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

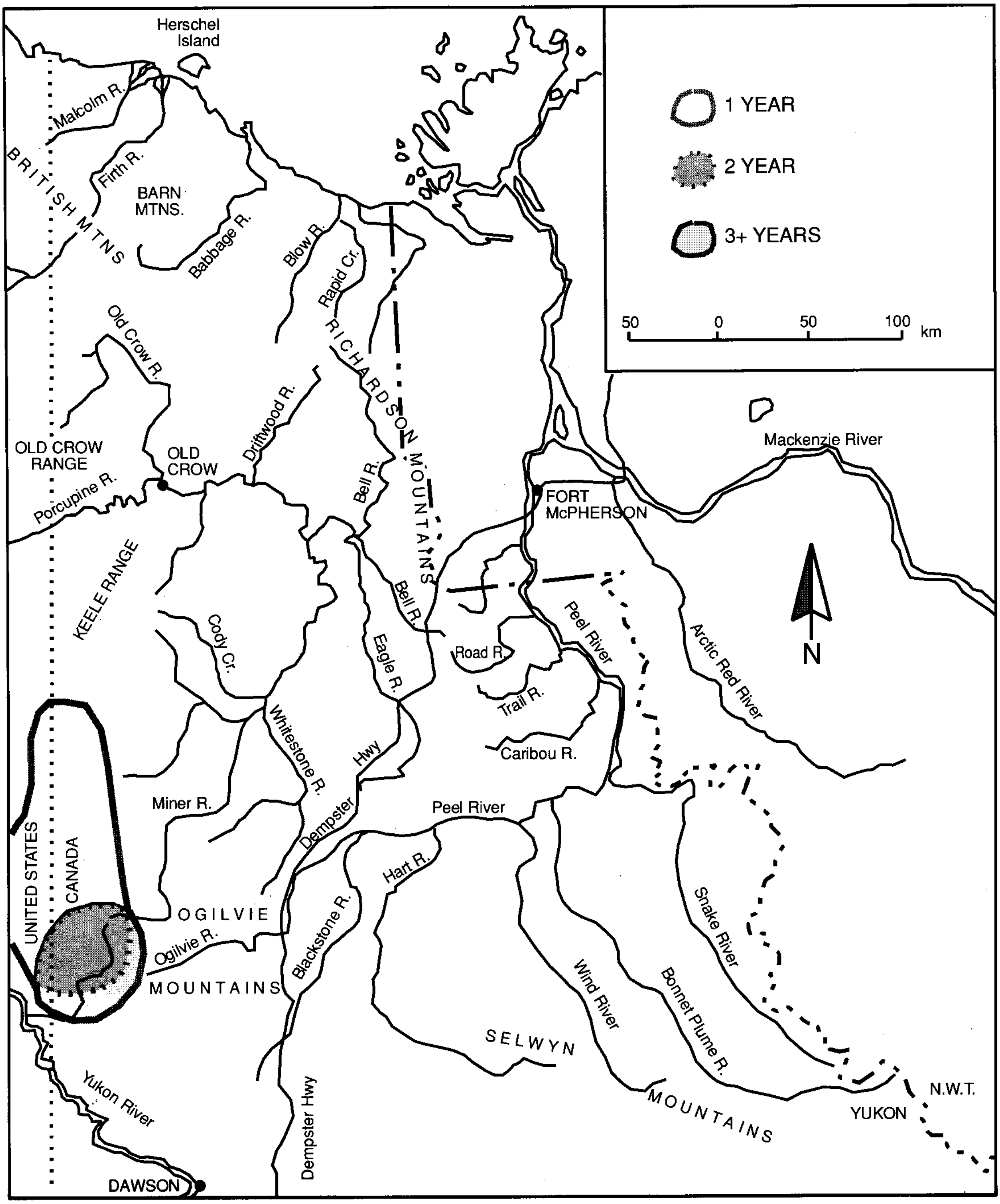

Figure 2.1. Alaskan border distribution of the Porcupine Caribou Herd in winter.

