FIRE - CARIBOU RELATIONSHIPS: (VIII)
BACKGROUND INFORMATION

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REPORTS IN THIS SERIES

1. Thomas, D.C. and H.P.L. Kiliaan. 1998a. Fire-caribou relationships: (I) Physical characteristics of the Beverly herd, 1980-87. Tech. Rep. Series No. 309. Can. Wildl. Serv., Prairie & Northern Reg., Edmonton, Alberta. 178pp.

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7. Thomas, D.C. 1998b. Fire-caribou relationships: (VII) Fire management on winter range of the Beverly herd: final conclusions and recommendations. Tech. Rep. Series No. 315. Can. Wildl. Serv., Prairie & Northern Reg., Edmonton, Alberta. 100pp.

8. Thomas, D.C. 1998c. Fire-caribou relationships: (VIII) Background information. Tech. Rep. Series No. 316. Can. Wildl. Serv., Prairie & Northern Reg., Edmonton, Alberta. 104pp.

FORWARD

This report was drafted in 1980, added to in 1982, and edited and printed in 1998. It was initiated in response to two initiatives. In 1977, a review of fire management in northern Manitoba was requested by Joe Robertson, a Conservation Officer who worked for many years in northern Manitoba for the Department of Natural Resources. In 1980, Rich Golden, a manager in the same department, initiated a multi-agency panel to review fire management and Steve Kearney and I were assigned the task of reviewing the literature.

The 1980 survey estimate of 38 000 to 40 000 for the Kaminuriak herd initiated a start to a status report for the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). There was a possibility that the herd would be classified as "rare" or "threatened."

The much higher survey results for the Kaminuriak herd in 1982 caused both initiatives to be suspended. The Manitoba government decided not to attempt to control fire on the forested winter range of the Kaminuriak herd.

This report is presented here because it contains some historical information that is difficult to obtain by most scientists. Some of the publications and reports referred to here are out of print and many of them are unknown to most researchers. It also presents data by earlier researchers in new ways.

There are conflicting viewpoints about the value of historical information. On the one hand, it provides information on such things as maximum and usual distribution of caribou, which is important in defining historic range. We may even try to establish cause and effect of changes in distribution, numbers, or recruitment using demographic, climatological, fire history, or hunting data. On the other hand, historical data may have little value in predicting future events if global warming or higher variability in weather variables continue to occur. Additionally, the range is gradually being influenced by industrial developments and human activities.

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1. INTRODUCTION

1.1. General description of the Kaminuriak and Beverly populations

The Kaminuriak population of barren-ground caribou (*Rangifer tarandus groenlandicus*) is one of 10 identified populations in Canada (**Fig. 1**, Calef 1978, 1980). Some of the populations (herds) were flourishing in 1978, while others were considered to be dwindling in numbers (**Table 1**). Those data indicate that (1) the 1977 density of the Kaminuriak herd was extremely low relative to other major populations in the NWT and Quebec-Labrador, which winter in the taiga and summer on the tundra (Table 1), and (2) the winter ranges of the Kaminuriak and Beverly populations are known to overlap extensively.

The reported sharp decline in reported numbers of the Kaminuriak herd, from 149 000 - 173 000 in 1955, to 63 000 in 1967 (**Table 2**), to 44 000 in 1977, and 39 000 in 1980 was a serious concern to managers of the population. The trend was alarming even if numbers probably were under-estimated by factors of 2-3.

The 1982 survey of caribou on their calving grounds was extrapolated to an estimate of 134 000 caribou in the Kaminuriak herd. Recruitment of 1-year-old caribou to the Kaminuriak herd averaged 18% from 1980 through 1983 (C. Gates pers. comm.). If crippling losses and unreported kills were 20%, the kill estimates in 1979 and 1980 were 9829 and 7706. Many biologists and Game Management Officers believe that crippling losses and unreported kills amount to 30%. If true, the 1979 and 1980 kills were 11 228 and 8804, respectively. Therefore, if the 1980 population was 39 000, the kill represented 10.2% (7880/39 000) of caribou >1 year old (assuming calves accounted for 10.5% of the kill) (Gates pers. comm.). Only high recruitment could sustain such a high kill rate or the population was vastly under-estimated.

With recruitment equalling the harvest, the population must decrease because of natural mortality of caribou >1 year. Natural mortality estimates range from 5% (Kelsall 1968) to 7.3% (Caribou Technical Committee, unpubl. data).

The estimate of almost 54 000 on calving grounds of the Kaminuriak herd in

Figure 1.

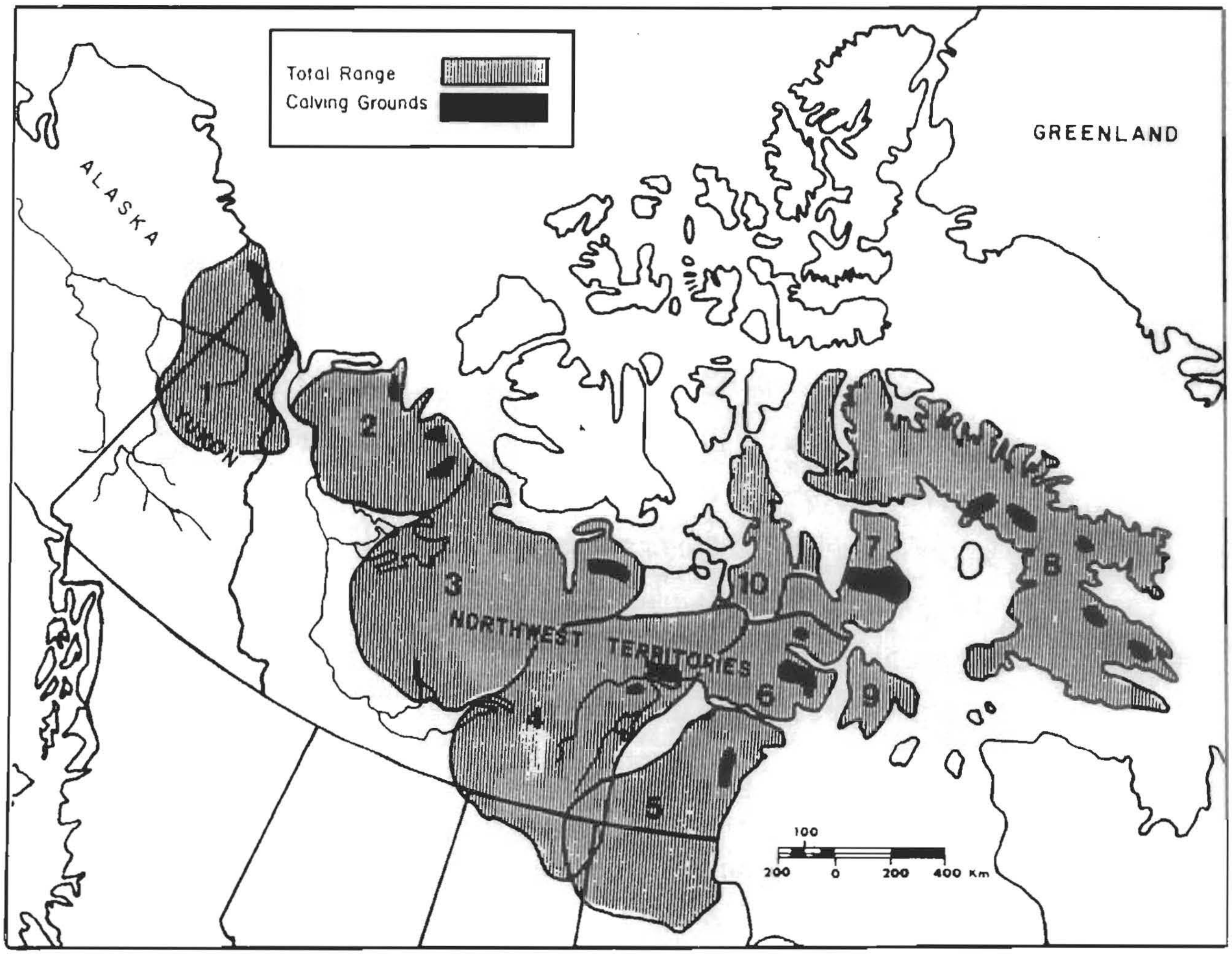


Figure 1. Ranges of herds of caribou in the NWT in 1977 (Calef 1980). Herd names are in Table 1.

Table 1. Status in 1977 of eight herds of caribou in the NWT (Calef 1978, 1980) and the George River herd in Quebec-Labrador (Dauphiné et al. 1975).

Map loc.[1]	Herd	Range area (km²)	Herd estimate	Suspected trend	Kill	Kill as % of herd	Caribou/ km²
1	Porcupine	220 000	100 000[2]	Stable	1554	1.6	0.45
2	Bluenose	194 000	90 000	Increasing	1124	1.2	0.46
3	Bathurst	518 000	150 000	Stable/decr.	6300	4.2	0.29
4	Beverly	389 000	124 000	Stable/decr.	5900	4.7[3]	0.32
5	Kaminuriak	282 000	44 000	Decreasing	3890	8.8	0.16
6	Wager Bay		29 000	Increasing.	0	0.0	
7	Melville Pen.		52 000[4]	Increasing	518	1.0	
8	Baffin		45 000	Decreasing	2485	5.5	
	George R.	256 000	155 000	Increasing			0.61

[1] See Fig. 1
[2] 93 000 - 103 000.
[3] Includes Saskatchewan kill.
[4] Includes Lorrilard herd listed at 17 000 in 1977 (Calef 1978).

1982, and a population total of 133 000, differed markedly with population trends to 1980 (Gates 1985 & pers. comm.). The kill adjusted for 30% underestimation represents 8.4% and 6.6% of the 1982 population, respectively. Some of the earlier population estimates obviously were low.

The estimated numbers in the Beverly herd varied from 275 000 in 1948-49 (Banfield 1954) (adjusted to account for missed caribou) to about 100 000 in 1955 (Kelsall 1968), 159 000 in 1967 (Thomas 1969), 210 000 in 1971 (Heard, pers. comm.), 177 000 in 1974 (Heard pers. comm.), 105 000 in 1980 (Gunn pers. comm.), and 150 000 in 1982 (Heard pers. comm.). Actual numbers probably were much higher as reflected by numbers adjusted to account for missed caribou and under-estimation of numbers in observed groups (**Table 3**).

Recruitment to the Beverly herd was 12.0% in 1967 and the over-winter kill in forested range was estimated at 3375 (Thomas 1969) or 2.1% of the herd estimate.

The southern extent of ranges of barren-ground caribou in Canada changed little between 1850 (Clarke 1940) (**Fig. 2**), and 1950 (Banfield 1954). However, it

Table 2. Estimated numbers in the Kaminuriak herd from 1948 to 1982.

Year	Month	Number	Adjustment 1[1]	Adjustment 2[2]	Source
1948	Apr-May	120 000	150 000	188 000	Banfield 1954
1955	May-June	149 000	186 000	233 000	Loughrey 1955
1968	June	63 000	included	79 000	Parker 1972a
1974	June	65 284	included	82 000	Heard pers.comm.
1976	June	42 376	included	53 000	Fisher et al. 1977
1977	June	44 000	included	56 000	Calef 1978
1980	May	39 000	included	49 000	Gunn pers. comm.
1982	June	133 000	included	166 000	Heard pers. comm.

[1] Assumes that 20% of the caribou are missed (x 1.25).
[2] Assumes that groups are under-estimated by 20%.

retracted northward in the 1970s and 1980s. One explanation for range reduction was changes in herd size (Tables 2 & 3). A concern of the Manitoba and NWT governments and the Caribou Management Board is a recent change in winter distribution. From 1973-74 through 1982, with the exception of 1974-75 and 1979-80, the majority of the population has wintered on the tundra near the settlements of Baker Lake, Rankin Inlet, and Eskimo Point rather than in northern Manitoba. To people in Keewatin settlements, there appears to be more caribou than ever, while hunters in the forest must travel long distances to secure a few animals. The northern boundary of the Kaminuriak herd remains undefined but it may have extended 50-100 km north of Chesterfield Inlet in historical times.

The winter range of the Beverly herd, at its known maximum, extended as far south as the Churchill River in Saskatchewan as far west as central Wood Buffalo Park and central Great Slave Lake, and as far east as Brochet, the Cochrane River, and Ennadai Lake. The summer range was bordered by Yathkyed Lake, Baker Lake and the Quoich River on the east, the Back River system on the north and MacKay Lake on the west. The northern boundary is uncertain and trails across the Back

Table 3. Estimated number of caribou in the Beverly herd from 1948 to 1982.

Year	Month	Number	Adjustment 1 [1]	Adjustment 2 [2]	Source
1948	Apr-May	275 000	343 750	429 700	Banfield 1954
1955	May-June	100 000	125 000	156 250	Kelsall 1960, 1968
1958	May	100 000	125 000	156 250	Kelsall 1960
1960	Apr-May	73 000	91 250	114 100	McEwan 1960
	July	90 000	112 500	140 600	McEwan 1960
1967	May	159 000	included	198 750	Thomas 1969
1971	June	210 000	included	262 500	Heard pers. comm.
1974	June	177 000	included	221 250	Heard pers. comm.
1980	June	105 000	included	131 250	Gunn pers. comm.
1982	June	150 000	included	187 500	Heard pers. comm.

[1] Assumes that 20% of the caribou are missed (Thomas 1969).
[2] Assumes numbers in groups are underestimated by 20% (Thomas 1969) (see Parker 1971).

River and around Garry Lakes suggest that the Beverly herd may travel north of Garry Lakes in some years.

1.2. **General review of the Kaminuriak and Beverly herds**

The first survey of the Kaminuriak population in 1948 indicated three subpopulations or herds numbering an estimated 120 000 caribou (Banfield 1954). A close look at the survey methodology, subsequent data on survey inaccuracies, and harvest data for that period, suggests that numbers were much higher than Banfield (1954) estimated. Similarly, the estimates from the next survey in 1955 (Loughrey 1955) must be considered an underestimate. Surveyors will readily admit that they could miss 20% of caribou and underestimate numbers in aggregations larger than 30 or 40 caribou by the same amount. They are reluctant to increase their estimates by 1.56 to account for those under estimations.

After further work on the population in 1956 (Loughrey 1956), field research on caribou in the next 9 years was focussed largely on the adjacent Beverly population

Figure 2

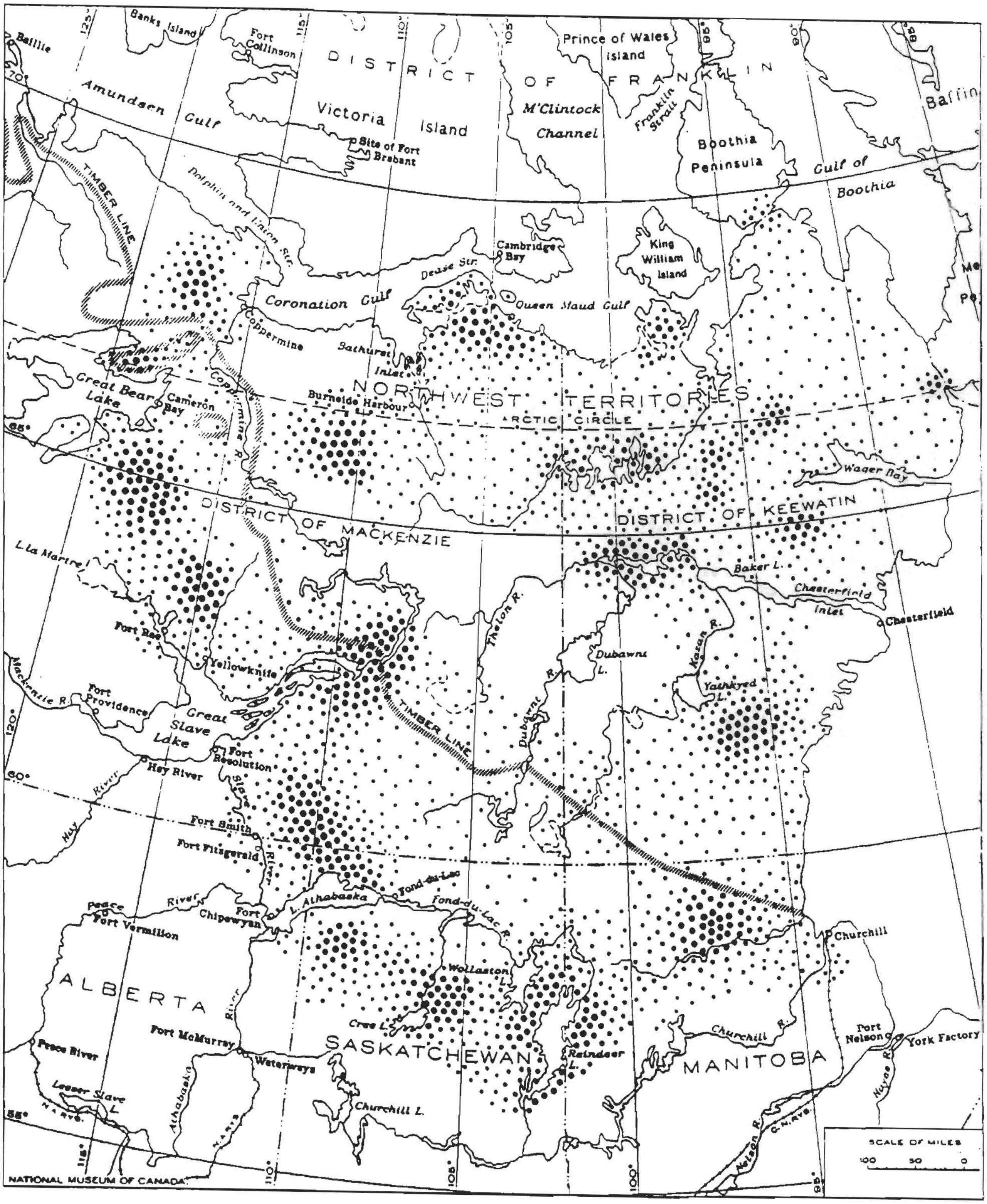


Figure 2. Distribution and relative density of caribou in mid-winter about 1850 (Clarke 1940).

(Kelsall 1968). The exceptions were distributional information on the population through tagging studies conducted at Duck Lake and vicinity, 1959-1970 (Miller and Robertson 1967) and air photo interpretation of burns (Beckel 1965).

Intensive studies of the Kaminuriak herd were conducted from 1966 through 1968. Phases included numbers and distribution (Parker 1972a), age determination and social structure (Miller 1974), diet and range (Miller 1976a), and growth, reproduction, and energy reserves (Dauphiné 1976). Those studies were followed in 1970 by a study of mortality factors in young calves (Miller 1974), and in 1972 and 1973 by a study of the effect of fires on caribou that used winter ranges in Manitoba and Saskatchewan (Miller 1976b).

Each year from 1971 to 1977, except for 1975, the NWT Wildlife Service surveyed the Kaminuriak population on their calving grounds (Calef pers. comm.). The first "adequate" survey, in 1974, indicated a population decline from an estimate of 68 000 in 1968 (Parker 1972a). This trend was supported by results of surveys in 1976, 1977, and 1980. During the 1970s, the Manitoba Government recorded winter distributions and continued to obtain harvest data as did the NWT Government. In 1977, the Manitoba Government hired a caribou biologist who has obtained fire incidence data and conducted range studies.

The Beverly herd was traversed by Clarke (1940) while conducting an investigation of the Thelon Game Sanctuary. He pulled together much of the historical data relating to that herd and others on the central mainland of Canada. Banfield (1954) surveyed the winter ranges of the herd in 1948-49 and described some movement patterns of population segments be named the Saskatchewan herd. In 1957-58, the herd was the focus of a 17-month general ecological study to ascertain causes of a perceived marked decline in the herd (Kelsall 1960, 1968). That was followed by a study of migration, reproduction, and calf mortality from 1959 to 1962 (McEwan 1960, 1963).

Individuals in the Beverly herd were tagged at water crossings from 1960 to 1967 (Kelsall 1968, Parker 1972b), 1972, 1973, and 1977 (Heard 1985 & pers. comm.).

Studies on winter range of the Beverly herd commenced in 1959 (Scotter 1964) and continued from 1973 through 1975 (Johnson and Rowe 1975) and from 1973 through 1975 (Kershaw et al. 1975). Those rather intensive studies were followed by a broad-based ecological mapping project in the late 1970s (Bradley et al. 1982).

From 1978-1982, the movements of the Kaminuriak and Beverly herds were monitored from 15 May to July 31 as part of the Land Use Regulations pertaining to exploration and proposed mining development on summer ranges.

In 1980 and 1981, a study of diets and forage digestibilities was conducted from a base in Fort Smith using rumen contents of caribou collected on winter range of the Beverly herd. In March 1982, a sample of 82 caribou was obtained northeast of Fort Smith to begin a study of potential effects of burns on caribou movements and feeding behaviour and to evaluate adequacy of winter range.

1.3. **A "Task Force on Fire Management"**

A "Task Force on Fire Management on Barren-Ground Caribou Wintering Range in Manitoba" was established 25 July, 1978, on initiative by the Manitoba Government. Seven members included a mix of caribou and fire specialists and managers. The Terms of Reference of the Task Force were as follows:

1. To evaluate the role of fire on winter range of the Kaminuriak herd in Manitoba.
2. To consider related factors such as predation, climatic changes, and herd condition.
3. To recommend, based on evaluation of available information, whether a program of protection and enhancement of winter range was necessary, at various caribou population levels.

The Caribou Management Group, with members from management jurisdictions of Manitoba, Saskatchewan, and NWT, and the Department of Indian Affairs and Northern Development, recognized that steps must be taken to conserve and rehabilitate the population. Three management options were possible:

1. Stop or sharply reduce the harvest of caribou.

2. Reduce the wolf population.
3. Reduce the loss of winter range in Manitoba through fire suppression.

The task force was restricted to feasibility of the third option in light of conflicting viewpoints on effects of forest fires on winter range of caribou (Scotter 1964; Johnson and Rowe 1975; Rowe et al. 1975; Kershaw et al. 1975; Miller 1976b, 1980).

1.4. **Purpose of this review**

The purpose of this review is to bring together pertinent literature and unpublished data on caribou winter range-fire interrelationships up to 1982. This review was intended to form a basis for discussion by task force members, who would then make recommendations. The scope of this review was extended to the ranges of the Beverly herd in 1980. That herd was selected for a study of potential effects of burns on caribou use of forested range and evaluation of the adequacy of winter range.

The task force project was abandoned in 1979 when the Government of Manitoba changed its emphasis from fire management to consultations with communities as a means of solving the caribou crisis. By that time much of this review was assembled and its completion was deemed to be important as a source of background information.

2. USE OF WINTER RANGE IN MANITOBA, SASKATCHEWAN, AND NWT

Historical use of northern Manitoba by barren-ground caribou is spotty, anecdotal, confused with observations of woodland caribou (*R. t. caribou*), and of questionable veracity, e.g., an observation of over 3.5 million in one migration in 1792 (Banfield 1954, Parker 1972a). Parker (1972a) concluded that seasonal movements and total numbers were similar in the recorded past to those existing in 1966-69. The Churchill River historically was the southern limit of winter distributions. Reindeer Lake was a traditional wintering region, and, occasionally, large numbers of forest-tundra caribou wintered on the tundra. There was considerable evidence for a southern expansion of caribou on winter range in Manitoba starting in the late 1930s and continuing until the late 1940s.

Banfield (1954) identified three herds in northern Manitoba in the winter of 1948 **(Fig. 3.)**, all with common calving grounds:

1. The Brochet herd (40 000) wintered around Reindeer Lake (No. 9 in Fig. 3).
2. The Duck Lake herd (25 000) wintered in the vicinity of South Indian Lake and Nelson House (No. 10 in Fig. 3).
3. The Churchill herd (55 000) occupied the lower Nelson and Hayes watersheds in winter (south of the Churchill River) (No. 11 in Fig. 3).

Defining wintering areas once during a winter or even based on several winter seasons can lead to faulty conclusions. The distributions in late-winter 1957 (Loughrey 1957) (**Fig. 4)** was quite different from that given by Banfield (1954). In fact, Banfield (1954) provided a good overview in his Figure 9 (**Fig. 5**), which showed a large maximal wintering area extending almost to The Pas and Island Lake in the south and a central core region. The region occupied by wintering caribou shifted to the north and west during the 1950s and 1960s (Robertson 1977).

Parker's (1972a) surveys indicated extensive movements during winters of 1966-67 and 1967-68. Distributions were different on every survey. In both winters there was a movement of the main body of caribou from east to west as winter progressed, such that by the end of April most caribou had moved out of Manitoba. On 1 May 1967, the Kaminuriak population was in two widely separated groups: one along the Saskatchewan-Northwest Territories border centred 80 km west of Manitoba, the other (20%) in Keewatin District along the Hudson Bay coast. One year later, most of the population was in the vicinity of the Manitoba-Saskatchewan border west of Misty Lake (Parker 1972a).

Robertson (1977), in a plea for management of the Kaminuriak population, mapped the southern limit of winter distributions in Manitoba at intervals from 1950-51 to 1975-76 (**Fig. 6**). He indicated a progressive shrinkage of the winter range in

Figure 3.

