ADMD. In contrast to these values, Cameron (1972) found that the ADMD of lichens was about 55 percent. This low value may have resulted from the inclusion of relatively indigestible mosses in the forage samples (R. Cameron pers. comm.).

Estimation of Digestible Energy, Nitrogen (N), and Phosphorus (P) of Seasonal Diets

The term "digestible energy" in this study refers to apparent in vivo digestible energy. The relationship between digestible energy and ADMD has been investigated for several ruminants and has been found to be nearly a 1:1 relationship in all cases (Table 16). To predict digestible-energy values for the dietary components of the Denali caribou herd, I have used the relationship developed for white-tailed and mule deer (Robbins et al. 1975; Table 16).

Table 16. The relationship between apparent in vivo digestible energy (Y) and apparent in vivo digestible dry matter (X) in white-tailed and mule deer, cattle, and sheep.

Species	Number of Observations	Predictive Equation	R	Source
white-tailed and mule deer	45	$Y = -0.713 + 0.991X$	0.97	Robbins et al. (1975)
cattle	82	$Y = 0.54 + 1.02X$	0.969	Rittenhouse et al. (1971)
sheep	36	$Y = -2.013 + 1.006X$	0.998	Moir (1961)

An attempt was also made to estimate the seasonal changes in the true protein digestiblity of dietary components using data on the N content of the diets, feces, and neutral-detergent residue of the feces (NDRF), as proposed by Robbins et al. (1975) for white-tailed deer. This relationship failed to predict reasonable estimates of true protein digestibility because the N content of the NDRF averaged 2 to 5 times higher in caribou fecal samples than in white-tailed deer feces. Recent experiments by Robbins have found that this discrepancy often occurs when non-graminoid species occur in the diet and is associated with a complexing of proteins by phenolic compounds (R. White pers. comm.). The Palmer Research Center assured me that their analytical results on neutral-detergent extraction and N content were correct, but would not provide similar assurance that N in the NDRF represented N in indigestible plant material (G. Mitchell pers. comm.).

Since it was impossible to calculate true N digestibility of the diets using the above method, I estimated apparent N digestibility of the seasonal diets using estimates of the N content of the forage and feces (collected on a seasonal basis) together with seasonal estimates of the daily DMI and ADMD. The ADMD estimates of the diets together with estimates of DMI allowed calculation of daily fecal output. The proportions of N in the daily DMI and fecal output allowed estimation of the apparent N digestibility, through subtraction of the grams of N in the food from the grams of N in the feces. The apparent digestiblity of P was estimated using the same method.

Estimation of Daily Dry Matter Intake (DMI) Requirements

The DMI requirements described in this paper are simply the caribou's energy requirements expressed on a dry matter basis. Estimates of DMI were based on the species composition of the seasonal diets (Chapter 1), the metabolizable energy of dietary components, and the metabolizable energy requirements of the Denai caribou herd (Chapter 2). The metabolizable energy of the dietary components is directly related to the gross energy X the digestible energy (expressed as a percentage) of the dietary components. The average gross energy value of forages was computed for shrubs, forbs, graminoids, lichens, and berries from calorific values reported by West and Meng (1966), Pegau (1968), and Klein (1970b) in Alaska and Miller (1976) in Canada. The calorific value of mosses was averaged from several estimates made on alpine tundra species collected on Mt. Washington in New Hampshire (Bliss 1962). A gross energy value for mushrooms was calculated based on calorific values of the protein, fat, and carbohydrate in mushrooms (Watt and Merrill 1963) and the content of these constituents in mushrooms (Appendix F; Kelsall 1968). Ash content of mushrooms was assumed to be negligible (Appendix C). Metabolizable energy of dietary components was calculated as $(0.82 \times \text{gross energy } (\text{kJ} \cdot \text{gm}^{-1}) \times \frac{\text{percent digestible energy}}{100})$. This appears to be a very good average estimate with little variability, as witnessed from work on white-tailed deer (Mautz et al. 1974, 1976), eland and wildebeest (Rogerson 1968), and cattle and sheep (Agricultural

Research Council 1965; Blaxter et al. 1966; National Research Council 1971).

All estimates of DMI were made as illustrated in the following brief example, where metabolizable energy is expressed as ME. Assuming a winter diet of 70 percent lichens and 30 percent graminoids, the diet would contain 9.84 kJ ME • g^{-1} of dry matter, calculated as (0.70 x 10.41 kJ ME • g^{-1} of lichens) + (0.30 x 8.50 kJ ME • g^{-1} of graminoids). If they fed on this diet, adult female caribou in winter (November to mid-May) in Denali National Park would require 2.20 kg • day^{-1} (dry weight), calculated as 21.65 MJ of ME • day^{-1} required (Table 15) ÷ 9.84 kJ ME • g^{-1} dry matter. This value takes into consideration that caribou are burning fat to meet energy requirements in winter. Lichens contributed 1.63 kg • day^{-1} to the DMI, calculated as (ME intake of lichens) ÷ (total ME of diet) x (total DMI). Data for these calculations have been summarized on a seasonal basis in the following section. No allowance was made for the decrease in dietary metabolizable energy that could occur with increasing food intake in summer. Due to the high quality of the summer diets of caribou (i.e. high ME of diets), the influence of this relationship was considered insignificant (Agricultural Research Council 1965).

Results and Discussion

Digestibility and Fiber Content of Diets

The relationship between estimated ADMD and fiber content of the seasonal diets is illustrated in Figure 3 from values in Appendices C and D and Tables 17 to 20. The fiber components discussed here are structural carbohydrates making up the cell walls (neutral-detergent fiber), as opposed to soluble carbohydrates in the cell contents. Cell contents are considered 98 percent digestible, whereas the digestibility of the cell walls will depend on the proportions of particular structural carbohydrates, primarily lignin, cellulose, and hemicellulose (Goering and Van Soest 1970). In general, hemicelluloses are of greater value to ruminants than cellulose, and lignin is considered indigestible. Through fermentation hemicelluloses provide a major portion of the digestible carbohydrates in the ruminant diet (Maynard and Loosli 1956). The digestibility of cellulose depends on its state of lignification (e.g. the stage of plant maturity) (Sullivan 1962). I did not observe the intake of senescent vegetative tissue in summer or late spring, so this was not a factor in lowering the digestibility of spring and summer diets.

It is evident from Figure 3 that the proportion of lignin in the seasonal diets is nearly constant, varying only from about 4 to 6 percent throughout the year. Wallmo et al. (1977) estimated that the lignin content of the major forages of white-tailed deer in north-central Colorado varied from about 0 to 17 percent, but they did not give seasonal values weighted for diet composition. For the most

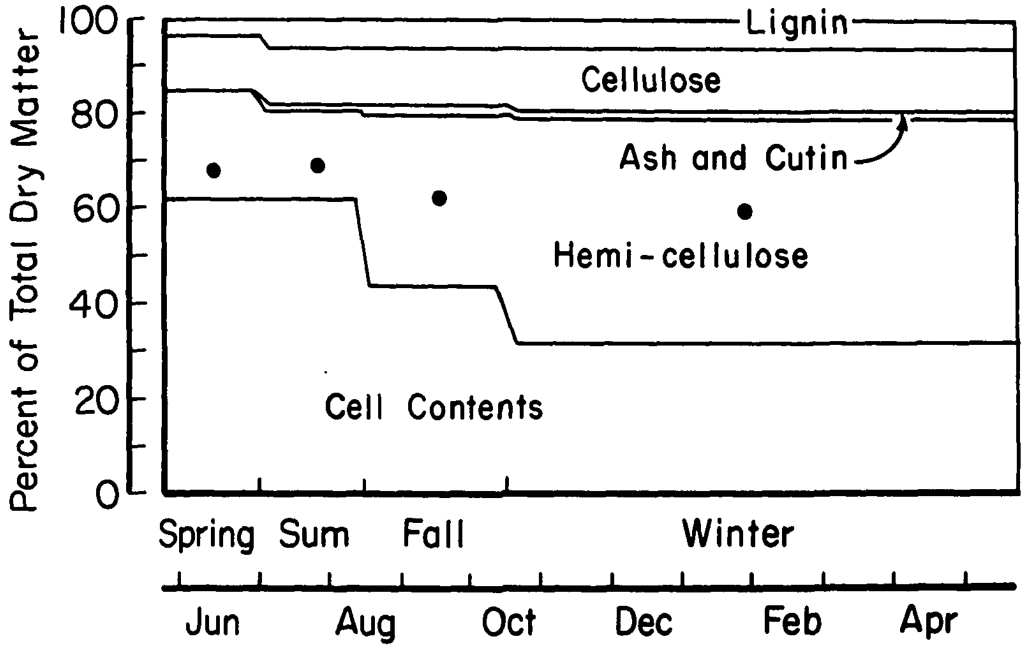

Figure 3. Structural fiber components and estimated apparent dry matter digestibility (•) of seasonal forages, weighted for diet composition (see Appendix C and Tables 17-20), Denali caribou herd, 1978-1979.

Table 17. Fiber content and estimated apparent dry matter digestibility (ADMD) of spring (mid-May to July) dietary components of the Denali caribou herd, 1978-1979. Values are summarized from Appendix E. Means[a] and standard deviations are given.

Spring Diet		Fiber (% dry wt)				
Plant Group	Intake % of Diet	Cell Walls	ADF[b]	Lignin	Cellulose	ADMD (% dry wt)
Berries	2	20.0 ± 11.5	14.6 ± 8.8	3.0 ± 1.1	11.5 ± 7.0	78 ± 8
Deciduous Shrubs	45	19.8 ± 1.8	15.4 ± 1.2	4.2 ± 0.4	11.2 ± 0.8	67 ± 2
Evergreen Shrubs	0					
Forbs	16	18.6 ± 8.1	15.5 ± 6.8	3.3 ± 1.3	11.5 ± 3.5	73 ± 6
Graminoids	12	62.6 ± 4.0	25.7 ± 1.9	3.1 ± 1.0	22.2 ± 1.1	65 ± 0
Lichens	25	72.9 ± 17.8	9.9 ± 4.1	2.9 ± 1.9	6.4 ± 2.5	70
Mosses	0					
Mushrooms	0					
Weighted means (n = 100)		38.0 ± 24.5	15.3 ± 4.5	3.6 ± 0.6	11.4 ± 4.5	69 ± 3

[a] Means are weighted in terms of the proportions of individual plant species within each plant group in spring diet (81 fiber analyses and 15 in vitro analyses are represented in the spring diet).

[b] ADF = acid-detergent fiber.

Table 18. Fiber content and estimated apparent dry matter digestibility (ADMD) of summer (July to mid-August) dietary components of the Denali caribou herd, 1978-1979. Values are summarized from Appendix E. Means[a] and standard deviations are given.

Summer Diet		Fiber (% dry wt)				
Plant Group	Intake % of Diet	Cell Walls	ADF[b]	Lignin	Cellulose	ADMD (% dry wt)
Berries	2	20.0 ± 11.5	14.6 ± 8.8	3.0 ± 1.1	11.5 ± 7.0	78 ± 8
Deciduous Shrubs	48	27.5 ± 0.3	21.6 ± 1.1	8.2 ± 0.5	13.4 ± 0.7	67 ± 2
Evergreen Shrubs	1	32.0 ± 4.2	23.9 ± 0.6	8.1 ± 1.5	15.4 ± 0.1	54
Forbs	10	25.9 ± 8.9	22.0 ± 7.9	4.6 ± 2.3	14.2 ± 3.8	69 ± 5
Graminoids	10	51.9 ± 4.1	22.3 ± 1.5	3.3 ± 1.8	18.2 ± 1.7	59 ± 8
Lichens	17	75.6 ± 16.2	10.4 ± 4.5	3.1 ± 2.1	6.3 ± 2.6	70
Mosses	0					
Mushrooms	12	31.7 ± 2.6	17.5 ± 3.4	5.0 ± 1.0	8.1 ± 0.8	90 ± 1
Weighted means (n = 100)		38.4 ± 18.5	19.2 ± 4.3	6.0 ± 2.3	12.1 ± 3.6	70 ± 8

[a] Means are weighted in terms of the proportions of individual plant species within each plant group in the summer diet (64 fiber analyses and 25 in vitro analyses are represented in the summer diet).

[b] ADF = acid-detergent fiber.

Table 19. Fiber content and estimated apparent dry matter digestibility (ADMD) of autumn (mid-August to mid-October) dietary components of the Denali caribou herd, 1978-1979. Values are summarized from Appendix E. Means[a] and standard deviations are given.

Autumn Diet		Fiber (% dry wt)				
Plant Group	Intake % of Diet	Cell Walls	ADF[b]	Lignin	Cellulose	ADMD (% dry wt)
Berries	3	20.0 ± 11.5	14.6 ± 8.8	3.0 ± 1.1	11.5 ± 7.0	78 ± 3
Deciduous Shrubs	14	27.3 ± 0.1	21.7 ± 2.1	8.3 ± 1.1	13.3 ± 1.1	66 ± 4
Evergreen Shrubs	2	41.4 ± 9.7	34.7 ± 10.5	12.2 ± 6.6	21.6 ± 4.5	59 ± 7
Forbs	9	29.6 ± 12.7	26.4 ± 13.3	6.3 ± 3.2	17.7 ± 6.8	43 ± 5
Graminoids	14	65.5 ± 5.4	34.3 ± 2.5	5.3 ± 1.4	27.1 ± 2.0	47 ± 7
Lichens	43	73.3 ± 17.5	10.3 ± 4.3	3.0 ± 1.9	6.4 ± 2.5	70
Mosses	5	78.9 ± 7.2	50.4 ± 4.4	21.6 ± 4.8	25.0 ± 4.2	7 ± 6
Mushrooms	10	31.5 ± 2.6	17.7 ± 3.4	5.1 ± 1.0	8.1 ± 0.8	90 ± 1
Weighted means (n = 100)		55.7 ± 21.3	20.1 ± 11.2	5.7 ± 4.2	12.8 ± 7.8	63 ± 8

[a] Means are weighted in terms of the proportions of individual plant species within each plant group in autumn diet (60 fiber analyses and 28 in vitro analyses are represented in the spring diet).

[b] ADF = acid-detergent fiber.

Table 20. Fiber content and estimated apparent dry matter digestibility (ADMD) of winter (mid-October to mid-May) dietary components of the Denali caribou herd, 1978-1979. Values are summarized from Appendix E. Means[a] and standard deviations are given.

Winter Diet		Fiber (% dry wt)				
Plant Group	Intake (% of diet)	Cell Walls	ADF[b]	Lignin	Cellulose	ADMD (% dry wt)
Berries	0					
Deciduous shrubs	1	36.0 ± 2.1	33.4 ± 1.4	12.3 ± 1.6	20.8 ± 4.6	60
Evergreen shrubs	7	36.5 ± 5.2	29.3 ± 5.6	8.8 ± 3.6	19.3 ± 2.4	64
Forbs	7	46.7 ± 1.5	40.8 ± 7.1	8.7 ± 2.7	24.7 ± 2.8	46 ± 0
Graminoids	11	71.1 ± 3.4	38.5 ± 1.2	5.9 ± 1.3	30.7 ± 0.6	54 ± 0
Lichens	62	73.4 ±17.2	10.4 ± 4.3	3.0 ± 1.9	6.4 ± 2.5	70
Mosses	10	78.9 ± 7.2	50.4 ± 4.4	21.6 ± 4.8	25.0 ± 4.2	7 ± 6
Mushrooms	2	29.9 ± 3.4	19.8 ± 7.2	5.7 ± 3.9	7.6 ± 2.0	91 ± 2
Weighted mean (n=100)		68.0 ±13.2	21.4 ±15.0	6.1 ± 5.6	13.3 ± 9.6	60 ± 20

[a] Means are weighted in terms of the proportions of individual plant species within each plant group in the winter diet (44 fiber analyses and 11 in vitro analyses are represented in the winter diet).

[b] ADF = acid-detergent fiber

part, only evergreen shrubs and mosses in the caribou's diet had lignin contents comparable to values in white-tailed deer forages (Tables 17 to 20). Cellulose values were also much lower in the caribou seasonal diets (11 to 13 percent) than in white-tailed deer forages (16 to 37 percent). Evergreen shrubs, mosses, graminoids, and *Equisetum* spp. in the caribou's annual diet have cellulose contents comparable to those in white-tailed deer forages, but these plant groups contribute most signficantly to the caribou's diet in autumn and winter, when lichens are the primary forage. Lichens have notably low proportions of lignin (3 percent) and cellulose (6 percent) which accounts for the low proportions of these components in the caribou's autumn and winter diets. Also, the low proportions of lignin and cellulose in lichens likely contributes significantly to the high digestibilities of the autumn and winter diets. Hemicellulose values of caribou diets (19 to 47 percent) on a year-round basis were extremely high compared to white-tailed deer forages (0 to 13 percent). This difference is due almost exclusively to the extremely high proportion of hemicellulose or hemicellulose-like compounds in lichens (63 percent) (see Table 4 for seasonal diets). This high proportion of hemicellulose also contributes significantly to the high estimated digestibilities of the caribou's seasonal diets (60 to 70 percent), particularly in autumn and winter when lichens dominate the diet. It should also be recognized that *Cetraria cucullata* has a high proportion of soluble carbohydrates (cell contents) (Appendix C) which also likely contributes to the high digestibility of the lichen component of the diets.

The relative constancy in the estimated digestibilities between seasons appears to be due primarily to the high proportion of cell contents of forbs and deciduous shrubs (leaves only) in the spring and summer diets and the high hemicellulose values of lichens in winter. A combination of these factors act to influence the digestibility in autumn. The relative constancy of undisturbed rest periods throughout the year (Chapter 2) also predicts that the digestibility of diets of the Denali caribou herd is relatively constant between seasons.

It appears that one can predict the digestibilities of the diets quite well by assuming lignin to be indigestible, cellulose to have a very low digestibility (less than 10 percent), hemicellulose to have a digestibility of 30 to 50 percent, and the cell contents to be 100 percent digestible. Data, however, should be obtained on apparent in vivo digestibilities of these diets to confirm these relationships.

The role of plant secondary metabolites (toxins and/or digestion inhibitors) in affecting the in vivo digestibility of natural caribou diets also needs to be evaluated in combination with data on fiber analyses. The high diversity of food items in spring and summer caribou diets is likely related to the avoidance of potential ill-effects of secondary compounds. For instance, Kuropat and Bryant (1980) suggest that caribou optimize the intake ratio of nutrients: secondary metabolites in their summer foraging strategies. The influence that plant secondary metabolites have on caribou population declines, however, is likely of minimal importance. For instance, one may surmise that secondary metabolites would have increasingly more significance as a regulatory factor in caribou population ecology when forage diversity was reduced. This might occur when vegetation transitions resulted from overgrazing, and caribou/reindeer were restricted to consuming largely evergreen shrubs, which are high in plant secondary metabolites (Rhodes and Cates 1976). However, vegetation transitions resulting from overgrazing by caribou/reindeer have only been documented on St. Matthew Island (Klein 1968), in southern Norway (Gaare et al. 1975), and in West Greenland (H. Thing pers. comm.), all in instances where predators were absent or very scarce and where animals either could not or did not expand or abandon their traditional range areas. In each of these cases, lichens have been observed to be replaced by monocots, mosses, and shrubs. Reimers (1980) has suggested that if caribou/reindeer survive the change from a lichen-based winter diet, as suggested in the case of Svalbard reindeer, the animals are faced with a more stable vegetation complex which is less subjected to overgrazing. In regard to the ecology of plant secondary compounds as chemical defenses against herbivores (Chapin 1980; Kuropat and Bryant 1980), I believe it is important to stress the defensive strategies that plants also must exert in relation to competing plants (e.g. in regard to vegetation transitional changes that occur with overgrazing). However, this subject is largely extraneous to the results of this study.

The effect of forage digestibility on the total caribou-range relationship is likely most critical on winter ranges where highly digestible fruticose lichens are largely lacking. However, this situation demands clarification because reindeer/caribou have adapted to the extreme scarcity of lichens in certain areas. For example, on Svalbard mosses and graminoids have largely replaced lichens in the reindeer's diet (Punsvik et al. 1980). Apparently, Svalbard reindeer have adapted to the low quantity of lichens on their ranges, in part, by evolving a greater efficiency for the digestion of mosses (Trudell et al. 1980), increasing intake of high quality vascular plant forage in summer, and decreasing energy expenditure, particularly during winter (Reimers 1980). These factors allow large quantities of fat to be stored which makes the animals less dependent upon winter grazing conditions. Reimers (1980) concluded that caribou/ reindeer unable to accumulate large quantities of fat (e.g. animals disturbed frequently by insects, predators, or humans) will suffer when lichens become overgrazed. The susceptibility of lichens to overgrazing is well known. Reimers also summarized evidence indicating that caribou/ reindeer are very likely not limited by either qualitative or quantitative characteristics (including digestibility) of summer forage. Instead he stressed that factors affecting the time spent on foraging activities were most important in influencing relative nutritional status of reindeer/caribou by autumn. Of course, qualitative and quantitative summer range characteristics can vary considerably.

In conclusion, it appears that by changing their diets seasonally, the Denali caribou maintain a nearly constant dry matter digestibility throughout the year, despite chemical and structural changes in plants.

Therefore, controls over energy expenditure (Chapter 2) and time spent in non-foraging activities (not range quality) are the main determinants of annual energy balance. This relationship, however, may change if lichens are extremely scarce on the wintering range.

Dry Matter Intake (DMI) Requirements

Seasonal estimates of DMI (Figure 4; Tables 21 to 24) were calculated as metabolizable energy requirements (Table 15) divided by the metabolizable energy of the diet. As such, estimates of DMI can be regarded as energy requirements expressed on a dry matter basis. Obviously, then, these estimates assume that range productivity was not limiting food intake. This assumption is likely valid but clarification is needed. First, it should be understood that winter range conditions, and primarily lichens, are most susceptible to overgrazing and that lichen availability in winter is often considered the limiting factor in the carrying capacity of reindeer/caribou ranges (Baskin 1970). Secondly, the present density of the Denali herd on the wintering range (0.4 caribou • km^{-2}) is very likely less than 10 percent of the winter range's carrying capacity (about 5 caribou • km^{-2}).