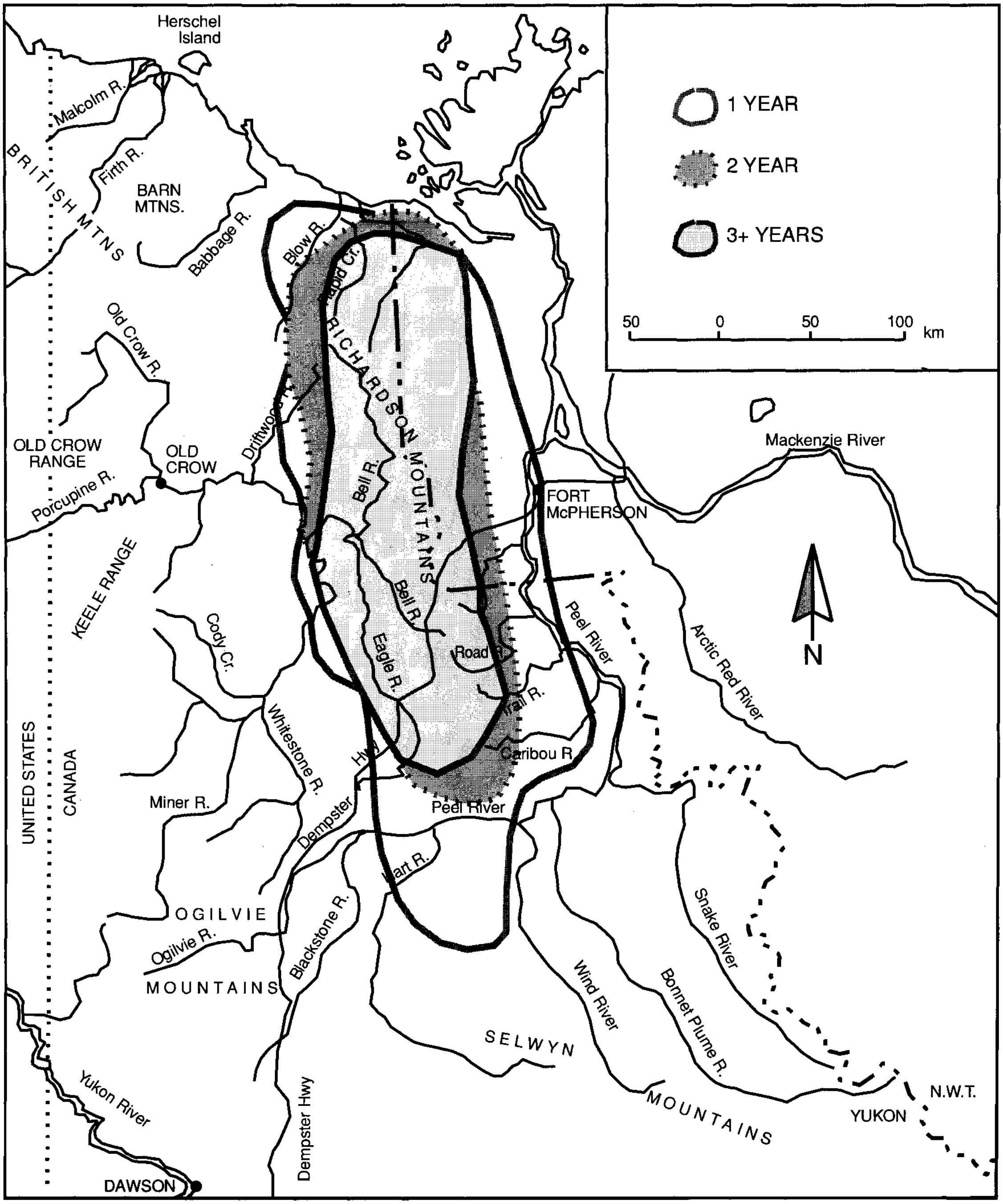

Figure 2.2. Richardson Mountain distribution of the Porcupine Caribou Herd in winter.