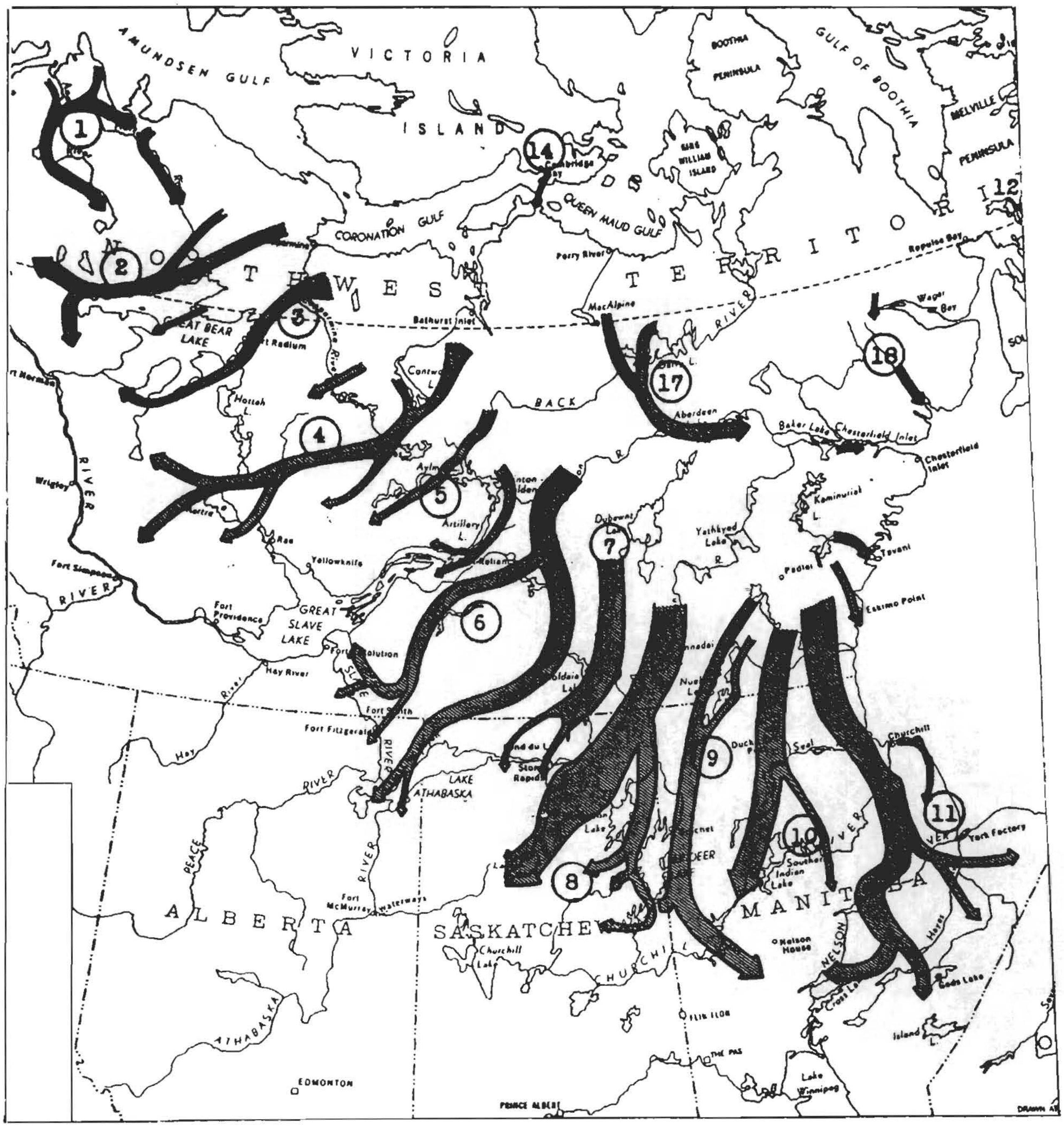


Figure 3. Autumn migration routes of the Brochet (# 9), Duck Lake (# 10), and Churchill herd (# 11) identified in northern Manitoba by Banfield (1954).

Figure 4.

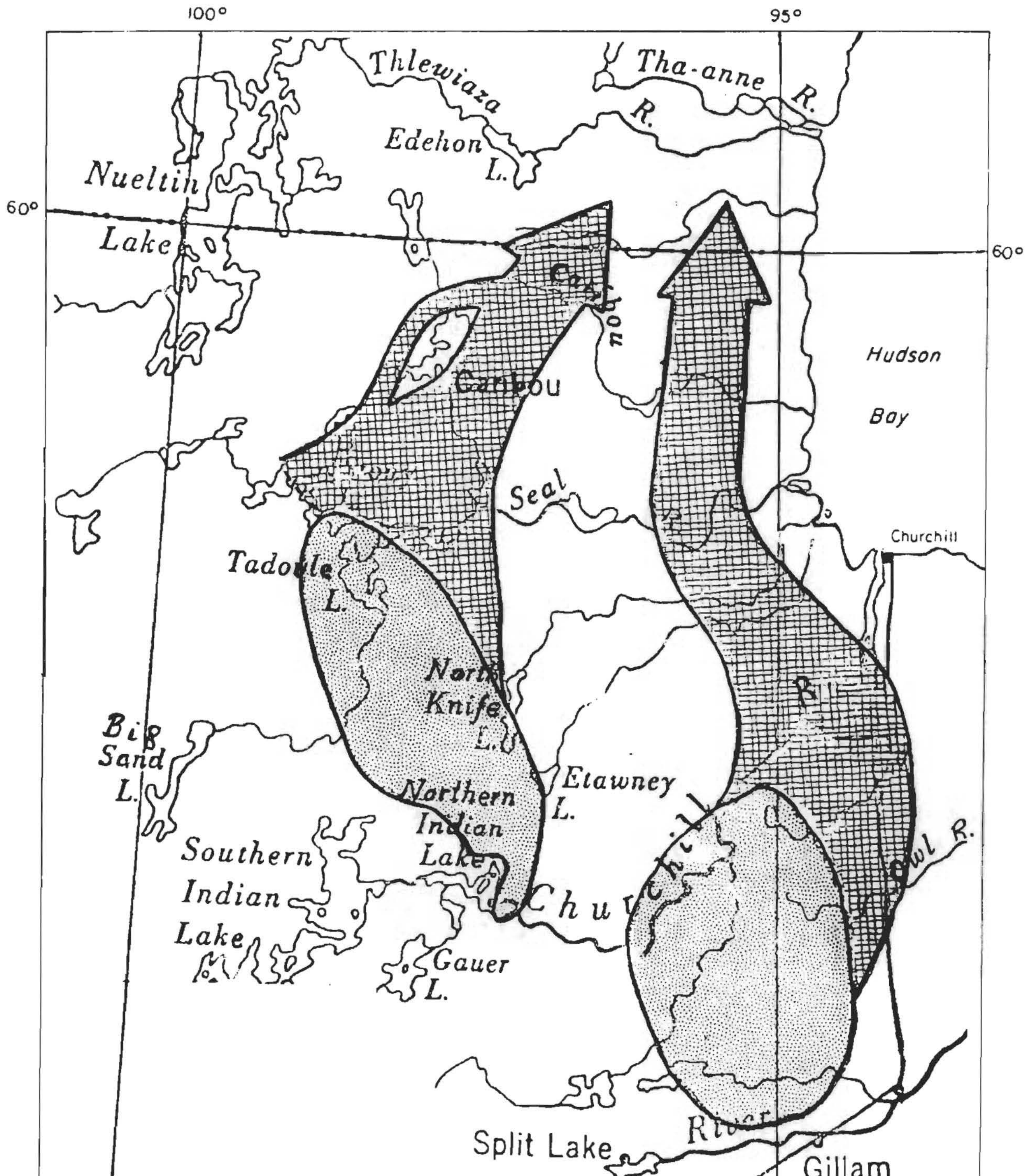


Figure 4. The late-winter distribution and spring migration routes of the Duck Lake and Churchill caribou herds in 1957 (Loughrey 1957).

Figure 5.

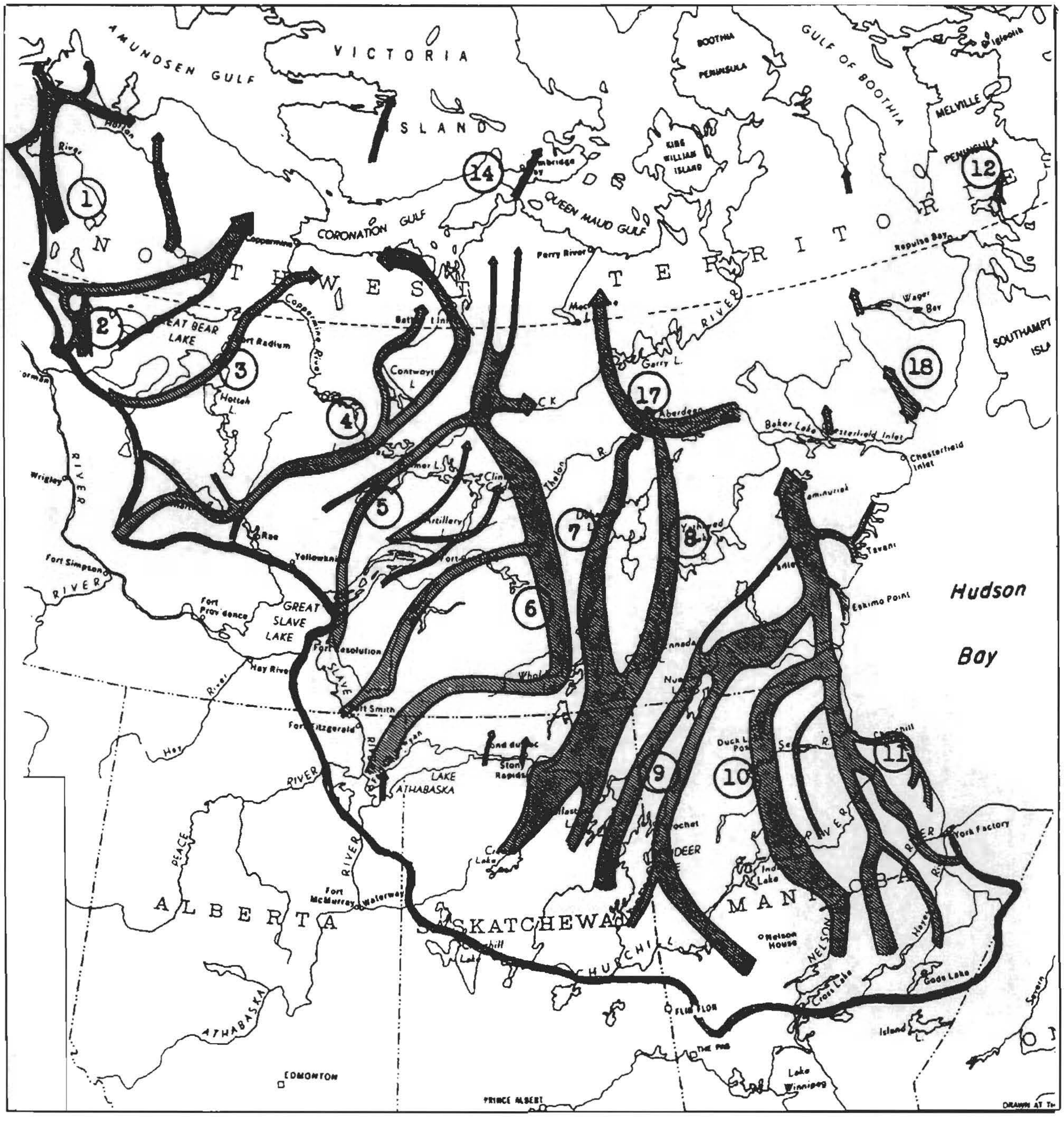


Figure 5. Spring migration routes of caribou herds and winter range limits (Banfield 1954).

Figure 6.

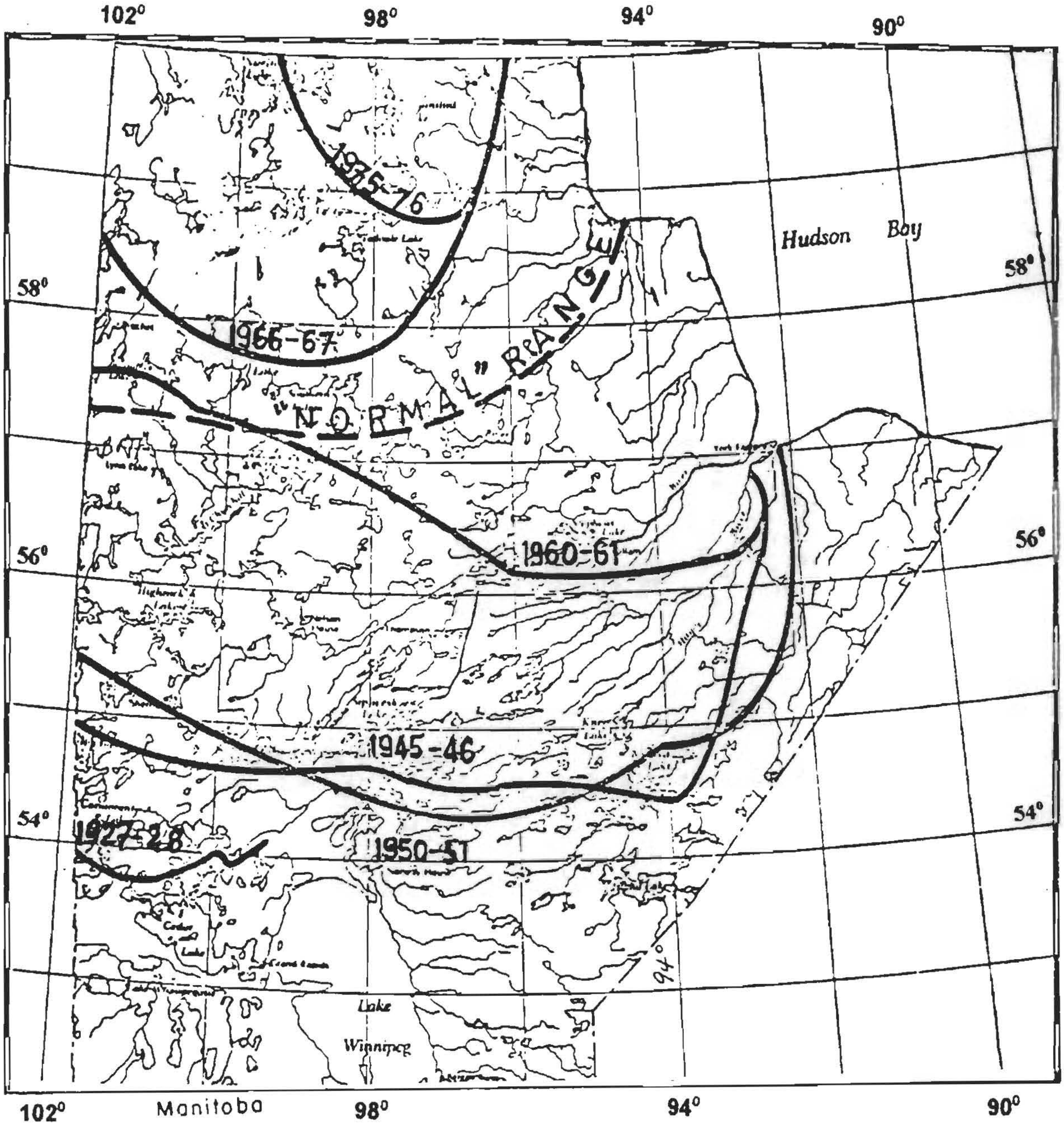


Figure 6. Withdrawal northward of winter range of the Kaminuriak herd at successive decade intervals, according to Robertson (1977).

northern Manitoba, from 373 000 km^2 in the 1940s and 1950s to 143 000 km^2 in most winters (the traditional or "favoured" range), to a complete withdrawal in 1976-77. In 1977-78, caribou re-entered Manitoba a short distance but stayed only until March. They did not return again until 1979-80 and 1981-82 (Kearney pers. comm.).

3. CHARACTERISTICS OF WINTER RANGE

3.1. **Climate**

Average annual precipitation by month for several stations in the winter range indicate relatively high values for northwestern Manitoba compared with other winter ranges. Annual precipitation at Brochet was 38.9 cm compared with 33.0 cm at Stony Rapids, 21.7 cm at Ennadai, and 21.0 cm at Fort Reliance (Bone et al. 1973, **Table 4**). Climatic data to 1970 (Environment Canada 1973), indicate a rainfall cline from Uranium City to Brochet: Uranium City 20.3 cm, Stony Rapids 24.4 cm, and Brochet 26.3 cm. Average snowfall at Brochet was 169 cm compared with 140 cm at Stony Rapids and 184 cm at Uranium City. Those data must be treated with caution because they were based on different time spans: Stony Rapids <10 years, Uranium City 10-14 years, and Brochet 20-24 years.

According to a map in Banfield's (1954) report (**Fig. 7**) north-central Manitoba and southern Keewatin District is in a zone of high snowfall (152 cm) relative to Stony Rapids (85 cm).

3.2. **Landform**

The major landforms in northern Manitoba (Ritchie 1962) are patternless and drumlinized drift plains overlying Precambrian granites and gneisses, which outcrop in places. According to Scotter (1965), outcrops are far more frequent in northwestern Manitoba than in northeastern Saskatchewan. Long sandy eskers are especially abundant in the northwest corner of Manitoba. Patternless drift plains are characterized by low relief but sufficient to impede drainage and thus create extensive bogs (Miller 1976b). This drumlin-dominated landform has greater relief

Table 4. Climatic means for several stations on or near caribou winter range in north-central Canada (metric conversion of data in Bone et al. 1973).

Station	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Year
					Temperature (C°)								
Brochet	-27.4	-24.3	-15.7	-6.3	3.3	9.8	15.4	14.4	8.1	1.3	-11.7	-23.3	-4.7
Stony Rapids	-27.8	-23.4	-18.2	-2.7	6.2	10.8	16.3	13.9	7.4	1.6	-11.0	-20.6	-4.0
Ennadai	-32.5	-29.1	-23.4	-12.8	3.1	6.4	12.6	12.1	4.0	5.5	-14.7	-25.4	-9.3
Fort Smith	-25.2	-22.6	-14.8	-3.2	7.3	13.0	16.2	13.8	6.8	-0.2	-12.3	-21.7	-3.6
Fort Reliance	-31.1	-27.5	-20.4	-9.8	1.3	8.2	12.9	13.4	6.6	-2.8	-13.0	-24.6	-7.2
					Precipitation (mm)								
Brochet	11.8	11.9	9.1	17.3	20.3	42.9	72.9	52.1	64.0	40.1	25.9	21.1	389.4
Stony Rapids	16.5	8.9	16.3	18.5	19.8	33.0	32.3	77.5	34.8	28.2	21.1	23.1	330.0
Ennadai	8.1	8.4	6.6	10.2	15.2	18.5	42.9	28.7	30.2	24.1	12.7	11.4	217.2
Fort Smith	13.5	16.8	17.0	13.2	24.6	35.8	50.6	41.9	39.1	24.4	21.8	22.1	320.8
Fort Reliance	9.9	11.4	8.6	7.6	11.7	15.5	24.9	25.4	25.4	26.4	24.6	18.8	210.3

Figure 7.

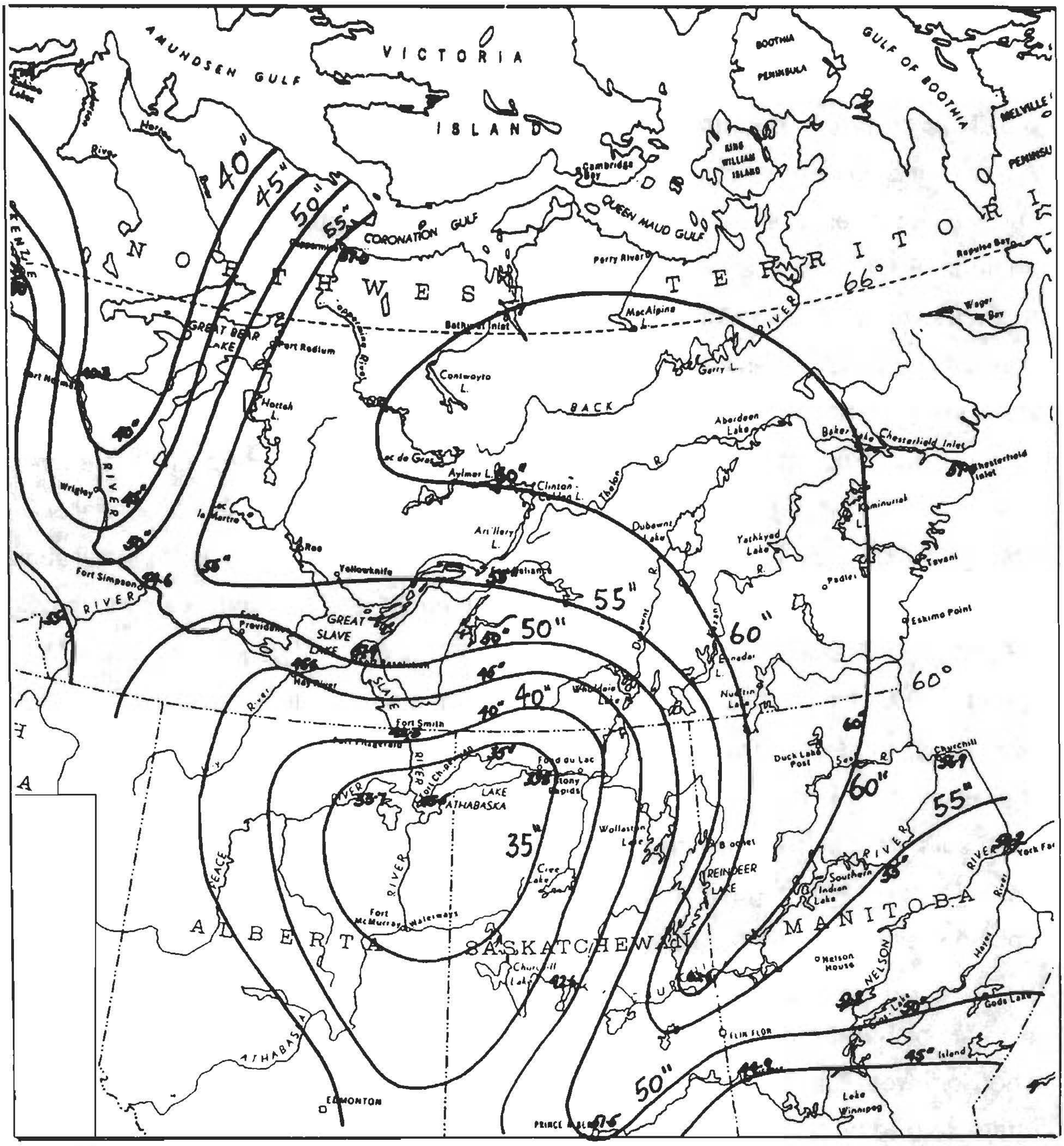


Figure 7. Snowfall isolines (inches) in northern Manitoba (Banfield 1954).

with small lakes, bogs, fens, and streams aligned with the drumlins.

The Hudson Bay Lowlands, an area of extensive bogs and muskegs caused by flat topography and poor drainage, occurs in the Seal and Hayes watersheds.

3.3. **Topography and soils**

A basic division used by range biologists is uplands and lowlands, crudely defined by surface characteristics such as hydrology and vegetation rather than a specific contour. For example, Miller (1976b) found that lowlands occupied 36% of the total surface in northwestern Manitoba but only 17% in Saskatchewan. If water surface was excluded (18% Manitoba, 20% Saskatchewan) by Miller 1976b, the ratios of lowland to upland in Manitoba and Saskatchewan were 43:56 and 21:79, respectively. Robertson (1977) found that water occupied 31.l% of the total area of four 1:250 000 (scale) map sheets in northwestern Manitoba and 22% of a smaller area (Whiskey Jack 1:250 000 scale map sheet) studied by Miller (1976b). Lowlands were subdivided into muskeg and fen. In Manitoba, 81% of lowlands were muskeg, 19% fens; in Saskatchewan 76% were muskeg, 24% fens. Of non-water surface, 35% and 9% of the surface were muskeg and fen, respectively, in Manitoba; 16% and 5% in Saskatchewan (**Table 5**).

Kelsall (1968), in a review of soil characteristics on caribou ranges, indicated that most soils were acidic, calcium content was low, and magnesium content was very low. Scotter (1965) suggested that the soils in northern Manitoba were podzols on upland sites derived from glacial drift or till.

3.4. **Major habitat types**

The Northwest Transition Zone of the Boreal Forest Region (Rowe 1972) is characterized by coniferous forest dominated by black spruce (*Picea mariana*) with lesser cover of jack pine (*Pinus banksiana*), white spruce (*P. glauca*), tamarack (*Larix laricina*), and white birch (*Betula papyrifera*). According to Miller (1976b), trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) were common

Table 5. Proportions (%) of land surface in upland, lowland, and water categories of sample areas on the caribou winter range in northwestern Manitoba and northeastern Saskatchewan (Miller 1976b).

		Lowlands			
	Water	Muskeg	Fens	Total	Uplands
Total surface:					
Manitoba	18	29	7	36	46
Saskatchewan	20	13	4	17	63
Non-water surface:					
Manitoba		35	9	44	56
Saskatchewan		16	5	21	79

only on southern exposures in the southern portion of the range in Saskatchewan.

Scotter (1965), who provided detailed descriptions of the vegetation of northwest Manitoba, stated that black spruce (*Picea mariana*) dominated open subarctic woodland in northern portions of winter range, but jack pine (*Pinus banksiana*) forests were abundant in the south. He summarized existing data on vegetation and fires in northern Manitoba. Of particular value was the work of Ritchie (1959, 1960, 1962), who noted that as little as 5% of "stable", mature vegetation (old growth) occurred in some regions of northern Manitoba.

Systematic classifications of major range (habitat) types were avoided by most workers. A crude one has evolved but it has not been formalized or standardized. Initial stratification was by dominant tree type, e.g., black spruce forest. Other authors (e.g., Ritchie 1960) added the dominant vegetation of the ground to the name, e.g., black spruce-lichen forests. Most authors have introduced the topographic modifiers, uplands and lowlands to some of their vegetation types. Several also added cover modifiers, i.e., open and closed (forests) or sparse and dense (tree cover).

Landscape or range-type classifications rarely are pure and those used to

Table 6. Major habitat types on taiga winter range of barren-ground caribou as compiled from several authors.

1. Black spruce dominated	6. Lake shore
1.1 Black spruce	6.1 Willow
1.2 Black spruce-white birch	6.2 Alder
1.3 Black spruce-jack pine	6.3 Sedge
2. Jack pine dominated	7. Stream (River, Creek)
2.1 Jack pine	7.1 Willow
2.2 Jack pine-spruce	7.2 Alder
2.3 Jack pine-white birch	7.3 Sedge
3. White birch dominated	8. Esker
3.1 White birch	9. Rock outcrop
3.2 White birch-black spruce	10. Boulder field
3.3 White birch-jack pine	11. Water
4. Muskegs (swamps) (bogs) (fens)	
4.1 Black spruce	Modifiers
4.2 Black spruce-larch	A. Topography
4.3 Larch	A1 Upland
4.4 Willow	A2 Lowland
4.5 Alder	B. Tree Cover
4.6 Sedge	B1 Closed (dense)
4.7 Open	B2 Open (sparse)
5. Meadows	C. Vegetation layers
5.1 Sedge	Mid: Shrub
5.2 Shrub and sedge	Ground: Lichen
	Moss

describe caribou winter range are no exception. Thus, physiognomic types such as muskegs, fens, boulder fields, eskers, etc. are listed as major range types along with those based on vegetation. To maintain a pure classification, based on major species at one to three canopy levels, the topographic and physiognomic features must be relegated to subtypes or modifiers.

Classifications used by various authors (**Table 6**) could be restructured into several combinations based on primary criteria including major species, species stratification (vertical and horizontal), cover classes, topography, physiognomic type, moisture regime, or various combinations.