This estimate of carrying capacity assumes that 20 hectares of winter range are needed per caribou per winter, in contrast to estimates of 8 to 10 hectares of lichen range required per caribou per winter as calculated by Davis et al. (1978) in interior Alaska, Poijarvi (1945) and Andreev (1954) in the Soviet Union, Skunke (1963) in Sweden, and Helle (1966) in Finland. Davis et al. (1978) calculated their estimates based on measurements in the literature of the annual production of lichens. Lichen biomass levels in interior Alaska were also taken from the literature, and caribou were assumed to be eating

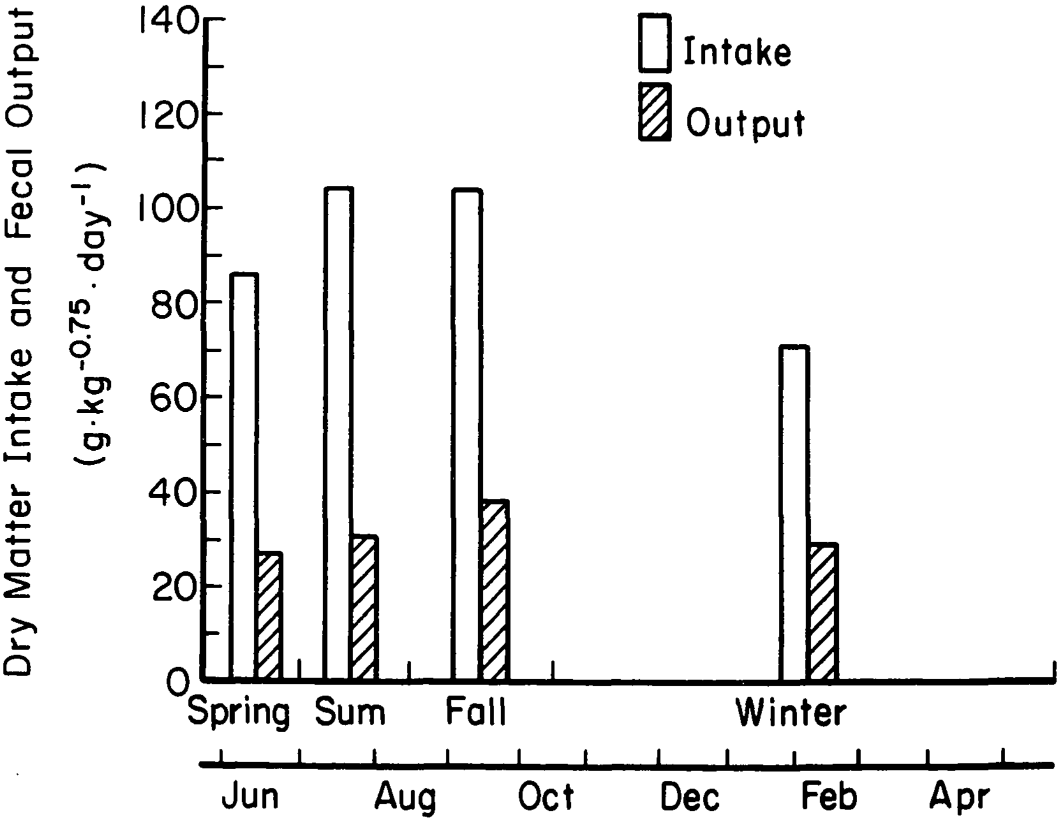

Figure 4. Seasonal estimates of the daily dry matter intake and fecal output of adult female caribou of the Denali caribou herd, 1978-1979. Fecal output was approximated from estimates of dry matter intake and ADMD of seasonal diets (see Methods).

Table 21. Estimates of the energy value ($kJ \cdot g^{-1}$) of spring (May 22 to June 30) dietary components and estimated dry matter intake (DMI) of adult female caribou, Denali caribou herd, 1978-1979. Spring metabolizable energy requirements were estimated to be 29.28 $MJ \cdot day^{-1}$ (Table 15) and a body weight of 100 kg was assumed. See Methods for explanations.

Dietary Component	% of Diet	Gross Energy (GE) ($kJ \cdot g^{-1}$)	(n)	Digestible Energy (DE) (% DE x GE) ($kJ \cdot g^{-1}$)	Metabolizable Energy (ME) (0.82 x DE) ($kJ \cdot g^{-1}$)	DMI[a] ($kg \cdot day^{-1}$)
Berries	2	19.30	(12)	14.78	12.12	0.06
Deciduous shrubs	45	20.05	(21)	13.17	10.80	1.23
Forbs	16	19.38	(9)	13.88	11.38	0.46
Graminoids	12	19.64	(17)	12.51	10.26	0.31
Lichens	25	18.49	(29)	12.70	10.41	0.66
Total Diet		19.49 ± 0.63[b]		13.12 ± 0.49[b]	10.76 ± 0.40[b]	2.72

[a] Total DMI = (energy requirement) · (ME of diet)$^{-1}$

[b] Values are weighted for diet composition (n=100). Means and standard deviations are given.

Table 22. Estimates of the energy value (kJ · g^{-1}) of summer (July 1 to August 15) dietary components and estimated dry matter intake (DMI) of adult female caribou, Denali caribou herd, 1978-1979. Summer energy requirements were estimated to be 37.66 MJ · day^{-1} (Table 15) and a body weight of 105 kg was assumed. See Methods for explanations.

Dietary Component	% of Diet	Gross Energy (GE) (kJ · g^{-1})	(n)	Apparent Digestible Energy (DE) (% DE x GE) (kJ · g^{-1})	Metabolizable Energy (ME) (0.82 x DE) (kJ · g^{-1})	DMI[a] (kg · day^{-1}
Berries	2	19.30	(12)	14.78	12.12	0.08
Deciduous shrubs	48	20.05	(21)	13.17	10.80	1.61
Evergreen shrubs	1	20.64	(13)	11.02	9.04	0.03
Forbs	10	19.38	(9)	13.12	10.76	0.33
Graminoids	10	19.64	(17)	11.35	9.31	0.29
Lichens	17	18.49	(29)	12.70	10.41	0.55
Mushrooms	12	19.76	(1)	17.49	14.34	0.53
Total diet		19.63 ± 0.57[b]		13.43 ± 1.63[b]	11.01 ± 1.34[b]	3.42

[a] Total DMI = (energy requirement) · (ME of diet)$^{-1}$

[b] Values are weighted for diet composition (n=100). Means and standard deviations are given.

Table 23. Estimates of the energy value ($kJ \cdot g^{-1}$) of autumn (August 16 to October 15) dietary components and estimated dry matter intake (DMI) of adult female caribou, Denali caribou herd, 1978-1979. Autumn metabolizable energy requirements were estimated to be 34.11 $MJ \cdot day^{-1}$ (Table 15) and a body weight of 110 kg was assumed. See Methods for explanation.

Dietary Component	% of Diet	Gross Energy (GE) ($kJ \cdot g^{-1}$)	(n)	Digestible Energy (DE) (%DE x GE) ($kJ \cdot g^{-1}$)	Metabolizable Energy (ME) (0.82 x DE) ($kJ \cdot g^{-1}$)	DMI[a] ($kg \cdot day^{-1}$)
Berries	3	19.30	(12)	14.78	12.12	0.13
Deciduous shrubs	14	20.05	(21)	12.97	10.64	0.55
Evergreen shrubs	2	20.64	(13)	11.93	9.78	0.07
Forbs	9	19.38	(9)	8.12	6.66	0.22
Graminoids	14	19.64	(17)	9.01	7.39	0.38
Lichens	43	18.49	(29)	12.70	10.41	1.64
Mosses	5	18.45	(7)	1.14	0.94	0.02
Mushrooms	10	19.76	(1)	17.49	14.34	0.53
Total diet		19.14 ± 0.67[b]		11.76 ± 3.49[b]	9.64 ± 2.86[b]	3.54

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[a] Total DMI = (energy requirement) · (ME of diet)$^{-1}$

[b] Values are weighted for diet composition (n=100). Means and standard deviations are given.

Table 24. Estimates of the energy value (kJ · g^{-1}) of winter (October 16 to May 21) dietary components and estimated dry matter intake (DMI) of adult female caribou, Denali caribou herd, 1978-1979. Winter metabolizable energy requirements were estimated to be 22.40 MJ · day^{-1} (Table 15) and a body weight of 107 kg was assumed. See Methods for explanations

Dietary Component	% of Diet	Gross Energy (GE) (kJ · g^{-1})	(n)	Digestible Energy (DE) (%DE x GE) (kJ · g^{-1})	Metabolizable Energy (ME) (0.82 x DE) (kJ · g^{-1})	DMI[a] (kg · day^{-1})
Deciduous shrubs	1	20.05	(21)	11.83	9.69	0.03
Evergreen shrubs	7	20.64	(13)	12.94	10.61	0.20
Forbs	7	19.38	(9)	8.70	7.13	0.13
Graminoids	11	19.64	(17)	10.37	8.50	0.25
Lichens	62	18.49	(29)	12.70	10.41	1.74
Mosses	10	18.45	(7)	1.14	0.93	0.03
Mushrooms	2	19.76	(1)	17.69	14.51	0.08
Total Diet		18.87 ± 0.67[b]		11.10 ± 3.66[b]	9.10 ± 3.00[b]	2.46

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[a] Total DMI = (energy requirement) · (ME of diet)$^{-1}$

[b] Values are weighted for diet composition (n=100). Means and standard deviations are given.

100 percent lichens. Calculations made in the Soviet Union and Sweden were based on reindeer ranges with known long-term stocking levels, and Helle (1966) in Finland considered the effects of snow on the availability and utilization of forage. I assumed that 20 hectares, rather than 10 hectares, of winter range were needed per caribou because lichens are rather scarce on portions of the winter range (though caribou winter diets still consisted largely of lichens (Chapter 1)).

I suggest that my estimate of carrying capacity on the winter range (5 caribou • km^{-2}) is very conservative, and that the herd never reached even 50 percent of this carrying capacity during the herd's peak estimated density in the late 1930's (about 2.3 caribou • km^{-2} on the former winter range). It is also relevant that, at present, essentially all caribou populations in North America are at densities of 0.4 to 0.8 caribou • km^{-2} or less (Bergerud 1980). Densities on the winter ranges are undoubtedly slightly higher, but probably do not reach even 50 percent of my estimate of the carrying capacity of the Denali herd's wintering range. Thus I suggest that range productivity is likely not presently limiting caribou populations (Miller 1976; Davis et al. 1978). The small range in densities of caribou populations results, in part, because an expansion of range area occurs with increases in population numbers (Skoog 1968).

Although densities are quite similar between North American caribou populations, it is likely that these populations experience vastly different degrees of energetic stress. These differences in energetic stress presumably result primarily from differences in factors controlling energy expenditure and time spent in non-foraging activities rather than differences in range quality (see previous section) or range productivity. This relationship may be different if lichen stands are extremely scarce on the winter range. Nutritional-based carrying capacities (Moen 1973; Wallmo et al. 1977), as opposed to conventional range or food carrying capacities, take into account the factors influencing energy balance and/or protein balance, and therefore should be used in comparing the relative value of caribou/reindeer ranges.

A vivid example of the relative importance of assessing nutritional-based carrying capacities versus conventional food carrying capacities occurred on the northern portion of the Baldwin Peninsula in Alaska during mid-July of 1980 in relation to a fenced reindeer population. Several reindeer starved to death during this period and all animals were in extremely poor condition. Starvation resulted from a dramatic increase in energy expenditure and time spent in non-foraging activities which occurred primarily as a result of prior herding of the animals and high levels of insect harassment (R. Dieterich pers. comm.). Less than 5 percent marrow fat occurred in the starved animals. Overgrazing was not observed. Body condition should have begun to increase by this time of the year, but the high levels of harassment undoubtedly prevented an increase in nutritional status. This exemplifies the importance of energy expenditure and harassment in assessing the sometimes critical nutritional balance of reindeer/caribou populations. Estimation of caribou/reindeer forage requirements based on energy requirements and forage quality allows a more comprehensive assessment of the role that nutrition plays in caribou population ecology, in contrast to conventional estimates of range carrying capacities.

White (1979) summarized the extrinsic and intrinsic factors which control food intake of reindeer/caribou. Extrinsic factors limiting food intake include food availability, food digestibility, and the proportion of time spent in non-foraging activities, which is dependent on time spent reacting to harassment and time spent in social activities. Intrinsic factors regulating intake include a searching for specific minerals and a drive to maintain energy balance and maximize growth rate. Theoretically, by combining data on activity budgets, energy requirements, and food digestibility, my estimates of intake rates take into account all of the above extrinsic and intrinsic factors, except food availability. Since range productivity is likely not limiting food intake, as discussed above, then food availability would likely only limit food intake when forage is protected by snow or by dead plant material. It is unlikely that snow conditions pose a problem in limiting food intake in the Denali herd in most years, due to the wind-swept condition of the wintering areas as discussed in Chapter 2.

In consideration of these factors, my method of estimating intake rates should be quite reliable. However, definition of an upper limit to intake rates is needed. For instance, if caribou are feeding through deep snow (high energy requirements) on a non-lichen winter diet (low digestibility), my prediction of required intake rates would likely exceed the intake capabilities of the ruminant, particularly in respect to the slow rate of passage of low digestible forage. Ammann et al. (1972) found that rumen fill limited intake in white-tailed deer when the apparent digestible energy of a basal ration (diluted with increasing proportions of sawdust) decreased below about 9.1 kJ • g^{-1}. None of the estimates of apparent digestible energy of seasonal diets in this study fell below 11.1 kJ • g^{-1} (Tables 21 to 24). As such, I doubt that intake was limited by low digestibility of the diets. However, this may occur in areas where lichens are scarce and in animals that presumably have not adapted to non-lichen diets, e.g. caribou that occasionally or regularly spend the winter on Alaska's Arctic Slope.

The estimated intake rates of the adult female caribou of the Denali herd appear to be very reasonable approximations. For instance, using esophageal-fistulated reindeer, White and Trudell (1980) estimated that maximum DMI of summer forage was 99 to 137 g • $kg^{-0.75}$ • day^{-1}, when the reindeer were grazing high-center polygons and lake margins on Alaska's arctic coastal plain. My estimates of DMI during the period of green growth (86 to 104 g • $kg^{-0.75}$ • day^{-1}) (Figure 4) do not exceed those of White and Trudell (1980). Apparently, caribou/reindeer can increase intake dramatically if they do not undergo long movements and are undisturbed throughout the summer, as in Svalbard (Reimers 1980). The result, of course, is the storage of large quantities of fat during a very short time period. Calculated winter intake requirements of caribou of the Denali herd (2.46 kg • day^{-1}) are also very reasonable in comparison with intake rates given by Holleman et al. (1979) (2.89 kg • day^{-1}) using esophageal-fistulated reindeer grazing primarily lichens. My estimates of food requirements in winter take into account that fat deposits are being utilized and that winter maintenance metabolic requirements are much lower than in summer. High intake rates therefore are not required unless digestibility is low or energy requirements are extremely high. The added costs of cratering through deep snow throughout the early to late winter periods (Tables 14 and 15) would increase intake requirements to about 2.56 kg • day^{-1}. It is noteworthy that intake values, without cratering costs, predict a 31 percent reduction in caloric intake from summer to winter, whereas Steen (1968) reported comparable values of 30 to 35 percent for adult semi-domestic reindeer.

Dietary Nutrients and Nutrient Balance

Seasonal changes in nutrient content of the diets of adult female caribou of the Denali herd are presented in Figure 5 and Tables 25 to 28 from data in Appendices E and F. Concentrations of N, P, and K in the diet decreased during the growing season, although concentrations of N, P, and K in mushrooms in autumn were very high. The proportions of Ca and TNC in the diet increased during the growing season and declined in the autumn and winter, whereas concentrations of Na remained relatively constant throughout the year. Dietary concentrations of Mg were nearly constant during the growing season and declined thereafter. These trends were similar to those described by Chapin et al. (1980) and Whitten and Cameron (1980) for vascular plant species analyzed from spring to autumn on Alaska's Arctic Slope. It should be noted that very few forage samples were analyzed for K and Mg, and these forage samples represented only a small proportion of the total diet composition (Tables 25 to 28; Appendix E).

Several authors have documented the qualitative dietary characteristics of caribou/reindeer. Most of these studies have involved analysis of forage samples for nutrients and/or fiber constituents. The results of several of these studies are summarized by Bergerud (1977) and Luick (1977). The nutrient quality of esophageal-fistula contents (Skjenneberg et al. 1975) and rumen contents (Klein 1962; Reimers 1980) has also been measured in an attempt to estimate the qualitative dietary characteristics of free-ranging

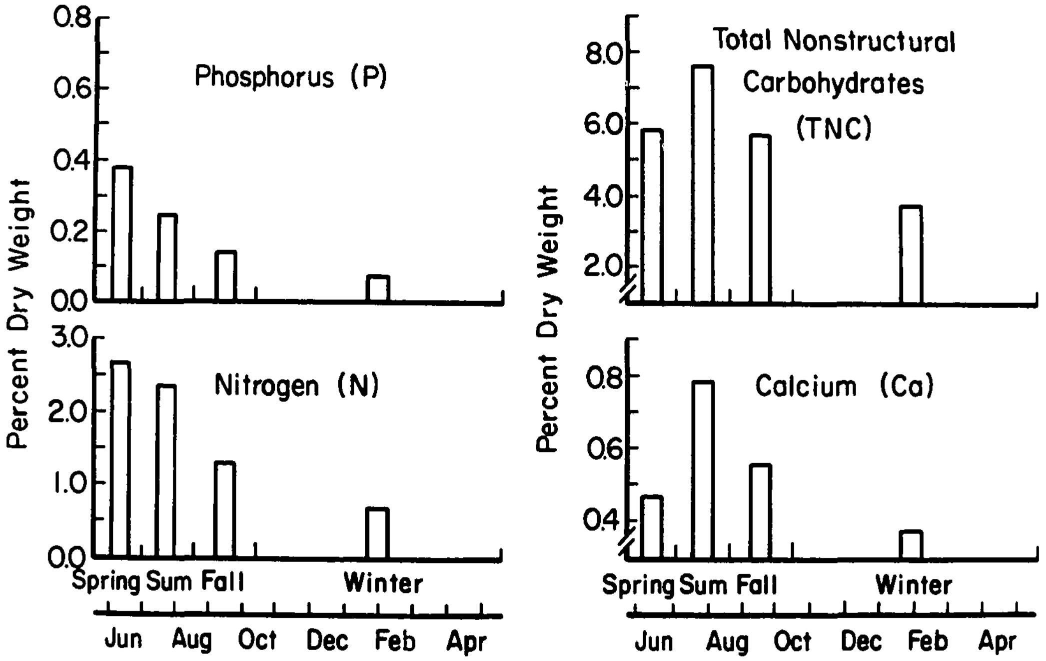

Figure 5. Seasonal variation in the nutrient content of caribou forages, weighted for diet composition (see Tables 25-28 and Appendix F), Denali caribou herd, 1978-1979.

Table 25. Nutrient content of spring (mid-May to July) dietary components of the Denali caribou herd, 1978-1979. Values are summarized from Appendix F. Means[a] and standard deviations are given.

Spring Diet		Nutrients (% dry wt)						
Dietary Component	Intake (% of diet)	N	P	K	Ca	Mg	Na	TNC
Berries	2	0.60 ± 0.15	0.11 ± 0.03	0.54	0.04 ± 0.02	0.06	0.08	29.4 ± 9.8
Deciduous shrubs	45	3.69 ± 0.25	0.54 ± 0.05	1.20 ± 0	0.65 ± 0.08	0.16 ± 0	0.11 ± 0.03	6.1 ± 1.2
Evergreen shrubs	0							
Forbs	16	3.77 ± 0.89	0.55 ± 0.16	2.99 ± 0.43	0.70 ± 0.27	0.18 ± 0.02	0.11 ± 0.05	5.8 ± 3.1
Graminoids	12	2.73 ± 0.54	0.30 ± 0.02	1.42 ± 0.28	0.25 ± 0.12	0.14 ± 0.01	0.15 ± 0.04	8.6 ± 1.5
Lichens	25	0.40 ± 0.35	0.04 ± 0.02	0.16 ± 0	0.15 ± 0	0.04 ± 0	0.04 ± 0.04	2.3 ± 3.9
Mosses	0							
Mushrooms	0							
Weighted mean (n=100)		2.70 ± 1.43	0.38 ± 0.22	1.24 ± 0.90	0.47 ± 0.24	0.13 ± 0.05	0.10 ± 0.04	5.9 ± 2.4
No. of forage samples represented		81	81	9	53	9	37	77

[a] Figures are weighted in terms of the proportions of plant species in the spring diet.

Table 26. Nutrient content of summer (July to mid-August) dietary components of the Denali caribou herd, 1978-1979. Values are summarized from Appendix F. Means[a] and standard deviations are given.

Summer Diet		Nutrients (% dry wt)						
Dietary Component	Intake (% of diet)	N	P	K	Ca	Mg	Na	TNC
Berries	2	0.60 ± 0.15	0.11 ± 0.03	0.54	0.04 ± 0.02	0.06	0.08	29.4 ± 9.8
Deciduous shrubs	48	2.43 ± 0.09	0.22 ± 0.01		1.26 ± 0		0.09 ± 0.02	6.5 ± 0.8
Evergreen shrubs	1	1.50	0.17		0.08		0.12	10.2
Forbs	10	2.15 ± 0.38	0.29 ± 0.11		0.94 ± 0.28		0.08 ± 0.03	9.4 ± 3.4
Graminoids	10	2.31 ± 0.22	0.17 ± 0.01		0.56 ± 0.17			17.4 ± 2.0
Lichens	17	0.43 ± 0.40	0.04 ± 0.02	0.16	0.15	0.04	0.04 ± 0.04	1.8 ± 3.5
Mosses	0							
Mushrooms	12	5.55 ± 1.26	0.70 ± 0.13	2.59 ± 0.20	0.03 ± 0.01	0.08 ± 0.01	0.11 ± 0.01	6.4 ± 0.5
Weighted mean (n=100)		2.38 ± 1.40	0.25 ± 0.18	1.13 ± 1.19[b]	0.79 ± 0.52	0.06 ± 0.02[b]	0.08 ± 0.02[c]	7.6 ± 5.1
No. of forage samples represented		64	64	8	28	8	44	60

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[a] Figures are weighted in terms of the proportions of plant species in the summer diet.

[b] Only 31% of the diet is represented in this figure.

[c] Only 90% of the diet is represented in this figure.

Table 27. Nutrient content of autumn (mid-August to mid-October) dietary components of the Denali caribou herd, 1978-1979. Values are summarized from Appendix F. Means[a] and standard deviations are given.

