



A STUDY OF CARIBOU RANGE USE AND POTENTIAL IN AND NEAR  
DENALI NATIONAL PARK AND PRESERVE

A synthesis report to the  
National Park Service  
(Contract No. CX-9000-7-E080)

May 15, 1983

Prepared by:

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## Preface

Work under this contract was initiated in September 1977 by Michael Davis, who was recruited to undertake the vegetative analysis of the rangelands of the Denali Caribou Herd as part of his MS thesis project. He carried out preliminary range reconnaissance work during early winter 1977 with David Klein, during which caribou wintering areas were visited. Smith accepted a permanent position as a range specialist with the Bureau of Land Management in summer 1978 and resigned his research fellowship with the Wildlife Research Unit. Rodney Boertje began field work on the grazing ecology, associated behavior and energetics of the caribou in June 1978 with initial assistance from Michael Davis. Gary Schultz was subsequently recruited to replace Michael Davis on the range evaluation component of the project and he began field work in June 1979. Rodney Boertje completed field investigations on this project in April 1980 and the data analysis and thesis preparation was completed in May 1981 (Boertje 1981). Boertje's thesis draws heavily on the data collected by Schultz on community type description and plant productivity and is a comprehensive assessment of the nutritional ecology of the Denali Caribou Herd and provides a model of the annual energy balance of these caribou. His thesis has been abstracted as the primary basis for this report. For specific details of the research methodology, data analysis methods and detailed results, reference should be made to Boertje's thesis. Schultz has provided the summary of forage productivity by plant communities that is included in the report. Information on the distribution and extent of vegetation types within

the study area were obtained from the work of Deborah Heebner, as reported in her MS thesis (Heebner 1982).

## Introduction

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 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  $\cdot$  km<sup>-2</sup> about 2 caribou  $\cdot$  km<sup>-2</sup> maximum over the entire range). The Denali Caribou Herd probably reached extremely high densities 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  $\cdot$  km<sup>-2</sup>), 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 wild-fires 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. 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 detail in relation to caribou population ecology in Chapters 2 and 3 of Boertje (1981), 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). 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.

Experience with other Alaskan caribou herds indicates that as populations decline traditional patterns of range use become fractured, with associated reductions in seasonal migration distances and range areas occupied (Hemming 1975). These patterns of more restricted range use may reflect reduced pressure of the animals on their food resource, loss of traditions of movement associated with smaller aggregations of animals, loss of stimulus for movement as a consequence of lower density of animals or other factors. These changed patterns of range use associated with caribou population declines may yield advantages to the caribou through the conservation of energy and reduced exposure to environmental stimuli as a result of the loss of social cohesiveness of the herd which could lead to increased pressures on the population through poor calving conditions, increased predation and reduced availability of high quality forage. Feeding selectivity and quality of forage consumed in relation to energetics are key factors in understanding the status of depressed caribou populations (Klein 1970b). The research, analysis of data and subsequent write up of findings has drawn heavily on literature and available reports on historical use of range lands by the Denali Caribou Herd. Similarly, the fire history of the range lands that have been used by the herd was reviewed and forage productivity work was based on fire history information. Heebner (1982) has also mapped the fire history of vegetation in Denali National Park and Preserve.

Past use of range lands of the Denali Herd was reviewed on the basis of available literature and reports, however, actual field work

was primarily restricted to areas of current use to assure an adequate data base for the development of a comprehensive model of the annual nutritional and energy cycle of the herd under present conditions.

Primary emphasis during the project was placed on the following objectives:

1. Determine present seasonal use by the herd of vegetation types and forage selection within types on a year-round basis. Relate forage quantity and quality to topographic and floristic variables and snow cover.
2. Determine feeding energetics through field observations of feeding behavior and forage selectivity. Relate feeding energetics to characteristics of snow cover and quality and quantity of forage consumed and its availability.
3. In so far as available population and growth data permit, assess the relationship of forage quality and quantity to past and present population numbers and distribution and to future range potentials.

