Range Ecology of the Porcupine Caribou Herd in Canada

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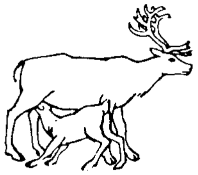

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Acknowledgements

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Executive summary

Introduction

The large Porcupine Caribou Herd of Grant's caribou (*Rangifer tarandus-granti*) migrates annually from summer range on the arctic coastal plain of Alaska and Yukon to winter in the forested valleys and plains of north-central Yukon and western Alaska. Concern for the well being of the herd in response to existing and proposed developments within their range, and the need for more knowledge on the range ecology of the species prompted this study. The work was conducted primarily by the Canadian Wildlife Service, initially as a joint project with the Yukon Department of Renewable Resources and continued from 1979 to 1987. We have divided the report into three major chapters, covering the winter, the late spring and the summer. Throughout these chapters we refer to 15 periods in the annual life cycle of the herd. In the final chapter, we discuss the energetic implications of our findings.

Winter

Characteristics of the range

The Yukon portion of the winter range of the herd occupies an extensive area in the north-central Yukon, from just north of Dawson City in the south, to the Beaufort Sea in the region of the Richardson Mountains in the north. This region was largely unglaciated during the last ice age and offers a wide diversity of habitats, from the sheltered valleys of the Ogilvie and Hart Rivers, to the mountainous terrain of the Richardson Mountains and to the lichen-rich habitats of the Eagle Plains, Whitestone and Miner Rivers.

The herd appears to occupy the core wintering regions on a rotational basis, using the Ogilvie/Hart region for a few years and then occupying the Richardson Mountains (Russell *et al.* 1992b). These two regions receive less snow than adjacent areas. Two major storm systems affect the area. The Pacific system moves north from the Gulf of Alaska and deposits considerable snow on the southern flanks of the Ogilvie Mountains, forming an effective barrier to southward expansion of the winter range. The other system, originating in the Bering Sea, moves eastward, gradually depositing snow as it swings around the Nahoni Range and across the Eagle Plains, leaving the Ogilvie/Hart basins in the snow shadow of both systems.

The Richardson Mountains, although appearing to receive normal snowfall for the region, are characterized by strong winds. Many portions of the Richardson Mountains are blown free of snow for the major part of the winter. We recognized nine snow regions within our study area, based on snow courses along the Dempster Highway and extensive spring snow surveys.

For the 118 stands used to document vegetation characteristics (described in Russell *et al.* 1992a) we sampled lichen biomass, which varied between 0 and 500 g/m^2 with a mean of 65 g/m^2. Among the genera, *Cladina* and *Cetraria* were the major contributors. The Eagle Plains had significantly greater lichen accumulations than other regions, comparing favourably with winter ranges of other herds.

Sixty-eight of the stands were sampled for fire history and a mean interval between fires of 120 years was determined. Lichen biomass tended to decline with stand age for all genera except *Cetraria*. Shrub communities tended all to be in a young age class. The tundra (graminoid communities) were not sampled.

Food habits

Fecal pellets were collected during five periods in each of three winters. The composition of the fecal samples remained remarkably constant from late September through early May. Fruticose lichens predominated (64%), followed by evergreen shrubs (11%), moss (8%), horsetails (6%), foliose lichens (5%), graminoids (3%), deciduous shrubs (2%), forbs ($< 1\%$) and mushrooms ($< 1\%$). Feeding trials with captive animals suggest that those proportions are a reasonable estimate of the ingested diet except for fruticose lichens (71%) and evergreen shrubs (4%). Snow conditions did not have a major influence on the diet although increasing snow cover over winter may have caused decreased use of horsetails and increased use of evergreen shrubs and forbs.

Activity

The activity of the Porcupine Caribou Herd was documented from October to April for the three years of the study (1979–80 to 1981–82). Activity pattern, the alternation between active and rest cycles, was tuned to sunrise and sunset. Animals were most active at sunrise and sunset resulting in one lying period in late fall, early and mid winter, two in early fall and late winter, or three in spring. Mean length of the active/lying cycle decreased from late fall (298 min) to early winter (238 min), increased to a peak in mid-winter (340 min) then declined in late winter (305 min) and again in spring (240 min). The mean length of the lying period increased through the winter from 56 min in early winter to 114 min in mid-winter and 153 min in late winter.

Winter activity budgets (the proportion of the day spent in various activities) reflected season, daylength and snow conditions. Although daylength was the main factor influencing the proportion of the day in which caribou were inactive, lying also increased under adverse snow conditions. The proportion of time spent moving (walking, trotting and running) tended to be greatest in October-November and April, likely related to seasonal migration, and was least during periods of adverse snow conditions. Feeding intensity (the proportion of the active period spent feeding) tended to be least in October-November and greatest during periods of adverse snow conditions. It is suggested that the increased lying time and feeding intensity, and decreased mobility of the animals that were observed at times of adverse snow conditions, reflected a decrease in forage availability rather than forage quality. We propose methods of using activity budgets as a means of assessing range quality for caribou herds.

Cratering dynamics

Cratering dynamics were examined under mild (1980–81), moderate (1979–80) and adverse (1981–82) snow conditions. In the mild snow years, animals dug many small craters in a day. Forage selectivity, assessed by the amount of cratered area animals fed upon per second of feeding time, was low. In the moderate snow year caribou dug an average number of large craters and were highly forage selective. In contrast, during the adverse snow year, caribou dug a few, large craters and exhibited forage selectivity similar to the mild year. A logarithmic relationship was determined between the energy cost of digging a crater and the number of craters dug per day.

While in the crater, caribou spent most time feeding and least pawing in the mild snow year (89% and 5%, respectively) compared to the moderate snow year (83% and 15%) and the adverse snow year (70 % and 25%) . Average searching time, time spent between craters, varied from a mean of 18 sec in the mild year to 54 sec in the moderate year and 63 sec in the adverse year.

Displacement of one caribou by another from craters was related to snow conditions and the energy cost of digging craters, although the relationship differed in each winter, indicating that animal condition may have been a complicating factor.

Late spring

Characteristics of the range

The period from mid-May to the end of June is the most dynamic time of year in northern Yukon. Snow is melting rapidly and new green vegetation is changing quantitatively and qualitatively. These changes occur at a time when caribou, migrating north from their winter ranges, are in the poorest physical condition in their annual cycle and during the period when lactating females face the highest energetic demands of the year. The Porcupine Caribou Herd uses the foothills and southernmost portion of the coastal plain during the critical calving period, with repeated use concentrating in the Jago uplands of Alaska and along the adjacent foothills and coastal plain of the Yukon north slope.

We conducted a three year study of the range ecology of female caribou on the Yukon north slope from 1979 to 1981. This area spans two distinct ecoregions; (1) the Northern Mountains ecoregion, including the foothills of the British Mountains and (2) the Coastal Plain ecoregion, with low elevation and subdued relief. There were marked differences in the weather among years; in 1979 spring was generally cool and wet with a relatively warm calving period; 1980 was the warmest year with temperatures during calving similar to 1979; 1981 had a cooler calving and a warmer and windier post-calving period than in 1979.

We used eight range types to stratify most of our sampling; alluvial willow, alluvial gravel, alluvial heath, wet sedge meadows, tussock meadows, sedge heaths, dwarf shrub heaths and alpine barrens. The warmer 1980 resulted in advanced phenological development in most range types. Alpine barren communities were the most advanced. Foothills were generally 10 days earlier than coastal communities.

Biomass sampling, although not intensive, showed that deciduous shrubs contributed most to new green annual growth followed by graminoids. Biomass change of graminoids peaked by 25 June, forbs by 5 July and shrubs after 12 July. We also documented the relative biomass of the major plant groups in the range types.

Our study area contained tussock densities comparable to those in other studies. We noted an annual variation in mean tussock flower production, confirming suggestions made by others that flower production in a given year is greatly influenced by the weather of the previous summer. In 1981, following the warm summer of 1980, we measured significantly higher *Eriophorum* flower production than in the previous two years.

The nutrient concentrations of the major plant groups showed a similar trend toward rapidly changing quality in the vegetation at this time of year. All the factors that we documented to characterize the calving grounds of the herd pointed to the importance of the two week period following calving. Most of the dynamics of the vegetation occurs between 4 June and 24 June. The region chosen for calving offers a diverse complex of range types, providing a wide array of available habitats in various stages of phenological development.

Habitat selection

Over the three years of the study, more than 50% of the animals used the tussock meadow community, particularly in the pre-calving and calving periods. Wet sedge meadows (especially in the post-calving and movement periods), alluvial heath and sedge heath were the only other types used in greater than 10% of our scan observations. We noted significant shifts in use of communities in response to early phenological development (1980) and abundant resources (*Eriophorum*, 1981). Avoidance of certain communities was attributed to both avoidance of predators (alluvial willow) and low vegetative cover (alpine barren).

Food habits

In all years, fecal fragment density switched from predominantly moss/evergreen shrub/graminoid in the pre-calving and calving periods to primarily deciduous shrub in the post- calving and movement periods. Feeding trials from captive caribou indicated that fecal fragments in late spring tend to overrepresent evergreen and deciduous shrubs at the expense of forbs and lichens.

We observed shifts in diet among years, with animals taking advantage of early phenology in 1980 and abundant *Eriophorum* in 1981.

Activity

Total cycle lengths (active+bedded) increased from the pre-calving to the post-calving period and then declined sharply in the movement periods. The percent of time spent feeding declined in the movement period (38%) from earlier stable values (55% average). The proportion of time spent walking was highest in the pre-calving (21%) and movement periods (29%) and lowest in the calving period (7%). Walking and feeding in the pre-calving period appeared to occur at the expense of time spent lying while in the movement period, increased walking reduced time spent feeding.

Based on continuous observations of focal animals, adults spent a significantly higher percent of their active time grazing than calves while calves spent a higher proportion of their active time running. Nursing bout frequency declined from pre- calving to post-calving while an increase in the duration of bouts was noted from calving to post-calving.

The period of calving was characterized by a reduction in movement, smaller group sizes and an increase in lying time. The post-calving period was marked by a further increase in lying time, a reduction in movement rates and a further increase in the median length of the active and bedded cycles. Activity budgets did not differ between the calving and post-calving periods. The movement period showed the most dramatic change in the activity of the animals. Group sizes increased dramatically, the proportion of time and rate of walking increased significantly, the proportion of time spent feeding declined significantly and the alternation between active and rest cycles was significantly reduced.

Late spring range use by bulls

By late May 1983 the bulls and non-productive females were distributed south of the mountains, where snowmelt was more advanced than farther north. Caribou used tussock meadows, dwarf shrub heaths and alpine barrens but avoided low-lying wet sedge meadows and alluvial willow thickest where snowmelt was slower. Diet consisted primarily of lichens and evergreen shrubs which were widely distributed in the habitat types used. By early June, as snowmelt progressed south of the mountains and on the eastern coastal plain, males moved northward to those areas. Intermountain basins, where snowmelt was retarded, were avoided. As the season progressed, males continued to use, and avoid, essentially the same habitat types but there was less use of dwarf shrub heaths. They continued to feed on lichens and began to use *Eriophorum* as it came into flower. In mid-June, males moved into intermountain basins as snowmelt there progressed. Caribou used tussock meadows and alluvial willow thickets as the diet shifted to *Eriophorum* and *Salix*. At that time, large aggregations of caribou formed in intermountain basins and they spent more time lying, less time walking, and had a lower rate of movement than in other periods. By late June, males began to use the tussock meadows, wet sedge meadows and alluvial willow thickets of the western coastal plain. *Salix*, which was common in all three habitat types, predominated in the diet. At that time, *Salix* on the coast was at a similar phenological stage to inland sites two weeks earlier when it was not used as heavily as *Eriophorum*. However, by late June, *Eriophorum* was in seed and therefore not as desirable a food for caribou. In late June average band size increased significantly and rate of movement was greatest as males moved westward towards Alaska. The mean length of active/rest periods decreased by about one-third. This sharp decrease may reflect both the high availability and high digestibility of young willow leaves.

In general, the distribution of male caribou followed the pattern of snowmelt and plant phenology and diet reflected both preference and phenological stage. Activity and movements were not related to snowmelt, plant phenology or diet appearing to follow a temporal pattern.

Summer

Our study was conducted from 1984 to 1986 with the objective of determining what role insect harassment played in the summer ecology of the Porcupine Caribou Herd.

Movements and distribution

Historical and recent movements and distribution of the herd pointed to the importance of the Richardson Mountains and the Muskeg Basin regions of northern Yukon during the summer insect season. Radiotracking relocations during the study showed that frequent fracturing and reformation of large aggregations occurred throughout the insect season.

Insects and weather

Wind and, to a lesser extent, temperature were the primary factors dictating mosquito activity. Mosquitoes were relatively inactive at wind speeds greater than 6 mps and temperatures less than 7°C. A wind/temperature index is provided to predict levels of activity. Others factors influencing insect activity were region, time and date.

Climate and weather patterns

The study area is influenced by two interacting regional climates; the subarctic continental climate, characterized by warm summers and a rapid transition from winter to spring, and the arctic coastal climate, characterized by cold long winters and cool moist summers. The line between these two systems shifts, depending on the relative strengths of the two air masses supporting these climates. To determine the weather patterns among the three permanent stations within the study area, we established nine temporary stations in 1986. These stations allowed us to classify the study area based on regional weather patterns. Sites in the Richardson Mountains were significantly cooler and moister than other stations.

Caribou response to insects

Groups tended to be larger earlier in the season but denser during conditions favourable to insects. While in these dense groups, animals displayed similar responses to insects, regardless of sex and degree of coat shedding. The responses increased in frequency as conditions favouring insect harassment improved. At low wind speeds, it was advantageous to be in the centre of the group rather than the periphery. At higher wind speeds, the opposite was true.

Activity, food and habitat

The effects of insect harassment showed not only in the formation and maintenance of large aggregations, but also in activity budgets, diet and habitat selection. During our study, animals moved an average of 10.9 km/day.

Based on scan observations, the activity budgets between1984 and 1985 were similar, except for a higher proportion of walking in 1985. When insects were active there was a significant decrease in time spent feeding and an increase in the time spent standing. Feeding intensity, the proportion of the feeding period spent ingesting food, was 14% lower when insects were active. Based on focal animal observations, the proportion of time spent moving (walking, trotting, and running) increased when insects were active.

Caribou responded to increases in insect activity either by moving to higher, and presumably windier, locations of the same habitat or choosing habitats with less «risk», based on moisture and vegetation cover.

Remains of deciduous shrubs were, by far, the most frequent in the fecal analysis. However, based on correction factors obtained from diets of captive caribou, deciduous shrubs and forbs were equally important. Samples collected after extended periods of harassment were not significantly different in composition from samples collected after no insect harassment. It appears either that diet remained relatively stable or rumen turnover time increased greatly during insect harassment, thus dampening the effect of diet shifts. Near the end of the mid- summer period, we noted a shift toward more lichen in the diet.

Energetic implications

Using a computer simulation model that combines rumen function with energy allocation, we explored the energetic implications of our results. The peaks in metabolizable energy intake and energy requirements coincided in early July, pointing to the crucial importance of the timing of calving. The annual trends in digestibility, fat deposition or mobilization and energy balance are also presented. One application of the model that proved quite useful was to «force» a pregnant female to follow the spring strategy of bulls, remaining on the winter range late into spring and tracking the phenological changes in vegetation in the pediments and intermountain basins of northern Yukon. Conversely, we «forced» an adult bull to stay with the pregnant females, migrating early to snow - covered calving grounds. In both instances the animals entered the insect season at higher body weights if they followed the strategy they would normally employ (although differences for bulls were slight). Pregnant females can survive on the poor late spring diet, and take advantage of forage allowing high metabolizable energy intake when the vegetation flushes. Bulls on the other hand, must obtain a higher energetic intake constantly to meet the high maintenance energy requirements that their large body size demands.

CHAPTER 1. Introduction

The «Porcupine Caribou Herd» was first named in the early 1950s, after a few years of cooperative surveys by the U. S. Department of Agriculture and the Canadian Wildlife Service. Until then the large number of observations of caribou concentrations in north eastern Alaska, northern Yukon and northwestern Northwest Territories (NWT), were attributed to the existence of either a number of seemingly discrete herds or parts of a large amorphous caribou population that inhabited all of Alaska and Yukon with various centres of habitation. Murie (1935) recognized the somewhat discrete nature of caribou in the region. After noting the obvious «centres of abundance» of caribou he concluded that:

> . . . there is free communication among the caribou, a connected distribution, all the way from the headwaters of the Porcupine and Peel rivers in the Yukon to the Brooks range in Alaska, including the Chandalar animals.

We are relatively certain that the herd has acted as an entity for several thousand years. Archaeological work at Old Crow has uncovered evidence of caribou crossings on the Porcupine River as much as 27,000 years B.P. These crossing sites coincide with present crossing sites of the herd. The entire home range of the herd is approximately 250,000 sq km, encompassing three jurisdictions (Fig. 1.1). Although the herd can be found anywhere north of Dawson in a given year, the wintering concentrations in Canada normally occur south of the Porcupine River in the west and from the headwaters of the Peel River to the Beaufort Sea in the eastern portion of the Yukon (Russell *et al.* 1992b). Most of the herd arrive on the winter range by mid-November and move little until March. Pregnant females begin to group up in early March and move north, generally along two migration routes (Fig. 1.1); the Richardson Route along the western flank of the Richardson Mountains and the Old Crow route, through the Ogilvie basins, Whitestone, Fishing Branch and Miner rivers, along the Keele Range and across the Porcupine River. The two routes tend to converge in the Old Crow Pediments north and east of the Old Crow Flats. Movement then proceeds through the valleys of the Babbage River and the British Mountains, joining any Alaskan wintering groups near the lower reaches of the Firth and Malcolm rivers. Arrival on the calving grounds can occur from early May to early June with the peak of calving during the first week of June. There are two areas where animals have concentrated during the calving period over the last two decades – in the foothills of the British Mountains near the Yukon/Alaska border and in the uplands of the Jago River in Alaska (Garner and Reynolds 1986, Russell *et al.* 1992b).

After calving, movement tends to follow the receding snowline north. At this time, the non-productive segment of the population (nonpregnant cows, bulls and juveniles), have moved from their wintering areas, generally along the same routes as the cows but three weeks later. During the peak of calving, this segment can be found in a crescent south and east of the calving locations. After calving, these animals move west along the foothills and coastal plain of the Yukon to join the nursery groups on the coastal plain of Alaska.

By early July, larger and larger aggregations begin to form and move in response to insect harassment. Movement can be south through the Brooks Range or southeast, through the British Mountains, eventually arriving in the Richardson Mountain region by the latter part of July (Russell *et al.* 1992b). After

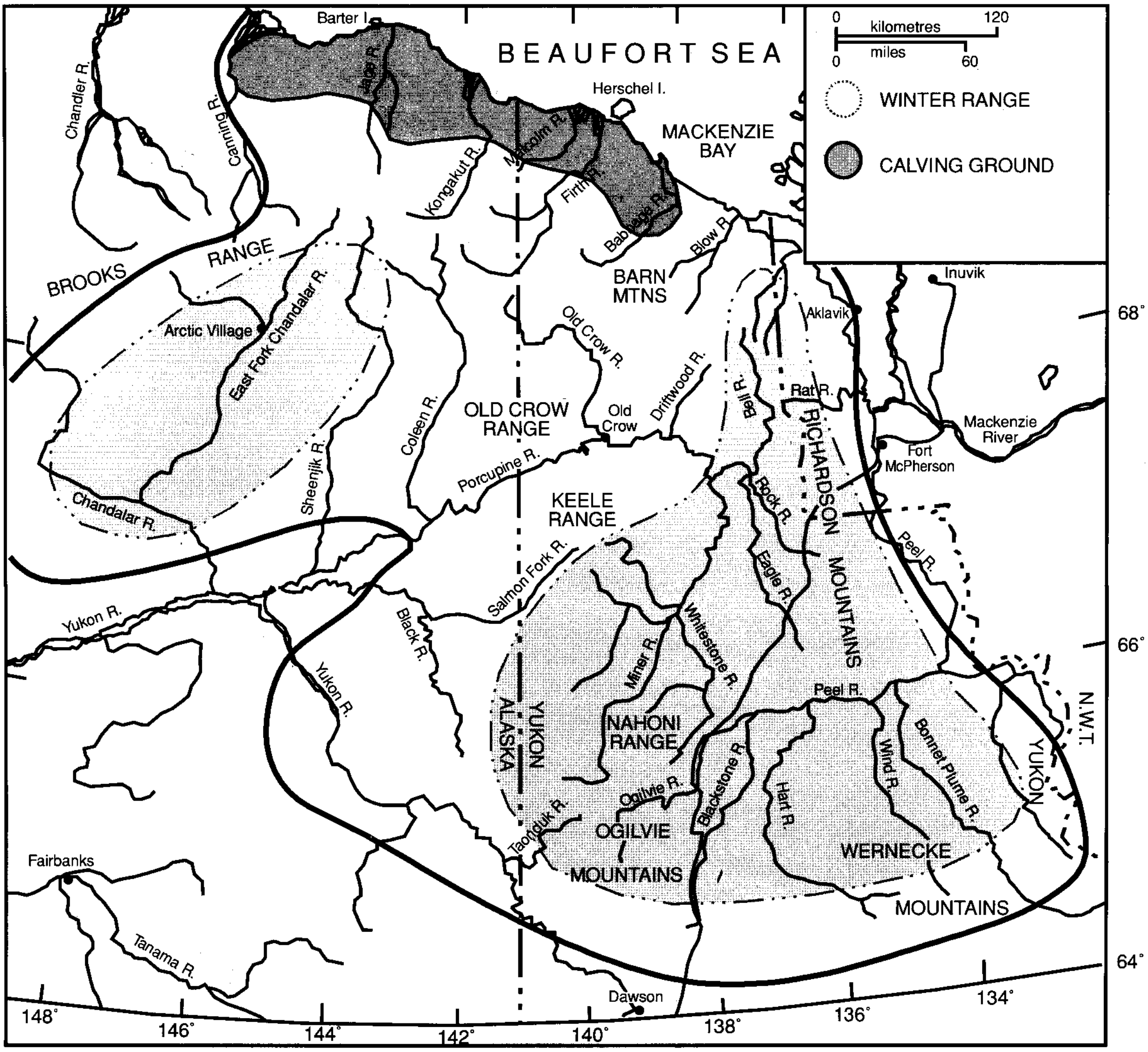

Figure 1.1. Home range of the Porcupine Caribou Herd.

insects become less of a nuisance, the large groups tend to fracture and smaller bands, generally of less than 100 animals, move continuously in August and early September. Movement of animals that arrived in the Richardsons in mid to late July is primarily east to the Canoe Lake area of NWT or to the west along the north end of the Old Crow Flats and into the southern flank of the Brooks Range in Alaska. In early September, most animals return to the Yukon retracing the August movement along the north part of the Old Crow Flats. The herd can remain north of treeline well into October if snow storms are late and mild weather prevails. However, by mid-September, snow storms will result in rapid southerly movements of the herd, south of treeline and across the Porcupine River. As in spring, this fall migration movement can funnel into two migration routes - the Old Crow route and the Richardson Mountain route. Rutting occurs in mid-October, wherever the herd happens to be at the time. By November, the herd has greatly reduced its movement and can be considered to be on winter range again.

We have divided the annual cycle of the herd into 15 periods that reflect changes in the environmental conditions that influence the behaviour and energetics of the individual (Table 1.1). We identified

Table 1.1. The 15 periods in the annual life cycle of the Porcupine Caribou Herd.

Season	Dates	Characteristics
Chapter 2. Winter[1]		
Rut	8 - 31 October	snow but melting
Late fall	1 - 30 November	beginning of winter snow cover
Early winter	1 December - 10 January	snow-cover shallow; shortest daylength very cold
Mid Winter	11 January - 20 February	snow-cover increasing; very cold
Late winter	21 February - 31 March	snow-cover peaking; longer daylength
Spring	1 - 30 April	snow-cover decreasing
Chapter 3. Late spring		
Spring migration	1 - 19 May	80 - 100% snow-cover; snow rotting; animals move north of treeline
Pre - calving	20 - 31 May	10 - 50% snow-cover, disappearing rapidly; cottongrass in bud
Calving	1 - 10 June	0 - 10% snow-cover; cottongrass in full flower; willow leaves in bud
Post - calving	11 - 20 June	cottongrass past flowering; willow leaves unfolding
Movement	21 - 30 June	willow in leaf; biomass increasing rapidly
Chapter 3. Summer		
Early summer	1 - 15 July	biomass peaking; mosquitoes peaking
Mid summer	16 July - 8 August	biomass at peak; mosquitoes past peak; oestrid flies peaking
Chapter 4. Energetic implications		
Late summer	9 August - 7 September	vascular forage quality declining
Fall migration	8 September - 7 October	early snow storms

1: chapters in this report that present data for included periods.

five late fall/winter periods influenced by changing snow conditions and daylength. Spring migration was recognized as a separate period. The most dynamic time of year (late May to the end of June) was divided into four periods reflecting the rapidly changing nutrient dynamics. Summer was divided into three periods, tracking the changing insect populations. The final two periods were fall migration and rut.

The overall strategy for these range studies was a response by the government agencies to the increasing number of potential and real industrial developments within the range of the herd with requirement to gain a better insight into the range relations of these large migratory caribou populations (Klein and White 1978).

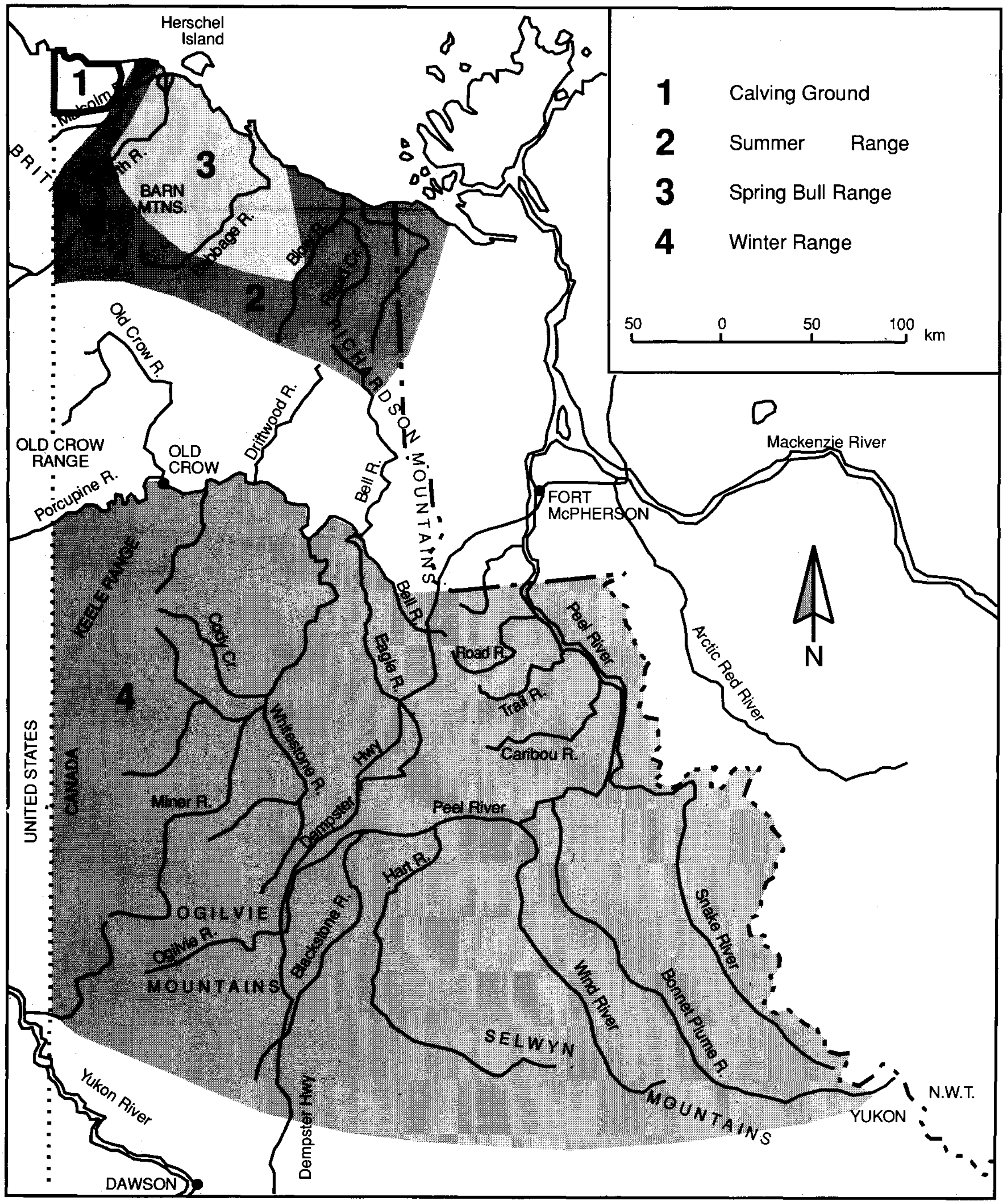

Figure 1.2. Study areas for the three range studies, 1979-86.

The format of the report roughly parallels three specific field projects conducted between 1979 and 1986 (Fig.1.2). Chapter 1, based on work conducted between 1979-82 documents the winter ecology of the herd. The presence of the Dempster Highway, initiated in 1958 and completed in 1979, resulted in a significant amount of concern about the potential impacts of the road to wintering Porcupine caribou. The road bisected the winter range and it was felt that significant harassment could cause the herd to abandon wintering areas south and east of the highway.

Concurrent with this work, we conducted a three year study on the use and characteristics of the core calving grounds in the Yukon (1979–81). Caribou biologists have long identified the core calving grounds of large migratory caribou as the most critical component of their annual range. This study focuses on the components that make up the core calving grounds in Yukon, how they are used by the herd and how the herd responds to changing environmental variables within a year and between years.

From 1984–86, we conducted an intensive study on the use of northern Yukon during the insect season. A formal review of potential hydrocarbon development on Yukon's north slope identified a need to document the range relations of the herd during the critical insect season and to assess the potential negative impacts of various development scenarios on the well being of the herd (Beaufort Environmental Assessment Review Panel 1983). In the summer study, we address the regional resources in the area, how the herd responds to these resources and examine the behaviourial and energetic response of individuals and groups to insect harassment (Chapter 3).

In Chapter 4, we bring together much of the information presented and examine the energetic implications of our findings in terms of weight changes of reproductive females and the birth and weight gain in the calves utilizing a computer simulation model.

CHAPTER 2. Winter

Introduction

Proposed and ongoing development on the winter range of the Porcupine Caribou Herd prompted much concern for the welfare of the herd in the early to mid-1970s. Of prime concern was the possible disruption to migration caused by the presence of the Dempster Highway, then scheduled to be completed from Dawson City, Yukon to Inuvik, NWT. The roadbed itself, recreational and industrial traffic, and hunting activity were all cited as possible causes of disturbance (Surrendi and DeBock 1976). The Yukon Department of Renewable Resources and the Canadian Wildlife Service initiated a study on the winter range in response to these concerns.

In this chapter we examine the winter ecology of the Porcupine Caribou Herd. We have approached this objective systematically, first documenting the characteristics of the range, its snowfall patterns, its vegetation resources, with particular reference to the distribution and abundance of lichens, and its fire history. We then document caribou use of the range, how historically the animals have distributed themselves on the Yukon portion of their winter range, what their present food habits are, and how daylength and snow parameters affect their activity budgets, activity cycles and cratering dynamics.

Winter is a critical period in the ecology of caribou (Russell and Martell 1984). During this long time, the species must cope with low temperatures and continuous snow cover, often crusted or iced-over, that can further limit the already reduced food resources. The strategy of most large migratory herds of wild *Rangifer* is to migrate south to the sheltered taiga woodlands that are rich in terrestrial lichens. In the Yukon, the Porcupine Caribou Herd occupies an expansive winter range, varying annually from the north flank of the Ogilvie Mountains, near Dawson City in the south, to the northern flanks of the Richardson Mountains in the north (Fig. 1.1).

Although considerable data are available on the dependence of wintering caribou on lichens (Russell and Martell 1984), few research projects have addressed the relationship between lichen availability, as influenced by changes in snow cover, and changes in diet, both over winter and among years. Previous reports on winter diet of the Porcupine Caribou Herd are based only on late winter collections in single years (Thompson and McCourt 1981; Duquette 1984). The present paper reports on estimates of the diets of caribou throughout three winters.

Daily activity patterns of caribou and reindeer (*Rangifer tarandus*) are related to seasonal changes in physiology, food quality and quantity, photoperiod, environmental conditions, and harassment by other organisms (White *et al.* 1981). A number of recent studies have collected information on winter activity budgets of caribou and reindeer (Gaare *et al.* 1975; Roby 1978, 1980; Reimers 1980; Boertje 1981, 1985; Skogland 1984; Roby and Thing 1985) and some general patterns are beginning to emerge (Russell and Martell 1984). Winter activity budgets are strongly influenced by photoperiod (Eriksson *et al.* 1981) and range quality as reflected by food quality and quantity and by snow conditions (Gaare *et al.* 1975; Roby 1978, 1980; Boertje 1981, 1985; Skogland 1984; Russell and Martell 1984; Roby and Thing 1985). Knowledge of activity budgets, therefore, will assist managers to assess the relative quality of winter range, estimate the relative condition of the herd and, by understanding the factors that affect activity budgets, analyse more accurately the influence of human disturbance.

The proportion of time spent lying is inversely related to range quality, as dictated by forage quality and/or forage availability (Gaare *et al.* 1975; Roby 1978; Boertje 1981; Russell and Martell 1984). Animals ingesting poor quality forage require longer periods for rumination than those ingesting high quality forage (Blaxter 1962). When food is scarce (because of either low biomass or adverse snow conditions), animals face an energetic trade-off between the high energy expenditure of obtaining food and low energy intake by increasing lying time. By comparing percent lying (percent of the observation period that animals spend lying) between herds or temporally for the same herd, an indirect method of assessing range quality is available.

Rangifer cue their activity to sunrise (Gaare *et al.* 1975; Thomson 1977; Roby 1978; Eriksson *et al.* 1981), and daylength (percent of a day occurring between sunrise and sunset) affects activity patterns (Eriksson *et al.* 1981). This complicates direct comparison of percent lying among studies.

Snow-cover limits the availability of forage. The success of caribou, a species that feeds on plants under the snow, is related to their ability to adapt to changing snow conditions. The array of strategies that caribou are able to exploit include occupying areas of favourable long term snow conditions and selecting favourable microsites for feeding (LaPerierre and Lent 1977).

Characteristics of the winter range

Study area

The study area encompassed the major wintering range of the Porcupine Caribou Herd within the Yukon Territory, an area bordered on the north by the Porcupine and Bell Rivers, and on the south by the south flank of the Ogilvie Mountains (app. 64 degrees N, Fig. 1.2). Roughly half the area drains northeast into the Beaufort Sea via the Peel and Mackenzie Rivers, and the other half west into the Bering Sea via the Porcupine and Yukon Rivers.

Dawson and Old Crow are the only two Yukon communities bordering the winter range and only one all-season road, the Dempster Highway, transects the area (Fig. 1.2), providing access for hunters from communities to the north and south. Since this study was initiated, the importance of the central and northern Richardson Mountains as key winter range has increased considerably. Unfortunately, we did not include this region in our original study area and suggest that more work needs to be conducted in that region during winter.

Climate

The climate of the area is continental, with long cold winters and cool summers. Annual precipitation is low, varying from 200 mm in the low plains of the north to 750 mm in the southern mountains. The area is influenced to some extent by weather systems from both the Pacific and Arctic Oceans. Pacific air, either from the Gulf of Alaska or the Bering Sea, brings most of the precipitation, while Arctic air brings the extreme cold of winter. During the study, the mean monthly temperatures fell as low as -41.8°C (January 1981; Table 2.1). Pacific systems are more dominant in the south and Arctic systems dominate in the north.

Terrain

All or part of three broad physiographic regions – the Richardson Mountains, Porcupine Plateau and Ogilvie Mountains (Bostock 1948) lie within the Yukon winter range of the Porcupine Caribou Herd. The Richardson Mountains are characterized by moderate to steep slopes and rounded, north-south trending ridge crests which rise 700 m above the adjacent Porcupine Plateau. At their western edge the mountains become abruptly lower and appear to merge into the Porcupine Plateau (Terrain Analysis and Mapping Services Ltd. 1981).

Table 2.1. Mean daily temperatures at two locations on the Dempster Highway, 1979-82

		Temperature (°C)					
Winter	Station	Nov	Dec	Jan	Feb	Mar	Apr
1979-80	Eagle Plains	- 5.8	-20.5	-23.6	-14.7	-16.4	-11.3
	Ogilvie River	-11.2	-28.4	-31.7	-22.4	-19.1	- 8.6
1980-81	Eagle Plains	-17.2	-25.0	- 7.6	-20.2	-12.3	
	Ogilvie River	-19.2	-36.5	-14.2	-23.7	-15.1	-10.9
1981-82	Eagle Plains	-17.8	-18.4	-29.7	-23.0	-16.8	
	Ogilvie River	-21.6	-25.4	-41.8	-26.2	-22.8	

The Porcupine Plateau includes the Embankment Hills, Peel Valley, Eagle Plains and the unnamed low rolling area which parallels the west flank of the Richardson Mountains. The latter area generally has a relief of 100 m with some ridges rising up to 200 meters higher than the surrounding area. Rivers, arranged in a trellis pattern, cross this area as they flow westward from the Richardson Mountains. Only the Eagle River exhibits a flat-floored valley with terraced sides unlike the broad V-shaped valleys of the other streams. To the south of the Eagle Plain lies the 20 km wide, 200 m deep, flat-floored, steep-sided Peel Valley (Terrain Analysis and Mapping Services Ltd. 1981).

The Northern, Central and Southern Ogilvie Ranges and the Ogilvie and Taiga valleys comprise the Ogilvie Mountains. The Northern Ogilvie Ranges are a series of broad, steep-sided ridges. The Central Ogilvies consist of steep-sided, round topped east-west trending ridges that are transected by Engineer Creek. The Southern Ogilvies are the most rugged of all the mountain ranges in the area, with jagged crests and steep to precipitous flanked peaks, which rise 1000 m above the broad, flat-floored valleys. The Klondike, Tombstone and Blackstone Rivers dissect the ranges completely (Terrain Analysis and Mapping Services Ltd. 1981).

Surficial geology

Most of the winter range, including the Porcupine Plateau, the northern part of the Ogilvie Mountains, the extreme western ridge of the Richardson Mountains, shows no evidence of glaciation during the last ice age. On the Eagle Plains, fine texture clay silt overlays rubble material. In the Ogilvie Mountains a thinner coarser grained colluvium has evolved. Even though not glaciated, most surficial deposits along watercourses are of glacial-fluvial origin. Along the Eagle and Whitestone Rivers, for example, terrace formation resulted from the damming of meltwater from the Laurentide Icefields.

The study area is located on the northern extremity of the discontinuous permafrost region of North America (Brown 1969). The location of this region is largely determined by mean annual temperature. The mosaic of permafrost is largely influenced by such terrain features as relief, drainage, soil texture, vegetation and snow-cover (Brown 1969). Permafrost-free areas include steep south facing slopes in the south and gravel deposits along most of the river valleys and in lakes.

Two features combine to produce a unique winter range among Canadian migratory herds – mountains and unglaciated terrain. The mountainous nature of the range results in dynamic weather conditions with distinct regional snow and wind patterns (discussed later). The lack of extensive glaciofluvial deposits results in unique vegetation complexes and deeper more widespread permafrost, compared to more eastern winter ranges. Permafrost is believed to have developed in the Pleistocene ice ages (Brown 1969). The lack of recent glacial influence over the majority of the winter range means that the processes of erosion and mass wasting have continued for many years resulting in deep peat accumulations.

Historical winter distribution

Prior to 1970, sporadic fixed-wing flights and ground observations served to define the wintering areas of the Porcupine Caribou Herd as far back as the last century (Kevan 1970). In the early 1970s a proposal to move Alaskan natural gas from Prudhoe Bay, Alaska to the Mackenzie Delta and the construction of the Dempster Highway prompted intensive monitoring of the herd by industry and government. Since 1970, there has been relatively unbroken record of the movements and winter distribution of the herd

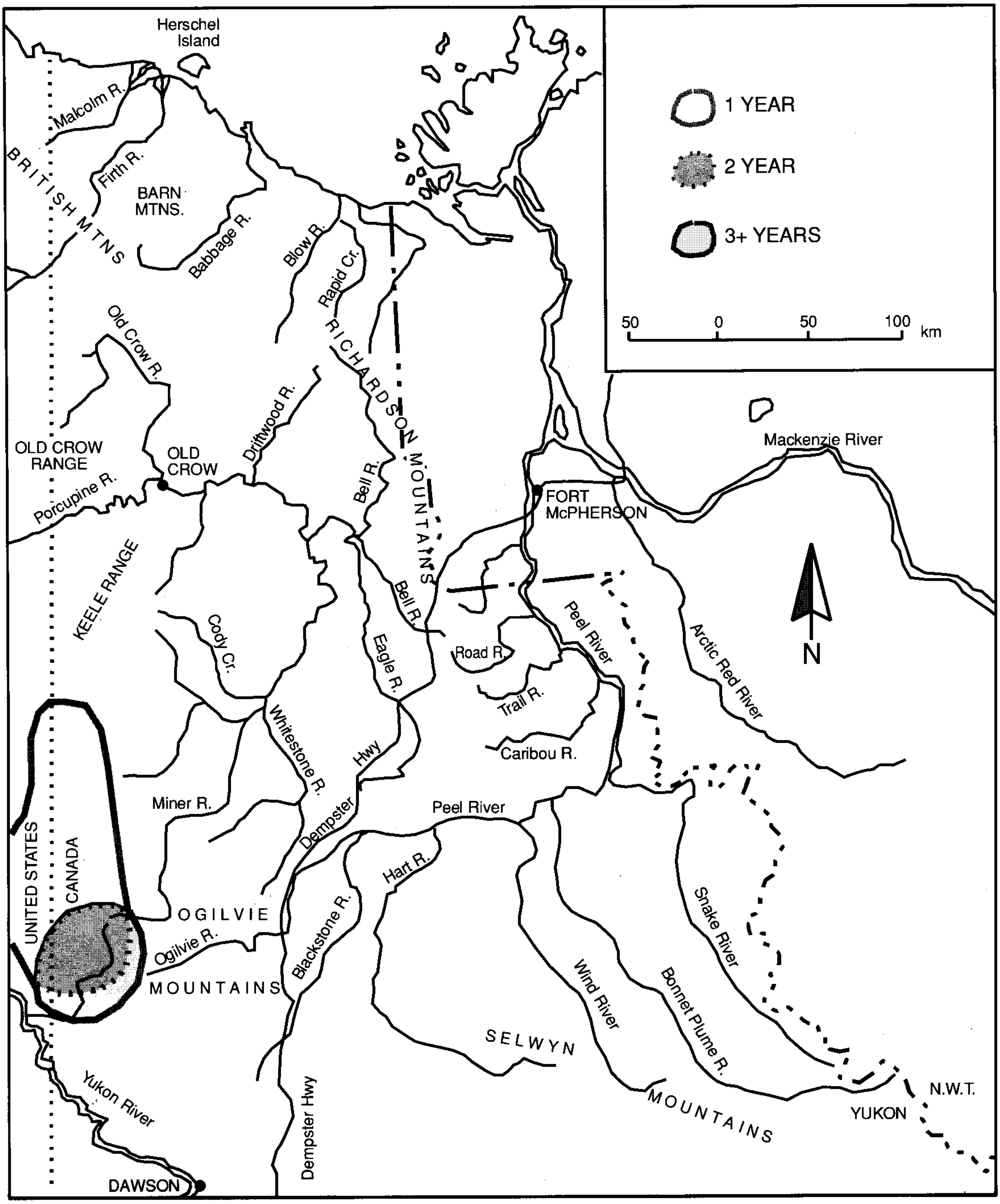

Figure 2.1. Alaskan border distribution of the Porcupine Caribou Herd in winter.

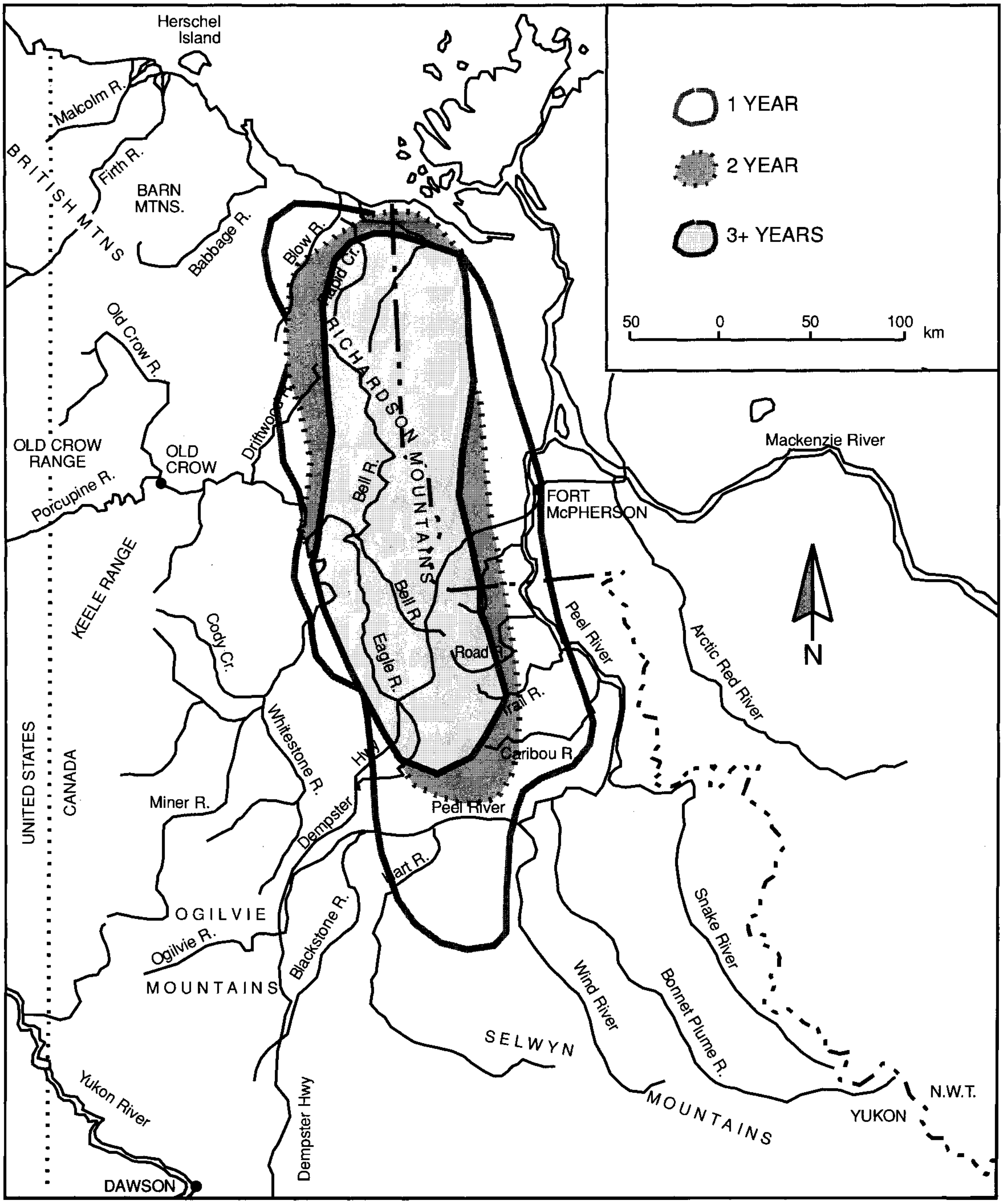

Figure 2.2. Richardson Mountain distribution of the Porcupine Caribou Herd in winter.

From these distributions and concurrent spring snow surveys conducted by the Department of Indian and Northern Affairs, Water Surveys Division in Yukon and the U. S. Department of Agriculture snow courses in Alaska, it appears that winter distribution of the herd is largely dictated by a combination of winter snow conditions and short-term traditional movements.

First, we can categorize distributions into four types that reflect winter snow conditions:

Border distribution – In two years the majority of the Yukon portion of the herd wintered along the Yukon/Alaska border from the Tatonduk to the headwaters of the Kandik River (Fig. 2.1). In both years (1979-80, 1981-82) snows were deeper than average in the south. We speculate from pre-1970 surveys that a similar distribution occurred in 1963-64. In 1963-64 and 1981-82 snowfall north of the Porcupine River (Shingle Point) was light throughout September, followed by extremely heavy snowfall in late September (1981) and early October (1963). In both of these years members of the Porcupine Caribou Herd moved across the Yukon River and inhabited the range of another migratory herd, the Fortymile Caribou Herd. We speculate that the invasion of this southern range was prompted by a

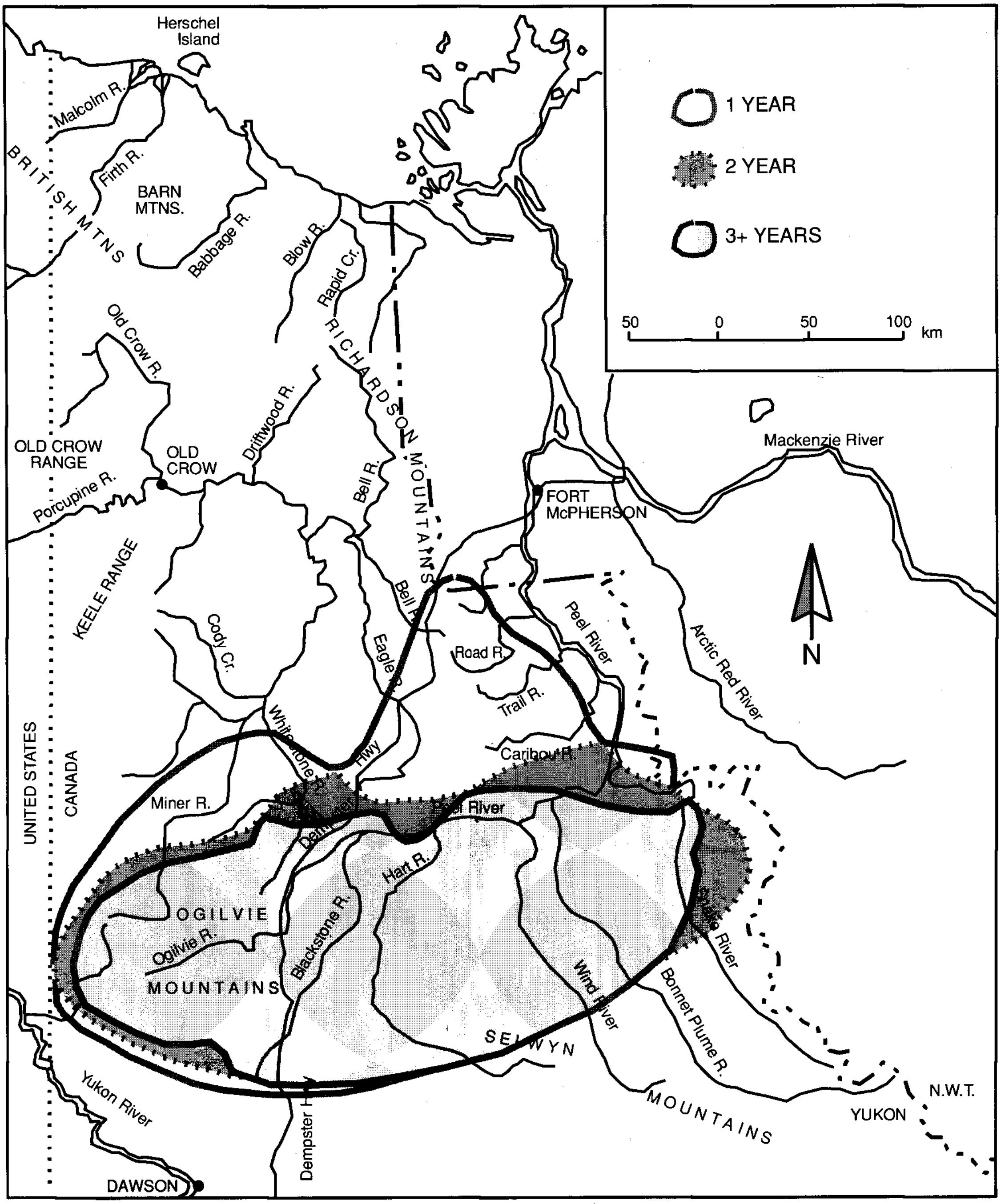

Figure 2.3. Ogilvie/Hart distribution of the Porcupine Caribou Herd in winter.

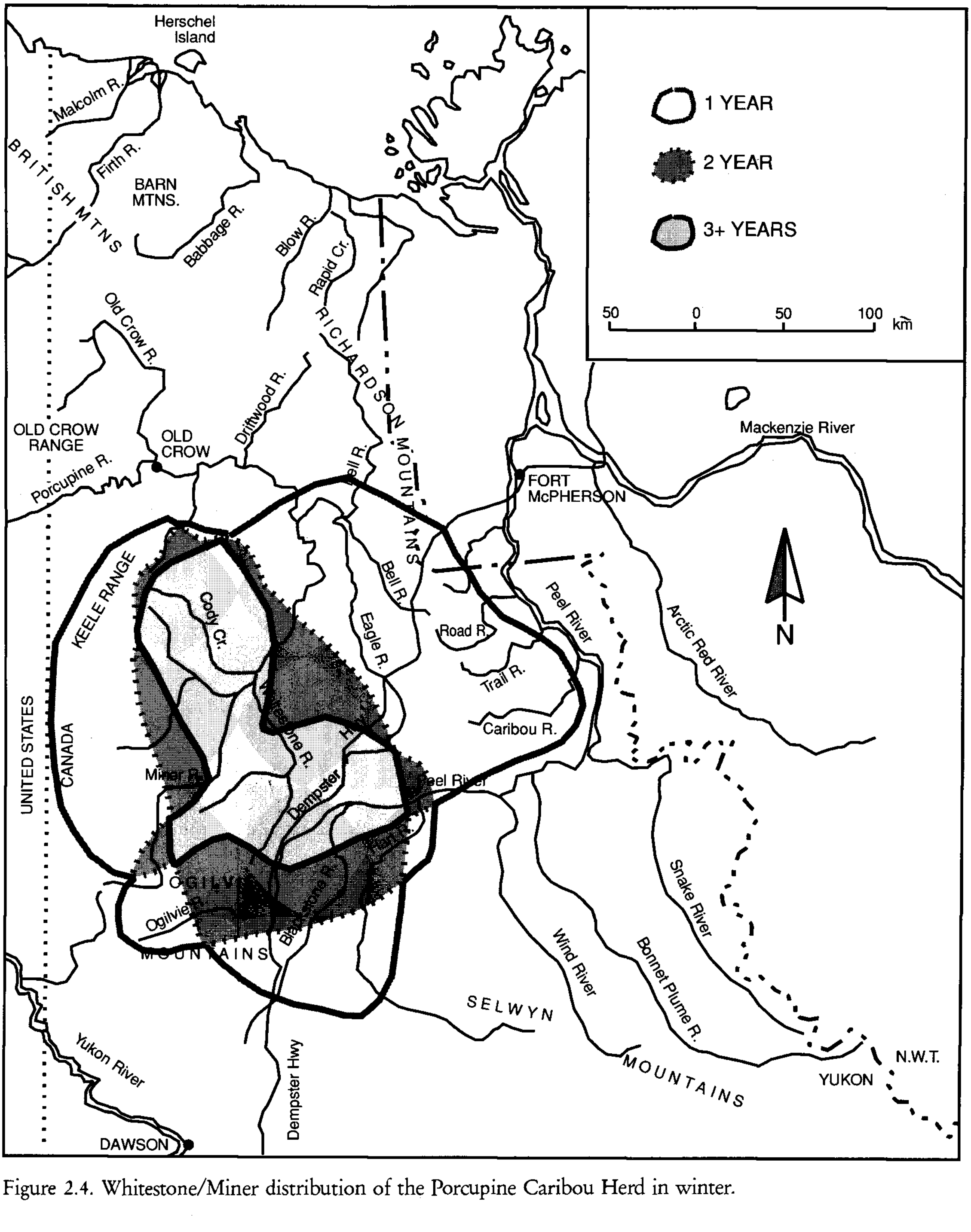

Figure 2.4. Whitestone/Miner distribution of the Porcupine Caribou Herd in winter.

late fall migration followed by heavy snowfall both north of the Porcupine River and within the other wintering areas of the herd (Ogilvie/Hart).

In 1978-79 a similar pattern occured with no significant snowfall until late October north of the Porcupine River, followed by extremely heavy snowfall resulting in the second heaviest accumulation in 25 years. The majority of the herd did cross the Porcupine River early in September, but after encountering mild weather they recrossed the Porcupine River until mid October, many then moving into Alaska. For those wintering in Canada, with fall migration stalled so late, animals utilizing the Old Crow route simply ran out of time and wintered further north on the migration route than they might do normally.

Richardson Mountains distribution – During the winters the majority of the Yukon wintering animals occupied the Richardson Mountains (Fig. 2.2), snow depth tended to be normal to above normal. The Richardson Mountains are characterized by high winds during winter, which results in an uneven distribution of snow with many areas blown completely bare.