Autumn Diet		Nutrients (% dry wt)						
Dietary Component	Intake (% of diet)	N	P	K	Ca	Mg	Na	TNC
Berries	3	0.60 ± 0.15	0.11 ± 0.03	0.54	0.04 ± 0.02	0.06	0.08	29.4 ± 9.8
Deciduous shrubs	14	1.59 ± 0.02	0.14 ± 0.07		1.43 ± 0		0.08 ± 0.01	7.7 ± 1.2
Evergreen shrubs	2	0.96 ± 0.37	0.14 ± 0.06		1.39		0.47	10.0 ± 9.1
Forbs	9	1.48 ± 0.52	0.13 ± 0.03	0.53 ± 0.38	1.95 ± 0.97	0.18 ± 0.04	0.02 ± 0.02	5.6 ± 3.1
Graminoids	14	1.25 ± 0.22	0.10 ± 0.02	0.58 ± 0.06	0.49 ± 0.10	0.13 ± 0.01	0.03 ± 0.01	9.1 ± 2.3
Lichens	43	0.41 ± 0.37	0.04 ± 0.02	0.16	0.15	0.04	0.04 ± 0.04	2.2 ± 3.7
Mosses	5	0.85 ± 0.33	0.12 ± 0.04	0.36	0.33 ± 0.12	0.20	0.01 ± 0	3.5 ± 2.4
Mushrooms	10	5.64 ± 1.23	0.71 ± 0.13	2.58 ± 0.19	0.03 ± 0.01	0.08 ± 0.01	0.11 ± 0.01	6.4 ± 0.5
Weighted mean (n=100)		1.35 ± 1.51	0.15 ± 0.19	0.58 ± 0.76[b]	0.56 ± 0.64	0.09 ± 0.06[b]	0.06 ± 0.07	5.7 ± 5.0
No. of forage samples represented		61	61	14	23	14	40	57

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[a] Figures are weighted in terms of the proportions of plant species in the autumn diet.

[b] Only 84% of the diet is represented in this figure.

Table 28. Nutrient content of winter (mid-October to mid-May) dietary components of the Denali caribou herd, 1978-1979. Values are summarized from Appendix F. Means[a] and standard deviations are given.

Winter Diet		Nutrients (% dry wt)						
Dietary Component	Intake (% of diet)	N	P	K	Ca	Mg	Na	TNC
Berries	0							
Deciduous shrubs	1	0.99 ± 0.32	0.09 ± 0.01		0.94		0.01	2.5 ± 3.3
Evergreen shrubs	7	1.15 ± 0.20	0.17 ± 0.03		1.39		0.47	14.6 ± 4.8
Forbs	7	1.07 ± 0.31	0.12 ± 0.02	0.61 ± 0.27	1.43 ± 0.79	0.27 ± 0.06	0.04 ± 0.02	5.9 ± 4.6
Graminoids	11	0.72 ± 0.07	0.07 ± 0.01	0.59 ± 0.07	0.36 ± 0.05	0.13 ± 0.01	0.03 ± 0.01	4.8 ± 0.5
Lichens	62	0.42 ± 0.37	0.04 ± 0.02	0.16	0.15	0.04	0.04	2.2
Mosses	10	0.85 ± 0.33	0.12 ± 0.04	0.36	0.33	0.20	0.01	3.5
Mushrooms	2	6.40 ± 1.23	0.79 ± 0.06	2.46	0.03	0.08	0.11	6.7
Weighted mean (n=100)		0.71 ± 0.86	0.08 ± 0.11	0.32 ± 0.37[b]	0.37 ± 0.43	0.09 ± 0.08[b]	0.07 ± 0.11	3.8 ± 3.2
No. of forage samples represented		33	33	9	19	9	23	32

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[a] Figures are weighted in terms of the proportions of plant species in the diet.

[b] Only 92% of the diet is represented in this figure.

reindeer. I have combined data on the qualitative characteristics of the seasonal diets with the estimates of intake rates. This has allowed estimation of daily nutrient intake rates which are compared with the approximate daily nutrient requirements of caribou (from estimates in the literature).

Nitrogen (N)

It is particularly important to discuss seasonal N requirements of free-ranging caribou because deficiencies of N and energy are most often implicated in limiting productivity and growth of ruminants. Both N and energy requiremnts have been considered at length in discussions of the nutritional carrying capacity of white-tailed deer range (Moen 1973; Robbins 1973).

The best estimates of the N requirements of caribou and reindeer have been made by McEwan and Whitehead (1970) on young animals during the first 2 years of growth, reared on a high plane of nutrition. The estimated amount of digestible N required for N equilibrium in these animals was 0.46 g N • $kg^{-0.75}$ • day^{-1}. This value can be compared with my estimates of digestible N intake of 1.57, 1.68, 0.63, and -0.01 g • $kg^{-0.75}$ • day^{-1} for the spring, summer, autumn, and winter caribou diets, respectively, calculated by difference from values in Figure 6. Thus adult female caribou on the Denali herd's range appear to be capable of storing N from late May to mid-October (about 4.5 months), since digestible N intake exceeds requirements. During winter (about 7.5 months) the caribou are unable to meet N

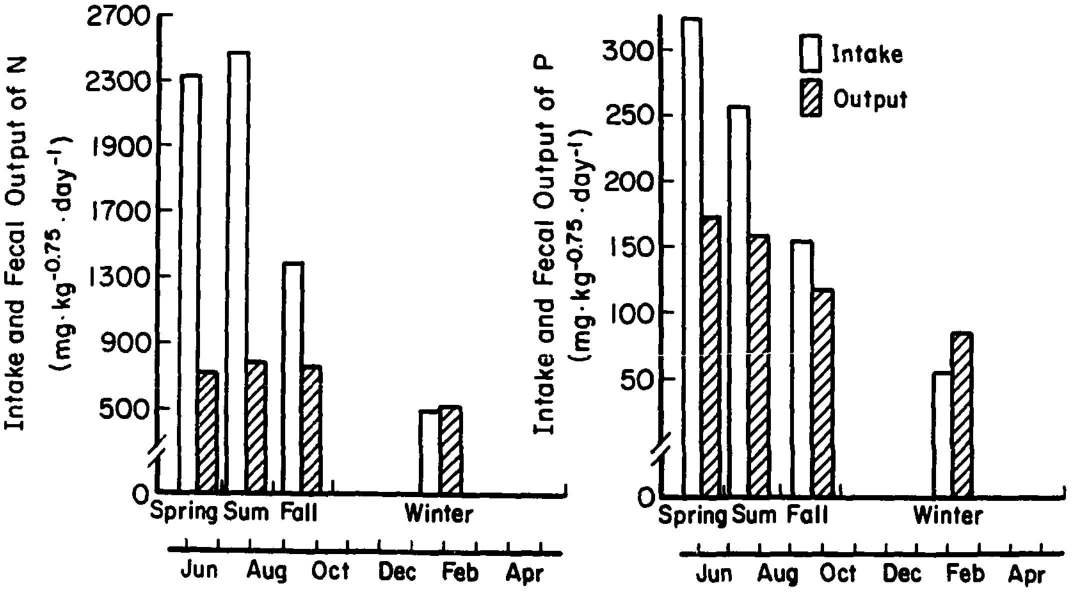

Figure 6. Seasonal variation in estimated intake and fecal output of N and P, Denali caribou herd, 1978-1979. Estimates are based on values from Figure 4, and N and P values from Tables 25-29 (see Methods).

Table 29. Seasonal variation in the nutrient content of caribou fecal samples, Denali caribou herd, 1978-1979.

Season	Dates	n	Nutrients (% dry wt)		
			N	P	NDRF[a]
Spring	June 1-30	2	2.78 ± 0.23	0.65 ± 0.01	2.25 ± 0.22
Summer	July 1-August 20	3	2.56 ± 0.01	0.51 ± 0.14	1.41 ± 0.16
Autumn	August 21-October 15	4	2.02 ± 0.35	0.31 ± 0.03	1.12 ± 0.29
Winter	October 16-May 31	7	1.78 ± 0.12	0.30 ± 0.04	0.93 ± 0.22

[a] NDRF is the nitrogen content of the neutral-detergent residue (cell walls) of the feces.

requirements, and if one considers the substantial additional daily loss of N in the urine (McEwan and Whitehead 1970; Jacobsen and Skjenneberg 1975) the caribou are undoubtedly experiencing a negative N balance. That is, the caribou are actually excreting more N than they are consuming, due to the low N content of the lichen-dominated diet and the continual metabolic fecal N and endogenous urinary N excretion. Using feeding trials, Nordfeldt et al. (1961), McEwan and Whitehead (1970), Jacobsen and Skjenneberg (1975), Jacobsen et al. (1978), and Syrjälä et al. (1980) have also reported that reindeer/caribou experience a negative N balance when fed a pure lichen diet. However, none of these studies have tested whether reindeer/caribou are in a negative N balance when fed a "natural" winter diet consisting of 50 to 75 percent lichens and 25 to 50 percent partially winter-green graminoids, Equisetum spp., and other forbs (see Chapter 1). The relatively high N content of these non-lichen species (Appendix E) is undoubtedly of importance in supplementing the low N content of lichen-dominated diets in autumn and winter.

Apparently caribou/reindeer consuming a lichen-dominated diet must confront the significant physiological stress that results from a negative N balance during long winters. However, certain physiological adaptations act to reduce this stress. For instance, young reindeer have been shown to have excellent capabilities of recycling urea when fed a low N diet (Hove and Jacobsen 1975). Wales et al. (1975) studied urea recycling in adult male reindeer and caribou and also found that the ability to recycle N improved on a low N diet. Also, reindeer are known to possess an important ability to excrete surplus water without losing solute (Valtonen 1979). It is also noteworthy that during the rutting period adult female and male reindeer/caribou exhibit markedly decreased N excretion and increased N deposition due to hormonal influences as discussed by McEwan and Whitehead (1970).

The role of the negative N balance in influencing caribou population ecology deserves special attention. Undoubtedly, the negative N balance in winter is most stressful to calves from 6 to 12 months old, because this cohort has extremely high N requirements for growth during their first spring, summer, and autumn and have little chance to store N. Doerr (1980) concluded that natural overwinter calf mortality was the initial regulating factor of large productive herds, in the absence of hunting. Bergerud (1980) summarized the factors involved in the overwinter mortality of calves in North America and concluded that malnutrition could be an important factor affecting these cohorts during severe winters, even on subarctic ranges in interior Alaska and Newfoundland. In addition, he suggested that malnutrition of calves in the arctic, and particularly the Canadian Arctic Islands, "may be severe enough and sufficiently frequent that caribou numbers are normally kept below limits that might be imposed by predation or ultimately by food supplies". Apparently, the Peary caribou on these islands are not as productive in the High Arctic environment as Svalbard reindeer, probably due to the influence of disturbances from insects and predators which act to decrease foraging time.

Doerr (1980) did not speculate on the causes of natural overwinter mortality of calves, and Bergerud (1980) simply indicated that this mortality is likely not a result of overgrazing. As suggested by Doerr (1980), there is a definite need to investigate the specific factors influencing late winter natural mortality of caribou. I have concluded that caribou are likely in a negative N balance in winter. This stress is presumably of similar importance to that imposed by energetic stress. Factors controlling seasonal variations in energy expenditure are essentially the same as those affecting N expenditure, as detailed by Moen (1973) and Robbins (1973). Therefore, it should be evident from discussions in Chapter 2 that migratory distances, snow conditions, length of the growing season, and disturbances by predators, humans, and insects all influence the annual N balance as well as the energy balance. These factors are particularly important in respect to limiting access to food and/or limiting the time available for feeding.

It is noteworthy that if caribou are experiencing particularly large energy costs and subsequently increase the proportion of lichen in the diet to meet these costs, then the drain on body N would likely increase excessively in a disproportionate manner. This result would likely occur because the intake of N on a lichen diet is lower than the N in other winter food items (Table 28), and the digestible N of these foods would probably show a similar ranking, except possibly for mosses. For instance, Robbins et al. (1975) have found a significant relationship between N of food and apparent and true digestibility of N in white-tailed deer. Increases in total dietary DMI to meet added energy costs would likely result in proportional increases in the drain on body N, as metabolic fecal N is proportional to DMI. If the animals are in a negative N-balance, the result would be less N in the body N pool by late winter. With these examples in mind, it is easy to visualize why caribou/reindeer have evolved a 30 to 45 percent voluntary reduction in caloric food intake during the winter, even in instances when young animals are fed a high quality diet (McEwan and Whitehead 1970). These examples should exemplify the critical interrelationships between energy and N balance. It should also be realized that if caribou reduce the proportion of lichens in the diet, presumably to increase N intake, then animals would be faced with lower digestibilities and a disproportionate decrease in digestible energy. Apparently, lichens are consumed to meet energy demands, and therefore energy is likely the most compelling requirement of caribou in winter.

Caribou calves are presumably largely adapted to the low winter intake of N, at least in the subarctic, because overwinter mortality of calves directly from malnutrition has rarely been observed, except during severe winters or unusual conditions (Bergerud 1980; J. Davis 1980a, pers. comm.). Dauphiné (1976) stated that malnutrition rarely becomes a widespread direct cause of death, but instead it renders calves more vulnerable to other forms of mortality, for example predation and disease. It is difficult to assess overwinter mortality of calves in the Denali herd because late winter calf counts have not been documented for the herd in recent years (Troyer 1976, 1977, 1978; Grosnick 1979). Instead counts have been made in early to mid-July as yearling-counts from post-calving aggregations, and are confounded by the large body size of yearlings by these dates (J. Davis pers. comm.; personal observation). Even more important is the comment by Davis et al. (1979) that, "it is common knowledge that substantial, but variable between years, numbers of yearlings may be absent from post-calving aggregations." It is likely that overwinter mortality of calves in the Denali herd, reported by Troyer (1976, 1977, 1978) and Grosnick (1979), was substanitally overestimated. Calves in the Denali herd presumably rarely suffer overwinter mortality from malnutrition at present as a result of several factors: (1) the longer summer growing season of the Denali herd compared to arctic herds, which allows sufficient time for the storage of energy N, and other nutrients, (2) the apparently equally nutritious forage of the Denali herd compared to arctic populations (as discussed later), (3) the usually wind-swept conditions of much of the wintering area, which, combined with the usually low snowfall and infrequent icing conditions, allows ready access to forage, and (5) a variety of other factors reported in Chapter 2; including the relatively short migrations, low proportion of time spent running, the virtual absence of harassment by mosquitoes and black flies, and the high availability of insect-relief sites. However, if the Denali herd was very large and expanding, the animals would presumably spend more time in social interactions, and the subsequent expansion in range area would require longer migratory distances. Also, there presumably would not be sufficient wind-swept foraging areas for the entire herd. Increases in disturbances would also likely accompany this increase in numbers, particularly from increased predator populations, hunting pressure, and social interaction. All of these factors would contribute to a decreased late winter nutritional status of caribou and could result simply from an increase in caribou numbers. A simultaneous increase in density would not necessarily have to occur, as an expanded range might occur along with an increase in caribou numbers. The high overwinter natural mortality of calves, in the large productive caribou populations studied by Doerr (1980), may have resulted directly from a combination of the above factors, particularly in regard to increased disturbance from hunters.

The usually high pregnancy rates (about 82 calves per 100 cows) of adult female caribou (greater than 3 years old) over much of North America (Bergerud 1980) indicate that this cohort has adapted somewhat to the negative N balance during the winter and the added N cost of pregnancy. However, many authors have stated that females in well-nourished caribou/reindeer populations ovulate and conceive at an earlier age than their counterparts in relatively poorly nourished populations (Klein 1968; Nikolaevskii 1968; Skoog 1968; Reimers 1972; Doerr 1980). Davis et al. (1980b) have recently reported that proportions of 2-year-old females giving birth in the rapidly expanding Delta caribou herd are similar to proportions of 3-year-olds giving birth in other established North American caribou herds. Also, they reported that the Delta caribou herd has yielded a higher percent of parous females on the calving grounds than any other established North American caribou herd. The influence that poor autumn body condition has on the inhibition of estrus and estrous behavior in adult ruminants is likely of less importance to a caribou population's pregnancy rates in most situations than early age-specific breeding, since summer conditions usually allow great improvement in body condition before the rutting season. Dauphiné (1976) discussed the relationship between breeding performance and fat reserves in female caribou and other ruminants. In brief, it can be stated that environmental conditions are limiting the reproductive potential of caribou over much of North America. Adult female caribou on the Canadian Arctic Islands have shown high variation in pregnancy rates (Miller et al. 1977), and this likely results from the added nutritional stress associated with the extremely short growing season and long winters.

It is important to recognize that nutrition also has an effect on neonatal survival of caribou calves. Dauphiné (1976) stated that survival of caribou calves must depend to some extent on the level of nutrition available to their dams during late gestation, in part because abandonment of calves would relieve the dam of part of the stress of lactation and ensure sufficient body condition for another pregnancy the following year. Nikolaevskii (1968), Preobrazhenskii (1968), McEwan and Whitehead (1972), and Hyvärinen et al. (1975) also stated that there is an apparent relationship between survival of neonatal calves and the nutritional status of their dams. McEwan and Whitehead further stated that environmental and social factors are important in this relationship, but they found these factors difficult to assess in free-roaming caribou populations. It has been noted that the influence of unusual nutritional stress during late pregnancy in caribou/reindeer increases the duration of the gestation period (McEwan and Whitehead 1972; Espmark 1980), decreases birth weight (Bergerud 1971; McEwan and Whitehead 1972; Espmark 1980), favors physical retardation and inactivity of calves at parturition (Espmark 1980), and may result in an increased incidence of abandonment of calves by free-ranging caribou (Espmark 1980). Kelsall (1960) and Miller and Broughton (1974) have reported significant mortality among young calves ultimately due to abandoment by their dams.

The proximate cause of this abandonment is likely unusual malnutrition of parturient females, and loss of the calf probably results from factors similar to those observed by Verme (1962) in undernourished white-tailed deer. In Verme's study the first 48 hours following birth was the crucial period which determined survival of calves. That is, calves surviving the first 48 hours of life also survived throughout the summer, except for deaths due to accidents or disease. Mortality during the critical 48-hour period resulted from one or more of the following factors: (1) poor condition of the fawn, (2) the fawn being too small to suckle, (3) the doe not permitting suckling, and (4) delayed lactation or no lactation by the doe (as cited by Klein 1970c). These factors, combined with the almost constant movement of the caribou, probably result in early mortality of calves when their dams are experiencing unusual nutritional stress.

It is interesting to note that Davis et al. (1980b) documented strong early cow-calf bonds among caribou of the apparently very healthy Delta caribou herd, even when these bonds were severely stressed. I noted the same strong early bonds among caribou of the healthy Denali herd, particularly during periods of disturbance initiated either by myself or by predators. This is in contrast to descriptions of human harassment causing females to abandon their calves in the Nelchina herd (Bos 1974).

It is also relevant that the Delta herd calved earlier in 1979 and 1980 than expected from previous reports from adjacent herds in interior Alaska (Davis et al. 1980b). This is important in view of McEwan and Whitehead's (1972) conclusion that wild caribou have a significantly longer gestation period compared with captive caribou on a high plane of nutrition, which suggest that an inverse relationship exists between gestation length and nutritional state. Also, Reimers (in Klein and White 1978) found that reindeer on a favorable range calved earlier than a comparable population on a poor range. Peak of calving in the Denali herd from 1976 to 1978 (Troyer 1978) was even earlier (by about 5 days) than reported for the Delta herd in 1979 (Davis et al. 1979). Yet, the Denali herd's calving areas are only about 160 km southwest of the Delta herd's calving grounds.

It is important to address Bergerud's finding that, although "hard" winters were related to decreased birth weights of caribou calves in Newfoundland, no relationship was found between birth weight and survival rate of calves (Bergerud 1971). He mentioned a 30 percent decrease in average birth weight between years (9.1 to 6.4 kg), yet his lowest weight here is greater than the average birth weight (about 6 kg) of caribou in Alaska and of reindeer in most populations in Alaska, Canada, and the Soviet Union (as summarized by Skoog 1968). Skoog stated that calves weighing less than 3.5 kg are weak and underdeveloped and will likely succumb. Bergerud's weights are probably high for several reasons. For example, the extremely moderate latitude of Newfoundland (about 50° N latitude) and the associated longer growing season likely contributes to a higher nutritional status of caribou in Newfoundland. Also, caribou in Newfoundland do not participate in a long pre-calving migration. An extensive migration to the calving grounds likely severely drains energy and N reserves during late gestation, particularly since foraging time is limited by the time required to migrate. Newfoundland caribou are also free of the energetic costs associated with disturbance by wolves.

It should be pointed out that predation on very young calves likely occurs independent of cow-calf nutritional status. For instance, within the first 2 to 3 weeks of birth, calves are vulnerable to predation by wolves and within about the first week of birth calves are vulnerable to predation by brown bears (Murie 1944; Skoog 1968; personal observations). After this critical period, predation will likely be much more dependent on nutritional status of the calves.

Predation on newborn calves of the apparently very healthy Denali herd could explain the low number of calves observed on the calving grounds (Troyer 1976, 1977, 1978; Grosnick 1979), particularly since predator populations are high in the park (see Study Area). Davis et al. (1979) have suggested that the extremely low calf counts on the calving ground of the adjacent Delta herd, prior to 1976, ($\overline{X}$ = 19 calves per 100 cows in 1973 and 1975, s.d. = 8) were due primarily to wolf predation on very young calves. This conclusion was reached following a wolf control program initiated in 1976, after which similar counts of calves on the calving ground showed great improvement ($\overline{X}$ = 40 calves per 100 cows, n = 5, s.d. = 12), even though weather conditions had apparently declined somewhat during calving. The predation on young calves, prior to 1976, likely occurred largely independent of the nutritional status of calves.

There has been some question whether low calf counts observed on the Denali herd's calving grounds were due to low natality rates and/or early loss of calves. Factors that suggest that the natality rates of the Denali herd are high include my observations of the relatively high nutritional status of the herd and observations by Troyer (1976) indicating a 79 percent pregnancy rate (as evidenced by udder distension) of 11 adult females radio-collared in late June, 1976. Of these 11 females only 1 was nursing, which strongly suggest an early loss of calves. I did not attempt to count udders on the calving ground in 1979 as this would often have demanded disturbing the caribou and my primary objective was to gather data on undisturbed activity patterns. However, antler counts (parturient caribou usually retain their antlers until calving (Bergerud 1980)) also suggested high natality rates. I believe the apparent high mortality of very young calves can only be explained through early losses to predation, although this has not been documented and needs intensive study. Vulnerability to predation likely decreases dramatically soon after calving because autumn and early winter calf counts, when compared to June counts on the calving ground, do not indicate a significant additional summer mortality (Troyer 1976, 1977, 1978; Grosnick 1979). This apparent decline in predation rates is probably related, in part, to the high nutritional status of the herd. Also, I suspect that a large majority of the calves that survive the initial mortality during and soon after calving (20 calves per 100 females in June and/or July, 1973 to 1980, s.d. = 9) (Haber 1977; Troyer 1980) are recruited into the population as yearlings. If this did not occur, the population would likely be declining (Bergerud 1978), yet the population appears to have been stable at about 1200 to 1500 animals from 1972 to 1980 (Haber 1977; Troyer 1976, 1977, 1978, 1980; Grosnick 1979).