In 1981, six vegetation cover maps at a scale of 1:250 000 were produced that encompassed most of the winter range of the Kaminuriak herd (58°N - 60°N latitude, 96°W - 102°W longitude) (Dixon 1981). Objective of this mapping was to determine quantity and quality of winter range. Twelve vegetation and three burn cover types were distinguished from colour enhancement of LANDSAT data. Ground checks were supported with aerial photography and visual checks from aircraft.

3.5. **Successional stages**

Ritchie (1959) and Scotter (1965) outlined successional stages on upland sites after fires in northwestern Manitoba. On glacial till, the sequence was herbs-grass-moss to white birch to white birch-black spruce to black spruce-white spruce to open black spruce. On rock ridges and sandy terrain the sequence was herbs-grass-moss to jack pine to jack pine-black spruce to black spruce-jack pine to open black spruce.

Kelsall (1960) concluded that presumed-climax spruce-lichen forest type were replaced in northern Saskatchewan by sub-climax jack pine-lichen forests. Spruce-lichen associations could only be found on islands in large lakes. He noted that south of Lake Athabasca and the Fond-du-Lac River, where substrates were sandy, the dominant cover was jack pine. Either jack pine is climax or succession from jack pine to spruce occurs slowly and a high incidence of fires precludes succession to spruce. A biophysical mapping project provided some of the answers north of 60°N

Figure 8.

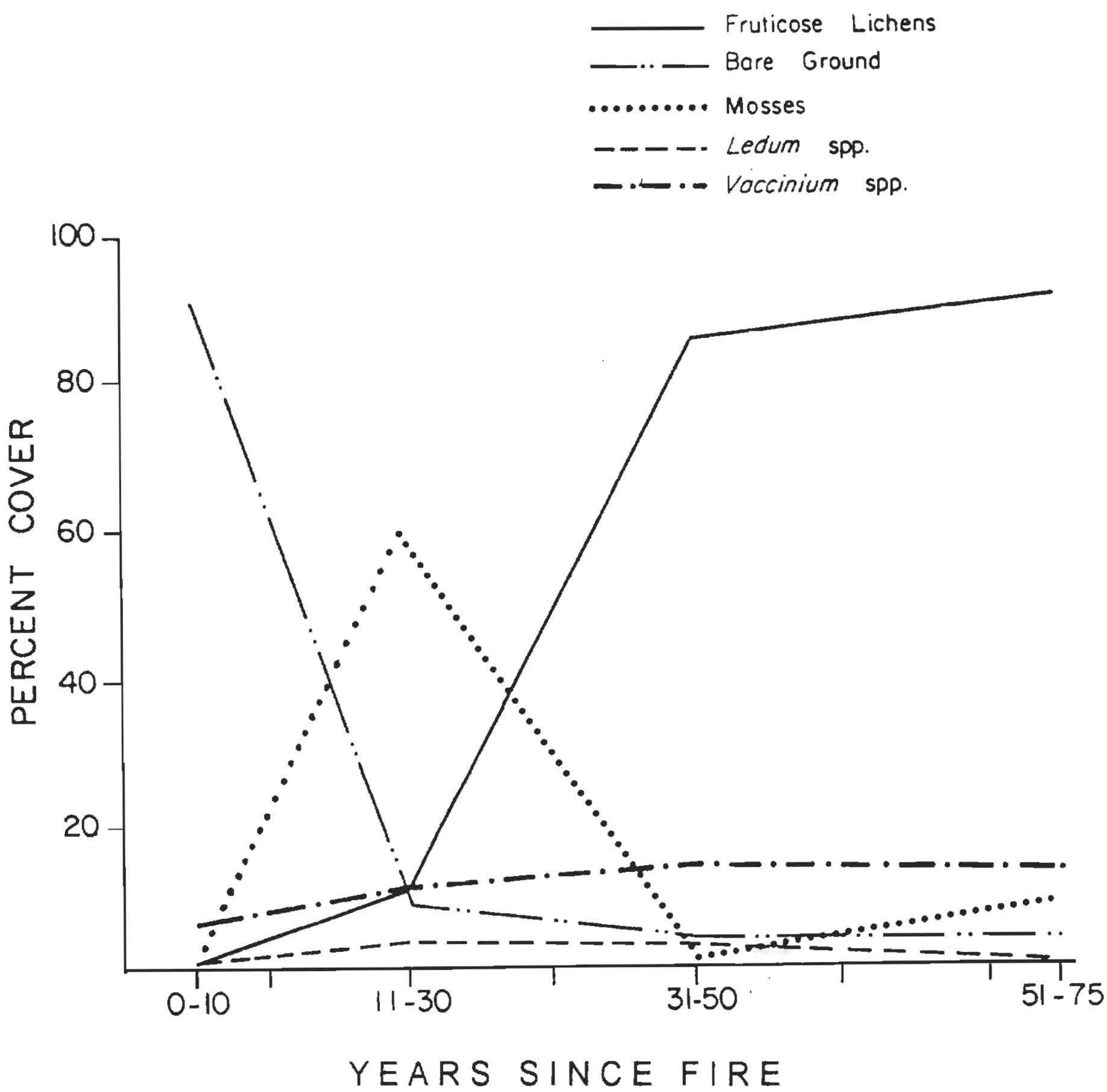


Figure 8. Percent cover of plant groups and bare ground at four phases of regeneration after fire on drumlins at Carleton Lake (Kershaw et al. 1975).

Table 7. Percent cover of vegetation at four phases of regeneration after fire on drumlins in the Dunvegan-Abitau lakes region, NWT (Kershaw et al. 1975).

Phase Years post fire	1A 3	1 12-23	2 32-52	3 67-70
Bare ground	91.4	8.7	4.5	2.1
Biatora granulosa		9.8	3.7	0.3
Cetraria spp.		0.7	16.6	11.4
Cladina spp.	1.0	1.3	44.2	45.1
Cladonia spp.		9.1	22.6	18.7
Stereocaulon paschale			1.6	20.8
Lecidea uliginosa		6.7	0.8	0.5
Ledum groenlandicum	0.7	3.9	2.8	
Vaccinium spp.	6.1	10.7	14.2	12.2
Carex leporina	0.2	0.4		
Polytrichum spp.		57.7	3.3	4.6

(Bradley et al. 1982).

Kershaw et al. (1975) documented successional changes in vegetation after fire on drumlins around Dunvegan-Abitau Lakes in NWT (**Fig. 8, Table 7**). Three years after a burn, dominant plant cover, on a background of 91% bare ground, was *Vaccinium uliginosum* (6%). Other species included *Cladina* spp. (l%), *Ledum groenlandicum* (1%), *V. vitis-idaea* (l%), and traces of *Carex* spp. At 12-23 years post burn, the surface was dominated by *Polytrichum* spp, (58%), mostly *P. piliferum* with lesser cover of *Vaccinium* spp. (11%), *Biatora granulosa* (a crust lichen, 10%), *Cladonia* spp. (9%), *Lecidea uliginosa* (a crust lichen, 7%), *Ledum groenlandicum* (4%), and others. In older phases, percent cover of lichen species increased sharply (**Fig. 9,** Table 7, **Appendix 1**) while shrubs, mosses, and sedges declined in cover.

In **Figure 10**, data in Kershaw et al. (1975) were grouped into six age classes: 3, 12, 23, 32, 47-52, and >67 years after fire. The number of sites included in each age class were 1, 1, 5, 4, 9, and 4, respectively.

Figure 9.

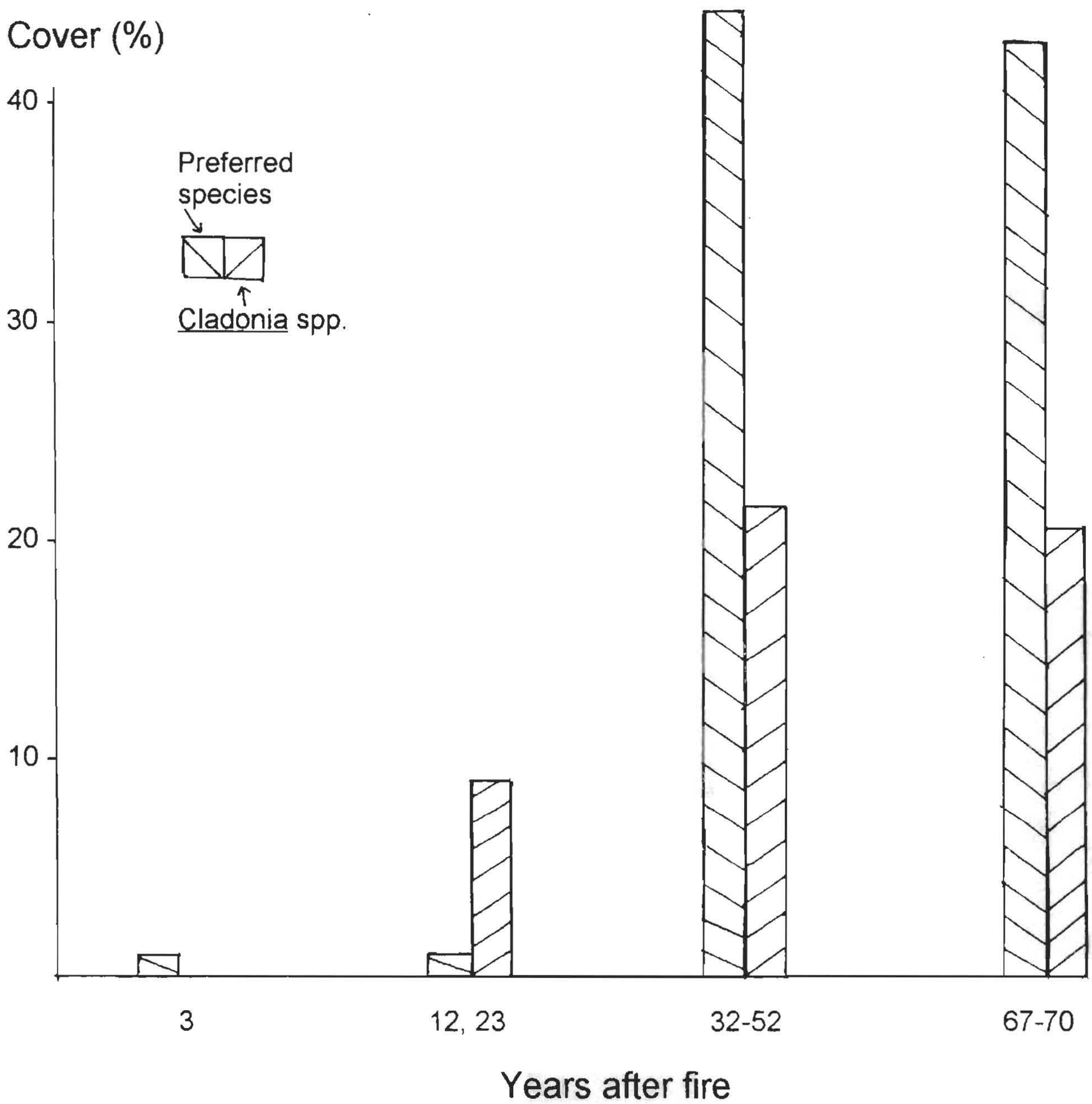


Figure 9. Percent cover of lichen species preferred by caribou (*Cladina* spp., *Cetraria* spp., and *Cladonia uncialis*) and less-preferred *Cladonia* spp. at four phases after fire at Carleton Lake, NWT (Kershaw et al. 1975).

Figure 10.

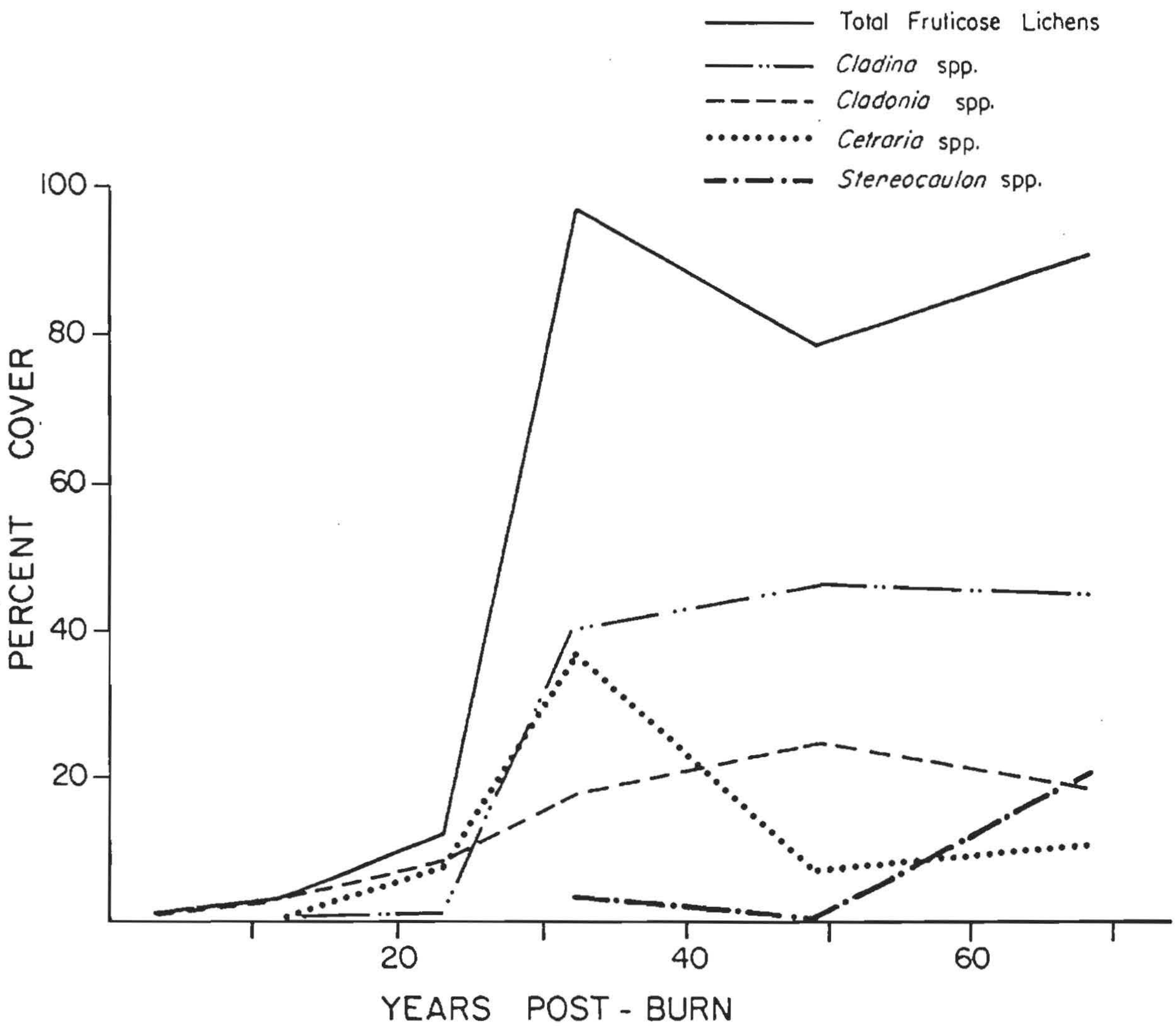


Figure 10. Percent cover of lichen genera at six intervals after fire on drumlins at Carleton Lake, NWT (data in Kershaw et al. 1975).

Table 8. Cover of terrestrial lichens (ocular estimates) at 53 sites in northern Manitoba and Saskatchewan (calculated from data in Miller 1976a, 1976b).

Age class (yr)[1]	Mean (%)	Standard deviation	Standard error	Sample size
21-40	32	45.3	45.3	2
41-60	75	8.7	6.1	3
61-80	75	10.5	2.7	16
81-100	80	10.2	4.2	7
101-120	77	14.0	4.9	9
121-140	75	12.1	5.4	6
141-160	80	8.4	3.2	8
161-180	79	2.8	2.8	2

[1] Ages in Miller (1976a & b) were increased 5 and 10 years for pine and spruce stands, respectively, to allow for time between fire and number of annulations in cores of representative trees. One lowland site with 38% cover was omitted.

Successioal changes noted in Kershaw et al. (1975) were presented here in detail because they showed a reasonably uniform change. Variability was reduced intentionally by selecting all sites on one landform type. The described succession is for spruce forests. In other studies, where data from a variety of habitat types and landforms were grouped, as was various burn severity classes, the extreme variability almost precludes generalizations. For example, consider Miller's data (1976b) (**Tables 8 and 9**). He noted rapid recovery of forbs, shrubs, mosses, spruce, and jack pine on sites in northwestern Manitoba burned 1 and 2 years before examination. Three years after a fire he estimated *Vaccinium* spp., *Ledum* spp., *Epilobium* sp., sedges, and *Equisetum* spp. collectively covered 60% of the surface. Three years after areas burned in north-central Saskatchewan, dense growth of one or more of the following species occurred: *Ledum* spp., *Pinus* spp., *Alnus* spp., *V. myrtilloides*, *V. vitis-idaea, Arctostaphylos uva-ursi*, and *Epilobium angustifolium.* Interestingly, lichens and mosses were placed in the "dense" rating only 9-12 years after burning.

Table 9. Terrestrial lichen biomass estimates at 53 sites with high lichen cover in northern Manitoba and Saskatchewan (calculated from data in Miller 1976a, 1976b).

Age class (yr)[1]	Mean (kg/ha)	Standard deviation	Standard error	Sample size
21-40	3075	2312	2312	2
41-60	4903	2163	1530	3
61-80	6518	3254	840	16
81-100	6141	688	281	7
101-120	9183	3348	1184	9
121-140	6817	1935	865	6
141-160	6103	1275	482	8
161-180	4460	1117	1117	2

[1] Ages in Miller 1976a & b) were increased 5 and 10 years for pine and spruce stands, respectively, to allow for time between fire and number of annulations in cores of representative trees. One lowland site with 38% cover was omitted.

3.6. Standing crop - productivity

Standing crop and productivity data for forage species are far more valuable than percent cover in assessing comparative productivity or theoretical carrying capacity. Unless landscape and fire severity factors are stratified, the data are likely to display extreme variability for reasons outlined in the previous section.

Scotter (1965) found, in northwestern Manitoba, a sharp increase in standing crop of the live component of terrestrial lichens to a 30-50 year post-burn class, then a more gradual increase to a maximum mean value of 98l kg/ha in a >120 year-class (**Table 10**). The standing crop of shrubs remained about constant after the first age class (1-10 years), whereas herbs and monocotyledons flourished only in the first 10 years after fire. Trends were similar in black spruce and white birch forests in

Table 10. Average standing crop (kg/ha) by age classes of air-dried forage in the Cochrane River region of northwestern Manitoba (Scotter 1965).

	Time since last fire (years)					
Plant group	1-10	11-30	31-50	51-75	76-120	>120
Grass-like	6	T	T	T	1	T
Herbs	39	T	T	1	2	8
Shrubs: High value	10	98	61	129	132	144
Mid value		2	1	2	4	8
Low value	61	113	72	122	119	62
(Totals)	(71)	(213)	(133)	(253)	(256)	(213)
Lichens: High value	T	168	405	573	731	861
Mid value	T	7	37	37	90	68
Low value	T	176	152	121	77	52
(Totals)	T	(351)	(594)	(731)	(898)	(981)
Others	1	T	T	T	T	
Totals	117	564	727	985	1157	1202

Values converted from pounds/acre to kg/ha by ratio 1.1208. T = trace

Saskatchewan (**Table 11**), although lichen biomass was generally lower and shrub productivity higher than in the Manitoba sample at equivalent age classes following fire (Scotter 1964). Standing crop of all ground lichens following fire in jack pine forests, although highly variable, changed little from 16 to 65 years post burn (**Table 12**). However, there was an upward trend in the living biomass of "high value" lichens (*Cladina* spp. and *Cladonia* spp.) (Scotter 1964) (**Fig. 11**).

Scotter (1971b) grouped all his data from 126 stands on caribou winter ranges to present a general picture of changes in standing crop of forage following fire (**Table 13**). To approximate *annual* production, I took 10% of his standing crop values for lichens and others at face value. The result (**Table 14**) indicates a gradual increase in forage productivity with age of forest.

The only other lichen biomass data was obtained by Miller (1976a, 1976b) on study plots, on fenced caribou exclosures, and on sites cratered by caribou. Data from study plots and exclosures in northwestern Manitoba indicated high variation and no change in biomass from 30 to 139 years after fires (**Fig. 12**). The data from

Table 11. Average standing crop (kg/ha) by age classes of air-dried forage in black spruce and white birch forests of northeastern Saskatchewan (Scotter 1964).

	Standing crop (kg/ha) Years since last fire					
Plant group	1-10	11-30	31-50	51-75	76-120	>120
Grass-like	71	10	1	1	4	2
Herbs	137	6	8	10	1	3
Shrubs: High value	20	262	324	253	399	374
Mid value	20	11	9	3	4	7
Low value	67	178	119	133	123	129
(Totals)	(108)	(452)	(452)	(390)	(527)	(510)
Lichens: High value	1	13	68	74	230	296
Mid value	2	18	99	205	140	201
Low value	2	53	49	38	28	44
(Totals)	(6)	(84)	(216)	(317)	(398)	(540)
Totals	325[1]	551	677	718	930	1056

[1] Includes "others" = 4. Values converted from pounds/acre to kg/ha by a factor of 1.1208.

Table 12. Average standing crop (kg/ha) of air-dried forage at intervals after fire in jack pine forests of northeastern Saskatchewan (Scotter 1964).

	Standing crop (kg/ha) Years since previous fire					
Plant group	5	15	16	35	43	65
Grass-like	24	20	T			
Herbs	37	74	1	T	T	4
Shrubs: High value	27	39	108	346	77	386
Mid value		24				4
Low value	8	156	325	338	210	28
(Totals)	(35)	(219)	(433)	(685)	(287)	(418)
Lichens: High value		6	35	62	228	37
Mid value	2	155		4	10	92
Low value		67	62	137	73	17
(Totals)	(2)	(228)	(96)	(203)	(310)	(146)
Totals	98	540	530	888	597	568

Values converted from pounds/acre to kg/ha by the ratio 1:1.1208. T = trace

Figure 11.

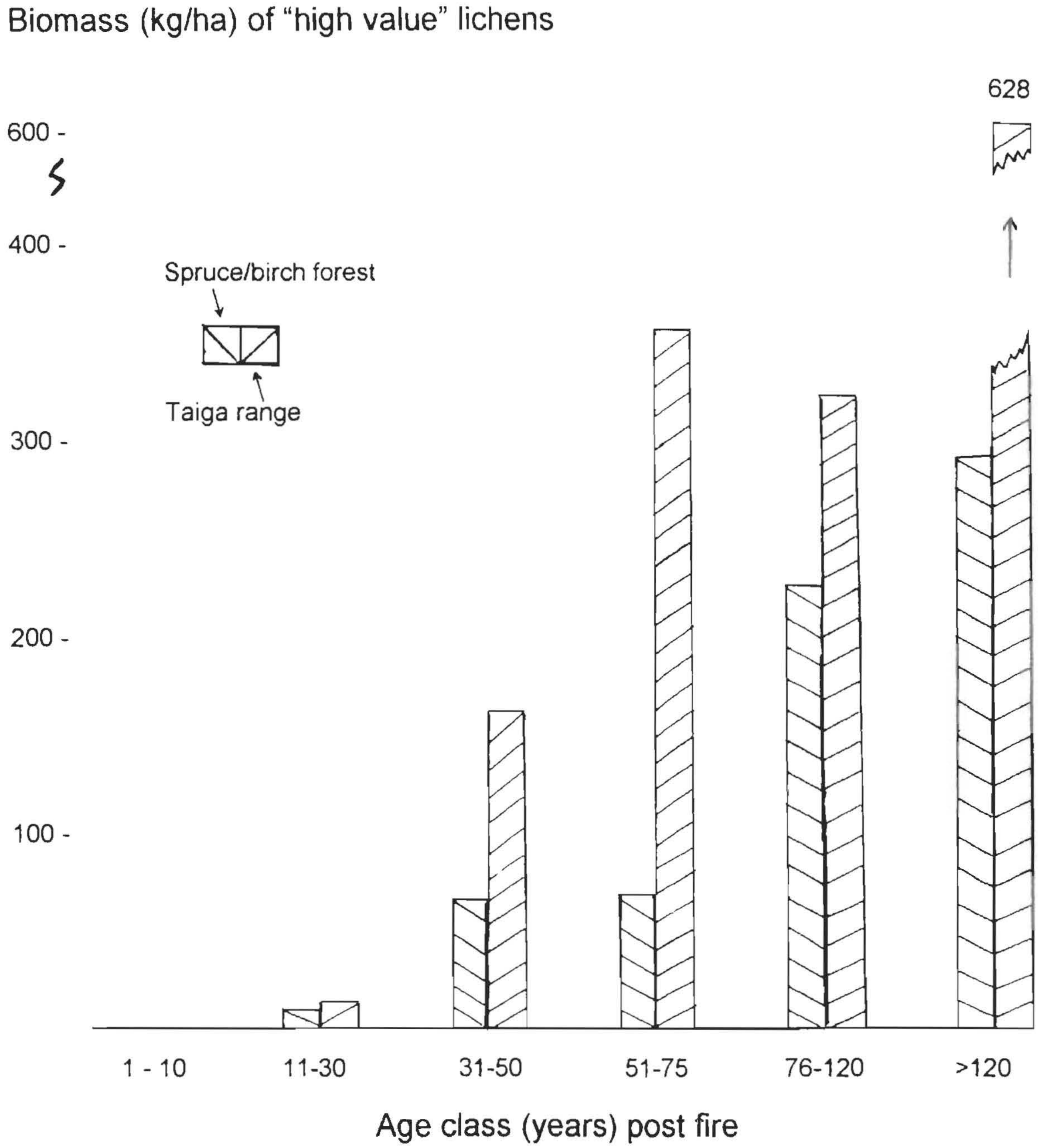


Figure 11. Standing crop of "high value" terrestrial lichens in black spruce and birch forests in Saskatchewan and in all sampled taiga range (data from Scotter 1964, 1971a).

Table 13. Average standing crop (kg/ha) of usable air-dried forage from 126 stands in upland forest habitats on the winter range of barren-ground caribou in north-central Canada (data from Scotter 1971b).

		Standing crop (kg/ha) Years since fire					
Plant group		1-10	11-30	31-50	51-75	76-120	>120
Grass-like		39	9	1	1	3	2
Forbs		76	10	2	3	5	8
Shrubs:	High value	16	139	212	189	278	284
	Mid value	11	9	2	3	5	7
	Low value	50	106	93	120	113	103
	(Totals)	(77)	(254)	(307)	(313)	(396)	(393)
Lichens:	High value	1	17	165	358	326	628
	Mid value	1	44	85	94	109	145
	Low value	1	56	100	74	39	40
	(Totals)	(3)	(117)	(350)	(526)	(474)	(813)
Totals		198[1]	390	660	843	878	1216

[1] Includes "others" = 3.

crater sites in both provinces produced similar results (**Fig. 13** and **14**). Mean standing crops (kg/ha) were 3849 (2611-10 653) in Manitoba and 6939 (951-13 756) in Saskatchewan. Much higher and more variable biomass for lichens obtained by Miller (1976b) is explained by differences in sampling technique and site selection and by calculation of total biomass *versus* estimated standing crop of living parts (Scotter 1964, 1965).