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

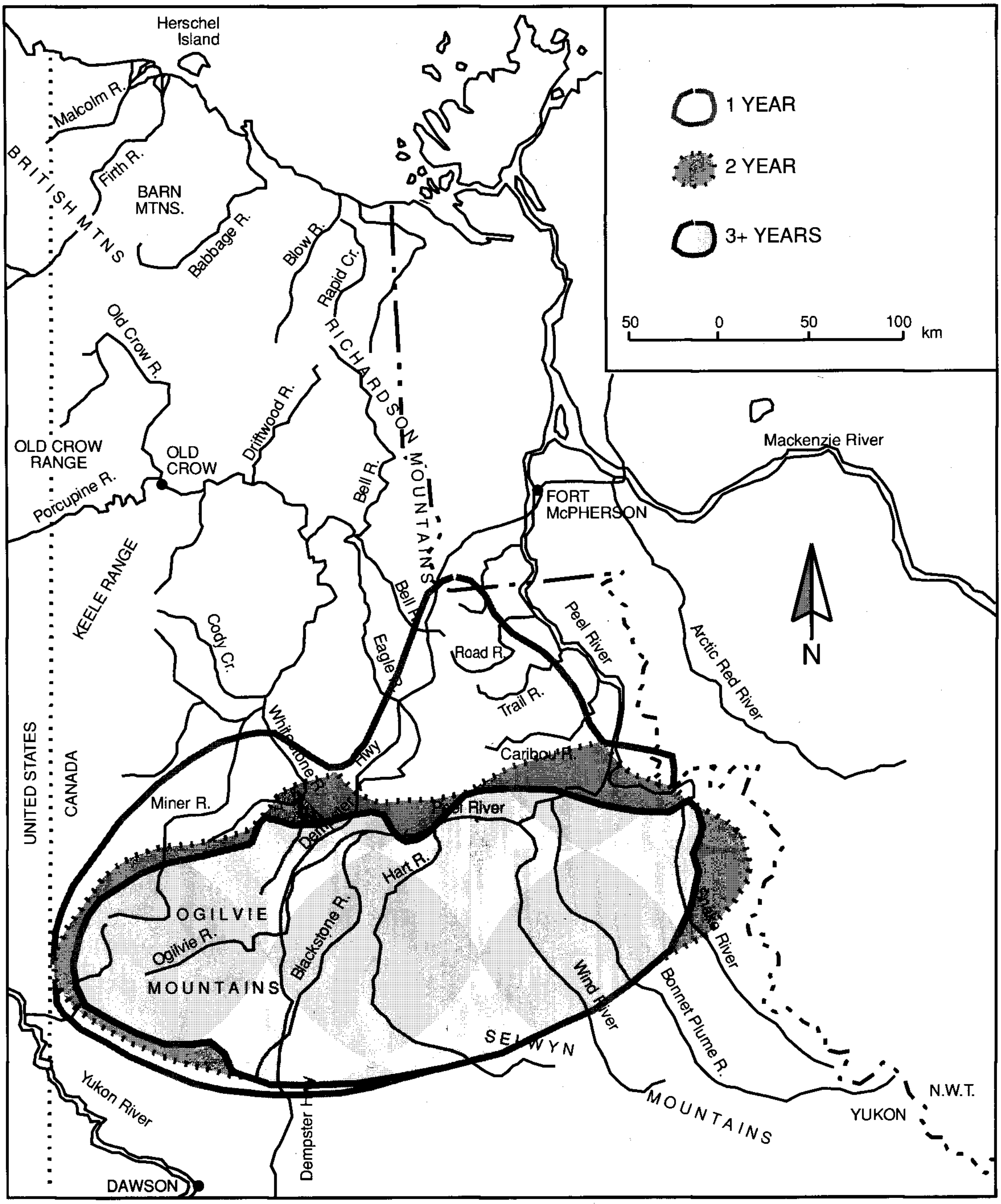

Figure 2.3. Ogilvie/Hart distribution of the Porcupine Caribou Herd in winter.