#### Forage Productivity

Productivity of vegetation types was found by using the double-sampling technique of weight estimate. With this technique, biomass of each species in 20 systematically located plots was estimated. Two plots were then clipped. The plant material was then saved to dry and weigh in the laboratory. This information was then used to convert the estimates of green plant material to a corrected weight of dry plant material. A total of 32 sites was sampled in 1979 and 50 sites were sampled in 1980. Vegetative productivity data is summarized in Table 1.

To determine the seasonal change in productivity of important caribou forage species, biomass of 12 species was measured at 2-3 week intervals throughout the growing season. Vegetation samples were collected at this time to use in assessing the change in forage quality. Approximately 190 plant samples were analyzed for nitrogen, phosphorus, calcium, total non-structural carbohydrates, acid-detergent fiber, neutral-detergent fiber, cellulose, lignin, and ash. These analyses were done by the Palmer Plant and Soils Laboratory, Alaska Agricultural Experiment Station. An additional 100 samples were analyzed for in vitro digestibility at the University of Alaska. These chemical and digestibility analysis data have been incorporated into the model of the annual nutritional regime of the Denali Caribou Herd.

#### Composition of Seasonal Diets

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

strategy. This migratory movement prior to calving may also be associated with the survival benefits of moving to a calving ground with relatively few predators 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). Approximate percentages of major forages in the seasonal diets of adult female caribou are shown in Table 2.

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. 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.

The autumn diet was dominated by lichens, 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.

Lichens also dominated the winter diet, whereas Equisetum spp., Vaccinum 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. 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 winter 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.

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.

#### Seasonal Activity and Estimated Energetics

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 animals in this herd 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 these 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 caribou in this area 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. Dauphine (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 (and included in Tables 12 and 13 in Boertje 1981). Subsequently, total daily energy

requirements of adult female caribou were calculated on a seasonal basis (Figure 1), 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. 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 expenditure (Figure 1) besides the 21-percent 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 contribute significantly to the large differences in food energy requirements in late summer and autumn versus winter. The high energy costs related to lactation are most important during the calving and post-calving season, 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. 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 1). 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  $2 \text{ MJ} \cdot \text{day}^{-1}$  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  $2 \text{ MJ} \cdot \text{day}^{-1}$  (comparing early and late winter activity costs) to an extreme of about  $6 \text{ MJ} \cdot \text{day}^{-1}$  (comparing activity costs between late winter and the insect season). Cratering costs, alone, can add about  $1.2 \text{ MJ} \cdot \text{day}^{-1}$  to winter energy requirements if cratering is prolonged and snow conditions are severe. 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  $665 \pm$

18 kJ · kg<sup>-0.75</sup> · day<sup>-1</sup> from February to May. Converting to metabolizable energy intake (MEI = 0.82 x DEI, Agricultural Research Council 1965), a value of 545 kJ · kg<sup>-0.75</sup> · day<sup>-1</sup> is obtained. This is about 1.43 times winter-BMR. The model developed from this study gives a value of about 652 kJ · kg<sup>-0.75</sup> · day<sup>-1</sup> (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. The 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 (1972) 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<sup>-0.75</sup> · day<sup>-1</sup> (1.50 times winter-BMR), while in this study we estimated a mean value of about 683 kJ · kg<sup>-0.75</sup> · day<sup>-1</sup> (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  $16.8 \text{ MJ} \cdot \text{day}^{-1}$  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  $20.3 \text{ MJ} \cdot \text{day}^{-1}$  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  $25.94 \text{ MJ} \cdot \text{day}^{-1}$  and  $27.20 \text{ MJ} \cdot \text{day}^{-1}$ , 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  $23.01 \text{ MJ} \cdot \text{day}^{-1}$ ) under the same conditions. Steen (1968) reported slightly lower winter maintenance values for MEI for penned female reindeer ( $21.3 \text{ MJ} \cdot \text{day}^{-1}$ ) 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 ours, 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 calorogenic effect of food, and (2) the extremely high energy

expenditure related to "trotting/running". Thomson's exclusion of the calorogenic effect of food accounts for the approximately 30 percent reduction in his values (exclusive of running costs) compared to ours. However, when running costs are considered, Thomson's values are often much higher than ours. 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 at a speed of  $10 \text{ km} \cdot \text{hr}^{-1}$ , compared to our value of  $30 \text{ kJ} \cdot \text{kg}^{-1} \cdot \text{hr}^{-1}$  at a speed of  $12 \text{ km} \cdot \text{hr}^{-1}$ . 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.