The extreme variability in apparent standing crops of lichens probably reflects a host of uncontrolled variables: range type, soils, canopy, shrub layer, moisture, aspect, topography, microclimate, microhabitat, including associated surface species, past use by caribou, completeness of previous burn, lichen species present, etc. For example, what is the effect of tree density on lichen biomass? Analysis of data in Miller (1976b) indicates that the highest mean standing crops of lichens occurred where densities of trees taller than 2 m were 6-15/100m^2 (**Table 15**). Those data were also highly variable, for the same reason, and differences may be chance ones.

Table 14. Estimated annual forage production (kg/ha, air dried) on 126 upland sites on the winter range of caribou in north-central Canada (data in Scotter 1971b).

	Annual forage production (kg/ha)					
	Years since fire					
Plant group	1-10	11-30	31-50	51-75	76-120	>120
Grass-like	39	9	1	1	3	2
Forbs	76	10	2	3	5	8
Shrubs	77	254	307	313	396	393
Lichens[1]	trace	12	35	53	47	81
Totals	194[2]	285	345	370	451	484

[1] Annual production assumed to be 10% of standing crop.
[2] Includes "others" = 2.

There are several limitations in Miller's (1976b) data: (1) he only considered ground lichens in appraising post-burn forage conditions, (2) he grouped all ground lichens together, (3) he calculated biomass of all lichen material, dead and alive, (4) he had no knowledge of past use of sites by caribou, (5) he had no data on annual productivity of lichens relative to age of forest, and (6) he grouped data from several habitat types and from different regions. Miller (1976b) obtained no data on standing crops or productivity of species other than ground lichens. For example, there are almost no data on standing crop of arboreal lichens because of sampling problems. Scotter (1964) sampled arboreal lichens on one tree at four sites each in mature jack pine and in black spruce forest in northern Saskatchewan. Mean standing crops in mature jack pine forests were 896 kg/tree, 2051 kg/ha total, and 381 kg/ha below 3 m (**Table 16**). Corresponding values in mature spruce forests were 622 kg/tree, 1198 kg/ha (total), and 679 kg/ha below 3 m (**Tables 16 and 17**). Those are the only data for that important reserve forage supply in north-central Canada. Biomass of arboreal lichens below 3 m level exceeded that of ground forms in both major forest types in northeastern Saskatchewan. An important data gap is the relationship between arboreal lichen productivity/biomass and age and type of forest.

Figure 12

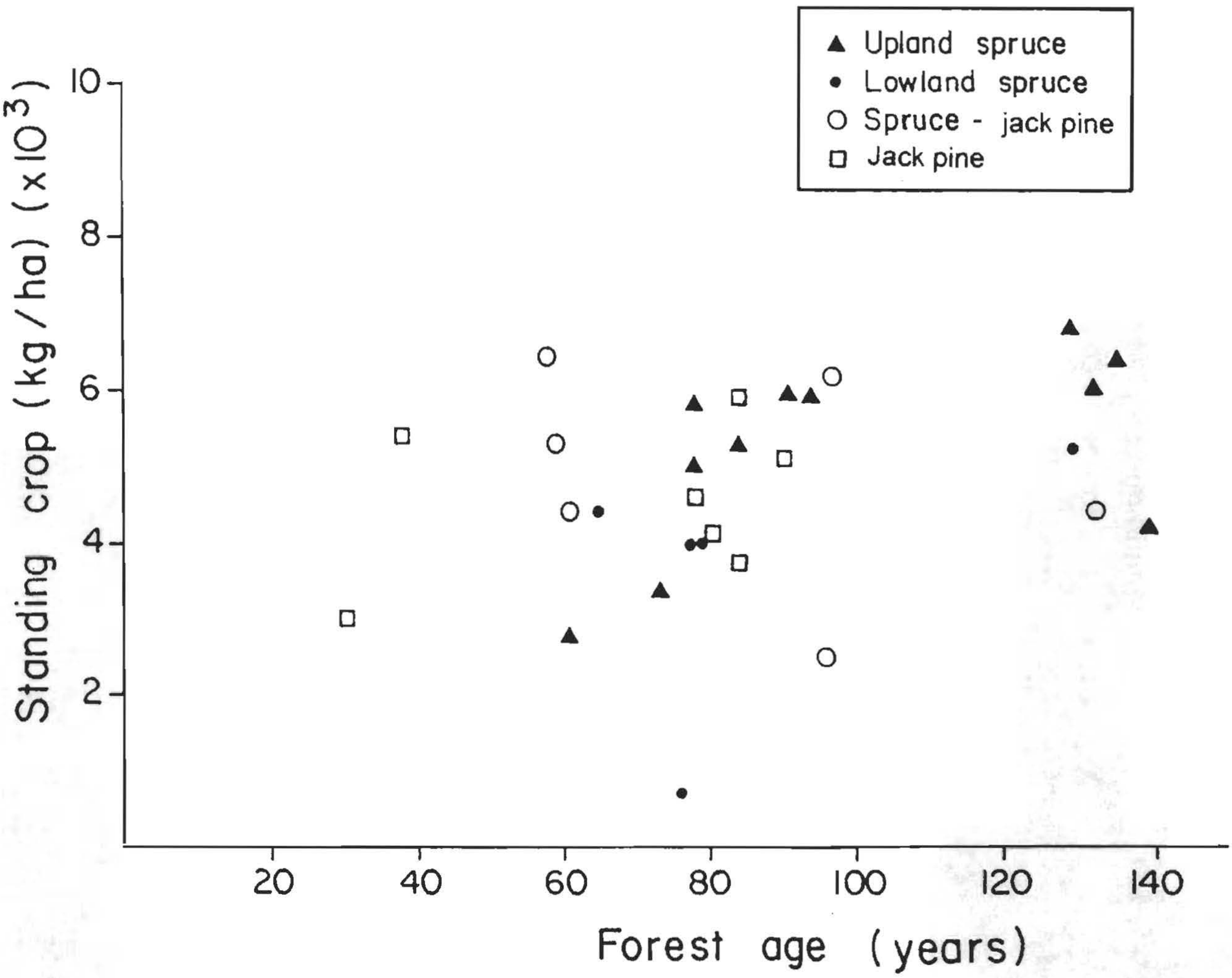


Figure 12. Biomass of terrestrial lichens with time after fire in four cover types in Manitoba (data from Miller 1976a, 1976b).

Figure 13

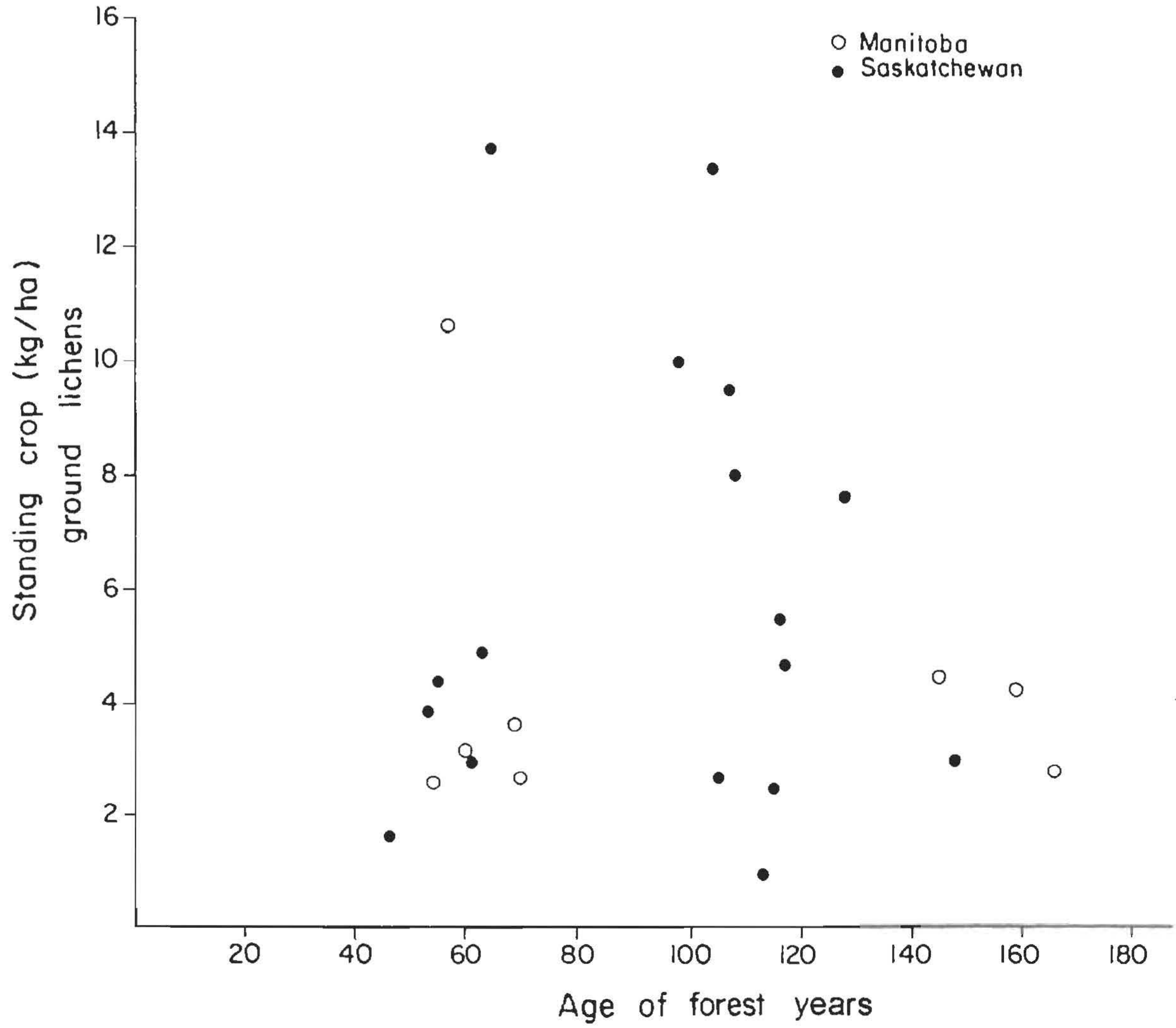


Figure 13. Biomass of terrestrial lichens with time after fire at crater sites in Manitoba and Saskatchewan (data from Miller 1976a, 1976b).

Figure 14.

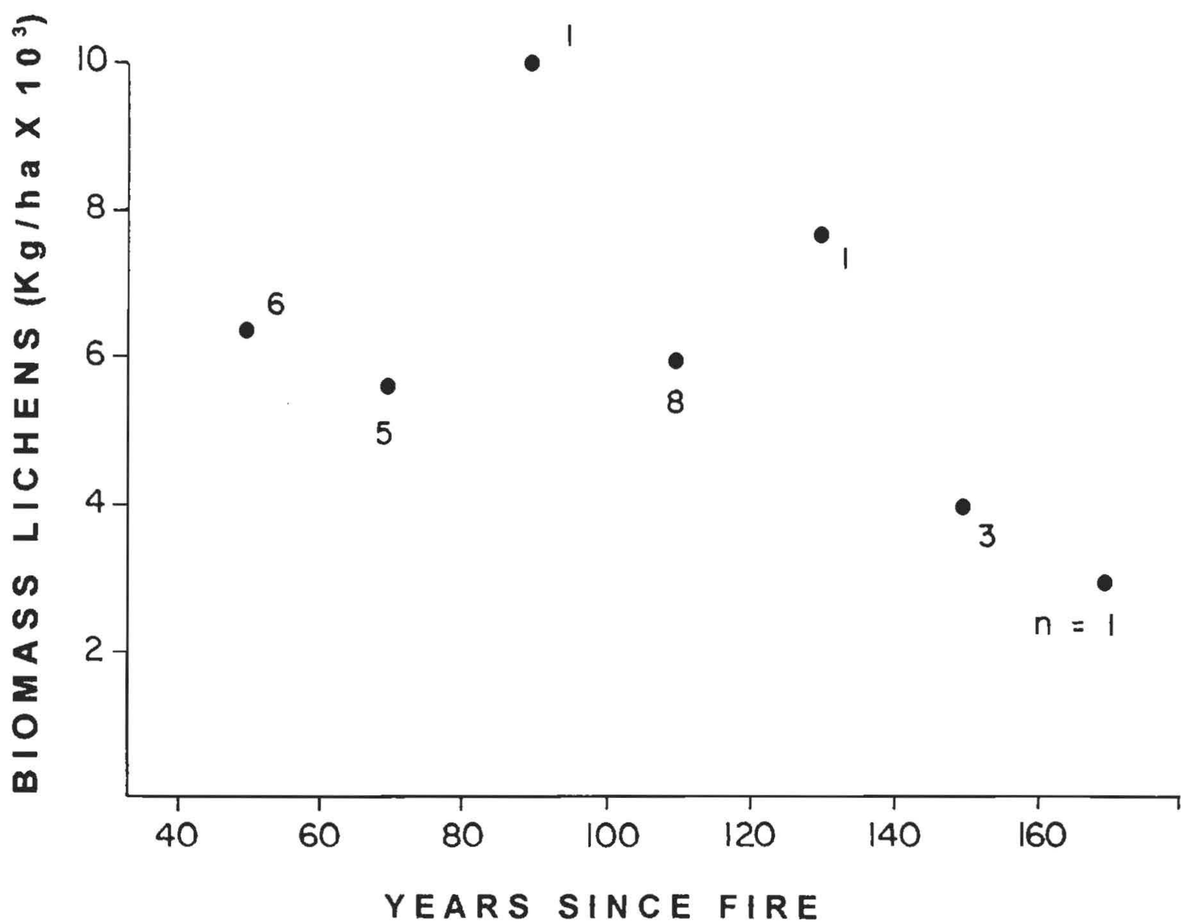


Figure 14. Mean biomass of terrestrial lichens with time in 20-year intervals after fire at crater sites in Saskatchewan (sample sizes beside points) (data from Miller 1976a, 1976b).

Table 15. Relationship between density of trees over 2 m in height and standing crop of lichens at 26 caribou feeding sites in northern Manitoba and Saskatchewan (data reworked from Miller 1976b).

No. trees >2 m/100 m²	No. of sites	Mean standing crop of lichens (kg/ha)
0- 5	6	4629
6-10	5	7240
11-15	5	6807
16-20	2	5428
21-25	2	2404
31-35	4	5138
>35	2	1828
Group 0-20	18	6048
Group >20	8	3627

FACTORS AFFECTING USE OF RANGE TYPES

The needs of caribou on winter range include abundant available forage of adequate quality, safe resting places, shelter, escape terrain, and favourable travel routes. Factors influencing relative use of range types include quantity and quality of forage present, its availability (affected by snow, wind, other climatic factors, tree cover, and topography), availability of safe resting places such as lakes, distribution of escape terrain, travel routes, and shelter. Where snow was shallow or soft, distribution of forage must be a major factor influencing winter distribution of caribou. What sort of surface vegetation is characteristic of caribou winter ranges in the study region?

Kelsall (1968), in a summary of the ground cover components found on caribou winter range in 47 locations in northern Manitoba and Mackenzie District in NWT, provided the following means and ranges (parentheses) for percent cover: bare ground 29% (4-67%), mosses 10% (0-44%), ground lichens 32% (4-62%), grass-sedge 4% (0-11%), *Empetrum* spp. 2% (0-17%), *Ledum* spp. 5% (0-37%), *Arctostaphylos* spp. 3% (0-8%), and *Vaccinium* spp. 9% (0-26%).

The listed vegetation species or types were present on almost every site examined. Other species occurred but they attained dominance only in small areas or unusual situations. Within lichens, *Cladina alpestris* occurred most frequently (51%) followed by *C. mitis* (33%). Descending abundance rank, when the most abundant class was grouped with the second most abundant class was *C. alpestris, C. mitis, Peltigera* spp. and *Umbilicaria* spp, (tied), *Cetraria nivalis, C. rangiferina, C. coccifera* and *Cetraria islandica* (tied), *C. gracilis, C. pyxidata*, and *C. multiformis* (from data in Kelsall 1968).

4.1. **Winter diet**

4.1.1. ***Rumen analysis***

The best available data on winter diets of caribou in northern Saskatchewan, Manitoba, and adjacent NWT was obtained from rumen analyses. The only large sample, approximately 559 rumens, obtained at several periods during the year indicated that, proportionately, lichens dominated all other forage groups in winter and were present in summer and autumn samples (**Table 18**, **Fig. 15**, from Miller 1976a). Lichens made up about half of the weight of rumen contents obtained in November, February, and April. Twigs and leaves each constituted about 20% of rumen contents in February and April samples. Further samples obtained in February and April of 1972 and 1973 again showed about 50% lichen species by weight in 1972; about 40% the following year (**Fig. 16**, Miller 1976b). However, lichen proportions may be grossly underestimated by that technique.

Lichens constituted 68.7% of the air dried weight of identified material in rumens of 20 caribou collected on winter ranges in northern Manitoba, Saskatchewan, and the NWT (Scotter 1967a, **Table 19**). The reindeer lichens (*Cladina alpestris, C. mitis, C. rangiferina*, and *C. uncialis*) made up 84.2% of the lichen component. In Miller's (1976b) collections of February and April 1972 and 1973 in northern Manitoba and Saskatchewan, rumens of all 28 caribou contained *Cladina* spp., *Cladonia* spp., and *Stereocaulon* spp. Only one rumen contained *Peltigera* spp. and *Cetraria* spp. However, Miller (1976b) indicated that the fixative (alcohol) used to preserve the

Table 16. Standing crop (air-dried weight) of arboreal lichens in mature jack pine forest at four sites in northeastern Saskatchewan, based on lichens present on one tree at each site (data in Scotter 1964).

			Standing crop (kg/ha)		
Site	Trees/ha	Lichens/ tree (g)	Wt. lichens (kg/ha)	Lichens 0-3 m (kg/ha)	Lichens >3 m (kg/ha)
1	1092	490	535	109	427
2	3338	671	2240	200	2039
3	2261	1276	2885	731	2155
4	2216	1147	2542	484	2058
Means	2227	896	2051	381	1670

rumens may have led to identification errors because of its bleaching action. In a subsample of 11 rumens examined in a fresh state in the field, percent occurrence of genera classified as abundant and present (parentheses) were as follows: *Cladina* 91% (100%), *Cladonia* 73% (91%), *Stereocaulon* 45% (100%), *Peltigera* 18% (64%), and *Cetraria* 9% (36%) (Miller 1976b). Therefore, data in Table 16 must be treated with caution.

The importance of *Cladina* spp. in winter diet of caribou is confirmed by percent occurrence data (Miller 1976a). In samples from November, January-February, and April, *Cladina* spp. occurred in 98% of rumen samples, followed by *Stereocaulon* spp. (59%), *Cladonia* spp. (48%), and *Cetraria* spp. (1%).

Leaves and twigs together made up, by weight, about 40% of rumen samples (Miller 1976a). His percent occurrence data, when grouped, yield unweighted mean values as follows: *Vaccinium vitis-idaea* (leaves) 100%, *Picea* spp. needles 96%, *Ledum* (leaves) 85%, *V. myrtilloides* (parts) 76%, *V. uligionsum* 69%, *Larix larcina* (leaves) 53%, *Pinus banksiana* (leaves) 48%, *Andromeda polifolia* 37%, *Kalmia polifolia* 37%, and *Betula* spp. 33%. The only entry under "grasslike plants" was *Equisetum* spp. with an average unweighted mean occurrence of 47%. Moss species occurred in 3-66% of the rumen samples and six species occurred in over 30%

Table 17. Standing crop (air-dried weight) of arboreal lichens in mature black spruce forests at four sites in northeastern Saskatchewan, based on lichens present on one tree at each site (data in Scotter 1964).

			Standing crop (kg/ha)		
Site	Trees/ha	Lichens/ tree (g)	Wt. lichens (kg/ha)	Lichens 0-3m (kg/ha)	Lichens >3m (kg/ha)
1	1287	1011	1301	121	1181
2	2965	477	1414	1305	109
3	1569	566	888	563	324
4	2745	434	1191	724	467
Means	2142	622	1198	679	519

of samples (Miller 1976a). *Equisetum* spp. averaged only 0.1% of the weight of material in Scotter's (1967) 20 samples.

The only woody plants of any appreciable weight in Scotter's (1967a) sample was *Picea* spp. (6.7%), *Pinus banksiana* (4.5%), *Vaccinium vitis-idaea* (3.4%), and *Ledum groenlandicum* (2.9%). All other woody plants constituted only 2.3% of the weight.

4.1.2. ***Crater examination***

Examination of forage present at the bottom of a large number of craters can provide some data on forage utilized provided that: (1) not all of a particular species is consumed, (2) evidence of parts of plants having been removed, (3) evidence of some species being avoided. Because some subjectivity is introduced, researchers have preferred to present lists of species present in craters. Some biologists compare such lists with lists of species in non-cratered, adjacent sites or with lists of species in the same general area.

Miller (1976a), who opted for a list of percentage frequency of forage items at feeding sites (**Table 20**), found that *Cladina* spp. occurred most frequently (unweighted average of 50%) of all lichen genera, followed by *Cladonia* spp. (34%), *Cetraria* spp., (30%), *Stereocaulon* spp. (26%), and arboreal lichens (14%). At sites,

Table 18. Proportion (%) by weight of five major forage classes in caribou rumens collected 1966-1968 in northern Manitoba, Saskatchewan, and NWT (sample sizes in parentheses) (data from Fig. 5 in Miller 1976a).

	Proportion (%) by weight				
Forage	Sep. (86)	Nov. (126)	Feb. (14)	Apr. (162)	Jun. (132)
Lichens	16.6	52.8	48.7	52.5	17.9
Grasses[1]	15.0	21.1	8.2	7.6	40.8
Leaves	18.4	8.1	20.6	19.8	11.2
Twigs	23.5	6.7	20.6	19.2	28.6
Mushrooms	26.5	11.3	1.9	0.9	1.5

[1] includes grass-like species, e.g., sedges and rushes.

frequency of all lichen species, except *Cetraria* spp., increased from early winter to later stages of winter. Lichens as a group increased in frequency occurrence from 47% in early winter to 81% and 82% in mid winter and late winter. Grass-like species decreased sharply from 59% in early winter to 19% and 14% late in winter. Frequency of woody plants at feeding sites increased markedly from 9% in November-December to 25% and 24% in mid winter and late winter. However, occurrence of individual woody species was highly variable. The most notable being *Vaccinium vitis-idaea* (13% as unweighted average) and *Ledum* spp. (10%).

Data from a site at Hara Lake (Saskatchewan) in late February and late April indicated a pronounced decrease during winter in occurrence of woody species at feeding sites: *Ledum groenlandicum* 41% to 15%, *Vaccinium uliginosum* 10% to 2%, *Empetrum nigrum* 12% to 2%, and a sharp increase in frequency of arboreal lichens from 0 to 46%. Frequency occurrence of ground lichens remained constant at 35-36% (Miller 1976a).

In 1972-73, Miller (1976b) marked craters in Manitoba and Saskatchewan during the winter and excluded caribou from them until cover data were obtained in

Figure 15.

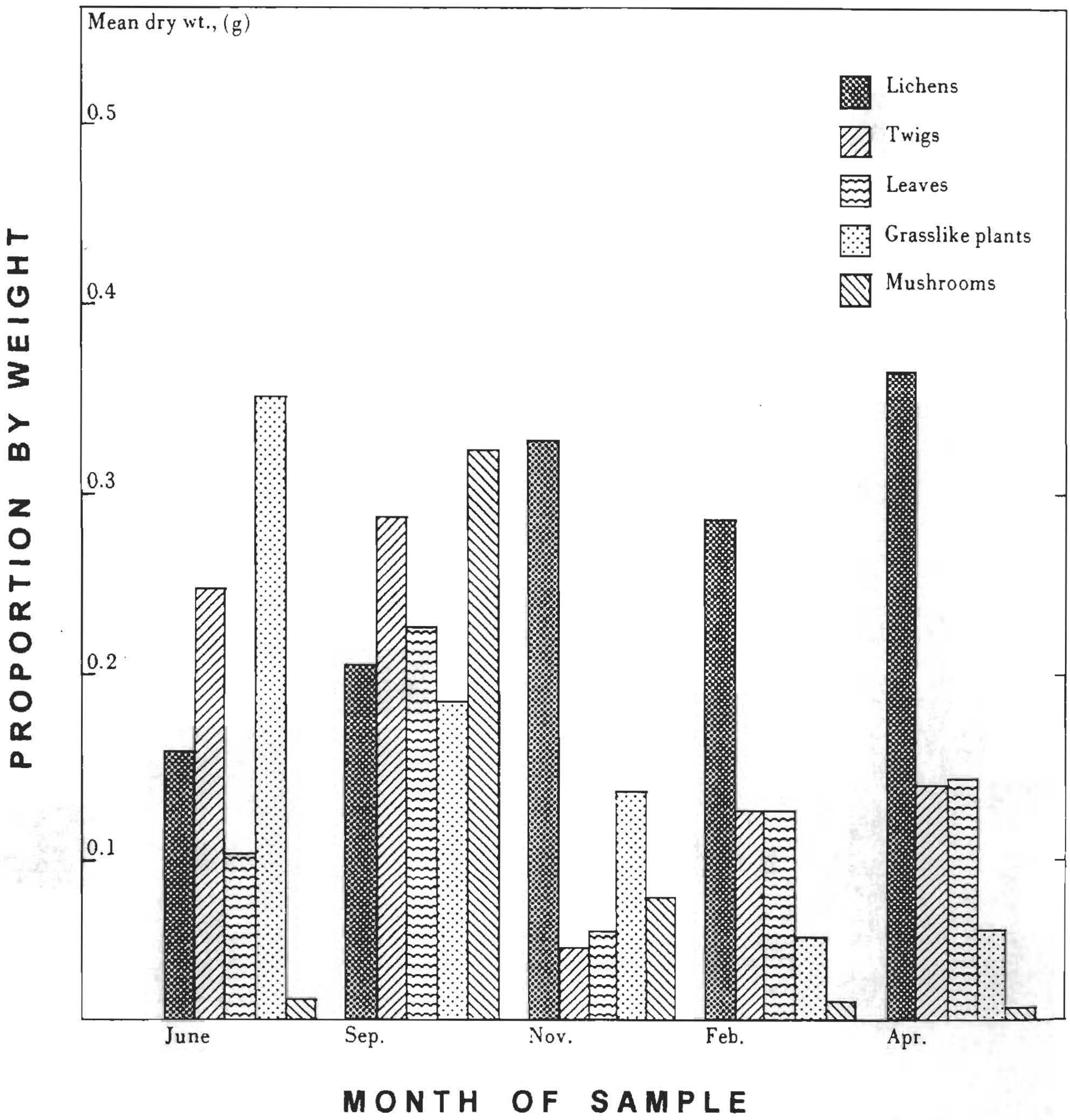


Figure 15. Proportionate occurrence by weight of plants in rumens of caribou obtained from June through April, 1972 and 1973 (Miller 1976a).