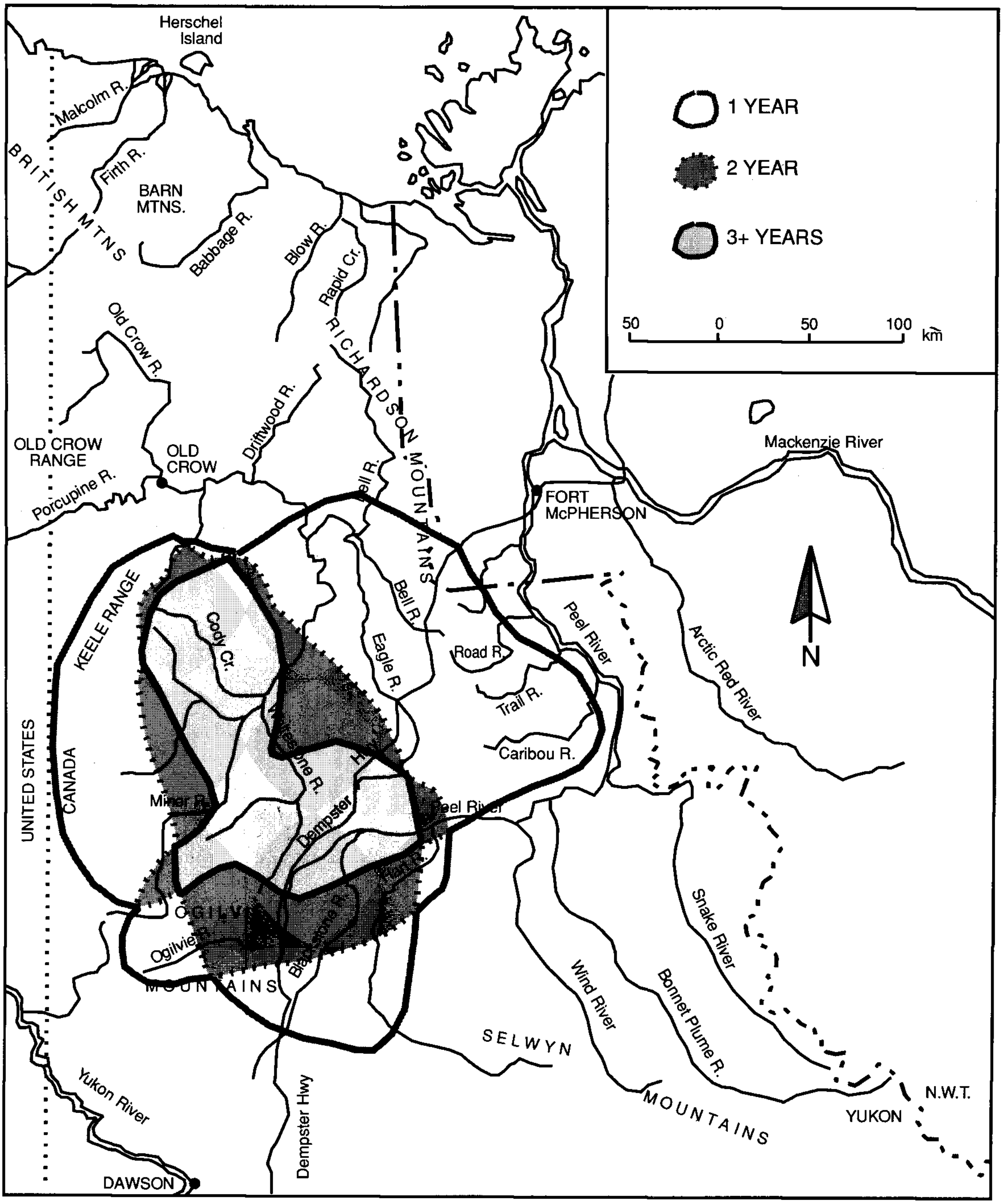

Figure 2.4. Whitestone/Miner distribution of the Porcupine Caribou Herd in winter.