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 our 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 ours.

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 (Dauphine\_ 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  $2.5 \text{ MJ} \cdot \text{day}^{-1}$  due to physiological stress, caribou would require about 76 MJ more annually if experiencing stress for an average of  $2 \text{ hr} \cdot \text{day}^{-1}$ . 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.

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 1974). 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).

#### Nutritional Ecology

It appears that dry matter digestibility 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 than 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  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$  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 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 lichens 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 deficiencies 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 activities 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 activities 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 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.

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.

#### 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 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 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 pres. 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 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, 1980). 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. 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 correspondingly 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 physiological 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 energetics/nutritional stresses between populations.

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Table 1. Vegetative productivity at time of peak plant growth (July) of plant communities available to the Denali Caribou Herd (Plant communities follow Viereck and Dyrness 1980 classification)(Data from G. Schultz).

Community Type and Species		Kg/Ha	±	S.E.
1-4-1	Willow Shrub Tundra			
	Graminoids	372.2		55.2
	Forbs	122.4		50.8
	<u>Salix pulchra</u>	731.7		169.3
1-5-1	Open Mat and Cussion Tundra			
	Graminoids	18.4		13.1
	Forbs	41.5		18.7
	<u>Salix rotundifolia</u>	126.6		126.6
	<u>Arctostaphylos alpinum</u>	38.4		35.0
	Lichens ( <u>Cetraria nivalis</u> ,	110.1		51.0
	<u>C. islandica</u> , <u>C. cucullata</u> , <u>Cladonia alpestris</u> , <u>C. gracilis</u> , <u>C rangiferina</u> , <u>C. mitis/arbus.</u> )			
1-7-1	Wet Sedge-Grass Tundra			
	<u>Carex aquatilis</u>	736.3		225.2
	<u>Equisetum arvense</u>	30.7		22.8
	Total Graminoids	786.6		212.1
	Forbs	29.7		28.3
	<u>Salix pulchra</u>	37.7		35.3
	<u>Salix reticulata</u>	17.6		14.4
	<u>Vaccinium uliginosum</u>	14.9		14.8
1-3-2	Sedge Tussock Shrub Tundra			
	<u>Eriophorum vaginatum</u>	143.4		70.6
	Total Graminoids	364.8		139.4
	Forbs	115.5		101.7
	<u>Betula nana</u>	228.0		106.9
	<u>Vaccinium uliginosum</u>	21.7		21.7
	<u>Salix pulchra</u>	77.1		58.2
Lichens ( <u>Cetraria cucullata</u> ,	69.9		58.6	
<u>Cladonia alpestris</u> , <u>C. rangiferina</u> )				
2-2-1	Dwarf Birch Low Shrubland			
	Total Graminoids	105.6		54.2
	Total Forbs	27.8		4.3
	<u>Betula nana</u>	487.4		256.2
	<u>Vaccinium uliginosum</u>	66.8		39.9
	<u>Betula glandulosa</u>	110.6		110.6
	<u>Salix barratiana</u>	47.4		47.4
	<u>Salix pulchra</u>	2.2		2.2
	Lichens ( <u>Cetraria cucullata</u> ,	271.6		125.4
<u>C. islandica</u> , <u>Cladonia alpestris</u> , <u>C. rangiferina</u> , <u>C. initis</u> )				

Table 1. (continued)

Community Type and Species		Kg/Ha	±	S.E.
2-1-1	Willow Tall Shrubland			
	Total Graminoids	194.9		148.8
	Total Forbs	211.0		81.1
	<u>Salix lanata</u>	663.4		663.4
	<u>Salix alaxensis</u>	71.7		45.5
	<u>Salix pulchra</u>	29.7		28.1
	<u>Salix glauca</u>	26.3		26.3
	Lichens ( <u>Cetraria cucullata</u> ,	34.5		34.5
	<u>C. islandica</u> , <u>C. nivalis</u> ,			
	<u>Cladonia gracilis</u> , <u>C. mitis</u> )			
1-4-2	Birch and Ericaceous Shrub Tundra			
	Total Graminoids	32.1		18.1
	Total Forbs	43.3		41.7
	<u>Betula nana</u>	282.5		147.3
	<u>Salix pulchra</u>	19.5		12.7
	<u>Vaccinium uliginosum</u>	224.6		59.6
	Lichens ( <u>Cetraria islandica</u> ,	166.7		114.7
	<u>C. cucullata</u> , <u>Cladonia alpestris</u> ,			
	<u>C. rangiferina</u> , <u>C. gracilis</u> )			

Table 2. Approximate percentages of major food<sup>a</sup> 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, in Boertje 1981).