Figure 16.

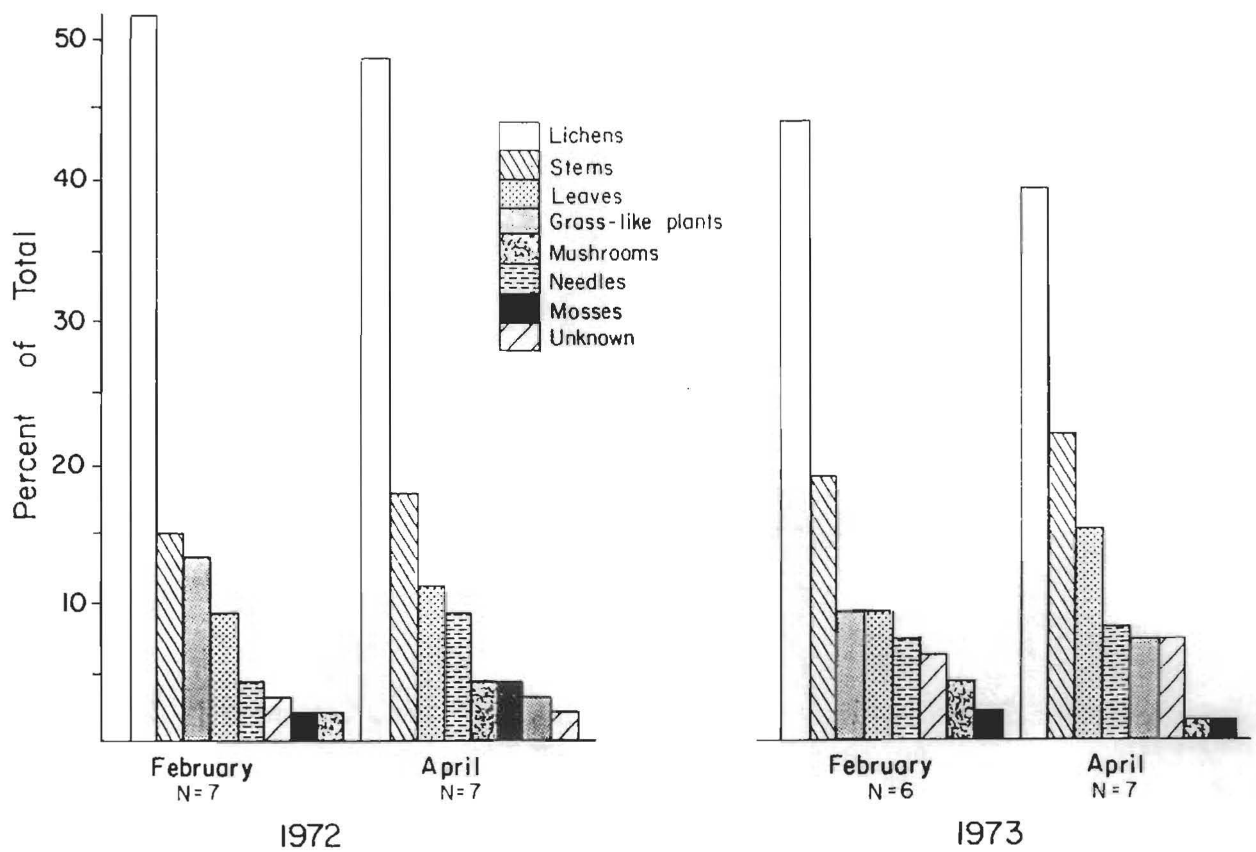


Figure 16. Proportionate occurrence by weight of plants in rumens of caribou obtained in February and April, 1972 and 1973 (Miller 1980).

Table 19. Percentages by weight of major classes of forage identified in the rumens of 20 caribou collected in winter in Saskatchewan (10 samples), Manitoba (6 samples), and the NWT (4 samples) (Scotter 1967a).

Species or group	Proportions in rumen samples[1]
Lichens:	68.7
Cladina spp.	57.8
Peltigera spp.	4.9
Stereocaulon spp.	2.9
Cladonia spp.	2.5
Woody plants	23.6
Bryophytes and fungi	4.2
Grass and grass-like	3.5

[1] Percentage by weight

following summers. Results (**Table 21**) show that surface vegetation at all sites was dominated by lichens, followed by *Vaccinium vitis-idaea, Ledum* spp., mosses, *V. uliginosum,* and *Empetrum nigrum.*

Kelsall (1960) collated frequency of occurrence data from several sites cratered in NWT and Saskatchewan (**Fig. 17**). Ground lichens, consisting mainly of *Cladina alpestris, C. mitis, C. rangiferina, Cetraria islandica, C. nivalis,* and *Stereocaulon tomentosum* totalled 47% of all species identified. *Vaccinium* spp., chiefly *V. vitis-idaea* and *V. uliginosum*, totalled 21.5% of species in craters. *Carex* spp. were third most common at 12.8%, followed by *Ledum* spp. (8.1%) and *Salix* spp. (4.l%). All

Table 20. Percent frequency of forage species found at feeding sites in northwestern Manitoba and northeastern Saskatchewan at three stages during winter 1967-68 (Miller 1976a).

Plant group	Frequency of occurrence (%) Nov.-Dec. (*n* = 32)	Feb. (*n* = 16)	Apr.-May (*n* = 145)
Lichens	47	81	82
Arboreal	9	19	13
Cladina spp.	34	56	61
Cladonia spp.	22	38	42
Stereocaulon spp.	16	31	30
Cetraria spp.	34	31	26
Peltigera & *Nephroma* spp.			4
Foliose			6
Grass-like	50	19	14
Woody plants	9	25	24
Lycopodium spp.		6	2
Myrica gale	3		
Empretrum nigrum			5
Ledum spp.		25	5
Kalmia polifolia	3		
Arctostaphylos uva-ursi			3
Vaccinium vitis-idaea	3	13	23

Table 21. Mean percent cover of plant groups in crater enclosures established in February and April, 1973, in Manitoba and Saskatchewan and examined in summer (Miller 1976b, p. 73).

	Percent cover						
	Manitoba			Saskatchewan			
Plant group	Feb. (*n*=8)	Apr. (*n*=2)	Comb. (*n*=10)	Feb. (*n*=8)	Apr. (*n*=9)	Comb. (*n*=17)	All[1] (*n*=27)
Lichens	63	82	69	77	73	75	72
Vaccinium vitis-idaea	32	26	30	29	20	24	27
Ledum spp.	23	5	17	17	13	15	16
Mosses	20	4	16	8	22	15	16
Vaccinium uliginosum	13	10	12	2	8	5	9
Empetrum nigrum	1	0	1	11	3	7	4

[1] Unweighted average for Manitoba and Saskatchewan. Column totals exceed 100% because of more than one stratum.

other species or groups occurred in less than 2% of 704 craters.

Kelsall (1968) compared data on frequencies of occurrence of plants in craters and in the same general region (**Fig. 18**). He interpreted the results as indicating that lichens, sedges, *Ledum* spp., and willows (*Salix* spp.) were highly preferred by caribou as winter forage, whereas *Vaccinium* spp., *Arctostaphylos* spp., *Empetrum nigrum*, and *Betula* spp. were eaten in amounts approximating their occurrence in ground cover.

Mosses and many other plant species were proportionately less frequent in craters than on the ground. However, Kelsall's (1968) data must be interpreted with caution for the two sets of data were obtained at different sites and different sampling procedures were used for each.

Figure 17.

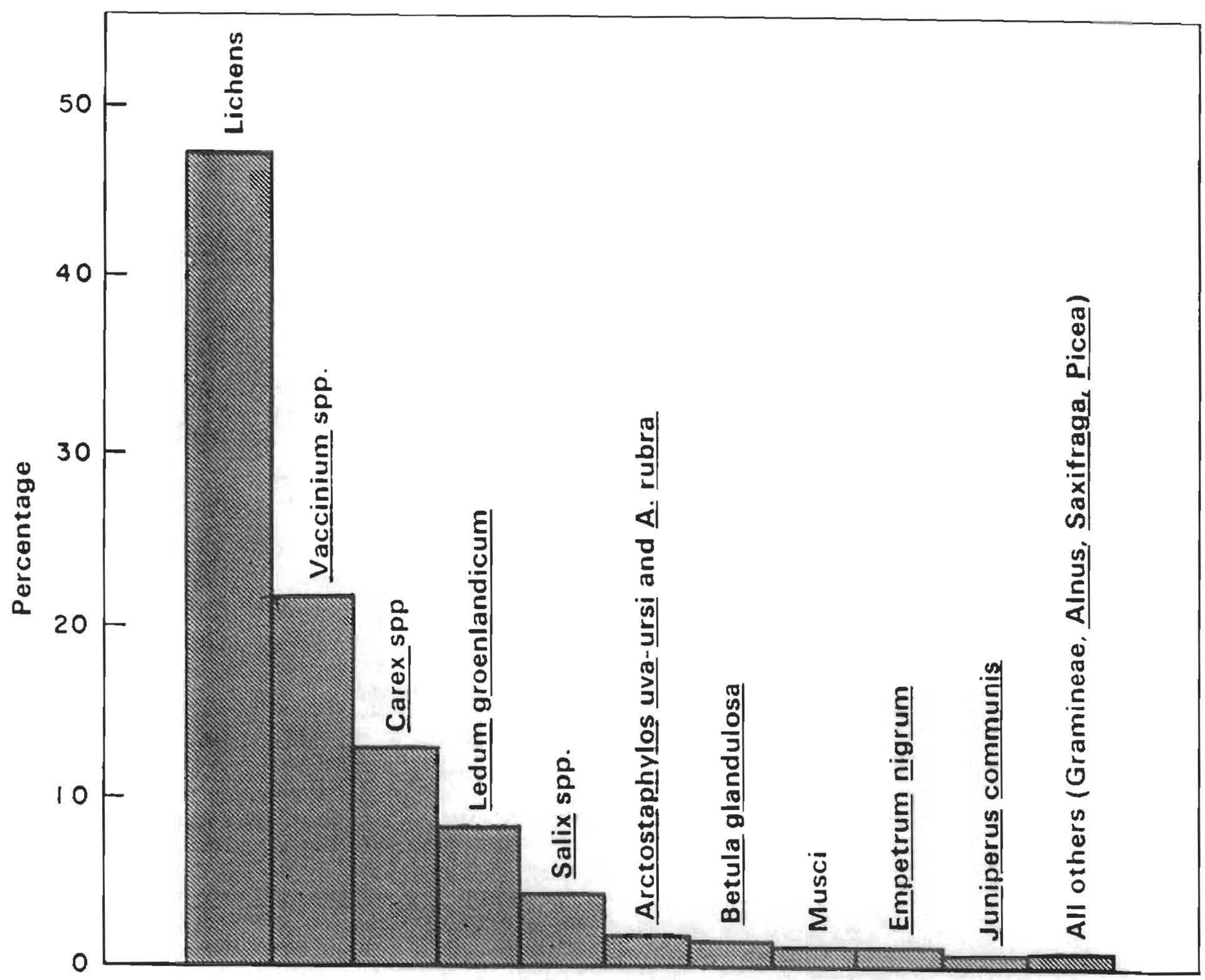


Figure 17. Frequency of occurrence of plants in craters dug by caribou in NWT and Saskatchewan (Kelsall 1960).

Figure 18.

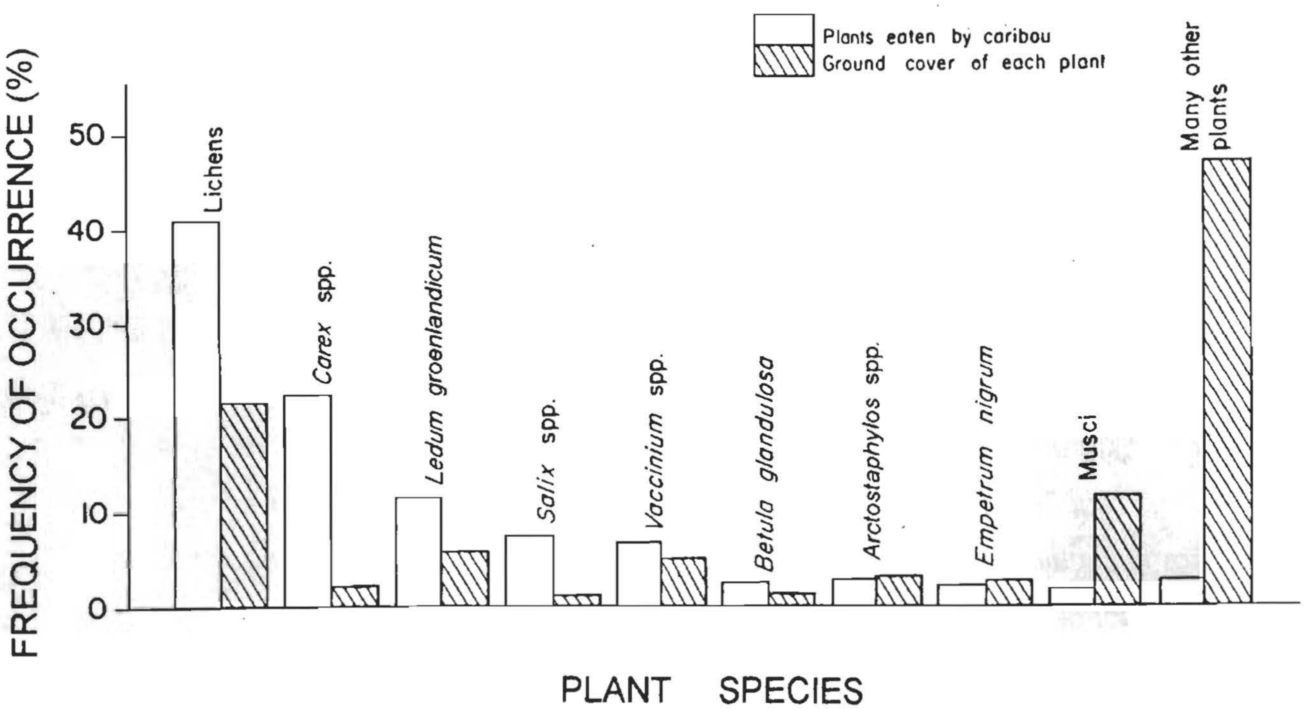


Figure 18. Frequencies of occurrence of plants in craters (open bars on left) and in the same general region (hatched bars) (Kelsall 1968).

Caribou actively sought out *Equisetum* spp. in winter according to Loughrey (1952) and Kelsall (1957). Kelsall (1968) considered that young leaves of *Ledum* spp. were important winter food, although Palmer (1944) suggested that species had low palatability.

4.1.3. ***Observations***

There are many generalized comments about winter food habits of caribou and reindeer. Single observations carry little weight; collectively they are of considerable value. Concerning the role of lichens in winter diet (Kelsall 1957) wrote:

> *"the preferred feeding areas in winter are those with spruce-lichen associations and, in descending order, those with associations having progressively less Sphagnum-lichen associations and spruce-jack pine-lichen associations. The only commonly-used non-lichen areas are the narrow margins of lakes, ponds, and rivers, where sedge-alder-willow growth and Equisetum are used occasionally by some caribou."* (p. 80).

Concerning preferences of reindeer for lichens in Russia, Zhigunov (1961) stated that *Cladina rangiferina, C. sylvatica* (~*mitis*), and *C. alpestris* were preferred species, *Cetraria cucullata* and *C. nivalis* ranked in second place, and *Stereocaulon paschale, Sphaerophorus globosus, Usnea* spp., and *Bryopogon* spp. were not preferred. However, in comments on individual lichen species he stated that *Usnea gossipoga* was readily eaten and greatly valued. *Spherophorus globusus* was of considerable importance as fodder in some regions. Zhigunov (1961) considered that *C. alpestris* was the chief lichen fodder in many areas of Russia. *Cetraria islandica* was important in autumn, especially during wet periods.

Helle (1966) listed *Cladina mitis, C. silvatica, C. arbusculata, C. rangiferina, C. alpestris* and *Stereocaulon paschale* as main species in winter diet of reindeer in Finland. *Vaccinium myrtilloides* was the only species consumed at all seasons.

Reindeer lichens constituted the main winter diet of reindeer in Russia (Davydov 1958, Sablina 1960). The latter author noted that reindeer preferred berries of three

Vaccinum spp., *Empetrum nigrum*, and *Rubus* spp.; when available they lived on those berries and mushrooms. *Vaccinium uliginosum* leaves and stems were eaten extensively but *V. vitis-idaea* was not a preferred species for it was eaten last. Sablina (1960) noted that reindeer seemed to prefer arboreal lichens to ground species in winter because they were consumed in that order when individual reindeer moved from one spot to another.

4.1.4. ***Palatability***

Good data on palatability (how readily eaten) and digestibility of forage are crucial to assessments of range based on forage biomass and productivity combined with range utilization. Kelsall (1968) speculated on palatability of 15 plant species or species groups to barren-ground caribou on the central mainland of Canada (**Table 22**). His ratings were based on proportionate occurrence in rumens (summer) or craters (winter) and on preferred range types, plus miscellaneous observations. Banfield (1954) constructed a similar list for summer forages of caribou in the same region. Kelsall's (1968) palatability evaluations differed little from those of Hadwin and Palmer (1922) and Palmer (1944) for Alaskan caribou (**Table 23**). More recently, Alaskan researchers found that reindeer selected five lichen species in the order *Cladina alpestris* (highest), *C. rangiferina, Stereocaulon paschale, Cetraria richardonii*, and *Peltigera aphthosa* (Hollemann and Luick 1977).

4.1.5. ***Digestibility***

Studies on digestibility of forages by caribou and reindeer were pioneered in the early 1970s by Alaskan *in vitro* ("in glass") techniques (Person et al. 1975, 1980a, 1980b). In the *in vivo* technique, nylon bags containing known quantities of dried forages are placed in rumens of fistulated caribou, followed by removal and re-weighing the sample after drying to determine dry-matter disappearance, the digested portion. The *in vitro* technique attempts to simulate, in test tubes, what occurs naturally in rumens. Dried, ground, and weighed samples of plant species are mixed with a rumen

Table 22. Quantitative analyses and palatability ratings of summer and winter foods eaten by barren-ground caribou (Kelsall 1968).

Genus or class	Summer foods		Winter foods	
	In stomachs, %	Palatability rating	In feeding craters %	Palatability rating
1. Fungi	1.2	high	absent	-
2. Lichens	31.3	high	47.0	high
3. Musci	T	low	1.1	low
4. *Equisetum*	0.6	high	absent	-
5. *Picea*	absent	-	0.1	low
6. *Juniperus*	absent	-	0.6	medium
7. Grass/sedge	28.1	high	13.1	high
8. *Salix*	15.7	high	4.1	high
9. *Betula*	15.5	high	1.3	high
10. *Alnus*	absent	-	0.3	medium
11. *Saxifraga*	absent	-	0.1	medium
12. *Empetrum*	0.1	low	1.1	medium
13. *Ledum*	1.2	medium	8.1	high
14. *Arctostaphylos*	1.3	low	1.6	medium
15. *Vaccinium*	3.8	medium	21.5	medium
16. Others	1.2	low		

inoculum-buffer mixture and incubated at 38-39° C under anaerobic conditions. Samples are recovered, dried, and re-weighed to obtain dry-matter disappearance (apparent digestibility) of the sample.

The results obtained by Alaskan researchers (**Tables 24 and 25**) should not be extrapolated to natural functions because rumen flora of captive animals fed commercial pellets or lichen mixtures for a month or so before the trials may differ from that of free-ranging animals. The micro-organisms are known to change as diet changes (Nieminen et al. 1980). When compared to the *in vivo* digestibility data, *in vitro* results generally are lower for lichens and shrubs and higher for grass-like

Table 23. Relative forage values of lichens according to Hadwin and Palmer (1922) and Palmer (1927, in Courtright 1959).

Value	Species		
1 High	*Cladina rangiferina* *Cladina alpestris* *Cladina sylvatica*[1]	*Cladonia amaurocraea* *Cladonia gracilis* *Cladonia uncialis*	*Cetraria cucullata* *Cetraria islandica*
2 Medium	*Cetraria nivalis* *Cetraria richardsonii* *Alectoria ochroleuca*	*Dactylina arctica* *Nephroma arctica*	*Stereocaulon alpinum* *Stereocaulon coralloides* *Stereocaulon tomentosum*
3 Low	*Alectoria nigricans* *Sphaerophorus colalloides*		*Thamnolia vermicularis* *Parmelia* spp.
4 Little or no	*Peltigera* spp. *Lecidea* spp. *Ochrolechia* spp.	*Alectoria jubata*[2] *Physcia* spp.	*Pertusaria* spp. *Psoroma* spp.

[1] *C. mitis.*
[2] *A. americana.*

species (Table 24). Person et al. (1980a & b) attributed relatively low *in vitro* digestibilities of lichens and shrubs to inhibitory actions of toxic substances in plants and to nitrogen deficiencies. Trudell et al. (1980) also mentioned variable inoculum sources and a buildup of fermentation end products as possible reasons why data from *in vitro* studies must be used with caution in ranking relative digestabilities of forage species.

The *in vitro* technique was tested on forages consumed by caribou in the Canadian Arctic Islands with inoculum obtained from rumens of free-ranging Peary caribou in summer and winter after sacrificing them (Thomas and Kroeger 1981). Apparent digestibilities of lichen species were *Cetraria cucullata* 76%, *C. islandica* 76%, and *Cladina mitis* 31%. The low value for the last-named species may be

Table 24. Apparent dry-matter digestibilities of forage species collected in Alaska and tested in fistulated reindeer and caribou (SD = standard deviation) (from Table IV D. 2. in Brown 1975).

	Dry matter disappearance (%)			
Plant species	*In vitro*	SD	Nylon bag	SD
Alectoria nigricans	41.9	4.0	94.8	4.1
Cetraria cucullata (Nome)	78.5	2.9	90.0	3.4
Cetraria cucullata (Cantwell)	82.4	6.1		
Cetraria islandica	28.6	0.6	61.6	2.5
Cladonia alpestris (Nome)	9.5	2.0	52.8	1.6
Cladonia alpestris (Kenai)			42.8	2.3
Cladonia alpestris (Cantwell)	18.2	8.7		
Cladonia rangiferina				
first stage of growth			52.3	2.1
entire podetia	37.4	1.0	40.9	2.5
decadent portion	18.1	1.8	20.5	0.6
live portions from Beltz			40.9	6.8
live portions from Snake			39.6	4.7
live portions from Cabin Rock 1			54.8	5.3
live portions from Cabin Rock 2	24.1	9.8	42.2	3.8
Cladonia uncialis	33.4	14.1	35.3	2.5
Peltigera aphthosa	40.6	1.9	49.2	6.5
Stereocaulon alpinum	13.9	0.3	39.5	13.8
Stereocaulon rivulorum (Kenai)			44.3	2.1
Thamnolia vermicularis	43.9	3.1	70.9	7.2
Betula nana	30.9	8.8	57.2	1.5
Ledum decumbens	18.5	1.3	47.6	4.2
Salix pulchra	20.1	1.5	66.5	9.5
Vaccinium vitis-idaea	19.8	4.4	64.4	1.3
Calamagrostis canadensis			36.2	1.3
Carex aquatilis				
green leaves			53.1	2.2
dead leaves			31.7	1.4
culms			35.5	1.5
bases			26.5	3.1
inflorescence			43.2	3.1
Eriophorum angustifolium	60.5	4.2	35.3	3.7
Eriophorum vaginatum	35.2	2.8	31.0	4.0
Festuca altaica	53.0	5.4	43.4	2.5
Hierochloe alpina	56.1	3.2	63.7	7.8
Hylocomium splendens	16.1	5.4	5.9	2.3
Polytrichum juniperinum	13.6	1.7	13.2	0.4
Sphagnum magellanicum	4.4	3.0	3.4	1.7

Table 25. Estimates of dry-matter digestibility (% ± SE) of hand-picked plant samples and esophageal egesta from reindeer incubated with rumen fluids from tranquilized caribou and tethered reindeer in Alaska (Brown 1975).

		Dry matter disappearance (mean±SE,%)		
		Source of inoculum		Unweighted
Plant sample	Plant parts	Caribou	Reindeer[1]	mean
Salix arctica	leaves/buds	71	52 ± 2	62
S. pulchra	leaves/buds		54	
S. reticulata	leaves/buds		38	
S. ovalifolia	leaves/buds	35	46 ± 6	41
S. lanata	live leaves		34 ± 2	
Dryas integrifolia	leaves/stem	33	33	33
	heads		21	
Carex aquatilis	live leaves	56	68 ± 4	62
Eriophorum angustifolium	live leaves	48	59 ± 3	55
	inflor.[2]+stem		56 ± 3	
E. vaginatum	mature leaves		28 ± 5	
Dupontia fisheri	live leaves		79 ± 2	
	inflor.	67	70	68
Arctophila fulva	live leaves	56	72	64
Oxtytropis sp.	live leaves		70	
Braya spp.	whole plant		68	
Parrya nudicalus	whole plant		67	
Artemisia richardsoiana	leaves	62	66 ± 3	64
Pedicularis spp.	inflor.+leaves		64 ± 6	
Saxifraga oppositifolia	inflor.+leaves		33 ± 1	
Cetraria alpestris		27 ± 14	16 ± 7	21
C. cucullata		74 ± 3	48 ± 1	61
Esophageal egesta	**Animal**			
Eriophorum meadow	reindeer 10		62 ± 0.2	
Eriophorum meadow	reindeer 12		49 ± 1.4	
Dryas heath	reindeer 12		49 ± 3.3	
Dupontia brook bank	reindeer 31		50 + 0.6	
	caribou C2	37 ± 2.2		
	caribou C3	43 ± 1.6		

[1] Rumen-fistulated reindeer were tethered on vegetation at Prudhoe Bay.
[2] inflor. = inflorescence or flower.

attributed to its scarcity on winter range and in the diet of Peary caribou in summer. Those species are utilized by caribou on mainland winter ranges.