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

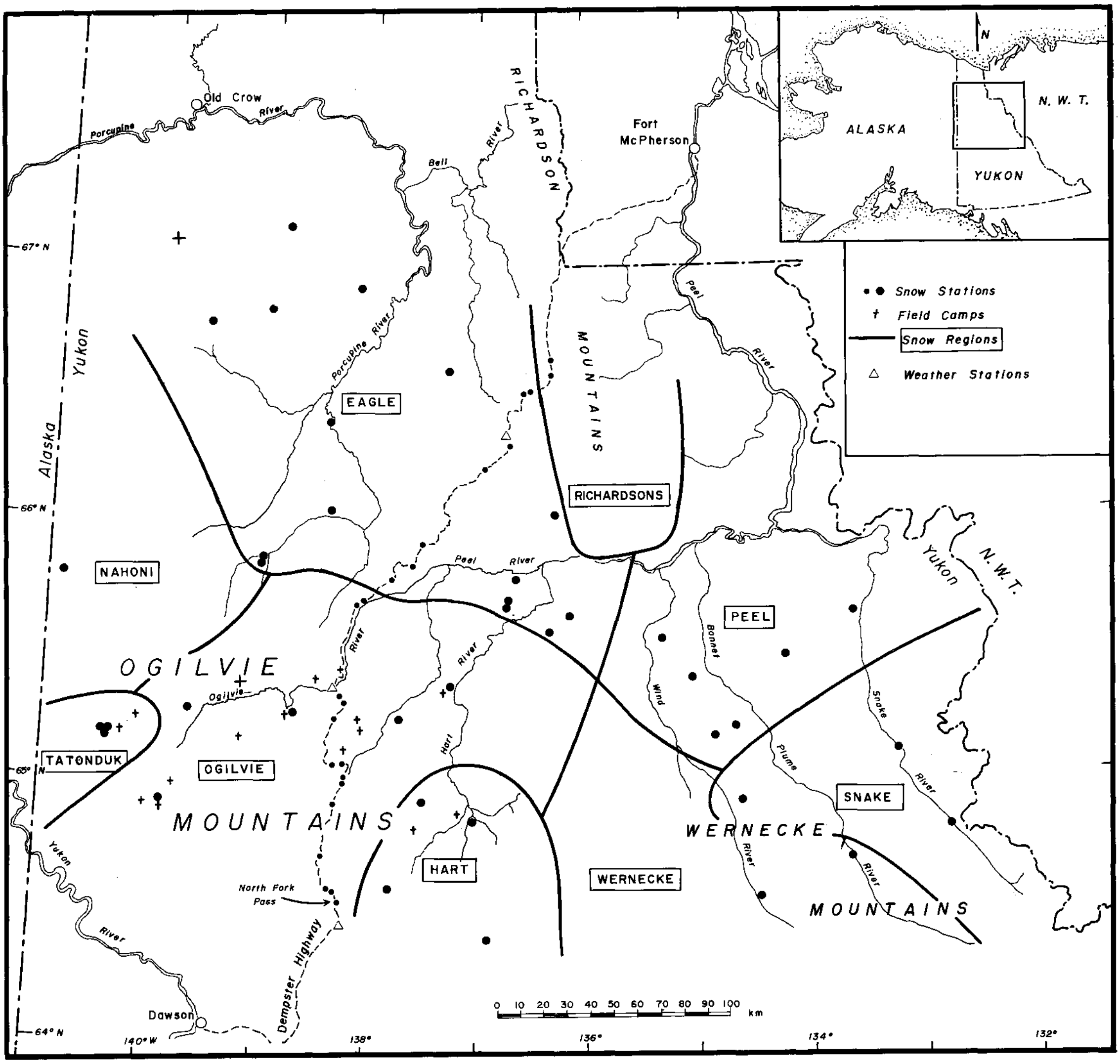

Figure 2.5. Winter range study area showing the snow stations and snow regions.

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:

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

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_t 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/cm^3) 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									
Riehardsons		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).

	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		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±57 (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.

Lichens	Regions					
	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).