Ogilvie/Hart distribution – Among the snow regions within the range of the Porcupine Caribou Herd, the Ogilvie/Hart region has the lowest mean snow accumulation. During the winters when the majority of the herd occupied this region throughout the winter (Fig. 2.3), snows were characterized by normal to high snowfall in the south combined with initial heavy snowfall from early to mid September in the north, resulting in a typical fall migration pattern. Animals moved into the Ogilvie/Hart basin, took advantage of the relatively shallow snow conditions (compared to adjacent regions) and remained in these regions until spring migration.

Whitestone/Eagle distribution – During the winters when the majority of the Yukon wintering population of the herd occupied this large region (Fig. 2.4), snow accumulation was invariably below normal. Movement during these winters fell into two patterns. If animals migrated early in September, they penetrated deeply into the Ogilvie/Hart basin, expanding into the Whitestone/Eagle area as winter progressed. If migration was late, animals drifted slowly south directly into the region. This region was shown to have the best lichen biomass accumulation, though snow depths were prohibitive in normal to deep snow years.

Trends in distribution types:

1970–74 From the winter of 1970–71 to 1973–74 the distribution was very consistent. The wide forested basins of the Ogilvie Mountains and the Hart and Ogilvie drainages, were occupied in all four winters. Concentrations of animals occurred from the Alaska to the NWT borders in this southern portion of the range. In only one year (1971–72) did concentrations occur north of the Peel River (Russell *et al.* 1992b).

1974–82 Over the next seven years (1974–75 to 1981–82), caribou moved from an exclusively Ogilvie/Hart distribution north and west into the wide basins of the Whitestone and Miner Rivers, occupying the Richardson Mountains only once. In deep snow years, the animals tended to use either the Tatonduk and Alaska border region or the Richardson Mountains, occupying the Whitestone/Miner region in the intervening shallow snow years (Russell *et al.* 1992b).

1982–89 From 1982–83 to 1988–89, concentrations were consistently found in the Richardson Mountains. The only year where the distribution occupied the Whitestone/Miner region was 1983–84, the lowest snow year during this period (Russell *et al.* 1992b).

Methods

Snow

Snow characteristics were measured between 1979–82 at three types of stations (Fig. 2.5):

1) 23 locations along the Dempster Highway from km 78–411, which were sampled in early winter (early December), mid-winter (late January), and late winter (early March);
2) 19 field camps adjacent to the Dempster Highway or further afield; and
3) Remote stations which were sampled during March each winter with the aid of a helicopter.

The habitat surrounding each station was classified as one of three forested (closed, open or scattered spruce) or four treeless habitat types (tussock, low shrub, tall shrub or exposed ridge tundra). At each station, 10 replicate measurements of depth and hardness were obtained, one every 5m along a 50 m transect. Depth was measured with a metre stick and hardness with a Ramsonde penetrometer. Ten snow cores were obtained at each site and weighed together to determine density. The Ramsonde penetrometer was incapable of measuring hardness less than about 500 g, which usually occurred in early winter with

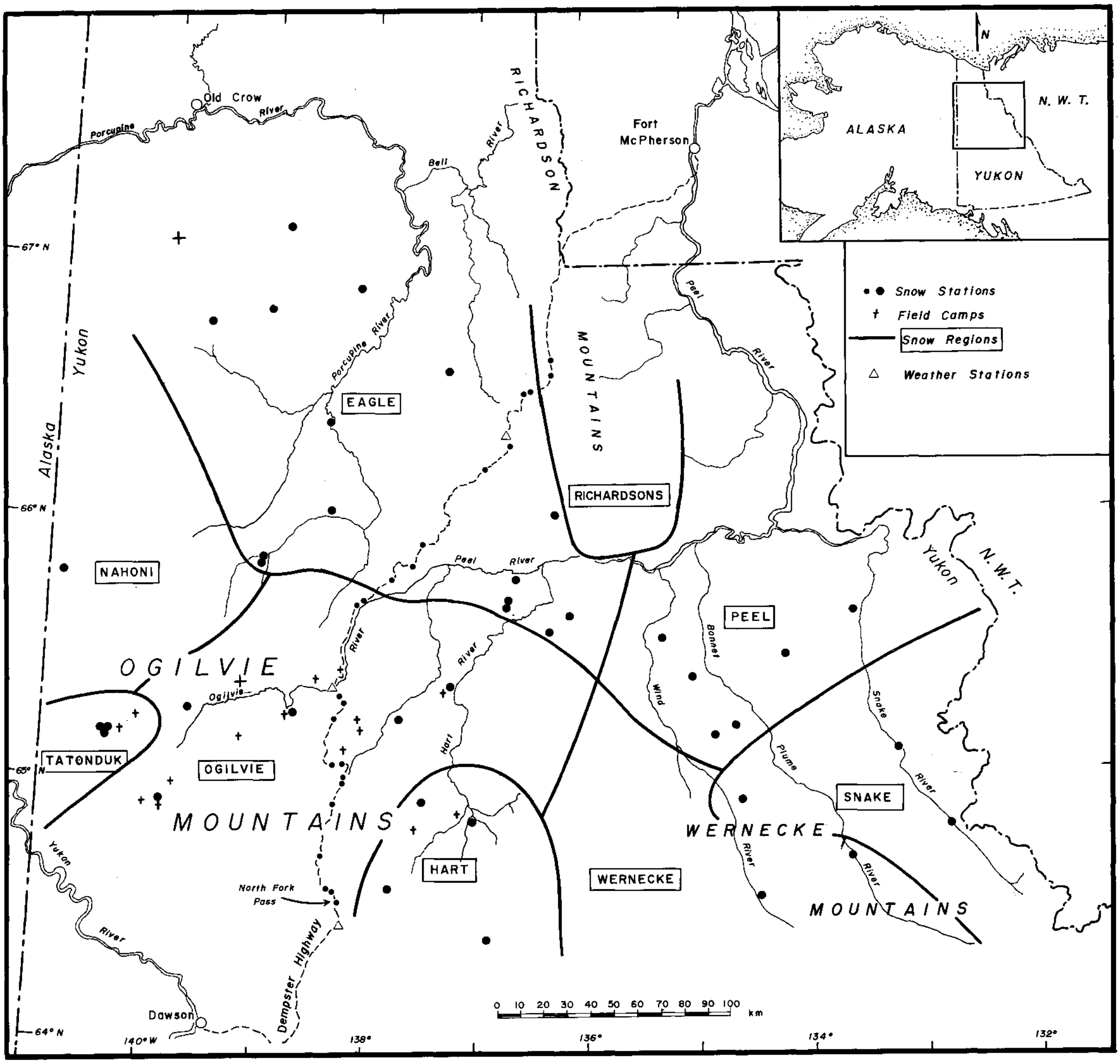

Figure 2.5. Winter range study area showing the snow stations and snow regions.

snow depths less than 30 cm. In these cases we arbitrarily assigned a hardness value of 100 g. We delineated areas having similar snow regimes (snow regions) primarily on the basis of snow depths in forested habitats. During this somewhat subjective process, we attempted to draw boundaries of regions along geographic features which we believed created the regional differences in snow characteristics.

Lichen biomass

In late May and early June of 1979 and 1980, prior to the emergence of most green vegetation, 32 random 25 x 25cm plots were established along a 100 m transect at each of the 116 stands. All lichen species cover and heights (only in second season) were recorded. As well, divot samples of the fruticose lichens were collected within the 25 x 25cm plots and air-dried in the field. In the lab, lichen samples were cleaned of debris, oven-dried to constant weight and for 32 stands separated and weighed by species. In 84 stands, all but five random plots were dried and weighed but not separated by species. In the five random plots, lichens were dried, separated and weighed by species.

The following method was used to determine total biomass by species in those stands not separated and weighed by species. For each species the average biomass associated with each cover value was calculated. If values were missing or sample sizes too small, interpolated or extrapolated values were used after plotting biomass versus cover value for each species. The resultant table of cover and corresponding biomass was applied to the frequency of cover values within each stand for each species in the stand. The resultant estimated total biomass of all species was then compared to the known total biomass of the stand. Individual species biomasses were then adjusted up or down in proportion to the total over or under estimate in order for the estimated total biomass to equal the known total biomass, calculated according to the following formula:

$$BIO_{jk} = (F_{ijk} \text{ x } B_{ij}) / \sum_{j=1}^{n} (F_{ijk} \text{ x } B_{ij}) / W$$

where BIO_{jk} is the biomass of species j for stand k, n is the number of species in stand, F_{ijk} is the frequency of cover value i for species j in stand k, B_{ij} is the average biomass in cover value i of species j, and W is the total weighed biomass of lichens in the stand.

Relationships of total biomass, *Cladonia* biomass, *Cladina* biomass and *Cetraria* biomass (except *Cetraria richardsoni*) with environmental variables were determined by Spearman rank correlation.

Aspect was transformed using the procedure proposed by Trimble and Weitzman (1956) and modified by Beers *et al.* (1966) to reflect a continuum from cold NE-facing slopes to warm SW-facing slopes.

Analysis of variance and Duncans multiple range test were used to test for significant difference of means among community type and range type.

Fire history

The fire history of sample stands was determined from tree discs, cut at ground level, sanded and examined under 8x to 40x magnification using a binocular microscope. Sampling was concentrated in the vegetation stands from trees where evident or suspected fire scars occurred (Arno and Sneck 1977). Trees were also sampled along obvious and accessible fire boundaries and randomly on either side of fire boundaries. On all sites it was assumed that the present stand was of fire origin and that establishment had occurred promptly following fire.

For stands that were uneven-aged, post-establishment fires were considered to have occurred if a second age class was clearly in evidence or definite fire scars were present.

Results

Snow

We divided the area into nine snow regions (Fig. 2.5). During the three years, late winter snow was generally deepest in the northern and extreme southern parts of the study area (Eagle, Peel, Richardsons, Tatonduk), and shallowest in the basins of the Ogilvie and Wernecke Mountains (Ogilvie, Hart, Snake; Table 2.2). Regional patterns of density and hardness were similar to those of depth for 1981–82, but were not consistent in the other years (Tables 2.3 and 2.4). Mid and late winter snow depth tended to be greatest in 1981–82 and least in 1980–81. Hardness and density also showed this year-to-year pattern in late winter, but not in midwinter. Snow was deeper, lighter, and softer in forest than in tundra habitats. Depth, and especially hardness, were more variable in tundra than in forest snow.

There was little correlation between late winter snow depth and density in either tundra or forest. The only significant relationship between these two was in 1981–82 in forests ($r=0.55$, $p=0.0002$, $n=41$). Overall, correlations were positive in all three years for forests, and negative in two of three years for tundra.

In all three winters, late winter snow depth was negatively correlated with hardness in tundra. In forest, the relationship was weakly positive overall, but within the range of hardness 600–1200 kg, depth varied

Table 2.2. Snow depths (cm) by snow regions in the winter range of the Porcupine Caribou Herd, winter 1979-80 to 1981-82. (Sample size).

	1979 - 1980			1980 - 1981			1981 - 1982		
Region	Early Dec.	Late Jan.	Early Mar.	Early Dec.	Late Jan.	Early Mar.	Early Dec.	Late Jan.	Early Mar.
Forest									
Richardsons		53 (1)	68 (1)		63 (1)	66 (1)	41 (1)	48 (1)	60 (1)
Eagle	23±4 (3)	46±1 (3)	64±1(11)	45±2 (3)	53±2 (3)	58±2(15)	61±6 (3)	66±3 (3)	78±2(15)
Nahoni			69 (1)						
Tatonduk			56 (1)			45 (1)			92±5 (2)
Ogilvie	20±1(12)	40±2 (8)	51±1 (9)	21±2(10)	24±3 (7)	35±2(12)	49±1 (8)	55±2 (7)	64±3(11)
Hart			48±2 (2)	21±4 (3)	17 (1)	35±5 (3)			60±1 (3)
Snake						18±4 (3)			54±3 (3)
Peel						39±9 (4)			92±3 (4)
Wernecke						48±8 (2)			70±4 (2)
Tundra									
Richardsons		20±1 (2)	23±6 (2)		19±6 (2)	18±6 (2)	20±5 (2)	18±4 (2)	21±7 (2)
Eagle	15±2 (2)	27±11(2)	37±4 (6)	33±7 (2)	31±9 (2)	41±8 (5)	61±7 (2)	62±7 (2)	57±9 (5)
Tatonduk			46±6 (2)			30 (1)			79±21(2)
Ogilvie	17±2 (9)	31±4 (6)	29±4 (6)	20±1 (8)	19±3 (6)	27±4 (5)	35±5 (6)	41±4 (7)	41±6 (6)
Hart			56 (1)	18 (1)	21±2 (3)	38 (1)			50 (1)
Peel						24±10(2)			53±11(2)
N. Fork Pass	35±3 (2)	73±5 (2)	77±2 (2)	41±1 (2)	71±1 (2)	82±3 (2)	75±4 (2)	73±1 (2)	85±7 (1)

Table 2.3. Snow density (g/cm³) by snow region in the winter range of the Porcupine Caribou Herd, winter 1979-80 to 1981-82. (Sample size).

	1979 - 1980			1980 - 1981			1981 - 1982		
Region	Early Dec.	Late Jan.	Early Mar.	Early Dec.	Late Jan.	Early Mar.	Early Dec.	Late Jan.	Early Mar.
Forest									
Richardsons		194 (1)	238 (1)		192 (1)	211 (1)	163 (1)	188 (1)	185 (1)
Eagle	143±3 (3)	183±9 (3)	167±3 (11)	159±6 (3)	200±13 (3)	153±10(15)	197±15 (3)	209±16 (3)	201±6 (15)
Nahoni			130 (1)						
Tatonduk			184 (1)			140 (1)			224±37 (2)
Ogilvie	144±6 (12)	182±9 (8)	165±8 (9)	126±9 (10)	169±15 (7)	159±7 (12)	194±10 (8)	185±6 (7)	203±5 (11)
Hart			176±6 (2)	113±17 (3)	186 (1)	144±17 (3)			179±11 (3)
Snake						146±35 (2)			182±7 (3)
Peel						177±22 (2)			231±11 (4)
Wernecke						213±27 (2)			216±25 (2)
Tundra									
Richardsons		240±1 (2)	236±18 (2)		176±19 (2)	213±45 (2)	190±17 (2)	191±27 (2)	249±22 (2)
Eagle	136±9 (2)	204±29 (2)	184±13 (6)	170±26 (2)	236±12 (2)	215±36 (5)	242±28 (2)	272±9 (2)	340±64 (5)
Tatonduk			227±19 (2)			155 (1)			244±28 (2)
Ogilvie	157±12 (9)	168±12 (6)	227±14 (6)	133±13 (8)	174±16 (6)	162±14 (5)	207±14 (6)	217±15 (7)	241±16 (6)
Hart			147 (1)	88 (1)	133±13 (3)	137 (1)			
Peel						194 (1)			259±37 (2)
N. Fork Pass	175±12 (2)	206±17 (2)	239±24 (2)	155±5 (2)	190±1 (2)	249±15 (2)	214±9 (2)	256±5 (2)	280±18 (2)

Table 2.4. Snow hardness (kg x 10^{-2}) by snow regions in the winter range of the Porcupine Caribou Herd, winter 1979-80 to 1981-82. (Sample size).

Region	1979 - 1980			1980 - 1981			1981 - 1982		
	Early Dec.	Late Jan.	Early Mar.	Early Dec.	Late Jan.	Early Mar.	Early Dec.	Late Jan.	Early Mar.
Forest									
Richardsons		122 (1)	214 (1)		102 (1)	108 (1)	75 (1)	124 (1)	106 (1)
Eagle	10 * (3)	84±3 (3)	86±2 (11)	10 * (3)	99±5 (3)	114±30(15)	127±21 (3)	332±35 (3)	245±23 (15)
Nahoni			71 (1)						
Tatonduk			83 (1)			79 (1)			378±134 (2)
Ogilvie	10 * (12)	71±10 (8)	90±4 (9)	10 * (10)	151±45 (7)	68±7 (12)	180±30 (8)	203±34 (7)	279±25 (11)
Hart			98±9 (2)	10 * (3)	47 (1)	106±37 (3)			148±64 (3)
Snake						115±105(3)			143±57 (3)
Peel						338±168(4)			379±107 (4)
Wernecke						362±196(2)			209±100 (2)
Tundra									
Richardsons		656±233(2)	740±55 (2)		612±277(2)	633±65 (2)	562±67 (2)	1137±79(2)	546±180 (2)
Eagle	10 * (2)	854±127(2)	338±11 (6)	10 * (2)	542±374(2)	298±120(5)	461±140(2)	796±172(2)	890±165 (5)
Tatonduk			293±102(2)			77 (1)			493±134 (2)
Ogilvie	10 * (9)	355±109(6)	430±51 (6)	10 * (8)	286±34 (6)	210±36 (5)	501±41 (6)	932±88 (7)	616±98 (6)
Hart			142 (1)	10 * (1)	40±15 (3)	70 (1)		385 (1)	
Peel						126±116(2)		666±381 (2)	
N. Fork Pass	10 * (2)	123±49 (2)	373±27 (2)	10 * (2)	112±1 (2)	142±2 (2)	234±88 (2)	545±45 (2)	402±29 (2)

* Hardness estimated, snow to soft to record.

Table 2.5. Average biomass of divot samples of each lichen species associated with each cover class (g/m²).

Species	Percent cover								
	0^+	<1	1–5	6–10	11–25	26–50	51–75	76–95	>96
Cladina rangiferina	29	90	202	502	1027	2617	4067	4515	–
Cladina mitis	22	45	141	246	531	851	1139	2016	–
Cladina alpestris	3	26	147	435	976	1664	2528	4880	–
Cladonia sp	42	99	221	323	720	1190	2112	2848	–
Cetraria nivalis	0	32	67	112	125	736	–	1942	–
Cetraria cucullata	6	48	124	278	509	851	1670	–	–
Cetraria islandica	10	67	134	326	496	1056	1290	–	–
Cetraria richardsoni	0	48	147	310	589	–	–	–	–
Stereocaulon alpina	6	29	109	400	752	1770	3552	4832	5536
Others*	0	13	80	112	234	–	–	–	–

+ result from species found in sorting but not recorded in field.

* minor species considered collectively include *Thamnolia subuliformis*, *Dactylna arctica* and *Alectoria ochroleuca.*

quite linearly from 30 to 80 cm. This probably indicates snow largely unaffected by wind or thaws. Including all years and all periods, there did appear to be a trend for increasing hardness at increasing depths, particularly in forest sites.

Density and hardness were positively but weakly correlated in both forest ($r=0.63$, $p<0.0001$, $n=183$) and tundra ($r=0.60$, $p<0.0001$, $n=133$). Hardness increased faster with increasing density in tundra than in forest.

Lichen biomass

For those stands not totally separated and weighed by species using the equation outlined earlier, total lichen biomass was determined . The average biomass determined for each cover value by species (Table 2.5) was multiplied by the frequency of the respective cover value in each stand to determine the estimated lichen biomass (g/m²).

To test the validity of the estimation technique for individual species, the estimated biomass was regressed against weighed biomass (both log transformed) for all stands completely separated and weighed. The results indicated that the estimation technique is most accurate for species with largest sample sizes (significant at 95% level), and least accurate as a predictor for sample sizes of less than 5 (Table 2.6).

Total lichen biomass varied between 0 and 501 g/m² with a mean of 65±7.2 g/m². The four major genera in terms of their contribution to total biomass were *Cladina* (57%), *Cetraria* (18%), *Cladonia* (15%), and *Stereocaulon* (10%, Table 2.7) . Among species *Cladina rangiferina* and *Cladina mitis* were the major contributors (Table 2.7).

Eagle Plains had significantly higher total fruticose lichen biomass than the other four regions ($F=5.80$, $p>0.003$) and a significantly higher reindeer lichen biomass than all regions but the North Fork Pass ($F=4.86$, $p>0.0012$; Table 2.7).

Table 2.6. Regression of log real versus log estimated biomass by species.

Species	Equation	R	N	Significance
Cladina rangiferina	log real = 0.105 + 0.96 log est	.96	21	**
Cladina mitis	log real = 0.703 + 0.669 log est	.71	26	**
Cladina alpestris	log real = 0.627 + 0.557 log est	.71	7	*
Cladina spp.	log real = 0.538 + 0.753 log est	.88	26	**
Cetraria nivalis	log real = 0.44 + 0.435 log est	.26	4	NS
Cetraria cucullata	log real = 0.387 + 0.8 log est	.88	22	**
Cetraria islandica	log real = 0.47 + 0.699 log est	.79	23	**
Cetraria richardsoni	log real = 0.254 + 0.798 log est	.75	4	NS

** at 99% level
* at 95% level

Individual species biomass and total lichen biomass were only weakly correlated to individual abiotic variables. Most species were negatively correlated to slope position and positively correlated to percent slope, indicating that biomass is greater on ridges than in valleys and greater on steep rather than gentle slopes.

Cladina, *Cetraria* (except *Cetraria richardsoni*), *Cladonia* and mean total lichen biomass were summarized for the seven range types. The open forest types (Needleleaf Woodland) tended to have the greatest lichen biomass (Fig. 2.6). Because sample sizes were small and within type variability was great, there were few significant differences.

Table 2.7. Summary of lichen biomass (g/m^2; mean±SD) by species or species group for the five geographic regions of the Dempster Highway.

	Regions					
Lichens	North Fork Pass	Chapman Lake	Ogilvie River	Eagle Plains	Richardson Mountains	All Regions
Cladina	37.8±15.34	19.4±9.81	23.4±4.63	67.7±11.12	18.3±5.48	37.8±15.34
C. rangiferina	17.4± 7.90	10.2±6.43	12.5±3.61	42.0± 8.26	14.0±4.40	22.5± 3.32
C. mitis	13.0± 3.79	7.1±2.16	10.0±1.56	15.1± 2.10	2.9±0.82	10.3± 1.00
C. alpestris	7.5± 4.84	2.1±1.61	1.0±0.38	10.8± 3.08	1.3±0.81	4.9± 1.17
Cetraria[1]	6.6± 2.44	8.7±1.86	13.8±2.19	11.0± 1.39	10.6±1.81	11.2± 0.93
C. nivalis	1.0± 0.75	<0.1±0.01	0.3±0.13	0.5± 0.16	0.3±0.15	0.4± 0.10
C. cucculata	4.2± 1.92	7.4±1.87	7.7±1.67	4.4± 0.17	5.5±1.24	5.9± 0.66
C. islandica	1.4± 0.41	1.4±0.51	5.9±0.94	6.1± 1.12	9.7±0.71	4.9± 0.51
C. richardsoni	0.2± 0.16	0.6±0.39	0.9±0.39	0.9± 0.48	0.8±0.26	0.8± 0.20
Cladonia	9.8± 3.72	8.1±1.60	7.2±1.22	16.5± 3.04	2.2±0.41	9.6± 1.90
Stereocaulon	0.9± 0.74	3.8±3.76	3.5±2.43	15.3± 8.38	0.1±0.05	6.4± 2.83
Other	0.3± 0.16	0.3±0.14	0.3±0.21	0.3± 0.15	0.5±0.17	0.3± 0.09
Reindeer lichens[2]	44.4±15.93	28.1±9.97	37.2±6.23	79.0±11.91	28.8±6.67	48.8± 5.10
Total	55.6±19.60	40.9±14.48	49.0±8.16	111.9±17.43	32.4±7.04	65.9±7.22

1. does not include *C. richardsoni*
2. refers to *Cladina* and *Cetraria*

Combining the region-specific biomass for the various range types with an estimate of the percent cover of the various range types within 5 km of the Dempster Highway, results in a closer approximation of the regional differences in lichen biomass (Table 2.8). For this purpose, the percent cover of range types was determined from a dot grid overlain on a visually interpreted Landsat MSS scene. While percentages are only approximate, Table 2.8 does reveal the dominance of the Eagle Plains compared to other regions occupied by the herd during winter (North Fork Pass not normally occupied by the herd). The lichen resources of the northern and central Richardson Mountains were not assessed in this study.

Fire history

Sixty-eight sites were sampled for fire history and summarized by community type (Table 2.9). The longest interval since a major fire event was 343 years in a *Picea mariana - Ledum - Vaccinium* community. Of sites sampled 23% had been burned in the last 50 years, 42% in the last 100 years and 63% in the last 150 years.

The mean interval between fires (for those stands where at least one fire scar was recorded) was 120 ± 95 years. However it was evident that not all fires caused scarring. Intensive examination of areas known to have been burned recently revealed only dead trees and healthy, undamaged specimens.

Even though too few stands were sampled to relate age of stand to understorey vegetation characteristics, a few generalizations emerged. All subalpine shrub communities sampled were young stands. Whether this phenomenon resulted from a greater frequency of fires in the zone or a greater susceptibility to scarring of trees in the subalpine than elsewhere, was uncertain.

For the purpose of our analysis stand age was divided into five age classes for the 68 stands where age was determined. Mean total lichen biomass declined with age class (Fig. 2.7) although the high variation with each class resulted in no significant differences between classes.

Although no significant differences were noted between classes, stands in the oldest age class had about one half as much *Cladina* biomass as those in younger age classes. *Cladonia* spp. biomass declined with age after an initial peak between 51–125 years. Again, no significant differences were noted. *Cetraria* biomass, on the other hand, tended to increase with age, while *Stereocaulon* decreased significantly with age class (Fig. 2.7).

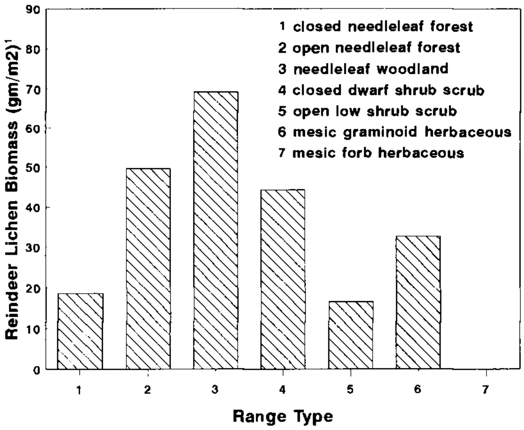

Figure 2.6. Reindeer lichen biomass versus range type.

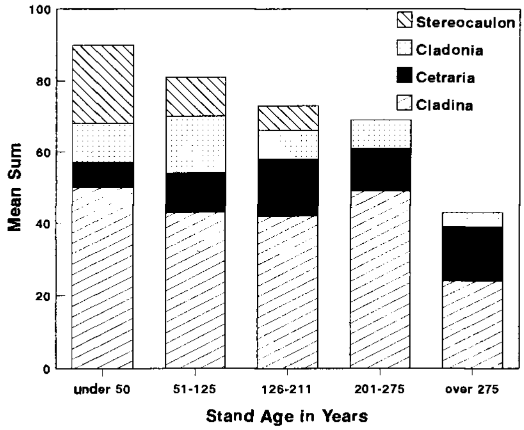

Figure 2.7. Lichen biomass versus stand age.

Discussion

Snow

The core Porcupine caribou winter range in Yukon is situated in the snow shadow of south and southwesterly Pacific storms that deposit most of their moisture on the south slopes of the Ogilvie and Wernecke Mountains. These large headwater basins of the Ogilvie and Hart Rivers also are relatively unaffected.

Table 2.8. The proportional area, mean biomass and proportional biomass of the six[1] range types within the five physiographic regions along the Dempster Highway.

Region Total biomass g/m²	Range type						
	Closed needleleaf	Open needleleaf	Needleleaf woodland	Open low shrub	Closed dwarf shrub	Mesic graminoid	Mean
North Fork Pass							
percent cover[2]	–	4.8	–	58.5	6.5	30.0	
mean biomass[3]	–	65.2*	–	48.2	16.5*	39.9	
prop. biomass[4]	–	3.1	–	28.2	1.7	12.0	45.0
Chapman Lake							
percent cover	–	–	–	27.1	2.9	66.8	
mean biomass	13.5	12.7	–	63.1	16.5*	23.9	
prop. biomass	–	–	–	17.1	0.5	16.0	33.6
Ogilvie Valley							
percent cover	–	21.1	26.7	6.0	3.1	31.1	
mean biomass	–	41.3	37.3	48.4*	16.5*	34.9	
prop. biomass	–	8.7	10.0	2.9	0.5	10.9	32.5
Eagle Plains							
percent cover	–	50.0	42.7	4.2	–	4.5	
mean biomass	47.4	78.1	85.3	43.8	–	21.6	
prop. biomass	–	39.1	36.4	1.8	–	1.0	78.3
Richardson Mountains							
percent cover	5.0	–	10.0	55.0	30.0	–	
mean biomass	0	–	37.3	38.5	16.5	–	
prop. biomass	0	–	3.7	21.2	5.0	–	29.9

1: the seventh range type (mesic forb) was not encountered on the mapping exercise.
2: the area of a given range type within 5 km of Dempster Highway.
3: mean fruticose biomass (g/m²) for range type specific to a given region.
4: calculated by – (percent cover x mean biomass) / 100 %.
* biomass not measured in given region, therefore, mean biomass for all regions used.

Lichen biomass

See and Bliss (1980) conducted field studies in our study area to determine the environmental factors that dictate vegetation community structure in lichen dominated alpine communities. They concluded that floristic composition was closely correlated to substrate pH, while species importance varied along a moisture gradient. For example, both *Cladina rangiferina* and *Cladina mitis* were common in wet sites on both acidic (Ogilvie) and basic (Nahoni) substrates, but reached greatest importance in the Ogilvie region. They concluded that moisture regime can override the correlation of species composition and substrate pH. However the lower quantitative values for these species in Nahoni sites suggests the influence of a secondary factor such as pH, or a factor correlated with it. *Cetraria cucullata*, on the other hand, reached its greatest abundance in moist basic sites but was generally considered a constant species throughout the environmental gradients.

Table 2.9. Summary of stand age by community type.

Range type	Mean age (yrs)	Community type	Mean age (yrs ± SD (n))
Closed needleleaf	160	*Picea glauca/Salix/Shepherdia*	-
		Picea glauca/Mertensia/Graminae	*160 (1)*
Open needleleaf	218	*Picea mariana/Betula/Carex*	160 ± 89 (6)
		Picea mariana/P. glauca/Betula/Vacc.	277 ± 33 (2)
Needleleaf woodland	136	*Picea glauca/Salix/Cladonia*	43 (1)
		Picea glauca/Dryas/Arctostaphylos	217 ± 90 (3)
		*Picea glauca/Dryas/*Moss	294 (1)
		Picea glauca/Stereocaulon	101 (1)
		Picea glauca/Stcreocaulon/Cladonia	54 (1)
		Picea mariana/Sphagnum/Cladonia	248 ± 84 (3)
		Picea mariana/Sphagnum/Eriophorum	175 ± 123 (2)
		Picea mariana/Ledum/Vaccinium	84 ± 71 (6)
		Picea mariana/P glauca/Alnus	168 ± 72 (3)
		*Picea mariana/P. glauca/*Lichen	26 (1)
Open low shrub	60	*Betula/Ledum/Vaccinium uliginosum*	43 (1)
		Betula/Vaccinium vitis-idaea/Ledum	-
		Salix/Betula	77 ± 53 (5)
		Alnus/Vaccinium/Ledum	-
		Betula/Ledum	-
Closed dwarf shrub	-	*Dryas*	-
Mesic graminoid	128	*Eriophorum/Ledum/Sphagnum*	-
		Carex/Ledum/Sphagnum	179 ± 30 (3)
		Carex/Ledum/Betula/Sphagnum	132 ± 90 (4)
		Eriophorum/Ledum/Sphagnum	-
		Eriophorum/Sphagnum/Betula	123 (1)
		Carex/Betula	78 (1)
Mesic forb	110	*Equisetum/*Moss	-
		Equisetum/Ledum	110 ± 142 (2)

Boyd (1984), working in east central Yukon, determined that lichens were unrelated to aspect and slope (among the species considered in Table 2.7). She found more *Cladonia rangiferina* than expected on rapidly drained sites while *Stereocaulon* species were associated with upper slopes and crests.

Although our data, based on species biomass, showed more relationships with environmental factors, all correlations were weak. The only consistent trend was that a number of species reached greatest abundance as we proceeded up the slope and the steeper the slope the greater the lichens. We did not measure the important factor of soil pH.

Lichen biomass falls in the general range of values reported for *Rangifer* winter ranges elsewhere (Table 2.11). Direct comparisons are not always possible since sampling techniques vary among studies. Some authors report on biomass of only lichen dominated community types (Trudell and White 1981; Parker 1975; Miller 1976), while others report the mean value of all community types present (this study, Scotter 1970). Some authors report only air dried values (Parker 1975; Miller 1976; Scotter 1970) while others

Table 2.10. Snow parameters from various *Rangifer* winter range studies.

Area	Forest		Tundra		Reference
	Depth (cm)	Density (g/cm^3)	Depth (cm)	Density (g/cm^3)	
Northern Finland	60–80				Helle and Saastamoinen (1979)
N. Saskatchewan	45–85				Miller (1976)
Greenland			14–26	0.29–0.55	Thing (1984)
Norway			50–70	0.30–0.50	Skogland (1978)
Denali			34	–	Boertje (1981)
Northern Alaska			13	0.32	Thing (1977)
N. Saskatchewan[1][2]	45	0.17			Pruitt (1959)
	45	0.25			»
Southern Yukon			23	–	Gauthier (1984)
Central Yukon[3][4]	57	0.18	39	0.22	this study
	45	0.17	40	0.18	»

1: characterizes area of concentrated use
2: characterizes area of occasional use
3: mean of all years, all regions
4: mean of all years, core (Hart/Ogilvie) regions

Table 2.11. Lichen biomass measurements from various *Rangifer* studies

Location	Range type	Sorted	Drying	Biomass (g/m^2)	Reference
Southampton Is., NWT	Lichen-heath plateau	no	air	75	Parker, 1975
	Lichen heath lowland	no	air	82	»
	Raised lichen – Dryas	no	air	70	»
	sedge – heath	no	air	48	»
	Patterned ground tundra	no	air	20	»
N. Saskatchewan	Lichen woodland	no	air	585	Miller, 1976
N. Manitoba	Lichen woodland	no	air	427	»
N. Saskatchewan	Lichen woodland	yes	air	81	Scotter, 1970
E. Finland	Lake islands	yes	oven	50	Lindgren *et al.* 1983
N. Finland	Heath forest	yes	oven	52	Helle, 1981
South Yukon	Sedge/grass	no	oven	19	Gauthier, 1984
Central Yukon	Closed needleleaf	no	oven	23	This study
	Open needleleaf	no	oven	65	»
	Needleleaf woodland	no	oven	99	»
	Open low shrub	no	oven	54	»
	Closed dwarf shrub	no	oven	21	»
	Mesic graminoid	no	oven	43	»

report oven-dried values (this study; Trudell and White 1981). In some studies, dead bases were separated and not included in the biomass estimates (Scotter 1970) while no such separations were made in other studies (Parker 1975). During our study, dead bases were not separated. Deep mats of lichen, where significant amounts of dead base existed, were infrequent enough that we felt that the caribou would have as much trouble as we in separating dead from live so that the animals probably ingested the whole thallus.

Fire history

Fire is undoubtedly one of the most important environmental factors affecting taiga ecosystems (Vierecke 1973). In an analysis of «fire weather» data, Simard (1973) indicated that the Yukon interior is rated as a high or very high risk area. In other words, few stands ever reach an edaphic climax. Vierecke and Schandelmeier (1980) postulated that, in the northern taiga zone, fire frequency may increase from west (Alaska and Yukon) to east following a similar trend in precipitation. This phenomenon may explain the long fire frequencies in New Brunswick (230 years; Wein and Moore 1977) and Newfoundland (400 years; Wilton and Evans 1974). Fire frequency in this study (about 120 years) is similar to estimates in Alaskan taiga (100 and 130 years) for white and black spruce forests, respectively (Heinselman 1978).

As the majority of our forest communities are black spruce, a brief description of successional trends in this forest type may help explain the vegetation communities. In their review of the effects of fires in Alaska and adjacent Canada, Vierecke and Schandelmeier (1980) describe the succession to black spruce/feathermoss community in five general stages:

1. Newly burned – from a few weeks to one year; primarily charred moss and mineral ash. Severity of burn important. If moderate, then shrub suckers may appear as well as *Calamagrostis* and *Polytricum.*
2. Herbaceous young herb stage – one to four years. Various mosses and herbs (notably *Epilobium*) and sprouting species (*Calamagrostis*, *Rubus chamaemorus*, and *Equisetum silvaticum*) dominate.
3. Shrub stage – six to 25 years. Shrubs dominate. Near the end of the stage, dead litter abounds, herb and moss cover increases and first lichens (*Peltigera*) appear.
4. Young black spruce – 26 to 50 years. Dense stands of black spruce while shrubs become reduced in cover.
5. Mature black spruce/feathermoss stage – final stage. Black spruce trees, saplings and seedlings dominate.

This description is very generalized. Actual successional trends and recovery vary according to the severity and frequency of the fire and site conditions. In our sampling, spruce/moss communities did tend to be the older stands. However, feathermoss was most often associated with white spruce (Pg/D/Ms – 294 years) while *Sphagnum* species were associated with black spruce (Pm/Sp/Ci – 248 years and Pm/Sp/Er – 175 years). For the two range types with significant samples, the closed-canopied open needleleaf were older (218 years) than the open-canopied, needleleaf woodland (136 years).

Successional trends and fire frequency in treeless communities are much more difficult to determine. From their review, Vierecke and Schandelmeir (1980) conclude that tundra vegetation is seldom completely destroyed by fire, and that recovery is usually rapid and by vegetative means. In most studies fire is not visually detectable after six to eight years. It is generally agreed that with lower fuels, cooler and moister conditions, tundra fires are a lot less frequent and of smaller size than forest fires. In our study all shrub communities aged were young (mean 60 years) compared to forest sites (mean 170 years). This may indicate that many of our shrub communities may have been early successional stages.

The only mesic forb community described in our study appeared to be an early successional stage in a severely burned black spruce stand. *Equisetum* is one of the few species whose rhyzoids penetrate the mineral soil, thus allowing it to survive and flourish after a fire.

Of major concern in this study was the effect of fire (or age of stand) on the lichen component in the understorey. Much controversy has surfaced in the last 25 years over the relationship between fire and lichens and caribou populations. What seems clear is that fire has both long and short term benefits and drawbacks to lichen abundance and distribution (Klein 1982). Of key importance is the perpetuation of a mosaic of age class stands. According to the literature, lichens are greatly reduced after fire, increase in abundance up to 125–175 years and decrease as canopy closes and microclimate for moss and shrubs improve. Therefore, although initially causing a decline in lichen biomass, fires ensure that large tracts of land do not succeed to lichen-poor forest moss communities. Our study noted a general decline in fruticose lichen biomass with age class of stand. However, the only species that declined significantly was *Stereocaulon*, virtually absent in stands greater than 200 years old. Because sample size was too small to split the youngest class into more classes, the majority of the early recovery rate dynamics documented by Scotter (1970) could not be assessed.

Summary

The Yukon portion of the winter range of the Porcupine Caribou Herd contains all the habitat elements necessary to ensure the long term viability of the herd at present population levels. We feel that the key to the quality of this range is the tremendous diversity of each of the elements addressed in this study – terrain features, snow parameters, vegetation types, forage resources and fire history. The unglaciated cordilleran terrain, with expansive intermontane basins and river valleys, provides a wide diversity of habitats to exploit throughout the winter as snow conditions change. Terrain and permafrost features also have resulted in a complex of vegetation types, from tussock tundra and alpine tundra to lowland white spruce stands. Lichen resources vary considerably within and between regions and appear to be average to above average compared to other *Rangifer* winter ranges. This lichen variability can be partially explained by the high fire frequency found in the study area. These fires are normally of limited extent (perhaps as a result of the dissected terrain) and serve to create a mosaic of successional stages.

Continental and local weather patterns have resulted in a reasonably predictable pattern of snow accumulation throughout the study area, with areas of heavy snow accumulation (North Fork Pass), moderate snow accumulation (Eagle, Peel and Tatonduk), regions of low snowfall (Ogilvie and Hart) and regions of low snow due to snow redistribution (Richardson Mountains). The long term distribution of caribou on the winter range appears to be largely dictated by our observed regional snow pattern.

Food habits

Methods

We collected composite fecal samples throughout the winter range of the Porcupine Caribou Herd in Yukon during five collecting periods in the winters of 1979–80 (n=16), 1980–81 (n=18), and 1981–82 (n=13); fall (11 October–12 November), early winter (1–17 December), mid-winter (24 January–7 February), late winter (2–12 March), spring (5–25 April). In addition, single samples were collected near Old Crow, Yukon, during fall migration (24 September 1979) and spring migration (8 May 1980). Each composite sample contained 20 fecal pellets, one from each of 20 fresh pellet groups. Fecal samples were analysed (Sparks and Malechek 1968) at the Composition Analysis Laboratory at Colorado State University, Fort Collins. The relative density of plant fragments was based on 100 fields per sample. All samples were analysed by the same technician and all samples from each winter were analysed at the same time. The accuracy of fecal analysis is influenced by differential digestion of plant species (Holechek *et al.* 1982). Therefore, the results represent proportions of discerned fragments in fecal samples, and consequently estimates of the diet, rather than actual proportions of the ingested diet.

Although the use of the same technician for all analyses removed a large source of potential error (Holecheck *et al.* 1982), the estimate fecal fragments may vary more among sampling sessions than within a single session. To examine this we chose two samples and submitted single replicates of those samples for analysis on four separate occasions as well as four replicates together on one occasion. All samples were blind.

Differences in diets over winter and among years were examined with a Kruskal-Wallis test for the major food groups (mosses, fruticose lichens, foliose lichens, horsetails, graminoids, deciduous shrubs, ever-

Table 2.12. Average percentages and coefficients of variation (CV) of discerned plant fragments in replicates of caribou fecal samples that were analysed at one time (o) and replicates that were analysed at different times (D).

Plant genus or group[1]	11 December 1979					10 March 1980				
	Mean[2]		CV		Ratio CV / CVo	Mean[2]		CV		Ratio CV / CVo
	O	D	O	D		O	D	O	D	
Moss	6.4	6.4	47.0	39.7	0.8	2.4	4.5	33.8	68.4	2.0
Fruticose Lichens	46.9	58.0	9.1	22.7	2.5	73.8	73.0	6.6	12.8	1.9
Cetraria - type	4.7	5.5	52.4	45.2	0.9	20.4	21.8	13.7	28.4	2.1
Cladonia - type	34.9	48.3	15.8	39.3	2.5	36.6	39.3	10.4	26.2	2.5
Stereocaulon	7.2	4.2	15.8	97.0	6.1	16.9	11.7	9.9	69.7	7.0
Foliose Lichens *(Peltigera)*	1.1	2.2	61.0	113.9	1.9	9.9	2.0*	53.1	117.0	2.2
Horsetails *(Equisetum)*	30.1	18.9*	14.2	29.2	2.0	0.4	1.5	115.4	60.5	0.5
Graminoids	1.6	1.1	55.8	41.1	0.7	1.2	1.0	75.0	67.5	0.9
Deciduous shrubs *(Salix)*	1.2	4.3	135.5	129.6	1.0	7.1	3.7	48.6	150.7	3.1
Evergreen shrubs	12.6	8.8	28.3	66.3	2.3	5.2	13.9	37.8	68.3	1.8
Vaccinium	8.4	4.6	31.7	109.8	3.5	3.5	11.2	59.1	85.3	1.4
Forbs	–	0.2	–	197.2	–	–	0.2	–	195.0	–

1: Genera which occurred at frequencies of less than 1% in any sample were not included.
2: Significant differences between means indicated by an asterisk ($* = p < 0.05$).

green shrubs, forbs) and major foods (*Cetraria*-type lichens, *Cladonia*-type lichens, *Stereocaulon, Peltigera, Equisetum, Carex, Eriophorum, Salix, Dryas, Ledum, Picea, Vaccinium*). Statistical procedures follow Siegel (1956), Sokal and Rohlf (1969), and Hollander and Wolfe (1973).

Results and discussion

Effect of analysis at different times

Only two significant differences were found in the average percentages of discerned plant fragments in replicates analysed at one time compared with those analysed at different times; foliose lichens in the March sample and horsetails in the December sample (Table 2.12). However, the replicates analysed at different times tended to have much greater coefficients of variation than those analysed at one time (Table 2.12). This was particularly true for *Cladonia*-type lichens, *Stereocaulon* and *Vaccinium*, and, to a lesser degree, for fruticose lichens, *Peltigera, Salix* and evergreen shrubs. Only moss, *Cetraria*-type lichens, *Equisetum* and graminoids showed relatively similar coefficients of variation and, therefore, are likely the only foods that can be compared with confidence between times of analysis. We do not know of any other studies which have examined this source of error in fecal analysis.

Differences among years

Several differences in discernible plant fragments were found among years. The percentages of fruticose lichens and *Cladonia*-type lichens were significantly greater and the percentages of *Cetraria*-type lichens, *Salix* and graminoids were significantly less during the winter of 1979–80 than during the other two winters, which were not significantly different from each other. The percentage of moss was significantly greater during the winter of 1980–81 than during the other two winters. The percentage of *Peltigera* was significantly greater and of *Vaccinium* was significantly less in the winter of 1981–82 than during the other two winters. However, considering the difficulties discussed previously in comparing results from different times of analysis, we consider only the low percentage of *Cetraria*-type lichens and graminoids in 1979–80 (8% and 1% respectively, compared with 11% and 4%, respectively in other years) and the high percentage of moss in 1980–81 (13% compared with 5% in other years) to be important differences among years. Although the high percentage of moss in 1980–81 coincides with the winter of lowest snow cover and perhaps the highest availability of the ground surface, the low percentage of *Cetraria*-type lichens and graminoids in 1979–80 do not appear to relate directly to snow conditions but may reflect the selective feeding strategy observed in that year (see section on Cratering Dynamics). The absolute differences, however are small.

Differences over winter

Only horsetails (*Equisetum*) showed a significant difference over winter; the percentage in late winter was significantly less than that in late fall and early winter. The percentage of forbs, evergreen shrubs and *Vaccinium*, were consistently less in late fall and early winter than in mid-winter to spring.

Snow conditions become increasingly severe for caribou as winter progresses. The decrease in use of horsetails may reflect decreased use of horsetail habitats as snow cover increases. The increased use of forbs, evergreen shrubs and *Vaccinium*, on the other hand, may reflect increased use of foods available in feeding craters, irrespective of palatability, as snow conditions become increasingly severe.

Seasonal diets

In general, the winter diet of the Porcupine Caribou Herd, as reflected in fecal samples is similar to that reported for other caribou populations wintering in taiga or in mountainous regions (Russell and Martell 1984). The diet remained remarkably constant from late September to early May (Table 2.13). Fruticose lichens (primarily *Cladonia*-type) predominated in the diet throughout, with only a slight reduction after late winter. Evergreen shrubs (primarily *Vaccinium vitis-idaea*) were the second most important component of the diet, followed by moss, horsetails (evergreen *Equisetum*) and foliose lichens (*Peltigera apthosa*). The shift to such a lichen-dominated diet may begin as early as late August (Thompson and McCourt 1981). Lichens start to decline in importance in May (Duquette 1984; this study).

Compared with previous reports on diet of the Porcupine Caribou Herd, also based on fecal analysis, our spring diet was similar to that reported by Duquette (1984) but contained noticeably less moss and more horsetails and evergreen shrubs than that reported by Thompson and McCourt (1981). Our single sample for fall migration contained noticeably less moss and more lichens, mushrooms and evergreen shrubs than that reported by Thompson and McCourt (1981) for the same period and our single sample for spring migration contained noticeably less *Salix* but otherwise was relatively similar to that reported by Duquette (1984) for the same period.

Fecal sample versus ingested diet

Boertje (1985) quite rightly cautions that fecal analyses often inadequately estimate caribou diets. Fecal analyses have been reported to overestimate mosses (Dearden *et al.* 1975) and underestimate mushrooms (Boertje 1981) and forbs (Boertje 1981; Samuel and Howard 1983). Dearden *et al.* (1975) developed correction factors for some caribou foods but over and underestimates of specific components can vary with diet composition (Gill *et al.* 1983).

Duquette (1984) conducted feeding trials on a captive caribou and a captive reindeer using a diet similar to that we observed. Fecal samples from those trials were also analyzed at Colorado State University. Compared with the actual ingested diet, fecal analysis significantly overestimated evergreen shrubs and

Table 2.13. Average percentages (±SE) of discerned plant fragments in fecal samples collected from the range of the Porcupine Caribou Herd, 1979–82.

	Season						
Plant genus or group[1]	Fall migration N=1	Fall N=6	Early winter N=12	Mid-winter N=7	Late winter N=15	Spring N=7	Spring migration N=1
Moss	3.4	7.0±1.28	7.4±0.72	9.3±1.98	7.4±1.50	8.3±2.56	12.2
Fruticose Lichens	78.1	62.8±3.15	65.6±3.22	62.3±6.58	66.3±3.36	58.7±2.80	43.8
Cetraria - type	-	10.1±2.66	8.4±1.22	9.7±1.75	12.1±1.76	10.4±0.66	-
Cladonia - type	78.1	48.3±5.74	53.3±3.85	46.8±7.84	48.4±3.72	43.2±3.66	43.8
Stereocaulon	-	4.4±1.52	3.9±1.19	5.8±2.19	5.8±1.38	5.1±1.78	-
Foliose Lichens (*Peltigera*)	0.6	6.7±4.29	5.0±2.69	4.6±3.17	6.2±2.57	4.6±3.28	10.9
Mushrooms	7.2	-	-	-	-	-	-
Horsetails (*Equisetum*)	1.7	10.2±1.17	8.8±2.24	3.6±1.36	2.8±0.68	6.4±3.83	3.2
Graminoids	1.1	4.0±1.64	2.6±0.56	3.0±1.16	2.4±0.39	5.0±1.20	4.0
Carex	-	1.0±0.40	1.1±0.35	1.8±0.79	1.3±0.32	4.2±1.23	4.0
Eriophorum	1.1	2.7±1.52	0.8±0.26	1.0±0.53	0.4±0.29	0.1±0.10	-
Deciduous shrubs (*Salix*)	0.6	1.6±0.59	2.2±0.68	3.1±1.66	2.3±0.54	2.8±1.31	-
Evergreen shrubs	7.3	7.6±1.33	8.4±1.08	12.9±3.15	12.4±2.63	13.9±2.99	25.9
Dryas	0.6	0.8±0.42	1.2±0.32	1.3±1.15	0.6±0.23	2.5±1.41	-
Ledum	5.6	1.5±0.58	1.9±0.40	1.8±0.76	1.1±0.25	1.1±0.34	2.4
Picea	-	0.1±0.13	0.6±0.24	0.8±0.31	1.3±0.41	1.4±0.66	3.2
Vaccinium	1.1	5.2±1.12	4.7±0.67	9.0±2.51	9.3±2.31	8.8±2.90	20.4
Forbs	-	-	-	0.9±0.76	0.3±0.10	0.2±0.14	-

1: *Arctogrostics, Artemesia, Astragalus, Bromus, Cassiope, Dupontia, Festuca, Hierochloe, Lupinus, Poa, Rubus, Saxifraga, Stellaria, Trisetum* and unidentified grass occurred at average frequencies of less than 0.5% in some seasons.

significantly underestimated lichens but gave a reasonable representation of moss, horsetails and graminoids (Table 2.14). The fecal analysis also estimated a small amount of deciduous shrubs (*Salix*) although none was present in the hand-mixed diet. The overestimate of evergreen shrubs likely reflects their low digestibility, although *Vaccinium vitis-idaea* is more digestible than other evergreen shrubs eaten by caribou (Boertje 1981). It is likely that the underestimate of lichens directly reflects the overestimate of evergreen shrubs, as has also been suggested by Boertje (1985). Dearden *et al.* (1975) found that *Cladina* and *Cetraria* were fairly represented in fecal analyses (correction factors of 0.81 and 0.91 respectively).

Although Duquette's feeding trials are limited, they are the only ones available for a winter diet which closely parallels the one we observed. Based on those trials, evergreen shrubs are overestimated at the expense of fruticose lichens. Also deciduous shrubs in small amounts may be an artifact of the technique. Therefore, to make our results better reflect the actual diet, they should be adjusted to reduce the proportion of evergreen shrubs to 38% of the fecal estimate and to add the amount of the reduction to the estimate for fruticose lichens. This would make only minor adjustments in most periods (Table 2.13.) and over-

Table 2.14. Average percentages of actual intake (mean ± SD [range]) and average percentages of discerned plant fragments in fecal samples from feeding trials on captive caribou and reindeer at the University of Alaska in 1982 by L. Duquette.

Plant Group^{+}	Actual Intake (n=8)	Fecal Estimate (n=8)	Correlation coefficient^{++}	Correction factor^{+++}
Moss^{1}	4.4±3.0 (2–1)	3.7±1.2	-0.28	1.17
Lichens^{2}	66.2±9.3 (50–78)	39.8±8.2	0.77*	1.66
Horsetails^{3}	5.2±2.0 (2– 7)	5.6±3.4	0.43	0.94
Graminoids^{4}	8.9±1.2 (7–11)	8.5±5.0	-0.66	1.05
Deciduous shrubs	0.0	2.7±1.8	–	–
Evergreen shrubs^{5}	14.9±4.9 (9–22)	38.7±8.4	0.76*	0.38

+ 1: *Hylocomium splendens*; 2: *Cladina stellaris*, *C. rangiferina*, *Cetraria nivalis*;
3: *Equisetum pratense*; 4: *Bromus* sp.; 5: *Vaccinium vitis-idaea*.
++* $p<0.05$
+++ Correction factor = mean actual intake/mean fecal estimate.

all would reduce the estimated proportion of evergreen shrubs in the diet to 4% and increase the estimated proportion of fruticose lichens to 71%. Those values are close to ones reported for the Beverly and Kaminuriak caribou herds based on rumen samples (Scotter 1967; Thomas and Hervieux 1986). The small amounts of *Salix* we observed (Table 2.13) may be artifacts.

Mushrooms and forbs are likely underestimated in our study, but we cannot develop correction factors for those groups. Both mushrooms and forbs, however, are normally only minor components of the winter diet of caribou (Russell and Martell 1984). Except for fall migration, the underestimation of those groups is not likely to be a serious problem.

Conclusions

The composition of fecal samples from the Porcupine Caribou Herd remained remarkably constant from late September through early May during three winters of collections. Overall, fruticose lichens predominated (64%) followed by evergreen shrubs (11%), moss (8%), horsetails (6%), foliose lichens (5%), graminoids (3%), deciduous shrubs (2%), forbs (< 1%) and mushrooms (> 1%). Based on feeding trials, those proportions are believed to be reasonable estimates of the ingested diet except for fruticose lichens and evergreen shrubs. Evergreen shrubs were likely overestimated in the fecal analysis at the expense of the fruticose lichens; evergreen shrubs were likely only 4% of the average ingested diet while fruticose lichens were 71%. The diet we observed was similar to that reported for other caribou populations wintering on a good lichen range in taiga or in mountainous regions (Russell and Martell 1984, Boertje 1985). Snow conditions did not have a major influence on the diet. Increasing snow depths, however, may have caused decreased use of horsetails and increased use of evergreen shrubs and forbs. There was a much greater variability among replicate samples analysed at different times than at the same time. Comparisons among samples analysed at different times should be made cautiously.

Winter activity

Methods

For seasonal comparisons, the field camps were established in each year in early fall (only 10–13 October, 1980), late fall (6–13 November), early winter (5–15 December), mid winter (26 January–6 February), late winter (5–12 March) and spring (5–25 April). These periods corresponded to significant changes in daylength and snow characteristics (Table 1.1).

We observed caribou with 15x–60x zoom spotting scopes at 17 field camps during the winters of 1979–80 through 1981–82. A band of caribou was defined as a socially interacting group of animals spatially distinct from other bands in the area. Activity data were collected using the instantaneous scan method (Altmann 1974). We scanned each band at 15-minute intervals and tallied the number of caribou engaged in each of six general activities which were identified primarily by posture.

1) feeding – standing or walking posture, including pawing in a feeding crater in snow, with the muzzle touching or nearly touching the ground;
2) lying – bedded on the ground, either upright or lying on its side, in a resting or ruminating position;
3) standing – stationary in an upright, standing posture with head elevated above the ground, and usually above the knees;
4) walking – similar to standing posture but moving at a slow gait (<5 km/h, 5 km/h, Thomson 1977);
5) trotting/running – similar to standing posture but moving rapidly in a two-timed symmetrical (trotting, 5–11 km/h) or asymmetrical (running, <11 km/h) gait (Thomson 1977); and
6) sparring – two individuals standing or walking with antlers in contact.

The proportion of caribou observed in each activity and their estimated 95% confidence limits were calculated by the ratio estimator method (Cochran 1977). The proportion of time spent in a given activity (R) and its estimated variance (v) and 95% confidence limits (CL) were calculated as follows:

$$R = \sum_{i}^{n} Yi \,/\, \sum_{i}^{n} Xi$$

$$v = \left(\sum_{i}^{n}(Yi^2) + R^2\sum_{i}^{n}(Xi^2) - 2R\sum_{i}^{n}(Xi \cdot Yi)\right) / \; n\,(X^2)(n\text{-}1)$$

$$CL = R \pm z\sqrt{v}$$

where

Yi = number of animals in sample (scan, band, etc.) engaged in given activity;
Xi = total number of animals in sample i;
n = number of samples; and
z = the normal deviate corresponding to a 95% confidence probability (1.96).

Differences were considered to be significant if the estimated 95% confidence limits did not overlap. Serial correlations occur among 15-minute observations of a given band of caribou because individuals continue some activities for periods longer than the time between observations and because the same individuals are observed for periods of up to several hours. Serial correlations are less likely to occur between bands of caribou although, in winter, caribou cue their activity to sunrise. Estimated confidence limits, therefore, were based on a single ratio for each band observed.