Mortality of adult female caribou directly from malnutrition is likely extremely rare, even in critical years, because females can abandon their calves prior to the additional stress from lactation. However, females at a very old age may be an exception. Mature bulls likely suffer mortality from malnutrition to a larger degree than females either directly or indirectly (de Bie and van Wieren 1980), because of the severe nutrient drains these animals experience during rutting activities just prior to winter. However, these animals can conserve considerable energy stores in later winter and early spring, compared to females, because they seldom participate in the relatively extensive pre-calving migrations of the females. Yearlings also conserve energy and N reserves to some extent by remaining behind in these migrations.

Finally, it is significant that the N content of caribou forages from the Denali herd's range (Appendix E) were very similar to seasonal values reported for comparable species in other caribou studies in Alaska and Canada (Pegau 1968; Hemming and Pegau 1970; Scotter 1972; Whitten and Cameron 1980). However, due to the small sample size or low number of species in most of these studies it was difficult to make definitive comparisons, except in the case of lichens.

In conclusion, caribou appear to be in a negative N balance in winter. This results primarily from the high intake of lichens in winter. Lichens have extremely low levels of N but contain high levels of digestible energy. Energy and N requirements are usually considered the most vital determinants of nutritional carrying capacities of ranges of wild ruminants (Moen 1973; Robbins 1973). Apparently, the most compelling nutrient requirement for caribou in winter is energy, or lichens would not dominate the winter diet. Thus factors controlling energy balance are likely the main determinants of nutritional status in caribou, although many of the same factors control N balance. Apparently, caribou are largely adapted to the negative N balance in winter.

Phosphorus (P)

Several factors indicate a wide variation in the seasonal P regime of caribou. For instance, P levels in the diet decline dramatically from summer to winter (Figure 5), due in part to the very low P content of lichens. Also, fecal output of P is greater than dietary intake in the winter (Figure 6), which indicates that caribou are in a negative P balance in winter. When one considers that significant quantities of P are also excreted in the urine in reindeer (Jacobsen et al. 1978), it may be hypothesized that caribou are not meeting P requirements through dietary intake as early as autumn, but instead are depleting body reserves.

Caribou/reindeer P requirements have not been defined. However, from experiments with reindeer calves fed a lichen diet with and without various mineral and protein supplements, Jacobsen et al. (1978) determined that calves were usually in a negative P balance, even when intake of P was as high as 5.80 g • day^{-1}. The estimated autumn intake of P in adult caribou in the Denali herd was only 5.31 g • day^{-1} (Figure 6) which also suggest that caribou may be in a negative P balance when feeding on the lichen-dominated autumn diet. However, the P balance of calves fed lichen-based diets is likely not directly comparable with the P balance of adult free-ranging caribou. Bjarghov et al. (1976) also found that reindeer calves fed lichen diets developed severe P deficiencies as indicated by low inorganic P levels in their blood serum compared to calves on a diet high in P.

Verme and Ullrey (1974) indicated that the minimum level of dietary P necessary to support maximum weight gain, bone strength, and antler development from weaning to 12 months of age in white-tailed deer was 0.35 percent. Cowan and Long (cited by Ullrey et al. 1975) reported that 0.20 percent dietary P was not limiting to antler development in 2-year-old males. The minimum P requirements generally recommended for maintainance of beef cattle (National Research Council 1970) and sheep (National Research Council 1968) under range conditions is 0.16 percent. However, the winter growth plateau observed in wild cervids may reduce nutrient requirements below the level required for maintainance of domestic animals. Based strictly on the above listed requirements, however, it is likely that caribou diets provide sufficient P in spring (0.38 percent P) and summer (0.25 percent P) for adult caribou, whereas autumn diets (0.15 percent P) may be deficient and winter diets (0.08 percent P) are undoubtedly deficient.

The increased demands for P during pregnancy in ruminants (Agricultural Research Council 1965) strongly suggest that pregnant caribou are in severe P stress during late gestation, particularly since they are still consuming a winter diet. This stress is likely comparable to the stress associated with energy and N deficiencies in late winter and early spring.

The influence of P on the population ecology of caribou likely closely follows that described for N. For instance, young animals and pregnant females are particularly susceptible to severe stress from deficiences of P, especially in environments with extremely short growing seasons and in conjunction with disturbances that act to limit the build-up of body reserves for winter use.

The P content of caribou forages in Denali National Park (Appendix E) were similar to seasonal values reported for comparable species in other caribou studies in North America (Hemming and Pegau 1970; Scotter 1972; Whitten and Cameron 1980). However comparisons are limited to data on the P contents of lichens and a few species of vascular plants.

Calcium (Ca)

Intake of Ca also varies markedly on a seasonal basis. Peak intake of Ca occurs in the summer (27.0 g Ca • day^{-1}), rather than in the spring as in N and P (Figure 5). It appears that Ca is probably not as limiting to caribou as energy, N, or P since the proportion of Ca in the winter diet is quite high (0.37 percent) compared to minimum maintainance requirements for adult beef cattle under range conditions (0.16 percent) (National Research Council 1970). Also, Bjarghov et al. (1976) found that serum Ca levels in reindeer calves fed lichens throughout the winter were very similar to serum Ca levels in reindeer calves fed a high Ca diet over the same period, even though lichen-fed calves lost 24 percent of their body weight. It is interesting, however, that Nieminen (1980) found that serum Ca levels decreased slightly in late winter in a group of free-ranging animals that were extremely malnourished. In fact, a large proportion of this population died from malnutrition subsequent to the collection of blood samples. It is likely that this decline in serum Ca did not result necessarily from the consumption of Ca-deficient food, but instead likely occurred largely from the lack of food intake. Decreased food intake likely occurred as a result of a hard crust of snow which prevented efficient cratering in the snow.

In Ca-balance trials with reindeer calves, Jacobsen et al. (1975) found a negative Ca balance on pure lichen diets. However, the intake of lichens was very low (0.69 to 0.85 kg DMI • day^{-1}), and calves consumed only 0.5 to 0.7 g Ca • day^{-1}. This is in contrast with the estimated intake of 9.1 g Ca • day^{-1} in adult caribou in Denali National Park in winter. Calves and pregnant females likely require the highest intake levels of Ca, but when food intake is not limited it is unlikely that severe Ca deficiencies occur.

According to Dietz et al. (cited by Scotter 1972), the optimum Ca:P ratio is between 2:1 and 1:2, and should not exceed 5:1 for domestic animals in a productive state. The Ca:P ratio of the caribou diets are within the optimum range only in spring (about 1.2:1), after which it slowly increases to about 4.6:1 in winter (Tables 25 to 28).

Although several forage samples were not analyzed for Ca, all plant groups except lichens were well represented (Appendix E). The value I used for lichens (0.15 percent Ca, n=1) (Appendix E) is likely a very good average estimate compared to the Ca content of 56 palatable lichen species collected on the Seward Peninsula (Hemming and Pegau 1970). It should be noted that _Cetraria_ _cucullata_ had a much higher Ca content (0.28 percent ± 0.15 (s.d.), n = 5) than _Cladonia_ spp. (0.07 percent ± 0.05, n = 51) (Hemming and Pegau 1970). These values are similar to values reported by Luick (1974) for lichens collected adjacent to Denali National Park. The proportion of _Cladonia_ versus

Cetraria species in the diet must be considered to obtain an average value of Ca intake (Appendix D). It is interesting that the Ca content of Cladonia spp., analyzed from northwestern Canada (Scotter 1972), appear to have higher proportions of Ca (0.12 percent ± 0.02, n = 15), than similar species on the Seward Peninsula (Hemming and Pegau 1970).

The Ca content of vascular plants in Denali National Park (Appendix E) appeared to be similar to the few values reported by Whitten and Cameron (1980) for Alaska's Arctic Slope, although there undoubtedly are Ca-deficient sites in both areas.

Total Nonstructural Carbohydrates (TNC)

Seasonal levels of TNC (Figure 5) are important indicators of the readily available energy of forages. Although fats and proteins have higher calorific values than TNC, the energy in TNC is considered completely utilizable by the ruminant. Peak intake of TNC occurs in the summer (260 g • day^{-1}), which is also the time when energy requirements are highest. Values in autumn, winter, and spring are 202, 93, and 160 g • day^{-1}, respectively. It is likely that the rapid deposition of fat in summer and autumn are related to the high intake of TNC during these periods. The TNC levels of caribou forages on Alaska's Arctic Slope (Whitten and Cameron 1980) are similar to my values (Appendix E), although few comparisons can be made.

Potassium (K) and Magnesium (Mg)

A large majority of samples were not analyzed for K and Mg (Tables

25 to 28; Appendix E). However, dietary K is likely adequate for all seasons, compared to K requirements for sheep and cattle (Agricultural Research Council 1965). The Agricultural Research Council (1965) stated that the likelihood of K deficiencies occurring in animals on conventional forage diets is remote. Also, Nieminen (1980) did not find any correlation between malnutrition and K content of blood serum in free-grazing reindeer, even in starved animals.

Likewise, Mg levels of caribou diets are likely sufficient to meet Mg demands of caribou, compared to sheep and cattle requirements (Agricultural Research Council 1965). However, lichens are low in Mg, and Bjarghov et al. (1976) found that severe malnutrition of lichen-fed reindeer calves was associated with significant declines in serum Mg levels. In contrast, Nieminen (1980) analyzed the effects of seasonal changes and nutrition on blood in 251 young and adult reindeer in northern Finland and found low serum Mg levels in only one extremely malnourished, probably starved, population in late winter. It is likely that Mg deficiencies occur very rarely among free-ranging caribou/reindeer, since pure lichen diets probably do not occur in the wild. Denali caribou continued to select forbs, especially Equisetum arvense, and graminoids in the winter, which are high in Mg. Mosses, too, are high in Mg, but the availability of Mg in mosses is unknown. The IVDMD trials suggest a very low digestibility of mosses (Appendix C), but actual measurements of the mineral digestibility of mosses are needed.

It should be mentioned that I observed a peracute attack and subsequent death of a lactating female caribou (5 years old) on August 16, 1978, from what may have been a case of grass tetany. Field observations for approximately 1 hour prior to the attack indicated this animal was grazing normally with a small group of caribou. Symptoms, including dizziness and imbalance, were observed immediately after an excitation leap which resulted from disturbance by an assisting biologist. The animal soon went into severe convulsions accompanied by muscle tremors, retraction of the head, and pawing of the forelegs followed by death about an hour later. A necropsy the following day by personnel of the Alaska Department of Fish and Game did not discover any unusual condition that could have resulted in the death of the caribou, but the symptoms suggest a case of grass tetany. Grass tetany results from a mineral imbalance associated with insufficient dietary Mg and excessive K. Analysis of this animal's feces indicated an unseasonally high intake of lichens (about 75 percent) which were abundant in the area. A subsequent high intake of mushrooms, which were abundant and frequently sought by caribou in the area, could possibly have created the onset of the disease. However, grass tetany, though relatively common in cattle and sheep, has not been documented among caribou in Alaska, and it would likely have been noticed if it occurs frequently since the symptoms are usually triggered by disturbance (R. Dieterich pers. comm.).

The K and Mg concentrations of lichens collected in Denali National Park (this study) and adjacent to Denali National Park (Luick 1974) were similar to values reported by Scotter and Miltimore (1973) for lichens from northwestern Canada. Also vascular plants collected in this study contained K and Mg levels similar to those reported by Whitten and Cameron (1980) for Alaska's Arctic Slope.

Sodium (Na)

The estimated concentration of Na in the seasonal diets ranged from about 0.10 percent in spring to about 0.06 to 0.07 percent in the autumn and winter (Tables 25 to 28). These proportions corresponded to a Na intake of about 2.7 g • day^{-1} in spring and summer, 2.0 g • day^{-1} in autumn, and 1.7 g • day^{-1} in winter. The Agricultural Research Council (1965) concluded that 2 g Na • day^{-1} is the minimum Na requirement for lactating sheep, whereas a minimum value of 12 g Na • day $^{-1}$ was given for dairy cattle. The Na requirements for growth in adult sheep (0.10 kg • day^{-1}) and cattle (0.33 kg • day^{-1}) were given as about 1 g Na • day^{-1} and 7 g Na • day^{-1}, respectively. Caribou Na requirements are probably intermediate between those for sheep and cattle, and therefore it is possible that caribou have sufficient Na in winter, but adult females in the Denali caribou herd likely suffer from Na deficiencies during lactation and fattening.

Staaland et al. (1980) have indicated that the combination of low Na and high K levels in the spring and summer forages of reindeer causes excretion of needed Na. Therefore the low Na and high K levels of the spring and summer forage are likely more critical than the lower Na and low K levels of winter forages. Weeks and Kirkpatrick (1978) also found that high K concentrations in spring forages can upset the Na:K balance of vertebrate herbivores, and lead to Na-deficiency symptoms. The "low" Na and "high" K values measured by Staaland et al. (1980) were very similar to my values and were collected in an area adjacent to Denali National Park. The Na:K ratios of spring versus winter caribou diets were about 1:12 and 1:5, respectively (Tables 25 to 28). Thus, males and young animals as well as lactating females may suffer from Na deficiencies in spring. A high intake of K from mushrooms in autumn may also lead to Na deficiencies at this time, or, alternatively, the very low Na:K ratio of mushrooms may deplete the Na pool (through added excretion of Na) to the extent that late winter or spring Na balance is particularly stressful.

It is well known that Na is often much more concentrated in animal-matter than in plants and that herbivores frequently use mineral springs or licks presumably to attain sufficient Na, particularly in early spring (Hall 1970; Weeks and Kirkpatrick 1976, 1978; Fraser et al. 1980). Likewise, adult female caribou of the Denali caribou herd visited mineral licks on several occasions just prior to and following the initiation of early spring vegetative growth (May 23 in 1979 on the Cantwell calving ground) and coinciding with the initiation of stresses from lactation. The frequency of use was highest from mid-May to the first week of June in 1979. During this period, groups of females (lick use by males is discussed later) often visited the "Dunkle lick" almost daily, particularly during late evening, and often trotted/galloped to the lick when within about a kilometer of the lick site. Caribou remained at the lick site for 30 to 60 minutes.

After the first week in June, these animals often visited the lick at about 10- to 14-day intervals in large groups (250 to 400 caribou) until the last days of June when caribou in the area migrated to the summering range.

Chronology of lick use is likely dependent on plant phenology. For instance, G. Schultz (pers. comm.) observed only moderate use of the "Dunkle lick" in 1980 compared to my observations in 1979. This may have occurred because vegetation in the area of the lick emerged 2 to 3 weeks later in 1980 than in 1979 due to a late snowmelt in 1980. Caribou, however, migrated to the summering range at about the same time in 1979 and 1980, indicating that lick use probably only controls local movements of caribou.

Adult female caribou were only observed to visit two mineral licks in Denali National Park, although other licks undoubtedly exist (Skoog 1968; K. Whitten pers. comm.). In addition to the "Dunkle lick" caribou visited the "Polychrome lick", which consisted of a brown soil bank along a reddish-colored creek bed. This lick is visible from the park road just east of Polychrome Pass and is situated on the migration route leading to and from the Cantwell calving ground. Female caribou used this lick throughout much of May and in early to mid-July. Occasionally a few bulls used this lick in July, but I was unable to follow use of this lick by bulls at other times of the year. Exceedingly few adult bulls (less than 5) traveled to the Cantwell calving ground where the "Dunkle lick" is situated, so I had little chance to observe lick use by bulls. However, it appeared that adult females used the licks much more intensively than bulls.

Undoubtedly, some individuals develop a taste for Na or are particularly deficient in Na and, therefore, use the licks more frequently than others. The "Dunkle lick" consisted of the overburden from the abandoned Dunkle coal mine operation in the center of the Cantwell calving ground. I collected soil samples at both licks, but the lab analyses were not complete at this writing.

Fraser et al. (1980) concluded that Na was the primary mineral sought at mineral licks and springs, and summarized the results of several studies that showed similar results. Fraser et al. (1980) also explained the problems associated with the sampling of licks and the interpretation of chemical analyses. These explanations rectify, at least in part, the conflicting findings of other studies. Tankersley (in prep.) has analyzed water samples from several spring-fed licks in Denali National Park and has found relatively high levels of Na. These licks were primarily used by moose, which likely also suffer from seasonal Na deficiencies in Denali National Park, similar to those suggested for caribou. Dall sheep also visit mineral licks in the park and snowshoe hares (*Lepus americanus*) have been known to congregate along certain sections of the park road to lick and ingest soil and gravel (K. Whitten pers. comm.). I have also observed hoary marmots (*Marmota caligata*) licking the road's surface in spring and summer.

It is interesting that caribou forages on Alaska's Arctic Slope contained about 10 times the Na levels (Whitten and Cameron 1980) found in forages in Denali National Park. The high values for the Arctic Slope presumably occur because this area formerly was submerged by the Arctic Ocean. However, further investigation is needed since Na levels in forages collected at Atkasook on the Arctic Slope (Chapin et al. 1980) were much lower than the values reported by Whitten and Cameron (1980). It is interesting that K. Whitten (pers. comm.) could not discern any differences in the Na content of forages collected along the coast compared to Na levels in forages collected 150 km inland. Caribou of the Central Arctic herd remain in this study area year-round, and apparently do not suffer from Na deficiencies as they are not known to use mineral springs or licks (K. Whitten pers. comm.). Skoog (1968) has reviewed studies in which reindeer visited ocean beaches for salt deposits. However, pregnant females of the Central Arctic herd have not been seen visiting beach areas near calving time to obtain salt, even though calving occurs near the coast. An adjacent herd, the Porcupine caribou herd, which winters south of the Brooks Range, regularly uses mineral licks prior to and during calving, mostly in early June, and again along the post-calving migration route in July (Calef and Lortie 1975). Calef and Lortie analyzed the soil in one lick and found high Na concentrations compared to control samples. Caribou used this lick frequently, even though the lick was only 21 km from the Arctic Ocean.

Skoog (1968) reported instances of the Fortymile, Nelchina, and Denali caribou herds using mineral licks, particularly near calving time and gives a lengthy summarization of reports on the use of salt by caribou/reindeer. However, Skoog (1968) suggested that Ca and P deficiencies may be more important in regard to lick use than Na. Kelsall (1968) had extensive experience with caribou herds in Canada, yet suggested that caribou do not use salt licks, which suggests, as in the case of the Central Arctic herd, that some caribou populations may have adequate access to Na in their forages.

Synopsis and Conclusions

It appears that dry matter digestibilty of the seasonal diets can be predicted by assuming that about 100 percent of the cell solubles, 30 to 50 percent of the hemicellulose, and less that 10 percent of the cellulose of the diet is digestible. Estimated dry matter digestibility of seasonal diets varied from about 60 percent in winter to 70 percent in spring and summer. High digestibilities in winter were maintained as a result of the high intake of lichens. Dry matter digestibilities of lichens are particularly well documented in the literature and average about 70 percent. The relative constancy in seasonal dietary dry matter digestibilities, regardless of strong seasonal variations in plant chemical and structural components, suggests that forage quality is not the main limiting factor influencing energy balance, particularly in regard to the direct relationship between dry matter digestibility and metabolizable energy of ruminant diets.

Estimated energy requirements were expressed on a dry matter basis (using estimates of the metabolizable energy of the diets) to approximate DMI requirements. Approximations of DMI amounted to 86, 104, 104, and 74 $g \cdot kg^{-0.75} \cdot day^{-1}$ in spring, summer, autumn, and winter, respectively. These values compared favorably with measurements of the daily DMI of esophageal-fistulated reindeer.

Except in the case of low Na levels, results of nutrient analyses on forages collected in this study were similar to results of forage analyses conducted on similar caribou/reindeer forages in other studies in Alaska and Canada. Forages were analyzed for N, P, K, Ca, Mg, Na, and TNC, and analyses were weighted for diet composition to estimate diet quality in spring, summer, autumn, and winter. Also, by combining these estimates with estimates of DMI, nutrient intake estimates could be assessed, and compared with estimated nutrient requirements of caribou. Fecal samples were analyzed for N and P on a year-round basis to assess N and P balance. Negative N and P balances were predicted in winter, resulting primarily from the large proportion of lichen in the diet. Dietary K, Ca, and Mg were probably not limiting nutritional status at any season. Dietary Na concentrations were extremely low on the Denali caribou range and the caribou were likely stressed by Na deficiences in spring. However, caribou, particularly adult females, frequently visited mineral licks in spring, presumably to supplement dietary Na levels.

It is particularly important to recognize that the factors controlling energy expenditure and time spent in non-foraging activites were apparently the main determinants of annual energy balance, rather than range quality or productivity. This relationship, however, may change if lichens are extremely scarce on the wintering range. It is also relevant that since lichens are the primary source of digestible energy in winter and, at the same time, are exerting strong detrimental effects on N and P balance, it seems reasonable to assume that the need for energy is the most compelling requirement of the animals in winter and even late winter and early spring (the most critical nutritional periods) when lichens continue to constitute a major proportion of the diet. Therefore, the key determinants of energy balance are likely also the main determinants of nutritional status. Caribou presumably have largely adapted to the low N and P content of lichen-dominated winter diets. This likely results, in part, because their summer diet, which contains high N and P concentrations, enable them to store these elements to meet winter requirements. Also, N and P requirements are lower in winter.

Factors controlling energy expenditure and the time spent in non-foraging activites appear to be the main determinants of nutritional status of the herd. These include snow conditions, length of the growing or fattening season, migratory distances, and disturbance by insects, predators, and humans. These factors were discussed in relation to an energetics model in Chapter 2 to aid in ascertaining the relatively high energetic and/or nutritional status of the herd. Independent observations that suggest a high nutritional status of the herd include relatively early calving and strong early cow-calf bonds (see Nitrogen section).