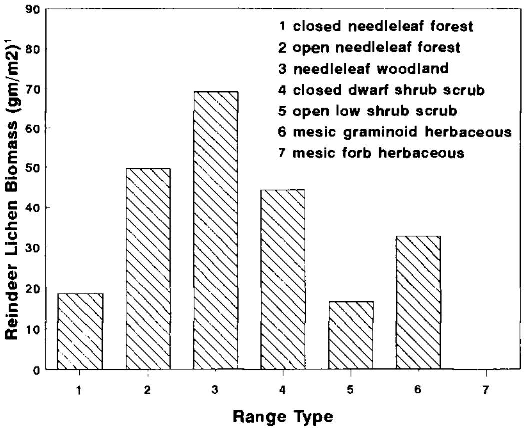

Figure 2.6. Reindeer lichen biomass versus range type.

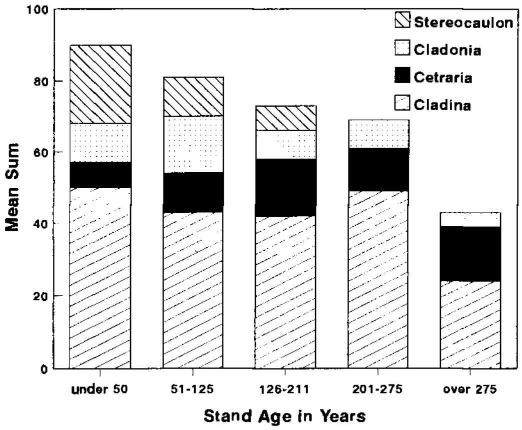

Figure 2.7. Lichen biomass versus stand age.

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/*Lichcn	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/cm³)	Depth (cm)	Density (g/cm³)	
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/m²)	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).

	11 December 1979					10 March 1980				
Plant genus or group[1]	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*-typc 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-idaca*) 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.

Plant genus or group[1]	Season						
	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:

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

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

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

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.