The relationships of activity budgets among sampling periods were examined through cluster analysis by the unweighted pair-group method using arithmetic averages (UPGMA) (Sneath and Sokal 1973). Similarity of activity budgets was based on percentage similarity (Pielou 1975) as an index.

The proportion of caribou lying was plotted in relation to time since sunrise. The length of the active/bedded cycle was calculated as the time between consecutive activity peaks. The area under the curve between activity peaks, when divided by the length of time between the activity peaks, was used to calculate the mean percent of time spent lying during that cycle. This mean was multiplied by the length of the active/bedded cycle to yield the mean length of the lying period.

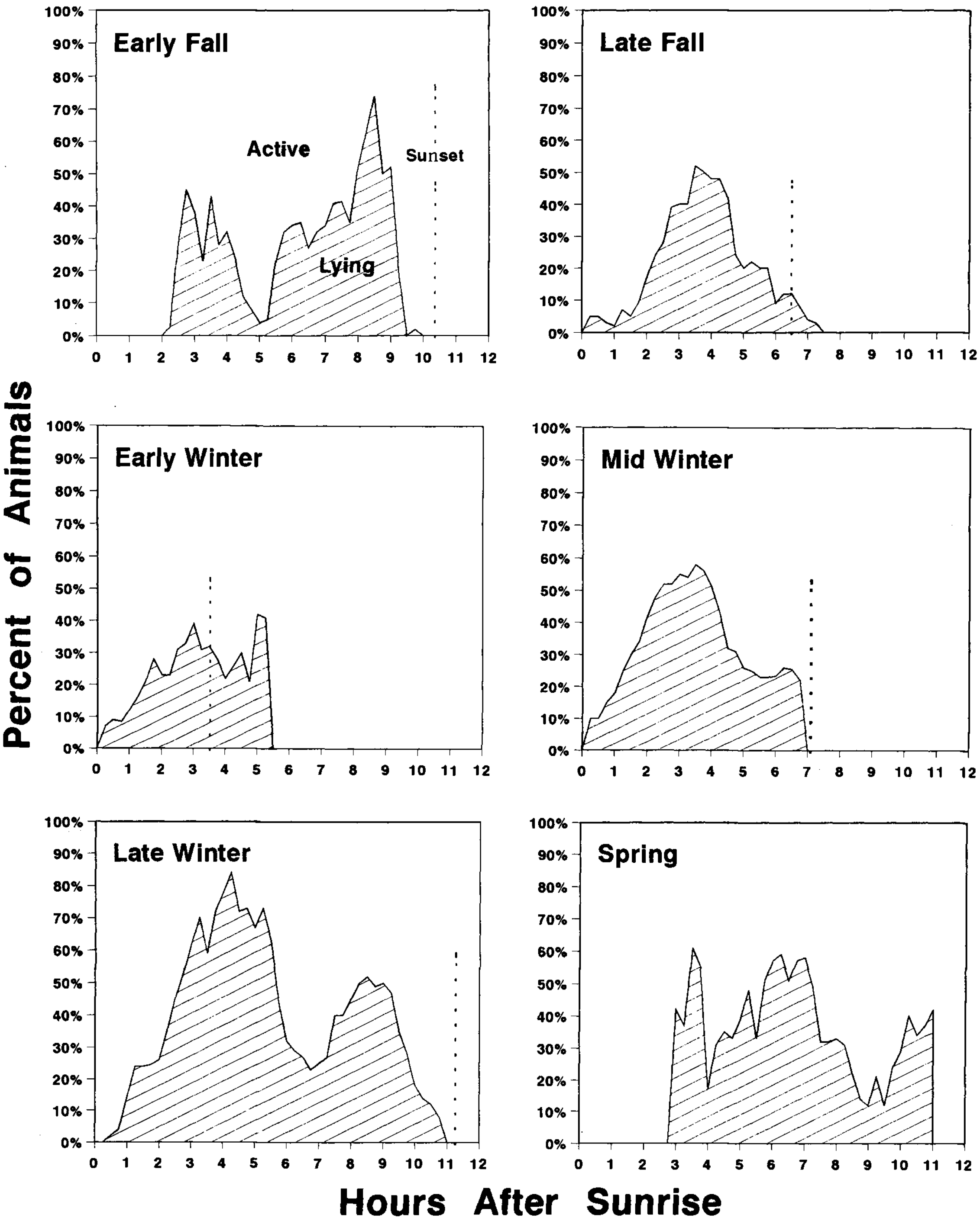

Figure 2.8. Percent of animals lying from 15 minute scans in relation to hours after sunrise for the six study periods.

Results

Band size

There was a trend each winter for the size of caribou bands observed at field camps to be largest in fall (96 ± 12.6; mean ± SE) and spring (80 ± 15.0), smaller in early winter (59 ± 12.9) and late winter (55 ± 9.3), and smallest in mid-winter (47 ± 4.6).

Activity pattern

During the six time periods examined, caribou were most active at sunrise and sunset (Fig. 2.8). The number of lying cycles was directly related to daylength, with periods of similar daylength yielding similar cyclic patterns. Thus, early winter (15% daylength) yielded one indistinct lying period (assessed visually from Fig. 2.8), late fall and mid winter (25%) yielded one distinct lying period, early fall and late winter (45%) yielded two full lying periods and, through extrapolation, in spring (60%), animals exhibited three lying periods.

The mean length of the active/bedded cycle varied from 238 min in early winter to 340 min in mid winter (Table 2.15). The mean length of the lying period decreased from late fall to early winter, then increased throughout the winter (Table 2.15).

Table 2.15. Length of winter lying and active periods and active/lying cycle for the Porcupine Caribou Herd, 1979-82.

	Total cycle (min)		Lying period (min)		Active period (min)	
Period	1st[1]	2nd	1st	2nd	1st	2nd
Early fall						
1980-81	206	285	38	102	168	183
Late fall						
1979-80	270		56		214	
1981-82	325		100		225	
Mean	298		78		220	
Early winter						
1979-80	255		54		201	
1980-81	230		47		183	
1981-82	280		68		162	
Mean	238		56		182	
Mid winter						
1979-80	310		93		217	
1980-81	375		101		274	
1981-82	335		147		188	
Mean	340		114		226	
Late winter						
1979-80	360	315	180	98	180	217
1980-81	270	240	124	87	146	153
1981-82	285	-	156	-	129	-
Mean	302	278	153	93	152	185
Spring						
1979-80		195		55		140
1980-81		225		112		113
1981-82		300		132		168
Mean		240		100		140

1: Length of 1st and (if applicable) 2nd period from Figure 2.8.

Activity budgets

Although we made observations in both taiga and tundra habitats at most field camps, 90% of the individuals and 85% of the bands observed were on tundra. Because there were few significant differences and no consistent difference (Wilcoxon test) in activity budgets between taiga and tundra, observations were combined.

Table 2.16. Activity budgets (% time ± estimated 95% confidence limits) of caribou in north-central Yukon in winter, 1979-82[1].

Winter	Fall	Early winter	Mid-winter	Late winter	Spring
1979-80					
Number of					
observations	82	61	89	111	110
bands	5	4	6	6	4
individuals	6331	1074	1457	6096	10899
Feeding	47.3 ± 8.8^{a,c}	64.4 ± 6.5^{b}	55.0 ± 4.2^{b,c}	46.0 ± 2.6^{a}	47.0 ± 1.7^{a}
Lying	19.8 ± 3.9^{a}	15.0 ± 8.5^{a}	29.8 ± 5.9^{b}	45.1 ± 5.5^{c}	33.0 ± 5.5^{b}
Standing	7.7 ± 3.4^{a}	6.9 ± 2.1^{a}	6.0 ± 3.3^{a}	5.1 ± 2.6^{a}	4.6 ± 2.6^{a}
Walking	22.7 ± 5.2^{a}	11.4 ± 2.4^{b}	6.7 ± 2.1^{c}	3.0 ± 2.2^{c}	14.8 ± 5.4^{a,b}
Trotting/running	1.3 ± 1.0^{a,b}	1.1 ± 0.7^{a}	1.4 ± 0.9^{a}	0.1 ± 0.1^{b}	0.5 ± 0.2^{a}
Sparring	1.3 ± 1.6^{a}	1.1 ± 1.3^{a,b}	1.1 ± 0.8^{a}	0.6 ± 0.4^{a,b}	0.1 ± 0.1^{b}
1980-81					
Number of					
observations	175	216	332	155	74
bands	12	19	23	10	12
individuals	15071	4949	11024	2464	3136
Feeding	40.7 ± 9.2^{a}	59.0 ± 4.8^{b}	54.5 ± 4.5^{b}	45.7 ± 10.2^{a,b}	44.2 ± 17.2^{a,b}
Lying	27.6 ± 14.2^{a,b}	20.6 ± 6.8^{a}	29.0 ± 5.5^{a,b}	42.5 ± 13.0^{b}	32.9 ± 13.8^{a,b}
Standing	7.7 ± 2.5^{a}	6.2 ± 1.7^{a}	5.4 ± 2.7^{a}	4.2 ± 1.7^{a}	1.6 ± 0.6^{b}
Walking	21.2 ± 4.6^{a}	11.7 ± 3.4^{a,b}	8.2 ± 2.3^{b}	5.9 ± 2.7^{b}	21.1 ± 20.8^{a,b}
Trotting/running	2.1 ± 0.7^{a}	0.6 ± 1.0^{a,b,c}	0.6 ± 0.5^{a,b}	0.3 ± 0.3^{b,c}	0.0 ± 0.0^{c}
Sparring	0.6 ± 0.4^{a,b}	1.8 ± 0.8^{b,c}	2.3 ± 0.6^{c}	1.4 ± 1.1^{a,b,c}	0.2 ± 0.2^{a}
1981-82					
Number of					
observations	183	154	293	149	94
bands	23	14	18	10	12
individuals	17191	13371	15305	13372	12566
Feeding	42.9 ± 5.1^{a}	53.4 ± 3.8^{b}	47.5 ± 3.9^{a,b}	44.9 ± 5.3^{a,b}	49.1 ± 3.7^{a,b}
Lying	28.1 ± 6.4^{a}	25.9 ± 6.9^{a}	39.5 ± 3.7^{b}	46.9 ± 5.7^{b}	44.4 ± 4.4^{b}
Standing	5.6 ± 1.5^{a}	4.9 ± 1.1^{a}	5.2 ± 1.2^{a}	4.6 ± 1.2^{a}	2.3 ± 0.7^{b}
Walking	21.6 ± 2.9^{a}	14.4 ± 4.8^{a,b}	7.2 ± 2.7^{b,c}	3.1 ± 0.4^{d}	4.1 ± 3.4^{c,d}
Trotting/running	0.5 ± 0.3^{a}	0.1 ± 0.0^{b}	0.1 ± 0.1^{b}	0.1 ± 0.1^{b}	0.1 ± 0.0^{b}
Sparring	1.3 ± 0.5^{a}	1.4 ± 0.7^{a,b}	0.5 ± 0.3^{b,c}	0.4 ± 0.2^{c}	0.0 ± 0.0^{d}

1: For each activity, within each winter, values with the same superscript are estimated not to be significantly different at the p=0.05 level.

Activity budgets show several seasonal patterns (Table 2.16). The proportion of time spent feeding was greatest in early and mid-winter. The seasonal trend in percent lying was consistent for all years, decreasing from fall to early winter, increasing throughout the winter and decreasing again in spring. In each year, values for percent lying in fall and early winter were significantly lower than those from mid-winter to spring (Table 2.16). Standing declined slowly over winter and was particularly low in spring. Walking was highest during fall and spring and lowest in mid- and late winter, except in 1981–82 when walking remained low in spring. Trotting and running tended to be lowest in late winter and spring. Sparring tended to decline over winter except in 1980–81 when sparring remained high until spring.

There were few significant differences in activity budgets among winters. In general, feeding tended to be greatest in 1979–80 (1979–80 was significantly greater than 1981–82 in mid-winter) and lying tended to be greatest in 1981–82 (1981–82 was significantly greater than 1979–80 in mid-winter and spring and significantly greater than 1980–81 in mid-winter). Standing tended to be greatest in 1979–80 and walking was significantly lower in 1981–82 than in 1979–80 in spring. Trotting and running tended to be lowest in 1981–82 and sparring tended to be greatest in 1980–81.

Cluster analysis of the activity budgets (Fig. 2.9) shows three distinct groups which can be characterized by their average activity budgets. Group 1 has high walking (20%) and low feeding (44%) and lying (28%) and reflects normal snow conditions in fall and spring. Group 2 has high feeding (55%), low lying (26%) and intermediate walking (11%) and reflects normal snow conditions in early and mid-winter. Group 3 has high lying (44%) and low feeding (47%) and walking (5%) and reflects normal snow conditions in late winter. In 1981–82, the winter of adverse snowconditions and delayed snowmelt, the activity budgets in mid-winter and spring were most similar to those in late winter in the other two years.

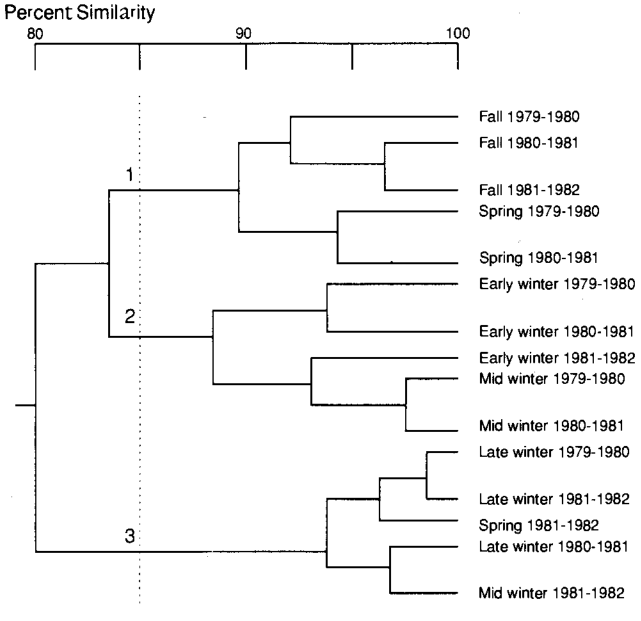

Figure 2.9. Cluster analysis of activity budgets of caribou in north-central Yukon.

The proportion of time spent in each activity (Table 2.16) was compared with average snow conditions on tundra in early, mid- and late winter each year (Pearson r, n = 9). Feeding (depth, -0.71; density, -0.71; hardness, -0.67), lying (density, 0.71) and sparring (depth, -0.72; density, -0.71) were significantly correlated with snow conditions. Snow depth, density and hardness were significantly intercorrelated (depth-density, 0.80; depth-hardness, 0.90; density-hardness, 0.82). Those relationships between activity and snow conditions may be influenced by the relationship between the proportion of time spent lying and daylength. Feeding (-0.63), lying (0.66), standing (-0.64), and sparring (-0.75) were all significantly correlated with daylength from fall through spring each year (Pearson r, n = 15), although snow conditions in early, mid- and late winter were not correlated with daylength. Because lying makes up a large percentage of daily activity budgets (Table 2.16) it potentially could mask changes in other activities. We, therefore, adjusted other activities to proportions of the active period to remove the effect of lying time. After adjusting, only sparring showed a significant correlation with daylength (r=0.67, n=15).

reduced our original sample size by 25% and consistently increased our estimate of percent lying for all time periods, although the change was not statistically significant for any period. Each spring and in late winter 1981–82, all our observations occurred well after sunrise or well before sunset.

Proportional use of active periods

The proportional use of active periods (Table 2.17) showed essentially the same seasonal patterns discussed previously for activity budgets. There were few significant differences in proportional use of active periods among years and the overall trends were similar to those for activity budgets, except for feeding. Overall, feeding tended to be lowest in 1980–81 and greatest in 1981–82 (1981–82 was significantly greater than 1979–80 in spring). Standing tended to be greatest in 1979–80 and walking tended to be lowest in 1979–80 except that 1981–82 was significantly less than 1979–80 in spring. Trotting and running tended to be lowest in 1981–82 (1981–82 was significantly lower than 1980–81 in fall) and sparring tended to be greatest in 1980–81 (1980–81 was significantly greater than 1981–82 in mid-winter).

Cluster analysis of the proportional use of active periods (Fig. 2.10) shows three distinct groups which can be characterized by their average proportional activities. Group 1 has low feeding (59%) and high walking (30%) and reflects normal fall conditions. Group 2 has high feeding (86%) and low walking (6%) and reflects late winter and spring with adverse snow conditions. Group 3 has intermediate feeding (75%) and walking (16%) and reflects normal conditions in early and mid-winter. It is notable that activity in 1980–81, the winter with the mildest snow conditions, in late winter was most similar to that in early and mid-winter in the other years and in spring was most similar to that in fall of the other years.

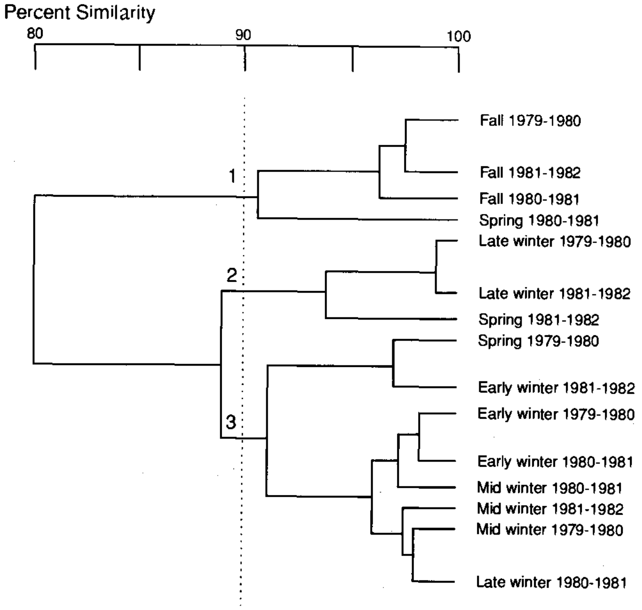

Figure 2.10. Cluster analysis of proportional use of active periods by caribou of north-central Yukon.

The proportion of time spent in each activity (Table 2.17) was compared with average snow conditions on tundra in early, mid- and late winter each year (Pearson r, n=9). No significant correlations were found.

Discussion

Effect of daylength on percent lying

Other authors have noted that caribou cue their winter activity to sunrise producing a conspicuous «midday» peak in lying (Gaare *et al.* 1975; Roby 1978; Eriksson *et al.* 1981). In our study, this «midday» peak generally occurred about 3.5 to 4.5 hours after sunrise, regardless of daylength. The pattern of active and bedded cycles for the remainder of the day is constrained by daylength since caribou also appear to exhibit another peak in activity at sunset.

Researchers normally employ the «50% rule» when determining mean length of lying and active periods (Roby 1978; Boertje 1981). By this method a lying period starts when 50% of the observed animals lie down and ends when over 50% get up again. Using the area under the curve method in our study, the length of the lying period increased throughout the winter from 56 min (early winter) to 153 min (late

Table 2.17. Proportional use of active periods (% time ± estimated 95% confidence limits) by caribou in north-central Yukon in winter, 1979–82.[1,2]

Winter	Fall	Early winter	Mid-winter	Late winter	Spring
1979–80					
Feeding	59.0 ± 11.0^{a}	75.8 ± 3.8^{b}	78.4 ± 6.8^{b}	83.8 ± 7.1^{b}	$70.2 \pm 7.9^{a,b}$
Standing	9.6 ± 3.9^{a}	8.1 ± 1.6^{a}	8.5 ± 4.4^{a}	9.3 ± 3.9^{a}	6.8 ± 3.5^{a}
Walking	28.3 ± 6.5^{a}	$13.5 \pm 2.7^{b,c}$	$9.6 \pm 2.4^{c,d}$	5.5 ± 3.5^{d}	$22.0 \pm 6.4^{a,b}$
Trotting/running	1.6 ± 1.2^{a}	1.3 ± 0.7^{a}	2.0 ± 1.2^{a}	0.2 ± 0.2^{b}	$0.8 \pm 0.4^{a,b}$
Sparring	$1.6 \pm 2.0^{a,b}$	$1.3 \pm 1.6^{a,b}$	1.6 ± 1.1^{a}	$1.1 \pm 0.9^{a,b}$	0.2 ± 0.1^{b}
1980–1981					
Feeding	56.3 ± 5.2^{a}	74.3 ± 3.3^{b}	76.7 ± 5.2^{b}	79.5 ± 4.4^{b}	$65.8 \pm 27.7^{a,b}$
Standing	10.6 ± 2.4^{a}	7.9 ± 2.1^{a}	7.6 ± 3.5^{a}	7.3 ± 3.0^{a}	2.4 ± 1.3^{b}
Walking	29.3 ± 3.8^{a}	14.7 ± 3.8^{b}	11.5 ± 2.8^{b}	10.2 ± 3.4^{b}	$31.4 \pm 27.7^{a,b}$
Trotting/running	2.9 ± 1.0^{a}	0.8 ± 1.2^{b}	0.9 ± 0.7^{b}	$0.5 \pm 0.6^{b,c}$	0.0 ± 0.0^{c}
Sparring	0.9 ± 5.7^{a}	$2.3 \pm 0.9^{a,b}$	3.2 ± 0.9^{b}	$2.4 \pm 1.6^{a,b}$	0.4 ± 0.2^{a}
1981–82					
Feeding	59.6 ± 4.8^{a}	72.0 ± 3.2^{b}	$78.5 \pm 5.2^{b,c}$	84.6 ± 2.4^{c}	88.3 ± 6.8^{c}
Standing	7.8 ± 1.8^{a}	$6.6 \pm 1.9^{a,b}$	8.6 ± 1.8^{a}	8.7 ± 2.2^{a}	4.1 ± 1.1^{b}
Walking	30.0 ± 3.5^{aa}	19.4 ± 4.8^{b}	$12.0 \pm 4.2^{b,c}$	5.9 ± 0.8^{d}	$7.4 \pm 5.9^{c,d}$
Trotting/running	0.7 ± 0.4^{a}	0.1 ± 0.0^{b}	0.1 ± 0.1^{b}	$0.2 \pm 0.2^{a,b}$	0.2 ± 0.0^{b}
Sparring	1.8 ± 0.7^{a}	$1.9 \pm 1.1^{a,b}$	$0.8 \pm 0.5^{a,b}$	0.7 ± 0.3^{b}	$< 0.1 \pm 0.0^{c}$

1: Numbers of observation and bands are identical with those in Table 2.16. Numbers of individuals are those in Table 2.16 less the number lying.

2: For each activity, within each winter, values with the same superscript are estimated not to be significantly different at the p=0.05 level.

winter). Other researchers maintain that the length of the lying period is consistent throughout the winter (Segal 1962; Roby 1978; Boertje 1981). In fact, Boertje (1981) concludes that his observed differences in percent lying among winter periods must be related to changes in the length of activity periods rather than the length of the lying periods. However, our data indicate that percent lying is significantly related to the length of the lying period (r=0.83, n=15) rather than the length of the active period (r=-0.43, n=15). We feel that the «50% rule» is inappropriate for individual bands during short daylength sampling times. Animals are normally active at sunrise and sunset and therefore complete active periods are seldom observed or if they are observed they are biased towards shorter periods. For example, using the «50% rule» we calculate that the mean length of the active period over all winter periods is 109 ± 11.1 min (mean ± SE, n=16). However, we had to disregard 42 incomplete active cycles (mean=200 min). By the area under the curve method the estimate of mean active period for all winter periods is 184 min. The major disadvantage of the area under the curve method is that no estimate of variation is possible.

In contrast, many complete lying periods were observed during the «midday» period. However, the 50% rule is not appropriate when lying periods are short and animals are somewhat asynchronous. The combination of these two factors normally results in observers seldom noting 50% of the band lying. The bias in this case is towards longer lying cycles. From our observations, these two factors do occur in the early winter period. Using the 50% rule we would estimate a lying period length of 108 min compared to 56 min using the area under the curve.

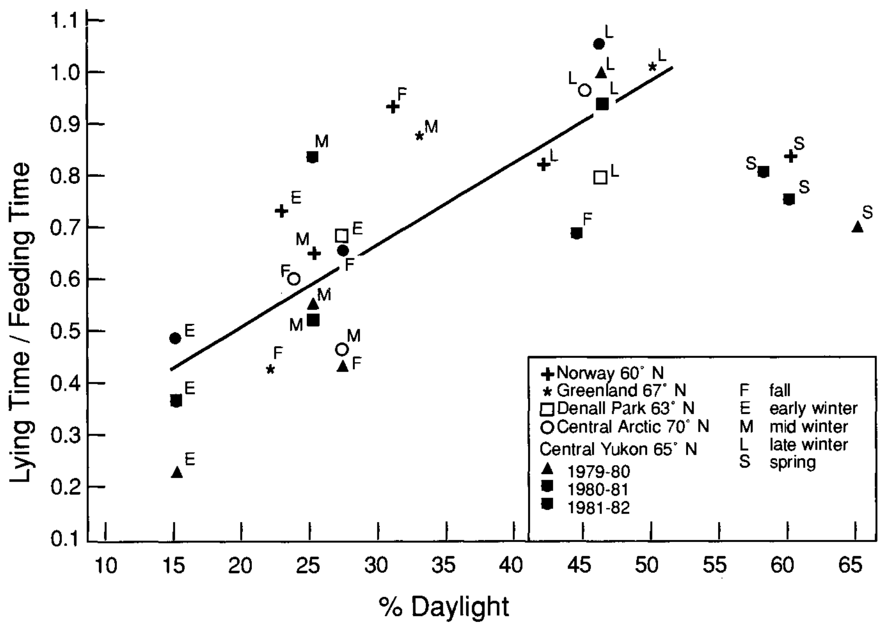

Figure 2.11. Relationship between day length and percent lying from various studies for fall (F), early (E), mid (M), and late (L) winter.

The fixed and thus predictable pattern of activity/lying peaks in relation to sunrise and sunset must be taken into consideration when comparing activity budgets between studies. In particular, the latitude, date, and time of daily observations are important when comparing winter activity among different herds. For example, comparing our results in early and mid-winter to data presented by Gaare *et al.* (1975) could be misleading. They observed Norwegian herds at approximately 60°N compared to 65°N for our study. The daylength in early and mid-winter in Norway is 25% and 38%, respectively, compared to 15% and 25% in central Yukon. It is not surprising, therefore, that Gaare *et al.* (1975) presented an early winter cycle similar to our mid-winter cycle (one very distinct lying peak) and a mid-winter cycle similar to our late winter cycle (two distinct lying peaks). Furthermore, Gaare *et al.* (1975) indicated that their observation period in mid-winter was only from 1.5 hours after sunrise to 1.5 hours before sunset, thus yielding an overestimate of percent lying compared to our estimates.

An examination of the literature indicates that few studies provide enough data points to compare winter activity patterns (% lying as the indicator) to daylength. Available data indicate that larger seasonal fluctuations in daylength (i.e. higher latitudes) correspond to larger fluctuations in percent lying (Fig. 2.11). Herds in Norway (Gaare *et al.* 1975), which exhibited the least variation in percent lying, were located at the most southerly latitudes. Our data (65°N latitude) generally exhibit a lower early winter minimum in lying and a higher late winter maximum. At even higher latitude, Roby (1978) recorded the greatest increase in percent lying from mid to late winter for the Central Arctic Herd.

The overall relationship between percent lying and daylength appears linear for daylight values of less than 50%. Although a straight line has been drawn through the data in Figure 2.11, we do not provide an equation because we do not know the exact observation dates for most studies. In Roby's (1978) study, for example, a five day change in the midpoint of his observation period could result in a 5% shift in daylength.

Activity budgets

Comparison of activity budgets among studies is complicated both by the effect of daylength and by the method of calculating the budgets. Unfortunately, details on method of calculation and statistical analysis of activity budgets are often unclear. Some studies have calculated a single ratio for each time period (Gaare *et al.* 1975, this study) while others have calculated a parametric mean of ratios based on individual cycles (Boertje 1981, 1985), bands (Skogland 1984) or scans (Roby 1978, 1980; Roby and Thing 1985). Because those means treat individual ratios equally, without regard for sample size, the mean can vary with the method of calculation. Subsequent analyses have then treated those ratios either parametrically (e.g. analysis of varience; Roby 1978, 1980; Skogland 1984) or non-parametrically (e.g. Chi-square test; Boertje 1981). Parametric treatment of ratios are often statistically invalid because of differing sample sizes and non-normal distribution without transformation. Non-parametric treatment of those ratios is not statistically valid because observations of individual caribou are not independent; the behaviour of the individual is influenced by the behaviour of the group. In addition, analysis based on scans is often biased because of serial correlation among sequential scans. Although the treatment of the data in the present study only estimates the significance of differences, it is a conservative approach and deals with the problems of caribou scan data: varying sample sizes, non-independence of individual animals, and serial correlations among sequential scans. Comparisons among studies should be made cautiously.

Although daylength was the main factor influencing the proportion of the day that caribou spend lying in winter, lying time also increased under adverse snow conditions (late winter each year and mid-winter and spring 1981-82) and was negatively correlated with the density of snow. Daylength was also the primary factor affecting the proportion of time spent sparring although it was also negatively influenced by the depth and density of snow. Sparring activity remained high during the winter of mildest snow conditions (1980-81).

The proportion of time spent moving (walking and trotting/running) was not influenced by daylength. Moving was greatest during fall and spring and was accompanied by a significant increase in the size of bands of caribou. Seasonal migrations likely had the greatest influence. Time spent moving was least during periods of adverse snow conditions (late winter 1979-80, late winter and spring 1981-82) although it was not significantly correlated with specific snow parameters.

The proportion of time spent feeding and standing were significantly influenced by the relationship between daylength and lying time. It is best, therefore, to consider those activities as proportions of the active period, or feeding intensity and standing intensity. Feeding intensity and standing intensity were not influenced by daylength. Standing intensity showed little variation but tended to be lower in spring than at other times. Feeding intensity tended to be lower in fall and spring than at other times, greatest during periods of adverse snow conditions (late winter 1979-80 and late winter and spring 1981-82) and least during the winter of mildest snow conditions (1980-81). However, neither feeding intensity nor standing intensity were significantly correlated with specific snow parameters.

Overall, activity budgets reflected season, daylength and snow conditions. The proportions of time spent lying, moving and the feeding intensity were influenced by adverse snow conditions, but not in a direct, linear manner. This is not surprising since caribou likely respond to thresholds in snow parameters rather than in a continuum (Russell and Martell 1984).

Range quality

Energy is likely the compelling requirement for caribou and reindeer in winter, and alteration of activity budgets is an important mechanism to help balance energy expenditure with metabolizable energy intake (Russell and Martell 1984). Roby (1980) and Roby and Thing (1985) suggested that feeding intensity, the proportion of time spent lying, and the mobility of animals reflects range quality, particularly from late January through April.

Lichen resources on the winter range of the Porcupine Caribou Herd are average to above average compared with other winter ranges and the winter diet of the Porcupine Caribou Herd is stable and indicative of good lichen range. We, therefore, suggest that the increased lying time, feeding intensity and the decreased mobility of animals that we observed at times of adverse snow conditions reflect a decrease in forage availability rather than forage quality. Those changes in activity budget result in a decrease in energy expenditure which enhances winter survival and body condition in spring. R. G. White (Univ. Alaska, pers. comm.) contends that caribou can physiologically reduce rumen volume at times of low food availability, thus requiring less feeding time to fill the rumen. Reduced rumen volumes in winter have been documented for field killed animals (Staaland *et al.* 1979). Increased lying time therefore should be caused by either longer rumination time (to extract the maximum amount from limited food supply) or by an energy conservation strategy whereby the lying period exceeds time necessary for rumination, as documented by Eriksson *et al.* (1981). Forage quality can also affect percent lying since ingestion of poor quality forage requires longer rumination times for digestion thus longer lying periods (Blaxter 1962; Cammell and Osborn 1972). With standardized observations plotted as in Figure 2.11, the points above the line should correspond to poorer quality or less available forage and points below the line should indicate the higher quality or more available forage.

Studies that indicated poor range conditions, with a few exceptions, do tend to fall above the line in Figure 2.11. Roby (1978) indicated that preferred forage (lichens) had low availability on the range of the Central Arctic Herd in northern Alaska. Range quality on Greenland was very poor and animals were near starvation (Roby 1980). Gaare (1968) indicated that a significant decline in lichen biomass had occurred on the Snohetta range in southern Norway (fall value for Norway, Fig. 2.11). Wild reindeer in Norway (Hardangervidda) have shown elevated lying times and high feeding intensities (Skogland 1984), particularly in mid- and late winter, which are likely related to adverse snow conditions (Skogland 1978) but could also be related to food quality because range quality and diet were variable (Skogland 1984). In the present study, fall values tend to be lower than mid winter values.

Cratering dynamics

Methods

Data on cratering dynamics were collected during the field sessions described in the Winter Activity section. During these camps, animals were observed through 15x60 power spotting scopes. Observations focused, when possible, on the individual crater, thus if an animal was displaced from a crater, observations were continued on the displacer in the same crater. Crater types were classified as;

1. new crater – one animal dug and voluntarily left crater;
2. recrater – one animal redug and voluntarily left old crater site;
3. displaced animal – crater animal displaced, observations on this record solely for displaced animal;
4. first displacer – observations of cratering dynamics on first displacer;
5. second displacer – as above but for second displacer

The data collected for each crater were total, feeding, standing, and pawing time, number of strokes for each pawing bout, and time between craters (whenever focal animal continued to be observed). Whenever an animal had its head in a crater and was not pawing, the animal was assumed to be feeding. Feeding intensity was calculated as the amount of time feeding divided by the total time in the crater. Pawing intensity was calculated as time pawing divided by total time in crater. Pawing rate was calculated as the number of strokes per crater divided by total time in a crater. Stroke time was calculated as the total time pawing in a crater divided by the number of strokes per crater. An index of forage selectivity was determined by examining the ratio of ground exposed (crater area) to the average time spent ingesting forage in a crater (units in cm^2/sec); the higher the ratio, the greater the forage selectivity. We assume that the forage resources among years and time periods are constant.

For each camp, crater dimensions were measured along transects through vegetation types where caribou had been observed cratering. Crater width and length were recorded for all camps while crater depth was recorded for all but the last three camps in the winter of 1979–80. Crater area was calculated as the area of an oval (width * length * 0.667) and volume as the product of the area times the depth.

Table 2.18. Crater measurements and regional snow parameters (SE in brackets).

		Regional snow			Crate					
Period	Habitat	Depth (cm)	Density (g/cm^3)	Hardness (g/m^3)	N	Depth (cm)	Width (cm)	Length (cm)	Area (m^2)	Volume (m^3x10^{-3})
1979–80										
Early winter	Forest	20 (1)	.144 (.006)	100	361	20.9 (0.43)	59.9 (2.35)	95.4 (4.00)	0.56 (0.17)	0.049 (0.009)
	Tundra	17 (2)	.157 (.012)	100	-	-	-	-	-	-
Mid winter	Forest	40 (2)	.182 (.009)	713 (97)	123	19.9 (0.51)	75.9 (4.40)	132.9 (8.9)	0.92 (0.25)	0.050 (0.010)
	Tundra	31 (4)	.168 (.012)	3548 (1085)	62	-	113.0 (8.2)	192.0 (16.4)	1.78 (0.52)	-
Late winter	Forest	51 (1)	.165 (.008)	802 (42)	62	-	98.6 (6.1)	192.0 (14.7)	1.47 (0.38)	-
	Tundra	29 (4)	.227 (.014)	4298 (509)	67	-	96.4 (5.7)	200.0 (13.5)	1.49 (0.37)	-
1980–81										
Early winter	Forest	21 (2)	.126 (.009)	100	144	25.2 (0.55)	47.3 (1.5)	63.5 (2.1)	0.21 (0.02)	0.052 (0.002)
	Tundra	20 (1)	.133 (.013)	100	185	23.4 (0.43)	41.3 (1.2)	57.5 (1.7)	0.17 (0.02)	0.043 (0.002)
Mid winter	Forest	24 (3)	.169 (.015)	1507 (447)	64	21.0 (0.51)	47.6 (1.9)	60.2 (2.4)	0.20 (0.03)	0.043 (0.003)
	Tundra	21 (3)	.174 (.016)	2861 (336)	64	16.8 (0.70)	43.1 (2.0)	59.4 (2.9)	0.19 (0.03)	0.033 (0.003)
Late winter	Forest	35 (3)	.159 (.007)	676 (70)	114	18.1 (0.55)	69.0 (2.8)	68.5 (2.2)	0.32 (0.04)	0.054 (0.004)
	Tundra	27 (4)	.162 (.014)	2097 (356)	127	11.2 (0.53)	33.5 (1.8)	44.2 (2.3)	0.13 (0.03)	0.020 (0.003)
Spring	Forest	-	-	-	100	47.4 (0.94)	77.6 (2.3)	101.8 (3.7)	0.53 (0.05)	0.250 (0.010)
	Tundra	-	-	-	60	16.2 (0.79)	41.5 (2.2)	55.1 (4.1)	0.17 (0.04)	0.031 (0.004)
1981–82										
Early winter	Forest	45 (1)	.181 (.010)	1413 (300)	60	44.1 (0.93)	72.8 (3.4)	112.3 (7.0)	0.61 (0.13)	0.268 (0.058)
	Tundra	32 (5)	.248 (.014)	6493 (411)	60	30.3 (0.81)	88.5 (5.8)	148.1 (9.9)	0.96 (0.23)	0.280 (0.067)
Mid winter	Forest	55 (2)	.185 (.006)	2032 (344)	-	-	-	-	-	-
	Tundra	48 (4)	.192 (.015)	14013 (878)	54	49.5 (1.33)	73.7 (4.6)	156.5 (9.8)	0.78 (0.14)	0.404 (0.081)
Late winter	Forest	97 (3)	.260 (0.005)	6107 (2 50)	50	64.2 (0.97)	104.2 (6.3)	160.3 (10.9)	1.14 (0.21)	0.736 (0.097)
	Tundra	79 (6)	.244 (.016)	4465 (977)	50	54.3 (1.47)	74.8 (6.3)	148.9 (10.6)	0.78 (0.19)	0.452 (0.104)

The number of craters dug in a day (CRATERS) was calculated as;

CRATERS = ACTIVE x 24 / (TOTAL + BETWEEN)

where,
ACTIVE = proportion of the day spent active (from Table 2.16)
TOTAL = total time in the crater (h), and
BETWEEN = mean time spent between craters (h)

The energy cost of digging a crater was determined from equations presented in Thing (1977). Specifically for his «slow« digging, the energy cost (joules) to dig a crater is:

ENERGY = (ED + EU + ESL) * TIME * PAW

where:
ENERGY is the energy cost to dig a crater, joules
ED is the energy cost of the downward stroke of the pawing movement (95.6 joules);
EU is the energy cost of the upward stroke of the pawing movement (205.5 joules);
ESL is the energy (joules) spent moving the snow load (calculated as the product of half the crater length, foot area, snow density, distance snow is moved divided by the time used to move the snow [0.17 sec]);
TIME is the time required to complete one pawing stroke (0.53 sec), and
PAW is the number of pawing strokes per crater

Results and discussion

The dimensions (length and width) of 1807 craters (1160 with depth) were taken during the three year study, 40% in forest communities and 60% in tundra communities (Table 2.18). Given equal weight for all periods, mean crater area was 0.649 ± 0.137 m^2 (mean $\pm$SE) and volume was 0.170 ± 0.057 m^3 (mean $\pm$SE). Crater volume was significantly correlated with regional snow conditions ($r=0.89$, $df=12$). Crater volumes recorded by Thing (1977), but recalculated using our formula, compared favourably with volumes recorded during our mild snow year (varying from 0.02 to 0.05 m^3 between his three study areas, cf Table 2.18).

Of the 1557 animals observed cratering, 78% were in tundra communities and 22% in forest communities (Table 2.19). Among the age/sex classes, bulls comprised the majority of the observations (51%), followed by cows (41%), and calves (8%, Table 2.19). New craters were the dominant crater type during all observation periods (83%), except for mid- and late winter 1982, when displacements were more common (Table 2.19).

The influence of caribou type, year and winter period on cratering activities were tested with a three-way analysis of variance. With few exceptions, year had the biggest influence (based on calculated F-value) and caribou type the least influence on cratering activities (thus, cratering activities are summarized by year and winter period, Table 2.20). Because year and period appeared the strongest correlates to cratering activities, we examined possible age/sex differences by performing a one-way analysis of variance controlling for winter and period where sample sizes were sufficiently large. Although some significant differences were noted, the only consistent difference was that bulls exhibited the lowest pawing intensity within all periods tested.

The possibility that snow parameters were the most important aspect of year-to-year variation in cratering activities was tested with stepwise multiple regression analysis using crater depth, area and volume and the regional snow parameters as independent variables (Table 2.21). Crater volume proved to be highly correlated to all cratering activities except pawing rate, stroke time and time between craters. Although regional snow parameters yielded significant relationships to most activities, the corresponding R^2's were generally lower. Both equations have been presented, as regional snow data may be all that is available to managers.

Table 2.19. Breakdown of cratering observations for the Porcupine Caribou Herd in winter and spring, 1979–82.

Habitat	Caribou type	Crater type	1979–80			1980–81				1981–82				Total
			Early	Mid	Late	Early	Mid	Late	Spring	Early	Mid	Late	Spring	
Forest	Cow	new	8	43	–	32	30	20	–	5	–	–	–	138
		recrater	–	–	–	–	–	–	–	–	–	1	–	1
		displaced	–	1	–	–	3	–	–	–	–	2	–	6
		1st displacer	–	–	1	–	4	–	–	–	–	1	–	6
		2nd displacer	–	–	1	–	2	–	–	–	–	1	–	4
	Calf	new	–	–	–	5	12	4	–	–	–	–	–	21
		displaced	–	–	–	–	1	–	–	–	–	–	–	1
	Bull	new	79	1	39	18	9	–	–	2	–	–	–	148
		displaced	4	–	2	–	3	–	–	–	–	–	–	9
		1st displacer	2	–	2	–	3	–	–	–	–	–	–	7
		2nd displacer	–	–	1	–	–	–	–	–	–	–	–	1
	Forest total		93	45	46	55	67	24	0	7	0	5	0	342
Tundra	Cow	new	16	31	43	96	51	–	53	44	38	2	14	388
		recrater	–	–	9	–	–	–	–	1	2	9	3	24
		displaced	1	5	2	2	1	–	–	7	8	2	1	28
		1st displacer	–	–	1	1	1	–	–	5	22	3	2	35
		2nd displacer	–	–	–	–	–	–	–	–	–	1	–	1
	Calf	new	–	5	11	47	14	4	9	1	5	–	–	96
		recrater	–	1	–	1	–	–	–	–	1	–	–	3
		displaced	–	2	1	1	1	–	–	–	1	–	–	6
		1st displacer	–	–	–	–	–	–	–	–	2	–	–	2
	Bull	new	–	24	70	67	53	264	–	11	7	2	6	504
		recrater	–	2	–	–	–	–	–	–	4	3	2	11
		displaced	–	1	12	2	5	9	–	1	1	2	1	34
		1st displacer	–	3	9	5	5	9	–	2	24	15	2	74
		2nd displacer	–	–	1	–	1	–	–	1	3	2	–	8
	Tundra total		17	74	159	222	132	286	62	73	118	41	31	1215

Grand totals:	Forest: 342	1979–80: 434	new: 1295
	Tundra: 1215	1980–81: 848	recrater: 39
		1981–82: 275	displaced: 85
	Early winter: 467		1st displacer: 124
	Mid winter: 436	Cow: 632	2nd displacer: 14
	Late winter: 561	Calf: 129	
	Spring: 93	Bull: 796	

Few studies have documented the time budgets of cratering *Rangifer.* Thing (1977) examined the energetic relationships of wintering caribou in northwestern Alaska, observing animals under snow conditions similar to the moderate winter (snow depths slightly shallower and densities higher) in the present study. In his October-November observations, animals spent 15.2% of the total observation time pawing declining to 14.1% in March-April. The proportion of time spent pawing in our study varied from 7.8% to 18.8% in early winter, from 8.2 to 23.7% in mid-winter, from 4.8 to 27.7% in late winter, and 1.3 to 5.6% in spring between the mild winter of 1980-81 to the severe winter of 1981-82, respectively (Table 2.20). Our percentages would be further reduced if time between cratering were included as it appears to be in Thing's study. In Greenland, caribou on poor ranges in areas of shallow but very dense snow, spent 15-20% of the feeding period in cratering activity (Thing 1984).

Pawing rates recorded in our study (overall mean of 13.8/min ± 0.43 [SE], n=553) compares favourably with literature values. Thing (1977) reported an early winter pawing rate of 13.1 paws/min increasing to 18.1/min in late winter. Our mean value of all periods increased from 9.9 paws/min in the mild snow year (1980-81) to 15.2 in the moderate year (1979-80) to 22.1 in the year of deepest, densest snow (1981–82). All three snow parameters were positively, although weakly, correlated to pawing rate (depth, 0.46; density, 0.56; hardness, 0.51). As calculated above, pawing rate does not represent the difficulty with which animals have in removing snow as indicated by Skogland (1978), but is more indicative of the amount of nonpawing activity in the crater. Thus as snow gets deeper and denser, pawing rate increases, not because animals paw faster but because they spend a greater proportion of their cratering time pawing. The major difference between our study and Skogland's is that we observed a positive correlation between depth versus density and hardness while Skogland (1978) recorded a negative correlation. When Skogland concludes that pawing rate declines with increasing density and hardness, it is because his depths decreased, resulting in a lower pawing intensity.

To determine the relationship between «paw rate» (a measure of speed) and snow, we should only consider the number of strokes/sec of actual pawing or the reciprocal, «stroke time», as defined by Thing (1977) and Fancy and White (1985). While we found that our snow parameters were not good predictors of stroke time, we noted that mean stroke time was slowest (0.69 sec) in the year of densest snow while the other two years were somewhat similar, being faster in the moderate snow year (0.53 sec) than in the mild snow year (0.59 sec). Our values compare favourably to Fancy and White (1985), who recorded a similar response (0.51 sec in soft snow and 0.67 sec in denser snow). On the other hand, Thing (1977) recorded a decrease in the time per stroke with increased snow hardness (0.53 sec in soft snow to 0.43 sec in hard snow). However, as explained by Fancy and White (1985), Thing was observing a «chopping» stroke which animals employ to break through a hard crust, a situation not encountered during our study.

Animals that are highly selective in their diet presumably exhibit this strategy to ingest higher quality forage, either in terms of digestibility, energy or protein content. If we accept that the most compelling component of a caribou winter diet is energy and that *Cladina*-type lichens are the most preferred energy source (Russell and Martell 1984). Also if we assume that the animals were occupying

Table 2.20. Summary of cratering activities (seconds) for the Porcupine Caribou Herd during the three

Period	Habitat	Total time in crater			Feeding time in crater			Pawing time in crater			Standing time in crater			Time sp betwe	
1979–80															
Early	Forest	87	91	17	87	79	16	69	10	3	69	2	1	37	31
	Tundra	16	26	6	16	23	5	16	3	1	16	0	0	–	–
Mid	Forest	44	112	23	44	99	20	44	12	3	44	1	1	37	24
	Tundra	55	207	41	55	178	34	55	22	7	55	7	2	14	99
Late	Forest	39	89	15	39	73	13	13	19	8	13	2	1	7	78
	Tundra	113	264	30	113	219	26	80	35	5	80	14	4	32	39
1980–81															
Early	Forest	50	79	10	50	72	9	50	5	1	50	2	1	34	15
	Tundra	163	87	8	163	74	7	163	8	1	163	5	1	99	1
Mid	Forest	39	131	33	39	109	28	39	14	4	39	9	3	25	14
	Tundra	104	69	7	104	59	6	104	6	1	104	4	1	79	22
Late	Forest	20	80	14	20	74	13	20	5	1	20	1	<1	11	32
	Tundra	262	105	9	262	98	8	262	3	<1	262	5	1	241	13
Spring	Tundra	53	45	5	53	44	5	53	1	<1	53	<1	<1	41	15
1981–82															
Early	Forest	7	340	103	7	252	76	7	59	16	7	29	15	5	77
	Tundra	55	315	67	55	242	54	55	63	13	55	9	2	41	40
Mid	Tundra	41	368	92	41	295	75	41	88	24	41	6	2	32	64
Late	Tundra	4	390	188	4	265	155	4	105	34	4	9	4	2	71
Spring	Tundra	20	142	49	20	134	48	20	8	3	20	<1	<1	14	21

range of similar forage conditions among years, based on our measure of forage selectivity (Table 2.22), we expect, and did indeed measure, a significantly larger proportion of *Cladina*-type lichens in the first year (63.3 ± 3.2) and similar but lower proportions in the final two years (44.8 ± 12.9 and 38.4 ± 5.0, respectively).

If we consider the time between craters largely a searching activity, then searching time was related to crater depth (Table 2.22). Although it does not appear that animals in the first year, when forage selectivity was the highest, spent a disproportionately longer time searching in relation to snow depth than did animals in the other years, if we compare the time between craters with the time spent from the initiation of one crater to the initiation of the next crater (Table 2.22), animals in the first year spent a higher proportion of time searching (26.2%) than animals in the other two years (16.9% and 14.9%). Thing (1984) indicated that the animals in Greenland spent 6-12% of their time searching in early winter increasing to 20-22% by late winter, although it is not clear how he defined searching time.

The number of craters dug in a day is another factor that animals can control to optimize energy balance. The daily crater output as defined here is a function of the amount of time animals were active, the total time spent in a crater and the total time between craters. The average number of craters dug in a day varied from 105 in the deep snow year to 433 in the mild snow year and 265 in the moderate snow year (Table 2.22).

1979–82 (n mean SE).

otal number f paw strokes			Stroke time			Pawing rate			Pawing bouts per crater			Paws per bout			Feeding intensity			Pawing intensity		
86	19	5	32	.47	.02	32	20	3	86	4	1	32	5	<1	87	.86	.02	69	.09	.01
16	7	1	5	.45	.02	5	18	4	16	3	1	5	4	2	16	.82	.03	16	.18	.03
22	22	5	22	.53	.03	22	19	3	44	6	1	22	4	<4	44	.83	.03	44	.17	.03
55	31	7	43	.51	.02	43	11	1	55	9	2	43	4	<1	55	.86	.01	55	.10	.01
39	16	4	11	.68	.07	11	9	1	39	4	1	11	5	<1	39	.81	.02	13	.11	.01
113	47	5	55	.59	.01	65	14	1	113	9	1	113	5	<1	112	.81	.01	80	.13	.01
23	8	1	23	.64	.05	23	9	1	50	3	<1	50	3	<1	50	.90	.01	50	.08	.01
79	13	2	79	.61	.02	79	13	1	163	3	<1	163	4	<1	163	.86	.01	163	.09	.01
21	23	7	21	.57	.03	21	13	1	39	5	1	39	5	<1	39	.83	.03	39	.09	.01
55	12	1	55	.55	.02	55	15	1	104	3	<1	104	4	<1	104	.86	.01	104	.09	.01
8	8	2	8	.63	.03	8	9	1	20	2	<1	20	4	<1	20	.93	.01	20	.05	.01
61	6	1	61	.61	.01	61	6	1	262	2	<1	262	4	<1	262	.93	.01	262	.03	.003
4	2	1	4	.53	.10	4	11	3	53	1	<1	53	3	<1	53	.96	.01	53	.02	.01
7	77	21	7	.78	.06	7	15	2	7	12	3	7	7	1	7	.74	.01	7	.20	.02
50	101	23	50	.69	.04	30	19	1	55	15	3	55	6	<1	55	.73	.02	55	.23	.02
35	126	23	35	.56	.03	35	27	2	41	18	3	41	7	<1	41	.74	.02	41	.23	.02
4	142	57	4	.57	.19	4	27	5	4	18	9	4	9	<1	4	.60	.07	4	.36	.08
8	12	5	8	.63	.09	8	13	4	20	3	1	20	5	1	20	.94	.02	20	.06	.02

We determined a 27.1 fold difference in the energy cost of digging a crater (Table 2.23, cf late winter tundra values for 1980-81 versus 1981-82). The mean values for all crater types were highest in 1981-82 (16911 joules) and lowest in 1980-81 (2457 joules). A significant logarithmic relationship exists between the number of craters dug per day and the energy cost associated with digging one crater (Fig. 2.12.), suggesting that a tradeoff exists between these two components.

No significant differences in cratering activity were determined among crater types based on an analysis of variance using only mid winter 1982 data (only period in which large enough sample sizes occured). However controlling for winter and

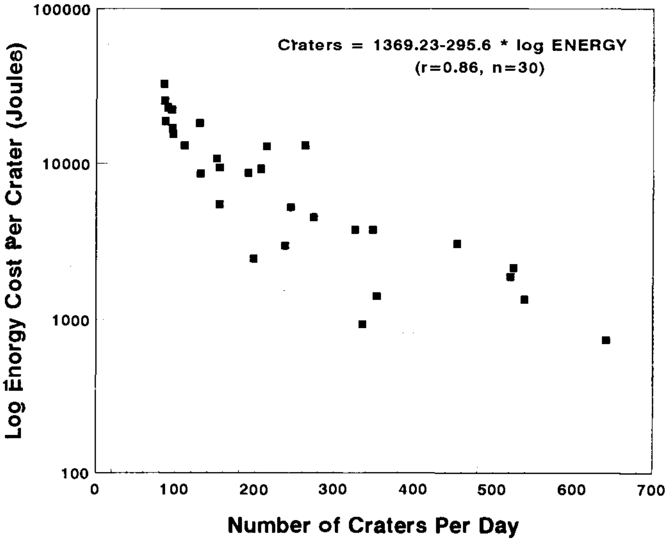

Figure 2.12. Log of the energy cost to dig a crater versus number of craters dug per day.

Table 2.21. Results of multiple regression relating caribou cratering activities to crater characteristics and regional snow parameters for the Porcupine Caribou Herd, 1979–82.

Activity	Best model	r^2 (n)	Regional snow model	r^2 (n)
Total time	65.485 + 797.83 Volume	.916 (12)	−249.09 + .0013 Hard + 2.3069 Dens	.698 (15)
Feed	62.610 + 561.47 Volume	.897 (12)	−160.80 + .0010 Hard + 1.6319 Dens	.707 (15)
Stand	not significant		not significant	
Pawing	-1.843 + 234.31 Volume	.981 (12)	-71.60 + .8815 Dep +.0003 Hard +.384 Dens	.851 (15)
Feed intensity	0.898 — 0.56 Volnme	.750 (12)	1.08 - .0026 Hard - .001 Dens	.653 (15)
Paw intensity	0.059 + 0.57 Volume	.823 (12)	-.117 + .0026 Dep + .001 Dens	.650 (15)
Paws/crater	0.414 + 323.68 Volume	.971 (12)	-101.841 + 0.971 Dep + .0005 Hard + .60 Dens	.834 (15)
Bouts/crater	1.719 + 39.56 Volume	.945 (12)	-12.270 + .0001 Hard +.1053 Dens	.781 (15)
Paws/bout	3.772 + 9.63 Volume	.776 (12)	2.438 + .0750 Hard	.656 (15)
Stroke time	not significant	.738 (12)	not significant	not significant
Pawing rate	4.228 + 0.0011 Area + 0.218 Depth	.738 (12)	not significant	
Between	-9.519 + 1.552 Depth	.795 (12)	not significant	

Volume: crater volume (m^3)
Area: crater area (cm^2)
Depth: crater depth (cm)
Hard: regional snow hardness (kg)
Dep: regional snow depth (cm)
Dens: regional snow density (g/cm^3)

Table 2.22. Comparison of mean values for snow parameters and caribou cratering characteristics for the Porcupine Caribou Herd, 1979-82.

Parameter	1979-80	1980-81	1981-82
Snow depth (cm)	33.6	24.7	51.0
Snow density (g/cm^3)	.180	.154	.216
Snow hardness (gm)	1892	1224	6596
Crater area (m^2)	1.24	0.20	0.78
Crater volume (m^3)	-	0.04	3.46
Number of craters/day	265	433	105
Forage selectivity (cm^2/sec)	107	27	30
Searching time (sec)	54	18	63
Activity while in crater (%)			
feeding	83	89	70
pawing	15	5	25
standing	2	5	5
Activity from start of crater To start of next (%)			
feeding	61	74	60
pawing	11	4	22
standing *	1	5	4
searching **	26.2	16.9	14.9
Recrater (%)	2.5	0.0	10.2
Displacement (%) ***	8.3	5.0	40.0

* while in feeding crater

** defined as the time between craters (includes some standing, walking, trotting and/or sparring

*** total number of displacement craters / (total displacement + new + recrater). To calculate the number of displacement craters all 2nd displacer craters and the greater of the displaced versus 1st displacer craters were totalled.

period, Kruskal-Wallis analysis indicated that displacers exhibited lower pawing intensities and consequently higher feeding intensities compared to displaced animals.

Thomson (1977) and Shea (1979) examined the role of displacement in the social hierarchy of caribou in winter. Although he never had any direct measurements, Shea (1979) concluded that «food is the limited resource for which hierarchy establishes privilege and there is increased competition for forage as winter continues» and that «this increased competition is caused mainly by changing snow conditions which make cratering more energetically expensive in late winter». Our data lend support to Shea's (1979) conclusions as percent displacement increased from the mild snow winter (5.0%), to the moderate snow year (8.3%) and again to the adverse snow year (40.0%).