Nutritional status has important influences on caribou population ecology particularly in regard to its effect on overwinter survival of calves, age of sexual maturity, production of healthy calves, and early cow-calf bond. Nutritional status also influences caribou population ecology through the effect that nutritional status has on resistance to predators, parasites, and diseases. I suggest that, since nutritional status of the herd appears to be very high, the poor calf crops observed in the Denali herd probably result from early predation on very young calves (less than 1 to 4 weeks old), independent of cow-calf nutritional status. This predation on young calves has presumably been the key factor controlling the stability of the population since 1972.

CONCLUDING STATEMENT: THE ROLE OF NUTRITION IN CARIBOU POPULATION ECOLOGY

Considerable controversy exists concerning the key factors controlling caribou population ecology, particularly in respect to the relative importance of range relationships versus the importance of predators and hunting (Bergerud 1980). More significantly, there has been a need to assess the aspects of caribou population ecology in a manner that allows investigation of the effects that any combination of factors (e.g. those affecting energy expenditure or dietary characteristics) may have on the total caribou-range relationship. This is important both for general management purposes (e.g. during severe winters or when animals are at high densities) and to assess the influence that increasing northern development has on the caribou-range relationship.

This paper has combined data on seasonal food habits, forage quality, and activity of the Denali caribou herd. This data base allowed calculation of apparently very reasonable approximations of the energy requirements and qualitative and quantitative dietary characteristics of the adult female cohort of the herd. Also, modeling of the energetics and nutritional status of the herd is done in a manner that allows assessment of the varying effects that dietary, behavioral, and/or environmental interactions have on the nutritional status of caribou.

Range productivity was assumed to play a minor role in the nutrition of the Denali caribou herd, and this assumption seems well-founded based on several factors, including the low density of the population, the large proportion of lichens in the winter diet (lichens are the most susceptible of the forages to overgrazing), and the estimated carrying capacities of reindeer/caribou ranges in the literature. It has been suggested that the length of active periods within undisturbed active-rest cycles will allow assessment of the relative condition of caribou ranges. Caribou ranges undoubtedly vary on a qualitative and quantitative basis, but overgrazing has not been well-documented on caribou ranges in North America. This likely results, in part, because of the fastidious feeding behavior of caribou and because an expansion in range area, or changes in range use patterns often accompany increases in caribou numbers. Thus, grazing pressure could remain rather stable during large fluctuations in caribou numbers.

The consumption of large proportions of lichens by the Denali caribou in winter appears to be a key factor in their annual nutritional status. Measurements of the dry matter digestibility and digestible energy of lichens in the literature indicate that lichens are extremely high in digestible energy compared to other winter food items. However, lichens contain extremely low levels of N and P, and caribou are likely experiencing negative N and P balances in winter when lichens dominate the diet. The high preference of caribou for lichens over other food items suggests that energy is the most compelling requirement of caribou in winter. Also, ingestion of lichens allows caribou to maintain a high dietary digestibility in winter. This suggests that, as long as lichens are not extremely scarce on the wintering range, the factors controlling energy expenditure and time spent in non-foraging activities exclusive of range quality or productivity, are the main determinants of energy balance and nutrition in winter. When consuming a non-lichen winter diet, low dietary digestible energy may be the major determinant of energy balance. However, more favorable snow cover characteristics and/or lack of or reduced harassment by predators or insects may compensate for the energetic stress imposed by the reduced energy availability of a non-lichen winter diet, as appears to be the case for Svalbard reindeer (Reimers 1980).

Activity budgets of adult female caribou/reindeer in late winter and early spring (Gaare et al. 1975; Roby 1980), calf weights in late winter, and percentages of parous females in young age classes are good indicators of nutritional/energetic status. These indicators should be used in combination with the nutrition and energetic models to determine critical levels of nutritional/energetic stress. Production and early survival of calves may also be good indicators of nutritional status, however particular care must be made in estimating these indices. For instance, early survival of calves appears to be very low in the Denali herd (Troyer 1980), yet the nutritional status of the herd is currently relatively high (see Synopsis and Conclusion of Chapters 2 and 3) compared to Arctic herds experiencing successful calf production. Caribou calves are particularly vulnerable to wolf predation during the first two weeks following birth, and brown bear predation on young calves can also be important (Murie 1944; Bergerud 1980; J. Bryant pers. comm., J. Davis pers. comm.). This susceptibility to predation undoubtedly occurs independent of the nutritional status of newborn calves, and the rate of predation during this calving and early post-calving period is likely related largely to the density of predators on the calving areas.

High predator densities are present in Denali National Park (see Study Area), and there is recent circumstantial evidence that suggests that wolves can cause substantial calf mortality during the immediate post-calving period. This was indicated by the increase in early calf survival in the Delta caribou herd following a wolf control program Davis et al. 1979, 1980b). Predation rates on caribou calves are probably more directly related to nutritional status of the animals after the 3 or 4 weeks following calving, particularly during late winter. However, accurate determinations of calf survival throughout the first summer and winter are largely lacking in the literature (Davis et al. 1979, pers. comm.). These determinations need to be measured on populations under different nutritional regimes and levels of predation to assess what effect nutritional status has on the resistance of caribou populations to wolf and bear predation. Nevertheless, it appears that survival of calves in the Denali herd after the initial 3 or 4 weeks of calving is very high (even with high wolf populations) as indicated by the stability of the population over the last 8 years (Haber 1977; Troyer 1980). For instance, during this 8-year period from 1973 to 1980, June and/or July calf counts have averaged about 20 calves per 100 females (Haber 1977; Troyer 1980) which would not allow sufficient recruitment to maintain a stable population level unless recruitment of these animals was high (Bergerud 1978).

Caribou nutritional status appears to be a decisive controlling factor in caribou population dynamics. This control results primarily from the influence that nutritional status has on resistance to predators (after the first few weeks of life), parasites, and disease, and from the effect that nutritional status has on overwinter survival of calves, age of sexual maturity, production of healthy calves, and the cow-calf social bond (see Nitrogen section in Chapter 3). In turn, the nutritional effects related to predator harassment, insect harassment, human disturbance, snow conditions, migratory distances, duration of the growing season, diet composition, and diet quality are corespondingly important. The effects of each of these environmental influences has been considered in an assessment of the nutritional status of adult females of the Denali herd. However, comparisons between caribou/reindeer populations are difficult to make since these environmental parameters can vary considerably between populations. Comparisons become even more complicated in view of the specialized behavioral, morphological and physiologial adaptations that some populations have acquired under the influence of a particular set of environmental conditions. Nevertheless, the need to measure the various parameters mentioned above should be obvious if one is to compare energetic/nutritional stresses between populations.

APPENDIX A

Percent relative density of discerned plant fragments in fecal samples collected primarily from adult female caribou, Denali caribou herd, 1978-1979.

Table A.1. Spring fecal sample analyses. Samples were collected primarily from adult female caribou.[a] Analyses were based on 100 fields per sample (100X). Each sample contained 25 fecal pellets collected from 25 different, fresh defecations.

Collection Dates	5/26/79	6/3/79	6/11/79	6/15/79	6/17/78	6/20/78	6/23/79	6/25/78	Mean ± s.d.
	(% relative density of discerned plant fragments)								
Plant Species									
Forbs									
Equisetum	3.2	1.3	0.4					0.6	1.4 ± 1.3
Graminoids									
Arctophila					0.6	0.9		0.6	
Carex	1.8	1.3	2.5	2.7	7.0	11.7	11.1	5.6	5.5 ± 4.1
Eriophorum						0.6		0.6	
Festuca	0.4	1.3	1.7	0.4	1.0	0.6	0.8	0.6	0.8 ± 0.5
Hierochloe	0.4								
	2.6	2.6	4.2	3.1	8.6	13.8	11.9	7.4	6.7 ± 4.4
Deciduous Shrubs									
Arctostaphylos					1.2	0.3		0.9	
Salix	6.1	35.2	62.5	70.2	46.1	67.2	43.4	68.2	50.0 ±22.2
Vaccinium		2.9	2.5						0.7 ± 1.3
	6.1	37.1	65.0	70.2	47.3	67.5	43.4	69.1	50.7 ±22.2

Table A.1. (Continued)

Evergreen Shrubs									
Ledum	0.9								
Vaccinium	3.6	2.0	—	—	—	—	—	—	0.7 ± 1.4
	4.5	2.0	0	0	0	0	0	0	0.8 ± 1.6
Nonvasculars									
Lichen I[b]	.9						0.4		
Lichen II[c]	77.2	54.5	27.8	24.9	37.6	15.6	42.2	19.1	
Peltigera	.4	1.3	.4	0.4	—	—	0.4	—	
	78.5	55.8	28.2	25.3	37.6	15.6	43.0	19.1	38.0 ±21.0
Mosses	5.1	.4	2.1	1.5	6.6	3.0	1.6	4.0	3.0 ± 2.1

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[a] Spring fecal samples were collected on the Cantwell calving area, except the May sample which was collected on the Stampede calving area.

[b] "Lichen I" is represented by the genera Dactylina, Cetraria, and Alectoria.

[c] "Lichen II" is represented by the genera Cladonia and Thamnolia.

Table A.2. Summer fecal sample analyses. Samples were collected primarily from adult female caribou.[a] Analyses were based on 100 fields per sample (100X). Each sample contained 25 fecal pellets collected from 25 different, fresh defecations.

Collection Dates	7/20/78	7/28/79	8/6/79	8/13/78	8/18/79	Mean ± s.d.
	(% relative density of discerned plant fragments)					
Plant Species						
Forbs						
Boykinia	0.2					
Equisetum	0.2					
Hedysarum		0.4 -	0.5			
	0.4	0.4	0.5	0	0	0.3 ± 0.2
Graminoids						
Arctophila	0.2					
Carex	3.2	8.3	2.4	2.8	2.3	3.8 ± 2.5
Festuca		2.0		1.7	.8	0.9 ± 0.9
Hierochloe		0.8		0.6		
	3.4	11.1	2.4	5.1	3.1	5.0 ± 3.1
Deciduous Shrubs						
Salix	91.7	55.9	59.9	43.2	28.3	55.8 ± 23.6
Vaccinium		0.4	1.4		3.1	1.0 ± 1.3
	91.7	56.3	61.3	43.2	31.4	56.8 ± 22.8
Evergreen Shrubs						
Dryas	0.2	1.2	2.4	0.6	0.8	1.0 ± 0.8

Table A.2. (Continued)

Nonvasculars						
Lichen I[b]		0.8		2.3		
Lichen II[c]	1.7	21.3	29.0	43.2	40.2	
Peltigera					1.5	
	1.7	22.1	29.0	45.5	41.7	28.0 ± 17.5
Mosses	2.8	1.6	1.4	2.9	0	1.7 ± 1.2
Mushrooms	0	0	2.9	2.9	23.0	5.7 ± 9.7

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[a] Summer fecal samples were collected in the vicinity of the upper Slippery Creek drainage.

[b] "Lichen I" is represented by the genera *Dactylina*, *Cetraria*, and *Alectoria*.

[c] "Lichen II" is represented by the genera *Cladonia* and *Thamnolia*.

Table A.3. Autumn fecal sample analyses.[a] Samples were collected primarily from adult female caribou. Analyses were based on 100 fields per sample (100X). Each sample contained 25 fecal pellets collected from 25 different, fresh defecations.

Collection Dates	9/20/79	9/30/79	10/1/78	10/11/79	Mean ± s.d.
	(% relative density of discerned plant fragments)				
Plant Species					
Forbs					
Equisetum	2.2	3.1	0	1.4	1.7 ± 1.3
Graminoids					
Carex	1.1	1.2	1.3	2.4	1.5 ± 0.6
Festuca	1.6			.5	0.5 ± 0.8
Hierochloe	0.5	0.6	2.0	—	0.8 ± 0.9
	3.2	1.8	3.3	2.9	2.8 ± 0.7
Deciduous Shrubs					
Salix	10.0	16.5	5.6	0	8.0 ± 7.0
Vaccinium	—	1.2	3.4	3.3	2.0 ± 1.7
	10.0	17.7	9.0	3.3	10.0 ± 5.9
Evergreen Shrubs					
Dryas	0.5	0.6	0.7	0.5	0.6 ± 0.1
Empetrum			0.7		
Ledum	—	0.6	—	—	
	0.5	1.2	1.4	0.5	0.9 ± 0.5

Table A.3. (Continued)

Nonvasculars					
Lichen I[b]	1.6	1.9	11.7	1.9	
Lichen II[c]	50.7	54.3	68.4	67.7	
Peltigera	3.9	2.5	0.7	4.9	
	56.2	58.7	80.8	74.5	67.5 ± 12.0
Mosses	23.2	11.3	3.4	15.1	13.3 ± 8.2
Mushrooms	4.5	6.0	2.0	2.4	3.7 ± 1.9

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[a] Autumn fecal samples were collected within 5 km of the park road between mileposts 70 and 76.

[b] "Lichen I" is represented by the genera *Dactylina*, *Cetraria*, and *Alectoria*.

[c] "Lichen II" is represented by the genera *Cladonia* and *Thamnolia*.

Table A.4. Winter fecal sample analyses.[a] Samples were collected primarily from adult female caribou. Analyses were based on 100 fields per sample (100X). Each sample contained 25 fecal pellets from 25 different, fresh defecations.

Collection Dates	11/20/78	11/21/78	11/21/78	1/5/79	1/5/79	1/7/79	3/7/78	3/10/79	3/12/79	5/9/79	Mean ± s.d.
	(% relative density of discerned plant fragments)										
Plant Species											
Forbs											
Equisetum	0.5	2.1	3.0						1.0	0.5	0.7 ± 1.0
Hedysarum	1.4	0.6		0.5					1.5	4.6	
Lupinus					0.6					0.5	
Stellaria	—	—	—	—	—	0.5	—	—	0.5	—	
	1.9	2.7	3.0	0.5	0.6	0.5	0	0	3.0	5.6	1.8 ± 1.8
Graminoids											
Carex	3.9	1.1	6.2	1.6	1.2	1.0	1.0	1.9	2.0	2.9	2.3 ± 1.7
Festuca								1.4	1.0	0.5	
Hierochloe	0.5	—	—	1.6	—	0.5	—	0.9	1.5	0.5	0.6 ± 0.6
	4.4	1.1	6.2	3.2	1.2	1.5	1.0	4.2	4.5	3.9	3.1 ± 1.8
Deciduous Shrubs											
Betula						0.5					
Salix	—	—	—	—	—	—	4.8	—	—	—	
	0	0	0	0	0	0.5	4.8	0	0	0	0.5 ± 1.5

Table A.4. (Continued)

Evergreen Shrubs											
Dryas				0.5	0.6						
Ledum	2.9				2.9		1.8	1.9	1.5	2.9	1.4 ± 1.3
Vaccinium	5.4	4.4	8.1	8.1	9.3	5.2	10.3	7.5	11.6	4.9	7.5 ± 2.5
	8.3	4.4	8.1	8.6	12.8	5.2	12.1	9.4	13.1	7.8	9.0 ± 3.0
Nonvasculars											
Lichen I[b]	2.4	1.6	0.6	1.1	1.7				0.5	1.4	
Lichen II[c]	75.2	77.0	70.4	58.1	49.6	77.5	52.0	60.6	54.4	45.3	
Peltigera	2.9	6.1	4.2	1.6	2.3	4.9	4.8	1.4	2.0	0.9	
	80.5	84.7	75.2	60.8	53.6	82.4	56.8	62.0	56.9	47.6	66.1 ± 13.4
Mosses	4.9	6.7	7.5	26.6	31.2	9.9	25.5	18.5	21.1	29.7	18.2 ± 10.1
Mushrooms	0	0.5	0	0	0.6	0	0	5.4	1.0	0.5	0.8 ± 1.7

[a] November collections were made in the vicinity of the upper drainage of Slate Creek. January and March samples were collected in the Stampede Hills.

[b] "Lichen I" is represented by the genera *Dactylina*, *Cetraria* and *Alectoria*.

[c] "Lichen II" is represented by the genera *Cladonia* and *Thamnolia*

APPENDIX B

Percent relative density of discerned plant fragments in miscellaneous caribou and reindeer fecal samples, Denali National Park, 1978-1979.

Appendix B. Percent relative density of discerned plant fragments in miscellaneous caribou and reindeer fecal samples, Denali National Park, 1978-1979. Based on 100 fields per sample (100X).

	Calf Samples		Bull Samples			Tame Reindeer Sample
Collection Date	6/23/79	7/28/79	7/12/78	8/28/78	9/9/78	8/25/78
Plant Species						
Forbs						
Boykinia			0.1			
Equisetum			0.1		0.7	
Lupinus					1.3	
Mertensia						0.7
Petasites		0.5				
Stellaria					0.7	
	0	0.5	0.2	0	2.7	0.7
Graminoids						
Arctophila				0.5		
Carex	5.7	4.5	1.0		3.4	0.7
Eriophorum						0.7
Festuca		2.4	0.3		1.3	
Hierochloe				0.5		
	5.7	6.9	1.3	1.0	4.7	1.4

Appendix B. (Continued)

Deciduous Shrubs						
Salix	28.7	40.9	96.9	86.5	15.5	53.9
Vaccinium				1.4	18.9	5.8
	28.7	40.9	96.9	87.9	34.4	59.7
Evergreen Shrubs						
Dryas		1.4	0.1	0.5	2.7	6.9
Ledum	0.3					
	0.3	1.4	0.1	0.5	2.7	6.9
Nonvasculars						
Lichen I[a]	0.6	1.4	1.0	1.0	4.8	0.7
Lichen II[b]	63.8	43.2		5.0	34.7	29.9
Peltigera	0.3					
	64.7	44.6	1.0	6.0	39.5	30.6
Mosses	0.6	2.8	0.4		8.4	
Mushrooms				4.7	7.7	

[a] "Lichen I" is represented by the genera *Dactylina*, *Cetraria*, and *Alectoria*

[b] "Lichen II" is represented by the genera *Cladonia* and *Thamnolia*

APPENDIX C

Fiber content and in vitro dry matter disappearance (IVDMD) of forage samples collected in and near Denali National Park, 1978-1979.

Table C.1. Fiber content and in vitro dry matter disappearance (IVDMD) of berries. Values are presented on a % dry wt basis.

		Fiber					
Species	Collection Date	Cell Walls	ADF	Lignin	Cellulose	Ash	IVDMD (mean±s.d.)[a]
Empetrum nigrum	8/22/79	32.9	24.5	4.2	19.4	0.8	68 ± 6
Vaccinium uliginosum	8/25/78	10.7	7.8	2.0	6.2	0	83 ± 1
Vaccinium vitis-idaea	8/28/78	16.4	11.4	2.7	8.8	0	82 ± 2

[a] n=4

Table C.2. Fiber content and in vitro dry matter disappearance (IVDMD) of deciduous shrubs. Samples contained leaf tissue. Values are presented on a % dry wt basis.

Species	Collection Date	Fiber				Ash	IVDMD (mean±s.d.)[a]
		Cell Walls	ADF	Lignin	Cellulose		
Arctostaphylos spp.[b]	1/7/79	26.1	24.2	11.6	11.5	1.1	41 ± 1
Arctostaphylos spp.	6/2/79	16.6	10.6	1.6	9.0	0	
Arctostaphylos spp.	6/7/79	18.1	10.3	2.0	8.3	0	
Arctostaphylos spp.	6/19/79	15.2	10.8	2.6	8.0	0.2	
Arctostaphylos spp.	6/25/78	15.6	10.2	2.6	7.5	0	51 ± 2
Arctostaphylos spp.	7/31/79	13.5	10.0	3.7	6.0	0.2	
Betula nana	6/3/79	23.0	18.9	4.7	14.1	0.3	
Betula nana	6/10/79	22.3	15.6	3.9	11.1	0.7	51 ± 2
Betula nana	6/18/78	28.2	19.9	6.4	14.7	0	
Betula nana	7/20/78	25.7	17.8	6.9	10.6	0.3	
Betula nana	8/16/78	26.4	14.5	4.8	9.6	0	52 ± 2
Betula nana	9/10/78	27.6	18.6	6.8	11.8	0.1	
Salix alaxensis	6/20/78	28.0	19.1	6.2	15.4	0	
Salix alaxensis	7/14/78	31.5	19.3	6.5	15.2	0	
Salix alaxensis	7/16/78	32.2	26.0	7.6	17.6	0.8	
Salix alaxensis	8/5/78	29.8	24.0	7.7	15.9	0.4	
Salix alaxensis	9/8/78	30.1	20.3	8.1	12.0	0.2	60 ± 5

Table C.2. (Continued)

Salix arctica	6/18/79	14.7	12.8	3.2	9.1	0.5	
Salix arctica	7/14/78	30.9	22.4	10.2	13.5	0	
Salix arctica[c]	7/30/79	31.5	24.6	8.1	15.5	0	46 ± 3
Salix arctica	8/11/79	24.4	20.8	8.1	12.2	0.5	
Salix arctica	8/21/79	29.7	24.3	7.4	16.6	0.3	
Salix commutata	6/4/79	20.7	14.6	3.7	10.0	0.7	
Salix commutata	6/10/79	29.0	17.3	3.3	14.0	0.1	
Salix fuscescens	6/28/79	26.5	19.0	4.2	14.3	0.5	
Salix glauca	7/28/78	27.4	23.0	9.8	13.8	0.3	
Salix glauca	8/1/78	29.4	22.2	8.7	11.8	1.8	
Salix glauca	8/14/78	21.2	17.3	6.0	10.2	1.1	
Salix glauca	8/25/78	25.0	18.4	4.6	12.5	1.4	69 ± 4
Salix glauca	9/9/78	21.8	16.8	7.2	11.9	0	
Salix pulchra[b]	1/5/79	34.5	32.4	11.2	21.1	0	23 ± 4
Salix pulchra	6/2/78	15.5	12.9	4.5	8.4	0.1	
Salix pulchra	6/2/79	20.4	16.4	5.2	11.1	0	42 ± 2
Salix pulchra	6/5/78	17.4	13.8	4.6	9.0	0.2	
Salix pulchra	6/7/79	16.9	14.2	4.6	9.5	0.2	45 ± 2
Salix pulchra	6/11/79	18.6	12.5	3.2	9.3	0	

Table C.2. (Continued)

Salix pulchra	6/18/78	17.1
Salix pulchra	6/19/79	14.6
Salix pulchra	6/20/79	18.3
Salix pulchra	6/25/78	17.6
Salix pulchra	6/28/79	20.3
Salix pulchra	6/29/79	18.1
Salix pulchra	7/7/78	25.8
Salix pulchra	7/16/78	24.8
Salix pulchra	7/20/78	24.6
Salix pulchra	7/24/78	29.8
Salix pulchra	8/1/78	31.9
Salix pulchra	8/11/78	21.2
Salix pulchra	8/18/78	28.2
Salix pulchra	8/25/78	17.9
Salix pulchra	9/8/78	30.0
Salix pulchra[b]	9/20/79	37.5
Salix reticulata	6/3/79	20.5
Salix reticulata	6/10/79	17.4
Salix reticulata	6/18/79	17.2

14.8	6.0	10.9	0	
13.0	3.6	9.3	0.1	52 ± 5
15.6	5.3	10.2	0	48 ± 1
16.1	7.1	9.1	0.1	
14.9	4.8	10.0	0.1	39 ± 3
15.6	3.4	12.3	0	43 ± 1
18.6	7.0	11.2	1.2	
18.6	8.7	11.2	0	37 ± 3
18.1	8.3	10.4	0	
23.6	7.7	15.9	0	
22.3	8.6	13.6	0	
18.9	8.2	9.1	1.6	45 ± 1
21.6	8.7	12.4	0.5	
15.4	4.1	11.2	0	
26.2	14.0	12.6	0	32 ± 1
34.4	13.4	20.4	0.6	
18.6	4.1	14.3	0.3	
14.6	2.3	12.1	0.2	
14.8	2.6	11.5	0.8	46 ± 2

Table C.2. (Continued)

Salix reticulata	6/25/78	19.7	16.6	6.3	11.2	0	
Salix reticulata	6/29/79	19.2	14.5	2.8	11.0	0.7	
Salix reticulata	7/7/78	22.9	17.6	7.9	11.7	0	
Salix reticulata	7/20/78	29.3	24.2	9.4	15.5	0	
Salix reticulata	8/2/79	25.2	24.1	9.4	14.6	0.1	
Salix reticulata	8/22/79	26.6	24.9	10.7	13.5	0.7	46 ± 1
Salix rotundifolia	6/18/79	17.7	14.8	3.4	11.4	0.1	51 ± 4
Salix rotundifolia	6/27/79	20.4	15.0	3.0	11.9	0	56 ± 2
Salix rotundifolia	7/28/79	30.3	28.5	9.4	17.7	1.2	46 ± 1
Vaccinium uliginosum	6/4/79	31.3	20.1	6.0	13.1	1.0	
Vaccinium uliginosum	6/10/79	28.6	19.6	4.7	14.6	0.3	
Vaccinium uliginosum	6/20/79	27.3	20.6	5.3	15.0	0.3	

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[a] n=4

[b] Sample contained only senescent tissue.