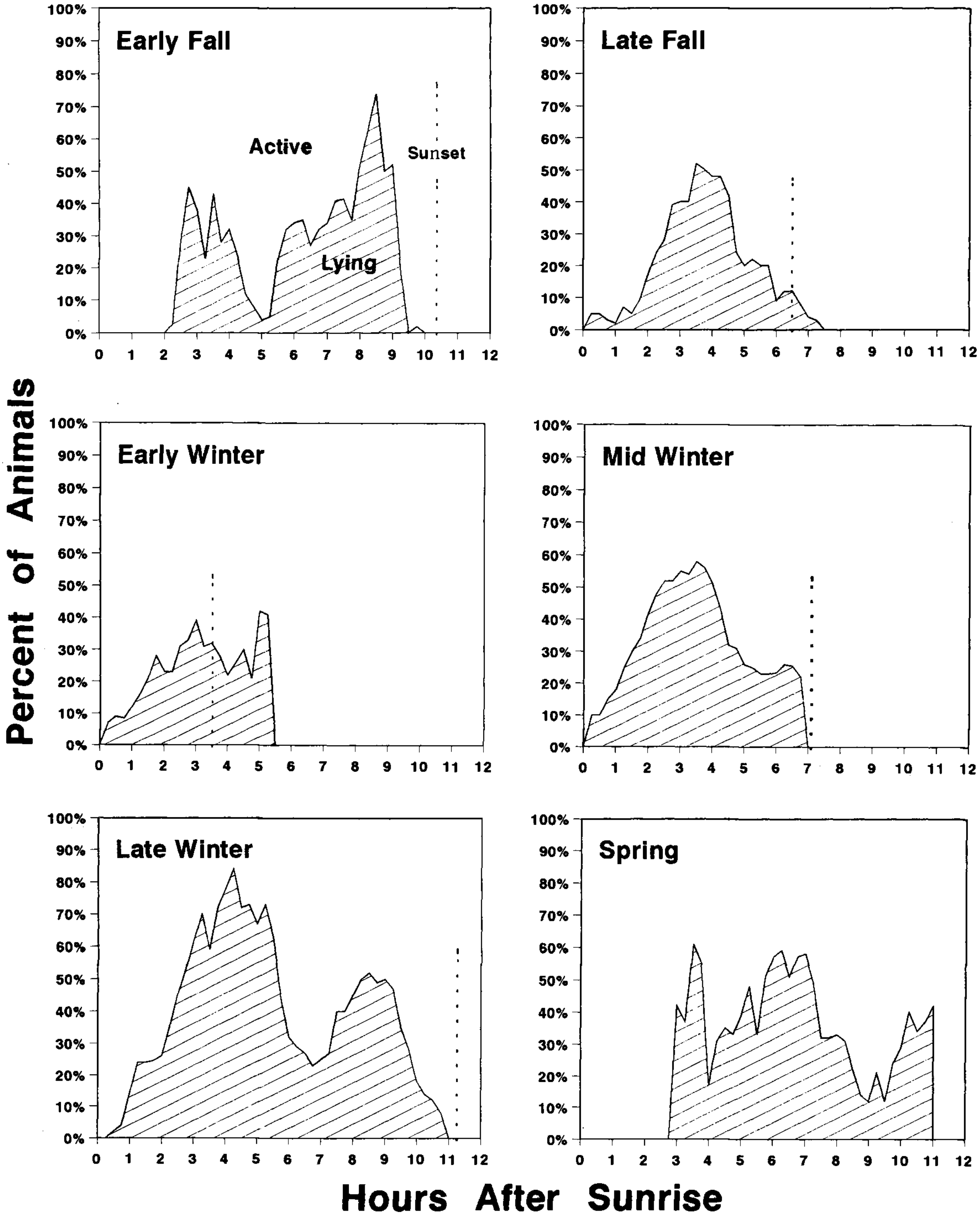

Figure 2.8. Percent of animals lying from 15 minute scans in relation to hours after sunrise for the six study periods.

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.

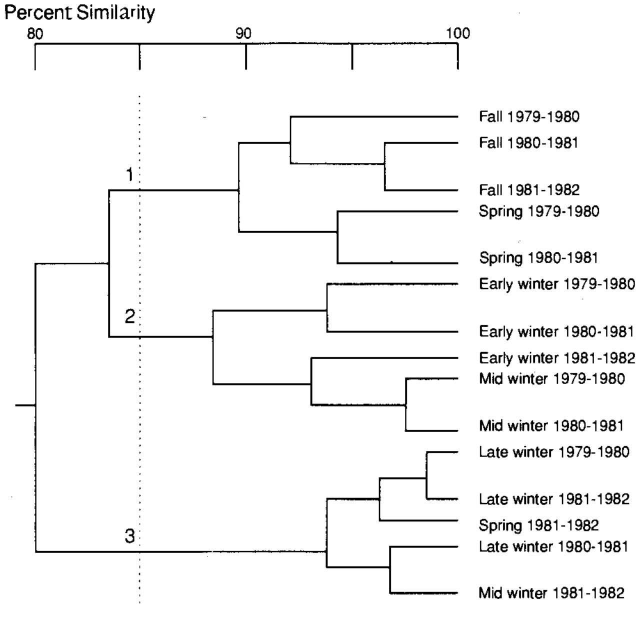

Figure 2.9. Cluster analysis of activity budgets of caribou in north-central Yukon.

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.

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.

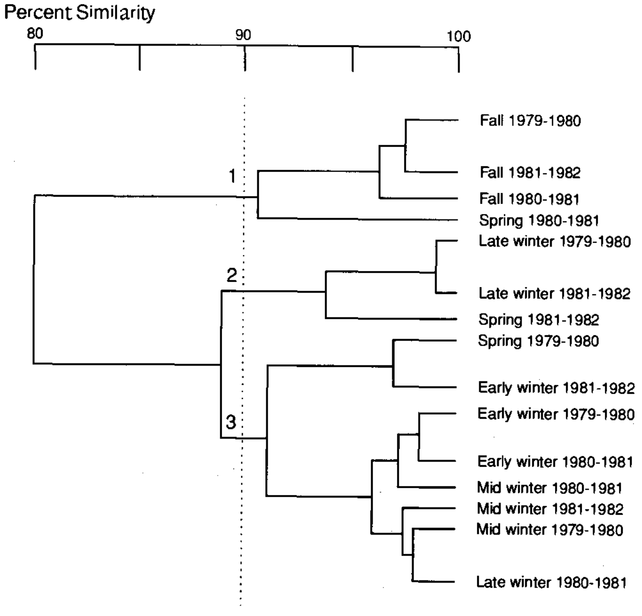

Figure 2.10. Cluster analysis of proportional use of active periods by caribou of north-central Yukon.