Animals tended to redig previously excavated craters as snow conditions worsened. The proportion of recrater types increased from 0% in the mild snow year to 2.5% in the moderate snow year to 10.2 % in the adverse snow year, (Tables 2.19 and 2.22). The energetic advantage of not having to entirely dig a new crater must occasionally offset the poorer forage quality remaining in an old crater as snow conditions deteriorate.

Conclusions

Caribou during our study were faced with a wide variety of snow conditions which influenced their cratering activities, presumably dictating the area and volume of craters to be dug, the number of craters, the degree of forage selectivity and the amount of search time available. Thus in the first year (moderate snow), animals

1. dug an average number of craters,
2. exposed the most forage per crater,
3. were highly selective of the exposed forage,
4. spent the largest percent of active time searching, and
5. exhibited a relatively low degree of displacement and recratering.

In the second winter when mild snow conditions prevailed, animals

1. dug the greatest number of craters per day,
2. exposed the least forage per crater,
3. were the least selective of forage, but similar to third winter,
4. spent the least time searching between craters, and
5. exhibited the least amount of recratering and displacement.

In the final year snow conditions were adverse and animals

1. dug the fewest number of craters,
2. exposed less but similar forage compared to the first year,
3. exhibited similar forage selectivity to the second year,
4. spent a similar proportion of time searching as animals in the first year, and
5. exhibited the greatest displacement and recratering activity.

The options available for animals in a year of deep, dense snow are extremely limited. Craters must be few because energy costs of digging craters probably exceed energy intake. As well, animals cannot afford to be highly selective of forage, although in 1981-82 animals did consume a relatively high quality diet (see winter food habits section).

One aspect of the study that was somewhat surprising was that strategies employed in early winter remained consistent throughout the winter. Moreover, as snow conditions in early winter 1979 and 1980 were essentially the same, snow condition apparently did not determine overall cratering strategies and animal condition may have been the overriding factor.

Conclusions from winter

Winter range has classically been described as one of the most critical habitats in the ecology of large migratory caribou herds. While our studies should only reflect the winter ecology of the Porcupine Caribou Herd, we conclude that considering the diversity of the range; the availability of large expanses of range with abundant availability of high quality forage; and the behavioural repertoire available to the species to cope with adverse winter conditions; that winter range for the Porcupine Caribou Herd, although important, is not one of the most critical ranges requiring strong legislative protection.

In years of shallow snow, the Porcupine Caribou Herd will occupy the vast Whitestone/Eagle Plains region, an area of normally high snow and abundant lichens. While in this forested region, animals can exploit the abundant lichen, obtained by cratering through relatively soft snow. The high lichen content in the diet, combined with a high proportion of the day spent feeding, probably results in a positive energy balance throughout the winter season (see Chapter 5).

In years of normal to deep snow, two regions are normally exploited; the Ogilvie/Hart Basins and the Richardson Mountains. Due to the effects of strong winds in the Richardson Mountains, this latter region is probably the most favourable in terms of snow conditions, however movement between valleys in this region may be a problem if deep drifts accumulate. We have evidence in diet samples, recently collected, suggesting that higher quality forage is typically obtained when the animals winter in the Ogilvie/Hart region.

Table 2.23. Energetic parameters determined for caribou cratering activites from the range of the Porcupine Caribou Herd.

Period	Habitat	Crater type	Number of craters/day	Energy cost per crater (joules)
1979–80				
Early winter	Forest	new	454	3072
Mid winter	Forest	new	348	3781
	Tundra	new	155	5501
Late winter	Forest	new	238	2928
	Tundra	new	131	8623
		recrater	87	18704
		displaced	151	10757
1980-81				
Early winter	Forest	new	539	1360
	Tundra	new	525	2156
		displacer	245	5277
Mid winter	Forest	new	326	3768
		displacer	274	4557
		2nd displacer	641	740
	Tundra	new	521	1888
Late winter	Forest	new	353	1423
	Tundra	new	335	935
		displacer	198	2468
1981–82				
Early winter	Forest	new	111	13090
	Tundra	new	130	18204
		recrater	85	32411
		displacer	191	8672
Mid winter	Tundra	new	95	22150
		recrater	96	16851
		displaced	214	12952
		displacer	90	22923
		2nd displacer	263	13086
Late winter	Tundra	new	86	25347
		recrater	207	9269
		displacer	97	15478
		2nd displacer	155	9418

CHAPTER 3 . Late spring

Calving grounds

Introduction

The critical nature of the calving grounds for large migratory caribou herds have long been recognized (Lent 1966; Skoog 1968; Kelsall 1968; Thomas 1969). In fact the fidelity of each population to this relatively discrete portion of their range led to the convention by caribou managers to name the herd after the geographical location of their calving grounds (Parker 1972).

Why are herds loyal to a unique calving ground? Many theories have been proposed, ranging from the ability of the parturient and lactating females to track the newly flushing, nitrogen rich vegetation (Klein 1970), the avoidance of insects, or the avoidance of high density predator populations (Kelsall 1968).

The calving grounds of most large migratory caribou herds tend to have at least one characteristic in common; they are generally found north of treeline at approximately the 0°C June 1 isotherm. During the onset and throughout the normal calving period these areas are characterized by a mosaic of newly flushing vegetation and melting snow patches. The annual variation in the pattern of snowmelt therefore has a large role to play in the exact location of calving (Lent 1980).

The exact location of the Porcupine caribou calving grounds has been determined only in the last 30 years. The Arctic Coastal Plain of Alaska and northern Yukon received little attention until coordinated surveys were initiated by the US Dept. of Agriculture and the Canadian Wildlife Service in the early 1950's. The «Porcupine Herd» was first named in 1953 after the river of the same name that best described the centre of habitation of a number of herds that were previously thought to be separate. As such the herd is not named after the location of their calving grounds.

Within the Yukon portion of the calving grounds of this herd, little human activity has disrupted the free movement of caribou during this critical stage in their life cycle. A proposal to construct a pipeline across the Yukon coastal plain linking gas reserves in Prudhoe Bay, Alaska with potential reserves in the Mackenzie Delta of the Northwest Territories, resulted in a number of investigations designed to document the movement patterns and extensive migration corridors of the Porcupine herd. The pipeline proposal was rejected by an inquiry in 1977 (Berger 1977). This and other proposals, however, caused concern among caribou researchers and managers and prompted a workshop in Fairbanks in 1978 to review our knowledge of large migratory caribou populations and suggest areas of research that should be conducted to better prepare ourselves for future development proposals (Klein and White 1978). Among the «first priority» recommendations of the workshop was the need to determine the «characteristics of caribou calving grounds» and the need to examine the «mechanisms of selection and factors governing selection of forage and habitats by caribou». This study was an attempt to fill in the knowledge gap in these two areas of concern.

The objectives of the present study were to;

- document the biophysical characteristics and annual variation of those characteristics on the area of most concentrated calving in the Yukon
- determine the patterns of range use exhibited by calving caribou in the area as reflected by habitat selection and food habits

- determine the energetic relationships of pregnant and lactating females as evidenced in activity budgets of the cow and the nursing behaviour of the calf.

Study area

The study area (Fig. 1.2) falls within the Northern Mountains and Coastal Plain Ecoregion, described by Oswald and Senyk (1977; Fig. 3.1). Annual precipitation in the region varies from 250 and 380 mm on the Arctic Plateau and British Mountains to about 125 mm along the Arctic Coast (Oswald and Senyk, 1977). Mean annual temperatures are about -10 to -11°C with extremes moderated by the coastal influence. The study area falls on the northern flank of interior mountains and is influenced by two maritime air masses that interact in the region. Pressure systems forming over the Gulf of Alaska frequently invade the area. However, because of the compact mountain barrier in Alaska, their access to the

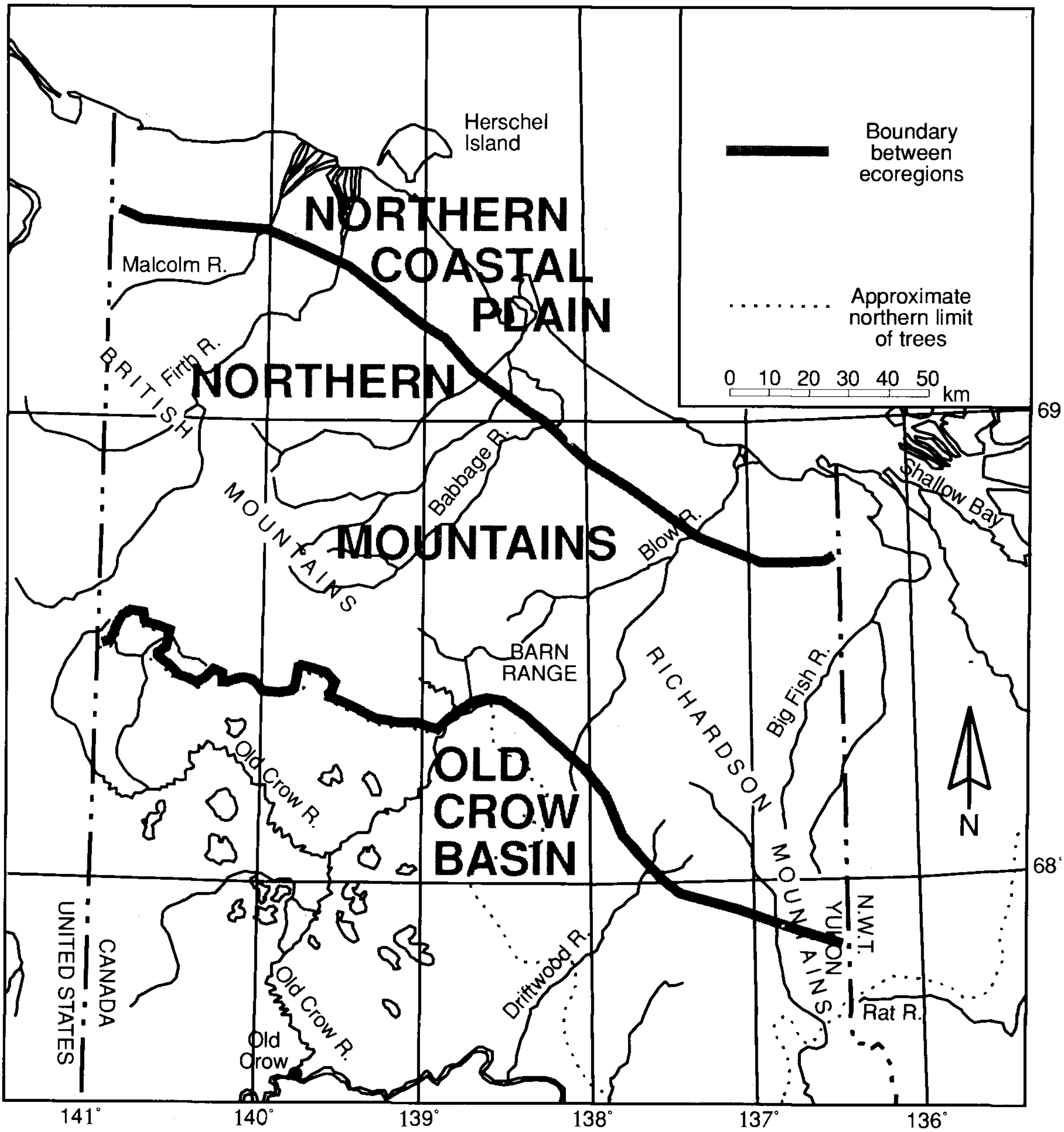

Figure 3.1. Ecoregions in the northern Yukon Territory.

northern Yukon is by sweeping along the coast. The second air mass is formed over the Beaufort Sea. This mass has a significant influence on the study area, but is barred from penetrating the interior by the mountain chain. The Beaufort Sea air mass introduces cold air to the region on its southerly course.

Within the Northern Mountains and Coastal Plain Ecoregion, Wiken *et al.* (1981) describe two ecodistricts that overlap our study area, the Komakuk Plains and Malcolm River Ecodistricts. In common with the entire Coastal Plain Ecoregion, the Komakuk Plains are characterized by their low altitude and subdued relief, and their abrupt termination along the foothills in the vicinity of our Camp 2 location. To the west the Plains continue into Alaska, while eastward there is a sharp change of geomorphology on to the King Plains Ecodistrict, which marks the extreme westward extent of the Quaternary glaciation. The Komakuk Plains are an unglaciated landform, covered by extensive fans and braided deltas, with low-lying areas covered with a blanket of patterned organic materials underlain with marine sediments. Soils are generally poorly weathered throughout the plains, primarily as a function of shallow depths to permafrost and the presence of free water in the active layer for prolonged periods. These soils tend to be acidic and nutrient poor, but rich in undecomposed organic matter (Wiken *et al.* 1981).

To the south of the Komakuk Plains lies the Malcolm River Ecodistrict, a region of highly variable relief. The generally rounded mountains of this ecodistrict offer a variety of geomorphic features. Bedrock summits, talus and solifluction slopes, fans, residual deposits, cryoplanation terraces, rock and gravel river terraces, and gravel-bed headwater streams abound. The majority of this ecodistrict is colluvium which is all but devoid of vegetation. Organic pediments form in lower slopes above the broad coarse-textured floodplains (Wiken *et al.* 1981).

Two camp locations were used during the study. The first, occupied in 1979 and 1980, was located approximately 20 km inland from the Beaufort Sea at 260 m elevation and observations were confined to 220 - 730 m elevation (generally under 350 m). The second camp, used in 1980 and 1981 was within 13 km of the coast at 140 m, with observations occurring between 120 - 470 m (generally under 250 m). The vegetation of the study area has been described elsewhere (Russell *et al.* 1992a), together with the relative availability of the significant range types at the two camp locations (summary in Table 3.1).

Porcupine caribou calving distribution

The calving distribution of the Porcupine Caribou Herd over the last two decades was reviewed by Garner and Reynolds (1986). We have included much of their review while giving a more detailed account for the three years of our study. The calving grounds of the Porcupine herd are international, extending along the arctic foothills (up to 1,100 m elevation) and arctic coastal plain to the Beaufort Sea coast from the Babbage River in Yukon to the Canning River in Alaska (Fig. 3.2). Over the past 14 years in which similar data have been collected, substantial variation in the distribution of calving has occurred, while certain «core» areas have been used often. The location of the previous wintering area, weather and snow conditions encountered on spring migration, and the snow melt pattern encountered on the calving ground all affect the distribution of the herd at the peak of calving in any given year. In years of difficult snow conditions, parturient cows can give birth along the migration route, south and east of the normal calving grounds (Lent 1980). For example in 1972 and 1982, both years of deep spring snow and late snowmelt, significant levels of calving activity occurred in the Old Crow Flats, British Mountains and on the Coastal Plain east of the Firth River (Roseneau *et al.* 1974, Mauer *et al.* 1983, and Whitten and Cameron 1984). In 1975, when snow conditions along the migration route were light and snow melt within the calving grounds was early, nearly all of the herd calved in the extreme west of the traditional area.

The area of major concentration during the peak of calving is centred in the uplands of the Jago River, extending west to the Sadlerochit River and east to the Aichilik River (Fig. 3.2). Within Canada, the foothills region between the Firth River and the Alaska border has consistently incorporated some of the calving distribution of the herd. However the limited area between the coastal plain and foothills may limit the number of calving caribou this area can sustain.

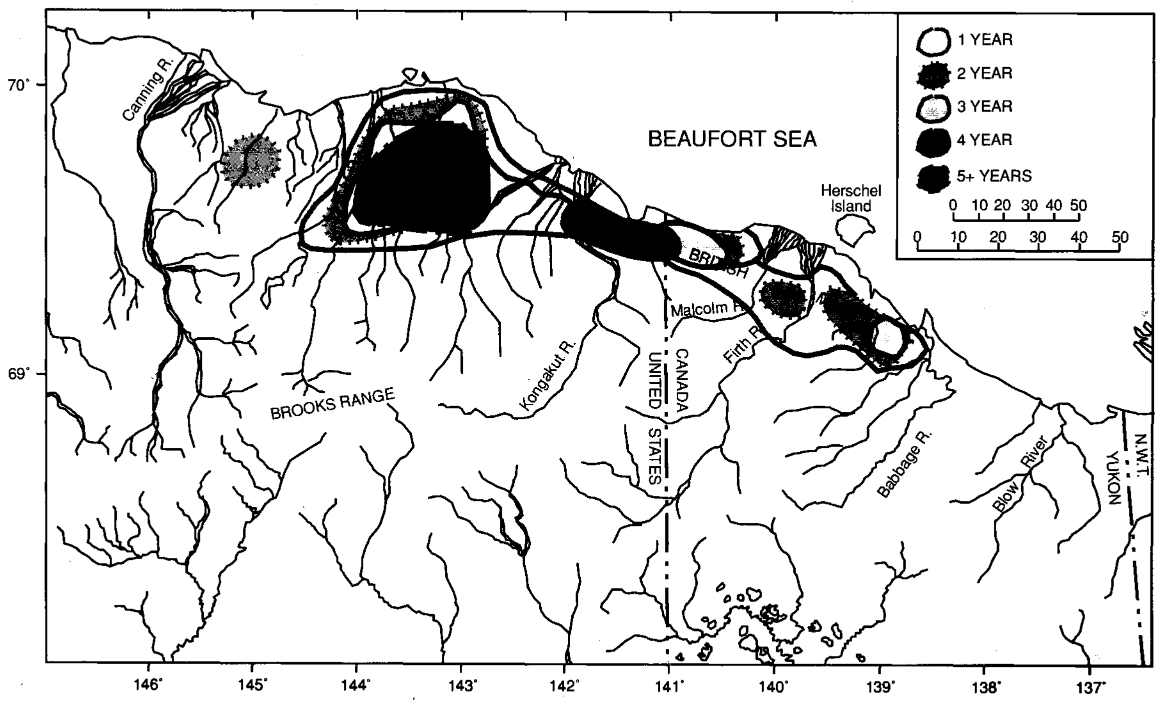

Figure 3.2. Porcupine Caribou Herd calving ground 1972-85

Movement of pregnant females to the «core» calving grounds is from the east and southeast along the foothills and mountain valleys where snow melts early. In years when snow melt is advanced, migration on to the calving grounds occurs along a more northerly, broad front across the foothills and coastal plain. Upon arrival within the core calving area, many caribou often move northward along corridors of early snow melt associated with major river courses.

The traditional calving ground of the Porcupine Caribou Herd is an area where snow melts early, along the foothills and the southern portion of the coastal plain from the Firth/Malcolm delta to the Canning River (Lent 1980). This area lies inland, is elevated sufficiently to experience frequent warming by spring-temperatures, and receives more solar radiation than the frequently fog-covered northern coastal plain.

Immediately after calving, the distribution of the nursery bands shifts northward, tracking the snow melt. The routes and patterns of movement are extremely variable. In general caribou that calve in Canada drift slowly, at first, westward toward the expansive coastal plains in the Jago region. Caribou that calve in the core Jago uplands tend to track the melting snow northward on to the coastal plain. Then, depending on the timing and intensity of insect harassment, the animals may move either to the Beaufort Sea shore (where caribou get some relief from insect harassment) or to the foothills and mountains returning to the coastal plain as harassment subsides.

In 1979, the calving distribution of the herd was very typical of the 14 year average (Russell *et al.* 1992b). Major concentrations of animals at the peak of calving were located in the Jago uplands and along the foothills from the Kongakuk River to east of the Clarence River (Fig. 3.3). Movement westward from the eastern concentration began about mid June and large aggregations formed in the region north of the Jago uplands. By the end of June the majority of nursery bands retraced their movements eastward, returning to Yukon in early July. Large aggregations were located at Demarcation Bay on July 4 and south of Komakuk Beach on July 5 (Fig. 3.3).

In 1980, calving distribution appeared to be greatly influenced by deep snow and late snow melt over much of the traditional calving grounds. On 4 June about 85% snow cover existed on all of the coastal plain with the exception of a narrow band of snow free terrain between Fish Creek and the Clarence

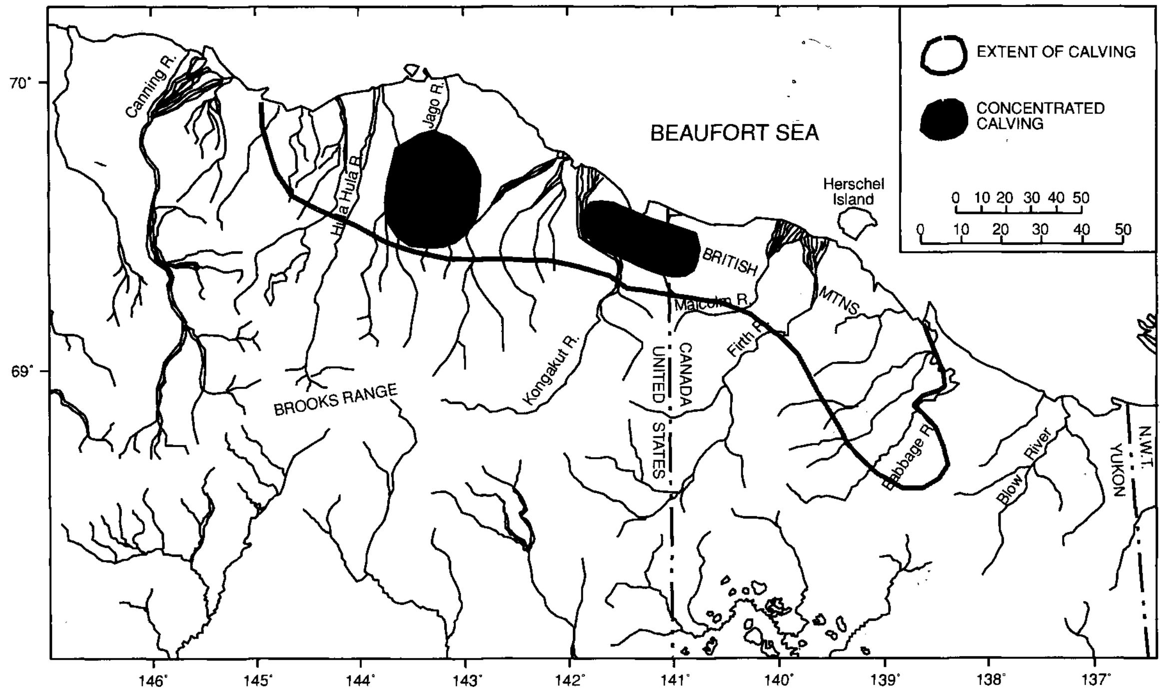

Figure 3.3. Porcupine Caribou Herd calving distribution, 1979.

River. The foothills regions along the north flank of the British Mountains and Brooks Range were relatively free of snow. The extent of calving corresponded closely to the snowfree areas, farther south and east than the usual concentration areas (Russell *et al.* 1992b). Areas of significant calving included the foothills reaches of the Trail, Crow, Spring and Firth Rivers, across the Fish Creek-Clarence River coastal

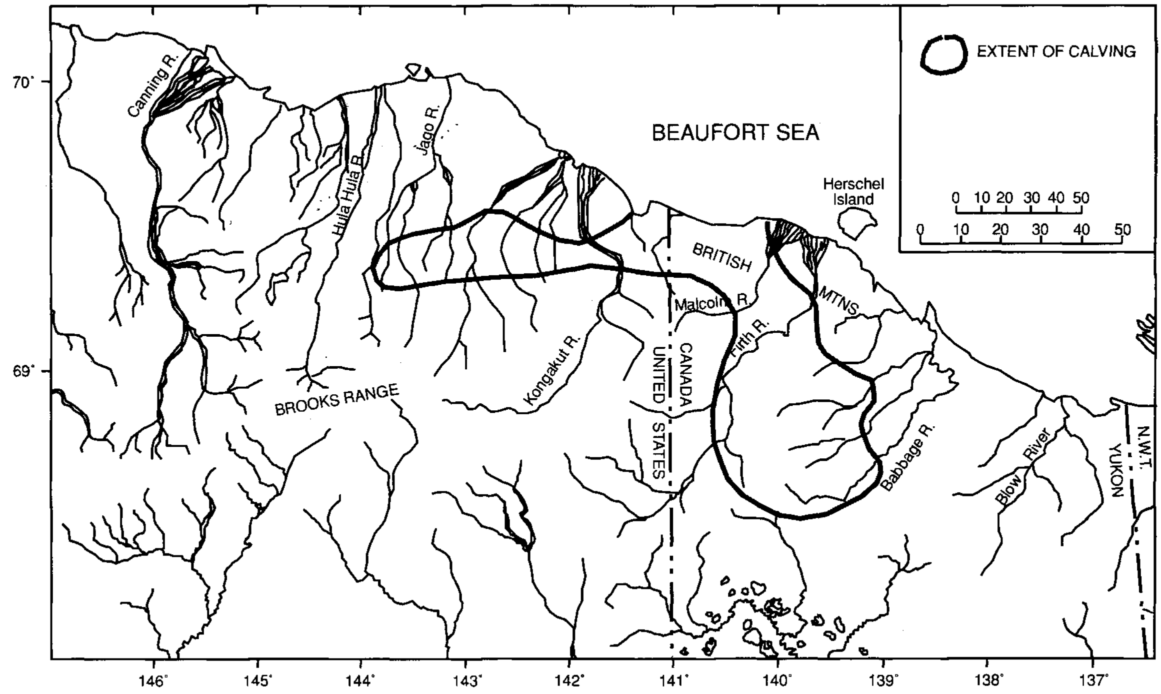

Figure 3.4. Porcupine Caribou Herd calving distribution, 1980.

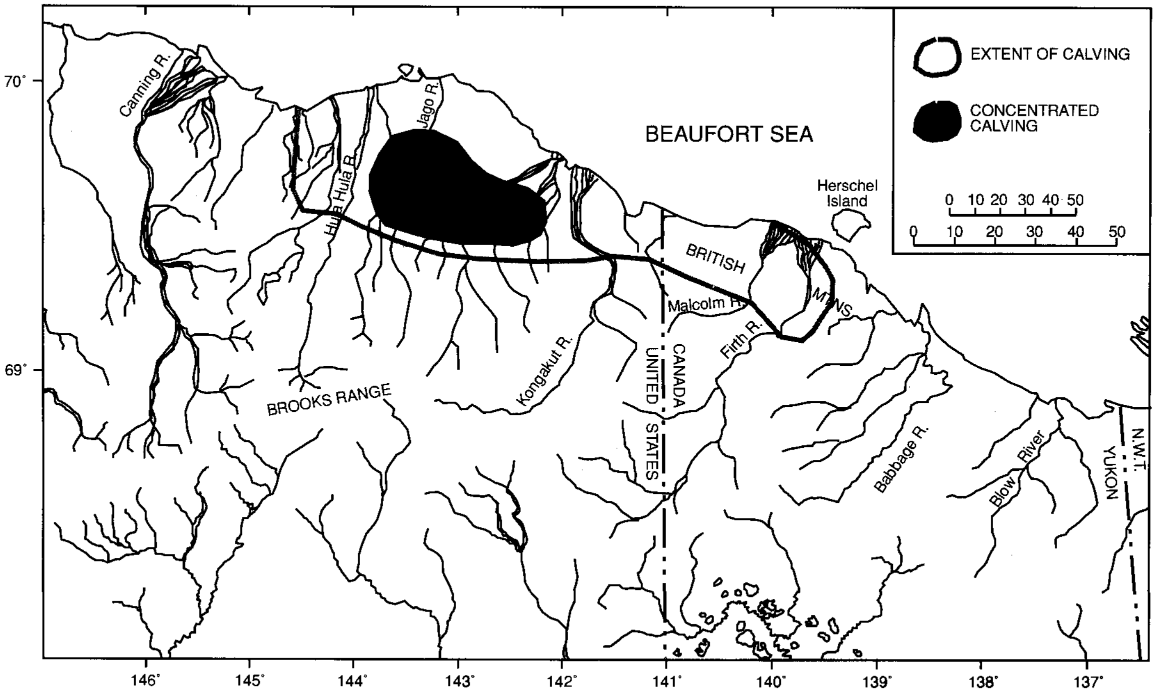

Figure 3.5. Porcupine Caribou Herd calving distribution, 1981.

plain area, into the Brooks Range foothills west to the Okpilak River (Fig. 3.4). After calving in 1980 the caribou moved swiftly westward and by late June the majority of the cows and calves were in the vicinity of the Jago River, drifting eastward along the foothills and coastal plain.

In 1981 most of the calves were born on the uplands of the Jago River in Alaska. The large concentrations there made extensive use of the foothills, primarily the dry snowfree uplands from the Okpilak River across the Jago River drainage to just east of the Egaksrak River in Alaska (Russell *et al.* 1992b). West of the Kongakut River, caribou bands appeared to consist almost exclusively of calving adult females, with few juveniles present. East of the Kongakut to the Firth River many more non-calving juveniles and a few bulls were mixed with the cows. Immediately after the peak of calving, movement of these eastern animals gradually drifted westward (Fig. 3.5). By June 29 the majority of the herd had moved from the Jago region to the northern foothills of the British Mountains, moving southeast from Alaska to the Yukon. Groups were scattered from the lower Firth River west to the lower Kongakut River (Fig. 3.5).

Characteristics of the range

Methods

Weather

Weather observations were made twice daily at approximately 0800 and 1600 hours. Temperature was recorded by maximum-minimum thermometers housed in a standard Stevenson screen and a thermograph mounted in the screen to provide a continuous measure of air temperature. Depth of fresh snow or the amount of rain from a standard rain gauge was recorded. Wind speed was measured from a totalizing anemometer mounted 1.5 m above ground surface. Weather observations were made at camp 1 in 1979 and 1980 and at camp 2 in 1981. Weather on the coast was obtained from Environment Canada records for Komakuk, approximately 26 km northeast of the study area.

Biomass

Biomass of fruticose and foliose lichens and new, green vascular matter was determined in the six major range types at 10-day intervals between 25 May and 15 July 1980. All vascular plants were clipped at moss or ground level in five 20 x 50 cm quadrats at 5 m intervals in each range type on each sampling date. Fruticose and foliose lichens were then collected from the clipped quadrats. One composite sample was made of each set of five quadrats. The vascular matter was then sorted to separate the new green biomass, floral parts and the lichens. It was not possible to separate «new green» leaves for some evergreen species (eg. *Ledum palustre*, *Vaccinium vitis - idaea*), therefore all green leaves were used. All materials were air dried in the field at approximately 40°C and later oven dried at 80°C until no further weight loss occurred, then weighed to the nearest milligram.

Tussock density

The density of cottongrass tussocks was determined in eight stands using the point-distance sampling technique (Batchelor 1971). In each stand 100 points were sampled at 2 m spacing. Distances to tussocks were not recorded if they exceeded 3 m. For each tussock the number of heads in flower, clipped by ptarmigan, or plucked by caribou were recorded. The proportion of tussocks covered with heath or heath-like species and the proportion grazed by small mammals were also estimated.

Phenology

The phenology of vascular vegetation was determined on 36 10x10 m permanent quadrats in the study area. Each range type in the study area was represented by three to 11 quadrats; larger numbers of quadrats were necessary for range types that varied dramatically in aspect. Eight quadrats were established at Clarence Lagoon for comparison. The phenology of all species present was determined at 10 - day intervals in nine classes: no development, flower buds, early flowering, full flowering, flowers senescing, seed or fruit, leaf buds, leaves unfolding, full leaf.

Nutrients

Twenty three species of plants were collected at ten day intervals between late May and early July 1980 to determine the level and change in the fibre and nutrient content of forage used by caribou. Each species was collected consistently from the same site and the portion of the plant collected mimicked that consumed by caribou. Samples were air dried in the field at approximately 40°C and later oven dried at 65°C until no further weight loss occurred (generally over 48 hours). A 7 g ground sample of each species collected was sent for analysis to the Plant and Soil Laboratory, University of Alaska, Palmer, Alaska. Samples were analysed for total nitrogen and phosphorus, acid detergent fibre, neutral detergent fibre, lignin, cellulose and residual and total ash.

Results and discussion

Weather

Mean daily air *temperature* increased gradually from the pre-calving period to the movement period, although there was significant between year variations. In all years the most dramatic increase in temperature occurred throughout the calving period (1-10 June) with mean values increasing approximately 1°C per day. Temperatures then oscillated lower and higher until the end of June. Only in 1981 did temperatures fail to recover to maximum calving period temperatures by the end of June. A significant warming period was observed in the pre-calving period in 1980 (Fig. 3.6). In general, 1980 was warmer than average throughout. In 1981 the calving period was cooler and the post-calving period warmer than 1979. The foothills were consistently warmer than the coast (Fig. 3.7), by 3 - 5°C during calving and post-calving.

In 1980 there was a significant increase in cumulative *degree days* in the foothills compared to the other years; no difference was apparent on the coast (Fig. 3.7).

In 1979 relatively high amounts of precipitation occurred from 20–25 May, from the 10–13 June and again from 20–25 June resulting in significantly higher levels of cumulative precipitation than in the other years, when the only period of high precipitation occurred in the calving period (Fig. 3.8).

Wind speeds varied considerably throughout the study, averaging approximately 8 km/h, with no general patterns emerging. The only noteworthy observations were the two peaks in wind speed recorded in the pre-calving (1980) and post-calving (1981) periods.

In summary, late spring in 1979 was wet and cool except during the calving period. In 1980, except for the calving period, temperatures were warm. The post-calving period in 1980 was very windy. The temperatures in 1981 were similar to 1979 except for a cooler calving and warmer and windier post-calving periods.

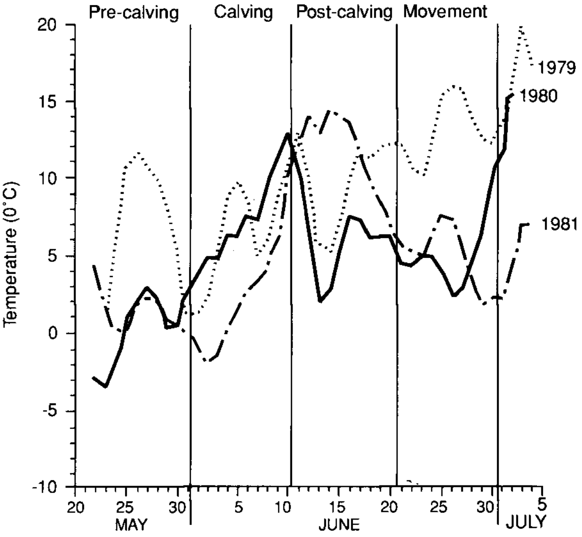

Figure 3.6. Mean daily air temperature recorded on the calving grounds of the Porcupine Caribou Herd, 1979–81.

Phenology

Definite trends were found in the timing and progression of phenological changes in plants among range types, between the foothills and the coast and among years of the study. *Dryas* and *Vaccinium uliginosum* are indicative of the general trend. Flowering and seeding on the alpine barren were generally earlier than on alluvial and heath range and were latest on meadows.

In 1979 and 1980 *Eriophorum vaginatum* and most other species produced seeds at least 10 days earlier in the foothills than on the coast. In 1981 the difference in phenology between the coast and foothills was less, presumably due to the smaller disparity in temperatures between these two regions that year.

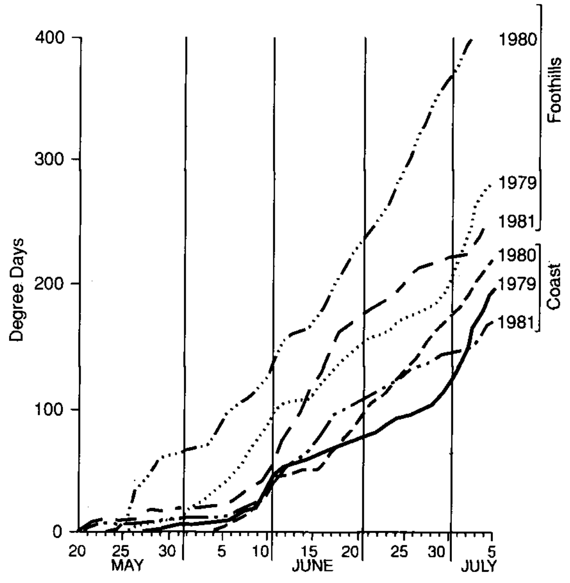

Figure 3.7. Cumulative degree days recorded on the Porcupine caribou calving grounds, 1979–81.

In 1980 phenology was most advanced in all communities and the transition from flower to seed was short. In 1979 flowering was early but the flowering period was elongated, possibly as a function of the cool, wet weather and almost constant cloud cover. In 1981, the flowering period was considerably later than in 1979 (Fig. 3.9).

Whitten and Cameron (1980) noted a similar trend in their latitudinal transect within the range of the Central Arctic Herd. They reported a 2 – 3 week advanced phenology in the southern foothills compared to coastal regions, with a strong south-north gradient along a 50 km transect.

Biomass

The relative physiognomic composition of the major range types have been reported earlier (Fig. 3.10). Evergreen shrubs contributed most to total green biomass in the study area throughout the study period (Table 3.1). Deciduous shrubs contributed the most to new annual growth, followed by graminoids. Graminoids peaked in new annual growth by 25 June and forbs by 5 July. Deciduous shrubs had not yet peaked by the final collection on 12 July.

If we focus on the five major plant groups and the major range types within the study area (> 5% of the study area, Table 3.2), each range type contributes a unique complex of plant groups. Mean lichen biomass was greatest in the alpine barren type (24 g/m²) with the remaining range types averaging about half (13 g/m², Table 3.3a - 3.3f). Graminoids were highest in the tussock tundra type throughout the sampling period, although biomass was low from late May to early June. Biomass of forbs appeared to peak in early July (Table 3.3). Most forbs were in the two heath communities and the alpine barren. The dwarf shrub heath type contained the highest biomass of deciduous shrubs in early June, but by mid June deciduous shrubs were found equally in all but the alpine barren range. After this period the tussock tundra community provided the highest biomass of shrubs.

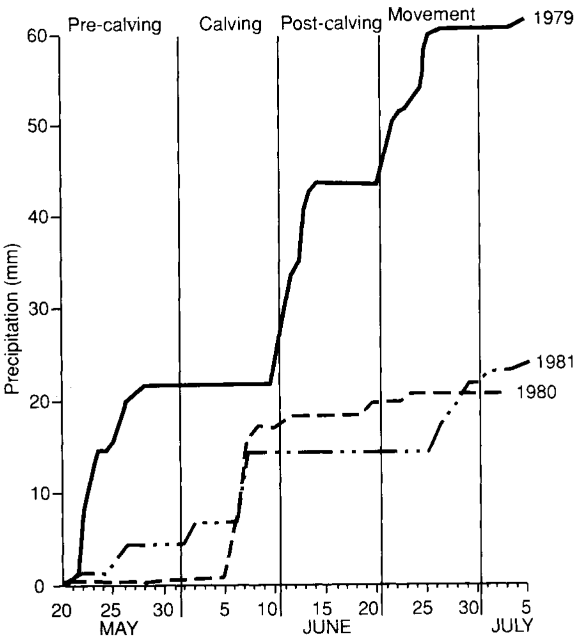

Figure 3.8. Cumulative precipitation recorded on the Porcupine caribou calving grounds, 1979-81.

Shrub biomass within wet sedge range types compared favourably to that measured in the Alaskan portion of the calving ground (Robus 1981) and both of these areas appear to have considerably higher *Salix* biomass than the calving grounds of the Western Arctic Herd (Kuropat 1984).

Table 3.1. New green biomass (g/m²) on the Yukon calving grounds of the Porcupine Caribou Herd, 1980.

Plant group	Collection date					
	23 May	7 June	14 June	25 June	5 July	12 July
Lichens	9.00[1]	21.17	9.73	14.39	13.30	17.84
Horsetails	-	0.09	0.03	1.03	0.97	0.88
Graminoids	3.40	7.35	19.23	30.02	32.18	34.47
Deciduous shrubs	-	0.78	4.13	20.15	23.92	46.55
Evergreen shrubs	41.78	46.21	50.83	64.41	69.56	69.56[2]
Forbs	0.23	1.30	2.45	7.88	13.79	10.46

1: weighted value reflected those communities snowfree on this date

2: adjusted value to reflect previous collection period (note low value recorded 12 July for tussock meadow community in Table 3.3c)

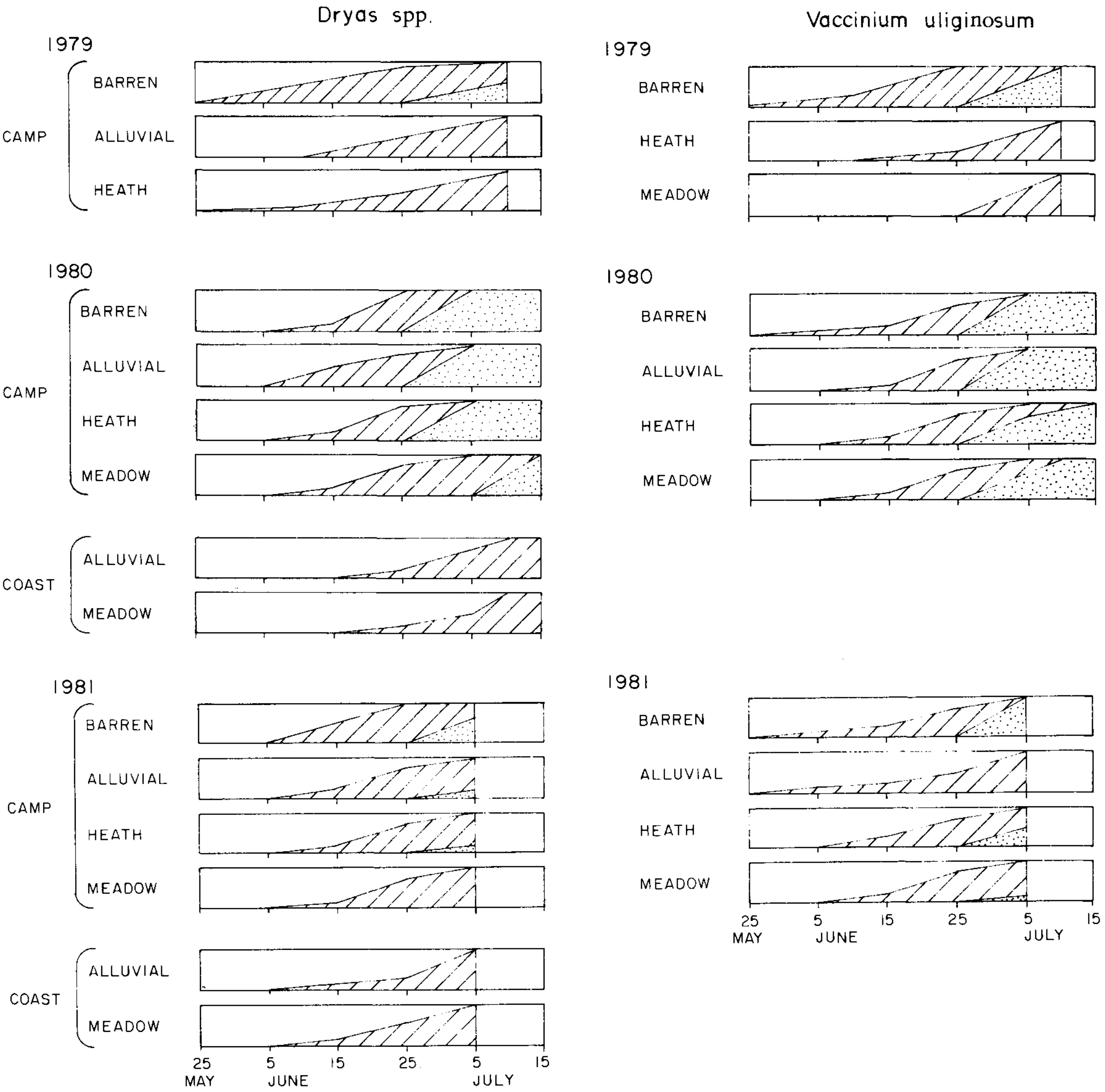

Figure 3.9. Phenological changes in key species over the three years of the study. Hatched area is proportion of sample flovering; stippled area is proportion in seed.

Tussock density

Eight stands were sampled to determine characteristics of tussocks in the study area; 4 in 1980, chosen to represent the wide range of tussock meadow communities, and 4 in 1981, chosen in large extensive meadows close to and on the coastal plain region. Stands sampled in 1980 tended to contain taller tussocks, with a lower heath component (except Stand 1) and fewer flower heads per tussock (except Stand 3, Table 3.4).

Within each stand, variables measured proved, at best, weakly correlated with the number of flowers produced per tussock (Table 3.5). Diameter and percent heath were the best predictors. Percent of the tussock grazed by microtines was significantly correlated to number of flowers in stand 6. Using multiple regression, the best model only accounted for 27% of the variability of total flowers (Stand 6, Table 3.6).

None of the stands chosen exhibited a strongly clumped distribution of tussocks; three (stands 1, 3, 4) tended to be uniformly distributed (based on an index of non-randomness of greater than 1.0, Table

Table 3.2. Percent coverage of range types on the calving grounds of the Porcupine Caribou Herd as determined from aerial photographs. Total area mapped (ha) in parentheses.

	Camp 1 (2563)	Camp 2 (3964)	Total (6527)
Alluvial gravel	2.8	4.1	3.6
Alluvial willow	0.8	2.6	1.9
Alluvial heath	3.7	15.4	10.8
Wet sedge meadow	1.4	8.0	5.4
Tussock meadow	32.5	53.3	45.2
Sedge heath	4.2	3.6	3.8
Dwarf shrub heath	13.4	4.6	8.1
Alpine barren	41.0	8.4	21.2

3.7, Pielou, 1977) while the rest tended to be slightly clumped (index less than 0.8). Bachelor's (1971) method of estimating density is not designed for stands with a uniform or close to uniform distribution of attributes. All of our estimates of tussock density, therefore, were based on all points sampled and varied between 1.62 m^{-2} (stand 1) to 5.89 m^{-2} (stand 8, Table 3.7). All stands sampled in 1981 contained a higher density of tussocks then those sampled in 1980.

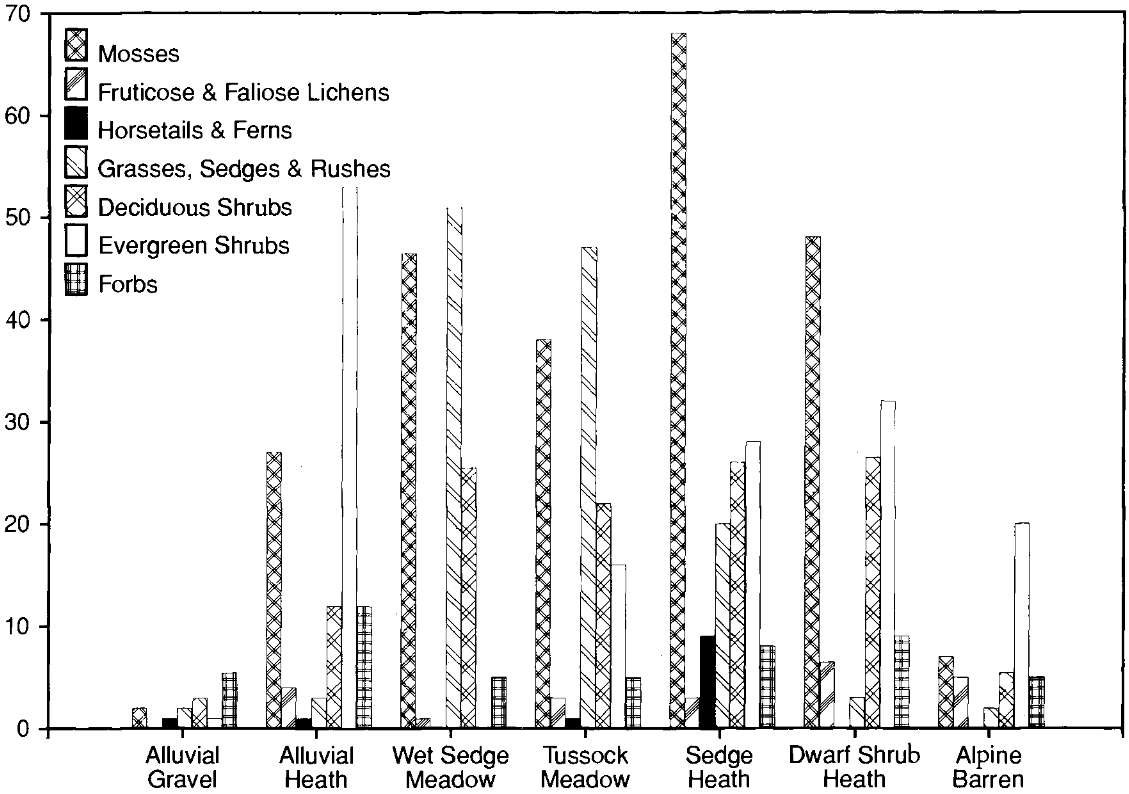

Figure 3.10. Physiographic composition of the seven range types encountered on the study area. Range type eight, *alluvial willow* was not sampled.

Table 3.3. New green biomass (g/m^2) in different range types on the calving grounds of the Porcupine Caribou Herd in northern Yukon, 1980.

Plant group	Collection date					
Alluvial heath						
	6 June	16 June	24 June	3 July	12 July	
Lichens	18.20	7.51	15.78	18.23	6.25	
Horsetails	0.15	–	–	0.22	–	
Graminoids	0.83	0.21	5.38	3.12	3.12	
Deciduous shrubs	–	2.11	26.32	13.31	39.00	
Evergreen shrubs	8.05	9.66	43.59	36.08	39.60	
Forbs	1.57	0.39	6.59	25.12	14.87	
Wet sedge meadow						
	6 June	16 June	24 June	3 July	12 July	
Lichens	9.26	–	3.15	3.71	17.04	
Horsetails	0.29	–	–	–	–	
Graminoids	21.87	57.23	70.88	65.48	91.48	
Deciduous shrubs	–	8.88	19.23	32.30	66.40	
Evergreen shrubs	0.37	–	0.54	5.88	–	
Forbs	0.18	0.23	5.47	9.47	1.35	
Tussock meadow						
	23 May	7 June	14 June	25 June	5 July	12 July
Lichens	7.31	22.59	8.36	10.51	8.19	18.87
Horsetails	–	–	–	–	–	–
Graminoids	7.12	11.45	31.24	49.83	54.22	56.05
Deciduous shrubs	–	–	6.03	30.57	39.87	76.77
Evergreen shrubs	87.41	83.30	82.93	86.10	93.49	22.68
Forbs	0.48	–	0.29	2.83	7.55	8.76
Sedge heath						
	9 June	14 June	27 June	6 July	13 July	
Lichens	3.73	5.56	–	4.28	0.06	
Horsetails	–	0.78	25.05	20.64	20.55	
Graminoids	7.98	10.86	18.92	18.08	34.71	
Deciduous shrubs	0.22	3.94	4.56	12.55	9.01	
Evergreen shrubs	10.48	44.05	11.47	39.41	28.99	
Forbs	3.22	6.28	10.31	12.50	8.80	

(Table 3.3. cont.d.)

Dwarf shrub heath

	9 June	18 June	26 June	6 July	13 July
Lichens	25.94	11.03	12.40	6.13	16.80
Horsetails	0.68	–	–	1.18	0.46
Graminoids	0.72	2.28	2.94	9.99	4.15
Deciduous shrubs	9.08	0.98	12.76	11.32	14.17
Evergreen shrubs	23.45	22.07	49.59	67.22	75.56
Forbs	4.27	4.14	21.32	22.43	22.24

Alpine barren

	8 June	18 June	27 June	6 July	14 July
Lichens	24.15	16.58	28.26	28.63	25.49
Horsetails	–	–	–	–	0.01
Graminoids	0.67	1.64	2.31	2.62	1.55
Deciduous shrubs	–	1.13	0.77	0.14	–
Evergreen shrubs	13.53	28.58	60.61	58.47	60.55
Forbs	2.76	7.35	14.41	19.44	10.03

Our tussock densities were consistent with those measured in other studies in the region. Shaver *et al.* (1986) determined that microsite or broad regional differences in *Eriophorum* flower production were less significant than annual differences. 1981 and 1983 were above average everywhere while 1980 and 1982 were below average everywhere. Kuropat (1984) found that on the calving grounds of the Western Arctic Herd, *Eriophorum* inflorescent density averaged 23.2 in 1977 and 22.7 flowers per m^2 in 1978. This compares with 13.6 in 1980 and 48.9 flowers per m^2 in 1981 in this study.

Table 3.4. Summary of tussock variables for the eight stands sampled on the calving grounds of the Porcupine Caribou Herd.

Variable	Stand								
	1	2	3	4	5	6	7	8	All ± SE
Sample size	261	300	297	297	300	300	300	300	2355
Diameter (cm)	30.8	26.8	28.4	28.2	26.8	23.4	22.5	25.3	26.4 ± 0.17
Height (cm)	18.7	20.4	18.9	20.4	15.0	11.3	13.8	16.5	16.8 ± 0.14
% heath	37.1	18.8	13.9	16.4	39.2	29.2	37.0	37.4	28.5 ± 0.54
% grazed	0.1	0.5	0.2	0.0	3.1	9.0	9.1	9.4	4.0 ± 0.25
Flowers	1.9	4.0	10.0	5.2	12.7	8.2	6.5	11.2	7.6 ± 0.19

Table 3.5. Correlation of variables measured during estimation of tussock density to the total number of flowers per tussock.

Variable	Stand 1	 2	 3	 4	 5	 6	 7	 8
Diameter		*	***	***	***	***		**
Height	***	**					***	***
% heath[1]	***	**	**	**	***	***	***	***
% grazed[1]						**		

1: negative correlation
* $p<0.05$ ** $p<0.01$ *** $p<0.001$

Table 3.6. Results of stepwise multiple regression and r^2 at inclusion of independent variable in the prediction of number of flowers.

	Variable		
Stand	1	2	3
1	Heath (0.05)	Height (0.09)	
2	Height (0.08)	Heath (0.11)	Diameter (0.13)
3	Diameter (0.13)	Heath (0.15)	
4	Diameter (0.06)	Height (0.13)	
5	Heath (0.17)	Diameter (0.23)	
6	Heath (0.11)	Diameter (0.25)	Grazed (0.27)
7	Heath (0.11)	Height (0.19)	
8	Diameter (0.09)	Heath (0.17)	Height (0.20)

Table 3.7. Estimate of tussock density, probable limit of error and Pielou's Index of Nonrandomness for the eight stands sampled.

Stand	Number of points	Density	Probable limit of error	Pielou's index
1	86	1.62	0.543	3.22
2	99	3.13	0.134	0.63
3	98	2.56	0.316	1.90
4	97	2.60	0.254	1.01
5	100	4.74	0.150	0.77
6	100	5.10	0.158	0.82
7	100	5.29	0.154	0.79
8	100	5.89	0.138	0.72

Nutrients

Appendix A describes the characteristics of plants collected for nutrient analysis in 1980 while Appendix B details the fibre, ash and nutrient content of the samples. General trends are evident if we use *Cetraria cucullata*, *Eriophorum vaginatum*, *Salix pulchra*, *Vaccinium vitis-idaea*, and *Pedicularis kanei* as representative of the various plant groups. The proportions of lignin, cellulose and the ADF fraction increased later in the season while the proportions of nitrogen and phosphorus declined (Table 3.8). Total ash and NDF remained relatively constant (Table 3.8). The pattern and quantity of lignin reported for lichens is somewhat surprising since lichens do not contain lignin and this value must reflect an index of plant hardening in the analysis process. Lichens were characterized by low values for ADF, nitrogen, cellulose and phosphorus and high values for total ash. Graminoids contained high NDF, ADF and cellulose fractions, while deciduous shrubs exhibited high values for nitrogen and phosphorus early in the season and high lignin values later. *Vaccinium*, representing evergreen shrubs, showed the least seasonal variation in NDF, ADF, lignin and cellulose, with relatively low values for nitrogen throughout the sampling period. Forbs contained relatively high nitrogen and phosphorus and low NDF values throughout the season.

The magnitude of and trends in nutrient concentrations compare well with similar studies in areas to the west in northern Alaska (Robus 1981; Whitten and Cameron 1980; and Kuropat 1984; White *et al.* 1975). From our data it would seem that evergreen shrubs could prove to be a valuable constituent

Table 3.8. Fiber, ash and nutrient content (% dry weight) of key species collected in 1980.