Rate of digestion or turn-over time of species appears to be highly variable. Sablina (1960) quoted studies which indicated retention times up to 13 days, although 85% of rumen contents were eliminated within 4 days. Alaskan studies, in which a radioactive marker was used, suggested turn-over times as long as 5 days for a mixture of lichen species, however, White and Trudell (1980) reported summer and winter turn-over times in reindeer of 10 and 17-20 hours, respectively.

Rates of digestion and turn-over times must be measured to improve analysis of rumen contents. For example, if retention time of species A is twice that of species B, then species A will be over-represented in rumens by 100% relative to species B, assuming equal ingestion rates.

4.1.6. ***Chemical composition***

A primary breakdown of plant constituents is carbohydrates (*ca.* 75%), protein, fats, and ash. Carbohydrates include sugars, starches, cellulose, hemicellulose, and lignin. Sugars and starches (storage form) provide quick energy but a major source of energy is contained in cellulose, which comprise the major structural framework of plants. Protein provides amino acids used by rumen micro-organisms to digest carbohydrates and fats. Protein is particularly concentrated in reproductive parts and active growing portions of plants. Generally it decreases in percent content as plants mature. Fats, subdivided in fats, lipids, and ether extracts, are stored chiefly in fruits and seeds. Certain fatty acids are termed essential, i.e., they are required nutritional compounds that animals cannot synthesize. Ash, what remains after complete combustion, is the mineral component: calcium, phosphorus, magnesium, lithium, etc.

A proximate analysis technique produced estimates of carbohydrates as two fractions: nitrogen-free extract and crude fiber. The former contains soluble sugars and starches plus some moderately soluble cellulose and lignin; the latter included relatively indigestible cellulose and lignin, etc.

Table 26. Chemical analyzes of muskox food plants, Thelon Game Sanctuary, winter range, 1957 (Tener 1965, p. 35).

Date collected	Plant species	Protein (N x 6.25)	Fat	Crude fibre	Ash	N-free extract	Ca[1]	P[1]
Winter 1								
Aug. 8	*Cetraria cucullata*	3.71	2.38	11.2	2.56	80.0	0.32	0.07
Aug. 8	*Polytrichum juniperinum*[2]	4.99	3.90	28.6	5.16	57.3	0.36	0.10
Aug. 8	*Betula glandulosa*	9.28	6.00	20.2	1.87	62.8	0.27	0.14
Aug. 8	*Empetrum nigrum* L.	5.15	10.43	23.1	2.40	58.9	0.46	0.07
Aug. 8	*Ledum decumbens* L.	7.26	6.43	25.9	1.89	58.5	0.46	0.09
Aug. 8	*Andromeda polifolia* L.	6.29	4.04	23.9	3.85	61.9	0.56	0.08
Aug. 8	*Arctostaphylos alpina*	8.55	2.54	9.5	5.37	74.9	0.57	0.13
Aug. 8	*Vaccinium uliginosum*	6.74	3.10	31.1	1.88	57.2	0.36	0.09
Aug. 8	*V. vitis-idaea* L.	5.43	3.34	19.9	2.25	69.0		
Winter 2								
Aug. 9	*Polytrichum juniperinum*	4.64	2.89	27.9	8.61	56.0	0.36	0.09
Aug. 9	*Betula glandulosa*	8.69	5.53	25.4	1.80	58.6	0.35	0.17
Aug. 9	*Empetrum nigrum* L.	4.17	10.38	23.0	3.01	59.5	0.48	0.06
Aug. 9	*Ledum decumbens* L.	6.38	7.14	27.3	2.30	56.9	0.40	0.09
Aug. 9	*Vaccinium uliginosum* L.	6.76	3.19	31.7	4.26	54.1	0.33	0.11
Aug. 9	*V. vitis-idaea* L.	6.09	2.93	20.5	3.07	67.4	0.56	0.10

[1] Ca = calcium, P = phosphorus.
[2] & *Aulocomnium turgidum*.

Kelsall (1968) summarized data from Tener (1965) (**Table 26**) and Courtright (1959) on chemical composition of caribou and reindeer forages (**Table 27**). Unfortunately, plant parts used for analysis and phenological state of each species, both critical factors, were not given. Relatively high protein values indicate that the samples were new-growth parts taken during the growing seasons. Three of four *Cladonia* (now *Cladina*) spp. had relatively high (40%) crude fiber values and all had protein values under 3%. *Stereocaulon* spp. at 8% and *Peltigera* spp. at 20% contained much higher levels of protein. Miller's (1976a) sample of 95% *Stereocaulon paschale* contained 10% protein, again much higher than his mixed samples predominantly of *Cladina* spp. and *Cetraria* spp. (Table 27).

Table 27. Chemical composition (%) of caribou and reindeer food plants (Kelsall 1968).

		Chemical composition (%)				
Plant species or group	No. of analyses	Protein	Fat	Crude fibre	Ash	N-free extract
Fungi	2	34.76	4.76	20.8	8.12	31.6
Cladonia rangiferina	5	2.21	1.58	42.3	1.49	51.4
C. alpestris	3	2.75	1.52	44.5	1.87	49.1
C. sylvatica (*mitis*)	2	1.86	1.16	44.0	2.21	50.8
C. mitis	1	2.54	1.67	23.0	2.18	65.6
Cetraria cucullata	3	3.77	3.82	11.2	2.14	80.0
C. islandica	5	4.60	3.38	7.9	1.51	82.7
C. nivalis	4	2.47	3.95	5.1	2.15	86.3
Stereocaulon (2 spp.)	4	8.02	1.78	24.6	2.55	63.1
Peltigera spp.	1	19.77	1.29	25.3	9.14	44.5
Musci (2 spp.)	2	4.81	3.39	28.3	6.88	56.6
Equisetum (3 spp.)	6	11.36	3.31	18.8	13.55	53.0
Carex aquatilis	3	10.55	3.21	35.4	5.95	44.8
Salix (8 spp.)	15	20.99	3.10	16.7	6.53	52.7
Betula glandulosa & *nana*	15	15.59	7.16	16.2	3.32	57.7
Epilobium angustifolium	4	13.37	3.09	27.1	6.60	49.8
Empetrum nigrum	4	4.60	9.98	23.1	3.33	59.0
Ledum decumbens	3	6.52	6.52	27.3	2.17	57.5
Arctostaphylos alpina	1	8.55	2.54	9.5	5.37	74.1
Vaccinium uliginosum	2	6.75	3.14	31.4	3.07	55.6
V. vitis-idaea	2	5.76	3.13	20.2	2.66	68.2

Note: Data from Tener (pers. comm.) and Courtright (1959). Data were selectively chosen as being comparable and, where necessary, were averaged by group or species and converted to dry weight (Kelsall 1968).

The proximate analysis data presented by Kelsall (1968), Tener (1965), Courtright (1959), and Miller (1976a) (Table 27 & **28**) help explain why caribou seek out mushrooms (protein 34.8%, ash 8.1%), *Equisetum* (horsetail) spp. (protein 11.4%, ash 13.6%), *and Salix* spp. (protein 21%, ash 6.5%) (Table 27).

A recently-developed system of forage evaluation, termed the detergent or "Van

Table 28. Protein and energy values of forage plant samples taken in summer from 1-m² plots in northern Manitoba. Protein was calculated by multiplying total nitrogen by 6.25 (Miller 1976a).

Plot no.	Forage type	Date collected	% Protein	Energy (K cal./100 g)
1	Lichen, 75% *Cladina alpestris*	19 June	2.04	434
2	Lichen, 95% *Stereocaulon paschale*		10.16	480
3	Lichen, 50% *Cladina rangiferina*		2.00	425
4	Lichen, 50% *Cetraria nivalis*		2.54	426
5	Lichen, mixed	20 June	3.99	454
6	Lichen, mixed		2.92	416
7	Lichen, 65% *Stereocaulon paschale*		6.42	455
9	Lichen, mixed *Cladonia* & *Cetraria*	21 June	2.71	431
10	*Ledum groenlandicum*		8.27	566
11A	*Vaccinium vitis-idaea*	22 June	5.77	509
11B	*Empetrum nigrum*		6.27	551
12	Lichen, mixed	25 June	2.82	433
13	Lichen, mixed		1.96	435
14	Lichen, mixed *Cladonia* & *Cladina*	26 June	2.24	431
16	Lichen, mixed		2.10	428
18	Lichen, mixed		2.12	434
20	*Carex aquatilis*	17 Sept.	6.54	463
21	*Carex aquatilis*	18 Sept.	5.25	452
22	*Equisetum fluviatile*		13.71	383
23	*Ledum groenlandicum*		8.36	569
25	*Equisetum fluviatile*	24 Sept.	6.76	488
	Cladina alpestris[1] live podetia		2.63	656
	dead podetia		1.82	345
	Cladina rangiferina[1] live podetia		4.14	366
	dead podetia		2.18	357

[1] additional samples.

Soest method", divides a plant cell into cellular contents and cell wall constituents. The former consists of sugars, soluble carbohydrates, protein and lipids, which are almost completely available to a herbivore. Cell walls, composed of hemicellulose, cellulose, lignin, and minerals, are of limited but variable availability to an animal. Some results for summer vegetation on the North Slope of Alaska are duplicated in **Table 29**. Those data are quite variable within similar species of vegetation and are difficult to interpret. The data for *Cladonia* (*Cladina*) *alpestris* are in error in terms of digestibility and perhaps cell contents. Caribou generally select forages with low lignin content.

4.2. **Availability of forage**

Availability of forage in winter may be more important than quantity and quality of forage. Ecologists generally agree that absolute quantity of forage on caribou winter ranges in Canada is not limiting. Caribou, like other ungulate species, have evolved mechanisms to compensate for poor-quality forage in winter (e.g., fat storage, nitrogen recycling, reduced forage intake). Climatic factors, especially deep snow and ice, can drastically reduce quantity and quality of forage available to caribou and increase their energy output in obtaining food, travelling, and avoiding predators.

4.2.1. ***Climatic factors***

As winter progresses, snow accumulates and it becomes a major factor in regional and local distributions of caribou. Pruitt (1959) suggested that caribou moved from deeper snow to shallower snow and from harder snow to shallower snow where foraging was easier. Higher mean snowfalls in northern Manitoba (e.g. Brochet 169 cm) compared with Saskatchewan (e.g. Stony Rapids 140 cm) may explain why the Kaminuriak herd sometimes moves westward towards or into Saskatchewan in late winter (Parker 1972a). If snow conditions are more favourable on the tundra, a herd may leave the taiga. In March 1958, for example, the Bathurst herd occurred for several weeks in the Mackay Lake-Muskox Lake region north of tree line where snow was soft and shallow.

Table 29. Chemical composition of plant material collected at Prudhoe Bay, 12-25 June 1972 (Brown 1975). Analysis by the detergent technique of Van Soest (1963) and Goering and Van Soest (1970). Values are expressed as g/100 g dry matter.

Sample	NDF	ADF Ligno-cellulose (crude fiber)	CC cell contents	CWC Hemi-cellulose	Cellul-ose	Lignin	*In vitro* dry-matter digest.%
Shrubs							
Salix arctica	18.5	16.4	81.5	2.1	11.9	4.5	52
S. pulchra	27.2	17.4	72.9	9.8	11.4	6.0	54
S. ovalifolia	31.2	27.3	68.8	3.9	18.6	8.7	46
Dryas integrifolia							
leaves/stem base	35.4	33.3	64.6	2.3	14.0	19.1	33
inflorescence	46.2	48.1	53.8	2.0	21.2	27.1	21
Sedges							
Carex aquatilis	58.2	21.7	41.8	36.5	18.6	3.2	68
Eriophorum angustifolium							
live leaves/10% dead	68.5	24.6	31.5	43.8	19.1	5.1	59
inflorescence + stem	57.5	21.3	42.5	36.0	16.3	4.7	56
Grasses							
Dupontia fischeri							
live leaves/10% inflor.	45.1	19.6	54.9	25.4	15.8	3.9	79
inflorescence + stem	62.1	31.0	37.9	31.1	25.5	5.5	70
Arctophila fulva	67.7	29.0	32.3	38.8	27.3	1.7	72
Herbs							
Artemisia richardsonii	42.3	29.2	57.7	13.1	24.2	5.0	66
Pedicularis spp.	25.9	20.8	74.1	5.1	14.3	6.5	64
Saxifraga oppositifolia	26.9	35.9	73.1	8.5	20.5	15.4	33
Lichens							
Cetraria cucullata	31.6	3.7	68.4	27.8	0.6	4.3	77
Cladonia alpestris	83.0	4.6	17.0	78.3	1.7	2.9	16
C. alpestris (Nome)	83.3	2.3	16.7	81.0	1.3	3.6	16
Esophageal fistula egesta (regurgitated)							
Caribou 1	67.4	35.2	32.6	32.2	25.3	9.8	43
Caribou 2	69.9	36.2	30.1	33.6	26.7	9.4	43
Caribou 3	62.8	35.0	37.2	27.8	23.0	12.0	41
Caribou 4	52.5	32.9	47.5	19.7	25.5	7.2	41
Artificial Foods							
Mixed reindeer hay[1]	78.0	24.6	22.0	53.4	18.3	6.3	30
Purina cattle starter No. 1	48.6	27.4	51.4	19.1	24.4	2.9	68

NDF, Neutral detergent fibre: ADF, acid detergent fibre; CC, cell contents; CWC, cell wall constituents; lignin was determined as the mineral, acid-resistant component of ADF. *In vitro* digestabilities were taken from Table 16. *Cell constituents=100-NDF, hemicellulose=NDF-ADF, cellulose=ADF-lignin*
[1] 78% lichen and 22% *Carex aquatilis* and brome hay.

Table 30. Proportionate occurrence of land surface (less water) and use as cratering sites in lowlands, lake-shore, and uplands in Manitoba and Saskatchewan in February 1972-73 (data in Miller 1976b).

		Proportionate occurrence (%)					
		Lowlands		Lake Shore		Uplands	
Province	Year	% of land	% use	% of land	% use	% of land	% use
Manitoba	1972	45	57	NA	11	55	42
	1973	45	48	NA	3	55	49
Sask.	1972	20	28	NA	14	80	58
	1973	20	34	NA	16	80	50

Note: NA = not available. Proportionate occurrences and use are not from the same area.

4.2.2. *Topography*

Analysis of data in Miller (1976b) indicate that caribou use lowlands as feeding sites more frequently than their occurrence (**Table 30**). Those results may be biased, however, because the two sets of data were not from the same area nor were they estimated the same way. Proportionate occurrence of land types was obtained from air photographs. Proportionate use was obtained from other regions and land types were estimated on snow covered terrain from an aircraft.

According to Miller (1976b), caribou showed a preference for feeding on tops of ridges and hills and on sides of eskers. On ridges and hills in Manitoba and Saskatchewan, 77% and 70% of feeding sites were on tops of hills. Although proportionate areas of tops and sides were not given, the latter would be larger in absolute extent.

4.2.3. *Exposure*

Caribou have such good insulation that they seldom seek protection from cold and wind. On the tundra, caribou will seek the lea of hills when the temperature is -40° C with winds of 50-60 kmph (pers. observations).

4.3. *Escape terrain*

Caribou rely on their speed for escape and escape terrain or cover types are used mainly by injured caribou. For example, caribou with injured legs or feet will stay beside water. They escape predators by swimming.

4.4. *Travel routes*

Travel routes in winter are across lakes and along streams and lowlands between lakes. During migration, travel can be amazingly directional with trails nearly parallel over many kilometres. Migrating caribou travel over all types of terrain but in general they take routes of least resistance. In spring migration many thousands of caribou will follow a few trails that snake through a series of lakes and waterways.

5. WINTER RANGE-FIRE RELATIONSHIPS

5.1. **General principles**

Principle 1:

Over a period of half a century, a large percentage of total area burned in that period occurs in only a few years. Supporting data:

- Saskatchewan caribou range (Stony Rapids map sheet) 1956-71 (incl.): One fire of 384 km^2 in 1970 accounted for 60.6% of area burned during that 16-year period (Miller 1976b).
- Fourteen tundra fires recorded in 1973 between 60°N and 65°N and west of 96° W longitude burned 129.5-155.4 km^2 (Wein 1976), which was probably equal to the area burned in all other years between 1950 and 1973.
- The area burned on the Whiskey Jack map sheet (northwestern Manitoba) in 1973 (1073 km^2) was 6l% of the total area burned (1758 km^2) over 16 years from 1956-67 and 1973-76 (data from Miller [1976b] and Robertson [1977]).
- In one region of Alaska during a 10 year period, 1956-65, 58%, 85%, and 96% of lichen habitats burned in 1, 2, and 3 of the 10 years, respectively (Davis 1978).
- According to Robertson (1977), fires burned large areas in portions of northern Manitoba in 1960 and 1961.

Principle 2:

A few large burns account for most of the area burned over a prolonged period of say 30-50 years. Supporting data:

- In north-central Saskatchewan, 1944-71 (incl.) (28 years), large burns in 1955 and 1970 account for 60% of area burned during that period (Miller 1976b).
- Northwestern Manitoba, 1963-64: "less than 7% of forest fires caused 91.5% of the destruction ..." (Scotter 1965).
- Less than 10% of fires on "caribou range," 1966-73, were larger than 4000 ha but they accounted for *ca*. 80% of the total area burned (Johnson and Rowe 1974).
- Fires larger than 200 ha account for about 95% of the area burned in the North (Rowe et al. 1975).
- One fire accounted for 53% of the total area of 16 burns examined on winter range north of Yellowknife (Kelsall 1960).

Principle 3:

In a period of half a century there are short periods of high fire incidence, i.e., periods of high fire incidence do not occur at random. Supporting data:

- Periods of high fire incidence (various authors): 1910-11, 1933-35, 1941-45, 1944-45, 1960-61, 1970-73, and 1979-80.
- Periods of low fire incidence: 1967-69, 1974-78.
- Prior to 1974, over 50% of forested areas of northern regions of Wood Buffalo Park were burned in 1941-45 (Johnson and Rowe 1974).
- Fires in the early 1970s in northwestern Manitoba and northeastern Saskatchewan burned as much forest as all other fires from 1950 through 1978.
- In 1960-61, fires were numerous and large north of Great Slave Lake.

Principle 4:

Lightning fires account for almost all of the *area* burned. Supporting data:

- From 1966-73 lightning accounted for 99.9% of area burned on "caribou range" in the Northwest Territories (Rowe et al. 1975).
- Lightning accounted for 97% of area burned in the upper Mackenzie Valley (Rowe et al. 1975).
- Lightning was responsible for 99-100% of area burned by fires in the late 1960s and early 70's in 9 of 10 regions of the NWT (Rowe et al. 1975).

***Principle 5*:**

Large fires occur in years with a high number of fires. Supporting data: Data in 1970, 1971, 1973, and 1979 for "caribou range" (Ferguson 1983).

***Principle 6*:**

The probability of fire starting naturally is directly related to time since previous burning. Supporting data: Empirical observations. Most fires started in mature or old stands. Fires tend to remove old stands. Lightning flows through tall trees to and from ground and dead trees probably are more likely to ignite than live ones.

***Principle 7*:**

The effectiveness of fire control is inversely related to numbers of fires in a season. Supporting data: Observations. Many fires can originate with one storm and fires spread rapidly if stands are dry and there is wind. There are insufficient numbers of fire fighters, aircraft, and equipment to attack many fires at once.

Principle 8:

Small fires, which occur in the majority of years, burn predominantly upland sites near human habitation; large fires burn uplands and lowlands nearly in proportion to their occurrence.

Principle 9:

In any 1 year, there is considerable regional variation in area burned. For example, in 1979, extensive burning occurred in western parts of the Beverly herd's range but not in the east. The reverse occurred in 1973.

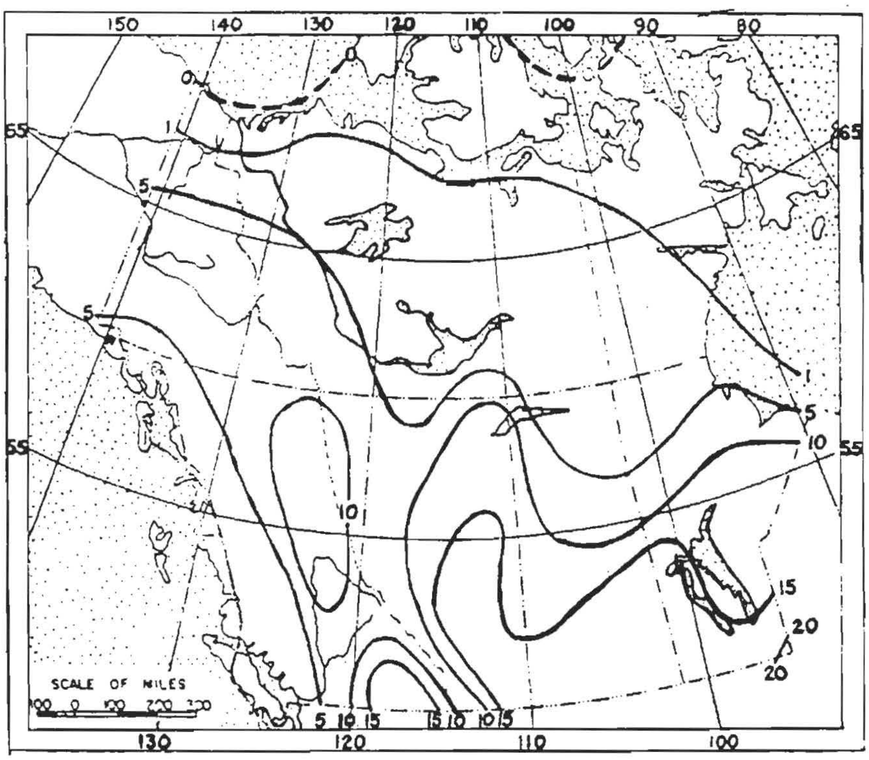
5.2. **The cause of fires**

The cause of most fires on caribou winter range is lightning striking dry fuels. Lightning is usually associated with convection storms in which vertical air motion produce electrical charge separation and create electric potential differences. Discharge of that potential produces a lightning strike (Rowe et al. 1975). Origins of convection storms are (1) frontal activity (the meeting of cold and warm air masses), (2) solar heating of terrain with upward movement of air, and, (3) upward deflection of air currents by topographic relief. Rowe et al. (1975) demonstrated clearly that fires north of Yellowknife occurred along storm fronts. Johnson and Rowe (1974) showed that frontal activity moved towards tree line in June and July and retreated to the southwest in August.

Data on thunderstorm frequencies (Kendrew and Currie 1955) indicate relatively high (5 days annually) values north and south of Lake Athabasca (**Fig. 19a**). Number of thunderstorm days increases in the series Fort Reliance, Yellowknife, and Fort Smith, each progressively more distant from tree line (**Fig. 19b**). Frequency of thunderstorms and other climatic characteristics, principally rainfall and surface features, combine to create variable "forest fire weather zones" (**Fig. 20**). Fire hazard is high or very high between Great Slave and Great Bear lakes and between Great Slave and Athabasca lakes and to the south of Lake Athabasca (Simard 1973).

Figure 19.

a



b

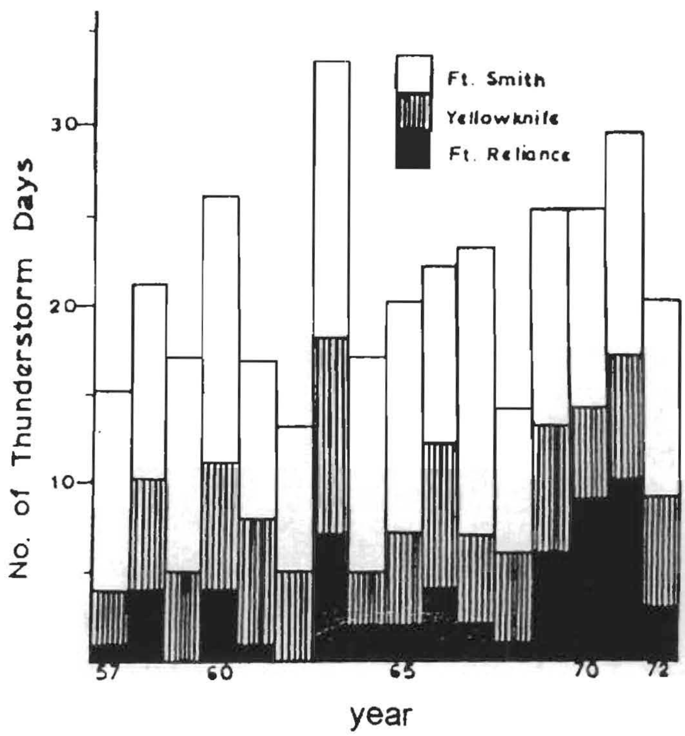


Figure 19. Mean number of summer (June-August) days with thunderstorm activity on (a) winter range of the Beverly herd of caribou (Kendrew and Currie 1955) and (b) at Fort Reliance, Yellowknife, and Fort Smith (Rowe et al. 1975).

Figure 20.