[c] Fiber content was measured on four subsamples of this sample. Means and standard deviations follow: Cell walls=31.15 ± 1.9, ADF=24.6 ± 1.1, Lignin=8.1 ± 2.4, Cellulose=15.5 ± 2.3

Table C.3. Fiber content and in vitro dry matter disappearance (IVDMD) of evergreen shrubs. Samples contained almost entirely leaf tissue. Values are presented on a % dry wt basis.

		Fiber					
Species	Collection Date	Cell walls	ADF	Lignin	Cellulose	Ash	IVDMD (mean±s.d.)[a]
Dryas octopetala	6/7/79	32.2	28.2	6.6	21.4	0.2	
Dryas octopetala	7/14/78	34.9	24.3	9.1	15.5	0.3	48 ± 2
Dryas octopetala	8/9/79	29.0	23.4	7.0	15.3	1.2	
Dryas octopetala[b]	9/20/79	48.2	42.1	16.9	24.7	0.5	6 ± 2
Ledum palustre[c]	10/1/78	36.4	33.3	12.5	20.3	0.5	11 ± 2
Vaccinium vitis-idaea[d]	6/13/78	34.5	27.2	7.5	18.4	1.3	44 ± 2

[a] n=4

[b] Sample contained only senescent tissue.

[c] IVDMD of *Ledum* was analyzed from a sample collected on the Seward Peninsula on 5/26/78.

[d] Fiber content and IVDMD of *Vaccinium* was analyzed from a sample collected on the Seward Peninsula.

Table C.4. Fiber content and in vitro dry matter disappearance (IVDMD) of forbs. Values are presented on a % dry wt basis.

Species	Plant Part	Collection Date	Fiber Cell Walls	ADF	Lignin	Cellulose	Ash	IVDMD (mean±s.d.)[a]
Anemone parviflora	FP[b]	6/25/78	24.7	18.3	4.3	14.0	0	
Anemone richardsonii	FP	6/15/79	19.6	15.2	2.8	11.7	0.7	83 ± 1
Artemesia arctica	FP	7/28/79	26.8	26.6	3.4	16.8	6.4	62 ± 2
Artemesia arctica	FP	8/11/79	29.6	24.4	7.2	15.5	1.6	
Boykinia richardsonii	LP[c]	7/14/78	22.0	16.5	6.8	10.2	0	69 ± 1
Boykinia richardsonii	FP	7/16/78	30.2	28.7	8.2	14.2	6.3	
Boykinia richardsonii	FP	7/20/78	22.8	20.4	3.4	16.8	0.1	
Boykinia richardsonii	LP	8/28/78	15.9	13.3	2.9	8.6	1.7	
Dodecatheon frigidum	LP	7/28/79	14.9	15.8	1.5	12.3	2.0	
Epilobium angustifolium	LP	6/2/79	11.4	9.6	1.1	8.4	0.1	
Epilobium angustifolium	LP	6/10/79	14.2	11.4	2.6	8.7	0.1	64 ± 6
Epilobium angustifolium	LP	6/20/79	13.2	12.2	4.3	9.5	0	
Epilobium latifolium	LP	6/6/78	11.0	10.2	1.1	9.1	0	
Epilobium latifolium	LP	6/10/79	11.6	11.6	2.7	8.6	0.2	71 ± 4
Epilobium latifolium	LB[d]	6/20/78	13.5	11.3	4.0	9.6	0	
Epilobium latifolium	LB	6/27/79	10.8	10.3	1.0	9.5	0.1	69 ± 2
Epilobium latifolium	LB	7/9/78	14.3	11.6	3.2	9.7	0	

Table C.4. (Continued)

Epilobium latifolium	LB	7/14/78	14.4
Epilobium latifolium	LP	8/4/78	14.5
Epilobium latifolium	LF[e]	8/4/78	16.5
Equisetum arvense	UP[f]	6/18/79	25.5
Equisetum arvense	UP	7/28/79	32.1
Equisetum arvense	UP	8/25/78	25.3
Equisetum arvense[g]	UP	9/29/78	46.6
Equisetum arvense[g]	UP	10/10/79	46.9
Equisetum arvense[g]	UP	11/20/78	47.8
Equisetum variegatum	UP	6/10/79	40.2
Equisetum variegatum	UP	6/20/78	42.2
Equisetum variegatum	UP	11/20/78	45.3
Hedysarum alpinum	LP	8/25/78	27.2
Mertensia paniculata	LP	6/6/78	14.9
Pedicularis langsdorfi	FP	6/26/78	46.6
Petasites frigidus	FP	6/6/78	20.2
Petasites frigidus	FP	6/15/79	18.0
Petasites frigidus	LP	8/25/78	18.2
Potentilla palustris	LP	6/26/78	23.3

11.5	3.2	9.1	0	
7.5	1.8	5.3	0.4	75 ± 4
15.0	2.7	10.4	1.9	
20.9	3.7	14.8	2.3	
23.7	3.5	15.8	4.5	69 ± 1
28.8	7.0	13.6	8.3	47 ± 1
46.3	10.2	23.1	13.0	
46.0	11.7	21.7	12.6	46 ± 1
47.0	12.2	25.4	9.4	
36.9	2.6	24.1	10.2	71 ± 1
38.5	9.5	21.5	8.6	
40.0	7.4	27.4	5.2	
20.9	10.2	10.4	0.2	
13.9	3.0	10.3	0.5	
21.0	8.3	11.6	1.1	68 ± 4
17.3	3.9	13.8	0.2	
15.6	3.5	11.7	0.4	
15.4	3.2	11.2	1.0	
15.4	5.6	11.4	0	

Table C.4. (Continued)

Sanguisorba stipulata	LP	6/4/79	12.2	9.7
Sanguisorba stipulata	LP	6/10/79	13.8	11.1
Sanguisorba stipulata	LP	6/18/79	14.2	10.0
Sanguisorba stipulata	LP	6/25/78	13.4	8.6
Sanguisorba stipulata	LP	8/24/78	15.8	12.7
Sanguisorba stipulata	LP	9/15/79	19.8	14.5
Stellaria longipes[h]	LP	11/21/78	49.5	26.5
Streptopus amplexifolius	LF	6/10/79	19.0	15.8
Streptopus amplexifolius	LF	6/25/78	20.9	18.8
Valeriana capitata	LF	6/26/78	18.1	12.7

[a] n=4

[b] FP=floral parts

[c] LP=leaf parts

[d] LB=leaf and floral buds

[e] LF=leaf and floral parts

[f] UP=upper portion of plant

[g] Sample contained only senescent tissue.

[h] Sample contained senescent tissue and small quantities of green tissue.

1.0	8.6	0.1	
1.5	9.3	0.3	72 ± 2
0.3	9.4	0.3	
1.9	7.9	0	
3.1	9.0	0.6	45 ± 2
3.3	10.0	1.3	39 ± 5
4.8	20.3	2.7	
2.1	13.6	0.1	86 ± 1
4.3	15.6	0	
5.4	6.7	0.1	76 ± 4

Table C.5. Fiber content and in vitro dry matter disappearance (IVDMD) of graminoids. Samples contained leaf tissue unless otherwise indicated. Values are presented on a % dry wt basis.

		Fiber					
Species	Collection Date	Cell Walls	ADF	Lignin	Cellulose	Ash	IVDMD (mean±s.d.)[a]
Carex aquatilus	6/26/78	70.1	29.3	3.5	26.1	0.1	
Carex aquatilus	6/28/79	63.6	22.5	1.7	20.8	0.1	
Carex aquatilus[b]	11/20/78	72.9	36.0	5.2	30.6	0.1	54 ± 3
Carex bigelowii	6/5/78	67.9	27.0	3.5	23.1	0.4	
Carex bigelowii[c]	8/3/79	56.8	20.9	3.6	16.5	0.7	52 ± 2
Carex bigelowii	8/15/79	55.1	22.1	3.2	17.1	1.8	53 ± 3
Carex bigelowii	8/21/79	57.2	23.4	3.7	19.0	0.8	
Carex bigelowii[d]	9/15/79	65.9	34.0	6.1	25.5	2.4	34 ± 1
Carex bigelowii[d]	10/1/78	73.8	40.7	8.4	30.0	2.3	
Carex podocarpa	6/10/79	66.5	21.4	1.1	19.2	1.1	63 ± 2
Carex podocarpa	6/20/79	60.8	21.2	1.6	18.6	1.1	66 ± 3
Carex podocarpa	7/28/79	53.2	20.6	2.2	17.1	1.3	
Eriophorum angustifolium[e]	6/10/79	66.7	24.5	2.0	20.9	1.5	
Eriophorum angustifolium[f]	6/26/78	36.2	29.3	8.1	21.4	0	
Eriophorum vaginatum[f]	6/5/78	72.1	27.9	3.1	24.6	0.1	
Eriophorum vaginatum[d]	10/1/78	76.4	42.6	7.9	34.0	0.8	

Table C.5. (Continued)

Festuca altaica[e]	6/15/79	53.7	24.8	2.0	20.7	2.1	
Festuca altaica[e]	6/26/78	60.8	34.4	4.2	30.0	0.2	
Festuca altaica[e]	7/28/79	45.7	24.5	0.8	20.8	3.0	68 ± 1
Festuca altaica	8/22/79	47.9	29.7	1.6	23.3	4.7	63 ± 1
Festuca altaica[d]	9/20/79	65.1	40.6	4.0	31.6	4.9	
Hierochloe alpina	8/4/79	47.4	24.5	3.2	19.5	1.8	70 ± 1
Hierochloe alpina	8/12/79	50.3	22.7	2.5	19.1	1.1	
Hierochloe alpina	8/21/79	46.7	24.4	3.6	18.6	2.2	
Hierochloe alpina[d]	9/9/79	63.9	37.6	4.0	30.5	3.1	
Hierochloe alpina[d]	11/21/78	69.3	36.8	4.5	31.1	1.2	

[a] n=4

[b] Sample contained about 30% green tissue. Remaining tissue was senescent.

[c] Fiber content was measured on four subsamples of this sample. Means and standard deviations follow:

Cell walls=56.8 ± 2.6, ADF=20.9 ± 0.3, Lignin=3.6 ± 0.6, Cellulose=16.5 ± 0.5, Ash=0.7 ± 0.6.

[d] Sample contained only senescent tissue.

[e] Sample contained floral parts and lesser quantities of leaf tissue

[f] Sample contained floral parts only.

Table C.6. Fiber content and in vitro dry matter disappearance (IVDMD) of lichens. Samples contained upper, live portions of lichens. Values are presented on a % dry wt basis.

Species	Collection Date	Fiber				Ash	IVDMD (mean±s.d.)[a]
		Cell Walls	ADF	Lignin	Cellulose		
Cladonia alpestris	6/25/78	82.2	7.2	2.6	3.2	1.3	39 ± 5
Cladonia alpestris	8/12/78	84.9	5.1	0.3	3.4	1.4	27 ± 10[b]
Cladonia rangiferina	8/12/78	84.0	12.1	3.0	8.0	1.0	36 ± 17[b]
Cladonia rangiferina	9/21/78	87.0	13.4	5.2	7.5	0.1	43 ± 3[c]
Cetraria cucullata	9/21/78	43.0	8.2	1.8	6.4	0.1	29 ± 8[c]
Lobaria linita	6/28/79	76.9	24.4	4.0	18.3	2.0	
Masonhalea richardsonii	8/12/78	16.9	4.0	0.9	1.7	1.4	22 ± 3
Peltigera aphthosa	1/7/79	64.0	14.5	7.3	6.9	0.5	32 ± 2
Peltigera aphthosa	6/25/78	74.7	27.5	11.6	14.2	1.8	27 ± 1
Stereocaulon sp.	1/7/79	73.4	18.8	4.1	9.9	4.8	31 ± 1
Stereocaulon sp.	6/1/78	69.8	17.8	4.3	12.1	1.4	
Stereocaulon sp.	6/25/78	72.0	18.6	6.6	11.9	0.4	29 ± 3
Stereocaulon sp.	7/16/78	70.2	16.0	3.1	11.0	1.9	
Thamnolia vermiculata	7/16/78	72.2	[d]				20 ± 3

[a] n=4

[b] n=12

[c] n=20

[d] Sample was too gelatinous to filter.

Table C.7. Fiber content and in vitro dry matter disappearance (IVDMD) of mosses. Samples contained upper portions of mosses. Values are presented on a % dry wt basis.

		Fiber					
Species	Collection Date	Cell Walls	ADF	Lignin	Cellulose	Ash	IVDMD (mean±s.d.)[a]
Hylocomium splendens	8/14/78	76.2	44.0	16.8	25.0	2.3	
Hylocomium splendens	8/22/79	82.3	48.6	16.4	29.8	2.4	8 ± 2
Polytrichum juniperinum	8/21/79	84.2	50.6	24.1	22.5	3.8	0 ± 2
Tomenthypnum nitens	3/14/79	67.5	53.9	23.3	28.4	3.2	
Tomenthypnum nitens	10/10/79	84.5	54.9	27.2	19.5	8.2	12 ± 1

[a] n=4

Table C.8. Fiber content and in vitro dry matter disappearance (IVDMD) of mushrooms. Values are presented on a % dry wt basis.

Species	Collection Date	Fiber				Ash	IVDMD (mean±s.d.)[a]
		Cell Walls	ADF	Lignin	Cellulose		
Amanita pantherina	8/18/78	30.4	16.0	9.6	6.4	0	
Boletus edulis	8/22/79	28.7	26.2	2.0	6.1	0.1	89 ± 1
Boletus edulis[b]	8/22/79	27.3	21.1	9.7	9.9	2.0	91 ± 3
Boletus scaber	8/18/78	33.7	12.0	5.3	6.7	0	92 ± 1
Clitopilus sp.	8/18/78	31.1	9.4	4.0	5.3	0.1	
Cortinarius spp.	8/18/78	32.5	13.6	2.5	11.1	0.1	
Laccaria laccata	8/18/78	33.0	12.7	3.5	9.0	0.2	
Lactarius spp.	8/18/78	43.0	16.8	6.6	10.0	0.1	
Lactarius sp.	8/18/78	43.2	14.8	3.8	11.0	0.1	84 ± 2
Pluteus cervinus	8/18/78	28.6	9.5	0.9	8.5	0.1	

[a] n=4

[b] Sample contained only caps of mushrooms.

APPENDIX D

Fiber content and estimated apparent dry matter disappearance (ADMD) of seasonal diets of the Denali caribou herd, 1978-1979

Table D.1. Fiber content and estimated apparent dry matter digestibility[a] (ADMD) of the spring (mid-May to July) diet. Calculations were based on spring data presented in Table 4 and Appendix C. Means and standard deviations are given.

Spring Diet			Fiber (% dry wt)					
Plant Species	Intake (% of diet)	n	Cell Walls	ADF	Lignin	Cellulose	ADMD (% dry wt)	n
Berries[b]	2	3	20.0 ± 11.5	14.6 ± 8.8	3.0 ± 1.1	11.5 ± 7.0	78 ± 8	3
Deciduous shrubs								
Arctostaphylos spp.	1	4	16.4 ± 1.3	10.5 ± 0.3	2.2 ± 0.5	8.2 ± 0.6		
Betula nana	2	3	24.5 ± 3.2	18.1 ± 2.3	5.0 ± 1.3	13.3 ± 1.9	57[a]	
Salix spp.	41	23	19.4 ± 3.8	15.3 ± 1.9	4.2 ± 1.3	11.1 ± 1.9	67[a]	
Vaccinium uliginosum	1	3	29.1 ± 2.0	20.1 ± 0.5	5.3 ± 0.7	14.2 ± 1.0	———	
	45	45	19.8 ± 1.8[c]	15.4 ± 1.2	4.2 ± 0.4	11.2 ± 0.8	67 ± 2	43
Forbs								
Epilobium angustifolium	3	3	9.6 ± 7.1	11.1 ± 1.3	2.7 ± 1.6	8.9 ± 0.6	64	1
Epilobium latifolium	1	4	11.7 ± 1.2	10.8 ± 0.7	2.2 ± 1.4	9.2 ± 0.5	70 ± 1	2
Equisetum arvense	1	1	25.5	20.9	3.7	14.8		
Equisetum variegatum	1	2	41.2 ± 1.4	37.7 ± 1.1	5.1 ± 6.3	22.8 ± 1.8	71	1
Sanguisorba stipulata	3	4	13.4 ± 0.9	9.9 ± 1.0	1.2 ± 0.7	8.8 ± 0.7	72	1
Other forbs	7	10	21.5 ± 9.2	16.4 ± 2.5	4.3 ± 1.8	12.0 ± 2.5	79 ± 10	3
	16	16	18.6 ± 8.1[c]	15.5 ± 6.8	3.3 ± 1.3	11.5 ± 3.5	73 ± 6	15
Graminoids								
Carex spp.	7	5	65.8 ± 3.6	24.3 ± 3.7	2.3 ± 1.1	21.6 ± 3.1	65 ± 2	2
Eriophorum spp.	4	3	58.3 ± 19.4	27.2 ± 2.5	4.4 ± 3.3	22.3 ± 2.0		
Festuca altaica	1	2	57.3 ± 5.0	29.6 ± 6.8	3.1 ± 1.6	25.4 ± 6.6	———	0
	12	12	62.6 ± 4.0[c]	25.7 ± 1.9	3.1 ± 1.0	22.2 ± 1.1	65 ± 0	7

Table B.1. (Continued)

Lichens[d]	25	25	82.9 ± 17.9[c]	9.9 ± 4.1	2.9 ± 1.9	6.4 ± 2.5	70[a]

[a] ADMD was assumed to be equivalent to IVDMD except for shrubs and lichens (see Methods).

[b] All analyses were applied, regardless of collection dates.

[c] Figures are weighted in terms of the proportions of plant species in the diet.

[d] Lichens contributing to the diet were assumed to be *Cladonia alpestris* (8%), *Cladonia rangiferina* (8%), *Cetraria cucullata* (6%), *Peltigera* (1%), and *Stereocaulon* (2%). Lichen analyses were applied regardless of collection dates.

Table D.2. Fiber content and estimated apparent dry matter digestibility[a] (ADMD) of the summer (July to mid-August) diet. Calculations were based on summer data presented in Table 4 and Appendix C. Means and standard deviations are given.

Summer Diet			Fiber (% dry wt)					
Plant Species	Intake (% of diet)	n	Cell Walls	ADF	Lignin	Cellulose	ADMD (% dry wt)	n
Berries[b]	2	3	20.0 ± 11.5	14.6 ± 8.8	3.0 ± 1.1	11.5 ± 7.0	78 ± 8	3
Deciduous shrubs								
Betula nana	2	2	26.1 ± 0.5	16.2 ± 2.3	5.9 ± 1.5	10.1 ± 0.7	57[a]	
Salix spp.	46	19	27.6 ± 3.7	21.8 ± 3.2	8.3 ± 1.1	13.5 ± 2.5	67[a]	
	48	48	27.5 ± 0.3[c]	21.6 ± 1.1	8.2 ± 0.5	13.4 ± 0.7	67 ± 2	48
Evergreen shrubs								
Dryas octopetala	1	2	32.0 ± 4.2	23.9 ± 0.6	8.1 ± 1.5	15.4 ± 0.1	54[a]	
Forbs								
Artemesia arctica	2	2	28.2 ± 2.0	25.5 ± 1.6	5.3 ± 2.7	16.2 ± 0.9	62	1
Boykinia richardsonii	2	3	25.0 ± 4.5	21.9 ± 6.2	6.1 ± 2.5	13.7 ± 3.3	69	1
Dodecatheon frigidum	1	1	14.9	15.0	1.5	12.3		
Epilobium latifolium	2	4	14.9 ± 1.1	11.4 ± 3.1	2.7 ± 0.7	8.6 ± 2.3	75	1
Equisetum arvense	2	1	32.1	23.7	3.5	15.8	69	1
Equisetum variegatum	1	1	42.2	38.5	9.5	21.5		
	10	10	25.8 ± 8.9[c]	22.8 ± 7.9	4.6 ± 2.3	14.2 ± 3.8	69 ± 5	8
Graminoids								
Carex spp.	6	3	55.0 ± 1.0	21.2 ± 0.8	3.0 ± 0.7	16.9 ± 0.3	53 ± 1	2
Festuca altaica	2	1	45.7	24.5	0.8	20.8	68	1
Hierochloe alpina	2	2	48.9 ± 2.1	23.6 ± 1.3	2.9 ± 0.5	19.3 ± 0.3	70	1
	10	10	51.9 ± 4.1[c]	22.3 ± 1.5	3.3 ± 1.8	18.2 ± 1.7	59 ± 8	10

Table D.2. (Continued)

Lichens[d]	17	17	75.6 ± 16.2[c]	10.4 ± 4.5	3.1 ± 2.1	6.3 ± 2.6	70[a]	
Mushrooms[e]	12	12	31.7 ± 2.6[c]	17.5 ± 3.4	5.0 ± 1.0	8.1 ± 0.8	90 ± 1	12

[a] ADMD was assumed to be equivalent to IVDMD except for shrubs and lichens (see Methods).