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.

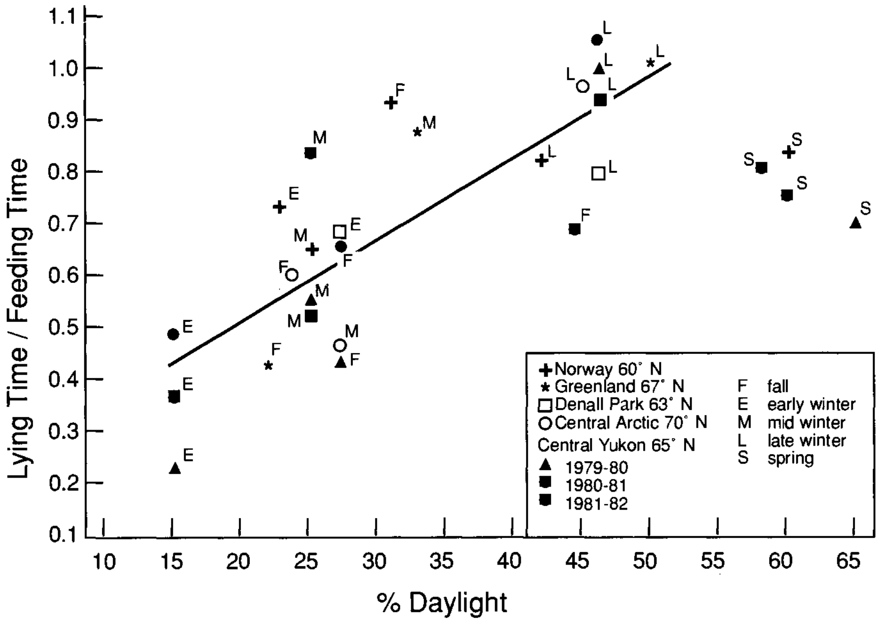

Figure 2.11. Relationship between day length and percent lying from various studies for fall (F), early (E), mid (M), and late (L) winter.

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^{3}x10^{-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)	0.432 (0.104)

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

$$\text{CRATERS} = \text{ACTIVE} \times 24 / (\text{TOTAL} + \text{BETWEEN})$$

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:

$$\text{ENERGY} = (\text{ED} + \text{EU} + \text{ESL}) * \text{TIME} * \text{PAW}$$

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

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

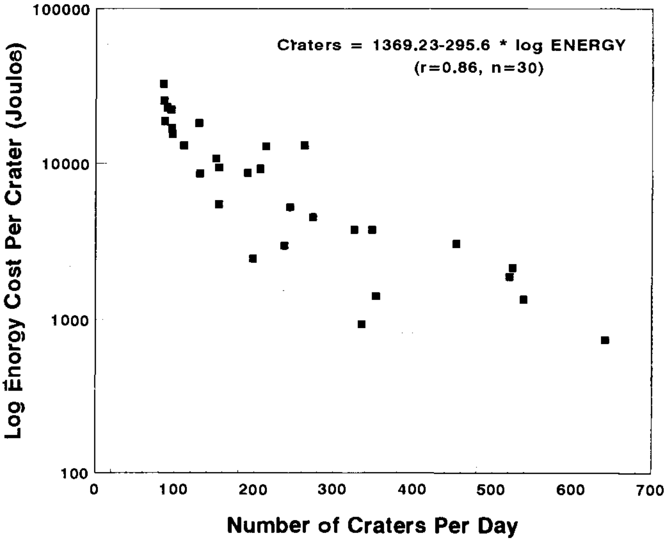

Figure 2.12. Log of the energy cost to dig a crater versus number of craters dug per day.

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 Volume	.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/cm³)	.180	.154	.216
Snow hardness (gm)	1892	1224	6596
Crater area (m²)	1.24	0.20	0.78
Crater volume (m³)	-	0.04	3.46
Number of craters/day	265	433	105
Forage selectivity (cm²/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