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

Table 2. (Continued)

Graminoids				
<u>Carex</u> spp. <sup>e</sup>	7	6	9	7
<u>Eriophorum</u> spp. <sup>f</sup>	4		1	
<u>Festuca altaica</u>	1	2	2	2
<u>Hierochloa alpina</u>		2	2	2
	<u>12</u>	<u>10</u>	<u>14</u>	<u>11</u>
Lichens <sup>g</sup>	25	17	43	62
Mosses <sup>h</sup>			5	10
Mushrooms <sup>i</sup>		12	10	2

<sup>a</sup>Plant parts selected are given in Appendix C of Boertje (1981).

<sup>b</sup>Species of berries selected included primarily Vaccinium uliginosum and V. vitis-idaea with less use of Empetrum nigrum.

<sup>c</sup>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.

<sup>d</sup>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.

<sup>e</sup>Species of Carex selected included primarily C. aquatilis, C. bigelowii, and C. podocarpa (see Appendix C of Boertje 1981 for their comparative uses).

<sup>f</sup>Species of Eriophorum selected included primarily E. vaginatum and E. angustifolium.

<sup>g</sup>Lichens species selected included primarily Cladonia spp. and Cetraria cucullata, with comparatively little use of Sterocaulon spp. and Peltigera spp.

<sup>h</sup>Species of mosses consumed were not identified to genera.

<sup>i</sup>Mushrooms consumed included primarily Boletus spp., although several other genera were selected (see Appendix C of Boertje 1981).

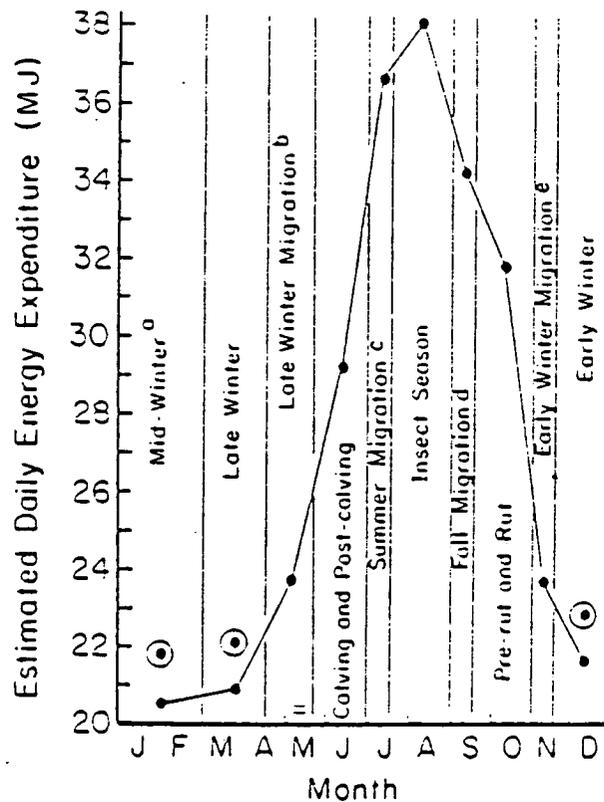


Figure 1. Year-round estimates of daily energy requirements of an adult female caribou with calf in the Denali Caribou Herd, 1978-1980. Circled values include foraging costs in extreme snow-cover conditions, compared to foraging in the absence of snow (see Methods in Boertje 1981).

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

<sup>b</sup>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). Body weight was assumed to be 100 kg, and the period lasted 36 days.

<sup>c</sup>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.

<sup>d</sup>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 105 kg, and the period lasted 15 days.

<sup>e</sup>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.