Plant group *	Date	Fiber				Ash		Nutrients	
		NDF	ADF	Lignin	Cellulose	Residual	Total	Nitrogen	Phosphorus
Lichens	Pre-calving								
	Calving	31.8	5.2	4.0	1.2	0	11.7	0.4	0.1
	Post-calving	28.5	4.5	2.0	2.0	0.4	14.0	0.4	0
	Movement	28.9	5.6	3.0	2.0	0.9	13.1	0.4	0
	Early summer ..	30.9	6.4	5.0	1.0	0.4	12.8	0.4	0
Graminoids	Pre-calving	56.6	19.2	1.6	17.1	0.4	4.1	3.1	0.5
	Calving	58.2	19.6	1.7	17.1	0.8	4.2	2.5	0.4
	Post-calving	64.3	23.6	1.3	22.2	0.0	3.4	2.1	0.3
	Movement	64.1	25.4	2.1	23.0	0.4	3.3	2.2	0.3
	Early summer ..	63.3	27.6	3.5	23.8	0.3	3.4	1.9	0.3
Deciduous shrubs	Pre-calving								
	Calving								
	Post-calving	12.9	12.6	4.5	6.4	1.7	5.0	4.8	0.7
	Movement	16.6	14.8	6.3	7.3	1.2	4.2	3.9	0.4
	Early summer ..	19.4	15.0	5.7	9.3	0.0	3.6	2.5	0.2
Evergreen shrubs	Pre-calving	28.6	20.8	4.4	15.8	0.6	2.7	0.9	0.1
	Calving	30.0	20.4	6.4	13.7	0.3	2.4	0.9	0.1
	Post-calving	30.7	18.7	5.4	13.3	0.1	2.6	0.9	0.1
	Movement	31.3	18.6	5.5	13.4	0.0	2.5	0.9	0.1
	Early summer ..	33.7	21.1	6.3	14.8	0.0	2.6	0.9	0.1
Forbs	Pre-calving								
	Calving	17.5	14.1	2.5	11.3	0.4	7.1	3.5	0.5
	Post-calving	19.8	13.7	6.7	7.0	0.0	6.7	3.2	0.4
	Movement	20.2	15.7	3.8	11.5	0.4	6.6	2.7	0.4
	Early summer ..	37.5	23.0	3.0	19.7	0.2	5.1	3.6	0.3

* Lichens : *Cetraria cucullata;* Graminoids : *Eriophorum vaginatum* flowers; Deciduous shrubs : *Salix lanata* leaves; Evergreen shrubs : *Vaccinium vitis-idaea* leaves; Forbs : *Pedicularis kanei* flowers

of the diet in late spring, being high in biomass and cell solubles (100 – NDF). However, Kuropat (1984), points out that the leaves of evergreen shrubs can contain high levels of secondary compounds. These compounds can bind with endogenous and microbial protein and may cause an inhibition of rumen function, toxicity and/or lowered digestibilities (Trudell and White 1981). Kuropat and Bryant (1980) provide us with information on the trends and magnitudes of secondary compounds in the major plant groups, an aspect of forage chemistry that we did not document in our study. They found that new inflorescences and leaves (particularily *Salix*) were poorly defended by toxic compounds. They argue that the subsequent increase in concentration of secondary compounds and decline in nitrogen and phosphorus, require caribou to seek early phenological stages in plants.

Summary

The pre-calving to movement periods are by far the most dynamic time of the year in terms of nutrient dynamics within the calving grounds of the Porcupine Caribou Herd. Parturient females arrive on the calving grounds when a significant portion of the area is still covered with snow, when available nutrients are scarce and when they are at an energetic low in their annual energy and nutrient reserves. As well, once they have calved, the energetic demands of the animal are very high due to lactation.

Thus, calving occurs just prior to the period of maximum growth and nutrient dynamics in the vegetation. As we have documented, most changes in the vegetation occur between 4 June and 24 June, during the two week period after the peak of calving. The region chosen for the majority of calving in the Yukon, as represented by our study area, offers a diverse complex of range types from the alpine barren communities to wet sedge meadows, damping the between year extremes in timing of snowmelt and phenological development.

Within each range type habitat quality was a function of species composition, forage biomass, phenological development, and nutrient quality. In late May, snowmelt pattern and topography determined which range types offered potential forage. Digestible solubles were generally restricted to lichens, best provided by the alpine barren communities. Nitrogen sources were scarce until early June. Between 4 and 14 June graminoids were the best available source of both cell solubles and nitrogen. Thus the tussock tundra communities became the best range type to use. Between 14 and 24 June the emergence of deciduous shrubs and the declining importance of graminoids reduced the importance of tussock tundra. Although lower in biomass, the highly digestible, nitrogen-rich forb species gained in importance in the latter part of June, thus elevating the importance of heath type communities.

During the three years of this study, 1980 stood out as being advanced phenologically due to higher than average temperatures throughout the study period. Consistent with previous work in Alaska we observed an interesting carry-over effect of that good year; the apparent abundance of *Eriophorum* flowers in the next year. Shaver *et al.* (1986), also noted a good flowering year in 1981 and speculated that since flower setting occurred early in *Eriophorum*, the weather in the previous year may play an important role in determining flowering density in any given year. This carry-over effect can have important implications for the well-being of parturient females. In 1981, when *Eriophorum* flowering was high in spite of cool temperatures in May and early June, the density of flowers probably reflected the favourable conditions in 1980.

Habitat selection

Methods

We divided the area of each camp location into eight range types (Russell *et al.* 1992a), and determined the proportion of each type by plotting on aerial photographs (Table 3.1). During 15 minute scan observations, the habitat type occupied by the animals observed was recorded. Preference for a particular type

Table 3.9. Percent of animals observed in the eight range types on the Yukon calving grounds of the Porcupine Caribou Herd, 1979–81.

Period	Tussock meadow	Wet sedge meadow	Sedge heath	Dwarf shrub	Alpine barren	Alluvial heath	Alluvial gravel	Alluvial willow	Total caribou observed
1979									
Pre-calving	19.7	4.1	4.8	8.0	1.7	60.9	0.9	–	4823
Calving	17.6	0.9	23.2	4.6	2.7	46.6	4.4	–	2949
Post-calving	10.5	18.6	54.5	9.6	0.3	5.7	0.7	0.2	8095
Movement	12.0	0.1	23.4	38.8	12.4	13.2	–	–	4240
1980									
Pre-calving	87.9	1.6	2.3	0.4	1.2	6.5	0.3	–	39008
Calving	51.8	0.8	10.2	1.4	2.5	30.7	2.3	0.2	13134
Post-calving	38.4	29.7	20.6	0.5	0.1	9.1	1.1	0.5	60422
Movement	–	58.9	–	–	–	37.6	3.6	–	6515
1981									
Pre-calving	72.4	3.1	–	2.3	–	21.7	0.5	0.1	23973
Calving	80.1	8.8	–	2.4	–	8.2	0.4	0.1	4668
Post-calving	13.2	39.4	–	–	–	32.9	13.7	0.9	2774
Movement	31.6	56.9	–	–	–	2.2	1.2	8.2	1560

was calculated as the ratio (use-availability)/(use+availability). In 1980, when observations were made at both camp locations the contribution of each camp to the index was proportional to the number of animals observed. The biophysical characteristics in the location of the observations also were recorded (Appendix C).

Results and discussion

Over 50 percent of the animals used the tussock meadow community in each of the three years of the study (Table 3.9). Wet sedge meadows, alluvial heath and sedge heath were used by over 10 % of the animals (Table 3.9). In all years tussock meadows received the most use in the pre-calving and calving periods, declining later in June. Wet sedge meadows were used primarily in the post-calving and movement periods. Use of alluvial heaths showed no consistency (Table 3.9). Alluvial willows and alpine barren types were seldom used.

Selection for or against any community type was determined for all periods of the study (Table 3.10). In 1979, animals selected alluvial heath and sedge heath communities throughout the study period. They showed a strong preference for wet sedge meadows in the post-calving period and for dwarf shrub heaths in the movement period. In 1980, tussock meadows and sedge heaths were the only communities favoured from the pre-calving to the post-calving periods. Wet sedge meadows were strongly selected in the post-calving and movement periods in both 1980 and 1981. In 1981, tussock meadows continued to be preferred in the pre-calving and calving periods. Throughout the study alluvial willows and alpine barrens were strongly avoided by caribou.

Phenologically, 1980 was the most advanced year and 1981 the most retarded. Density of *Eriophorum* flowers was greatest in 1981. These observations may help explain the early preference for tussock tundra communities in 1980 and 1981. The tussock tundra communities, although least advanced phenologi-

Table 3.10. Habitat preference of animals observed in the eight range types on the calving grounds of the Porcupine Caribou Herd, 1979–81.

Period	Tussock meadow	Wet sedge meadow	Sedge heath	Dwarf shrub	Alpine barren	Alluvial heath	Alluvial gravel	Alluvial willow
1979								
Pre-calving	–0.25	0.48	0.06	–0.25	–0.92	0.89	–0.52	–1.00
Calving	–0.30	–0.23	0.69	–0.49	–0.88	0.85	0.22	–1.00
Post-calving	–0.51	0.85	0.86	–0.17	–0.99	0.21	–0.60	–0.60
Movement	–0.46	–0.87	0.69	0.49	–0.54	0.56	–1.00	–1.00
1980[1]								
Pre-calving	0.32	–0.55	0.25	–0.90	–0.89	–0.26	–0.84	–1.00
Calving	0.06	–0.75	0.45	–0.70	–0.78	0.47	–0.22	–0.81
Post-calving	0.08	0.68	0.69	–0.88	–0.99	–0.10	–0.53	–0.59
Movement	–1.00	0.83	–1.00	–1.00	–1.00	0.55	–0.00	–1.00
1981								
Pre-calving	0.15	–0.44	–1.00	–0.33	–1.00	0.17	–0.78	–0.90
Calving	0.20	–0.05	–1.00	–0.31	–1.00	–0.30	–0.82	–0.90
Post-calving	–0.60	0.66	–1.00	–1.00	–1.00	0.36	0.54	–0.36
Movement	–0.26	0.75	–1.00	–1.00	–1.00	–0.75	–0.55	0.62

Note: preference was determined as (use-availability)/(use+availability)

1: in 1980 availability was calculated as the average of the two camps, weighted by the number of animals observed at each camp.

cally compared to other range types in any given year, offer the highest concentration of cell solubles and nitrogen in the pre-calving and calving period. In 1980 this community was well advanced and used early by the caribou. In 1981, the unusually abundant *Eriophorum* inflorescences, along the edge of the retreating snow, may have attracted the large numbers of caribou observed.

In 1979, alluvial heaths were much more preferred in the pre-calving and calving period, perhaps due to the unavailability of the tussock meadow type (due to snow cover) and the abundance of lichens and mosses in this heath type.

Although the alpine barren community contains relatively high biomasses of lichens, its low relative use in the early part of the season may be due to the lack of other vegetative cover in this type. Caribou must be able to maintain a full rumen and if little else is available will fill the rumen with poorly digestible forage types such as moss. The alpine barren community (*Dryas/Vaccinium uliginosum*) contains only 4% cover of moss and only 31% cover of total vegetative matter.

Another reason for not utilizing lichens in the alpine barrens may be the low moisture content. Trudell and White (1981) reported an avoidance of sites with dry lichens, even though lichens formed a major constituent in the diet of their animals. They attribute this avoidance to severe lip abrasion from ingesting dry lichens.

In the post-calving and movement periods, the preference for wet sedge meadows may be associated with the abundance of freshly flushing willow and the emergence of young basal shoots of *Eriophorum angustifolium* and *Carex aquatalis*, a species which reaches its greatest abundance in wet sedge communities.

The early season use of tussock meadow communities has been documented in most range studies of caribou in spring and early summer (Skoog 1956; Lent 1966; Kelsall 1968; White *et al.* 1975; Kuropat 1984). The traditional calving grounds of the Western Arctic Herd contain a complex of vegetation types similar to those we have described, though our study area contained more alpine barren and less tussock meadow (Kuropat 1984). Kuropat (1984) reported that, following anthesis of *Eriophorum*, caribou moved from the lowland tussock communities to drier upland meadows to take advantage of new forb growth, particularly *Lupinus*. When *Salix* leaves began to unfold, they shifted to the lowland wet meadows, high in *Salix* biomass. We also noted a shift to wet meadows following the calving period in all years except movement period 1979.

The avoidance of the alluvial willow community may be a result of predator avoidance. Other authors have noted the reluctance of caribou to enter tall willow communities, which provide excellent ambush cover for wolves and grizzlies (Roby 1978; Boertje 1981; Kuropat 1984). The avoidance of the alluvial willow type also may be related to the poorer quality of willow leaves in these communities compared to those species present in the meadows (*Salix pulchra* versus *S. glauca* and *S. alexensis*).

Food habits

Methods

We collected composite fecal samples throughout the study area during five life cycle periods over the three years; precalving (n=7), calving (n=4), post-calving (n=5), movement (n=4) and early summer (n=5). The methods of analysis of fecal fragments and statistical treatment of the data were described earlier. We submitted two identical samples for analysis on four separate occasions and four replicates on one occasion.

Results

Effect of analysis at different times
The frequency of discerned plant fragments in replicates analysed at one time compared with those sampled at different times was significantly different for deciduous shrubs in the 1979 sample (Table 3.11). For most species, samples analysed at different times tended to have a much higher coefficient of variation than those analysed at the same time. This was particularly true for moss (1979 and 1980), *Eriophorum* (1979), deciduous shrubs (1979) and evergreen shrubs (1979 and 1980). Only *Cladonia*-type lichens, *Dryas* and forbs showed relatively similar coefficients of variation. They are therefore the only foods that can be statistically compared with confidence between times of analysis (Table 3.11).

Differences between periods
Several significant differences occurred between periods. Moss, *Vaccinium*, and *Eriophorum* were significantly higher in pre-calving and calving than in later periods, while lichens and *Equisetum* were significantly higher in pre-calving compared to post-calving, movement and early summer. *Dryas* was significantly higher in the pre-calving period than all other periods and *Salix* was significantly higher after the calving period (Table 3.12).

Differences among years
Recognizing the limitations of comparing samples analysed at different times, we did note some striking differences among years for some of the plant groups. Graminoids comprised over 30% of the fecal fragments from the pre-calving to the movement period in 1981, but were virtually absent from the diet after the calving period in the other two years (Table 3.13). Deciduous shrubs did not become the dominant component in fragments until the movement period in 1981, compared to the post-calving period in the other two years. In 1980, moss was represented in over 50% of fragments in the pre-calving and calving period, nearly twice as often in the other two years.

Table 3.11. Average percentages and coefficients of variation (CV) of discerned plant fragments in replicates of caribou fecal samples that were analysed at one time (O) and replicates that were analysed at different times (D).

	21–28 May 1979					28 May 1980				
	Mean		CV		Ratio	Mean		CV		Ratio
Plant genus or group	O	D	O	D	CV(D)/ CV(O)	O	D	O	D	CV(D)/ CV(O)
Moss	13.5	30.9	13.8	60.4	4.4	27.1	25.6	18.0	50.4	2.8
Lichens	10.8	6.6	48.0	48.1	1.0	25.4	32.3	20.6	35.0	1.7
Cetraria-type	2.7	1.1	57.2	86.4	1.5	4.9	4.7	61.4	71.1	1.2
Cladonia-type	6.8	4.9	62.5	47.9	0.8	15.9	24.1	27.7	45.1	1.6
Stereocaulon	1.3	0.5	51.2	68.1	1.3	4.6	2.6	69.0	133.6	1.9
Peltigera	–	0.2	–	206.3	–	–	1.0	–	123.4	–
Horsetails	8.6	9.1	33.8	58.4	1.7	20.9	11.4	39.3	32.6	0.8
Graminoids	12.3	18.5	17.3	36.7	2.1	9.4	12.6	37.4	36.5	1.0
Carex	4.0	2.2	74.5	123.4	1.7	1.3	2.9	16.1	81.5	5.1
Eriophorum	7.4	16.0	15.3	58.5	3.8	7.5	9.0	38.5	47.0	1.2
Deciduous shrubs*	42.6	14.7	16.1	107.4	6.7	5.3	4.1	33.3	59.7	1.8
Evergreen shrubs	11.3	19.6	23.0	61.2	2.7	10.5	12.6	16.7	50.3	3.0
Dryas	6.0	5.3	28.7	26.0	0.9	1.7	4.0	53.0	43.6	0.8
Vaccinium	5.0	14.1	36.2	92.6	2.6	7.0	7.6	38.3	62.5	1.6
Total shrubs	53.8	34.4	8.7	58.3	6.7	15.9	16.7	4.6	26.0	5.7
Forbs	1.0	0.5	106.4	67.6	0.6	1.3	1.4	94.9	75.4	1.3
Total vascular	74.9	62.5	6.8	25.8	3.8	47.5	42.1	14.5	4.3	0.3

Significant differences between means indicated by an asterisk (*=$p<0.005$).

Fecal sample versus ingested diet

Fecal samples from Duquette's trials using a summer diet similar to that observed in this study and analysed in Colorado were used to assess the over or under estimation of certain components of the summer diet. Compared with actual ingested diet, fecal analysis significantly under- estimated lichens, mushrooms and forbs while over-estimating deciduous shrubs (Table 3.14). The apparent high digestibility of forbs probably influences the estimation of the other components of the diet. Therefore, to correct the diet to better reflect actual intake, we applied correction factors to lichens and to evergreen and deciduous shrubs and assigned the remaining portion of the diet (to add to 100%) to forbs (Table 3.15). These correction factors were based on regressions of actual versus fecal-estimated diet for both summer and winter trials.

Discussion

The progression of diet change over the five periods measured in this study indicate that the caribou are rapidly changing diet as the quantity and quality of foods change. Between year comparisons indicate that the animals are taking advantage of annual variations in forage as well. In an average year, when the pregnant cows reach the calving grounds, many of the communities are unavailable due to snow cover, especiallly the widespread tussock tundra community. The objective at this time of year is to fill the rumen with whatever is digestible, and if digestible forage is unavailable, to fill the rumen with anything else. Thus we see the use of lichens, evergreen shrubs and mosses in the pre-calving and calving period in

Table 3.12. Average percentages (±SE) of discerned plant fragments collected from the calving grounds of the Porcupine Caribou Herd, 1979–81

			Season		
Species name	Pre-calving	Calving	Post-calving	Movement	Early July
	n = 7	n = 5	n = 5	n = 4	n = 5
Moss	32.4±8.19	49.5±8.78	5.6± 4.56	0.3±0.14	–
Selaginella	8.9±2.13	4.6±0.95	1.0± 0.50	0.1±0.07	0.1±0.05
Total mosses	41.3±7.06	49.1±7.85	6.5± 5.02	0.5±0.17	0.1±0.05
Cetraria-type	1.7±0.99	0.4±0.20	0.1± 0.13	–	<0.1±0.04
Cladonia-type	7.8±3.49	1.2±0.66	0.2± 0.12	–	0.1±0.08
Total lichens	10.8±4.81	2.0±0.84	0.5± 0.24	–	0.1±0.09
Equisetum	2.6±1.05	0.7±0.31	0.3± 0.34	0.2±0.08	<0.1±0.04
Total horsetails and ferns	2.6±1.05	0.7±0.31	0.3± 0.34	0.2±0.08	<0.1±0.04
Carex	2.3±0.78	2.5±1.34	0.9± 0.47	0.3±0.32	0.2±0.10
Eriophorum	17.2±5.17	20.7±9.71	6.8± 6.67	1.3±0.75	0.1±0.05
Total graminoids	20.0±4.77	23.9±8.09	7.7± 7.08	1.6±0.66	0.4±0.07
Salix	5.0±1.58	6.8±3.24	80.0±13.72	96.3±1.50	98.0±0.22
Total deciduous	5.0±1.58	6.8±3.24	80.1±13.71	96.3±1.50	98.0±0.22
Dryas	4.4±0.76	0.9±0.48	1.3± 0.90	0.6±0.54	0.7±0.11
Vaccinium	14.7±6.11	16.0±4.51	2.8± 1.52	0.9±0.40	0.5±0.17
Total evergreen shrubs	19.7±6.17	16.9±4.50	4.1± 1.87	1.6±0.91	1.2±0.22
Total shrubs	24.7±5.24	23.7±3.22	84.2±12.39	97.8±0.65	99.2±0.23
Total forbs	0.6±0.17	0.7±0.31	0.8± 0.39	0.1±0.06	0.2±0.11
Total vascular content	47.9±6.54	48.9±8.34	93.0± 5.23	99.5±0.17	99.8±0.10

1: *Sphagnum, Peltigera, Stereocaulon, Arctagrostis, Dupontia, Festuca, Luzula, Poa, Ledum, Artemisia, Astragalus, Draba, Lupinus, Saxifraga,* and unknown forbs occurred at average frequencies of less than 1.0 % in some seasons.

most years. In 1979, a normal to poor year for *Eriophorum* flower production, animals utilized the most available digestible forage, lichens and ingested significant quantities of moss and evergreen shrubs. In 1980, with early phenological development, animals were able to utilize a wider variety of forage types, including early flowering *Eriophorum* and deciduous shrubs. The relatively high moss intake recorded in the pre-calving and calving period in 1980 may indicate that the animals were selecting roughage to offset the highly digestible forage available early in the season. In 1981, with the excellent production of *Eriophorum*, animals quickly focussed on graminoids, evergreen shrubs and moss.

As snow melts, the first component of fresh vegetation is the heads of *Eriophorum*, high in cell solubles, nitrogen and phosphorus and with significant biomass. Other forage such as forbs are of high quality but scarce early in the season. In 1981, a year of very abundant flowering of *Eriophorum*, caribou ate the heads of this species early in the pre-calving period and continued its use longer than in 1979 and 1980.

As deciduous shrubs and forbs become more available, animals quickly shift to the freshly unfurled leaves of *Salix*. These leaves are high in digestible cell solubles, phosphorus and nitrogen at a time when these components in the *Eriophorum* heads are rapidly declining in value. In 1980, a year of early snowmelt and advanced phenology, caribou began shifting to *Salix* in the calving period compared to a shift in the post-calving period in 1981. Deciduous shrubs and probably forbs (based on corrected diet, Table 3.15), remain the main component of the diet into July as the sequential leafing and blooming of different species of these plant groups become available.

Table 3.13. Annual differences in the major food types based on discerned plant fragments for the Porcupine Caribou Herd, 1979–81.

Study period	n	Plant group Graminoid	Lichen	Forbs	Deciduous Shrub	Evergreen Shrub	Moss	Horsetail
1979								
Precalving	1	11.4	31.4	0.6	1.2	22.0	22.9	8.7
Calving	–	–	–	–	–	–	–	–
Post-calving	1	0.4	0.6	0.1	97.5	1.1	0.3	0.0
Movement	–	–	–	–	–	–	–	–
Early summer	1	0.6	0.4	0.6	97.0	0.9	0.1	0.0
1980								
Pre-calving	4	15.1	8.6	0.6	8.3	11.3	54.0	2.1
Calving	2	9.9	1.9	1.1	12.4	11.6	61.9	1.1
Post-calving	4	1.0	0.6	0.9	90.3	3.7	2.1	0.6
Movement	2	0.8	0.1	0.1	97.9	0.7	0.5	0.0
Early summer	4	0.4	0.1	0.1	98.1	1.3	0.1	0.1
1981								
Pre-calving	2	34.1	3.8	0.8	0.4	35.3	25.3	1.0
Calving	2	37.8	2.1	0.3	1.2	22.1	36.3	0.3
Post-calving	1	36.2	1.3	1.3	27.3	8.1	26.1	–
Movement	2	2.4	0.0	0.0	94.6	2.5	0.4	0.2
Early summer	–	–	–	–	–	–	–	–

Table 3.14. Average percentages of actual intake and average percentages of discerned plant fragments in fecal samples from feeding trials on captive caribou and reindeer at the University of Alaska in 1982 by L. Duquette.

Plant group	Actual intake x̄ ± SD(range)n=8	Fecal estimate x̄ ± SD(range)n=8	Correlation coefficient*
Moss[1]		0.3	–
Lichens[2]	18.1 ± 4.8(14–28)	4.8 ± 1.5	0.72
Mushrooms	3.1 ± 0.6 (2–4)	0	–
Graminoids[3]	5.4 ± 2.9 (2–11)	3.4 ± 2.4	–0.54
Deciduous shrubs[4]	43.1 ± 2.5 (41–47)	90.3 ± 2.8	–0.74
Evergreen shrubs[5]	2.5 ± 0.5 (2–3)	1.2 ± 0.8	–0.12
Forbs[6]	27.6 ± 2.6 (22–30)	<0.1 ± 0.1	–

1: *Hylocomium splendens*; 2: *Cladina stellaris, C. rangiferina, Cetraria nivalis*, 3: *Bromus, Carex aquatilis*; 4: *Salix alexensis, S. lanata*; 5: *Vaccinium vitis-idaea*; 6: *Epilobium latifolium, Medicago falcata, Trifolium repens.*
* $p<0.05$

Table 3.15. Adjusted diet of the Porcupine Caribou Herd, adjustment based on correction factors derived from Table 3.14.

Plant group	Pre-calving	Calving	Post-calving	Movement	Early July
Moss	41	49	6	<1	<1
Lichens	27	15	13	12	13
Horsetails	3	1	<1	<1	<1
Graminoids	20	24	8	2	<1
Deciduous shrubs	1	1	38	46	47
Evergreen shrubs	9	8	3	2	2
Forbs	0	2	32	38	38

Regressions used;
Lichens (n=16) Actual = 12.44 + 1.33 estimate R=0.96
Evergreen shrubs (n=16) Actual = 1.91 + 0.34 estimate R=0.90
Deciduous shrubs (n=16) Actual = -1.2 + 0.49 estimate R=0.99
Forbs 1.00 – sum of rest.

Caribou activity

Methods

Scans – see methods described in Winter Activity budget section.

Focal animal – In 1980 and 1981 we watched focal animals to determine the individual variation in active and bedded cycles, nursing behaviour of the calves and to document how individuals partitioned their active time. Only complete active and bedded cycles were used in the analysis. Activity criteria follow from the activity scans. We further divide feeding into;

feed – standing in one place with head to the ground ingesting forage,
graze – head down ingesting forage while walking, and
search – head down or moving from side to side but not ingesting forage.

A successful suckle was considered any suckle lasting at least five seconds. Suckling duration and time between successful suckles were recorded.

Results

Band size

Mean band size weighted by period was 69.1 ± 15.01 (mean ± SE, Table 3.16). The maximum group size was generally in the movement period and the minimum in the calving period. In 1979, animals tended to stay in smaller groups until the movement period when considerable aggregation occurred.

Movement rate

Caribou tended to reduce their movement rate from pre-calving to the calving period and increase again after the post-calving period. Animals tended to have higher movement rates in 1980. The reduced rate in the pre-calving period for 1979 is noteworthy (Table 3.17).

Active and bedded cycles

Total cycle lengths (active + bedded) increased from the pre-calving to post-calving periods and then declined sharply in the movement periods, largely as a result of the significant decline in the active cycle length (Table 3.18).

Table 3.16. Group sizes of the Porcupine Caribou Herd during different periods of the life cycle, 1979–81.

Study period	Group size			
	n	Mean	SE	Range
1979				
Pre-calving	52	17.1	2.00	2 - 64
Calving	29	13.3	2.22	2 - 50
Post-calving	24	36.8	8.28	5 - 163
Movement – early July .	7	192.8	103.41	5 - 550
1980				
Pre-calving	73	77.5	9.61	6 - 442
Calving	61	30.9	4.34	6 - 232
Post-calving	59	142.3	28.53	8 - 1168
Movement	7	127.1	28.53	23 - 202
1981				
Spring migration	13	90.9	20.16	3 - 239
Pre-calving	25	73.8	22.51	8 - 578
Calving	18	37.9	5.51	4 - 110
Post-calving	7	31.0	9.75	5 - 81
Movement	5	85.4	28.99	14 - 152

Table 3.17. Movement rate of the Porcupine Caribou Herd based on scans from pre-calving to early July, 1979–81.

Study period	Movement rate (km/h)		
	n	Mean	SE
1979			
Pre-calving	278	0.20	0.031
Calving	177	0.20	0.029
Post-calving	232	0.20	0.028
Movement	19	0.45	0.171
Early July	15	0.31	0.131
1980			
Pre-calving	533	0.97	0.060
Calving	571	0.25	0.024
Post-calving	629	0.53	0.032
Movement	44	0.98	0.184
1981			
Spring migration	134	0.24	0.276
Pre-calving	187	0.59	0.077
Calving	168	0.24	0.043
Post-calving	109	0.25	0.073
Movement	35	0.40	0.145

Table 3.18. Summary of average active and bedded cycle lengths for the Porcupine Caribou Herd during the late spring - early summer, 1979-81.

Study period	Cycle lengths	
	Active (n, mean ± SE)	Bedded (n, mean ± SE)
Pre-calving	(13) 86 ± 8.0 a,b*	(29) 88 ± 5.6 a
Calving	(17) 99 ± 7.4 a	(37) 75 ± 5.4 a
Post-calving	(35) 102 ± 8.1 a	(55) 83 ± 3.9 a
Movement	(4) 42 ± 7.2 b	(7) 66 ± 8.6 a

* periods with the same suffix (a, b) are not significantly different.

Activity budgets

The proportion of time spent feeding declined from the pre-calving period through to the movement period. The magnitude of this decline was greatest in 1979 and least in 1980. In all years the proportion of time spent feeding was lowest in the movement period, but not significantly lower in 1980. In all years, the decline in feeding from post-calving to movement period was marked by a concurrent increase in the proportion of time spent walking. In 1979, the decline in feeding from pre-calving to calving was associated with an increase in lying time (Table 3.19). In 1980 and 1981, lying time increased from pre-calving to calving, while walking time decreased.

In 1979 and 1980 lying time increased from the pre-calving to the post-calving period, then declined in the movement period. The proportion of time spent walking declined from pre-calving to post- calving and increased in the movement period (Table 3.19). The proportion of time spent walking was notably low in the pre-calving period of 1979.

Focal animal observations

No significant differences were measured among the classes of adults. Within an active cycle, adults spent a significantly higher proportion of time grazing, while calves spent a higher proportion of their active time running (except post-calving) and standing (except pre-calving, Table 3.20). In the pre-calving period adults spent a significantly higher proportion of time walking while calves walked more in the post-calving period.

Adults spent a higher proportion of active time grazing in the calving and post-calving periods compared to the pre-calving period, and a higher proportion of time walking in the pre-calving period compared to the post-calving period. Calves spent the highest proportion of time grazing in the calving period and the lowest proportion in the pre-calving period, and all periods were significantly different from each other (Table 3.20). Feeding intensity (graze-search/100) was extremely high throughout the seasons (0.98 for adults and 0.99 - 1.0 for calves).

Due to their skewed frequency, the mean length of active and bedded cycles are misleading (Tables 3.21 and 3.22). The median lengths of the active and bedded cycles, probably a more appropriate measure, increased for both adults and calves from the pre-calving to the post-calving period (Tables 3.21 and 3.22). The most dramatic increase for both adults and calves was from the pre-calving to the calving period, possibly due to the pregnant females preparation to give birth and/or the constant interruption from nursing and the calves frequent nursing bouts (see next). Adults had much longer median active and bedded cycles than calves.

Nursing

We analysed 386 bouts of nursing behaviour involving 39 different individual calves. We noted a decline in bout frequency from pre-calving to post-calving (significant between pre-calving and calving) and

Table 3.19. Summary of activity budgets of the Porcupine Caribou Herd in late spring and early summer, 1979–81.

Study period	n	n	Activity	(mean±95%CL)			
	(groups)	(animals)	Feed	Lie	Stand	Walk	Trot
1979							
Pre-calving	52	4823	.58±0.042	.28±0.057	.03±0.006	.11±0.025	.01±0.008
Calving	29	2961	.48±0.061	.34±0.086	.02±0.006	.15±0.049	.02±0.011
Post-calving	24	8143	.44±0.045	.45±0.045	.01±0.005	.08±0.024	.01±0.013
Movement*	5	4240	.30±0.135	.20±0.084	<.01±0.001	.48±0.175	.02±0.022
1980							
Pre-calving	73	39015	.56±0.040	.20±0.082	.01±0.003	.23±0.063	<.01±0.000
Calving	61	13363	.54±0.055	.35±0.071	.01±0.003	.10±0.027	.01±0.007
Post-calving	59	60380	.56±0.053	.37±0.051	.01±0.003	.06±0.015	<.01±0.002
Movement	7	6515	.44±0.024	.32±0.178	<.01±0.003	.22±0.173	.02±0.014
1981							
Pre-calving**	38	23973	.59±0.048	.21±0.079	.01±0.004	.19±0.095	<.01±0.002
Calving	18	4668	.60±0.055	.30±0.072	.02±0.006	.07±0.027	.01±0.019
Post-calving	7	2774	.51±0.037	.39±0.069	.01±0.004	.08±0.038	.01±0.005
Movement	5	1560	.36±0.059	.49±0.121	.02±0.011	.13±0.094	<.01±0.001
All years							
Pre-calving	163	67811	.58±0.028	.21±0.055	.01±0.003	.21±0.050	<.01±0.001
Calving	108	20992	.54±0.040	.33±0.050	.01±0.003	.10±0.020	.01±0.006
Post-calving	90	71297	.54±0.048	.38±0.044	.01±0.002	.07±0.013	<.01±0.002
Movement	17	12315	.38±0.075	.30±0.115	.01±0.003	.29±0.163	.01±0.009

* contains some observations in early July.
** contains some observations in mid May.

Table 3.20. Summary of caribou activity based on continuous observations of active individuals for the Porcupine Caribou Herd, late spring to early summer, 1978–83.

Activity	Pre-calving		Calving		Post-calving	
	Calves n= 171	Others n=54	Calves n=64	Others n=35	Calves n=34	Others n=12
Feeding	<.01±.002	.30±.051	.20±.026	.57±.064	.10±.027	.70±.080
Walking	.37±.028	.25±.039	.22±.026	.19±.037	.31±.043	.05±.014
Standing	.47±.028	.42±.051	.46±.038	.24±.054	.49±.050	.25±.086
Running	.05±.013	<.01±.002	.04±.013	<.01±.001	.01±.004	<.01±.001
Nursing	.08±.013	–	.04±.013	–	.10±.031	–
Other*	.03±.013	.02±.016	<.01±.001	<.01±.001	<.01±.001	<.01±.001

n = number of complete cycles observed.
* other activity includes sparring, swimming, drinking, etc.

Table 3.21. Frequency of complete active cycles for calves and adults of the Porcupine Caribou Herd, late spring - early summer, 1978-83.

Cycle length	Calves			Adults		
	Pre-calving	Calving	Post-calving	Pre-calving	Calving	Post-calving
<10 min	170	52	33	35	14	3
11 - 30 min	1	9	1	3	2	2
31 - 50 min	–	2	–	5	2	–
51 - 70 min	–	1	–	7	5	2
71 - 90 min	–	–	–	4	8	2
91 - 110 min	–	–	–	–	–	1
111 - 130 min	–	–	–	–	2	–
>130 min	–	–	–	–	2	2
median value (min)	.67	1.4	2.6	2.5	44.7	67.7

an increase in bout duration from pre-calving to calving (significant only based on bouts). The percent of active time spent nursing declined from calving to post-calving (Table 3.23).

Discussion

At our camp location, pre-calving cows were either still migrating west to calving sites in Alaska or were in preparation for calving within our study area. In 1979, concentrated calving occurred in the study area (Fig. 3.3). In the pre-calving period cows tended to have lower movement rates, lower proportion of time walking and smaller group sizes than the other two years. Although calving did occur in the study area in 1980 and 1981, most animals present in the study area in the pre-calving period appeared to be moving into Alaska. Animals that did calve in the area in 1980 and 1981 were those further back on migration during the pre-calving period.

Table 3.22. Frequency of complete bedded cycles for calves and adults of the Porcupine Caribou Herd, late spring - early summer, 1978-83.

Cycle length	Calves			Adults		
	Pre-calving	Calving	Post-calving	Pre-calving	Calving	Post-calving
<10 min	156	36	19	35	11	1
11 - 30 min	9	12	12	13	8	2
31 - 50 min	5	10	4	4	4	3
51 - 70 min	1	3	2	7	8	1
71 - 90 min	–	2	–	3	5	4
91 - 110 min	–	2	–	3	4	–
111 - 130 min	1	–	–	–	3	1
>130 min	1	1	1	2	–	1
median value (min)	1.1	8.2	10.2	7.6	45.3	55.0

Table 3.23. Frequency and duration of nursing bouts of calves of the Porcupine Caribou Herd, late spring – early summer, 1979–81.

Study period	Time observed (h)	(n)	Frequency[1] (bouts/100min) mean ± SE	Duration (sec) mean ± SE	% time nursing
Based on bouts					
Pre-calving	27.6	120	7.2	23.3 ± 2.13 a	2.8
calving	70.3	193	4.6	37.8 ± 2.66 b	2.9
post-calving	41.6	73	2.9	32.9 ± 3.68 b	1.6
Based on calves					
pre-calving		11	9.7 ± 1.92 a[2]	26.2 ± 5.46 a	4.2
calving		16	5.1 ± 0.87 b	39.9 ± 5.56 a	3.4
post-calving		12	3.8 ± 1.13 b	36.7 ± 5.36 a	2.3

1: bouts > 5 sec duration.

2: Values with the same suffix (a, b) are not significantly different.

The period of calving was characterized by a reduction in movement (both rate and proportion), smaller group sizes, and an increase in lying time. Although group cycle lengths, based on scans, did not differ from the pre-calving to the calving period, focal animal investigations indicated a tendency toward longer median active and bedded cycles. The high frequency of short cycles shown by focal individuals would be masked by the synchronous alteration in active/rest cycles dictated by groups.

The post-calving period was marked by a further increase in lying time, a reduction or maintenance of movement rates and/or proportion of time walking and an increase in the median length of active and bedded cycles. Activity budgets did not differ significantly between the calving and pre-calving periods.

The movement period showed the most dramatic change in the activity of the animals. Group sizes increased dramatically, the proportion of time and rate of walking increased significantly, the proportion of time spent feeding declined significantly and the alteration between active and rest cycles was significantly reduced. In 1980, group sizes had already increased in the post-calving period. This was associated with an increase in rate of movement, which indicated that animals moved from the study area earlier than in previous years (although this is not reflected in an increase in the proportion of time spent walking).

Individual calves decreased the frequency of nursing bouts and increased the duration of an individual bout within a few weeks of birth. In the pre-calving period all the calves seen were probably less than a week old. In the calving period we were observing calves from newborn to two weeks old and in the post-calving period from newborn to three weeks old. The increase in bout duration and decrease in bout frequency would be much more pronounced for an individual calf than our data suggest. Using a captive herd in which individuals were marked, Parker *et al.* (1990) reported an exponential decline in the frequency of feeding bouts with age of calf while bout duration remained relatively constant.

Few data exist on the activity of newborn caribou calves. Our data agree well with those presented by Parker *et al.* (1990), who observed that calves spent less than 1 % of the day grazing post-partum, increasing to between 10 – 20 % by the end of one month of life. The percent of day spent lying [bedded cycle length/(bedded+active cycle length)] varied between 65 – 85%, comparing favourably with the observations of Parker *et al.* (1990). They also noted a sharp decline in the time spent running from birth to one month of age, similar to our findings.

Summary discussion

In 1979 pregnant cows moved out of wintering areas in northcentral Yukon along the ridges of the Old Crow route. Snow was relatively deep in the forested habitats below the ridges. Once on the north slope animals dropped out of migration randomly and occupied calving areas by late May. The two regions of concentrated calving were the foothills areas between the Kongakuk and Malcolm rivers and the uplands of the Jago River. Weather conditions in late May prevented early exposure of the tussock tundra communities; precipitation was high 20 - 25 May and temperatures were coldest among the years recorded in this study. As a result of the late snowmelt and cool temperatures the timing of flowering in the key forage species was late. Once on the core calving area for that year, many females remained, not moving further west. Movement rates were slow, and group sizes small as animals fed primarily on lichens, evergreen shrubs and *Equisetum* available in sufficient quantities in the alluvial heath communities. These habitats open up early compared to the tussock tundra communities. Lichens at that time in 1979, provided necessary digestible solubles while moss and evergreen shrubs provided roughage to maintain a full rumen.

Weather remained cool and wet throughout the calving period. As vegetation became available, animals switched to a graminoid based diet and then to deciduous shrubs by mid June. Habitats primarily utilized were the sedge heath communities, a range type with abundant willows and sedges. By mid June animals began to bunch up and move west towards Alaska, reflected by an increase in movement rate, group size, and proportion of time spent walking in the last 10 days of June.

In 1980, spring migration was greatly slowed by the deep snow and late snowmelt along the migration routes. The area of snow free habitat was limited up to early May, but subsequent warm weather from the middle to the end of May resulted in early snowmelt in the foothills. Animals that occupied the study area in mid May continued westward to the foothills habitats of Alaska. Thus the pre-calving period was characterized by relatively large group sizes, high movement rates and a high proportion of time spent walking, in direct contrast to the same period in 1979. These animals were able to take advantage of the early melt in the tussock tundra communities along the foothills and the resultant early phenology. Diet in late May was primarily moss, evergreen shrubs, and graminoids. It was a poor year for the production of *Eriophorum* flowering due to the inclement weather in 1979. The tussock tundra communities were the favoured type in the pre-calving to calving period. By calving, early phenological changes were evident and we noted an early shift from graminoids to deciduous shrubs associated with a shift to the wet sedge meadow communities, abundant in deciduous shrubs.

In the post-calving period the animals began early aggregations with group sizes of over 1000 animals recorded. The movement rate, date and radio-tracking information (Russell *et al.* 1992b) indicated that the animals moved rapidly and early (after the peak of calving) to Alaska. This movement was further evidenced by the high rate of movement in the post-calving period. Although the proportion of time spent walking (based on scans) did not show an increase in the post-calving period, evidence from the focal animal studies indicate that animals in the grazing period tended to move while feeding much more than in 1981. Therfore we suggest that during the important post-calving period nursery bands displayed highly oriented feeding rates towards Alaska. We further suggest that this rapid movement from our study area may have been due to the compressed flowering period compared to other years. If phenology was progressing rapidly in 1980 and if animals were attempting to track phenology then the logical movement was north and west. We would suggest therefore that early and rapid phenological development, although beneficial in late May and early June may prove detrimental later as key forage species decline quickly in nitrogen and phosphorus and lignify earlier.

The warm weather in 1980 resulted in a very high production of *Eriophorum* in 1981. The progress and timing of spring migration was relatively normal in 1981 and animals arriving on the calving ground appeared to be continuing on to core calving areas in the Jago River region of Alaska, similar to 1980 and in contrast to 1979. The weather in 1981 was cool and plant growth was slowed and prolonged compared to 1980. The normal snowmelt and high production of *Eriophorum* flowers resulted in the early exploitation of tussock tundra communities with animals able to pluck newly exposed flowers at the edge of the snow. Use of *Eriophorum* continued into the post-calving period, and thus the use of *Salix* was delayed compared to previous years. This prolonged use of graminoids may be due to the abundance of *Eriophorum* flowers and/or the retarded phenological development of the willows. Similar to 1980, the animals switched from a preferred tussock tundra community before calving, to the utilization of the wet sedge communities after it.

Movement from the calving area westward was a slow drifting compared to the rapid movement in 1980. The prolonged phenology may have been an important factor. Continuous observations of calves in 1981 indicated that there was an increase in the proportion of active period spent nursing from the calving to the post-calving period (compared to a decline in 1980). In both years the proportion of the adult's active period spent standing mirrors the proportion of the calves active period spent nursing indicating that the frequency and duration of nursing has an effect on the activity budget of the female. Perhaps this is the reason for the high frequency of short active and bedded periods observed with focal adults in the pre-calving and calving periods; the frequent nursing bouts constantly interrupted the activity of the female. These shorter cycles were not evident in the scan observations of the groups. Group activity better reflects the overall alternation of ingestion (or movement) and digestion.

In all years we noted a decline in the length of both active and bedded cycles in the movement period and we have evidence that this phenomenom occurred early in 1980. The use of willow and forbs in the latter part of June may help to explain this sharp reduction in cycle lengths. White and Trudell (1980) noted that the rate of dry matter disappearance was highest for forbs followed by deciduous shrubs. Thus the rate of digestion and passage would increase and lying periods would be reduced. White and Trudell (1980) and Kuropat (1984) reported a relationship between increased biomass and increased bite size and bite rate and this was most pronounced with forbs (*Lupinus*) and shrubs (*Salix*). Kuropat (1984) contrasted the high eating rates on forbs (8.2 g per min) and deciduous shrubs (6 g per min) with the lower values for *Eriophorum* (1.7 g per min). White *et al.* (1975) indicates that a curvilinear relationship exists between biomass and intake in some of the key plant groups and further that the slope of the line for forbs is particularily steep because animals can increase the effective biomass of forbs by walking while grazing and consuming almost all of the aerival biomass. Thus the short active cycles in the movement period may not reflect a reduced intake but may reflect a combination of higher intake rates and higher rates of digestion and passage.

Our data suggests that calving caribou are able to react rapidly to the quickly changing environment experienced in the month between arriving on the calving grounds and leaving. They are able to track rapidly the quantity and quality of vegetation as dictated by weather and terrain. The fact that they do react quickly suggests that uninterrupted movement in response to these changing conditions is an essential element in the survival of the calves and in the ability of females to regain reserves depleted over the winter and throughout spring migration. The transition from post-calving to the movement period appears to be the time of most dramatic change for the animals, a time when they attempt to maximize nutrient intake and minimize energy output. Our observations were conducted on animals that move westward after calving to the post-calving aggregation sites in the Jago region of Alaska. For that reason the activity budgets of our animals after mid June may not be indicative of those animals that reach the Jago region in the calving period. We would suspect that the high movement rates and low feeding rates, that we measured during the movement period, would not necessarily occur in the core calving regions of Alaska. We suspect that these latter animals would be able to enjoy a more energetically beneficial «movement» period. In fact their activity budgets may suggest that a prolonged post-calving period may extend to the end of June and that no «movement» period exists.

Spring range of bulls

Introduction

The general pattern of spring migration involves pregnant cows migrating early from wintering grounds to calving sites north of treeline. Meanwhile males, juveniles and non-pregnant females remain on the wintering areas until early May. Therefore, during calving, and for a variable period before and after calving, males are segregated from females. It has been suggested that this segregation occurs because males follow the northward initiation of growth of forage while pregnant females move quickly to the calving grounds for other reasons, such as predator avoidance (Whitten and Cameron 1980). Recent proposals for a seaport, quarries and roads in northern Yukon in the area used intensively by males in early summer have focused attention on the need for information on that component of the herd.

Study area

Investigations were conducted in northern Yukon, north of the Porcupine River (Fig. 1.2 and 3.11). The area can be divided from south to north into three broad ecoregion bands: Old Crow Basin, Northern Mountains and Northern Coastal Plain (Wiken *et al.* 1981; Fig. 3.1). These ecoregions will be described in some detail in Chapter 4.

Three campsites were used for observing caribou in 1983: Sam Lake, 21 May - 12 June; King Point, 13 - 21 June; Firth River, 22 - 30 June (Fig. 3.11). The Sam Lake camp was at the southern edge of the Barn Mountains and overlooked rolling, tundra-covered pediments. The King Point and Firth River camps both lay on the coastal plain in rolling arctic tundra. Sites for documenting plant phenology (Fig. 3.11) were established on the Old Crow pediments (Sam Lake, Bonnet Lake), in the intermountain basins (Cottonwood Creek, Anker Creek), on the inner coastal plain (Crow River, Walking River) and at the coast (Stokes Point, King Point).

Methods

Distribution

To follow the movements of caribou, radio transmitters on collars were placed on animals on the winter range. Between five and 15 caribou were available for relocation each year (1981 - 5; 1982 - 5; 1983 - 15). In 1981 and 1982, four relocation surveys were flown between 3 and 28 June and in 1983 six surveys were flown between 8 May and 1 July. In addition to the locations of radio-collared animals, the locations of all male caribou observed on aerial surveys and reported by other researchers were plotted on maps.

Activity

See methodology described in Winter activity budget section.

Phenology

We observed snowmelt and the development of vegetation in eight relatively flat cottongrass (*Eriophorum vaginatum*) tussock meadows (Fig. 3.11). We estimated the relative stage of development of the flowers of *Eriophorum vaginatum* (flower bud, early flower, full flower, past flower, seed) for 24 tussocks at approximately 5-m intervals along a transect at each site. Along the same transect we also documented the relative stage of development of the leaves of 24 plants of *Salix pulchra, Betula glandulosa* and *Ledum palustre* (leaf bud, leaf unfolding, full leaf).

Habitat selection

We divided the area of observation at each campsite into six distinct habitat types and determined the extent of each by mapping them on aerial photographs. These types were similar to those described in the Calving Ground study with the addition of an open White Spruce type. We also documented the use of late snow patches and sandy beaches at some camps. The areas observed at campsites appeared

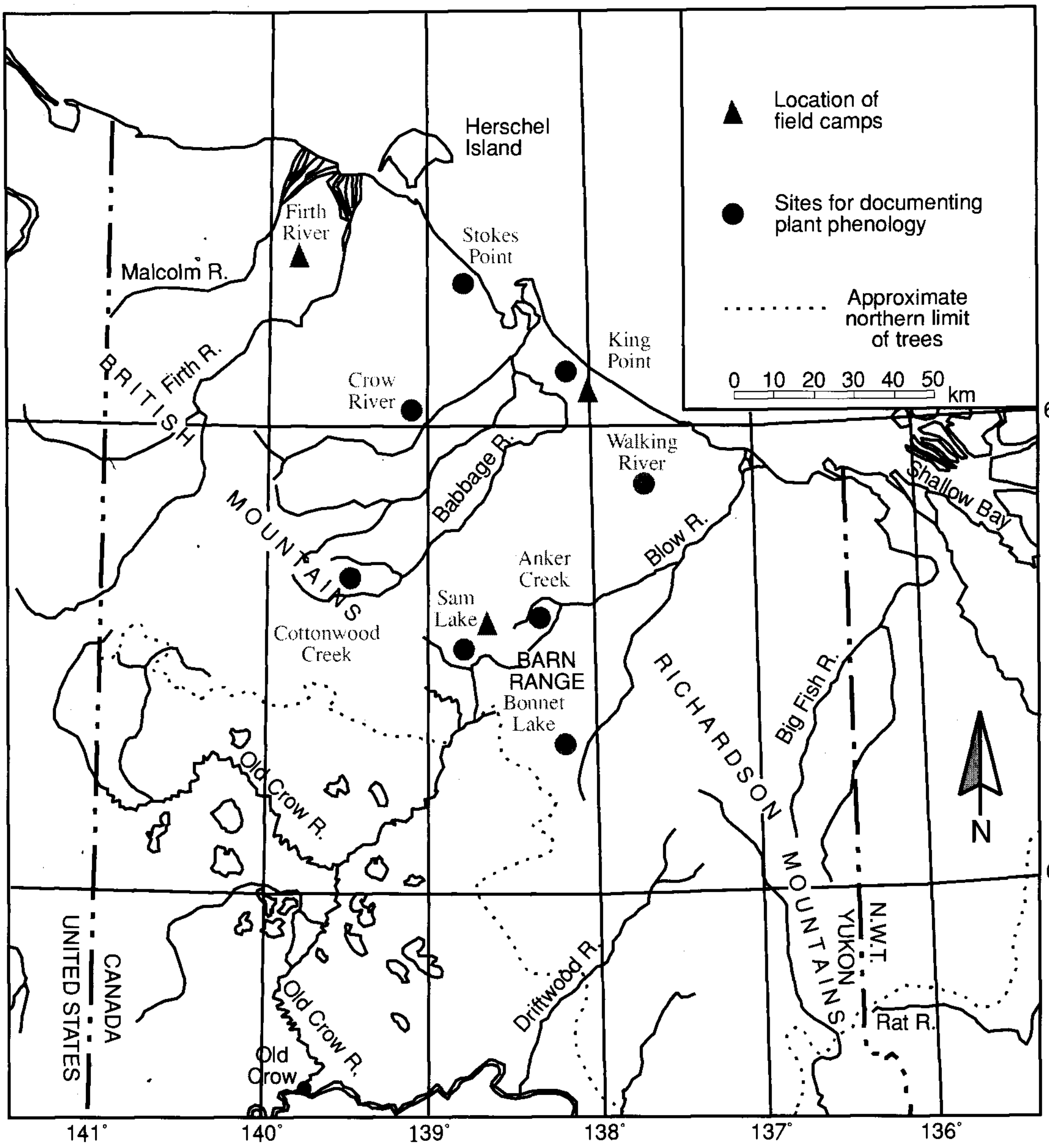

Figure 3.11. Location of study of males in spring, showing camp sites and phenological plots, 1983.

to be representative of much wider areas based on examination of aerial photographs and observations from aircraft.

Food habits

We collected composite fecal samples at Sam Lake (22 May, 4-5 June, 12 June), King Point (15-17 June), Firth River (26-27 June) and Stokes Point (15 June, 27 June). The method of fecal analysis and statistical treatment of the data follow those described in the Winter Food Habits section.

Data analysis

For the purpose of comparison, data analysis was consistent, in terms of time periods, with the calving ground study (Table 1.1).

Results and discussion

Distribution

Male caribou follow the females on spring migration along essentially the same routes leading from the two principal wintering areas, the Ogilvie Mountains of north-central Yukon and the Arctic Village region of northeastern Alaska. Females reach the calving grounds in mid to late May while males fan out in the rolling pediments north and east of the Old Crow Flats and into the wide basins near the headwaters of the Firth River (Fig. 3.12A). In early June, at the time of calving, males are distributed in a broad crescent south and east of the calving grounds (Fig. 3.12B). By this time, if not earlier, males from both the Alaskan and Yukon wintering areas are well mixed. Males then move eastward south of the British Mountains and northwestward from the Richardson Mountains. By mid June large aggregations begin to form in the intermountain basins near the headwaters of the Spring, Trail, Babbage and Running Rivers, and, in some years, on the Firth River (Fig. 3.12C). By late June males are found moving westward and northwestward towards the coast of the Beaufort Sea near the Alaska-Yukon border (Fig. 3.12D). At this time, band sizes frequently number in the thousands and smaller bands which have lingered behind move quickly to join the larger concentrations. Most males meet and mix with females and young on the Alaska-Yukon coastal plain by early to mid July before returning eastward to the Richardson Mountains.

Males, therefore are essentially segregated from females during May and June. The consistent pattern of distribution and movements among years and the formation of aggregations in mid June prior to joining females and prior to the insect season suggest a response to food resources combined with a form of social facilitation.

Activity

In late May, at Sam Lake, many females were moving through the area and males occurred in both male-dominated and female-dominated bands. Therefore, observations included both types of bands. After that time, only male-dominated bands were observed. The average size of bands was relatively constant from late May to mid June but increased significantly in late June (Table 3.24).

There was no significant difference in the proportion of time spent feeding or trotting/running among observation periods (Table 3.25). In mid June the proportion of time spent lying was significantly higher, and the proportion of time spent walking was significantly lower, than during other periods. The proportion of time spent standing was significantly lower in late June. The rate of movement (Table 3.24) mirrored the proportion of time spent walking (Table 3.25) and was conspicuously low during mid June.

It is not possible to make precise comparisons of activity budgets among studies because of differences in methods of calculation. In general, for the same season, Roby (1978) found that male caribou in north-central Alaska spent less time feeding (39%) and more time lying (47%) than males we observed.

Table 3.24. Size and rate of movement (km/h) of bands of male caribou in northern Yukon in 1983

Period	Size		Rate	
	(n)	$\bar{x} \pm$ SE	(n)	$\bar{x} \pm$ SE
Pre-calving	45	17.5 ± 1.78a[1]	574	0.35 ± 0.26a
Calving	55	24.2 ± 2.90a	730	0.54 ± 0.025b
Post-calving	65	19.9 ± 4.47a	1088	0.15 ± 0.007c

1: Means with same suffix (a, b) are not significantly different (p=0.05).

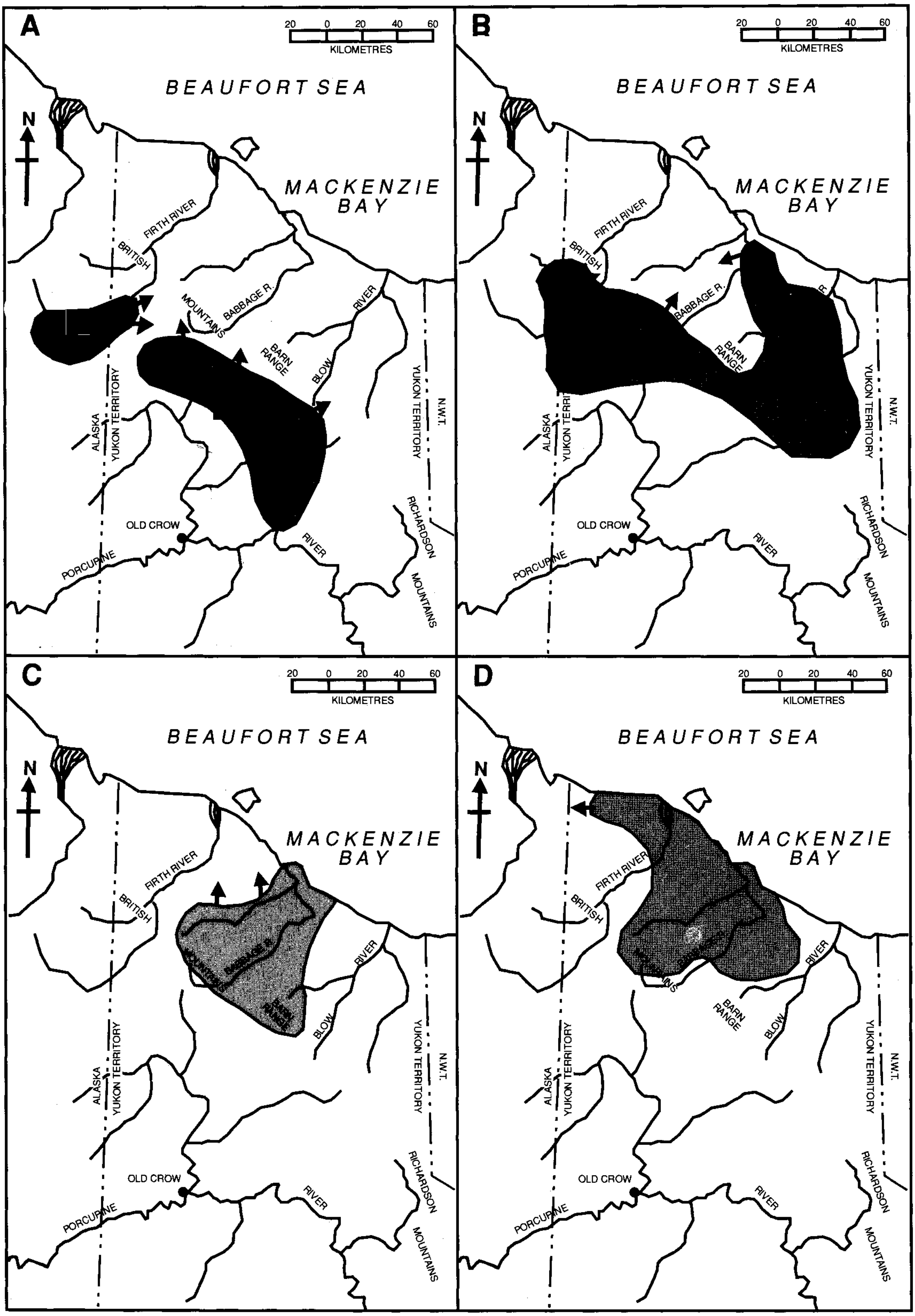

Figure 3.12. General distribution and direction of movement of male caribou in northern Yukon in late May (A), early June (B), mid June (C), and late June (D).