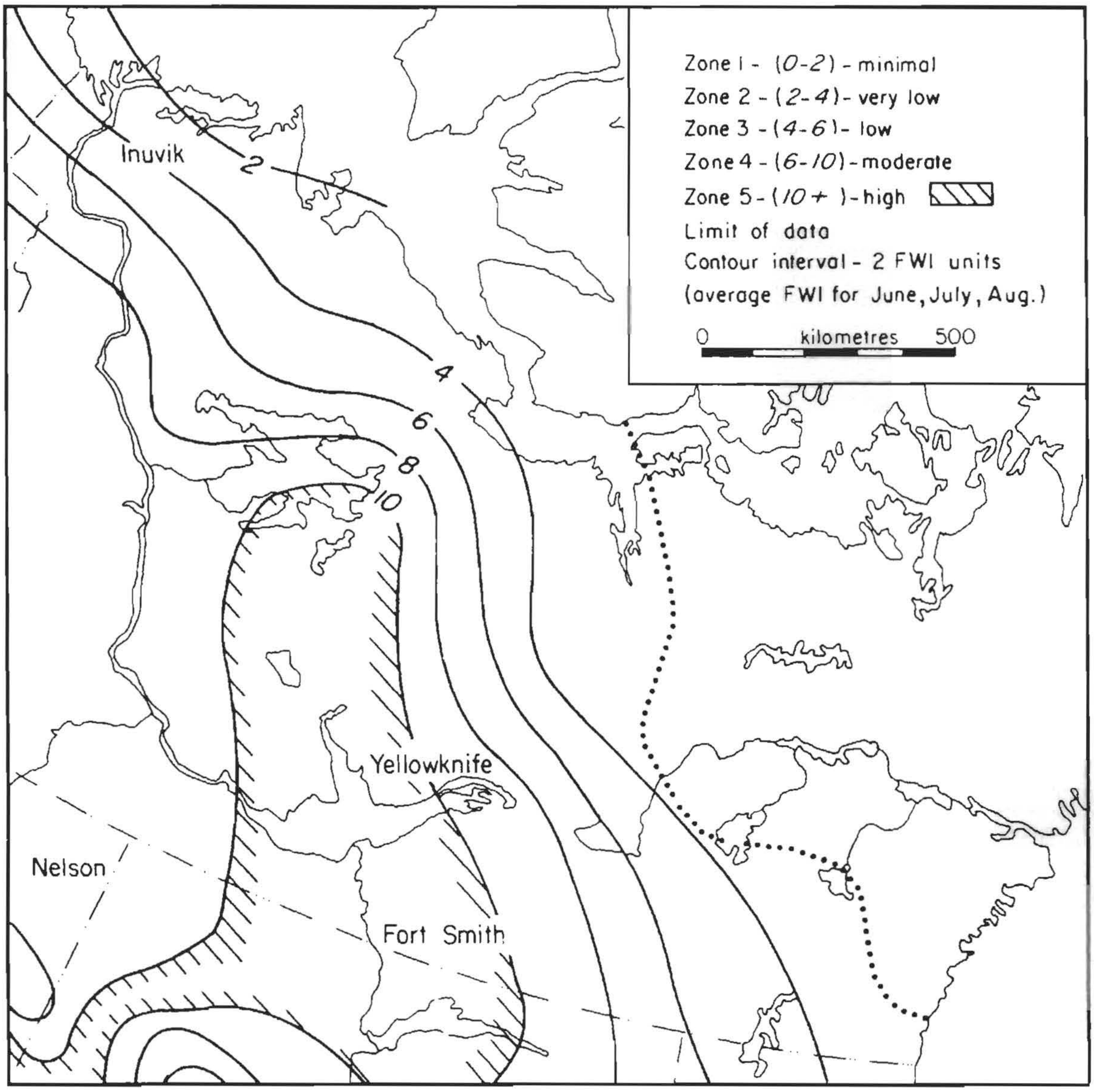


Figure 20. Average fire weather indices for June-August generating "forest fire weather zones" (Simard 1973).

5.3. **Fire behavior**

Behavior of fire on caribou winter range was vividly described by Johnson and Rowe (1974) from first-hand observation:

> *Fires seem to follow a more or less regular sequence of activity. Night, morning and evening find the humidity higher and fuel moisture higher. During this time fires burn mostly on the ground and move at a slow rate... If an inversion occurs at night the area around a fire is very smoky and the exact fire front is difficult to locate in the morning. By the afternoon the air has warmed and the humidity and fuel moisture have decreased. During this time, if fuel is present and meteorological conditions are suitable, a fire will increase greatly in size and will crown as well as burn on the ground... Given a strong and constant wind, "fire runs" in the vegetation are usual... In such "runs" the above-ground vegetation is destroyed, some of the litter layer is consumed, and most of the downed timber is ashed... Damage by fire varies greatly depending on whether the fire is active in the morning, afternoon, evening or night, some areas burning very hot and others completely escaping... One surprising fact came out of the few plots studies; ericaceous shrubs burn much more readily than do lichens... This is probably due to the lower flash point of the shrubs.*

Heat from crown fires turns all fuels on the ground to ash. Ground fires often burn shrubs and litter but only partially burn ground lichens, in some cases only the dry tops (Rowe et al. 1975).

5.4. **Fire incidence**

The rate at which fires have burned the total surface, land surface (less water), or drier sites (e.g. less muskeg) has been estimated at several locations on winter range of caribou (**Fig. 21**). The overriding themes of available data, which must be converted to a common denominator for comparative purposes, are its extreme spatial and temporal variability. Sources of data are recent fire history, distribution of stand ages (**Fig. 22**) and sizes at a point in time, and fire intervals (**Fig. 23**) at certain locations.

Data for northern Manitoba in two periods produce remarkably different average annual rates of area burned (**Table 31**). R.J. Robertson's data in Robertson's (1977)

Figure 21.

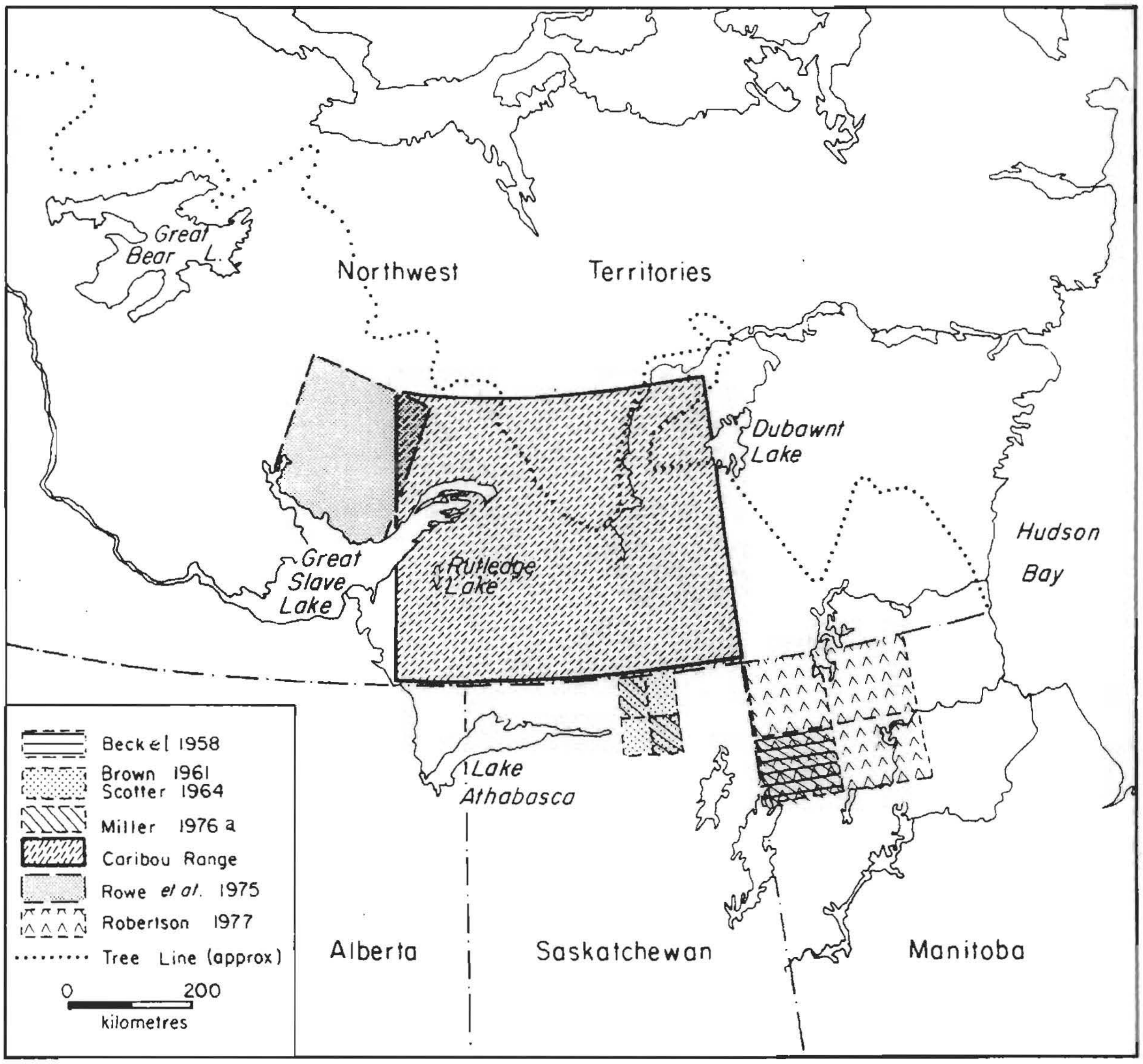


Figure 21. Areas of winter range of central herds of caribou where data are available on the rate at which fires have burned the landscape.

Figure 22.

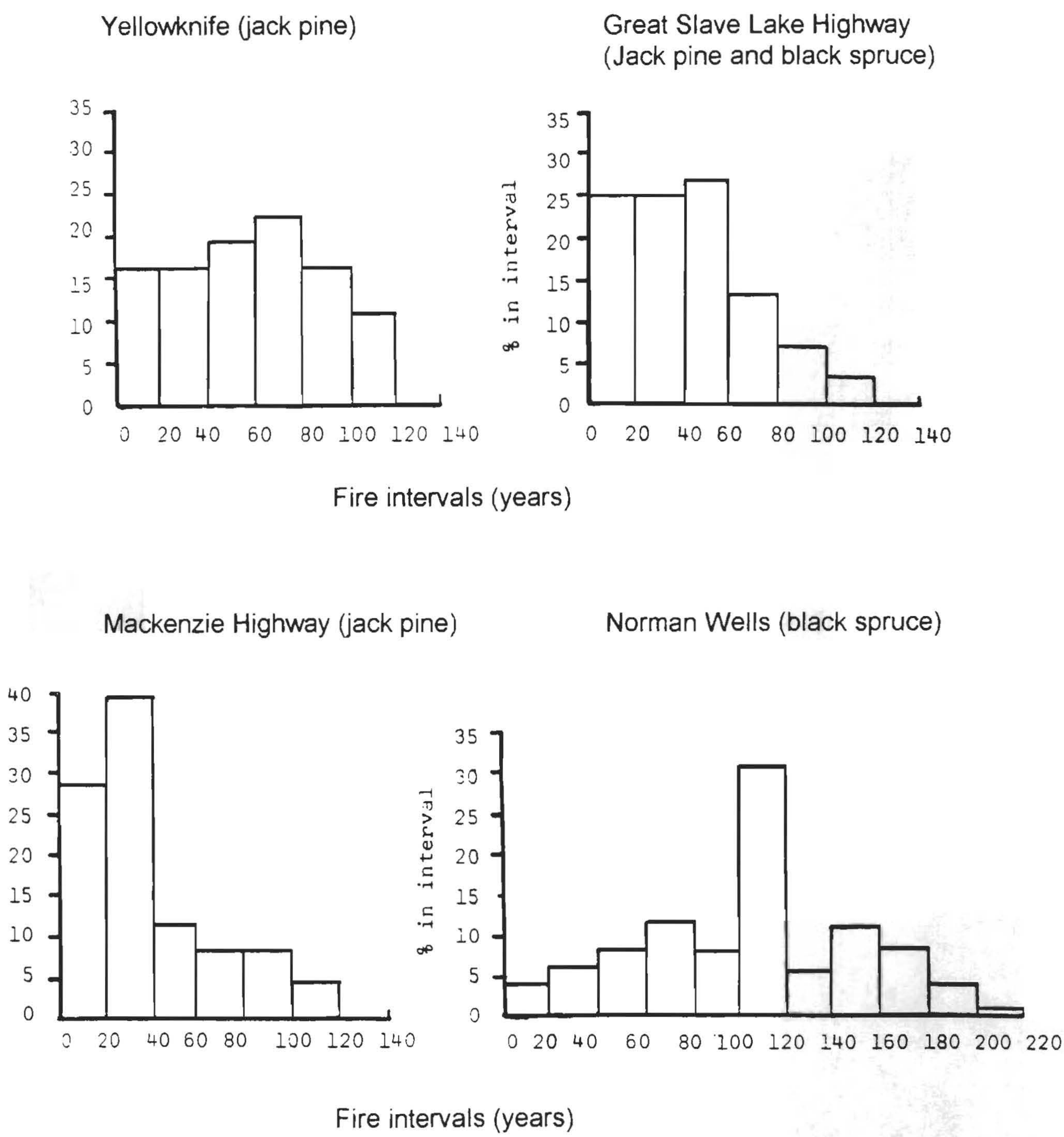


Figure 22. Distribution of fire intervals at four locations on winter range of the Beverly herd of caribou (Rowe et al. 1975).

Figure 23.

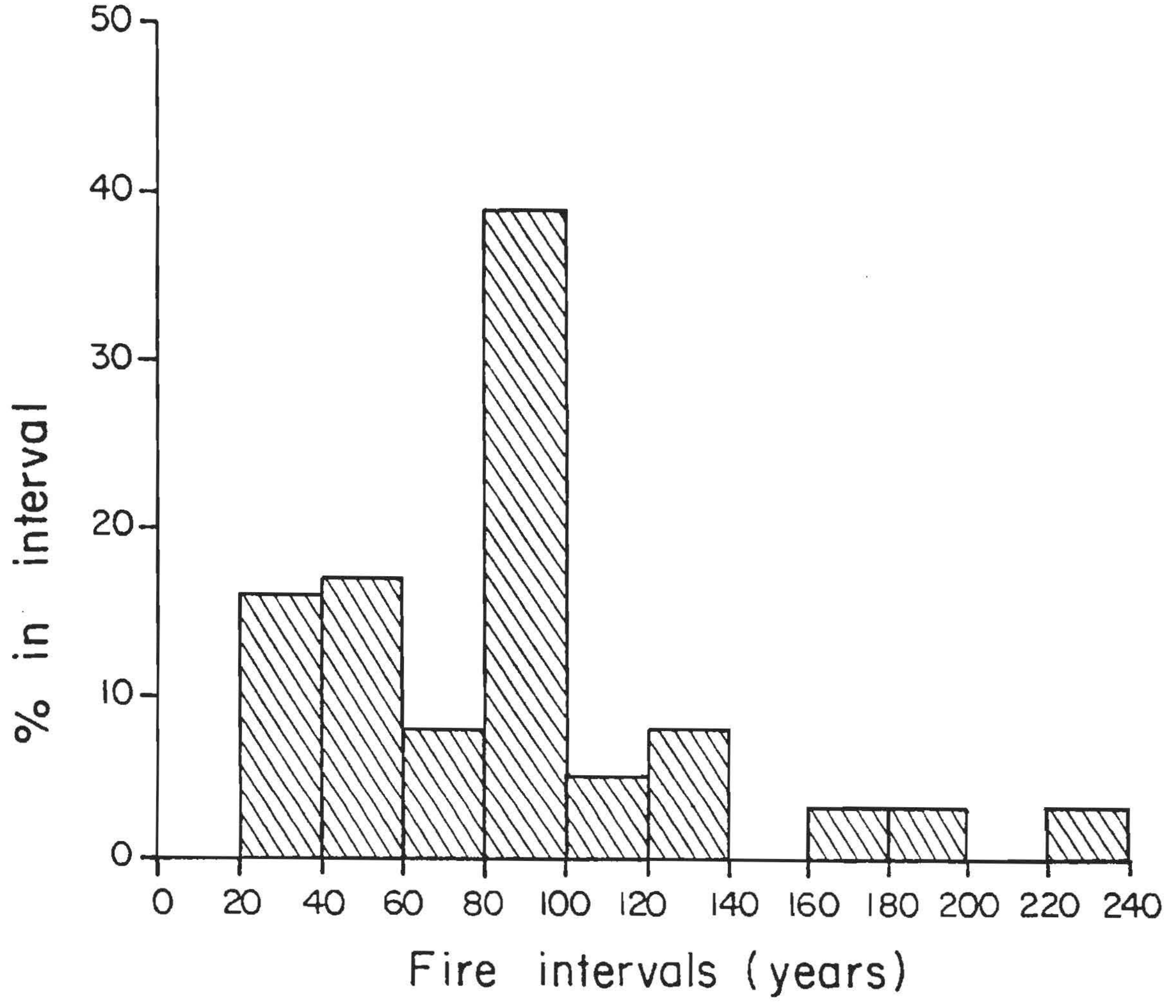


Figure 23. Frequency distribution of 35 fire intervals in 24 stands at Rutledge Lake, NWT, obtained from fire scars (Rowe et al. 1975).

Table 31. Average percentages of total surface and land surface (less water) burned annually in regions of winter range of caribou in north-central Canada.

Location	Period	Area surveyed (km²) Total	Land	Area burned (km²)	Percentage of area burned/year Total	Land[1]	Source
N.W. Man.	1956-1967	12 107	9 827	192.3	0.13	0.16	Miller 1976b
	1973-1976		42 899	4585.0		2.67	Robertson 1977
N.E. Sask.	1840-1884	12 727	10 182	26.7	0.21	0.26	Scotter 1964
	1885-1909	12 727	10 182	57.9	0.45	0.57	
	1910-1929	12 727	10 182	60.9	0.48	0.60	
	1930-1944	12 727	10 182	57.0	0.45	0.56	
	1945-1959	12 727	10 182	84.1	0.66	0.83	
	1956-1971	7 202	5 757	634.0	0.55	0.69	Miller 1976b
"Caribou range"	1966-1973	105 627		7648.8	0.91	1.13	Rowe et al. 1975
Yellowknife	1968-1973	43 706		2339.2	0.89	1.11	Rowe et al. 1975

[1] Assumes 20% water.

report indicate severity of the 1973 fire season on caribou winter range in Manitoba. Percentages of land area burned within an area covered by four 1:250 000 map sheets were as follows: Munroe 6.1%, Whiskey Jack 10.5%, Kasmere 11.5%, and Tadoule 14.3%. Corresponding average, annual values for the next 3 years were 0.4%, 0.7%, 0.2%, and 0.1%. Average area burned annually was 0.79% when data for the two periods were combined. Areal rate of burning in 1973 (9.76%/yr) was 3l.5 times the average rate (0.31%/yr) for the subsequent 3 years (1974-76). Average annual proportion burned in 1973-76, on the four map sheets, was 2.6%.

Robertson's (1977) calculations of time required to burn the remaining 36 422 km² were based on an invalid assumption. The mean rate for 1973-76 is inflated because 1973 was too atypical. The mean rate, on all four map sheets, for 1973-76 was 16.7 times the rate for the 12-year period 1956-67.

Scotter (1964), using data of Brown (1961), concluded that area burned, 1945-59, in a 12 727 km² area of north-central Saskatchewan was 1.4 times the rate from

Table 32. Rate of burning by three age class intervals at Rutledge Lake, NWT (Rowe et al. 1975).

Age class (yr)	Average percent burned per year in age class interval: 20 year	40 year	80 year
0 - 20	0	]	}
21 - 40	0.75	] 0.375	}
			}
41 - 60	1.10	)	}
61 - 80	0.70	) 0.90	} 0.64
81 - 100	4.81	]	)
101 - 120	1.05	] 2.93	)
			)
121 - 140	3.08	)	)
141 - 160	0	) 1.54	) 2.24
161 - 180	2.00	]	]
181 - 200	7.14	] 4.57	]
			]
201 - 220	0	)	]
221 - 240	10.0	) 5.00	] 4.79

1885-1944 and 3.1 times the rate from 1840-84 (**Table 31 & 32**). Those comparisons are not valid except for the two youngest classes because of expected recurrence of fires in stands older than 20 years, as shown graphically by Rowe et al. (1975) (Fig. 23) based on fire interval frequencies at Rutledge Lake, NWT. The "survivorship" curve generated from cumulative fire intervals for Rutledge Lake (**Fig. 24**) was used to adjust Scotter's (1964) data to account for older burns being masked by younger ones (**Table 33**). The converted data (**Table 34**) indicate a lower proportion of area burned in 1840-1884 but air photo interpretation inaccuracies in older classes could cause those apparent differences.

Figure 24.

Figure 24. A "survivorship curve" based on cumulative fire intervals for Rutledge Lake (Rowe et al. 1975).

Table 33. Apparent average annual rates at which forests were burned before 1960 in a 12 727 km² region of northeastern Saskatchewan (data reworked from Brown [1961] and Scotter [1964]).

Age of forest (years)	Area in age-class km²	(%)	Area burned per year[1] (km²)	Average annual burn rate (%) Specific surface[2]	Land surface[3]	Total surface[4]
1-15	1261	(15.4)	84.1	1.03	0.82	0.66
16-30	855	(10.5)	57.0	0.70	0.56	0.45
31-50	1217	(14.9)	60.9	0.75	0.60	0.48
51-75	1448	(17.7)	57.9	0.71	0.57	0.46
76-120	1202	(14.7)	26.7	0.33	0.26	0.21
>120	2186	(26.8)	00.0	NA	NA	NA
Totals/ave.	8169	(100.0)		81.6[5]	0.65[5]	0.52[5]

[1] Area burned/number of years in class.
[2] Area burned per year/8169.
[3] Average annual burn rate for specific surface x 0.80 (Miller 1976b).
[4] Average annual burn rate for specific surface x 0.642 (Scotter 1964).
[5] Average for 1-50 years (1929-1959).

Data for 1956-71 in northeast Saskatchewan (Miller 1976b) indicated annual burn rates (0.55% of total surface, 0.69% of non-water surface) somewhat lower than in 1945-59 according to Scotter's (1964) data (0.66% and 0.82%) but similar to past periods of 30 and 50 years (Table 33). Areal burn proportions north and south of Great Slave Lake for periods 1968-73 and 1966-73 were higher at 0.89% and 0.91%, annually (Table 31). However, the latter two rates included two severe years, 1970 and 1973, whereas data for Saskatchewan did not include 1973. Calculation of burn rates over short time periods is of interest but it tells us nothing about long-term natural fire cycles.

Fire frequency data for Rutledge Lake on "caribou range" were analysed mathematically by Rowe et al. (1975), Johnson and Rowe (1977), and Van Wagner (1978). The last named found that a negative exponential equation with a 100-year cycle fit reasonably well. Van Wagner (1978) defined fire cycle as the number of years required to burn over an area equal to a study area. His definition of a fire

Table 34. Adjustments to Scotter's (1964) data for northeast Saskatchewan (Table 33) to account for re-burn rates estimated at Dunvegan Lake (Fig. 26).

Period	Age class	Percent reburned	Correction factor	Adjusted % area burned annually Land[1]	Land[2]	Total
1945-1959	1- 15	0	0	1.03	0.82	0.66
1930-1944	16- 30	6	1.06	0.74	0.59	0.48
1910-1929	31- 50	21	1.21	0.91	0.73	0.58
1885-1909	51- 75	41	1.41	1.00	0.80	0.64
1840-1884	76-120	83	1.83	0.60	0.48	0.39

[1] Excludes water, muskeg, and rock (35.8%, Scotter 1964).
[2] Excludes 20% water (Miller 1976b).

cycle was the reciprocal of the average proportion of the whole area burned every year and the average interval between fires at a given location, but not over a region.

If a negative exponential model is accepted, mean age of stands in the Rutledge Lake area was 100 years, median age was 69 years, and mean rate of burning was 1% annually. The latter value, for an undetermined period, is intermediate to the rate of 0.91% (total area) and 1.09% (land surface) calculated for 1966-73, based on fire history data (Table 31).

The 20-30% water of Precambrian Shield areas of caribou winter range must be incorporated in calculations of fire cycles. Otherwise, fire cycles will be biased 20-30% longer than is the case. In theory, similar adjustments should be made for upland areas where most caribou feeding occurs. An end result is that areal extent of fire in uplands probably is underestimated even where data are not adjusted for unburned inclusions.

One assumption behind application of the negative exponential model is equal fire susceptibility with age of forest. Data on fire intervals (Rowe et al. 1975) suggest low susceptibility in the first 20 years after fire and relatively low susceptibility in forests aged 21-40 years. Fire susceptibility is somewhat academic in stands older than about 50 years because large fires sweep across a mosaic of different aged stands. In theory, if fire susceptibility increases with age of stand, the result is a higher frequency of younger-aged stands than expected with constant susceptibility. If fire susceptibility peaked at 81-100 years, that class would appear less frequently than expected.

Van Wagner (1978) suggested that use of a negative exponential was a method of deducing fire history from a distribution of stand ages at any given time. Data presented by Scotter (1964) for northeast Saskatchewan, when plotted on semi-log paper fit a straight line reasonable well, which indicated an 80-year cycle and an average burn rate of 1.25% annually on land exclusive of water (20%, Miller 1976b). muskeg (15%, Miller 1976b), and rock outcrops etc. (8%). The fire cycle south of Lake Athabasca is shorter (Black and Bliss 1978).

One index of fire burn rate is proportion of winter range in a mature or climax state, a somewhat subjective criterion. Kelsall (1960) reported that 20% of land (non-water) surface in a region south of Great Bear Lake was in sub-mature successional stages. In contrast, in 1958, in a 43 020 km² region in northern Saskatchewan, only 2% of the surface was considered to be in a climax (spruce-lichen) state (Kuyt in Kelsall 1968). Scotter's (1964) data reveal that, in 1960, only 24% of a landscape in northeastern Saskatchewan was older than 120 years. Sub-climax stages occur on sandy sites even after 120 years. Virtually all plotted burns were less than 30 years old in 1957-1958 (Kelsall 1968). Vast areas of recently burned landscape were noted in 1967 south of Lake Athabasca and the Fond-du-Lac River (Thomas 1967, 1969). Apparently, vast areas burned in the same region in 1969 and 1970 (**Fig. 25**).

Smaller or fewer fires occur in regions where lakes are numerous. For example, in Kelsall's (1960) study region, 23% of the surface was water. Within burned regions, water constituted 18% of the surface and, in unburned regions it comprised 36%.

The average annual proportion of burned landscape in two adjacent regions of

Figure 25.