[b] All analyses were applied, regardless of collection dates.

[c] Figures are weighted in terms of the proportions of plant species in the diet.

[d] Lichens contributing to the diet were assumed to be *Cladonia alpestris* (6%), *Cladonia rangiferina* (6%), *Cetraria cucullata* (3%), *Peltigera* (1%), and *Stereocaulon* (1%). Lichen analyses were applied regardless of collection dates.

[e] Mushrooms contributing to the diet were assumed to be *Boletus* spp. (8%) and the remaining species listed in Appendix C (4%), exclusive of *Amanita*. Mushroom analyses were applied regardless of collection dates.

Table D.3. Fiber content and estimated apparent dry matter digestibility^{a} (ADMD) of the autumn (mid-August to mid-October) diet. Calculations are based on autumn data presented in Table 4 and Appendix C. Means and standard deviations are given.

Autumn Diet			Fiber (% dry wt)					
Plant Species	Intake (% of diet)	n	Cell Walls	ADF	Lignin	Cellulose	ADMD (% dry wt)	n
Berries^{b}	3	3	20.0 ± 11.5	14.6 ± 8.8	3.0 ± 1.1	11.5 ± 7.0	78 ± 3	3
Deciduous shrubs								
Betula nana	2	2	27.0 ± 0.8	16.6 ± 2.9	5.8 ± 1.4	10.7 ± 1.6	57^{a}	
Salix spp.	12	9	27.4 ± 5.6	22.5 ± 5.8	8.7 ± 3.5	13.7 ± 3.0	67^{a}	
	14	14	27.3 ± 0.1^{c}	21.7 ± 2.1	8.3 ± 1.1	13.3 ± 1.1	66 ± 4	14
Evergreen shrubs								
Dryas octopetala	1	1	48.2	42.1	16.9	24.7	54^{a}	
Vaccinium vitis-idaea^{a}	1	1	34.6	27.2	7.5	18.4	64^{a}	
	2	2	41.4 ± 9.7^{c}	34.7 ± 10.5	12.2 ± 6.6	21.6 ± 4.5	59 ± 7	2
Forbs								
Boykinia richardsonii	1	1	15.9	13.3	2.9	8.6		
Equisetum arvense	2	3	39.6 ± 12.4	40.4 ± 10.0	9.6 ± 2.4	19.5 ± 5.1	47 ± 1	2
Equisetum variegatum	2	1	45.3	40.0	7.4	27.4		
Hedysarum alpinum	1	1	27.2	20.9	10.2	10.4		
Petasites frigidus	1	1	18.2	15.4	3.2	11.2		
Sanguisorba stipulata	2	2	17.8 ± 2.8	13.6 ± 1.3	3.2 ± 0.1	17.8 ± 11.0	39	1
	9	9	29.6 ± 12.7^{c}	26.4 ± 13.3	6.3 ± 3.2	17.7 ± 6.8	43 ± 5	4

Table D.3. (Continued)

Graminoids								
Carex spp.	9	4	67.5 ± 7.7	33.5 ± 7.3	5.9 ± 2.0	26.3 ± 5.4	44 ± 14	2
Eriophorum spp.	1	1	76.4	42.6	7.9	34.0		
Festuca altaica	2	2	56.5 ± 12.2	35.2 ± 7.7	2.8 ± 1.7	27.5 ± 5.9	63	1
Hierochloe alpina	2	3	60.0 ± 11.8	32.9 ± 7.4	4.0 ± 0.5	26.7 ± 7.1		
	14	14	65.5 ± 5.4[c]	34.3 ± 2.5	5.3 ± 1.4	27.1 ± 2.0	47 ± 7	11
Lichens[d]	43	43	73.3 ± 17.5[c]	10.3 ± 4.3	3.0 ± 1.9	6.4 ± 2.5	70[a]	
Mosses[b]	5	5	78.9 ± 7.2	50.4 ± 4.4	21.6 ± 4.8	25.0 ± 4.2	7 ± 6	3
Mushrooms[e]	10	10	31.5 ± 2.6[c]	17.7 ± 3.4	5.1 ± 1.0	8.1 ± 0.8	90 ± 1	10

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[a] ADMD was assumed to be equivalent to IVDMD except for shrubs and lichens (see Methods).

[b] All analyses were applied, regardless of collection dates.

[c] Figures are weighted in terms of the proportions of plant species in the diet.

[d] Lichens contributing to the diet were assumed to be *Cladonia alpestris* (14%), *Cladonia rangiferina* (14%), *Cetraria cucullata* (10%), *Peltigera* (2%), and *Stereocaulon* (3%). Lichen analyses were applied regardless of collection dates.

[e] Mushrooms contributing to the diet were assumed to be *Boletus* spp. (7%) and the remaining species listed in Appendix C (3%), exclusive of *Amanita*.

Table D.4. Fiber content and estimated apparent dry matter digestibiltiy^{a} (ADMD) of the winter (mid-October to mid-May) diet. Calculations are based on winter data presented in Table 4 and Appendix C. Means and standard deviations are given.

Winter Diet			Fiber (% dry wt)					
Plant Species	Intake (% of diet)	n	Cell Walls	ADF	Lignin	Cellulose	ADMD (% dry wt)	n
Deciduous shrubs								
Salix sp.	1	2	36.0 ± 2.1	33.4 ± 1.4	12.3 ± 1.6	20.8 ± 4.6		
Evergreen shrubs								
Dryas octnpetala	1	1	48.2	42.1	16.9	24.7		
Vaccinium vitis-idaea^{b}	6	1	34.5	27.2	7.5	18.4	64^{a}	
	7	7	36.5 ± 5.2^{c}	29.3 ± 5.6	8.8 ± 3.6	19.3 ± 2.4	64 ± 0	7
Forbs								
Equisetum arvense	3	3	47.1 ± 0.6	46.4 ± 0.5	11.4 ± 1.0	23.4 ± 1.9	46	1
Equisetum variegatum	3	1	45.3	40.0	7.4	27.4		
Stellaria longipes	1	1	49.5	26.5	4.8	20.3		
	7	7	46.7 ± 1.5^{c}	40.8 ± 7.1	8.7 ± 2.7	24.7 ± 2.8	46 ± 0	3
Graminoids								
Carex spp.	7	2	73.4 ± 0.7	38.4 ± 3.3	6.8 ± 2.3	30.3 ± 0.4	54	1
Festuca aitaica	2	1	65.1	40.6	4.0	31.6		
Hierochloe alpina	2	1	69.3	36.8	4.5	31.1		
	11	11	71.1 ± 3.4^{c}	38.5 ± 1.2	5.9 ± 1.3	30.7 ± 0.6	54 ± 0	7

Table D.4. (Continued)

Lichens[d]	62	62	73.4 ± 17.2[c]	10.4 ± 4.3	3.0 ± 1.9	6.4 ± 2.5	70[a]	
Mosses[b]	10	5	78.9 ± 7.2	50.4 ± 4.4	21.6 ± 4.8	25.0 ± 4.2	7 ± 6	3
Mushrooms[e]	2	3	29.9 ± 3.4	19.8 ± 7.2	5.7 ± 3.9	7.6 ± 2.0	91 ± 2	3

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[a] ADMD was assumed to be equivalent to IVDMD except in the case of shrubs and lichens (see Methods).

[b] All analyses were applied, regardless of collection dates.

[c] Figures are weighted in terms of the proportions of plant species in the diet.

[d] Lichens contributing to the diet were assumed to be Cladonia alpestris (20%), Cladonia rangiferina (20%), Cetraria cucullata (14%), Peltigera (3%), and Stereocaulon (5%). Lichen analyses were applied regardless of collection dates.

[e] Mushrooms contributing to the diet were assumed to be Boletus spp. Analyses were applied regardless of collection dates.

APPENDIX E

Nutrient and moisture content of forage samples collected in and near Denali National Park, 1978-1979.

Table E.1. Nutrient content of berries.

		Nutrients (% dry wt)						
Species	Collection Date	N	P	K	Ca	Mg	Na	TNC
Empetrum nigrum	8/22/79	0.43	0.08		0.02			35.3
Vaccinium uliginosum	8/25/78	0.65	0.12		0.04			34.8
Vaccinium vitis-idaea	8/28/78	0.71	0.13	0.54	0.06	0.06	0.08	18.1

Table E.2. Nutrient and moisture content of deciduous shrubs. Samples contained leaf tissue.

		Nutrients (% dry wt)							
Species	Collection Date	N	P	K	Ca	Mg	Na	TNC	H_2O(%)
Arctostaphylos spp.[a]	1/7/79	0.56	0.12				0.01	2.4	
Arctostaphylos spp.	6/2/79	2.45	0.33		0.48			12.8	74
Arctostaphylos spp.	6/7/79	2.13	0.24		0.46			13.9	74
Arctostaphylos spp	6/19/79	2.15	0.27		0.60			15.2	74
Arctostaphylos spp	6/25/78	1.72	0.19				0.33	11.1	
Arctostaphylos spp	7/31/79	1.43	0.16		0.72			14.8	60
Betula nana	6/3/79	4.02	0.49		0.40			6.5	71
Betula nana	6/10/79	3.67	0.47		0.34			8.2	71
Betula nana	6/18/79	3.32	0.42				0.09	0.6	
Betula nana	7/20/78	3.13	0.24				0.01	2.1	
Betula nana	8/16/78	2.54	0.21				0.01	3.7	
Betula nana	9/10/78	0.72	0.40				0.12	6.2	
Salix alaxensis	6/20/78	3.08	0.58				0.11	2.4	
Salix alaxensis	7/14/78	2.62	0.27				0.21	6.0	
Salix alaxensis	7/16/78	2.78	0.38				0.01	4.2	
Salix alaxensis	8/5/78	2.39	0.13				0.01		
Salix alaxensis	9/8/78	1.65	0.11				0.01	8.2	

Table E.2. (Continued)

Salix arctica	6/18/79	4.79
Salix arctica	7/14/78	2.36
Salix arctica[b]	7/30/79	2.67
Salix arctica	8/11/79	2.67
Salix arctica	8/21/79	2.23
Salix commutata	6/4/79	6.00
Salix commutata	6/10/79	4.73
Salix fuscescens	6/28/79	3.59
Salix glauca	7/28/78	1.94
Salix glauca	8/1/78	2.43
Salix glauca	8/14/78	2.28
Salix glauca	8/25/78	1.70
Salix glauca	9/9/78	1.18
Salix pulchra[a]	1/5/79	0.76
Salix pulchra	6/2/78	3.52
Salix pulchra	6/2/79	4.37
Salix pulchra	6/5/78	3.57
Salix pulchra	6/7/79	4.32
Salix pulchra	6/11/79	4.06

0.77		0.70			5.3	82
0.34				0.22	5.3	
0.22		1.50			9.6	70
0.18		0.60			11.6	64
0.22		1.92			9.9	69
0.83		0.34			11.4	79
0.86		0.86			9.4	78
0.57		0.82			9.5	77
0.19				0.13	10.5	
0.12				0.01	3.9	
0.13				0.01	4.4	
0.08				0.01	5.1	
0.09				0.26	13.2	
0.10				0.01	0.1	
0.52	1.13	0.32	0.14	0.10	2.5	
0.75		0.44			2.6	76
0.49	1.26	0.29	0.17	0.02	2.5	
0.72		0.40			3.2	
0.65		0.46			4.8	62

Table E.2. (Continued)

Salix pulchra	6/18/78	3.12
Salix pulchra	6/19/79	4.60
Salix pulchra	6/20/79	3.35
Salix pulchra	6/25/78	3.47
Salix pulchra	6/28/79	3.67
Salix pulchra	6/29/79	2.99
Salix pulchra	7/7/78	3.04
Salix pulchra	7/16/78	2.00
Salix pulchra	7/20/78	2.55
Salix pulchra	7/24/78	3.09
Salix pulchra	8/1/78	2.31
Salix pulchra	8/11/78	1.90
Salix pulchra	8/18/78	2.70
Salix pulchra	8/25/78	0.90
Salix pulchra	9/8/78	0.86
Salix pulchra	9/20/79	1.21
Salix reticulata	6/3/79	3.36
Salix reticulata	6/10/79	3.26
Salix reticulata	6/18/79	3.20

0.57		0.17	2.6	
0.75	0.76		7.3	79
0.50	0.52		4.8	74
0.55		0.15	1.9	
0.62	0.72		5.4	76
0.34	0.50		11.2	72
0.23		0.05	2.1	
0.33		0.23	4.9	
0.32		0.24	3.3	
0.19		0.04	3.1	
0.22		0.08	3.2	
0.11		0.01	7.0	
0.16		0.03		
0.06		0.01	8.4	
0.08		0.14	3.7	
0.08	0.94		4.8	33
0.51	1.04		5.0	78
0.45	1.22		7.3	78
0.43	0.98		7.0	79

Table E.2. (Continued)

Salix reticulata	6/25/78	2.70	0.27		0.12	3.1	
Salix reticulata	6/29/79	3.29	0.23	1.42		9.9	76
Salix reticulata	7/7/78	2.00	0.24		0.07	8.0	
Salix reticulata	7/20/78	1.65	0.16		0.01	7.4	
Salix reticulata	8/2/79	2.45	0.19	1.78		13.8	72
Salix reticulata	8/22/79	1.83	0.14	1.70		13.9	70
Salix rotundifolia	6/18/79	3.66	0.42	0.66		9.5	78
Salix rotundifolia	6/27/79	3.32	0.38	0.52		10.0	78
Salix rotundifolia	7/28/79	2.63	0.20	1.14		12.7	72
Vaccinium uliginosum	6/4/79	3.83	0.50	0.30		1.6	77
Vaccinium uliginosum	6/10/79	3.05	0.45	0.38		3.8	77
Vaccinium uliginosum	6/20/79	3.17	0.42	0.34		3.4	76

[a] Sample contained only senescent tissue.

[b] Nutrient and moisture content was measured on four subsamples of this sample. Means and standard deviations follow: N=2.67 ± 0.05, P=0.22 ± 0.01, Ca=1.50 ± 0.05, TNC=9.6 ± 0.9, H_2O=70 ± 1.

Table E.3. Nutrient and moisture content of evergreen shrubs. Samples contained almost entirely leaf tissue.

		Nutrients (% dry wt)							
Species	Collection Date	N	P	K	Ca	Mg	Na	TNC	H_2O (%)
Dryas octopetala	6/7/79	2.09	0.20		1.00			9.9	61
Dryas octopetala	7/14/78	1.45	0.19				0.09	9.1	
Dryas octopetala	8/9/79	1.54	0.15		0.80		0.14	11.3	60
Dryas octopetala[a]	9/20/79	0.70	0.09		1.39			3.6	49
Ledum palustre	10/1/78	1.41	0.13	0.33	0.24	0.11	0.01	8.8	
Vaccinium vitis-idaea[b]	6/10/77	1.22	0.18				0.47	16.4	

[a] Sample contained only senescent tissue.

[b] Sample was collected on the Seward Peninsula.

Table E.4. Nutrient and moisture content of forbs.

Species	Plant Part	Collection Date	Nutrients (% dry wt) N	P	K	Ca	Mg	Na	TNC	H_2O (%)
Anemone parviflora	FP[a]	6/25/78	2.86	0.38				0.05		
Anemone richardsonii	FP	6/15/79	3.72	0.42		0.50			20.8	88
Artemesia arctica	FP	7/28/79	2.53	0.35		0.92			11.3	81
Artemesia arctica	FP	8/11/79	2.11	0.29		1.04			12.2	79
Boykinia richardsonii	LP[b]	7/14/78	2.15	0.57				0.01	4.4	
Boykinia richardsonii	FP	7/16/78	2.61	0.42				0.01	3.3	
Boykinia richardsonii	FP	7/20/78	1.75	0.37				0.13	13.4	
Boykinia richardsonii	LP	8/28/78	1.03	0.08				0.01	6.8	
Dodecatheon frigidum	LP	7/28/79	2.37	0.17		1.36			15.0	81
Epilobium angustifolium	LP	6/2/79	5.40	0.90		0.64			2.3	87
Epilobium angustifolium	LP	6/10/79	4.21	0.70		0.64			0.8	86
Epilobium angustifolium	LP	6/20/79	3.38	0.66				0.15	0.9	
Epilobium latifolium	LP	6/6/78	4.90	0.68	1.92	0.41	0.22	0.01	1.2	
Epilobium latifolium	LP	6/10/79	3.75	0.50		1.06			7.2	84
Epilobium latifolium	LB[c]	6/20/78	2.97	0.48				0.01	2.2	
Epilobium latifolium	LB	6/27/79	4.17	0.56		0.82			6.4	84
Epilobium latifolium	LB	7/9/78	2.76	0.36				0.01	3.8	

Table E.4. (Continued)

Epilobium latifolium	LB	7/14/78	3.05
Epilobium latifolium	LP	8/4/78	1.63
Epilobium latifolium	LF[d]	8/4/78	2.07
Equisetum arvense	UP[e]	6/18/79	5.50
Equisetum arvense	UP	7/28/79	2.14
Equisetum arvense	UP	8/25/78	1.97
Equisetum arvense[f]	UP	9/29/78	1.04
Equisetum arvense[f]	UP	10/10/79	1.29
Equisetum arvense[f]	UP	11/20/78	1.16
Equisetum variegatum	UP	6/10/79	1.49
Equisetum variegatum	UP	6/20/78	1.10
Equisetum variegatum	UP	11/20/78	0.79
Hedysarum alpinum	LP	8/25/78	2.03
Mertensia paniculata	LP	6/6/78	5.50
Pedicularis langsdorfii	FP	6/26/78	2.74
Petasites frigidus	FP	6/6/78	3.18
Petasites frigidus	FP	6/15/79	3.99
Petasites frigidus	LP	8/25/78	1.87
Potentilla palustris	LP	6/26/78	2.20

0.48				0.13	5.3	
0.16				0.25	11.7	
0.23				0.01	3.2	
0.82		1.12			6.2	87
0.21		0.68			18.1	77
0.15				0.03	6.5	
0.13	0.20	1.51	0.14	0.09	0.3	
0.13		3.64			1.7	31
0.14	0.52	1.30	0.49	0.02	1.0	68
0.23		1.44			11.0	
0.15				0.11	10.8	
0.11	0.85	0.70	0.21	0.02	9.8	
0.12				0.01	6.1	
0.79	3.59	0.28	0.14	0.01	4.2	
0.28				0.01	7.2	
0.41	2.69	0.34	0.20	0.02	10.6	
0.44		0.86			3.5	84
0.13				0.01	7.2	
0.29				0.04	6.5	

Table E.4. (Continued)

Sanguisorba stipulata	LP	6/4/79	5.30	0.75	0.74		1.6	81
Sanguisorba stipulata	LP	6/10/79	3.94	0.64	0.78		7.5	81
Sanguisorba stipulata	LP	6/18/79	4.49	0.60	0.94		4.1	81
Sanguisorba stipulata	LP	6/25/78	3.13	0.46		0.19	1.2	
Sanguisorba stipulata	LP	8/24/78	2.01	0.17		0.01	1.5	
Sanguisorba stipulata	LP	9/15/79	1.96	0.15	2.58		7.7	84
Stellaria longipes[g]	LP	11/21/78	1.63	0.15		0.03	9.1	
Streptopus amplexifolius	LF	6/10/79	5.80	0.71	0.46		10.9	89
Streptopus amplexifolius	LF	6/25/78	3.49	0.55		0.20	8.6	
Valeriana capitata	LF	6/26/78	2.22	0.34		0.25	12.2	

[a] FP = floral parts

[b] LP = leaf parts

[c] LB = leaf and floral buds

[d] LF = leaf and floral parts

[e] UP = upper portions of plant

[f] Sample contained only senescent tissue.

[g] Sample contained senescent tissue and small quantities of green tissue (green nodes).

Table E.5. Nutrient and moisture content of graminoids. Samples contained leaf tissue unless otherwise indicated.

		Nutrients (% dry wt)							
Species	Collection Date	N	P	K	Ca	Mg	Na	TNC	H_2O (%)
Carex aquatilis	6/26/78	1.80	0.25				0.29	5.0	
Carex aquatilis	6/28/79	2.92	0.29		0.22			13.0	69
Carex aquatilis[a]	11/20/78	0.81	0.08	0.89	0.35	0.14	0.04	5.6	
Carex bigelowii	6/5/78	2.89	0.33	1.62	0.15	0.14	0.06	5.4	
Carex bigelowii[b]	8/3/79	2.47	0.19		0.56			15.5	63
Carex bigelowii	8/15/79	2.17	0.16		0.72			16.8	63
Carex bigelowii	8/21/79	1.94	0.14		0.58			15.4	66
Carex bigelowii[c]	9/15/79	1.41	0.10		0.74			3.5	66
Carex bigelowii[c]	10/1/78	0.54	0.08	0.20	0.40	0.13	0.01	3.8	76
Carex podocarpa	6/10/79	4.10	0.35		0.48			7.5	69
Carex podocarpa	6/20/79	4.15	0.36		0.52			9.7	82
Carex podocarpa	7/28/79	2.81	0.18		0.78			15.4	
Eriophorum angustifolium[d]	6/10/79	2.62	0.33		0.10			6.0	
Eriophorum angustifolium[e]	6/26/78	1.73	0.18				0.04	3.7	
Eriophorum vaginatum[e]	6/5/78	1.93	0.34	1.06	0.08	0.13	0.16	4.2	
Eriophorum vaginatum[c]	10/1/78	0.55	0.03				0.01	2.1	

Table E.5. (Continued)

Festuca altaica[d]	6/15/79	3.04	0.33		0.24			13.8	70
Festuca altaica[d]	6/26/78	1.37	0.18				0.13	11.0	
Festuca altaica[d]	7/28/79	2.15	0.16		0.40			19.4	67
Festuca altaica	8/22/79	1.58	0.12		0.36			18.7	62
Festuca altaica[c]	9/20/79	0.71	0.06		0.38			4.1	46
Hierochloe alpina	8/4/79	2.05	0.15		0.38			19.9	67
Hierochloe alpina	8/12/79	1.90	0.18		0.28			20.0	65
Hierochloe alpina	8/21/79	1.68	0.16		0.44			21.2	68
Hierochloe alpina[c]	9/9/79	0.69	0.06		0.38			7.9	45
Hierochloe alpina[c]	11/21/78	1.02	0.08	0.71	0.13	0.11	0.01	3.6	

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[a] Sample contained about 30% green tissue. Remaining tissue was senescent.