Table 3.25. Daily activity budgets (% time ± estimated 95% confidence intervals) for male caribou in northern Yukon in 1983.

Date	Pre-calving	Calving	Post-calving	Movement
Number of observations .	619	787	1,153	330
Number of bands	45	55	65	29
Number of individuals ...	8,443	14,498	19,554	25,592
Feeding	51.0±4.0	47.6±3.4	52.0±3.0	49.0±2.8
Lying	31.1±6.4	31.9±5.0	40.4±3.3	25.4±4.3
Standing	1.8±1.1	0.9±0.3	0.9±0.2	0.4±0.1
Walking	14.8±4.9	19.1±2.4	6.3±0.9	24.1±5.6
Trotting/running	1.2±1.1	0.5±0.3	0.3±0.3	1.0±0.4

The mean length of both active and resting periods declined significantly from late May to late June (Table 3.26). The decrease from mid June to late June was particularly conspicuous. The mean length of the active period that we observed late May to mid June (112 minutes) was shorter than that reported for male reindeer in summer (135 minutes; Segal (1962)), while the mean length of the resting period (104 minutes) was nearly identical (reindeer; 105 minutes).

Table 3.26. Length (minutes) of active and resting periods (x ± SE) for male caribou in northern Yukon in 1983. (Samples sizes).

	Pre-calving	Calving	Post-calving	Movement
Active period	(7) 118±18.4a[1]	(10) 111±12.9ab	(29) 110±6.4ab	(5) 78±11.0b
Bedded period	(23) 103±6.9a	(34) 98±5.2a	(46) 109±4.7a	(12) 69±6.5b

[1] Means with same suffix (a, b) are significantly different (p=0.05).

Phenology

On 18-19 May 1983, the Old Crow pediments were about 80% snow covered farther north all sites were about 95% snow covered. By 3 June the snow cover had declined to less than 5% on the Old Crow pediments and on the coast but was about 50% (30-70%) between those sites. By 10 June the intermountain and inner coastal plain sites were 10–20% snow covered and by 17 June all sites were essentially snow-free.

In general, the development of vegetation was most rapid on the Old Crow pediments (Table 3.27). In early June, the development of *Eriophorum vaginatum* was more advanced on the coastal plain than at inland sites but by mid June plant development on the coast was behind that at other sites and remained so. This was probably due to the temperature gradient which develops between the coast, strongly influenced by the ice-covered Beaufort Sea, and the thermal basin surrounding the Old Crow Flats (Pearson and Nagy 1976). In general, plant development on the Old Crow pediments was at least a week in advance of that on the coast.

Habitat selection

Tussock Tundra was weakly selected in late May and early June while Wet Sedge Meadow was strongly avoided until late June (Table 3.28). Dwarf Shrub Heath began to be avoided weakly after late May and Alluvial Willow shifted from being avoided in late May and early June to being selected in mid June and late June. Other habitat types were too poorly represented to compare.

Table 3.27. Phenology of vegetation in northern Yukon in 1983. The percent of plants in each stage of development is presented in sequence. Blank spaces indicate that the plant had not yet begun to develop.

	Date				
	June 3	June 10	June 17	June 24	July 1
Eriophorum vaginatum.	B/E/F/P/S[1]	B/E/F/P/S[1]	B/E/F/P/S[1]	B/E/F/P/S[1]	B/E/F/P/S[1]
Coast	0/33/67/0/0	0/6/92/2/0	0/0/0/100/0	0/0/0/0/100	0/0/0/0/100
Coastal plain........	0/48/52/0/0	0/0/88/12/0	0/0/0/100/0	0/0/0/0/100	0/0/0/0/100
Mountain basins.....	0/88/12/0/0	0/2/67/31/0	0/0/0/90/10	0/0/0/0/100	0/0/0/0/100
Pediments	0/60/40/0/0	0/4/46/50/0	0/0/0/0/100	0/0/0/0/100	0/0/0/0/100
Salix pulchra[3].........	B/U/L[2]	B/U/L[2]	B/U/L[2]	B/U/L[2]	B/U/L[2]
Coast	100/0/0	0/100/0	0/96/4	0/0/100	
Pediments	58/42/0	38/62/0	0/10/90	0/0/100	0/0/100
Betula glandulosa......			B/U/L[2]	B/U/L[2]	B/U/L[2]
Coast			56/27/17	2/54/44	0/0/100
Coastal plain........			46/50/4	0/0/100	0/0/100
Mountain basin.....			48/38/14	0/0/100	0/0/100
Pediments			2/29/69	0/0/100	0/0/100
Ledum palustre........					B/E/F/P/S[1]
Coast					86/14/0/0/0
Coastal plain........					80/20/0/0/0
Mountain basin.....					66/34/0/0/0
Pediments					0/0/100/0/0

1: flower bud/early flower/full flower/past flower/seed.
2: leaf bud/leaf unfolding/full leaf.
3: *Salix pulchra* was not sufficiently abundant to tally on the inner coastal plain and intermountain basin sites.

Food habits

In late May *Cladonia*-type lichens and *Vaccinium* (likely *V. vitis - idaea*) were the most important components of fecal samples (Table 3.29). Those species continued to be important in early June, although *Eriophorum* (likely *E. vaginatum*) was the most important item. *Eriophorum* predominated in the samples in mid June but declined sharply in late June. *Salix* increased markedly from early June to mid June and dominated the samples in late June.

There were no marked differences in diet, as reflected in fecal samples, at the two sample sites in late June. In mid June the proportion of *Eriophorum* increased from Sam Lake (50%) to King Point (61%) to Stokes Point (91%) while evergreen shrubs declined over the three sites (25%, 3%, 1%, respectively). *Salix* was highest at King Point (32%), lower at Sam Lake (16%) and lowest at Stokes Point (1%). Those variations did not appear to be precisely related to either availability or phenological stage.

Thompson and McCourt (1981) reported that *Eriophorum* (56%) and lichens (37%) were the most important components in fecal samples of the Porcupine Caribou Herd in late May and that samples were dominated by *Eriophorum* (77%) in early June and by *Salix* (99%) in late June. Although the proportions of lichen in late May and *Salix* in late June are consistent with our findings, the proportions of

Table 3.28. Availability (A, % area), utilization (U, % caribou) and selection (S)[1] of habitat types by male caribou in northern Yukon in 1983. Approximate area observed at each campsite in parenthesis.

	Sam Lake (29 km^2)			King Point (26 km^2)					Firth River (23 km^2)		
	Pre-calving			Calving		Post-calving			Movement		
Habitat type	A	U	S	U	S	A	U	S	A	U	S
Tussock meadow	51	60	0.47	82	0.71	88	97	0.11	76	80	0.05
Wet sedge meadow	18	3	-0.69	1	-0.88	10	1	-0.87	19	17	-0.05
Dwarf shrub Heath	21	18	-0.08	14	-0.20	–	–	–	4	2	-0.20
Alpine barren	1	1	0.00	1	-0.05	–	–	–	1	<1	-0.83
Alluvial willow	8	3	-0.36	1	-0.73	<1	1	0.54	<1	1	0.90
Open white Spruce	1	–	-1.00	<1	-0.87	–	–	–	–	–	–
Beach	-	–	–	–	–	1	<1	-0.75	–	–	–
Late snowpatch	-	15	–	–	–	–	<1	–	–	<1	–

1: selectivity measured as (U-A)/(U+A). Utilization values were adjusted by removing the snowpatches because their availability could not be measured.

Eriophorum are not; they appear high in relation to expected phenological stage, especially in late May. Duquette (1984) reported on diet of females of the Porcupine Caribou Herd based on fecal samples and found that in late (16-26) May samples were dominated by lichens (41%), *Salix* (22%) and evergreen shrubs (16%), with *Eriophorum* making up less than 1%. The high proportion of *Salix* is noticeably different either from that we observed (0%) or from that reported by Thompson and McCourt (1981) (0.1%). In late May, therefore, caribou of the Porcupine Herd apparently feed primarily on lichens but supplement the diet with whatever palatable green matter is available.

Summary and conclusions

In late May male caribou were distributed south of the mountains where snowmelt was more advanced than farther north. There they used tussock meadows, Dwarf Shrub Heaths and alpine barrens but avoided low-lying wet sedge meadows and alluvial willow thickets where snowmelt was slower. Diet consisted primarily of lichens and evergreen shrubs which were widely distributed in the habitat types utilized. By early June, as snowmelt progressed south of the mountains and on the eastern coastal plain, males moved northward to those areas. Intermountain basins, where snowmelt was retarded, were avoided. As the season progressed males continued to use, and avoid, essentially the same habitat types but made less use of Dwarf Shrub Heaths. They continued to feed on lichens but began to use *Eriophorum* as it came into flower. In mid June, males moved into intermountain basins as snowmelt there progressed. Caribou used tussock meadows and alluvial willow thickets as the diet shifted to *Eriophorum* and *Salix*. At the time, large aggregations of caribou formed in intermountain basins where they spent more time lying, less time walking, and had a lower rate of movement than in other periods. By late June, males began to use the western coastal plain where they used tussock meadows, wet sedge meadows and alluvial

Table 3.29. Average percentages of discerned plant fragments in fecal samples collected from male caribou in northern Yukon in 1983. Adjusted diet in parenthesis (see Table 3.14).

Food items	Pre-calving	Calving	Post-calving	Movement
Moss	8.6 (9)	4.3 (4)	2.6 (3)	0.1 (<1)
Lichens	33.9 (58)	34.9 (59)	3.0 (16)	0.3 (13)
Cetraria type	4.5	3.0	0.6	0.2
Cladonia-type	23.4	28.7	1.6	0.2
Stereocaulon	5.2	3.2	0.8	-
Horsetails *Equisetum*)	(0)	1.5 (2)	0.3 (<1)	0.1 (<1)
Graminoids	10.0 (10)	36.7 (37)	67.3 (67)	2.3 (2)
Carex	6.8	3.1	1.0	0.7
Eriophorum	3.2	33.6	65.8	1.5
Deciduous shrubs *(Salix)*	(0)	2.0 (0)	16.5 (7)	95.8 (46)
Evergreen shrubs	47.5 (18)	19.9 (9)	9.6 (5)	0.6 (2)
Dryas	1.5	0.7	5.0	0.3
Ledum	5.3	3.7	1.1	-
Vaccinium	40.8	14.7	3.6	0.1
Forbs	- (5)	0.6 (0)	- (2)	0.7 (37)

1: *Astragalus, Festuca,* fungi, *Lupinus, Peltigera, Picea, Poa, Saxifraga* and unidentified *Ericaceae* occurred at average frequencies of less than 1% in some sampling periods.

Note: There is a problem with correction factors when high graminoids and lichens and low deciduous shrubs are found in fecal fragments (see corrected calving diet).

willow thickets. *Salix*, which was common in all three habitat types, predominated in the diet. At that time, *Salix* on the coast was at a similar phenological stage to that at inland sites two weeks earlier, when it had not been used as heavily as *Eriophorum*. By late June *Eriophorum* was in seed and therefore not as desirable as a food for caribou. In late June average band size increased significantly and the rate of movement was greatest as males moved westward towards Alaska. The mean length of active/resting cycle decreased by about 35%. This sharp decrease may reflect both the high availability and high digestibility of young willow leaves.

In general, the distribution of male caribou followed the pattern of snowmelt and plant phenology and their diet reflected both preference and phenological stage of different species of plants. Activity and movements, however, were not related to snowmelt, plant phenology or diet. Rather, they appeared to follow a seasonal pattern.

Comparison of bulls and cows

Bulls are better able than cows to follow closely the progression of phenology (Whitten and Cameron 1980). In the Porcupine Caribou Herd the bulls tend to delay spring migration by at least two weeks, remaining on the winter range into May before migrating north. In the Central Arctic Herd, Whitten and Cameron (1980) reported that bulls wintering with the cows on the Arctic Coastal Plain actually move south in the spring to take advantage of earlier phenological stages available on south-facing slopes in the Brooks Range and the southern foothills.

Early to mid May is undoubtably an important time in comparing the activities of bulls and cows. However our field investigations were made only from late May to the end of June. Fecal samples we collected in 1987, from animals wintering north of treeline, indicated that lichens drastically decline in the diet with an associated increase in evergreen shrubs and moss. This suggests that animals moving north of treeline early would face a poorer quality range (prior to snowmelt).

In the pre-calving period bulls were found in the Old Crow Pediments, a region of early snowmelt in the northern Yukon. They foraged in smaller groups and with a lower rate of movement than cows, many of which were already north of the British Mountains.These bulls are switching from a lichen dominated winter diet, substituting evergreen shrubs, deciduous shrubs and graminoids as they become available. Meanwhile the diet of cows has a characteristically high component of moss.

While cows break into smaller groups and move slowly during the calving period, bull movement increases, oriented northward to the newly open areas towards the coast. Bulls maintain their intake of lichen but rapidly replace evergreen shrubs with newly exposed *Eriophorum* flowers. The cows are still feeding on moss, graminoids and evergreen shrubs. In 1983 a good production of *Eriophorum* was recorded (Shaver *et al.* 1986). We would expect *Eriophorum* intake that year to follow the pattern documented for cows in 1981, another good *Eriophorum* year. In 1983 cows did indeed consume more *Eriophorum* than did the bulls in the pre-calving period and equal amounts in the calving period, while the bulls consumed more *Eriophorum* in the post-calving period. The major difference in their diets still remains the high amount of moss eaten by cows and of lichens by bulls. Bulls may indeed be located in areas of better lichen stands than cows or have the ability during the calving period to travel to more favourable sites.

By the post-calving period both components of the herd reduce the proportion of time spent walking, although rate of movement of the cows tends to be higher, indicating that they may be moving more while feeding. By this time the cows have switched to a diet of deciduous shrubs whereas bulls have increased their intake of *Eriophorum* at the expense of lichens. This difference in diet was not due to the late flushing of shrubs in 1983, when shrub leaf unfolding occurred as early or earlier during our study of cows.

By the movement period, the diets and activity of both bulls and cows are similar, both having switched to a predominantly shrub and forb diet, increased group size and movement rate. We would assume that neither group would be at an energetic advantage during this period because advanced phenological development is so widespread and the females are no longer limited by the movement of their calves.

By moving from the Old Crow Pediments in late May to the coastal plain and intermountain basins east of the Firth River in late June, bulls are moving from the zone of earliest snowmelt in the Northern Yukon to the area of latest snowmelt. Their high intake of *Eriophorum* heads as late as the post-calving period indicates that they must be obtaining flowers prior to anthesis. Lent (1980) noted that the coastal plain loses snow later east of the Firth River than to the west. Bulls therefore can take advantage of early phenology and their mobility and inter-regional movement allows them to track the early phenological stages for longer than the cows.

Our data indicate similar trends in the length of active and rest cycles over the four periods observed, although those cycles were significantly longer for bulls which have proportionally larger rumen volumes (White and Trudell 1980) but not proportionally larger intake rates (g per min eating), so that they have to eat for longer to fill their rumens.

CHAPTER 4. Summer

Introduction

In early summer, small groups of caribou move north and west through the foothills and along the coastal plain. Following calving in the first half of June, large aggregations of mixed age and sex usually form on the coastal plain of northeast Alaska or northwest Yukon Territory (Garner and Reynolds, 1986). It is generally thought that these aggregations form to reduce harassment by flies or predators (Bergerud 1974; Roby 1978; Calef & Heard 1980).

By mid July, large groups of caribou drift east or south. Caribou summering in northern Yukon Territory historically have used the mountainous region and coastal plain but avoided the Old Crow Flats (Russell *et al.* 1992b).

The activity of the herd during summer appears largely influenced by the activity of blood sucking and parasitic insects. The period of insect activity coincides with the time when caribou are restoring body reserves depleted during winter (White *et al.* 1975) and growing new hair and antlers, when cows are lactating, and when bulls are accumulating fat reserves in preparation for the fall rut. This period is important nutritionally, primarily because green vegetation, high in digestible nitrogen, is available for approximately 6 weeks before senescence reduces nutrient content and plant digestibility (Kuropat and Bryant 1983). This nitrogen source is essential to growth and maintenance in caribou (Russell and Martell 1984).

To optimize nutrient intake, caribou must employ strategies to minimize the detrimental effects of insect harassment. Observations of other herds suggest that the tactics include: moving to regions that have few insects and favourable food resources, are typically cool and windy, and employment of various behavioural responses (eg. formation of large dense aggregations).

In the following section, we review the historical information on summer movements of the Porcupine Caribou Herd. Caribou do not use the summer range randomly; certain regions appear to be preferred. We have attempted to rationalize these consistent patterns, focusing on the effects of insect harassment on foraging opportunities. We have provided an inventory of vegetation complexes within the region (Russell *et al.* 1992a). We also investigated the factors that influence insect activity, and identified those abiotic variables that can be used to predict insect activity. The regional weather patterns within the Yukon summer range can be predicted from the records of permanent weather stations and assessed in relation to potential insect abundance. We document activity budgets, habitat selection and food habits of the herd during harassed and unharassed time periods using this information to assess the strategies employed by caribou in minimizing the negative energetic effects of harassment in terms of group dynamics and behavior of individuals. In the concluding section we attempt to integrate all these factors to account for the movements, activity and behaviour of the herd during this critical time period.

Study area

The climate in the study area (Fig. 1.2) is characterized as «polar continental» in the extreme north and «subarctic continental» to the south (Wiken *et al.* 1981) with mean daily summer temperatures above 3°C and mean daily winter temperatures below -10°C. Precipitation is low at all times of the year.

Wiken *et al.* (1981) defined 3 broad ecoregions in this area: the Northern Coastal Plain, the Northern Mountains and the Old Crow Basin (Fig. 3.1). The Beaufort Sea and the northern limit of tree line define the northern and southern limits of the study area. The Northern Coastal Plain ecoregion stretches northward from the 150m elevation contour to the Beaufort Sea coast. Cold north winds often blow off the Beaufort ice pack resulting in cool summer temperatures. There are numerous lakes and ponds on the coastal plain, many associated with thermokarst features. More lakes occur east of the Firth River as this area was glaciated.

In the Northern Mountains ecoregion the British, Barn and Richardson Mountain ranges are separated by the large drainage basins of the Babbage and Blow Rivers. In each mountain range there are numerous valleys and occasional upland plateaus. Peaks in the British and Richardson Mountains reach an elevation of 1500m while the central Barn Mountains do not exceed 1100m. This region was unglaciated, so most mountain valleys tend to be narrow and V – shaped. Summer temperatures are slightly warmer than on the coastal plain to the north, although cooler temperatures are still found at high elevations. Broad valleys to the south of these mountains merge with the Old Crow pediments which surround the Old Crow Basin (Wiken *et al.* 1981).

The Old Crow Basin ecoregion has elements of both arctic tundra and boreal forest. The pediments in the northern sector of this region rise to 450m elevation and merge with the foothills of the Northern Mountains ecoregion. The southern sector consists of a huge wetland complex at an elevation of approximately 300m. The climate of this region is much warmer in summer than that of the mountainous and coastal regions to the north.

Russell *et al.* (1992a) has described the vegetation communities of the northern Yukon Territory. The range types of interest in this study are: tussock meadow, wet sedge meadow, dwarf shrub heath, and alluvial willow. We also refer to the alpine barren described in the spring section, as «sparsely vegetated» because it occurs at low elevation in the study area, and identify two additional habitat types: low shrub tundra and sedge heath.

Summer movements

Historical

The post-calving movements of the Porcupine Caribou Herd begin about 15 June, two weeks after the peak of the calving period (Calef 1974). Calving usually takes place on the Alaskan coastal plain during years of normal to early snowmelt. If snowmelt is delayed, pregnant cows may be dispersed south of the coastal plain throughout the hills north of the British and Brooks Mountains and in the intermountain basins. In the years when caribou calve in northern Yukon, they travel west to the Alaskan coastal plain after calving. Westerly movement continues as the caribou begin to coalesce into increasingly larger aggregations, usually on the uplands between the Jago and Hulahula Rivers (Garner and Reynolds 1986). The caribou move on to the coastal plain as the snowmelt progresses.

With the onset of insect harassment during the last week in June, the caribou often move to the coast, aggregating on the coastal plain from the Canning River delta to Beaufort Lagoon. In 1976 and 1981, severe inclement weather (fog, rain and cold) may have reduced insect activity as coastal aggregations did not form (Curatolo and Roseneau 1977; Whitten pers. comm.). Although insect harassment has often been postulated as the stimulus for formation of large dense groups, large groups have formed prior to insect activity in some years. Large groups have also formed in years of few insects, as in 1973 (Roseneau *et al.* 1974), though these aggregations were probably not as tightly spaced as those which form when weather conditions favour insect harassment.

During «normal» years, the caribou remain near the coastal plain in Alaska until the first week in July, when a concerted movement to the southeast begins. At this point, the cow calf component of the

Porcupine Herd is usually in several large groups of tens of thousands of animals, which may join into one or two huge groups totaling 70,000 – 80,000 animals as they progress towards the Yukon/Alaska border. These cow/calf groups usually encounter bull/juvenile groups in the vicinity of the Clarence River between 7 – 15 July, although some bulls may already have joined the cows on the coastal plain. These caribou usually move south into the foothills later in July. In 1972 and 1982, 10,000–15,000 caribou remained on the coastal plain for the summer, seeking relief from insects by wading in the Arctic Ocean or resting on ice pans along the shore (McCourt *et al.* 1974; Russell *et al.* 1992b).

After crossing the Yukon-Alaska border, the majority of caribou usually continue southeast through the foothills of the British Mountains in early July, crossing the Malcolm River and on into the valley of the Firth River. The lower Firth River cuts into a deep canyon which poses a major obstacle to the herd as they move up the Firth River valley searching for suitable crossing points. Many calves are separated from cows or drown during these crossings (Farnell pers. comm.). Upon reaching the southeastern end of the British Mountains, between the headwaters of the Babbage River and the Muskeg Creek, the caribou normally halt their concerted movement and stall at the northern edge of Muskeg Basin. As slower or later arriving caribou begin to gather over the next few days, the herds once again become more concentrated. Thus the south-eastern edge of the British Mountains (Muskeg Basin) appears to be consistently used as a «staging area» where caribou congregate before moving again around mid July.

From 1971 through 1975, the majority of post-calving caribou continued to travel southeastward crossing the southern flanks of the Barn Mountains and into the Richardson Mountains northeast of Bonnet Lake in the latter half of July (Roseneau and Curatolo 1976). In August, the caribou dispersed across the northern edge of Old Crow Flats and westward into Alaska. This pattern began to change in 1976 when the herd remained in the Richardson Mountains in August and did not return to Alaska (Curatolo and Roseneau 1977).

In 1977, the majority of the herd was last observed on 18 July – still on the coastal plain. One large group was south of Barter Island (60,000) and another group south of Herschel Island (30,000; Bente 1977). This was the first year, since studies began in 1971, in which the cow/calf aggregations did not travel to Alaska after calving. The large herd south of Herschel Island was seen to turn east rather than west after emerging from the Firth Valley onto the coastal plain. Unfortunately, their late movements were not observed.

The year 1978 marked another significant change in the post-calving movement pattern. Most of the herd did not move east across the Firth River, but travelled south within Alaska along the headwaters of the Firth and Malcolm Rivers (Russell *et al.* 1992b). This route to the west of the Firth retraced the spring migration route of that year, which had been abnormally far west, because an unusual snowmelt pattern resulted in easier travelling on the western side of the Old Crow migration route. As caribou tend to follow fresh trails, this unusual post-calving movement pattern may have been an artifact of the unusual spring migration route taken one month previously. As a result, in 1978, only 15,000 caribou reached the staging area at the south-eastern edge of the British Mountains. These caribou did continue along their «normal» route eastward and arrived in the Richardson Mountains later in July.

In 1979, it appeared that the majority of the herd again swung southwest into Alaska after the segregated cow/calf and bull /juvenile groups joined up on the coastal plain, but poor weather prevented full documentation of this movement. In that year 30,000 caribou reached the staging area on the southeast edge of the British Mountains. Then, instead of continuing to the Richardson Mountains, half of the herd split off and moved back into Alaska via the Firth River headwaters. This movement scenario seemed to be followed in subsequent years.

In conclusion, the post-calving movements of the Porcupine Caribou Herd followed a general pattern (Fig. 4.1) which persisted 1971–76, then changed abruptly in 1977-78. Since 1979, the majority of the herd has travelled to the staging area on the southeast side of the British Mountains, usually in the first half of July. From this point, a majority of the herd has moved back into Alaska, by-passing the

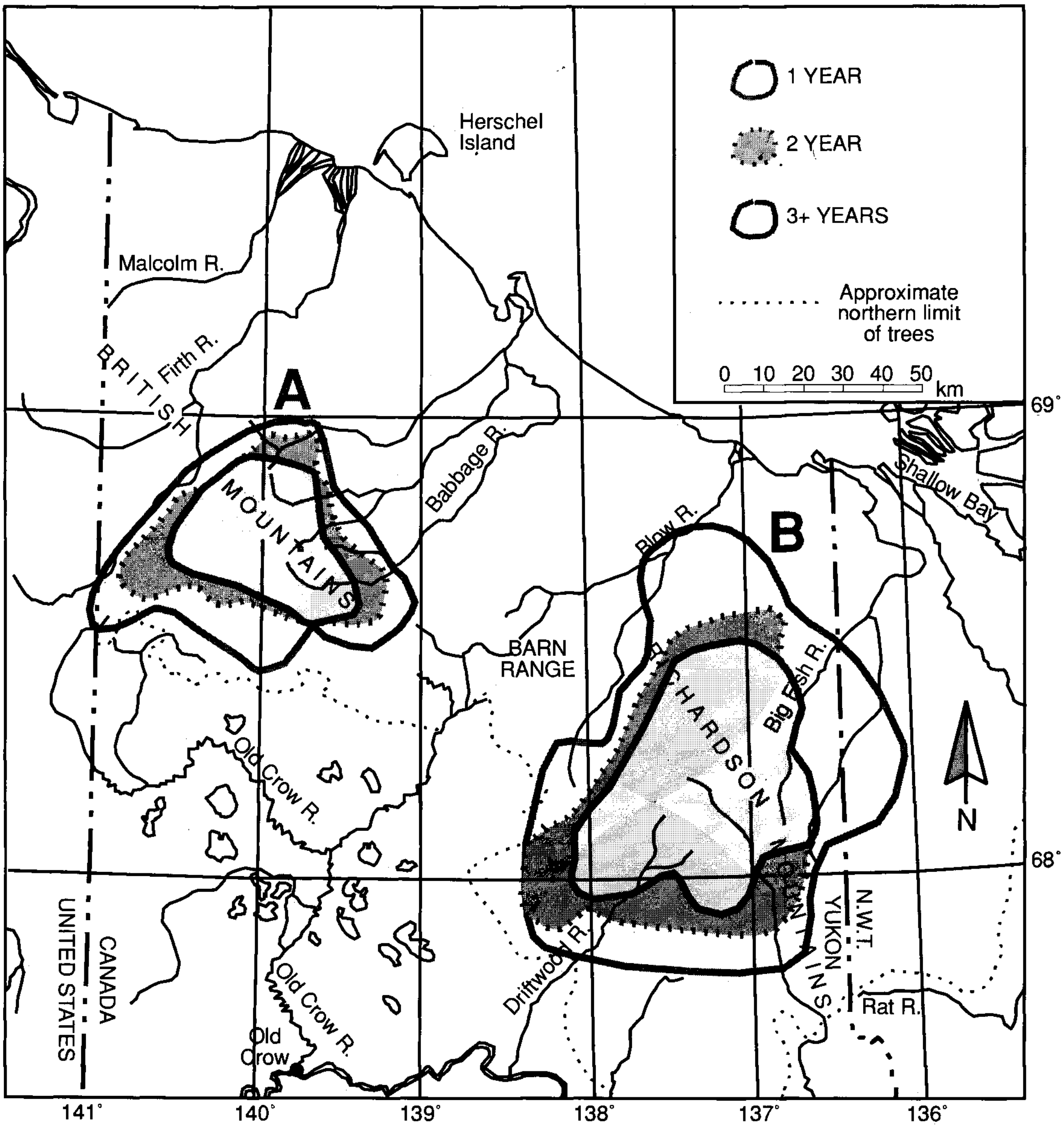

Figure 4.1. Mid summer insect relief habitat of the Porcupine Caribou Herd in Yukon.

Richardson Mountain insect relief areas traditionally used by the large post-calving aggregations. The Richardson Mountains still remain important to a smaller segment of the herd.

Herd movements - 1984, 1985

Methods

During our study period, intensive radio-telemetry flights and ground surveys provided a detailed account of group movements and distribution which could be related to known historical movements of the herd. We also wished to examine herd dynamics during periods of insect harassment, using radio-collared individuals as a means of keeping track of groups as they dispersed and coalesced.

Results

Caribou distribution April – August, 1984

The spring movement northward in 1984 was primarily west of the Richardson Mountains through the Barn Range, the Babbage River drainage, and the British Mountains. In May, other caribou (probably bulls and barren cows) were seen moving northward west of the Old Crow Flats.

By 5 July, large groups of post-calving cows joined with bulls and barren cows in the British Mountains by the Yukon/Alaska border to form a number of discrete groups. Our radio-telemetry flights indicated that about 100,000 caribou were in the Yukon in 13 groups. The largest of these groups was followed through the season. This group, located on the Spring River, contained close to 40,000 caribou including 32 with radio-collars. On 6 – 7 July strong winds blew from the southwest preventing us from monitoring the group. On 8 July winds had subsided enough to allow us to relocate it, greatly fragmented, approximately 50 km to the southwest at the head of the Trail River. For the next five days mosquitoes were

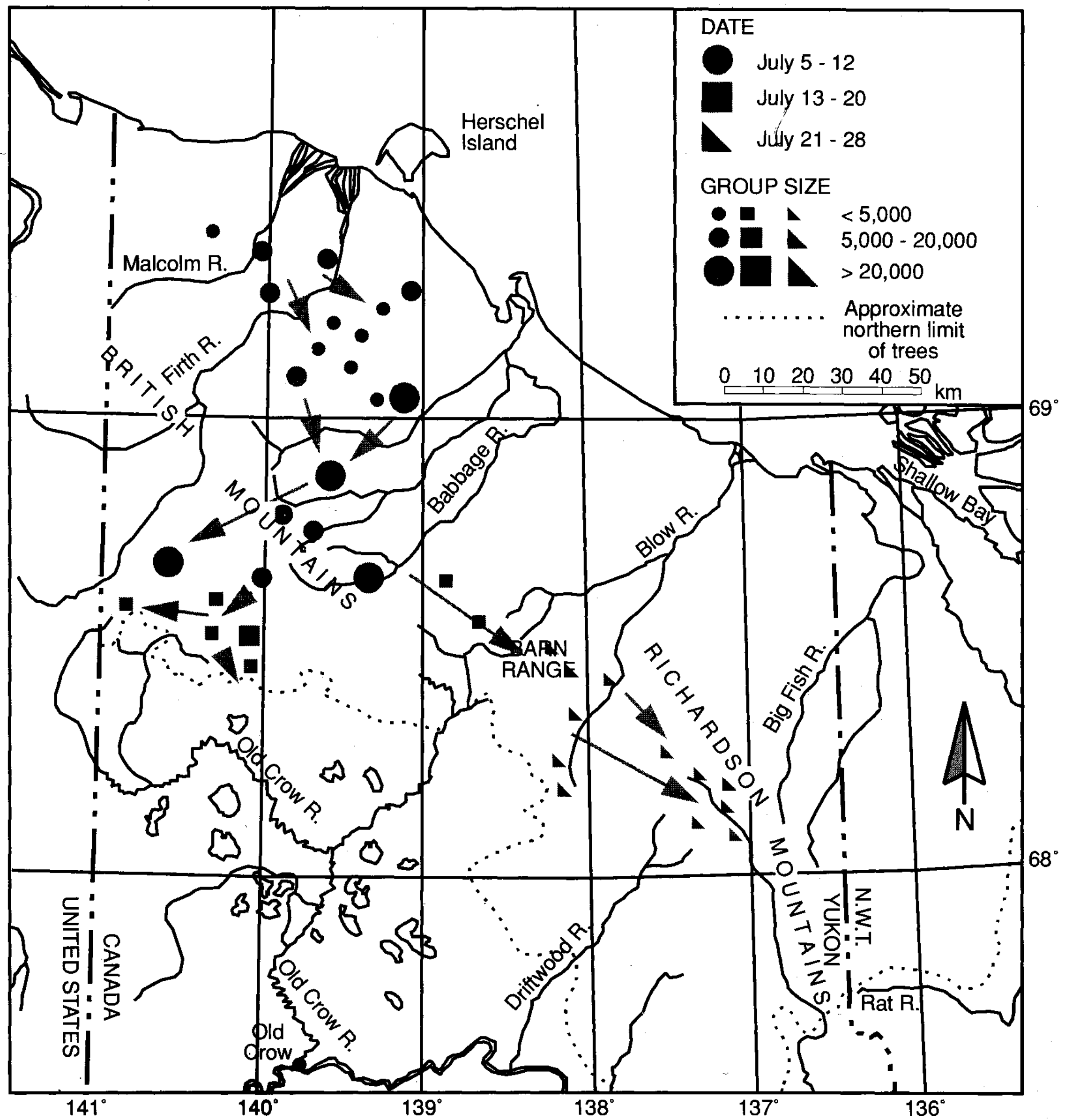

Figure 4.2. Movements of the Porcupine Caribou Herd in the summer of 1984.

bothersome and the caribou moved only short distances between lowland feeding areas and «insect relief habitat» on wind exposed ridges and uplands on the southeast edge of the British Mountains. The typical diurnal pattern for caribou was to forage at lower elevations at night, move up in elevation to wind exposed slopes by 0800, and remain in these areas until evening. As temperatures dropped and insect activity subsided, the caribou moved down into the basin of Muskeg Creek/Babbage River headwaters for another period of feeding.

On 12 July another storm began and continued until 15 July. The large group split into at least 6 smaller groups, all but two of which moved westward into Alaska along the northern edge of Old Crow Flats (Fig. 4.2).

By 19 July, only about 8,000 caribou remained in the Yukon. In groups of various sizes, they moved quickly eastward through the Barn Range, across the Blow valley, and remained in the northern Richardson Mountains until 1 August. In early August, the frequent storms and cool weather suppressed insect activity and served to disperse the larger groups. The maximum group size rarely exceeded 100 caribou in August.

Caribou distribution 22 June – 6 August, 1985

In 1985, approximately 40,000 caribou wintered in the Richardson Mountains north of the Dempster Highway. By late May, nearly half of them had moved west into Alaska along the coastal plain and north of the Old Crow Flats. Those remaining in northern Yukon in late May (approximately 22,000) were in the British Mountains and west of the Babbage River.

Fifty radio-collared caribou were located in a survey of the Yukon north slope on 22 June. These were primarily cows distributed in small bands (< 200 caribou) from west of the Babbage River to the Alaska border. Most of these bands were in the foothills and on the coastal plain between the Babbage and Malcolm Rivers. A brief survey flown on 23 June along the coastal plain and foothills indicated a steady westward movement of caribou. By 27 June, most were west of the Malcolm River and moving into Alaska.

Poor weather interfered with flying early in July. Relocation surveys on 5 and 6 July indicated an eastward movement of caribou from Alaska through the British Mountains, in groups ranging from 3,000 to 20,000 caribou. These animals made extensive use of the upland areas east of the Firth River, at the headwaters of the Crow and Trail Rivers. These groups periodically split up and reformed during the second week of July, varying in size from approximately 1,000 to 25,000. During this time, the caribou started moving south and east making extensive use of the Muskeg Creek drainage (Fig. 4.3).

By 11 July, several thousand caribou were moving eastward through the headwaters of the Babbage River. By mid July, approximately 20,000 caribou were found in the middle of the Barn Range. These caribou continued moving east and were found east of the Blow River 18 July in groups of 4,000 to 12,000 caribou.

Approximately 25,000 caribou used the Richardson Mountains in the last week of July and first week of August. Maximum group size varied from 1,000 to 9,000 depending on weather conditions and thus, insect activity. Movement was generally southward in the last week of July (as far as 68° 00'lat.) and then northward by 2 August to the Rapid Creek and Purkis Creek drainages. In the final survey on 6 August most caribou in northern Yukon were found in the hills north of the Richardson Mountains, on the edge of the coastal plain (Fig. 4.3).

Discussion

The Porcupine Caribou Herd and other barren-ground caribou herds move long distances to summer range and continue to move throughout the summer. These long range movements may be in response to predators, insects or food availability and quality.

The search for a combination of insect relief habitat and prime feeding areas may best explain caribou summer movements in northern Yukon. The large groups seen in early summer must move or they would quickly overgraze an area. Overgrazing by caribou has been documented recently on Rideout Island

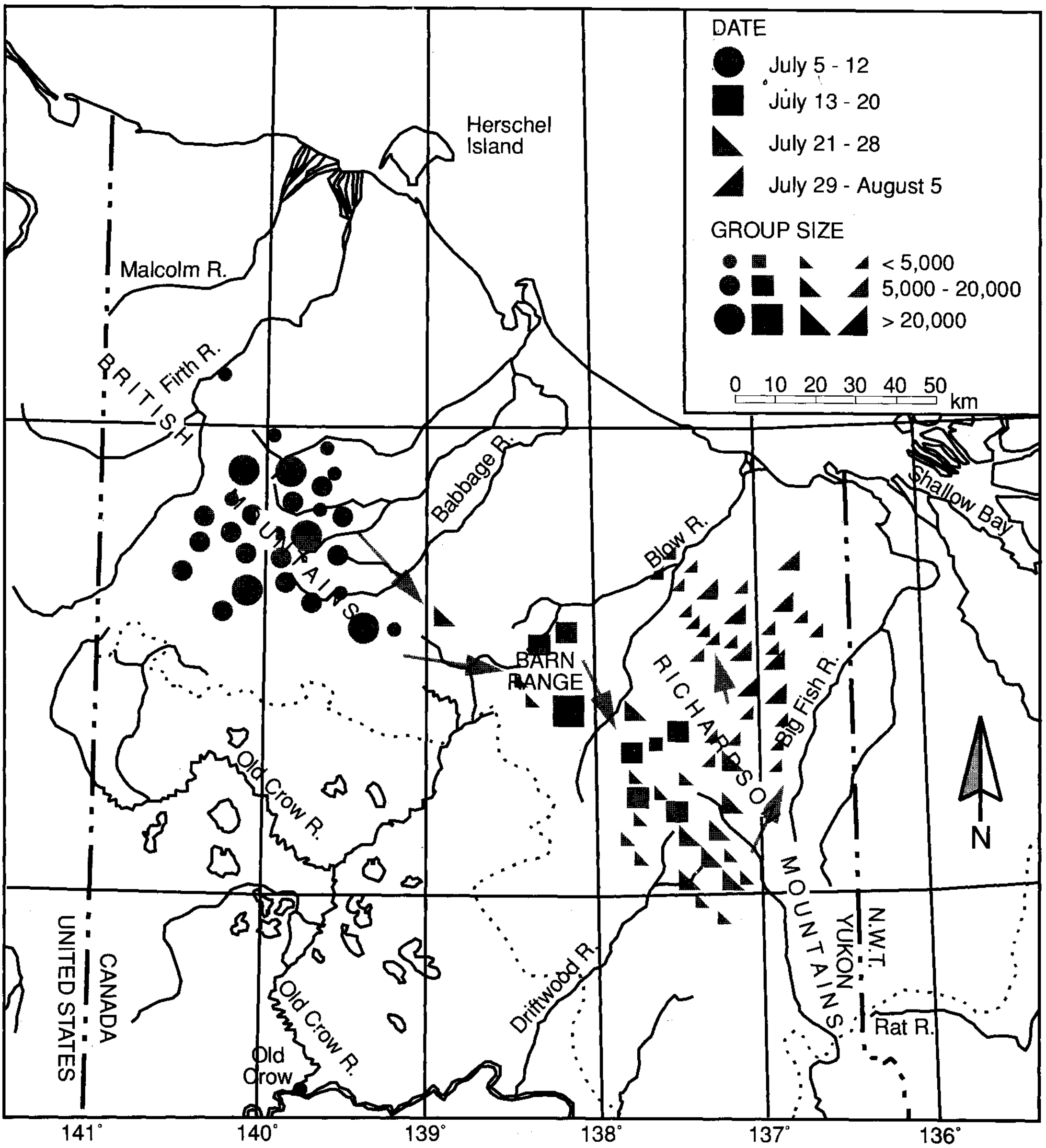

Figure 4.3. Summer movements of the Porcupine Caribou Herd in 1985.

N.W.T. (Heard 1988) and by reindeer on St. Matthew Island (Klein 1968). In addition to overgrazing, we have observed that trampling can destroy much of the vegetation in narrow valleys which several thousand caribou have passed through. Much of the western portion of northern Yukon is mountainous and therefore sparsely vegetated. These areas generally offer good wind exposure on uplands and are therefore good insect relief habitat. However, they are of limited use to caribou because they are not in proximity to extensive habitats with some shrub component.

The intensive monitoring of herd movements during this study confirmed the consistent patterns of distribution and use described historically. The shift from important staging areas on the southeast side of the British Mountains and the movement corridor to, and use of, the Richardson Mountains, must be considered as the «traditional» use pattern of the herd.

Activity of dipterans in relation to date and weather

Introduction

Approximately 12 species of mosquitoes (*Culicidae*) are found in northern Yukon Territory (Wood *et al.* 1979). Mosquitoes detect their prey by travelling in the direction of increasing CO_2 concentration (Wood *et al.* 1979) and they may travel several kilometers (Hocking 1953). At closer range, mosquitoes detect heat given off by the host and are also attracted visually to the target.

Adult nasal bot flies (*Cephenemyia trompe*) and warble flies (*Hypoderma tarandi*) mimic bees in appearance but do not feed and therefore have very reduced mouthparts. They emerge in early summer and mate. Mated females then search for caribou on which to deposit their larvae or eggs.

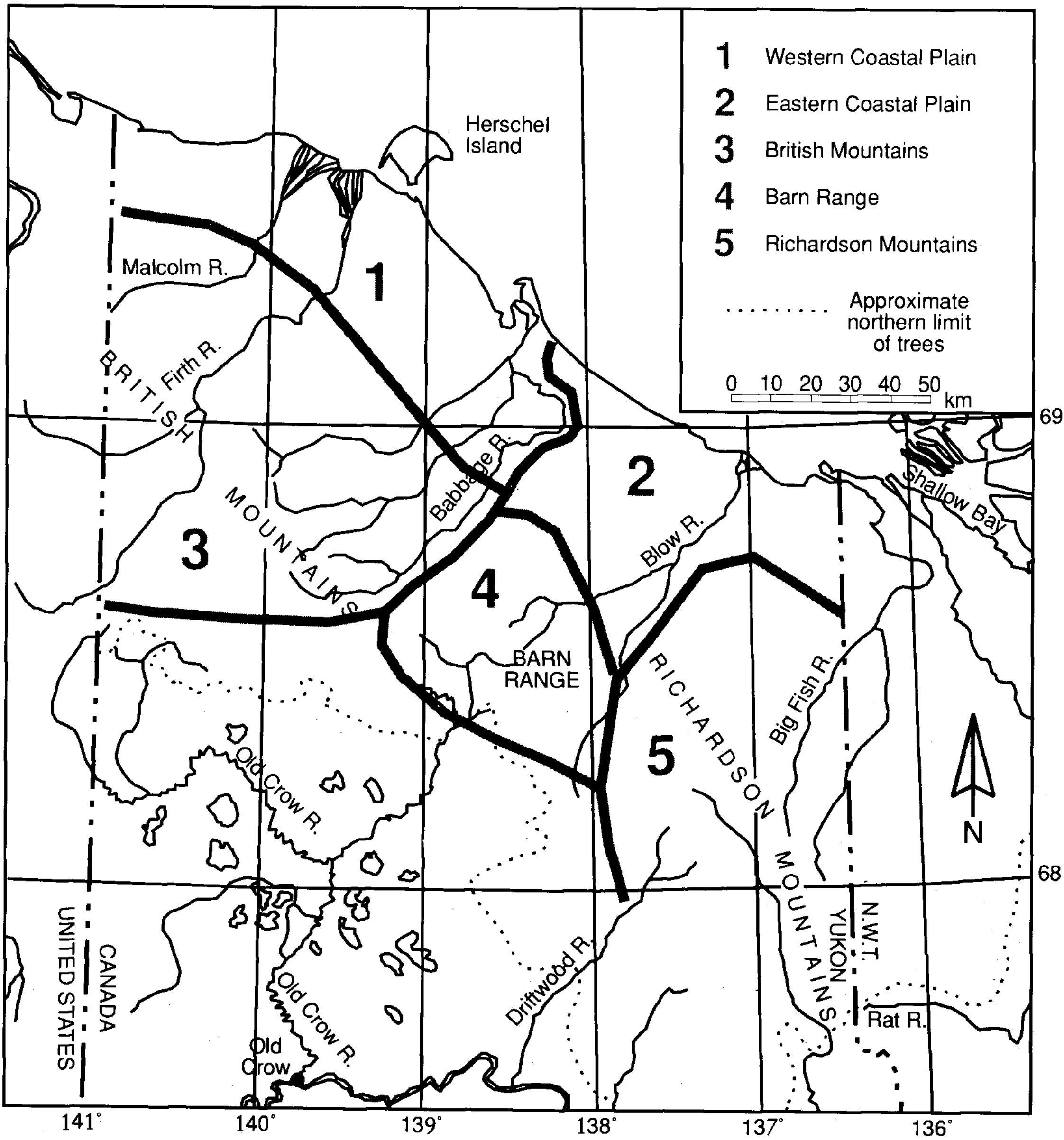

Figure 4.4. Sampling regions for mosquito sweep samples on the summer range of the Porcupine Caribou Herd, 1986.

The objective of this part of the study was to determine the abiotic factors, particularly weather conditions and season, that influence activity of mosquitoes. We predicted a negative relationship between wind speed and mosquito activity, and a positive relationship between temperature and mosquito activity. We were not able to determine how weather and season influenced activity of Oestrid flies, but we did infer from the literature how weather conditions influence the activity of these flies.

Methods

Weather

We recorded weather conditions concurrently with each mosquito sample. Wind speed (m/s) was measured at a height of about 1.5 m with a hand held Sims (TM) anemometer. Wind direction was determined by compass and recorded as north, northeast, east, southeast, south, southwest, west, or northwest. Cloud cover was estimated to the nearest 5%. Ambient temperature was determined from a mercury thermometer (°C) suspended 30-40 cm above the ground and shaded. In 1985 and 1986, we determined relative humidity with a hand-held sling psychrometer.

Mosquito sampling

Mosquitoes are relatively easy to capture because they are poor fliers and most northern species are attracted to any warm-blooded animal. Mosquitoes were sampled using a sweep net 40 cm in diameter on a 1.6 m dowel. With each sample we recorded weather conditions, habitat type, date, time and location.

The most complete sampling of mosquitoes was made in 1986, when sweep samples were collected systematically between 1 July and 5 August. Therefore, analyses to determine the effect of weather, date and time on mosquito activity were conducted only on the 1986 data.

Sampling sites were assigned to one of five geographic regions (Fig. 4.4), plus the Bonnet Lake base camp (where most of the samples were collected). Three of these regions fall within the Northern Mountains ecoregion (Fig. 3.1), but do not extend to it's northern limits. The two coastal regions (Fig. 4.4) extend as far south as the 350 m contour.

Only female mosquitoes were used in the analyses. In addition to actual and mean numbers of mosquitoes caught, we used the proportion of total sweep samples having one or more female mosquitoes for each degree of temperature or each m/s of wind speed. To consider interactions between temperature and wind speed, a functional response index was developed using the following equations;

If temperature $>18°C$ then $TI=1$
If temperature $<6°C$ then $TI=0$ $TI=1-((18-temp)/13)$
where $temp=temperature$ (°C)
If wind >6 m/s then $WI=0$
$WI=(6-wind)/6$
where $wind=wind$ speed (m/s)
$INDEX=TI x WI$

This INDEX is based on the following sampling results:
a. no mosquitoes were caught at temperatures <6°C in any year.
b. the proportion of samples with mosquitoes did not increase much above 18°C.
c. no mosquitoes were caught at wind speeds >6m/s.

Oestrid flies

These flies are difficult to study without specialized traps because they are not usually attracted to humans and are strong, fast fliers compared to mosquitoes. Limits to flight for oestrid flies therefore were taken from the literature. Kelsall (1975) cited studies on reindeer that set a minimum temperature of 13 to 15°C and an optimum of 15 to 27°C for oestrid flight. Kelsall (1975) also observed that warble flies were inactive at winds greater than 8 to 9 m/s even if other conditions were favorable. Based on these limits, a functional response index was developed for oestrid flies using the following equation;

If temperature $>18°C$ then $TI=1$
If temperature $<13°C$ then $TI=0$ $TI=1-((18-temp)/10)$
where temp=temperature (°C)
If wind >9 m/s then $WI=0$
$WI=(9-wind)/9$
where wind=wind speed (m/s)
$INDEX=TI \times WI$

Thus as INDEX values approach 1.0, weather conditions were considered more favorable to mosquitoes and oestrid flies.

Results

Mosquito sweeps

Seasonal effects

The number of female mosquitoes caught in sweep samples ranged from 0 to 141 with a mean of 3.2 ($n=399$, $SE=0.46$). In 1986, mosquitoes were caught throughout the sampling period and the maximum catch was greatest in the second week of July.

The overall mean mosquito catch was compared for the first and second half of the study period. The difference in means between 1 - 18 July and 19 July - 5 August (3.8 vs 2.0) was significant (Mann-Whitney, $U=-3.95$, $p<0.01$). The proportion of samples with mosquitoes was also lower in the second half (0.66 vs 0.46).

Diurnal variation

Mean mosquito catch was generally higher after 1900 hours. A quadratic regression of mean mosquito catch on time was significant ($r^2=0.47$, $p=0.001$). A quadratic regression of time on mean temperature was significant ($r^2=0.63$, $p=0.014$), indicating that the relationship between temperature and time of day was non-linear. The apparent relationship between time and number of mosquitoes caught is probably due to the increase in ambient temperature throughout the day. No collections were made between 2400 hrs and 0700 hrs, so a complete evaluation of diel pattern in mosquito catch was not possible.

Relative humidity

Mosquito catch was not significantly correlated with relative humidity (Spearman's correlation coefficient= -0.098, $p>0.05$).

Temperature

In 1986, no mosquitoes were caught below 7°C, and the catch remained low up to 10°C. The highest mean catches were at 18°C and 19°C. Mean catch of mosquitoes was regressed on temperature. The quadratic regresssion was significant. The regression curve indicates that the highest mean catch of mosquitoes was at approximately 18°C (Fig.4.5).

A quadratic regression of proportion of samples with mosquitoes on temperature was highly significant ($p<0.01$) at $r^2=0.82$.

Wind speed

The number of mosquitoes caught in sweep samples dropped off above wind speeds of 4 m/s, and no mosquitoes were captured above 6 m/s. The highest mean catch was at 1 m/s wind speed. A regression of the mean mosquito catch on wind speed was negatively related to wind speed (Fig. 4.6; note the regression line appears to increase above 11 m/s. This is simply an artifact of fitting a quadratic equation to the data.) The quadratic regression had a much higher r^2 than was found with temperature; therefore, wind speed appears to be the best single predictor of mosquito activity.

The proportion of samples with mosquitoes also was significantly related to wind speed; a quadratic regression had an $r^2=0.95$.

Wind/temperature index

The mean number of mosquitoes caught was higher above the 0.5 wind/temperature INDEX level though a quadratic regression of mean mosquito catch on INDEX was not significant. A quadratic regression of the proportion of samples with mosquitoes on wind/temperature INDEX was significant at $r^2=0.91$.

A quadratic regression of the proportion of samples with mosquitoes on wind/temperature INDEX was significant at $r^2=0.91$.

Region

It was difficult to compare differences in mosquito activity among regions because weather conditions often varied among sample sites. However, a Kruskal-Wallis test on mean mosquito catch indicated that there were locational differences in number of mosquitoes caught (X^2 approximation=16.33, p=0.01).

Among the regions sampled, the highest mean number of mosquitoes caught in sweep samples was in the area west of the Babbage River (including Trout Lake), and the second highest mean was in the Blow River Valley (Table 4.1.). There was a significant difference in mean mosquito catch between the Blow River Valley vs. the British, Barn, and Richardson Mountains ($p<0.05$).

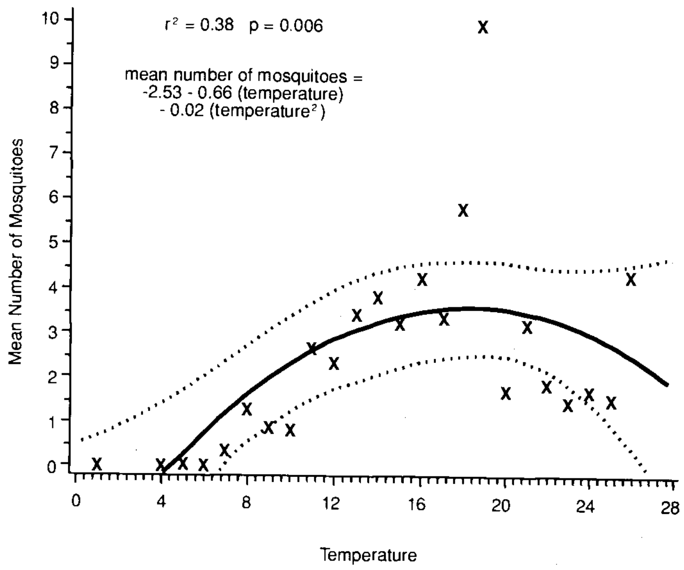

Figure 4.5. Quadratic regression (with 95% confidence intervals) of mean number of mosquitoes on temperature (°C).

Wind speeds recorded with each mosquito sample were compared among regions and no significant difference was found ($p<0.05$). It appears that difference in wind speeds alone do not account for the variation in mosquito catch in the different regions. Temperatures recorded with each mosquito sample were significantly different among regions (Kruskal-Wallis, X^2 approximation=10.80, p=0.002). In the Richardson Mountains, samples were taken at significantly lower temperatures than in each of the other regions ($p<0.05$).

Discussion

Influence of season and weather on Dipterans

The initial increase and subsequent decline in the mean number of mosquitoes caught suggest a seasonal change in the mosquito population. The lower mean catch of mosquitoes caught in the second half of the study period was not a result of inclement weather at the time of sampling. The same proportion of samples (87%) were taken within the limits for flight for both the first and second half of the study period. Thus, the changes that we observed in the number of mosquitoes caught in relation to date probably reflect changes in the population size.

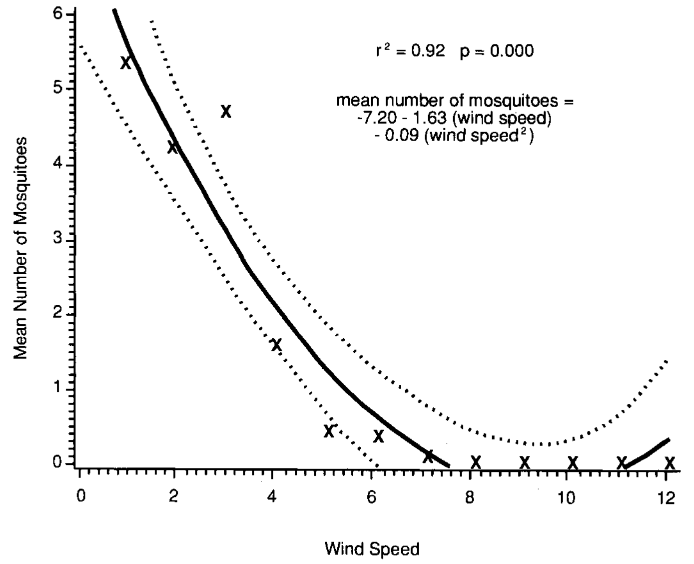

Figure 4.6. Quadratic regression (with 95% confidence intervals) of mean number of mosquitoes on wind speed (m/s).

Time of day did not appear to influence the level of mosquito activity, and no midday lull in activity was observed, unlike in southern latitudes (Taylor 1963; Downes 1965). Downes (1965) observed that the diel pattern of insects at northern latitudes is a function of weather rather than a response to light intensity, and reported that blood-seeking flies may have periods of very intense activity within their short life span as adults.

The strongest relationship between actual number of mosquitoes caught over the entire sample period and weather/temporal variables was with wind speed, which appears to be the best predictor of mosquito activity.

With regard to presence/absence of mosquitoes, the proportion of samples with mosquitoes had high r^2 values for quadratic regresssions with wind speed, wind/temperature INDEX and temperature. These results suggest that it may be more realistic to predict presence/absence of mosquitoes rather than actual level of activity based on known weather conditions.

The difference in mean mosquito catch between the Richardson Mountains and other regions was attributable, at least in part, to differences in temperature. Regional differences in the population of emergent mosquitoes were not measured, but may have contributed to the differences in mosquito catch between regions.

Table 4.1. Mean number of mosquitoes and proportion of samples with mosquitoes in each location.

Location	Number of mosquitoes			Proportion of samples with mosquitoes
	Mean	Standard deviation	Sample size	
Trout Lake and west of Lower Babbage River	14.3	38.3	13	.91
British Mountains	1.6	4.9	30	.66
Barn Range	1.6	2.5	34	.60
Bonnet Lake	3.1	6.8	238	.53
Richardson Mountains	2.9	5.6	32	.47
Blow River Valley and east of Lower Babbage River	3.7	4.4	30	.73

Though we did not quantify the wind and temperature thresholds for oestrid flight, incidental observations in this and previous studies suggest that oestrid flies are active at higher wind speeds than mosquitoes, but require a higher temperature to initiate flight. Because of the problems in sampling for oestrids, and the fact that the best relationships between weather conditions and mosquito activity were for presence/absence of mosquitoes, weather conditions were not used to predict dipteran activity beyond presence/absence. Thus, caribou group dynamics and behavior were related to weather conditions which either favoured both mosquitoes and oestrid flies (wind speed less than 6 m/s and temperature greater than 13°C) or limited their activity (wind speed greater than 6 m/s or temperature less than 13°C). Other subsets of weather conditions were used where indicated.

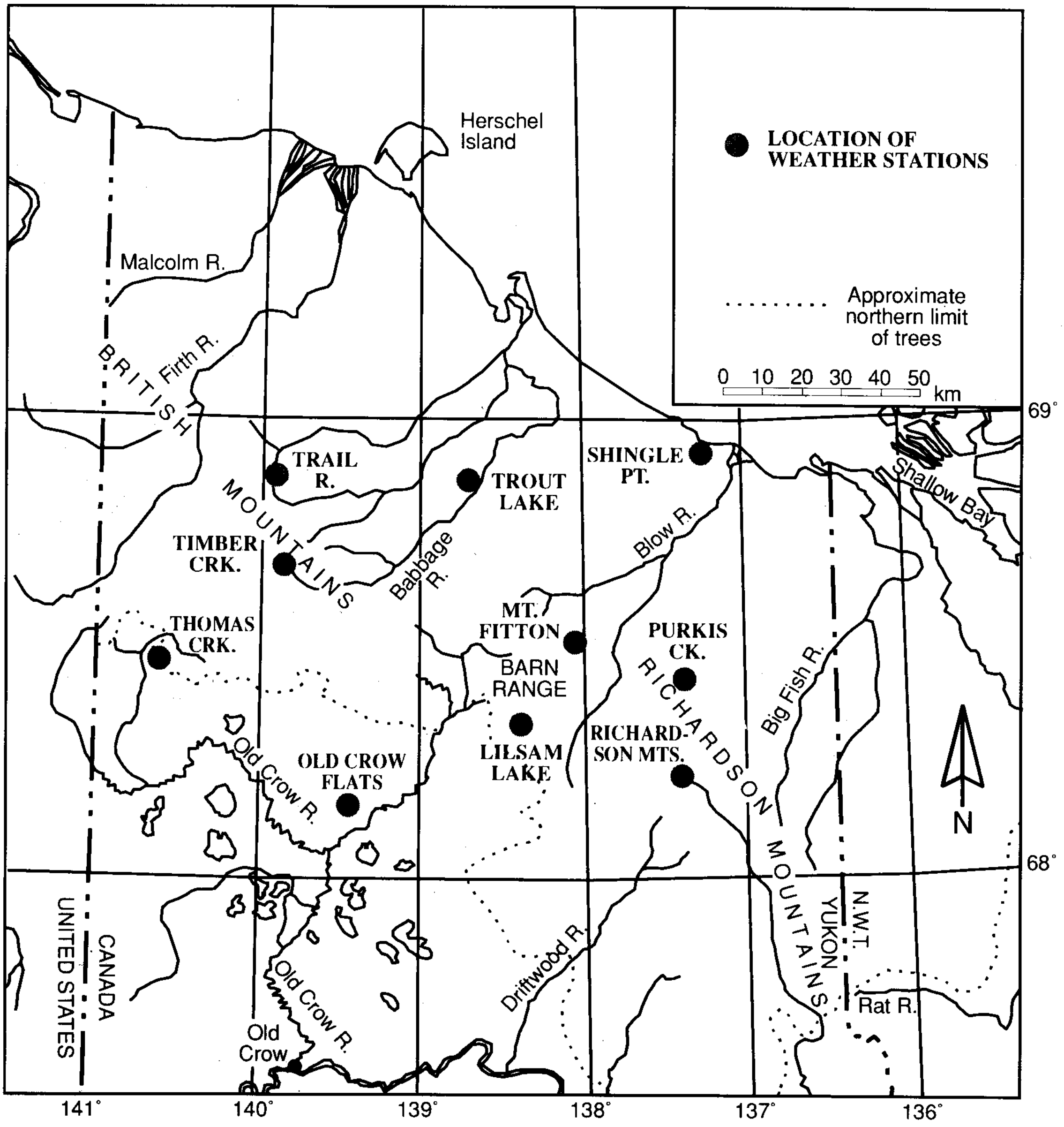

Figure 4.7. Location of weather stations.

Climate and weather patterns

Introduction

As the Porcupine Carbou Herd exhibits rather consistent movement patterns over the years during the insect season and the local activity of insects is strongly influenced by weather variables, it is important to explore the detailed regional weather patterns within the study area in an effort to understand the regional distribution of the herd.

The study area is influenced by two interacting regional climates; the subarctic continental climate and the arctic coastal climate (Ritchie 1984). These types are generally delineated by a line roughly paralleling the coast along the first set of foothills south of the coastal plain region. The line that delineates the two climates corresponds to a 30% isoline, areas south of the line being influenced by Pacific air for over 30% of July, areas to the north for less than 30%. The line shifts annually, dependent on the strengths of the interactions between the polar air mass and the warm, moist Pacific westerlies. The continental climate to the south is distinguished by a rapid transition from winter to spring and by warm, moist summers. Spring is greatly retarded in the arctic coastal climates (Ritchie 1984).

In the process of monitoring and predicting storms surges for Beaufort Sea drilling operations, Atmosphere and Environment Service determined that 8 storm patterns generally influence the study area (Atmospheric Environment Service 1985). In July and early August, the most prevalent patterns result in northeasterly/southwesterly air flows.

Methods

At the end of June, 1986, we deployed 10 remote weather stations throughout the study area (Fig. 4.7) intended to encompass the expected variation in weather patterns in northern Yukon. One station (Roland Creek) was destroyed by a grizzly bear. The remaining 9 provided data until the first week of August. Stations were deployed in similar sites, i.e. within tussock tundra vegetation communities, on flat relatively unobstructed terrain. Each station included CR-21 or CR-21x (Campbell Scientific) data recorders which were programmed to record hourly a range of information including: shaded air and ground temperature, relative humidity, wind direction, wind speed and solar radiation. In addition, weather information collected every 6 hours was obtained from the three permanent weather stations bordering the study area, Old Crow, Shingle Point and Komakuk. No recordings were available from Old Crow at night.

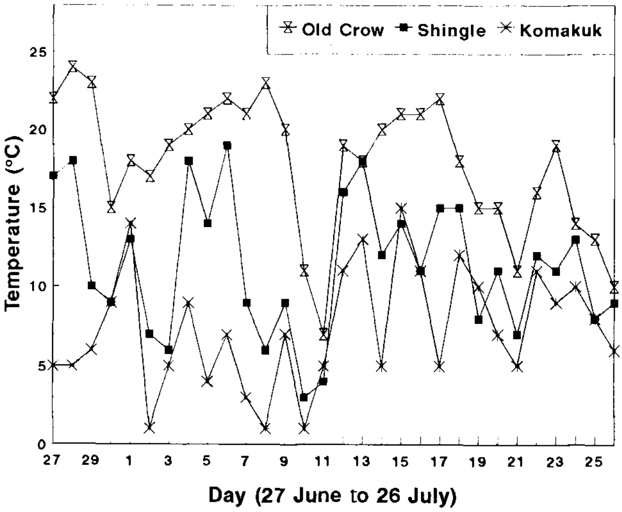

Figure 4.8. Average daily air temperatures at three sites on the summer range of the Porcupine Caribou Herd, 1986.

Results and discussion

Data summaries

There were several problems with the raw data from the automatic stations. Equipment malfunctions required us to disregard a portion of the data sets for Timber Creek and Trail River. Some air temperature values at Timber Creek, Purkis Creek, Thomas Creek and Old Crow Flats were well beyond the range of possibility. Where unrealistic values were evident, air temperature was calculated by multiple regression, using ground temperature, solar radiation and time of day as the independent variables. During the morning hours of 10 July, a strong low pressure system passed through the region, causing strong winds and a significant drop in temperatures. Due to the small size of some of the data sets, this phenomenon may affect all conclusions that are based solely on statistical analyses.

Average daytime air temperatures

At the permanent stations the mean daily temperature was calculated from the 1300 and 1900 hour temperatures. The daytime period was chosen because no nighttime temperatures were available from the Old Crow permanent station. The hours chosen reflect the hottest time of the day since solar noon at this latitude at this time of year is roughly 14:15 PM. Average daytime temperatures for the remote stations were calculated as the mean of recorded temperatures every two hours from 1100 to 2100.

Old Crow enjoys the warmest temperatures among the permanent stations while Komakuk is typically the coldest (Fig. 4.8). Mean daily temperatures at the temporary stations indicate that two groups emerge, those with warmer temperatures (Old Crow Flats, Timber Creek and Thomas Creek; overall mean 17.9°C), and those with cooler temperatures (Purkis Creek, Trout Lake, Trail River, Lilsam Lake, Mount Fitton and Richardson Mountains: overall mean 13.0°C). The Old Crow Flats was the warmest site (mean 19.2°C) and the Richardson Mountains the coolest (mean 10.7°C).

Average hourly air temperatures

The daily curve of the mean hourly air temperatures was of typical sinusoidal shape at five of the temporary stations (Mount Fitton, Purkis Creek, Lilsam Lake, Trail River, Trout Lake; Fig. 4.9A), with an obvious peak around 1600 - 1800 hours. At three of the

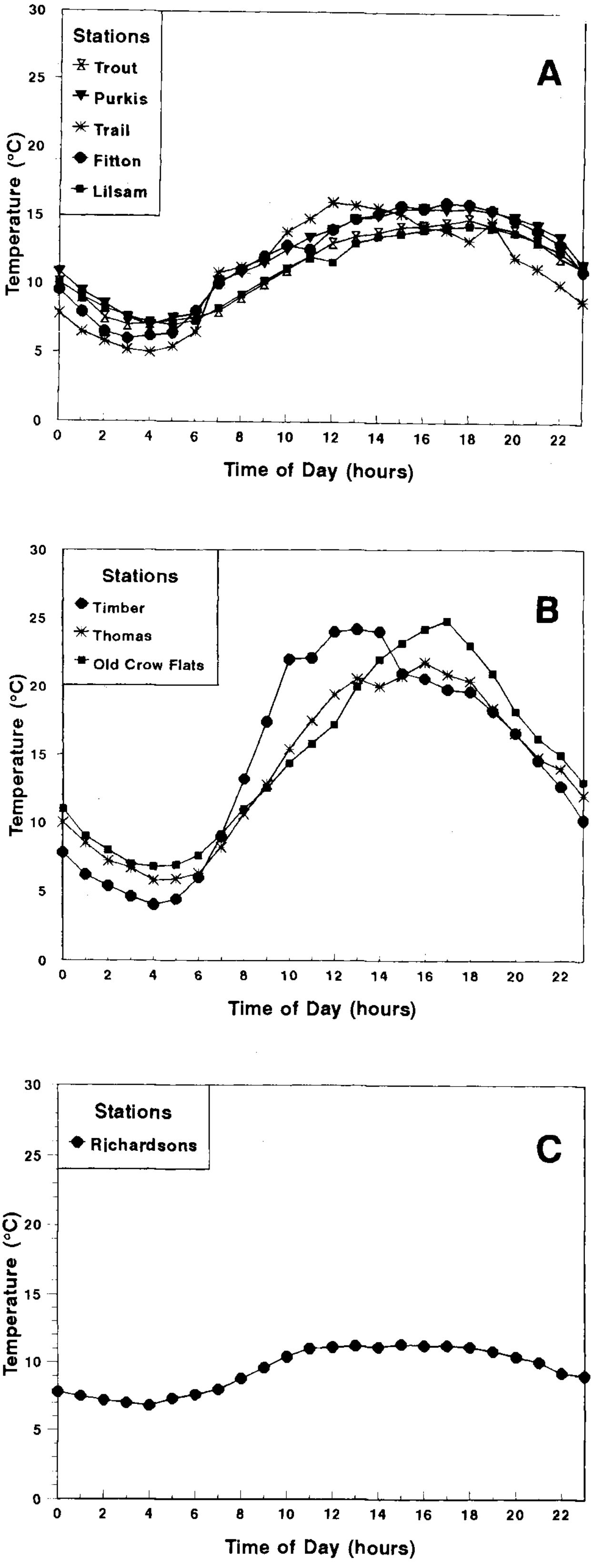

Figure 4.9. Average hourly air temperatures at nine sites on the summer range of the Porcupine Caribou Herd, 1986.

stations (Old Crow Flats, Timber Creek, Thomas Creek: Fig. 4.9B) a much more pronounced daily peak occurred (at 1400 hours at Timber Creek). At Richardson Mountains the daily peak was much dampened (Fig. 4.9C).

Average hourly wind speeds

There is a much less consistent relationship between windspeed and time, using hourly recordings, for the three temperature regions identified in Figure 4.9. This is not surprising as wind speed is more variable than temperature. In spite of the variability, all but one of the stations identified in Figure 4.9A had similar patterns of mean wind speed (Fig. 4.10A). The winds at the Lilsam site were significantly higher than elsewhere. Lilsam appeared to be on the boundary of two systems, as it was common to see winds coming from opposite directions on adjacent small lakes in the area. Most sites experienced a wind lull from 0600 to 0800 hours and a daily peak around 1800 hours (Figs. 4.10A and 4.10B). The Richardson Mountain region exhibited the least variation in daily wind speed, with moderate winds all day (Fig. 4.10C). Mean average daily wind speed was highest at Lilsam and lowest at the Trail River site.

Correlations between permanent and temporary sites

Correlation tables were calculated for the period 27 June – 26 July for readings at 0700, 1300 and 1900 hours. These tables include;

1. temperature and wind correlations between permanent and temporary stations (Table 4.2).

2. temperature and wind speed correlations between temporary stations (Table 4.3).

We were able to determine strong air temperature correlations for most stations. Komakuk was invariably the poorest predictor of temperature for all of the temporary sta-

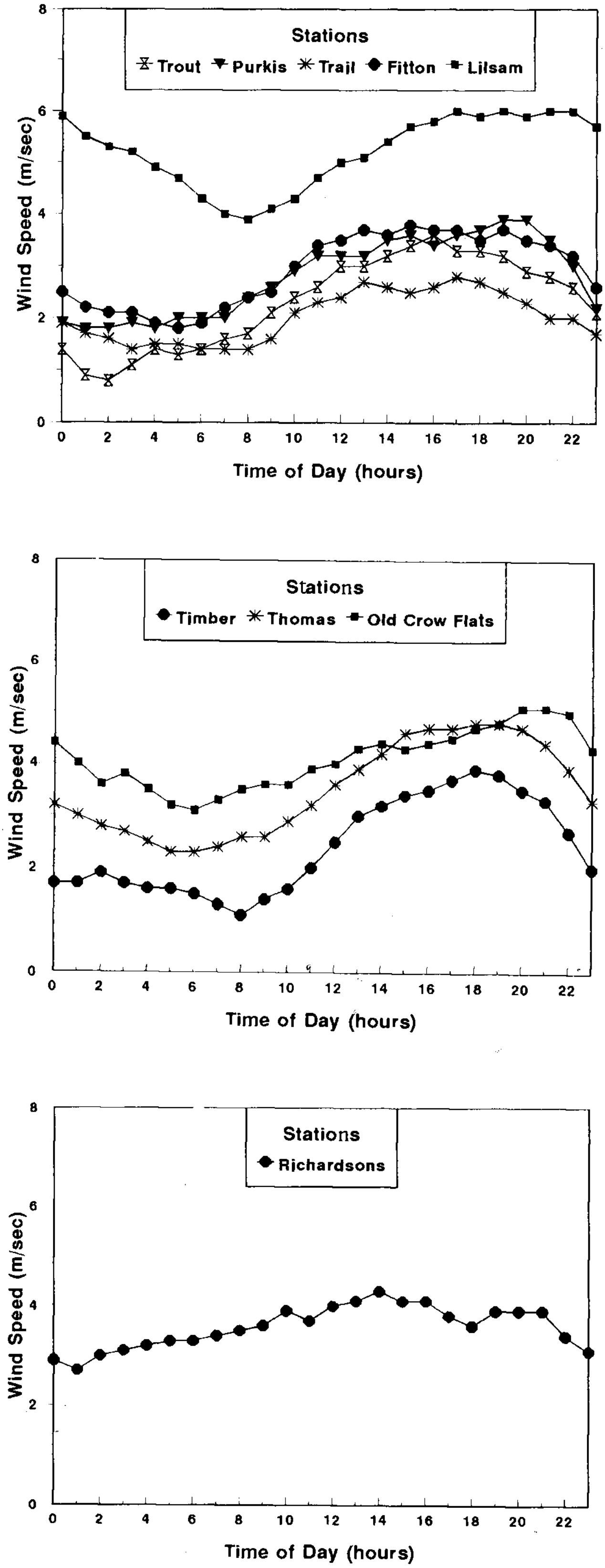

Figure 4.10. Average hourly windspeeds at nine sites on the summer range of the Porcupine Caribou Herd, 1986.

Table 4.2. Temperature and wind correlations between temporary and permanent weather stations on the summer range of the Porcupine Caribou Herd, July 1986.

	Permanent weather station								
Temporary weather station	Komakuk			Shingle			Old Crow		
	Wind	Temp	n	Wind	Temp	n	Wind	Temp	n
Trout	.22	.61	85	.46	.86	83	.24	.79	83
Purkis	.40	.60	79	.49	.88	77	.37	.78	77
Trail	.32	.32	48	.41	.56	49	.28	.64	48
Fitton	.14	.59	83	.55	.83	81	.58	.79	82
Timber	.15	.26	85	.44	.54	83	.43	.80	83
Lilsam	.02	.49	86	.35	.80	84	.54	.85	84
Richardson	.01	.34	86	.09	.65	84	.40	.83	84
Thomas	.24	.29	82	.43	.55	80	.40	.88	81
Old Crow Flats	.04	.38	82	.38	.63	80	.63	.91	81

tions. Shingle Point was a good predictor of temperatures for Trout Lake, Purkis Creek and Mount Fitton while Old Crow proved the best predictor of temperature at all the remaining temporary stations. Using this combination the lowest correlation coefficient we would have to employ is 0.80 with the single exception of Trail River (0.64). Among the temporary stations Lilsam Lake provided the highest mean correlation to all other stations (mean 0.86, range 0.72 - 0.96). For wind speed, the correlation coefficients were not as good as for temperature. Using the highest correlation coefficients between permanent and temporary sites, the mean correlation would be 0.49 (range 0.40 – 0.63). Although all of the correlations were significant, the resulting accuracy was less than we had hoped. Among the temporary stations, correlations were only marginally better. Mount Fitton provided the highest overall predictability among stations with a mean correlation coefficient of 0.57 (range 0.48 – 0.68). If only one remote station was to be established in the study area, the Mount Fitton site would be the most valuable, due to the highest correlation with wind and a very good correlation with temperature (0.83, range 0.66 – 0.96).

Regional weather versus insects

From the tabular summaries of average hourly temperatures, and using our algorithm for INDEX of mosquito and oestrid fly activity, we were able to rank the weather stations in terms of potential insect harassment (Table 4.4). One of the major factors that we were not able to consider was habitat type. We assumed that with equal weather parameters, wetland areas would produce more mosquitoes than drier terrain types. From our analysis, the Richardson Mountains and Lilsam Lake stations appeared to be significantly more favourable in terms of insect relief than all the other sites. Cool temperatures and moderate winds at the Richardson station indicated that it was the most favourable site for oestrid fly relief and the second most favourable site for mosquito relief. The Lilsam Lake site provided the best conditions to avoid mosquitoes, and the second best for avoiding oestrid flies. At the other end of the scale, Timber Creek, Trail River and Purkis Creek were the least favourable for mosquito relief, while Timber Creek, Old Crow Flats and Thomas Creek were the least favourable for oestrid fly relief.

Table 4.3. Temperature and wind Spearman correlation matrix among temporary weather stations on the summer range of the Porcupine Caribou Herd, July 1986.

		Temperature correlation								
		Trout	Purkis	Trail	Fitton	Timber	Lilsam	Richardson	Thomas	Old Crow Flats
WIND CORRELATION	Trout	–	.96	.68	.94	.77	.92	.81	.80	.82
	Purkis	.59	–	.67	.96	.76	.94	.85	.77	.80
	Trail	.60	.53	–	.66	.81	.72	.72	.70	.64
	Fitton	.68	.55	.52	–	.73	.96	.87	.76	.79
	Timber	.57	.36	.58	.65	–	.77	.75	.93	.86
	Lilsam	.31	ns	ns	.56	.64	–	.92	.81	.84
	Richardson	ns	.30	ns	.47	ns	ns	–	.77	.77
	Thomas	.55	.41	.58	.54	.69	.55	ns	–	.95
	Old Crow Flats	.38	.29	.41	.57	.68	.65	.39	.57	–

ns=not significant

Table 4.4. Mean daily oestrid fly and mosquito harassment indices for the temporary weather stations on the summer range of the Porcupine Caribou Herd, July 1986.

Station	Oestrid index	Mosquito index
Old Crow Flats	0.28	0.22
Timber Creek	0.36	0.31
Richardson	0.03	0.12
Trail River	0.21	0.29
Trout Lake	0.16	0.25
Mount Fitton	0.21	0.24
Purkis Creek	0.24	0.28
Lilsam Lake	0.09	0.04
Thomas Creek	0.26	0.20

Response of groups and individual caribou to insect harassment

Introduction

A few studies have attempted to quantify the relationship between caribou behavior and activity and the presence of insects on summer range. Roby (1978) found group size was positively correlated with his subjective measure of mosquito activity. White *et al.* (1975) showed that caribou in the Central Arctic Herd segregated and formed small groups on days with little or no insect activity, and formed larger mixed groups on days when mosquitoes and oestrid flies were active. Helle and Aspi (1983) attempted to quantify how group formation might serve to reduce attack of insects on reindeer in the middle of a group vs. reindeer on the periphery of a group or on solitary individuals outside the group. They conducted an experiment with insect traps that simulated the size and shape of reindeer and found that significantly fewer insects were caught in the middle of a group of traps. However, their results have limited application as the trials were run in the absence of wind on small groups of traps. The effectiveness of group formation in reducing contact between caribou and insects is unclear from these studies, although the occurrence of large groups during periods of insect harassment has been consistantly reported.

The first objective of this part of the study was to relate caribou group response to different weather conditions which either favored or limited insect activity. We predicted that when insects are active and winds are calm or low, caribou will form larger, tighter groups.

The second objective was to relate the display of annoyance responses to weather conditions that favored or inhibited insect activity, while considering possible sources of individual variation among caribou. Annoyance responses were used as an index of the level of harassment experienced by individual caribou. We predicted that when weather conditions favor insect activity, caribou will exhibit more frequent annoyance responses (head shaking, foot stamping, ear flicking, etc.).

The third objective was to determine the advantage or disadvantage of occupying certain positions in a group. We predicted that when insects are active and winds are low or calm, caribou in the core of a group will display fewer annoyance responses than those on the periphery. When insects are active and winds are moderate, caribou on the windward side of a group will display fewer annoyance responses than those in the core or leeward side of a group. We also predicted that caribou on the leeward side of the group will attempt to move to the centre or windward side of the group.

Methods

In past years, several caribou in the Porcupine Herd have been fitted with radio-collars (Garner and Reynolds 1986). During our study period, groups of caribou were located daily (when weather permitted) using radio-telemetry. Daily straight-line movement rates of individuals were determined from successive relocations of radio-collared caribou.

In 1984 and 1985, estimates of group size and group composition were recorded for each group of caribou located during radio-telemetry flights. From the air, a group was defined as three or more caribou within 100 m of each other. Group size was estimated to the nearest 1000 for groups larger than 1000, and to the nearest 100 for groups smaller than 1000. Group composition was recorded as: mixed age and sex, predominately bulls or predominately cows. Weather conditions were not consistently recorded in conjunction with these observations of group size. The data were combined with ground observations on group size to determine the relationship between group size versus date and weather conditions.

The average spacing between the majority of caribou in the group was recorded. Inter-animal spacing was gauged by estimating the number of adult caribou lengths between individuals, using 1.5 m as the approximate length of an adult caribou. The categories used for spacing were: less than 1m, 1 to 4.9m, 5 to 9.9m, 10 to 14.9m, 15 to 24.9m, 25 to 49.9m and 50 to 99.9m.

In 1985, detailed observations of caribou activity patterns and behavioural response to insects were made between 3 July and 6 August. Mosquitoes and oestrid flies were active during this period, though the timing and duration of insect activity varied with date and weather. When a group of caribou was located, two to four observers were placed within walking distance of a vantage point near the caribou. Observations were made by one observer with a 20–40 x variable power spotting scope, while a second person timed the behaviours using hand-held stop watches or recorded data directly into an Epson HX20 (TM) field computer.

On the ground, group size was estimated to the nearest thousand for groups larger than about 1000, and the nearest 100 for groups between about 500 and 1000. A total count was made of groups smaller than 500. For the focal animal observations, an individual was chosen from each of the windward, core or leeward positions. Although most groups observed were of mixed age and sex, the majority of animals (and observations) were of cows with calves. Spacing in the immediate area of the focal animal was recorded. Caribou annoyance responses were recorded as individual events because their short duration made accurate timing impossible. Annoyance responses included head shaking,shaking of back and rump, tail flicking, ear flicking, stomping of foot and leg, and head dropping to the ground.

Two quantitative methods were used to determine the degree of harassment experienced by individual caribou occupying different positions within a group. The first method measured frequency of annoyance responses and activity patterns on a focal animal for a five-minute period. The second method recorded the time interval between the start of an observation on a focal animal and the first annoyance response displayed by that animal.

In the first method, a caribou was observed continuously for five minutes while age/sex, proportion (%) of hair shed, activity, annoyance responses, habitat occupied, and local weather conditions were recorded. Individuals were classified as cow with a calf, cow without a calf, yearling, mature or immature bull. The amount of hair shed was estimated to the nearest 5% on each caribou.

For analysing the advantage or disadvantage of being in a certain position in a group, only groups with inter-animal distance of less than 10 m were used. Caribou that were 10 or more meters apart were assumed to have equal exposure to wind regardless of the configuration of the group and were defined as being in loose groups. A group had to have at least 7 animals in diameter in any direction so that the central caribou was at least three caribou bodies inside from any peripheral animal. This generally was not a problem as most groups observed were composed of several thousand caribou. Position in a group was categorized as windward, core or leeward. The windward and leeward positions were combined as «peripheral» position for some of the analyses. The core was defined as the centrally located 20% of individuals in a group.

Few caribou remained in the same position within a group for the entire five minute period, so position was recorded both at the start and end of an observation period. For analysing the advantage or disadvantage of occupying a certain position, only the start position was used, so long as the individual remained in a tightly spaced group for the entire period. The distance an individual moved in five minutes was categorized as 0, >0 and <10m, >10 and <100m or >100m.

The second method used to determine harassment experienced by individual caribou was designed to collect a large sample from different age/sex classes of caribou in different positions within a group. Individuals were chosen from each position and the time from the beginning of each observation to the time of the first annoyance response was recorded. This measure of time falls anywhere along the interval between two annoyance responses, so the mean of this measurement should be equal to half of the «real» interval time. A longer mean recorded time should reflect a longer mean interval between annoyance responses, indicating a lower frequency of annoyance responses. This measure of time is referred to as the «response interval» with the understanding that it does not represent the true interval. The type of annoyance response, age/sex of the caribou, proportion (%) hair shed, habitat occupied, activity and local weather conditions were recorded concurrently with these observations. Response frequency and response interval provided independent measures of harassment experienced by the caribou.

The level of harassment experienced by individual caribou in one position relative to another position in a group was tested by comparing the response frequency and the response intervals of individuals in different position categories.

Linear regression was used to test the relationship between group size and date. Kruskal-Wallis test, Mann-Whitney and Friedman's two-way analysis of variance on ranks of group size, spacing and movement rates were used to determine the relationships between each of these variables and categories of weather conditions and date. In many cases, date was treated as either the first half (1 July 1 - 18 July) or second half (19 July - 5 August) of the study period.

To analyse changes in group size, spacing and movement rate, the first record of these characteristics for each group on each day was used. If there was a significant change in weather (i.e. from weather conditions unfavorable for insects, to weather conditions favorable for insects or vice versa), a second observation of group size, spacing and movement rate was included in the data set.

Spearman's rank correlation coefficients were produced to determine the relationship between annoyance responses and all weather variables. Kruskal-Wallis tests, and Friedman's tests (two-way and three-way analysis of variance on ranked values of the dependent variables response frequency and response interval) used to determine their relationship with the independent variables: percent of hair shed, sex, date, location, habitat type, position in group, and weather conditions which either favored or limited insect activity. Few observations were made on yearlings and calves, so these were not included in the analyses done with the independent variables. Because of small sample sizes in the response frequency data, some of the categories of certain variables were grouped for analysis (e.g. habitat).

Results

Group dynamics

Based on radio-tracking surveys in 1984 and 1985, the maximum estimated group size observed was higher in early and mid July than in the last week of July. However the absolute number of animals in the study area also declined by the latter half of July.

In 1985, more detailed weather data were collected concurrent with observations of group size. There was no significant relationships between group size and weather conditions.

When all recorded observations of spacing were combined, we found no significant difference in spacing between the first and second half of the study period (Analysis of variance, F=0.93, p=0.33). We did find significantly tighter spacing (1-4.9 m) when weather was favorable for insects, compared to spacing of 5 to 9.9 m when it was unfavorable (Analysis of variance, F=38.55, p= <0.001).

Annoyance responses of individual caribou

Early in July, all cows had shed less than half their hair, while several bulls were already in an advanced stage of shedding. Later in July, about 85% of the cows observed had shed less than half their hair, while 86% of the bulls observed had shed more than half their hair. There was a significant relationship between sex and % shed over the entire study period (Kruskal-Wallis, X^2 approximation=682, p= <0.001, n=1352).

The most commonly observed annoyance responses were head shakes; head drops were the least common. Cows displayed a higher frequency of back shakes and head shakes, while bulls displayed more frequent head drops and foot stamps. There was no significant difference in mean response frequency or mean response interval between the sexes or between caribou less than 50% shed versus 50% or more shed.

Caribou annoyance responses in relation to date and weather

Linear regression analysis of mean response frequency vs. weather variables indicated that both wind speed (r^2=0.31, p=0.03) and temperature (r^2=0.41, p=0.001) were significant, although the r^2 values were low. A quadratic regression with wind/temperature INDEX (r^2=0.049, p=0.02) gave a higher r^2 than wind speed or temperature. Regression analysis with mean response interval was only significant for temperature (r^2=0.35, p=0.02). Regressions with date were not significant for response frequency or response interval.

Mean values of annoyance responses indicated a higher frequency earlier in later July (14.5/min vs. 7.5/min). and a lower response interval (27.5 s vs. 41.1s). The mean response frequency recorded for caribou increased when weather was favorable for insects, and the mean response interval declined. In the two-way analysis of variance on ranks of response frequency and response interval, the date – weather effects were not significant, so there was no interaction between the dependent variables.

Relationship between position in group and insect harassment

We examined position in a group to determine if any advantage in occupying the core position was gained at low wind speed (< =3.5m/s) vs. moderate wind speed (>3.5 to 9 m/s). For the response frequency and response interval measurements, position was significant for both categories of wind speed (Friedman's F= 12.5, n=54 for low wind speed; F=17.8, n=68 for moderate wind speed). At low wind speed, the mean response frequency was lowest in the core position (8.2/min – core vs. 16.3/min - peripheral), suggesting that caribou occupying that position were less harassed. The mean response interval was longer in the core at low wind speed (56.7 s – core vs. 36.5 s – peripheral), also suggesting that caribou occupying the core were less harassed.

When wind speed was moderate, the mean response frequency was lower in the peripheral positions (5.2/min) than in the core (14.1/min). Mean response interval was slightly longer in the peripheral positions (35 s) and shorter in the core (33 s). Thus, at moderate windspeed, caribou in peripheral positions were less harassed.

Discussion

Caribou group dynamics

Contrary to our hypothesis, weather conditions that favored or limited insect activity did not account for variations in group size. Groups size was strongly related to date. Assuming that formation of large groups is an adaptive response to insect harassment, it is possible that most groups observed were already large enough, and that further grouping would not increase the advantage of occupying a group. Baskin (1970) reported «little change in defensive capacity» against insects for groups larger than 3000 caribou. The mean group size we observed over the 1985 study period was approximately 4900.

The decline in group size after mid July probably coincided with a decline in the mosquito population, though mosquitoes were not sampled systematically in 1984 and 1985. In 1986, the mean number of mosquitoes caught did decline significantly after mid July. The reduction in mean group size could be explained by the reduction in the number of caribou in the study area in the latter half of July in both years.

An increase in genetic fitness, derived from forming large dense groups when insects are active, can be hypothesized. The ultimate cause of such behaviour may be «selfish avoidance» as suggested by Hamilton (1971). As a member of a group, the probability of attack (by a predator or parasitic insects) is reduced for individuals, providing that the group is not more easily detected by predators. If caribou in large groups have reduced contact with insects they would experience less irritation and blood loss from mosquitoes and have a smaller parasite load than caribou in small groups.

The decline in group size later in July may be related in part to forage quality. After first leaf-out, the quality of forage (especially shrubs) declines (Skogland 1980, Kuropat and Bryant 1983, this study). Caribou in smaller groups may have an advantage in selecting microsites where vegetation is in an earlier phenological stage. A combination of mosquito and oestrid fly harassment, forage quality, and/or presence of predators may influence group size, but it is difficult to sort out the ultimate causal factors.

The results of our study supported the hypothesis that tighter groups would form when weather favoured insect activity. Our observations agree with other studies on barren-ground caribou that report greater spacing in groups of caribou when weather conditions preclude insect activity (Curatolo 1975, Roby 1978, Dau 1986).

Behavioral responses of individual caribou

The lack of difference in mean response frequency or mean response interval between caribou of different sex or different degree of hair shedding suggests that warble flies were not cueing in on caribou with most hair shed. If warble flies are attacking both sexes equally, larvae that hatch out of eggs laid on female caribou may still be less successful in reaching the epidermis due to greater difficulty in traversing thick, dense winter pelage. We found a difference in the types of annoyance responses displayed by bulls and cows, but this would not necessarily explain the documented difference in warble larvae infestation (Kelsall 1975).

Our results supported the hypothesis that caribou display more frequent annoyance responses when weather conditions favored insect activity. The decline in annoyance responses later in the study period may reflect the phenology of the mosquito population. We have no data to relate this decline to phenology of oestrid flies.

The most common response observed among caribou – head shaking – may have indicated either oestrid fly or mosquito harassment. The types of annoyance responses attributed to mosquito harassment and oestrid fly harassment probably overlap considerably, apart from the «head drop» which is a characteristic response to nasal bot flies (Espmark 1967).

Position in a group

Our results regarding the advantage or disadvantage of occupying a certain position in a group suggest that, at the lower range of wind speed, caribou in the eore experience less harassment. Such caribou did display responses to insect attack, so they were not evading insects entirely. At the higher range of wind speeds there was an apparent advantage in occupying one of the peripheral positions.

Activity budgets, food and habitat selection

Introduction

In addition to forming aggregations, caribou and reindeer change their activity pattern at moderate or high levels of insect harassment, and spend less time feeding and more time moving or standing (Curatolo 1975, White *et al.* 1975, Thomson 1977, Boertje 1981, Fancy 1983, Thing 1984). Several studies have reported that, during periods of harassment, caribou and reindeer spend more time in habitats with typically fewer insects such as windswept ridges (Surrendi and DeBock 1976, Skoog 1968), gravel or sandy areas (White *et al.* 1975, Helle and Aspi 1984), or snowbeds (Thomson 1977).

The summer months are critical for the Porcupine Caribou Herd. In winter, caribou cows will draw heavily on their energy and nutrient reserves (Adamczewski *et al.* 1986). During the short season that green vegetation is available, they must replenish these reserves or their reproductive capability will be limited (Thomas 1982).

Disrupting the normal activity budgets of caribou can have important energetic implications. Modelling studies have demonstrated that the decrease in time spent feeding, with a corresponding increase in time spent running, has a surprising multiplier effect on the daily energy balance of an individual (S. Fancy and R. White pers. comm.). This consideration is even more dramatic when the caribou are close to, or in, a negative energy budget under normal conditions.

The first objective in this aspect of our study was to document the normal activity budgets of the Porcupine Herd on their summer range, paying particular attention to the role of insect harassment on the determination of activity budget. With such dynamic relationships in hand, we can then begin assessing the implications of additional man-caused disruptions during this critical period. We predicted caribou would alter their activity pattern, and reduce their feeding intensity when dipterans were active.

The second objective was to relate movement rate of individual caribou to weather conditions which favored or limited insect activity. We predicted that as insect activity increases, caribou increase their rate of movement, they move into the wind, and they spend more time moving.

Methods

Data were obtained during the summers of 1984-85 from early July until the first week of August, as described in the preceding section. Both 15 minute scans and 5 minute continuous observations were used to determine the relationship between insect harassment, activity, food and habitat selection. Activities included feeding, feeding intensity (eating time/total active time), walking, standing, lying, and trotting/running. Observations on caribou activity were analysed using presence or absence of mosquitoes and oestrid flies as catagories.

Nine composite fecal samples were collected during the summer of 1984. Our objective was to compare the composition of feces from caribou that were severely harassed by insects, and thus spent extended periods in sub-optimal forage areas (eg. barren ridges, scree slopes) with that from caribou which were relatively unharassed and thus able to forage freely. We assumed a 12 hour rumen turnover rate during the summer months (White and Trudell 1980) and therefore collected samples from groups of animals that had been under observation over a 24 hour period. For example if we observed caribou confined to ridge tops from 0800–1600 hours we collected the fecal samples from the same group around midnight of the same day. A collection consisted of 10 pellets from each of 20 fecal groups, thus 10 replicate samples could be analysed.

As in other phases of the study, fecal composition analysis was carried out at the Plant Composition Lab, Fort Collins, Colorado and correction factors were applied in order to correct for differential digestibility of the different plant groups, (Duquette 1984).

Results

Movement rates of caribou

A total of 667 locations of radio-collared caribou were plotted during the 1985 field season. Based on minimum straight line distances between successive locations, the mean movement rate was 10.9 km/day (range 1.5 - 21.2 km/day). Movement rates decreased significantly later in the study period ($r^2=0.21$, $p=0.01$). We could not record wind speed and temperature in the proximity of each radio-collared caribou

Table 4.5. Summary of proportion of time in summer the Porcupine Caribou Herd spent in various activities when insects were present or absent.

Year	Insects	Scans	Feed	Lie	Stand	Walk	Trot/run
1984							
All data		286	.32±.09	.16±.05	.24±.08	.19±.04	.09±.04
Mosquitoes	present[1]	175	.25±.03	.14±.03	.30±.05	.20±.03	.11±.03
	absent[2]	111	.44±.05	.20±.04	.14±.04	.16±.03	.05±.02
Oestrids	present[3]	165	.27±.04	.10±.02	.34±.05	.18±.03	.11±.03
	absent[4]	121	.40±.04	.25±.05	.10±.03	.19±.04	.06±.03
1985							
All data		873	.38±.04	.13±.05	.24±.08	.18±.02	.06±.02
Mosquitoes	present	646	.36±.02	.11±.01	.28±.03	.19±.02	.06±.01
	absent	227	.46±.04	.20±.03	.12±.03	.17±.02	.06±.02
Oestrids	present	530	.38±.02	.09±.01	.30±.03	.16±.02	.06±.01
	absent	343	.39±.03	.20±.03	.14±.03	.21±.02	.06±.02
All years							
All data		1159	.37±.04	.14±.04	.24±.06	.18±.02	.07±.02
Mosquitoes	present	821	.33±.02	.12±.01	.28±.02	.19±.01	.07±.01
	absent	338	.45±.03	.20±.03	.12±.02	.17±.02	.06±.02
Oestrids	present	695	.36±.02	.09±.01	.31±.02	.17±.01	.07±.01
	absent	464	.39±.02	.21±.02	.13±.02	.21±.02	.06±.02
Both	present[5]	589	.33±.02	.09±.01	.33±.03	.17±.01	.07±.01
	absent[6]	155	.45±.04	.25±.04	.10±.03	.16±.03	.04±.01

1: if wind speed less than or equal to 6 mps or temperature greater than or equal to 7°C
2: if wind speed greater than 6 mps or temperature less than 7°C
3: if wind speed less than or equal to 9 mps or temperature greater than or equal to 13°C
4: if wind speed greater than 9 mps or temperature less than 13°C
5: if wind speed less than or equal to 6 mps or temperature greater than or equal to 13°C
6: if wind speed greater than 9 mps or temperature less than 6°C

in order to test movement rates in relation to weather. After 18 July, when the majority of caribou were in a region that was subsequently found to have fewer mosquitoes (Richardson Mountains), they still moved an average of 8.9 km/day.

Movement rates determined from the instantaneous scan observations were tested in relation to weather and date. We predicted that movement rates would be significantly faster when weather favored insect activity. In 1984 and 1985, there were no significant differences in movement rates based on weather that favored or inhibited dipteran activity (1.6 km/h vs. 0.6 km/h). In 1984, movement rates declined significantly later in the season while in 1985 movement rates did not change significantly with date.

Direction of movement in relation to wind direction was also determined from the instantaneous scans. Chi-square analysis showed a significant relationship between direction of movement and wind direction in 1984 (X^2=0.64, p=0.01, n=219), but not in 1985 (X^2<0.01, p=0.98, n=645). In 1984, when weather conditions favored insect activity, more caribou moved into the wind than would be expected by chance.

Activity budgets and feeding intensity

A total of 1159 scans (286 - 1984; 873 - 1985) were recorded during July and August under a variety of weather conditions. There was no significant difference in activity budgets between the two years, except for proportion of time spent walking, which was higher in 1985, primarily in late summer. In 1984 there was no significant difference in activity budgets between early and late summer. In 1985, time spent feeding was significantly higher, while time spent standing and lying was significantly lower in early than in late summer.

The 15 minute scans showed a significant shift in activity budget when insects were active in both 1984 and 1985 (Table 4.5). Once weather conditions became favorable for mosquitoes and oestrid flies, there was a decrease in time spent feeding and lying, and an increase in time spent standing.

The 5 minute continuous observations also showed an increase in proportion of time spent standing (from 11% to 20%) when weather was favorable for insect activity (Mann-Whitney, U=2.11, p=0.03). Feeding intensity was 14% lower when insects were active (Mann-Whitney U=-3.6, p<0.01). However, there is a link between the different feeding intensities observed for caribou in different habitat types and under different weather conditions. When insects were active, more observations were made of caribou feeding in barren and sparsely vegetated *Dryas* habitat types than was expected by chance (Table 4.6). In these habitats we would expect to observe lower feeding intensities among caribou.

The 15 minute scans showed that the proportion of time caribou spent walking and running was not significantly affected by insect harassment (Table 4.5). However, the five minute continuous observations indicated that the proportion of time spent moving increased significantly (from 18% to 25%) when insects were active (Mann-Whitney, U=-2.2, p=0.03).

Diurnal activity

Using the weather data obtained during our observations, we calculated the mean mosquito and oestrid fly harassment levels throughout the day. The two values generally tracked each other with a strong increase from 0900 to 1100 followed by a gradual decline from 1700 to 2200. Our observations from 2300 to 0800 were too few to determine a total 24 hour pattern. However, from recordings at automatic weather stations, we know that mosquito harassment does occur most evenings (lesser amounts at cool temperatures) while oestrid fly harassment is essentially nonexistent from roughly 1100 to 1900.

We combined all observations on caribou for July and August, to determine if any diurnal activity patterns existed during the study period. Based on a combination of feeding, walking and running, caribou appeared most active prior to 1000 and after 1700. The patterns were not very distinct, possibly due to the variation in insect activity from day to day (Fig. 4.11). Feeding appeared sporadic throughout the day, with an indistinct lull at midday. Standing and lying appear to be almost

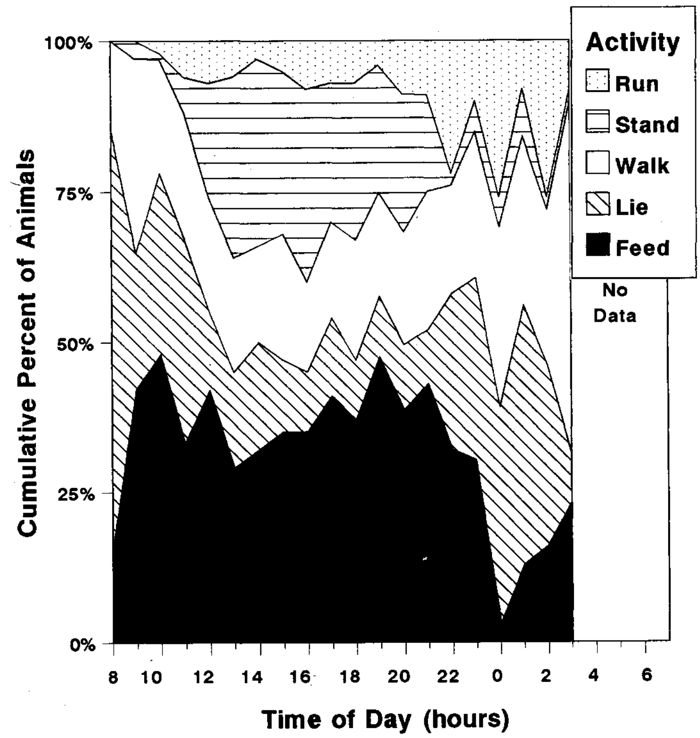

Figure 4.11. Diurnal pattern of various activities recorded for the Porcupine Caribou Herd in summer of 1984 and 1985.

Table 4.6. Vegetation types and position selected by the Porcupine Caribou Herd in relation to insect activity, n (%)[1].

Insect activity	Position	Tussock tundra	Sedge meadow	Sedge heath/ heath	Dryas barren	Forb heath	Alluvial gravel & rock	Dense willow	Lichen barren	Open spruce	Low shrub tundra	Total
Present	Crest	0 (0)[1]	0 (0)	8 (5)	21 (10)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	10 (25)	39 (7)
	Upper slope	0 (0)	0 (0)	50 (31)	91 (42)	1 (20)	15 (71)	1 (3)	0 (0)	0 (0)	21 (52)	179 (31)
	Mid slope	4 (21)	21 (32)	52 (32)	79 (37)	0 (0)	4 (19)	1 (3)	11 (92)	0 (0)	3 (8)	175 (30)
	Lower slope	0 (0)	0 (0)	8 (5)	7 (3)	4 (80)	0 (0)	26 (87)	1 (8)	7 (100)	1 (2)	54 (9)
	Valley floor	14 (73)	34 (52)	25 (15)	17 (8)	0 (0)	2 (9)	0 (0)	0 (0)	0 (0)	5 (13)	98 (17)
	Plain	1 (5)	10 (15)	18 (11)	0 (0)	0 (0)	0 (0)	2 (7)	0 (0)	0 (0)	0 (0)	31 (6)
	Total	19 (3)[2]	65 (11)	161 (28)	215 (37)	5 (1)	21 (4)	30 (5)	12 (2)	7 (1)	40 (7)	576
Absent	Crest	0 (0)	0 (0)	3 (1)	5 (2)	0 (0)	0 (0)	0 (0)	2 (33)	0 (0)	10 (1)	10 (1)
	Upper slope	0 (0)	0 (0)	58 (21)	82 (38)	0 (0)	2 (40)	2 (2)	2 (33)	0 (0)	146 (20)	146 (20)
	Mid slope	6 (11)	4 (13)	101 (37)	62 (29)	0 (0)	3 (60)	32 (33)	2 (33)	0 (0)	215 (29)	215 (29)
	Lower slope	8 (14)	13 (43)	74 (27)	32 (15)	1 (100)	0 (0)	25 (26)	0 (0)	0 (0)	159 (22)	159 (22)
	Valley floor	12 (21)	13 (43)	35 (13)	32 (15)	0 (0)	0 (0)	18 (19)	0 (0)	0 (0)	152 (21)	152 (21)
	Plain	31 (54)	0 (0)	18 (11)	0 (0)	0 (0)	0 (0)	19 (20)	0 (0)	0 (0)	50 (7)	50 (7)
	Total	56 (8)	30 (4)	271 (37)	213 (29)	1 (0)	5 (1)	96 (13)	6 (1)	0 (0)	54 (7)	732
Subjective insect risk level		High	High	High/ Medium	Low	Medium	Low	High	Low	High	High	

1: % of animals observed in vegetation type within a position and insect activity category.

2: % of animals in vegetation type within an insect activity category.

Table 4.7. Percent cover of land cover types found in each sub-region of mapped area.

	British Mountains	Barn Mountains	Richardson Mountains	Coastal plain west	Coastal plain east
Dense shrub slope	2.1	5.7	12.8	0.0	1.7
Low shrub tundra	0.4	2.2	13.5	0.0	1.4
Tussock tundra with 26–35 % shrubs	12.4	12.6	6.7	3.4	10.6
Tussock tundra with 16–25 % shrubs	20.9	26.9	21.1	16.7	23.9
Tussock tundra with 0–15 % shrubs	7.2	17.0	17.0	0.9	9.5
Heath	13.8	9.1	3.8	24.9	13.6
Dryas/sedge	4.5	2.1	1.2	15.9	1.1
Lichen/alluvial	29.3	18.9	17.6	20.6	19.3
Barren rock	9.5	5.6	6.3	9.0	13.3
Wet alluvial	0.0	0.0	0.0	8.6	5.4

inverse (Fig. 4.11). There was a strong peak in proportion of caribou standing between 1000 and 2000, while the proportion lying peaked at 0900 and 2200. We have shown that standing increased primarily at the expense of lying when insects were active. Therefore, standing appears to track the mean harassment levels during the day. Caribou movement (walking and running), although low throughout the study, is most prevalent during the evening hours. We can speculate that this movement corresponds to a decline in mosquito and oestrid fly activity, with caribou moving from insect relief areas toward preferred feeding areas.

Habitat use

Our measure of habitat use was based on the observed location of groups of caribou during the 15 minute scan observations. The 15 minute scans gave a better picture of habitat use than the 5 minute spells of continuous observation. If the groups were dispersed so that they occupied more than one habitat type, they were assigned to two or more habitat types with equal weight for each type. The range type used can be subjectively rated as high, moderate and low »risk» categories in terms of their potential for insect harassment. This subjective rating is based on vegetative characteristics (taller, denser – higher risk), moisture (wetter – higher risk), and physical location (valley bottoms – higher risk; Table 4.6). We hypothesized that caribou would respond to increased insect harassment by choosing lower risk habitats.

Throughout the study period, over one half of the observations on caribou were in heath/sedge heath or *Dryas* barren vegetation types (Table 4.6). When weather was favorable for insect activity, a higher proportion of observations were in *Dryas* barrens and at higher elevations (i.e. upper slopes). When weather was not favorable for insect activity, a higher proportion of observations were in heath/sedge heath and on mid-slope.

As weather became more favourable for insect activity, fewer observations of caribou were made in dense willow and tussock tundra. Both of these communities have a higher risk of potential insect harrasment (Table 4.6). Low shrub tundra was a high risk vegetation type which remained unchanged in percent use with increasing insect activity. However, when insects were active, more observations were made at higher elevations within this community.

From satellite mapping (Russel *et al* 1992a) we determined the relative availability of vegetation types in the British, Barn and Richardson Mountain subregions (Table 4.7). Combining habitat use (Table 4.6) with habitat availability (Table 4.7) we can determine habitat selection for the herd in the summer when insects are present and when they are absent (Fig. 4.12). Dense shrub slopes appear to be avoided when insects are present and selected when they are absent. There also appears to be a stronger selection for *Dryas* communities when insects are present.

Food habits

Deciduous shrubs were by far the most frequent plant group observed in the fecal sample slides, among all samples collected (Table 4.8). However, once correction fac-

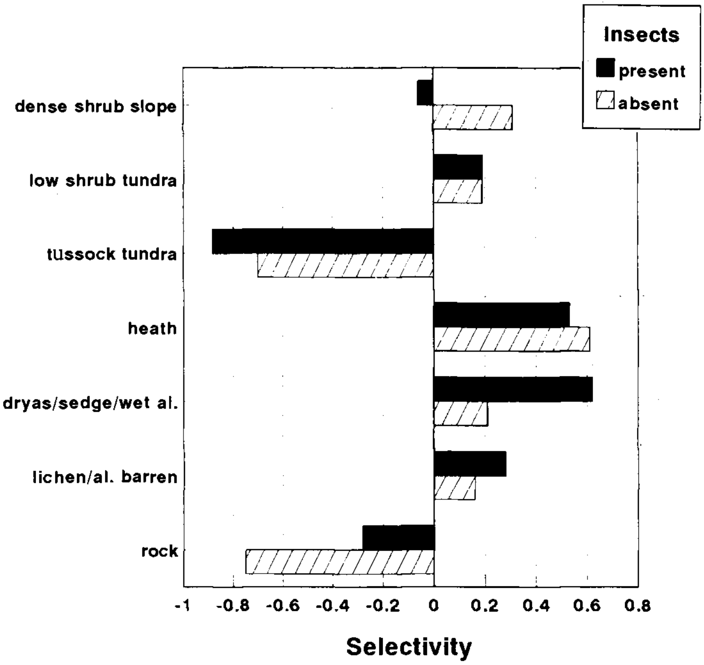

Figure 4.12. Selection of major range types on summer range by the Porcupine Caribou Herd during insect harassment and in the absence of insects.

Table 4.8. Proportion (%) of fragments from different types of plants in the feces of caribou from the Porcupine Caribou Herd in July 1984. The numbers in parenthesis represent an estimate of the composition of the diet of standard correction factors to the data from fecal analysis. (See Methods).

July Date	Insects present	Mosses	Lichens	Deciduous shrubs	Evergreen shrubs	Forbs
8	no	0 (0)	0 (0)	97.6 (47)	1.5 (3)	0.3 (49)
10	yes	0 (0)	0 (0)	95.9 (46)	1.6 (3)	2.1 (50)
15	no	0 (0)	0.7 (3)	96.0 (46)	0.3 (1)	2.7 (50)
20	no	0 (0)	0.3 (1)	96.5 (46)	2.5 (4)	1.1 (48)
22	yes	0.5 (1)	1.1 (4)	90.2 (43)	2.3 (4)	4.6 (45)
24	yes	0.6 (1)	3.2 (12)	80.5 (39)	1.8 (3)	12.3 (44)
25	yes	0 (0)	0 (0)	94.7 (45)	0.5 (1)	4.9 (54)
26	no	0.8 (1)	0.3 (1)	89.2 (43)	6.4 (10)	2.4 (42)
29	no	2.6 (3)	6.2 (23)	85.5 (41)	3.5 (6)	2.9 (24)
Mean		0.5 (1)	1.3 (5)	91.8 (44)	2.3 (4)	3.8 (45)

Correction factors:

Mosses	1.0	Graminoid	1.6
Lichens	3.8	Evergreen shrubs	2.03
Deciduous	0.48	Forbs	100 (total of others)

tors were applied, the contribution of deciduous shrubs was not significantly different from that of forbs (Table 4.8). This illustrates the importance of dietary correction factors.

From the samples collected we were not able to establish any differences between the diet of caribou harassed by insects and those not harassed (Table 4.8). More careful collection of samples would be required to detect actual dietary differences. An important illustration of this point is the composition of the 26 July sample. The group of animals from which the sample was taken was observed standing on a scree slope eating very little, if any, vegetation from 0800 to 2200, making only one brief foray into the valley below to feed. Collection of fresh fecal samples were obtained from where the animals were observed at midnight that night. The sample does not illustrate any difference in dietary composition from the other samples (Table 4.8). During the collection of fresh samples, however, field crews found it extremely difficult to find 10 pellets in any pellet group and those that were found were unusually small. This confirms that when little food is taken, fecal output is reduced, rumen turnover time is increased and the fecal composition reflects the diet of the individuals over much longer than 12 hours.

By contrast, the sample of feces collected on July 24 does reflect an apparent decline in deciduous shrub and forb intake and an apparent increase in lichen intake. During our observations, this group of caribou was confined to drier ridge habitats during insect harassment, however they were observed feeding at irregular intervals in this and adjacent habitats. In this case, total food intake may not have declined significantly, the only effect of the harassment being a shift in species intake from their preferred summer forage.