[b] Nutrient and moisture content was measured on four subsamples of this sample. Means and standard deviations follow: N=2.47 ± 0.07, P=0.19 ± 0.01, Mg=0.56 ± 0.04, TNC=15.5 ± 1.6, H_2O=63 ± 1.

[c] Sample contained only senescent tissue.

[d] Sample contained floral parts and lesser quantities of leaf tissue.

[e] Sample contained only floral parts.

Table E.6. Nutrient content of lichens. Samples contained only upper, live portions of lichens.

Species	Collection Date	Nutrients (% dry wt) N	P	K	Ca	Mg	Na	TNC
Cladonia alpestris	6/25/78	0.52	0.05				0.02	0.1
Cladonia alpestris	8/12/78	0.32	0.01				0.01	0.1
Cladonia rangiferina	8/12/78	0.34	0.03				0.01	0.1
Cladonia rangiferina	9/21/78	0.19	0.03				0.07	0.1
Cetraria cucullata	9/21/78	0.17	0.04				0.01	9.0
Lobaria linita	6/28/79	1.81	0.15		0.20			2.0
Masonhalea richardsonii	8/12/78	0.23	0.01				0.01	5.7
Peltigera aphthosa	1/7/79	2.41	0.14				0.01	3.0
Peltigera aphthosa	6/25/78	1.33	0.09				0.19	0.3
Stereocaulon sp.	1/7/79	0.86	0.06				0.01	0.3
Stereocaulon sp.	6/1/78	0.87	0.07	0.16	0.15	0.04	0.01	0.2
Stereocaulon sp.	6/25/78	0.85	0.08				0.41	0.1
Stereocaulon sp.	7/16/78	0.82	0.10				0.17	0.1
Thamnolia vermiculata	7/16/78	0.41	0.08				0.25	0.1

Table E.7. Nutrient and moisture content of mosses. Samples contained upper portions of mosses.

Species	Collection Date	Nutrients (% dry wt)						TNC	H_2O (%)
		N	P	K	Ca	Mg	Na		
Hylocomium splendens	8/14/78	1.09	0.12				0.01		
Hylocomium splendens	8/22/79	0.60	0.11		0.22			4.8	74
Polytrichum juniperinum	8/21/79	0.53	0.08		0.30			6.1	58
Tomenthypnum nitens	3/14/79	1.30	0.19	0.36	0.31	0.20	0.01	1.1	
Tomenthypnum nitens	10/10/79	0.75	0.10		0.50			1.8	31

Table E.8. Nutrient and moisture content of mushrooms.

Species	Collection Date	Nutrient (% dry wt) N	P	K	Ca	Mg	Na	TNC	H_2O (%)
Amanita pantherina	8/18/78	4.07	0.73	3.45	0.06	0.12	0.11	4.9	
Boletus edulis	8/22/79	7.30	0.85		0.01				92
Boletus edulis[a]	8/22/79	6.90	0.80		0.04			10.0	92
Boletus scaber	8/18/78	5.00	0.73	2.46	0.05	0.08	0.11	3.3	
Clitopilus sp.	8/18/78	4.89	0.90	2.47	0.04	0.08	0.35	4.6	
Cortinarius spp.	8/18/78	3.33	0.38	3.04	0.07	0.08	0.04	2.3	
Laccaria laccata	8/18/78	3.57	0.39	2.79	0.03	0.10	0.11	3.8	
Lactarius spp.	8/18/78	3.49	0.44		0.01			15.8	
Lactarius sp.	8/18/78	2.83	0.39	2.42	0.05	0.08	0.02	5.3	
Pluteus cervinus	8/18/78	5.00	0.62	3.57	0.05	0.09	0.06	2.1	

[a] Sample contained only caps of mushrooms.

APPENDIX F

Nutrient content of seasonal diets of the Denali caribou herd, 1978-1979.

Table F.1. Nutrient content of the spring (mid-May to July) diet. Calculations are made based on spring data presented in Table 4 and Appendix D. Means, standard deviations, and sample size (in parentheses) are given.

Sample Diet		Nutrients (% dry wt)						
Plant Species	Intake (% of diet)	N	P	K	Ca	Mg	Na	TNC
Berries[a]	2	0.60 ± 0.15 (3)	0.11 ± 0.03 (3)	0.54 (1)	0.04 ± 0.02 (3)	0.06 (1)	0.08 (1)	29.4 ± 9.8 (3)
Deciduous shrubs								
Arctostaphylos spp	1	2.11 ± 0.30 (4)	0.26 ± 0.06 (4)		0.51 ± 0.08 (3)		0.33 (1)	13.3 ± 1.7 (4)
Betula nana	2	3.67 ± 0.35 (3)	0.46 ± 0.04 (3)		0.37 ± 0.04 (2)		0.09 (1)	5.1 ± 4.0 (3)
Salix spp.	41	3.74 ± 0.76 (23)	0.55 ± 0.17 (23)	1.20 ± 0.09 (2)	0.68 ± 0.31 (14)	0.16 ± 0.02 (2)	0.11 ± 0.05 (6)	6.0 ± 3.2 (23)
Vaccinium uliginosum	1	3.35 ± 0.42 (3)	0.46 ± 0.04 (3)		0.34 ± 0.04 (3)			2.9 ± 1.2 (3)
	45	3.69 ± 0.25[b] (45)	0.54 ± 0.05 (45)	1.20 ± 0 (41)	0.65 ± 0.08 (45)	0.16 ± 0 (41)	0.11 ± 0.03 (44)	6.1 ± 1.2 (45)
Forbs								
Epilobium angustifolium	3	4.33 ± 1.02 (3)	0.75 ± 0.13 (3)		0.64 ± 0 (2)		0.15 (1)	1.3 ± 0.8 (3)
Epilobium latifolium	1	3.95 ± 0.81 (4)	0.56 ± 0.09 (4)	1.92 (1)	0.76 ± 0.33 (3)	0.22 (1)	0.01 ± 0 (2)	4.3 ± 3.0 (4)
Equisetum arvense	1	5.50 (1)	0.82 (1)		1.12 (1)			6.2 (1)
Equisetum variegatum	1	1.30 ± 0.28 (2)	0.19 ± 0.06 (2)		1.44 (1)		0.11 (1)	10.9 ± 0.1 (2)
Sanguisorba stipulata	3	4.22 ± 0.91 (4)	0.61 ± 0.12 (4)		0.82 ± 0.11 (3)		0.19 (1)	3.6 ± 2.9 (4)

Table F.1. (Continued)

Other forbs	7	3.57 ± 1.24 (10)	0.46 ± 0.17 (10)	3.14 ± 0.64 (2)	0.49 ± 0.23 (5)	0.17 ± 0.04 (2)	0.08 ± 0.10 (7)	8.1 ± 3.0 (9)
	16	3.77 ± 0.89[b] (16)	0.55 ± 0.16 (16)	2.99 ± 0.43 (8)	0.70 ± 0.27 (16)	0.18 ± 0.02 (8)	0.11 ± 0.05 (15)	5.8 ± 3.1 (16)
Graminoids								
Carex spp.	7	3.17 ± 0.98 (5)	0.32 ± 0.05 (5)	1.62 (1)	0.34 ± 0.18 (4)	0.14 (1)	0.18 ± 0.16 (2)	8.1 ± 3.3 (5)
Eriophorum spp.	4	2.09 ± 0.47 (3)	0.28 ± 0.09 (3)	1.06 (1)	0.09 ± 0.01 (2)	0.13 (1)	0.10 ± 0.08 (2)	
Festuca altaica	1	2.21 ± 1.18 (2)	0.26 ± 0.11 (2)		0.24 (1)		0.13 (1)	12.4 ± 2.0 (2)
	12	2.73 ± 0.54[b] (12)	0.30 ± 0.02 (12)	1.42 ± 0.28 (11)	0.25 ± 0.12 (12)	0.14 ± 0.01 (11)	0.15 ± 0.04 (12)	8.6 ± 1.5 (8)
Lichens[c]	25	0.40 ± 0.35[b] (25)	0.04 ± 0.02 (25)	0.16 ± 0 (2)	0.15 ± 0 (2)	0.04 ± 0 (2)	0.04 ± 0.04 (25)	2.3 ± 3.9 (25)

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[a] All analyses were applied, regardless of collection dates.

[b] Figures are weighted in terms of the proportions of plant species in the diet.

[c] Lichens contributing to the diet were assumed to be *Cladonia alpestris* (8%), *Cladonia rangiferina* (8%), *Cetraria cucullata* (6%), *Peltigera* (1%), and *Stereocaulon* (2%). Lichen analyses were applied regardless of collection dates.

Table F.2. Nutrient content of the summer (July to mid-August) diet. Calculations were made based on summer data presented in Table 4 and Appendix D. Means, standard deviations, and sample size (in parentheses) are given.

Summer Diet		Nutrients (% dry wt)						
Plant species	Intake (% of diet)	N	P	K	Ca	Mg	Na	TNC
Berries[a]	2	0.60 ± 0.15 (3)	0.11 ± 0.03 (3)	0.54 (1)	0.04 ± 0.02 (3)	0.06 (1)	0.08 (1)	29.4 ± 9.8 (3)
Deciduous shrubs								
Betula nana	2	2.84 ± 0.42 (2)	0.23 ± 0.02 (2)				0.01 ± 0 (2)	2.9 ± 1.1 (2)
Salix spp.	46	2.41 ± 0.39 (19)	0.22 ± 0.08 (19)		1.26 ± 0.51 (4)		0.09 ± 0.09 (15)	6.7 ± 3.6 (18)
	48	2.43 ± 0.09[b] (48)	0.22 ± 0.01 (48)		1.26 ± 0 (48)		0.09 ± 0.02 (48)	6.5 ± 0.8 (48)
Evergreen shrubs								
Dryas octopetala	1	1.50 ± 0.06	0.17 ± 0.03 (1)		0.80 (1)		0.12 ± 0.04 (2)	10.2 ± 1.6 (2)
Forbs								
Artemesia arctica	2	2.32 ± 0.30 (2)	0.32 ± 0.04 (2)		0.98 ± 0.08 (2)			11.8 ± 0.6 (2)
Boykinia richardsonii	2	2.17 ± 0.43 (3)	0.45 ± 0.10 (3)				0.05 ± 0.07 (3)	7.0 ± 5.5 (2)
Dodecatheon frigidum	1	2.37 (1)	0.17 (1)		1.36 (1)			15.0 (1)
Epilobium latifolium	2	2.38 ± 0.65 (4)	0.31 ± 0.14 (4)				0.10 ± 0.11 (3)	6.0 ± 3.9 (4)
Equisetum arvense	2	2.14 (1)	0.21 (1)		0.68 (1)			
Equisetum variegatum	1	1.10 (1)	0.15 (1)				0.11 (1)	10.8 (1)
	10	2.15 ± 0.38[b] (10)	0.29 ± 0.11 (10)		0.94 ± 0.28 (5)		0.08 ± 0.03 (5)	9.4 ± 3.4 (6)

Table F.2. (Continued)

Graminoids								
Carex spp.	6	2.48 ± 0.32 (3)	0.18 ± 0.02 (3)		0.69 ± 0.11 (3)			15.9 ± 0.8 (3)
Festuca altaica	2	2.15 (1)	0.16 (1)		0.40 (1)			19.4 (1)
Hierochloe alpina	2	1.98 ± 0.11 (2)	0.17 ± 0.02 (2)		0.33 ± 0.07 (2)			20.0 ± 0.1 (2)
	10	2.31 ± 0.22[b] (10)	0.17 ± 0.01 (10)		0.56 ± 0.17 (10)			17.4 ± 2.0 (10)
Lichens[c]	17	0.43 ± 0.40[b] (17)	0.40 ± 0.02 (17)	0.16 (1)	0.15 (1)	0.04 (1)	0.04 ± 0.04 (17)	1.8 ± 3.5 (17)
Mushrooms[d]	12	5.55 ± 1.26[b] (12)	0.70 ± 0.13 (12)	2.59 ± 0.20 (12)	0.03 ± 0.01 (12)	0.08 ± 0.01 (12)	0.11 ± 0.01 (12)	6.4 ± 0.5 (12)

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[a] All analyses were applied, regardless of collection dates.

[b] Figures are weighted in terms of the proportions of plant species in the diet.

[c] Lichens contributing to the diet were assumed to be *Cladonia alpestris* (6%), *Cladonia rangiferina* (6%), *Cetraria cucullata* (3%), *Peltigera* (1%), and *Stereocaulon* (1%). Lichen analyses were applied regardless of collection dates.

[d] Mushrooms contributing to the diet were assumed to be *Boletus* spp. (8%) and the remaining species listed in Appendix D (4%), exclusive of *Amanita*. Mushroom analyses were applied regardless of collection dates.

Table F.3. Nutrients content of the autumn (mid-August to mid-October) diet. Calculations were made based on autumn data presented in Table 4 and Appendix D. Means, standard deviations, and sample size (in parentheses) are given.

Autumn Diet		Nutrients (% dry wt)						
Plant Species	Intake (% of diet)	N	P	K	Ca	Mg	Na	TNC
Berries[a]	3	0.60 ± 0.15 (3)	0.11 ± 0.03 (3)	0.54 (1)	0.04 ± 0.02 (3)	0.06 (1)	0.08 (1)	29.4 ± 9.8 (3)
Deciduous shrubs								
Betula nana	2	1.63 ± 1.29 (2)	0.31 ± 0.13 (2)				0.07 ± 0.08 (2)	5.0 ± 1.8 (2)
Salix spp.	12	1.58 ± 0.62 (9)	0.11 ± 0.05 (9)		1.43 ± 0.69 (2)		0.08 ± 0.10 (6)	8.2 ± 4.1 (7)
	14	1.59 ± 0.02 (14)	0.14 ± 0.07 (14)		1.43 ± 0 (12)		0.08 ± 0.01 (14)	7.7 ± 1.2 (14)
Evergreen shrubs								
Dryas octopetala	1	0.70 (1)	0.09 (1)		1.39 (1)			3.6 (1)
Vaccinium vitis-idaea[a]	1	1.22 (1)	0.18 (1)				0.47 (1)	16.4 (1)
	2	0.96 ± 0.37 (2)	0.14 ± 0.06 (2)		1.39 (1)		0.47 (1)	10.0 ± 9.1 (2)
Forbs								
Boykinia richardsonii	1	1.03 (1)	0.08 (1)				0.01 (1)	6.8 (1)
Equisetum arvense	2	1.43 ± 0.48 (3)	0.14 ± 0.01	0.20 (1)	2.58 ± 1.51 (2)	0.14 (1)	0.06 ± 0.04 (2)	2.8 ± 3.3 (3)
Equisetum variegatum	2	0.79 (1)	0.11 (1)	0.85 (1)	0.70 (1)	0.21 (1)	0.02 (1)	9.8 (1)
Hedysarum alpinum	1	2.03 (1)	0.12 (1)				0.01 (1)	6.1 (1)

Table F.3. (Continued)

Petasites frigidus	1	1.87 (1)	0.13 (1)				0.01 (1)	7.2 (1)
Sanguisorba stipulata	2	1.99 ± 0.04 (2)	0.16 ± 0.01 (2)		2.58 (1)		0.01 (1)	2.4 ± 3.6 (2)
	9	1.48 ± 0.52 (9)	0.13 ± 0.03 (9)	0.53 ± 0.38 (4)	1.95 ± 0.97 (6)	0.18 ± 0.04 (4)	0.02 ± 0.02 (9)	5.6 ± 3.1 (9)
Graminoids								
Carex spp.	9	1.37 ± 0.70 (5)	0.11 ± 0.04 (5)	0.55 ± 0.49 (2)	0.56 ± 0.18 (5)	0.14 ± 0.01 (2)	0.03 ± 0.02 (2)	9.0 ± 6.5 (5)
Eriophorum spp.	1	0.55 (1)	0.03 (1)				0.01 (1)	2.1 (1)
Festuca altaica	2	1.15 ± 0.62 (2)	0.09 ± 0.04 (2)		0.37 ± 0.01 (2)			11.4 ± 10.3 (2)
Hierochloe alpina	2	1.13 ± 0.50 (3)	0.10 ± 0.05 (3)	0.71 (1)	0.32 ± 0.16 (3)	0.11 (1)	0.01 (1)	10.9 ± 9.2 (3)
	14	1.25 ± 0.22 (14)	0.10 ± 0.02 (14)	0.58 ± 0.06 (11)	0.49 ± 0.10 (13)	0.13 ± 0.01 (11)	0.03 ± 0.01 (12)	9.1 ± 2.3 (14)
Lichens[a]	43	0.41 ± 0.37[b] (43)	0.04 ± 0.02 (43)	0.16 (3)	0.15 (3)	0.04 (3)	0.04 ± 0.04 (43)	2.2 ± 3.7 (43)
Mosses[a]	5	0.85 ± 0.33 (5)	0.12 ± 0.04 (5)	0.36 (1)	0.33 ± 0.12 (4)	0.20 (1)	0.01 ± 0 (2)	3.5 ± 2.4 (4)
Mushrooms[d]	10	5.64 ± 1.23[b] (10)	0.71 ± 0.13 (10)	2.58 ± 0.19 (10)	0.03 ± 0.01 (10)	0.08 ± 0.01 (10)	0.11 ± 0.01 (10)	6.4 ± 0.5 (10)

[a] All analyses were applied, regardless of collection dates.

[b] Figures are weighted in terms of the proportions of plant species in the diet.

[c] Lichens contributing to the diet were assumed to be Cladonia alpestris (14%), Cladonia rangiferina (14%), Cetraria cucullata (10%), Peltigera (2%), and Stereocaulon (3%). Lichen analyses were applied regardless of collection dates.

[d] Mushrooms contributing to the diet were assumed to be Boletus spp. (7%) and the remaining species listed in Appendix D (3%), exclusive of Amanita.

Table F.4. Nutrient content of the winter (mid-October to mid-May) diet. Calculations are based on winter data presented in Table 4 and Appendix D. Means, standard deviations, and sample size (in parentheses) are given.

Winter Diet		Nutrients (% dry wt)						
Plant Species	Intake (% of diet)	N	P	K	Ca	Mg	Na	TNC
Deciduous shrubs								
Salix sp	1	0.99 ± 0.32 (2)	0.09 ± 0.01 (2)		0.94 (1)		0.01 (1)	2.5 ± 3.3 (2)
Evergreen shrubs								
Dryas octopetala	1	0.70 (1)	0.09 (1)		1.39 (1)			3.6 (1)
Vaccinium vitis-idaea[a]	6	1.22 (1)	0.18 (1)				0.47 (1)	16.4 (1)
	7	1.15 ± 0.20[b] (7)	0.17 ± 0.03 (7)		1.39 (1)		0.47 (1)	14.6 ± 4.8
Forbs								
Equisetum arvense	3	1.16 ± 0.13 (3)	0.13 ± 0.01	0.36 ± 0.23 (2)	2.14 ± 1.29 (3)	0.32 ± 0.25 (2)	0.06 ± 0.05 (2)	1.0 ± 0.7 (3)
Equisetum variegatum	3	0.79 (1)	0.11 (1)	0.85 (1)	0.70 (1)	0.21 (1)	0.02 (1)	9.8 (1)
Stellaria longipes	1	1.63 (1)	0.15 (1)				0.03 (1)	9.1 (1)
	7	1.07 ± 0.31[b] (7)	0.12 ± 0.02 (7)	0.61 ± 0.27 (6)	1.43 ± 0.79 (6)	0.27 ± 0.06 (6)	0.04 ± 0.02 (7)	5.9 ± 4.6 (7)
Graminoids								
Carex spp.	7	0.68 ± 0.19	0.08 ± 0 (2)	0.55 ± 0.49 (2)	0.38 ± 0.04 (2)	0.14 ± 0.01 (2)	0.03 ± 0.02	4.7 ± 1.3 (3)
Festuca altaica	2	0.71 (1)	0.06 (1)		0.38 (1)			4.1 (1)

Table F.4. (Continued)

Hierochloe alpina	2	0.86 ± 0.23 (2)	0.07 ± 0.01 (2)	0.71 (1)	0.26 ± 0.18 (2)	0.11 (1)	0.01 (1)	5.7 ± 3.0 (2)
	11	0.72 ± 0.07[b] (11)	0.07 ± 0.01 (11)	0.59 ± 0.07 (9)	0.36 ± 0.05 (11)	0.13 ± 0.01 (3)	0.03 ± 0.01 (9)	4.8 ± 0.5 (11)
Lichens[c]	62	0.42 ± 0.37[b] (62)	0.04 ± 0.02 (62)	0.16 (5)	0.15 (5)	0.04 (5)	0.04 ± 0.04 (62)	2.2 ± 3.7 (62)
Mosses[d]	10	0.85 ± 0.33	0.12 ± 0.04 (5)	0.36 (1)	0.33 ± 0.12 (4)	0.20 (1)	0.01 ± 0 (2)	3.5 ± 2.4 (4)
Mushrooms[e]	2	6.40 ± 1.23 (3)	0.79 ± 0.06 (3)	2.46 (1)	0.03 ± 0.02 (3)	0.08 (1)	0.11 (1)	6.7 ± 4.7

[a] Sample was collected on June 10, 1977, on the Seward Peninsula, rather than in winter.

[b] Figures are weighted in terms of the proportions of the plant species in the diet.

[c] Lichens contributing to the diet were assumed to be *Cladonia alpestris* (20%), *Cladonia rangiferina* (20%), *Cetraria cucullata* (14%), *Peltigera* (3%), and *Stereocaulon* (5%). Lichen analyses were applied regardless of collection dates.

[d] All analyses were applied, regardless of collection dates.

[e] Mushrooms contributing to the diet were assumed to be *Boletus* spp. Analyses were applied regardless of collection dates.

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