Our observations cover the transition period from a typically graminoid/shrub diet in late May/June to a lichen diet by early September. The high lichen value documented in the latest sample (24%, 29 July), may be the beginning of a shift toward the lichen dominated fall and winter diet. This shift corresponds with a shift in quality of *Salix* as the season advances. Graminoids were not a significant component of the July diet.

Discussion

Movement of groups and individuals

Our observations did not support the hypothesis that caribou increase their movement rate when weather conditions favored insect activity. However, the proportion of time spent moving did increase significantly. Roby (1978) and Downes (1985) found that the proportion of time spent moving (i.e. running and walking) increased significantly during periods of mosquito harassment. Curatolo (1975), Fancy (1983) and Dau (1986) found that caribou increased their rate of movement, particularly during periods of mosquito harassment. Dau (1986) found more stationary caribou when oestrids were present.

The successful evasion of insects by mobile caribou would depend on the exact rate of movement, the wind speed and the direction of movement in relation to wind direction. Our observations in 1984 support the hypothesis that caribou orient their movement into the wind, but in 1985 there was no relationship between wind direction and direction of movement. Other factors may influence direction of movement, such as orientation toward sparsely vegetated areas or other habitat types that have characteristically fewer insects.

Activity

The relationship between insect harassment and activity of caribou was more clearly defined than the relationship between insect harassment and habitat used by caribou. This may be due in part to the fact that most observations were made during the day, and insects were active most days, although some days had only low levels of harassment. Observations were therefore weighted toward habitats that caribou occupied during the day when insects were bothersome. The few observations that were made on days with few or no insects probably show caribou using lower elevation sites and lusher vegetation communities. Another reason that change in activity is the more clearly defined variable is the fact that it is an immediate response while change in habitat is a latent response.

We found the predominant use of *Dryas* communities throughout the study period surprising, considering that this community type is sparsely vegetated compared to others. It seems possible that one important effect of sporadic, perhaps unpredictable bouts, of insect harassment is that caribou are faced with a trade-off between occupying good forage sites and places where there are few insects. The ideal conditions would then be when good forage sites coincide with good foraging conditions. This combination is found in coastal vegetation communities early in the season when graminoid vegetation provides most of the diet. As willows and forbs increase in importance, the caribou move inland.

The increase in use of the wet sedge communities is significant because they often contain lush willow species in close proximity to windswept ridgetops. Tussock tundra, the most abundant community type at lower elevations, was seldom used even when insects were absent. We conclude that tussock tundra was not utilized primarily because there were few convenient opportunities to reach these communities from the high elevation/ low risk *Dryas* communities. *Dryas* barren communities may provide the optimal trade-off.

Feeding intensity and activity

The decline in feeding intensity with increase in insect harassment was related in part to the habitat occupied by the caribou when weather conditions favoured insect activity. Some sparsely vegetated habitat types were almost devoid of vegetation, so that the caribou could do little feeding. Other studies have also reported a decrease in time spent feeding when insects were active (Baskin 1970, Curatolo 1975, White *et al.* 1975, Dau 1986, Murphy 1988). Thing (1984) reported a five to six fold decline in feeding intensity between periods of no harassment and severe harassment. This has important implications with regard to the energy budget. Fancy (1986) found that reduced ingestion time (ie. energy intake) was more important in overall energy balance than increased walking/running time. Helle and Tarvainen (1984) found that the level of insect harassment in summer affected the yearly variation in calf weights recorded in the fall. The significance of reduced energy intake is important at both the individual and population level, because body condition affects reproductive success (Couturier *et al.* 1988) and adult cows that have not replenished their energy and nutrient reserves by the time of autumn rut are less capable of reproducing successfully (Thomas 1982).

We found that caribou spent proportionally less time feeding and more time standing and running/walking when weather was favorable for insect activity. Other studies have also reported an increase in time spent standing (Baskin 1970, Curatolo 1975, White *et al.* 1975, Dau 1986, Murphy 1988). Stationary *Rangifer* are often vigilant for insects (primarily oestrid flies). Certain annoyance responses are only exhibited when they are standing as opposed to lying (Espmark 1968, Thomson 1977). More time spent standing may better enable caribou to detect oestrid flies and make the appropriate annoyance responses.

Conclusions

Caribou in the Porcupine Herd consistently form large aggregations in early July, a time of year when they are at an energetic low and face a horde of summer insects. We found a significant relationship between insect activity and the density of these groups. By remaining in large, dense groups, the harassment of individuals is reduced. Local insect populations could be swamped by several thousand caribou. However, by opting to remain in large aggregations, an individual caribou severely limits its choice of insect relief habitat. The areas that caribou travel to at this time of year must provide both insect relief and sufficient forage to sustain up to 50,000 caribou for several weeks. Furthermore, the region chosen must be the one that in the long term has the most stable, thus most predictable, environmental conditions. Once in the region, the caribou maximize their energy balance by exploiting habitats and subregions as the conditions of that particular year permit.

Our intention in this study was to determine the relationship between caribou and insects and to assess how the caribou respond to insect harassment while they concurrently maximize their opportunity to feed. We believe that the key to regional, subregional and localized habitat selection by caribou at this time of year is a continuous evaluation of these two factors. The herd has many regional options to avoid insects and there are numerous locations where caribou could obtain optimal forage. Only a few locations offer both in close proximity and sufficient abundance to sustain 50,000 or more caribou for several weeks.

The only criterion for good insect relief is a lack of insects. Using this criterion, obvious choices are sites generally devoid of vegetation and/or exposed to wind such as strips of land along the Beaufort Sea coast and in the water itself, late snowbeds, gravel bars and high windswept ridges. We have documented the use of all of these habitats. Gravel bars and late snowbeds are too few and too small to accommodate large aggregations of caribou. Coastal strips are indeed an important habitat early in the summer (late June - early July). In the northern Yukon the foothills become free of snow first, then melting proceeds northward to the coast. The intermountain regions are last to be snowfree. In late June, coastal habitat provides new vegetation that is high in nitrogen and weather conditions that generally limit mosquito activity.

Once willow leaves emerge in late June, caribou quickly shift their diet. Willows are not very abundant on the coastal plain, so the shift in diet also involves movement inland to the intermountain regions. However, when weather is warm and calm, caribou would encounter mosquitoes in these vegetated areas. Thus groups of caribou must seek relief on mountain slopes and ridges, areas where high convective winds limit insect activity and sparse vegetation offers insects little protection from the wind.

Ideal regions for occupation in early July, when mosquitoes are the major consideration, should provide windy, sparsely vegetated habitat in close proximity to valleys with lush willows and forbs. The region used in late July should contain optimum foraging conditions, as the first part of August marks a decline in insect harassment and a fragmenting of large groups into smaller scatterred bands of caribou.

The herd must constantly be evaluating options. In years of inclement weather, with few insects, the herd can shift into regions with more favorable forage. However, even in those years there appears to be a tendency for herds to remain relatively close to insect relief areas, so that they would not be vulnerable should conditions become more favorable for insects.

One of our tasks was to identify critical insect relief habitats to be protected or avoided should development occur. As an outcome of our work we have attempted to differentiate «primary» insect relief habitat from «secondary» insect relief habitat. By primary relief habitat we mean those areas that are consistently used and provide relief and forage for the herd. These are «destination» areas, the areas caribou remain in for an extended period of time during the brief summer. Secondary relief areas are used opportunistically by the herd while moving to a destination area. While primary areas tend to provide the ideal combination of conditions for that particular year, secondary sites lack certain attributes and cover a smaller area. Because the relief areas may be required by 50,000 or more caribou at one time primary areas tend to be regions rather than isolated sites. Our movement data indicated that even within a primary relief region, caribou still move four to five kilometres per day.

The northern Yukon is comprised of an extremely diverse complex of environments, from wet coastal plains in the north to rocky, windswept ridges in the mountains to the warm pediments in the south. The northern region is influenced primarily by weather systems coming off the Beaufort Sea, the southern region by the warmer northeasterly flows from central Alaska and the intermountain region appears to be influenced by both. If we were asked to predict the weather within the three regions we would say the northern region would be cold, the southern region warm and the intermountain region windy. The upslope wind conditions of the intermountain region provide the relief from insects that the caribou seek. Within this intermountain region three areas have a higher density of shrubby vegetation that form the staple summer diet of caribou; the southeast edge of the British Mountains, the north flank of the Barn Mountains and the entire Richardson Mountains. All three areas could provide adequate forage for the large aggregations of summering caribou, however, they are not used equally.

The southeast edge of the British Mountains appears to be an important region in early to mid July. Caribou use the windswept slopes for insect relief during the days, venturing into the more densely vegetated valleys to the south and southeast when conditions permit. The large aggregations tend to linger in this region in mid July before «deciding» to move east or west. In most years the aggregations split up - some returning west through the upper Firth River into Alaska, the remainder turning east toward the Richardson Mountains which appear to provide the required relief from insect harassment for the remainder of the summer. This area was documented to have the coolest temperatures within the study area. Once in the Richardson Mountains, caribou use the higher elevations of the upper Bell River, and the ridges and valleys to the north. These areas have extensive slopes of lush willow in close proximity to wind exposed ridges, if relief from insects is required. The north flank of the Barn Mountains is used only when insect levels are low, either due to inclement weather or the advance of the season. This region is too far inland to benefit from the coastal breezes and it is too low to produce upslope wind conditions or significantly cool temperatures.

Any land based development in northern Yukon should not proceed without due consideration to protection of the primary insect relief areas we have identified and equally important, unobstructed access to those areas. Finally, any disturbance that could cause large aggregations of caribou to fragment during periods of insect activity, or alter activity patterns such that energy intake is reduced and energy expenditure increased, should not be permitted.

CHAPTER 5. Energetic implications

Introduction

In the previous three chapters we have reported on range ecology at important periods in the life cycle of the Porcupine Caribou Herd. We have linked the characteristics of the biophysical environment with the movements, distribution, food habits, and activity of the herd. We have demonstrated that all factors are inextricably linked and that the herd's viability in the long term is probably dependent upon their ability to respond to annual changes in the environment *and* to continue to have the opportunity to exploit key ranges thereafter.

In this section we take our integration one step further by employing computer-assisted simulation modelling to examine the energetic implications of changes in diet and activity budgets for an individual caribou. Recently researchers studying the Porcupine Caribou Herd have formulated a computerized energetics model that tracks the changes in body composition of a caribou throughout the year (Kremsater *et al.* 1989; Hovey *et al.* 1989).

As a group, we have deliberately constructed the model to incorporate much of the data presently available on the herd and its range. The model provides a valuable «bookkeeping service», allowing us, for example, to monitor energy intake over the year, based on our knowledge of feeding times, diet composition and nutrient quality of forage at various stages of phenology. The simulation program allows us to integrate observed changes in diet and activity within and between years, conduct sensitivity analysis to examine which variables contribute most to our estimate of caribou condition, and begin to utilize the model for predictive purposes (e.g. implications of development, climate change).

In this section we have utilized the model to reveal annual trends in activity budgets, diet and energy requirements, to determine how normal changes in these factors affect the energy balance of the individual, to determine if the timing of calving is related to forage variables, and to examine the energetic implications of the strategy of pregnant cows, which migrate earlier than bulls in the spring.

Methods

The model has two compartments, a rumen function submodel that allows the animal to ingest food based on activity budgets, empirical diet and plant community biomasses. Food items are classified into nine plant groups (lichens, evergreen shrubs, etc). The rumen function section then digests the food (on a hourly basis) and updates the three rumen pools (cell wall, cell contents and non-digestible pools). The resultant metabolizable energy intake (MEI) is tallied each day to be utilized by a growth submodel. MEI is allocated within the growth submodel to meet energetic demands of basal maintenance, activity, lactation and/or gestation. If excess energy remains, the animal is allowed to grow (allocated between lean tissue and fat).

After initial simulations we created three data sets for the activity budgets of an adult female; one representing a good year composed of the budgets of winter 1980-81, the late spring/early summer budgets

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[1] The detailed model writeups can be obtained from Environment Canada, Canadian Wildlife Service, Box 6010, Whitehorse, Yukon, Canada Y1A 5L7.

Table 5.1. Fecal fragment density and adjusted diet* (in parentheses) of the Porcupine Caribou Herd in late summer, fall migration and spring migration.

Plant group	Study period Late summer	Fall migration	Spring migration
Graminoids	7.7 (6.9)	3.8 (3.5)	4.0 (4.0)
Lichens	30.0 (39.3)	59.3 (58.0)	16.1 (49.6)
Forbs	0.8 (0.7)	0.8 (0.7)	14.4 (14.4)
Deciduous shrubs	32.7 (29.2)	0.0 (0.0)	0.0 (0.0)
Evergreen shrubs	21.1 (8.1)	9.9 (4.8)	53.6 (20.1)
Mosses	7.7 (6.9)	14.6 (13.3)	11.6 (11.6)
Horsetails	0.0 (0.0)	7.6 (6.9)	0.0 (0.0)
Mushrooms	0.0 (8.9)	0.0 (9.0)	0.0 (0.0)

* Adjusted diet determined from Table 2.17 except that mushrooms were assigned a value of 10% (before normalizing) based on observations of Boertje (1985).

of 1980 and the insect season of 1985; one representing a bad year composed of the winter of 1981-82, late spring early summer of 1979 and the insect season of 1984; and an average year composed of the weighted mean for each period. For the periods not reported previously in this report we used data on activity budgets (Table 5.1) and diet (Table 5.2) collected from limited field work in late summer and fall migration 1989, and from a pellet collection during spring migration (mid April 1987) when migrating females were in the northern Richardson Mountains. This latter sample contained a high component of *Ledum* and relatively low lichens. We conclude that the females are forced to switch to a poorer quality diet earlier than the bulls and non-pregnant cows, which remain back on their lichen-rich wintering areas well into May. We also assumed a spring migration activity budget similar to spring 1980, when animals migrated from winter range early (Table 2.16).

The diet composition used to simulate good, bad and average years for the adult female remained constant and represented the average fecal fragment analyses, corrected for differential disappearance in the form presented earlier (in Winter and Late Spring sections), for each period.

Table 5.2. Activity budgets (%) of the Porcupine Caribou Herd based on 15 minute scans for late summer and fall migration, 1989.

Activity	Study period Late summer	Fall migration
Number of scans	105	10
Number of groups	9	4
Number of animals	7915	47
Feeding (%)	62	52
Lying (%)	14	34
Walking (%)	12	12
Standing (%)	11	02
Running/Trotting (%)	01	00

To examine the energetic implications of spring strategies of bulls versus cows we ran two simulations for each of a single pregnant cow and for a mature bull. We simulated the pattern of metabolizable energy intake, energy balance and weight change for a 160 kg bull if he followed the cows to the calving grounds (i.e. assuming the energy budget and diet reported for the calving grounds) versus if he remained with the bulls on the winter range and migrated north with the rest of the bulls (i.e. assuming activity budgets and diet reported for bulls).

Similarly, we simulated the pattern of metabolizable energy intake, energy balance and weight change for a pregnant female for both scenarios: staying with the bulls or migrating early with the cows.

Results and discussion

Diet - Figure 5.1. illustrates the annual diet of an adult female and male used for the simulations. The figure 5.1. shows the relative importance of lichens to the diet of the Porcupine Caribou Herd over the majority of the year and illustrates the rapid shift in diet in late spring and early summer. These values represent the average diet for the years and periods that we observed. For most periods, diet composition did not vary between years with significantly different amounts of snow and/or insects. Annual variations in diet composition became obvious only from late spring to the movement period. This difference was largely attributable to the timing and pattern of plant phenology and differences in the mobility of the bulls and the pregnant cows.

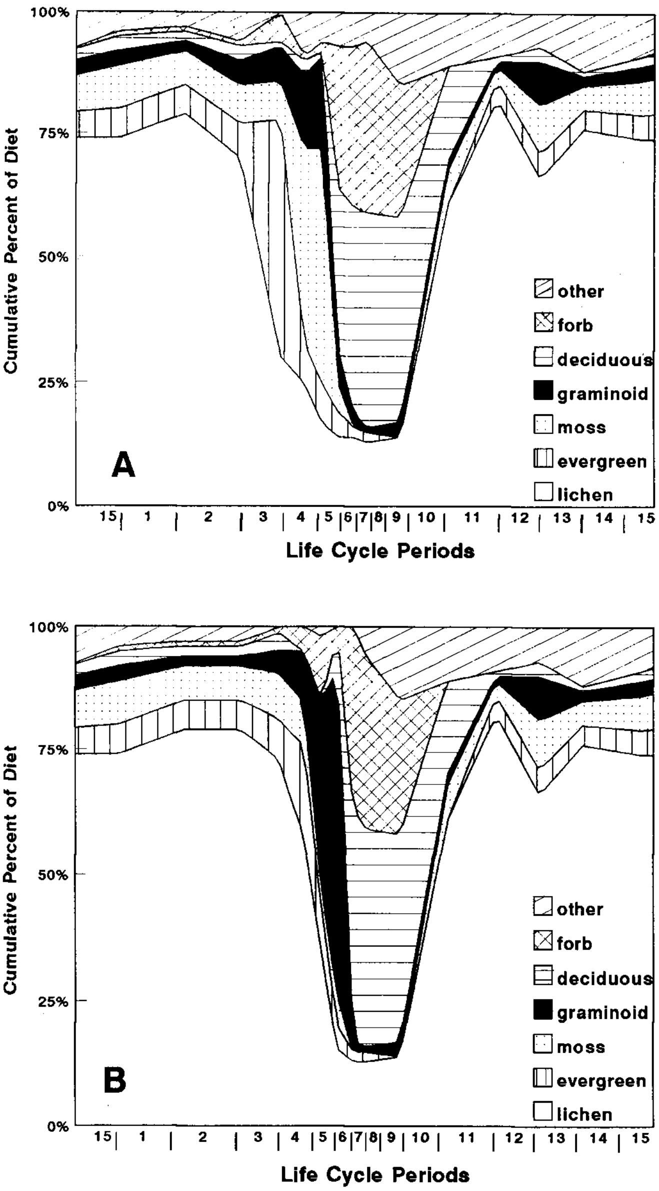

Figure 5.1. Percent of plant groups in the diet of Porcupine caribou adult cow (A) and bull (B). Life cycle periods: 1, mid winter, 2, late winter, 3, spring, 4, spring migration, 5, pre-calving, 6, calving, 7, post-calving, 8, movement, 9, 10, 11, early, mid and late summer, 12, fall-migration, 13, rut, 14, late fall, 15, early winter; dates as in Table 1.1.

Activity budgets - Figure 5.2. and Figure 5.3. presents the annual activity budgets for an adult female (Fig. 5.2A) and bull (Fig. 5.2B) and for an adult female in a «good» versus «bad» year (Fig. 5.3A and 5.3B, respectively) . We observed three distinct peaks in feeding throughout the year; immediately pre-calving, after insect season and again in mid December. There may be some problem with the observed high feeding times in December, because animals may have coincided active cycles with the very limited daylight hours. Thus we may be overestimating percent feeding if we extrapolate our observations to a 24 hour basis. The two other peaks in feeding do however seem predictable; the May peak occurs at the end of spring migration when animals are on a poor quality diet. Higher feeding times may be associated with the requirement to keep the rumen full while foraging in low biomass habitats. The August peak coincides with the decline in insect harassment. The early December peak and, to a lesser extent, the May peak in feeding came at the expense of walking time while the August feeding peak was at the expense of standing and running. The percent of time spent running and standing only became significant in the insect season and these increases coincided with a decrease in lying time.

During the late winter and spring seasons animals in a «good» year (Fig. 5.3A) have notably shorter lying times and longer feeding and walking times than animals in a «bad» year. «Good» year animals had shorter feeding and lying times and longer standing times in the insect seasons.

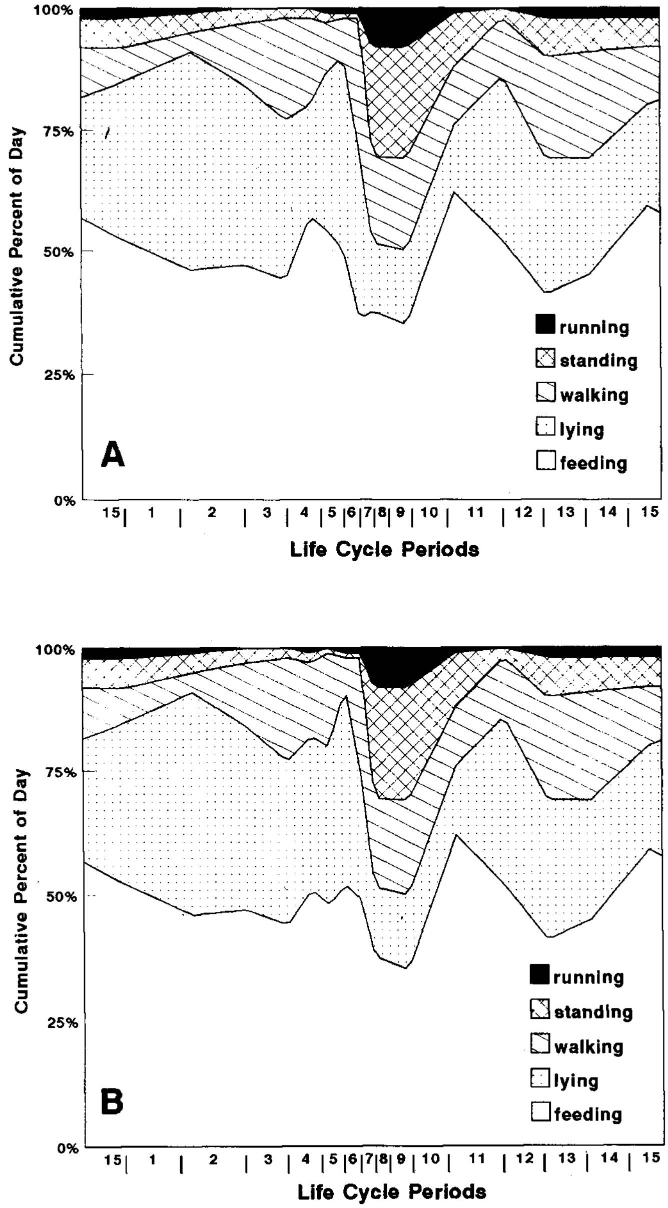

Figure 5.2. Annual activity budgets of an adult cow (A) and bull (B) of the Porcupine Caribou Herd. (Periods as in Fig. 5.1).

Total energy requirements of a lactating/pregnant female in an average year shows a distinct cycle peaking in mid July (Fig. 5.4), coincident with a peak in *metabolizable energy intake* (Fig. 5.5). The timing of calving and thus the timing of lactational demand appears to be highly tuned to phenological changes in the vegetation. In a year of severe insect harassment the MEI peak in July is significantly dampened (Fig. 5.5), as animals reduce the amount of time spent eating. These factors underline the importance of unrestricted movement and ready access to high quality prior to and during the insect season. The critical nature of the late spring/early summer periods cannot be overstated particularly for pregnant and lactating cows. This narrow window of time is critical to the viability of the calf, because it is the period when females are least tolerant to disturbance, when the highest nutrient content of the plants are potentially available and rapidly changing, and when the demands of lactation become the most significant energy expenditure.

The three troughs in metabolizable energy intake (Fig. 5.5) and energy balance (Fig. 5.6) are associated with a combination of poor forage (Fig. 5.7) and reduced intake. In the pre-calving period females are on a very poor diet. They have left the lichen-rich boreal forest in the south and arrive at the calving grounds prior, in most years, to new flushing vegetation.

Another trough in metabolizable energy intake occurs in August. Lactational demands are still relatively high at the same time that forage quality is rapidly declining due to plant senescence. The final trough in metabolizable energy intake occurs at the rut as a result of decreased feeding times. Pregnant and lactating cows can be in a negative energy balance from spring migration to fall migration in a year of late snowmelt and severe insect harassment («bad» year, Fig. 5.6).

Another parameter that we can use to monitor forage quality is the mean *digestibility* of the diet (Fig. 5.7). The pattern is similar to the MEI cycle, with cows on the poorest range (in terms of digestibility) in late spring and on best range by late June. Therefore, animals experience the lowest mean digestibility at the peak of calving and the highest mean digestibility at the time of peak lactational demand. The subsequent gradual decline in mean digestibility corresponds to declining forage quality. Such is not the case for the bulls that can track plants in early phenological development throughout the spring to pre-calving period and enjoy higher digestibilities than the cow (Fig. 5.7).

The integration of all these parameters to an individual caribou is tracked through the pattern of *fat change* throughout the year (Fig. 5.8). For the simulations of good and bad years we can see a wide divergence in the pattern and amount of fat. In good winters our data suggests that the animals can deposit fat until early spring and throughout the insect season. In poor years fat is lost during both winter and the insect season.

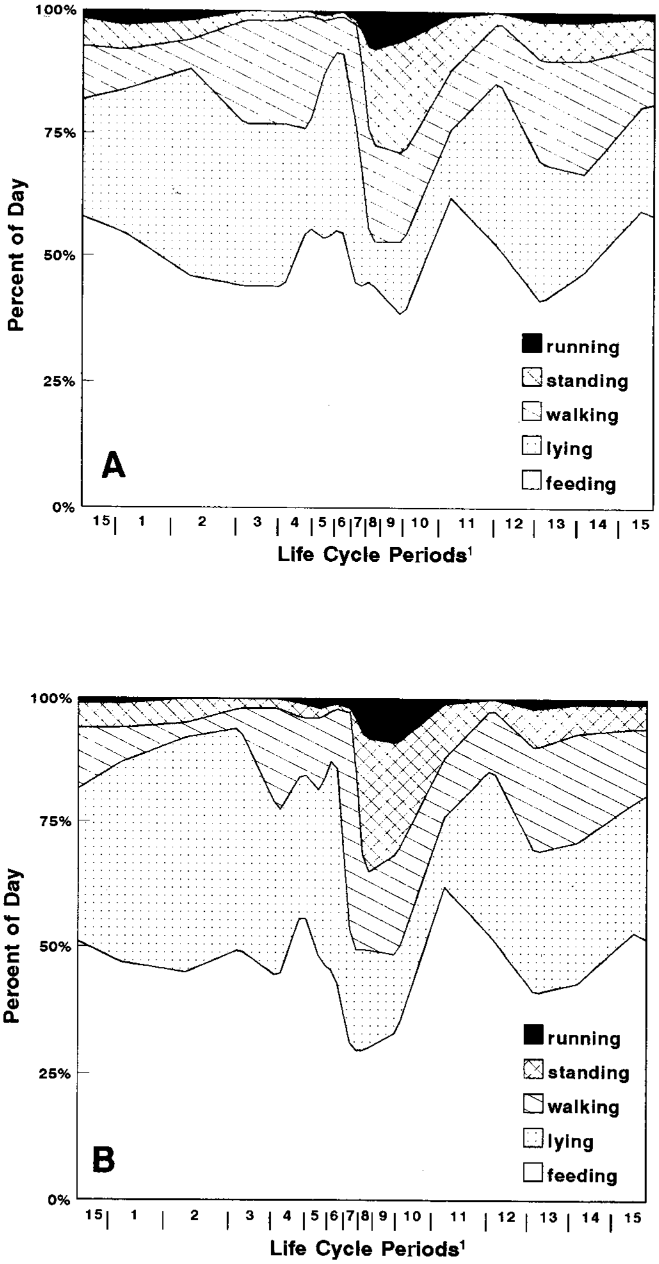

Figure 5.3. Annual activity budgets of a Porcupine caribou adult cow in a «good» (A) versus «bad» year. (Periods as in Fig. 5.1.)

If we look at average daily (Fig 5.9A) and total seasonal (Fig 5.9B) *fat change* change, in relation to our 15 time periods, we see that the greatest daily weight loss is in the calving period, largely as a result of high late gestational and early lactational costs and low forage biomass. Cows can then regain weight in the movement and early summer prior to insects becoming the major disruptive factor to food intake and prior to plant senescence. Fall migration is an important period in terms of replenishing fat reserves. From our simulations animals can gain fat throughout the winter seasons in an average year, although if our estimate of percent feeding in early winter is high, then the high fat gain values may be overestimated.

One of the values of the simulation models is that it allows us to assess energetically the strategies employed by caribou. In this section we discuss the energetic implications of the strategy employed by bulls versus pregnant cows at the critical time of year (1 April to 30 June). Bulls remain longer on the winter range, migrating north about three weeks later than the pregnant cows. They are thus better able than cows to track vegetation phenology in the pre-calving and calving period. Cows arrive on the calving grounds prior to initial new growth of the forage species.

The larger body size of the bulls imposes a higher energy requirement than smaller-bodied cows. Therefore, even with the added costs of gestation, energy requirements of bulls remain higher than cows until after calving, when the reverse situation occurs (Fig. 5.10). In fact, when the energy requirements of lactating females are beginning to peak, bull requirements begin to decline (Fig. 5.10). By remaining on the winter range longer, bulls can better meet their higher basal energy requirements. For the two bull scenarios, we can see that the bull remaining back and tracking phenology into late May is in a much more favourable energy balance than a bull migrating early with the cows (Fig. 5.11). It is only after calving that this latter bull gains some energetic advantage (Fig. 5.12). However, on average, the bull which remains with the bulls enters the insect season in slightly better shape compared to if he migrated early with the pregnant cows (Fig. 5.12).

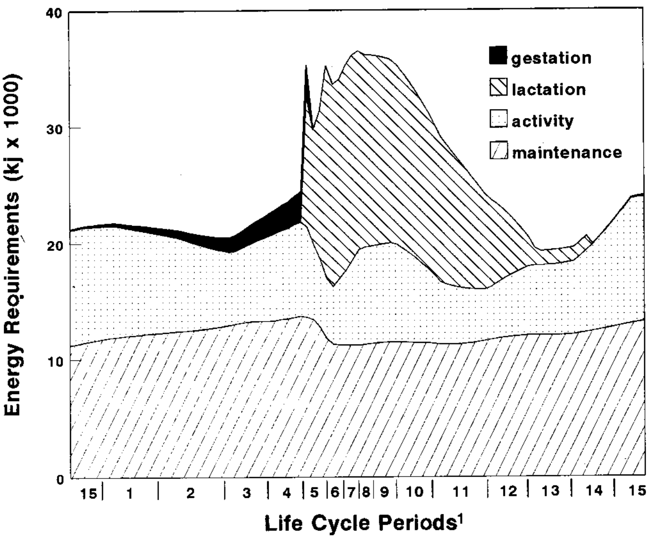

Figure 5.4. Total seasonal energy requirements of an adult female Porcupine caribou. (Periods as in Fig. 5.1.).

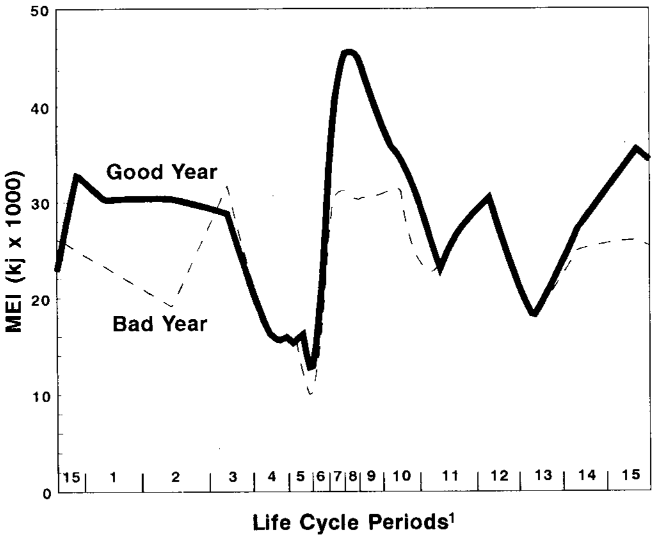

Figure 5.5. Metabolizable energy intake (MEI) – «good» year versus «bad» year for an adult female Porcupine caribou. (Periods as in Fig. 5.1.).

Because the cow has a lower basal metabolic demand, she is able to cope better with the poorer quality spring forage encountered north of treeline than could a bull. If a pregnant cow remained with the

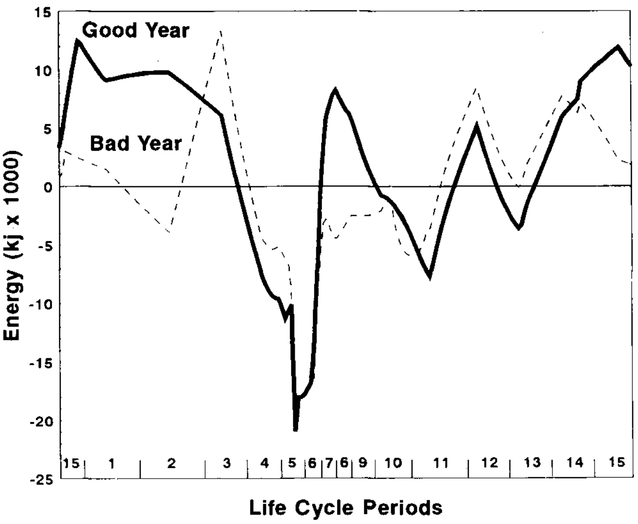

Figure 5.6. Energy balance – «good year» versus «bad» year for an adult cow of the Porcupine Caribou Herd. (Periods as in Fig. 5.1.).

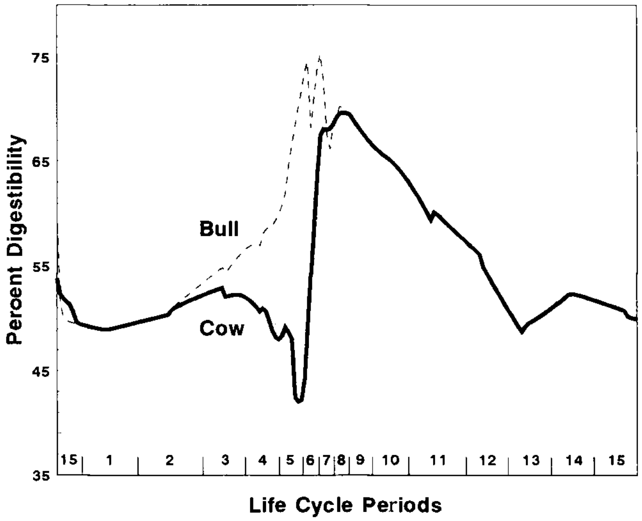

Figure 5.7. Seasonal digestibility of the diets of an adult cow and bull of the Porcupine Carihou Herd. (Periods as in Fig. 5.1.).

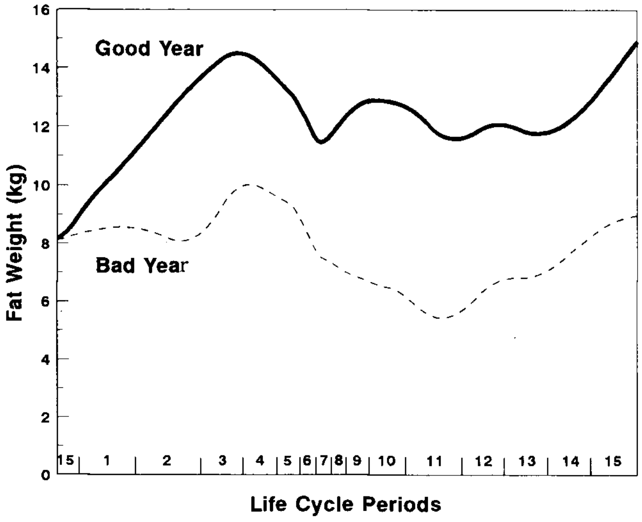

Figure 5.8. Weight of body fat reserves of a female Porcupine caribou in a «good» year versus «bad» year. (Periods as in Fig. 5.1.).

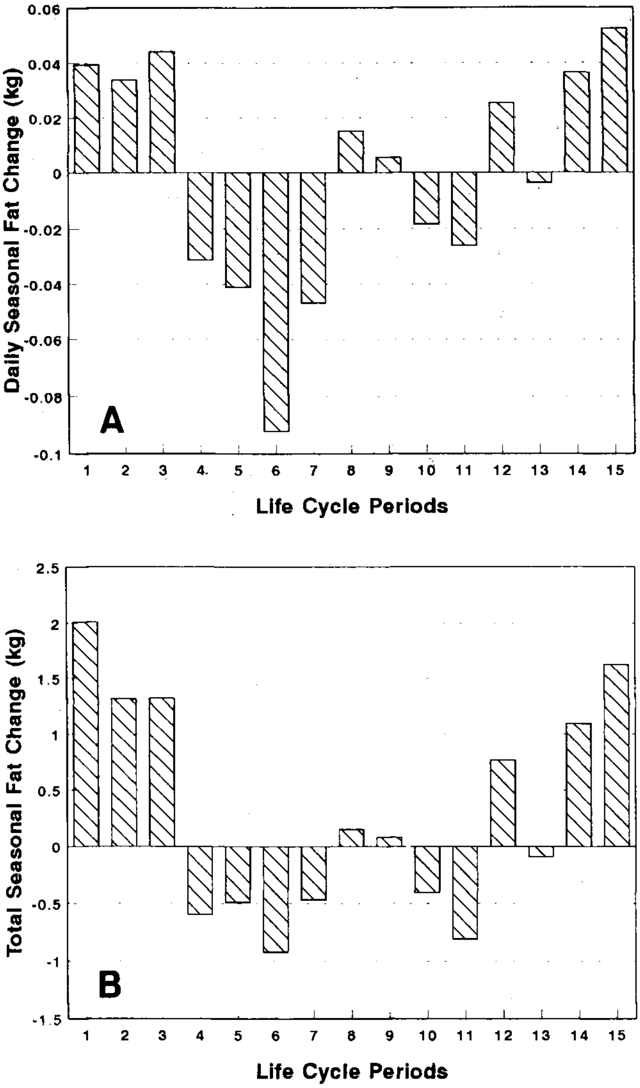

Figure 5.9. Average daily (A) and total (B) seasonal fat change for an adult female Porcupine caribou. (Periods as in Fig. 5.1.).

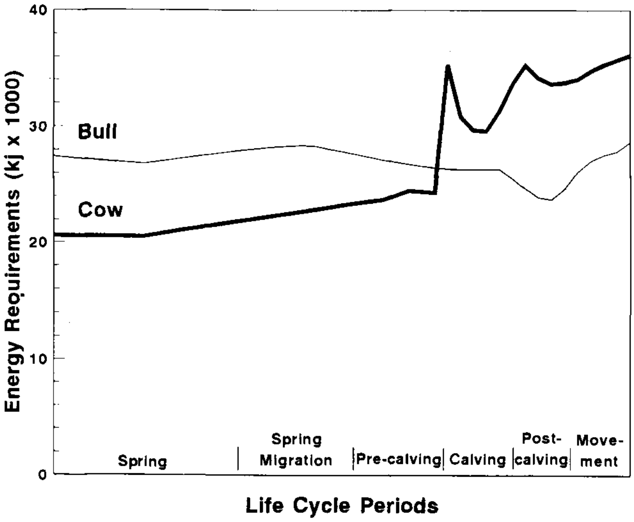

Figure 5.10. Total energy requirements for a bull and cow from the Porcupine Caribou Herd, from spring to the movement period. (Periods as in Fig. 5.1.).

bulls she would gain a energetic advantage until calving. As soon as lactational demands become significant the cows on the calving ground gain the energetic advantage (Fig. 5.11). The difference in the month of June is so significant that the cows moving early to the calving ground enter the insect season in significantly better shape than if they followed the strategy of the bulls (Fig. 5.12).

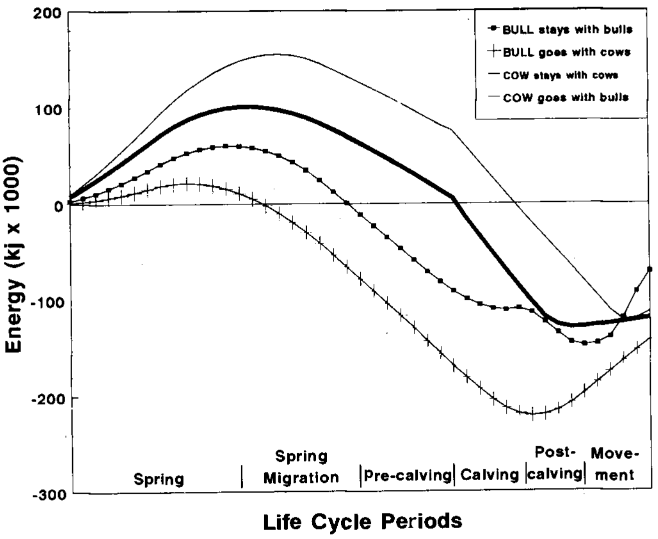

Figure 5.11. Cumulative energy balance for four simulated scenarios: bull staying with bulls; bull going to calving grounds with cow; cow staying with cows; and cow remaining on winter range with bulls, tracking early spring phenology.

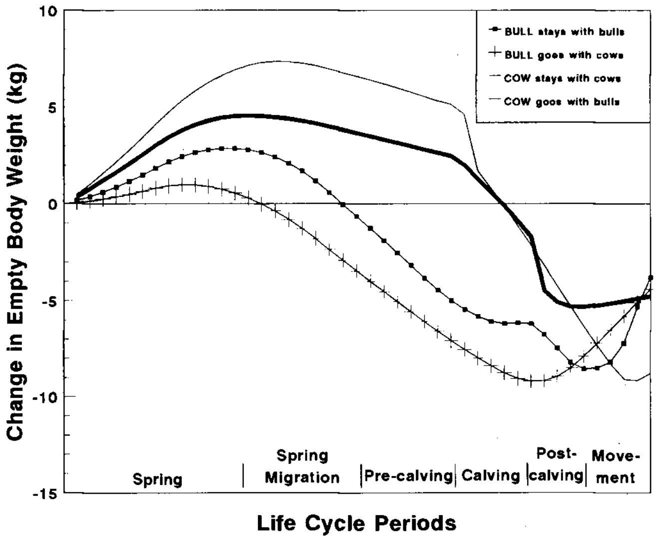

Figure 5.12 Empty body weight of bull and cow Porcupine caribou under four simulated scenarios: bull staying with bulls; bull going to calving grounds with cow; cow staying with cows; and cow remaining on winter range with bulls, tracking early spring phenology.

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Appendix A.

Mean wet weight (g) and mean dry weight (g) of parts of different species of plants collected for nutrient analysis of the calving ground of the Porcupine Caribou Herd in Yukon in 1980.

Species	Range type	Unit collected* (phenological stage)**	Date	n	Mean wet weight (g)	Mean dry weight (g)
Thamnolia vermicularis	alpine barren	whole plant				
Cetraria cuccullata	alpine barren	whole plant				
Equisetum variegatum	alluvial willow	whole plant				
Equisetum scirpoides	tussock meadow	whole plant				
Equisetum arvense	sedge heath	whole plamt				
Eriophorum angustifolium	wet sedge meadow	shoot	June 6	76	0.54	0.131
			June 14	85	0.68	0.158
			June 24	108	1.44	0.336
			July 3	114	1.63	0.425
			July 12	110	3.33	0.822
Eriophorum vaginatum	tussock meadow	flower (B)	May 24	876	0.11	0.029
		(F)	June 4	840	0.14	0.037
		(P)	June 14	260	0.40	0.093
		(S)	June 23	200	0.50	0.146
		(S)	July 2	150	0.69	0.218
		(S)	July 12	210	0.54	0.176
Carex aquatilis	wet sedge meadow	shoot	June 6	111	0.63	0.180
			June 14	120	0.75	0.184
			June 24	81	1.33	0.312
			July 3	73	1.36	0.404
			July 12	79	1.62	0.538
Salix glauca	wet sedge meadow	leaf				
Salix lanata	dwarf shrub heath	leaf				
Salix pulchra	wet sedge meadow	leaf				
Betula glandulosa	wet sedge meadow	leaf				
Vaccinium uliginosum	tussock tundra	leaf				
Dryas integrifolia	alluvial heath	flower (F)	June 23	1500	0.08	0.016
		(P)	July 3	1400	0.09	0.030
		(S)	July 12	1500	0.10	0.039
Polygonum bistorta	tussock meadow	flower (B-F)	June 23	168	0.81	0.116
		(F)	July 2	66	1.52	0.264
Boykinia richardsoni	dwarf shrub heath	inflor. (F)	July 12	114	2.28	0.385
Geum glaciale	alluvial heath	flower (B-F)	June 6	190	0.47	0.078
		(F-P)	June 14	190	0.53	0.120
		(S)	June 23	95	1.26	0.285
		(S)	July 3	130	0.73	0.233
Lupinus arcticus	alluvial heath	inflor. (B)	June 14	210	0.48	0.058
		(F)	June 23	85	2.04	0.221
		(F-S)	July 3	52	3.17	0.439
		(S)	July 12	25	5.48	0.822
Oxytropis maydelliana	alluvial heath	inflor. (B-F)	June 24	332	0.32	0.054
		(F-P)	July 3	275	0.39	0.082
		(S)	July 12	250	0.45	0.108

Appendix A (cont) .

Species	Range type	Unit collected* (phenological stage)**	Date	n	Mean wet weight (g)	Mean dry weight (g)
Oxytropis borealis	alluvial gravel	inflor. (B-F)	June 24	240	0.40	0.093
		(F-P)	July 3	310	0.34	0.056
		(S)	July 12	300	0.44	0.126
Epilobium latifolium	alluvial gravel	whole plant	June 14	190	0.47	0.079
			June 24	55	1.93	0.266
			July 3	68	1.91	0.361
			July 12	40	3.48	0.604
		inflor. (B-F)	July 3	91	1.16	0.229
		(F-S)	July 12	75	1.49	0.309
Pedicularis kanei	alluvial heath	flower (B)	June 6	122	1.20	0.109
		(B-F)	June 14	90	1.08	0.178
		(F-P)	June 23	70	0.65	0.270
		(P-S)	July 3	45	0.34	0.634
Artemesia arctica	alluvial gravel	inflor. (B)	June 14	-	-	-
		(B)	June 24	75	1.49	0.215
		(F)	July 3	45	2.67	0.475
		(F)	July 12	57	2.24	0.461

* – unit collected: whole plant – entire above ground plant,
shoot – leaves and stem plucked from basal sheath,
flower – flower head and pedicel,
inflorescence – flower head, upper stem and leaves

** – phenological stage; B – flower bud; F – flower open; P – flower past or senescent; S – seed or fruit.

Appendix B.
Fibre, ash and nutrient content (% dry weight) of vegetation collected in 1980.

		Fibre				Ash		Nutrients	
Species	Date	Ndf	Adf	Lignin	Cellulose	Residual	Total	Nitrogen	Phosphorus
Lichens									
Thamnolia vermicularis	June 9	52.2	16.7	12.6	3.3	0.8	13.1	0.6	0.1
	June 18	49.6	12.6	7.8	4.4	0.3	17.5	0.5	0.1
	June 27	57.2	13.2	8.0	4.7	0.4	13.3	0.6	0.1
	July 6	53.4	11.9	9.0	1.8	1.1	13.8	0.5	0.1
	July 13	53.6	13.0	10.1	2.0	0.4	14.9	0.6	0.1
Cetraria cucullata	June 8	31.8	5.2	4.0	1.2	0.0	11.7	0.4	0.1
	June 17	28.5	4.5	2.0	2.0	0.4	14.0	0.4	0.0
	June 26	28.9	5.6	3.0	2.0	0.9	13.1	0.4	0.0
	July 5	30.9	6.4	5.0	1.0	0.4	12.8	0.4	0.0
	July 12	30.5	4.4	1.7	1.8	0.9	13.0	0.4	0.0
Horsetails									
Equisetum variegatum	June 6	43.3	35.6	6.5	22.5	6.5	11.4	1.2	0.1
	July 12	37.9	31.0	4.4	20.9	5.6	10.7	1.8	0.1
Equisetum scirpoides	June 7	46.8	34.6	6.5	23.6	4.5	9.7	1.0	0.1
	July 12	46.4	35.2	6.1	22.9	6.1	10.7	1.0	0.1
Equisetum arvense	June 23	27.2	18.4	3.8	14.2	0.5	11.1	3.2	0.4
	July 2	26.9	18.2	3.1	13.1	2.1	10.7	2.2	0.2
	July 12	27.9	20.7	3.0	15.3	2.4	12.2	2.1	0.2
Graminoids									
Eriophorum angustifolium	June 6	60.3	25.2	2.8	21.5	0.9	4.0	1.8	0.3
	June 14	60.2	25.8	3.4	21.7	0.7	4.4	2.4	0.3
	June 24	62.1	26.8	3.2	23.4	0.3	4.1	2.2	0.3
	July 3	64.2	28.1	3.6	23.6	1.0	3.2	1.7	0.2
	July 12	60.1	26.5	4.1	21.7	0.8	3.1	1.4	0.2
Eriophorum vaginatum	May 24	56.6	19.2	1.6	17.1	0.4	4.1	3.1	0.5
	June 4	58.2	19.6	1.7	17.1	0.8	4.2	2.5	0.4
	June 14	64.3	23.6	1.3	22.2	0.0	3.4	2.1	0.3
	June 23	64.1	25.4	2.1	23.0	0.4	3.3	2.2	0.3
	July 2	63.3	27.6	3.5	23.8	0.3	3.4	1.9	0.3

Carex aquatilis	June 6	60.1	28.5	4.0	23.2	1.3	4.2	1.7	0.2
	June 14	63.1	27.7	3.6	23.1	1.0	4.5	2.3	0.4
	June 24	64.6	27.6	3.5	23.4	0.7	5.3	2.3	0.4
	July 3	65.9	29.0	3.2	25.3	0.5	4.5	2.1	0.3
	July 12	70.5	33.8	4.5	28.7	0.6	3.9	1.4	0.2
Deciduous shrubs									
Salix glauca	June 23	31.2	20.5	7.0	12.7	0.9	4.6	3.4	0.4
	July 2	23.2	17.6	5.7	11.3	0.6	4.4	2.8	0.2
	July 12	23.0	17.4	6.1	10.8	0.5	4.3	2.5	0.2
Salix lanata	June 14	20.4	15.2	3.0	12.1	0.1	7.2	4.9	0.6
	June 23	21.6	17.4	4.3	12.9	0.2	6.6	3.9	0.4
	July 3	19.6	16.6	4.4	12.2	0.1	6.2	2.8	0.2
	July 12	17.4	14.0	4.2	9.2	0.0	6.8	2.6	0.2
Salix pulchra	June 14	12.9	12.6	4.3	6.4	1.7	5.0	4.8	0.7
	June 24	16.6	14.8	6.3	7.3	1.2	4.2	3.9	0.4
	July 3	19.4	15.0	5.7	9.3	0.0	3.6	2.5	0.2
	July 12	19.9	15.2	4.6	10.4	0.2	3.8	2.2	0.2
Betula glandulosa	June 14	21.4	16.8	5.6	10.6	0.5	3.5	3.6	0.4
	June 24	21.9	18.4	6.3	12.1	0.0	3.0	3.0	0.3
	July 3	24.1	19.4	6.5	12.9	0.0	2.4	2.4	0.2
	July 12	25.3	17.4	3.2	13.9	0.3	3.0	2.2	0.2
Evergreen shrubs									
Vaccinium vitis-idaea	May 24	28.6	20.8	4.4	15.8	0.6	2.7	0.9	0.1
	June 7	30.0	20.4	6.4	13.7	0.3	2.4	0.9	0.1
	June 14	30.7	18.7	5.4	13.3	0.1	2.6	0.9	0.1
	June 25	31.3	18.6	5.5	13.4	0.0	2.5	0.9	0.1
	July 5	33.7	21.1	6.3	14.8	0.0	2.6	0.9	0.1
	July 12	31.4	22.0	6.4	14.8	0.8	2.8	0.8	0.1
Dryas integrifolia	June 23	25.3	17.1	3.9	13.2	0.0	3.2	1.8	0.3
	July 3	40.1	30.0	7.1	22.8	0.2	3.1	1.5	0.2
	July 12	46.1	34.0	10.4	22.4	1.2	3.4	1.6	0.2
Forbs									
Polygonum bistorta	June 23	23.9	22.4	4.1	16.1	2.2	5.6	3.1	0.4
	July 2	32.1	26.2	7.8	18.1	0.4	4.6	2.2	0.4
	July 12	36.2	31.0	9.0	21.2	0.8	4.9	1.8	0.2

Appendix B (cont.). Fibre, ash and nutrient content (% dry weight) of vegetation collected in 1980.

		Fibre				Ash		Nutrients	
Species	Date	Ndf	Adf	Lignin	Cellulose	Residual	Total	Nitrogen	Phosphorus
Boykinia richardsonii	July 12	18.8	16.4	3.8	12.2	0.9	4.0	2.0	0.4
Geum glaciale	June 6	31.7	23.4	3.6	18.5	1.2	6.3	3.1	0.4
	June 14	30.7	22.7	4.3	17.5	1.0	6.2	2.5	0.3
	June 23	34.7	27.6	6.2	20.0	1.4	6.2	2.0	0.3
	July 3	45.8	35.1	10.0	22.2	2.9	6.2	1.1	0.1
Lupinus arcticus	June 14	21.2	18.4	1.8	16.1	0.6	3.1	5.4	0.7
	June 23	30.0	23.5	2.6	20.8	0.0	6.9	2.9	0.4
	July 3	24.0	19.3	2.3	17.0	0.0	5.6	3.3	0.4
	July 12	34.9	25.4	4.1	21.2	0.0	5.4	2.1	0.2
Oxytropis maydelliana	June 24	24.5	18.0	2.3	15.5	0.2	5.9	4.1	0.4
	July 3	31.0	22.5	2.5	19.4	0.6	6.1	3.8	0.4
	July 12	38.1	27.1	7.4	17.7	2.0	5.8	1.9	0.3
Oxytropis borealis	June 24	25.9	21.1	3.4	16.8	0.9	5.6	3.6	0.4
	July 3	27.6	20.8	2.4	17.0	0.8	5.5	3.1	0.3
	July 12	39.2	27.0	4.4	21.5	0.2	6.0	3.6	0.3
Epilobium latifolium	June 14	13.0	11.0	2.0	8.5	0.5	9.6	4.2	0.5
(shoots)	June 24	17.2	15.5	3.0	11.5	1.0	10.3	4.1	0.4
	July 3	17.2	14.4	3.4	10.8	0.2	12.9	2.8	0.2
	July 12	18.8	16.6	3.9	12.5	0.2	12.7	2.6	0.2
(flowers)	July 3	14.9	12.1	2.5	9.0	0.5	8.9	2.5	0.3
	July 12	16.2	13.2	2.7	10.1	0.3	9.2	1.8	0.3
Pedicularis kanei	June 6	17.5	14.1	2.5	11.3	0.4	7.1	3.5	0.5
	June 14	19.8	13.7	6.7	7.0	0.0	6.7	3.2	0.4
	June 23	20.2	15.7	3.8	11.5	0.4	6.6	2.7	0.4
	July 3	37.5	23.0	3.0	19.7	0.2	5.1	3.6	0.3
Artemesia arctica	June 14	39.3	18.3	4.9	8.7	4.7	16.2	4.3	0.5
	June 24	25.6	19.1	6.6	11.6	0.9	13.3	3.6	0.4
	July 3	26.3	20.4	7.0	12.7	0.7	12.0	2.6	0.3
	July 12	32.9	24.8	7.8	15.1	1.9	11.4	2.0	0.2

Ndf: Neutral detergent fibre. Adf: Acid detergent fibre.

Appendix C.

Percent of caribou observed in each range type by physiographic characteristics. (Sample size).

	Alluvial gravel (2,030)	Alluvial willow (610)	Alluvial heath (26,382)	Wet sedge meadow (28,810)	Tussock meadow (89,056)	Sedge heath (25,841)	Dwarf shrub (4,963)	Alpine barren (1,526)
Slope								
none	100.0	72.6	99.8	73.4	17.0	3.6	3.4	2.1
slight (< 10%)	-	17.9	0.2	13.2	22.1	31.5	30.9	9.3
moderate	-	9.5	-	13.4	60.9	63.8	19.3	67.0
steep (> 30%)	-	-	-	0.<1	<0.1	1.2	46.4	21.6
Aspect								
north	-	12.1	-	1.6	5.6	17.3	1.7	2.6
north-east	-	-	-	4.8	0.6	12.2	20.3	3.7
east	-	4.6	-	11.4	29.4	55.5	59.8	58.4
south-east	-	-	-	-	2.3	1.1	2.6	16.3
south	-	-	-	2.7	1.4	1.8	0.1	12.6
south-west	-	-	-	-	1.3	0.1	3.7	-
west	-	10.7	0.2	6.1	37.9	6.6	6.6	0.9
north-west	-	-	-	-	4.4	1.9	1.7	3.5
Topographic position								
crest	-	-	-	-	0.4	0.2	0.2	2.1
upper slope	-	-	-	3.1	13.1	7.1	9.7	51.8
middle slope	-	21.6	-	17.3	46.0	72.4	76.9	38.3
lower slope	-	5.7	0.1	6.0	21.4	15.6	6.3	7.5
apron	-	-	0.1	0.1	0.6	0.6	2.7	0.4
valley floor	81.0	62.6	82.0	36.0	9.7	2.9	3.0	-
plain	19.0	10.0	17.8	37.4	8.8	0.9	0.2	-
terrace	-	-	-	-	-	0.4	0.9	-
Land form								
level	5.4	72.6	99.8	73.0	12.3	3.2	5.8	-
fan-pediment	-	-	-	0.3	-	-	-	0.1
rolling	-	27.4	0.2	26.7	87.7	96.4	93.0	93.2
ridged	-	-	-	-	0.1	-	0.3	3.1
terraced	-	-	-	-	-	0.4	0.9	3.7
recent fluvial	94.6	-	-	-	-	-	-	-

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