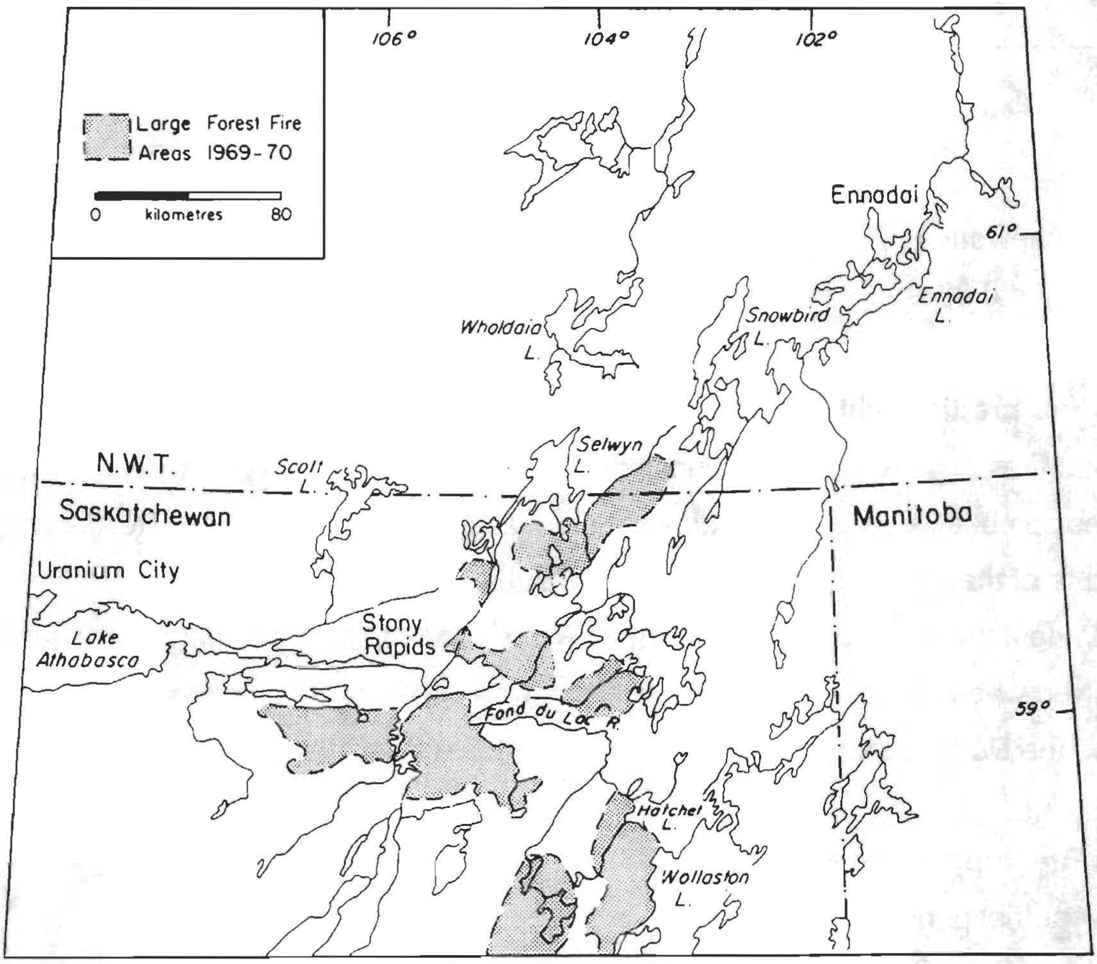


Figure 25. Burns in 1969-70 in northeastern Saskatchewan (Bone et al. 1973).

Table 35. Number of fires, area burned, and operating budget for the first 3 years of fire suppression on the "caribou range" (Naysmith pers. comm.).

Year	No. of fires	Total area burned (km^2)	Total cost (x $1000)
1966	39	80.9	116.8
1967	9	52.6	49.7
1968	1	T	42.1
Totals	49	33.0	208.6

Saskatchewan, 1956-71, was 1.06% (southeast quarter Stony Rapids 1:250 000 map sheet) and 0.38% (northwest quarter) (Miller 1976b, p. 37).

5.5. **Fire predictability**

Natural fires occur under two conditions (1) the fuel source is dry, and (2) lightning strikes combustible material. Indices of dryness developed by the Fire Research Institute of the Canadian Forest Service may be used to predict likelihood of fires occurring if the second condition is met. Rowe et al. (1975) found that few fires occurred when the Fire Fuel Moisture Code was less than 75 or when the second index, the Duff Moisture Code, was less than 45.

5.6. **Fire suppression**

A 3 year trial period of fire suppression on "caribou range" in NWT between Lake Athabasca and Great Slave Lake was initiated in 1966. In the first summer, 33 or 40 forest fires within a designated region of 103 600 km^2 were fought at additional costs of $95 000. Actual expenditures for the 3 years varied from the budget (**Table 35**). Costs decreased to $75 000 in the second and third years because few fires occurred. A second 3 year program (1969-71) was launched after the first one was deemed to be successful.

6. THE REGULATION OF CARIBOU POPULATIONS: FIRE IMPLICATIONS

Factors most commonly mentioned as regulators or controllers of caribou populations are forage restrictions, climatic extremes and changes, over-harvest, predation, parasites and diseases, and social factors.

6.1. **Forage**

Winter range is likely to be one of the key factors governing upper limits of population size (Klein 1970). Winter range encompasses the total winter environment including climate, landscape, vegetation, and fauna. Therefore, forage restrictions in winter and climate usually are considered together as they are inextricably related. Key variables are restricted availability of low quality forage and increased energy expenditures in obtaining forage, travelling, avoiding predators, and maintaining body temperature. Fat, accumulated during summer and autumn, may be utilized in winter and spring (April and May) when *Rangifer* spp. may be in a state of negative energy balance.

Rangifer spp. that winter of the tundra periodically are subject to mass starvation (Scheffer 1951, Klein 1970, Parker et al. 1975, Miller et al. 1975) and therefore they may seldom if ever attain the "carrying capacity" of their range. In some cases starvation conditions are attributed entirely to forage inaccessibility; in others a combination of range over-utilization and forage inaccessibility is implicated. Mass starvation of Peary caribou on the Parry Islands of Arctic Canada in winter 1973-74 was caused by severe snow and ice conditions (Parker et al. 1975, Miller et al. 1975).

The only documented cases of *Rangifer* spp. over-utilizing their entire range are in predator-free island environments. Reindeer introduced to St. Matthew Island in 1944 increased to 1350 individuals (4.1/km^2) in 1957, when overutilization of the range was evident, and to 6000 (18.5/km^2) in 1963 (Klein 1968). Fewer than 50 of those reindeer survived the severe winter of 1963-64 but we will never know how many would have survived had the numbers been kept within the carrying capacity. There was also a crash under similar conditions of the Pribiloff Islands in Alaska in the 1940s (Scheffer 1951).

The Coats Island (Hudson Bay) population of caribou increased from an estimated 500-600 in 1961 to 1400-1500 in 1970. Numbers in May 1974 were estimated at 4100-4400 and in 1975 the count was 6000 of which 4356 were dead (Gates 1979). The 72% mortality was attributed to greater than average snowfalls, although fall icing was a distinct possibility.

Rangifer spp. that migrate from tundra to taiga for the winter are not subject to population crashes. Incidents of starving caribou in taiga are rare (Scotter 1964) and mass mortality non-existent. The mobility of caribou coupled with their flexibility in range selection and use enables them to find range adequate for subsistence in all but exceptional winters, such as 1961-62 on the central mainland of Canada (Scotter 1964). That winter resulted in a missing cohort in the age structure of the Kaminuriak herd (Miller 1974). A second reason is presence of a reserve supply of arboreal lichens that are available in years of deep snow.

According to Bergerud (1974), supporters of a hypothesis that numbers decreased because of shortages of lichen supplies caused by fire and logging, included Leopold and Darling (1953), Edwards (1954), and Scotter (1964, 1967b). On the surface it appears as though these biologists fell into an old trap of looking for single factors to explain declines, when combinations of factors probably are involved. However, Scotter's (1967b) most extreme statement was:

"... *There can be little doubt that forest fires have been one of the principal causes of the decline...*"

The primary mechanism was believed to be destruction of slow growing and slow colonizing ground lichens, an important component of winter diet (Section 4.1). Other possible mechanisms include interference with migration and movement and avoidance of burned regions because of their odour.

No one has demonstrated that winter range was inadequate in aerial extent or quality because of fire. Only a small percentage of available winter range is used in any one season or over several winters.

6.2. **Climatic extremes and climatic change**

Climate (long-term) and weather (short term) affect caribou directly and impinges on all other factors. Severe storms during calving, as in 1958, can result in loss of a significant proportion of calves (Kelsall 1968), a direct effect. Climatic extremes in winter can result in mass mortality in insular populations and they no doubt affect all caribou populations, but occurrences are treated under forage as availability.

An early wet summer followed by a long period of warm days with little wind would result in severe insect harassment and blood loss and increased losses to predators because of disruption to caribou. Energy lost or, alternatively, not gained at that time may be crucial to the productivity of young females and survival in calves.

Obviously, climate is the principal factor effecting the incidence of fire on the winter range (the incidence of fire on the tundra is too low to be significant).

6.3. **Over-harvests by humans**

Collective over-harvest by humans is a theme common to most of the explanations of population declines. Over hunting by individuals is a separate issue. Collective over hunting was considered to be the primary cause in several declines in populations on mainland Canada (Banfield 1954; Kelsall 1968; Calef 1978, 1980; Thomas 1981) and in Alaska (Davis 1978). Over-harvest is the factor most readily documented. If, over a period of years, the known or presumed kill nears or exceeds recruitment to a population, then a downward trend in numbers is inevitable. Natural mortality will amount to at least 5% of adults in a herd and generally it is in the range of 5% to 10%.

Burns may influence migration routes and winter distributions. Harvest could increase or decrease, as a result, depending on whether distributional shifts were toward or away from communities.

6.4. **Predators**

I know of no evidence that predators have caused, as opposed to contributed to, declines of barren-ground caribou populations. Bergerud (1974, 1980) implicated predators (and disease) as important factors in declines of woodland caribou. His hypothesis was that predators and disease increased because fire and logging created new habitat and introduction of, or increase in, numbers of alternate prey species, some of which harboured parasites transmissible to and harmful to caribou.

That wolves cause significant mortality to caribou populations is not disputed. Average mortality rates of 5% of adults in central Canadian mainland populations were ascribed to wolf predation (Banfield 1954, Kelsall 1968, Parker 1972a).

In Newfoundland where wolves do not occur, the lynx (*Lynx canadensis*) was found to be a major cause of mortality in calf caribou (Bergerud 1971). Wolf predation was the primary cause of calf mortality on calving and post-calving grounds of the Kaminuriak and Beverly herds (Miller and Broughton 1974, Miller et al. 1983). Parker (1972a) estimated that wolf predation on the Kaminuriak population, then estimated to number 63 000, accounted for 4.8% of individuals over 1 year of age. There was some evidence of high mortality in calves in June 1978, and many wolves on calving grounds of the Beverly population (Calef, pers. comm.). In Alaska, Murie (1944) considered wolf predation on calves to be a significant source of mortality. Recently, Davis (1978) found there was a vast amount of evidence to suggest that wolf predation was the principal factor limiting the Forty-mile population in Alaska.

Rates of predation could change considerably if extensive burning of winter ranges caused a change in migratory behaviour and movements. For example, predation rate may be reduced if caribou winter on the tundra or in sparsely treed regions. Certain regions are used by wolves for denning. If caribou change their movement patterns, wolves may be forced into areas with few denning sites, or if they use traditional sites they may suffer food shortages and poor survival of pups.

Range deficiencies could go undetected without baseline information on normal changes in fat reserves, growth rate, maturation (age at puberty), and calf and yearling survival. For example, in 1967-68 the Kaminuriak herd showed relatively poor performance in all those areas. Most adults had used their subcutaneous fat reserves by March, calves lost weight over winter, made relatively small gains in their second summer, and thus were vulnerable in their second winter. Only about 2% conceived as yearlings, 48% as 2½-year-olds, and 82% at age 3½, a relatively slow attainment of puberty (Dauphiné 1976). Furthermore, there was evidence that, after conceiving for the first time at 1½ or 2½ years, some females failed to conceive the next year. Calf survival to age 1 year averaged only about 30% (Parker 1972a). These data, when compared with other populations, indicate inadequate nutrition, perhaps caused by forage restrictions or unusually large energy expenditures.

6.5. **Parasites, disease and insect harassment**

Those factors were not implicated in any major declines of barren-ground caribou but their actions could be significant but go undetected. Warble flies (*Oedemagena tarandi*) and nose bots (*Cephenemyia nasalis*) can cause severe harassment of caribou in summer, when replenishment of fat reserves is crucial. Blood sucking insects, especially mosquitos (*Culex* spp.), can cause mortality. Seldom are deaths attributed directly to insects but their cumulative effects in some summers may result in high losses to predators, significant energy losses, and reduced recruitment. Bergerud (1974) reviewed the topic relative to woodland caribou.

6.6. **Social pressures**

Skoog (1968) hypothesized that caribou declines in Alaska were caused by emigration to other ranges when populations exceeded a threshold density of 1.9-3.9 caribou/km^2. Haber (1977) and Haber and Walters (1980) subscribed to that theory, inferring that emigration was to less suitable range where mortality was higher.

6.7. **Combinations of factors**

Except for several cases where harvest has exceeded increment of yearlings and insular declines caused by inaccessibility of forage in winter, all other declines were attributed to combinations of hunting, predation, and unusual weather.

Bergerud (1974) argued that most or all declines in caribou populations around the turn of the century could be attributed to over-harvest and increased predation. There are many documented cases of over harvest but the increased-predation hypothesis must be examined more closely. Bergerud (1974) attributed a monotocous (one ovum) reproductive trait to evolutionary pressures from predators. An equally plausible argument for evolution of one offspring is energy limitations in a sometimes severe environment. Bergerud (1974) attributed high mortality in calves largely to wolf predation. But crucial to his arguments are data to show increased populations of wolves. The only supporting evidence is on southern fringes of woodland caribou ranges in British Columbia and southern Ontario. Bergerud (1974) introduces a third factor, parasites, as possibly contributing to declines where white-tailed deer invade the range of woodland caribou. Major declines in large barren-ground caribou populations cannot be explained by Bergerud's hypothesis. There are no data to support his argument for an increase in rate of predation on these populations. If rate of predation increased simply because fewer caribou are available to a fixed number of wolves, then over-hunting is the proximate cause.

Bergerud (1974) uses the term "range destruction" in his third hypothesis, attributed to Cringan (1957), and limits his comments to destruction of lichen by fire. He dismisses climatic extremes and climatic changes, which result in forage restrictions and lowered energy regimes. Marginal energy could result in the evolution of characteristics of caribou that Bergerud (1974) believes were adaptations to predators, namely single births and poor calf survival. Quantitatively it would be manifested in poor growth rates, and slow attainment of puberty, as noted in many barren-ground caribou populations.

There is no reason to implicate only one, two, or even three factors in declines of caribou populations. Climatic factors cause declines in insular populations (Parker et al. 1975, Miller et al.1975, Thomas et al. 1976). Chance snow storms during calving can wipe out a significant proportion of calves. Slight changes in climate could cause significant mortality in calves and adults through insect harassment. Reindeer can expand beyond carrying capacity of their ranges in the absence of predators and over-harvesting (Klein 1967). Certain components of range may be over-utilized e.g. bare patches of high ground along spring migratory routes, resulting in energy restrictions, which may influence survival of young and retard growth and puberty. Such changes are subtle and may go undetected.

Hunters with modern rifles can easily kill more individuals than a population can tolerate. Some hunting and trapping habits can provide an easy source of meat for wolves, e.g. wounded animals, meat caches, and caribou meat used to bait traps.

My view is that multiple factors are involved in population declines of barren-ground caribou that utilize taiga in winter. Unfavourable natural factors, over a period of years, largely climatic dependent or related, could cause population fluctuations in the absence of humans. Heavy hunting pressure coinciding with such periods probably results in population declines periodically observed in caribou populations. Once at a low level, recovery of populations is a slow process unless conditions are optimum, a likelihood of low probability.

7. STATUS OF WINTER RANGE

7.1. **The concept of carrying capacity**

The concept of carrying capacity implies that food or some other environmental factor limits the size of populations. Forage or its availability is usually implicated as a factor limiting herbivore numbers. Definitions of carrying capacity require climatic qualifications, e.g. maximum number of individuals of a species that a given region can sustain indefinitely based on average climatic conditions of the recent past.

There is little evidence for or against the hypothesis that winter ranges, under average snow conditions, have limited number of barren-ground caribou in North America. The key term is *under average snow conditions* because abnormally deep snow can cause malnourishment in caribou, which affects production and survival of calves e.g. 1961-62 Beverly population (McEwan 1963, Scotter 1964). Evidence supporting that hypothesis include:

1. Caribou are low in fat reserves in spring (Dauphiné 1976). However, that state

may be normal -- a consequence of high energetic costs of obtaining low quality forage through snow and migrating long distances.

2. There is high mortality of calves in their first year, which possibly is linked to poor nutrition during development and prenatal growth.
3. Growth in the first 2-3 years of life is slow or may stop during winter, e.g., Kaminuriak herd in 1967-68 (Dauphiné 1976).
4. Attainment of sexual maturity is slow e.g. Kaminuriak herd (Dauphiné 1976).

   The key question is whether the above characteristics are normal and, if not, do they indicate abnormally high "environmental resistance" in winter ranges.

Evidence contrary to the hypothesis that winter ranges have limited caribou populations in North America (Bergerud 1974) include the following:

1. Reports of starved barren-ground caribou are rare. Scotter (1964) received a report from a trapper of sick and aborting caribou in the Beverly population late in the severe winter of 1961-62. However, caribou can move to areas where food is available and deep snow places them in range of arboreal lichens, a reserve food supply. Furthermore, wolves may remove malnourished individuals.
2. Pregnancy rates in adult females remain at 80-90% every year (Kelsall 1968) in spite of varying conditions on winter range. That argument (Bergerud 1974) is contrary to numerous studies in ungulates which indicate that fertility declines in malnourished females. However, rapid recovery of fat reserves on summer range could result in a high conception rate in October.

7.2. **Estimating carrying capacity**

Several problems confound predicting average carrying capacity:

1. Climates is highly variable and averages may have little meaning outside sample periods. In fact, occasional climatic extremes may be more significant. Do we ignore them when estimating carrying capacity? A "long-term" climatic average of 20-40 years is extremely short term in the evolutionary history of caribou. According to some climatologists we have passed through a period of relative climatic stability and entered, about 1968, a period of instability of unknown consequence to carrying

capacities of caribou ranges. For example, Klein and White (1978) found that for some meteorological stations in reindeer winter habitat in Alaska, annual precipitation between 1901 and 1930 was twice that between 1931 and 1960. One consequence was marked differences in lichen growth rates and, hence, on winter range carrying capacity.

2. The habitat is not static. Caribou winter range in the taiga is a mosaic of various successional stages, some being long term gradual changes but most are a result of climatic related individual disturbances: fire, wind, disease, frost action etc.

There appear to be two methods of estimating range carrying capacities.

1. Empirical or trial and error.
2. Range studies combined with physiological and energetics data.

The first method is used to determine carrying capacities of cattle range-lands. Once that approximate stocking rates are established for a region, ranchers can use them as a guide for their operation. Excess stocking rates leads to obvious signs of overuse such as shortness of grass, growth of weeds, and heavy browsing of shrubs and trees. Similarly, our best information on average long-term carrying capacity of caribou ranges in Canada are based on past numbers and densities and not on any range studies. Present population estimates and past history suggests that ranges of the six major populations (Porcupine, Bluenose, Bathurst, Beverly, Kaminuriak, and George River) on the mainland of Canada can each support at least 200 000-400 000 caribou under average past climatic conditions (Table 1). The ranges may support two or three times those numbers because estimates may be low by that much. The range of the Kaminuriak population may support the lowest densities because of deeper winter snow and retarded plant phenology and succession attributed to the cooling effect of Hudson Bay. Conversely, portions of that herd usually winter on tundra and fire cycles appeared to be long before 1973.

Calef (1974) suggested then-current densities of *ca.* 0.4/km² (1/mi²) for the entire ranges of caribou in Tamyr (Russia), Alaska, and central Canada were "unusual" and that higher densities may be periodic eruptions (Table 2). Skoog (1968) postulated that the Alaskan population fluctuated around a mean of 600 000, i.e., 0.6/km² using Hemming's (1975) value of 41 927 km² as the total range in Alaska. These values are considerably lower than carrying capacities given by various authors for caribou and reindeer.

A second method of estimating carrying capacity is through range and animal studies. A labourious method is to determine standing crop and productivity of range. Mapping of range types is obviously necessary. Calculation can be made assuming complete availability and then correction factors are applied for inaccessibility because of snow or ice, for units not used by caribou, and for trampled vegetation. The ratio of annual growth of lichens to biomass is poorly understood, as is effect of annual or periodic use of lichens by caribou.

For example, Parker (1975) calculated winter carrying capacity of Southampton Island for caribou by assuming that (1) lichens were the staple winter forage, (2) 5 kg of dried forage/caribou/day was required, (3) half of the lichens were available in winter, (4) the lichens could withstand an annual grazing of 11% of standing crop.

More-sophisticated models will be developed when diets are known, digestibility and chemistry of each forage species are known, winter energetics of caribou can be estimated, and effect of snow on accessibility and energetics can be estimated from more data. Glaring data gaps at present are the digestibility and turn over time of forage species utilized on winter range and nutritional physiology (Nieminen 1980).

7.3. **The relationship between carrying capacity and burn incidence**

Carrying capacity is maximal in a given region at a certain optimum annual rate of burning of winter range. A trap that many biologists have fallen into when reviewing effect of fire on winter range of caribou is to omit all shades of grey, i.e., fire is detrimental to range or it is not. Obviously a key point is the rate at which the entire range or important components of it are burned. There is ample evidence that too-high a rate is detrimental. Some authors suggest that old stands are less productive than mature ones, because of closing canopies, lichen senescence, higher cover of mosses, growth of muskeg, and fewer shrubs, monocotyledons, and forbs (Scotter 1971a, Kershaw et al. 1975, Miller 1980). Perhaps a mix of ages from young to old provides a diverse range of forage species, which provide a wider array of nutrients than just old-aged stands.

We do not know what the average optimum rate of burning is, recognizing that it will vary as to range type and geographic location and according to future winter climates. The optimum age of upland forests for forage production would seem to lie in the 60-150 year range. The optimum rate will depend on the shape of the generalized forage production/age curve. For example if the curve fits a normal distribution with maximum annual yield of forage at 100 years, an annual burn rate of *ca.* 0.75% of the surface would be optimum. The curve appears to be skewed to the right which advances optimal fire return interval to 100-200 years and lowers the optimum rate of burning to perhaps 0.5% per year.

Davis et al. (1978), who calculated carrying capacity of a caribou range in Alaska strictly on lichen productivity, assumed the curve for lichen productivity in the first 100 years (post-fire) was linear. At a burn rate of 1%/year, he calculated that half the potential lichen production was available to caribou at any given time.

> "*From the standpoint of caribou management it appears that lichen recovery within 50 years after a fire is sufficient to allow caribou use. This suggests that a 50-year fire "rotation period" would not result in a reduced carrying capacity*" (Davis et al. 1978:37).

In other words, 2% of land surface could be burned annually and still there would be range adequate for the needs of caribou. This conclusion seems to be at odds with data for winter ranges in Canada (Kelsall 1960, Scotter 1971a, Miller 1980).

Of course, optimum rate of burning will vary geographically with climate and among lichen species and cover types. We do not have sufficient data on forage production and availability with time (post fire) to predict optimal rates but I suspect that the value lies between 0.3 and 0.5% annually.

8. DISCUSSION

In evaluating the effect of fire on forested winter ranges in north-central Canada, the key questions appear to be as follows:

1) What is the long term rate of burning?
2) Is there adequate winter range for the current population?
3) At present areal rate of burning, what population level can the range support?
4) What rate of burning is optimal to yield optimum winter habitat for caribou?

1. What is the long-term rate of burning?

The percent of land (non-water) surface burned annually in an area covered by the Whiskey Jack map sheet in northwestern Manitoba was 0.16% from 1956 to 1967 (Miller 1976b) and 2.67% from 1973 to 1976 on a larger area (Robertson 1977). Weighted mean burn rate for all 16 years was 0.79%. That value still may not be a good approximation of the long-term burn rate because the 1973 season was so atypical. The long term rate is, therefore, probably lower. Support for that contention is obtained by looking at burn rates in areas that are expected to have higher rates because of a drier summer climate and more frequent thunderstorms, e.g. northern Saskatchewan and the "caribou range" in the NWT between Great Slave and Great Bear lakes. The mean annual burn rate on areas north and east of Stony Rapids, 1956-71, was 0.69% of non-water surface (Miller 1976b). In a larger area of the Stony Rapids region, the annual burn rate, 1945-59 (note overlap in years), on land surface was *ca*. 0.83% (Table 32); 0.56% for the period 1930-44, adjusted to 0.63% to account for a 12% re-burn rate in that class. On "caribou range", 1966-73, mean rate for total area was 0.91% (Rowe et al. 1975), equivalent to an annual rate of *ca.* 1.09% of land (less water) surface assuming 20% water. Corresponding values for an area north of Yellowknife, 1968-73, were 0.89% and 1.07% (Rowe et al. 1975).

2. Is there adequate winter range for the current population?

There are conflicting viewpoints on how many caribou were in the Kaminuriak herd in historical times. One supposition is that large numbers must have been present to provide sufficient meat for aboriginal people before introduction of repeating rifles. The first survey in 1948 (Banfield 1954) yielded an estimate of 120 000 but that value should be scaled upward in light of subsequent data. There is a tendency to underestimate numbers in caribou in aggregations by about 20% (Banfield et al. 1955; Kelsall 1968, Thomas 1969, Parker 1972a). An unknown proportion of caribou, specific to each survey, are missed. Percentage missed is extremely variable within one survey but it can approach 50%. When caribou are scattered as on the winter range, before the start of migration, the first source of error may be insignificant. However, a large correction factor must be applied to Banfield's (1954) data to account for missed animals because his transects often were 6.4-8.0 km wide. A modest correct factor of 20% (x l.25) brings his estimate to 150 000. Further, Banfield (1954) did not survey caribou of the Kaminuriak herd that winter on tundra and he may have missed segments in the forest. There is reason to believe that the population was 200 000-400 000 in 1948-49. Kill estimates in the late 1940s and early 1950s for the population or just for the Manitoba region were in the 20 000 to 30 000 range (Banfield 1954) and some estimates were higher (Robertson 1977). Harvest could not have exceeded 10% of the population (200 000-300 000), even with high (15-20%) recruitment, without causing a sharp decline in numbers. According to a 1955 population estimate of 149 000 (Loughrey 1955), no such decline occurred. Subsequent data suggests that the 149 000 estimate should be scaled upward to at least 160 000 (Adjustment 1, Thomas 1969) or more reasonably to 233 000 (Adjustment 1 and 2, Table 2), to certain portions of the data (Parker 1972a).

Evidence suggests that populations in both Alaska and Canada were high in numbers in the mid-1930s. In Alaska, a decline presumably set in about 1938 and continued through the 1940s (Davis 1978). In Canada, a decline may have started later, perhaps in the mid-1940's (Kelsall 1968). Based on an assumption that area of occupied range is directly related to numbers, Parker (1972a) suggested that the Kaminuriak population in 1948-50 was exceptionally numerous, which accounted for the range extension into southern Manitoba at that time (Robertson 1977). Parker

(1971) suggested that his estimate of the 1968 population (63 000) probably was near a historical level because caribou occupied the "normal range." Calef (pers. comm.) supported a hypothesis that caribou maintain approximately a constant density as numbers fluctuate. There are data that refute that hypothesis. In fact, there was a decrease in range utilized by the Beverly population from 1957 to 1976, although estimated numbers increased from 120 000 to 160 000 in that period. All that can be concluded is that there is a general tendency for range size to be related to population size but the relationship is not sufficiently precise to speculate on numbers or trends if range size is known.

Winter range in northern Manitoba probably was able to support upwards to 500 000 caribou in the past. There are no data to suggest that condition and health of caribou was impaired by overuse of range during the 1940s and early 1950s. A population of 40 000 would require only 20% of range needed by 200 000 caribou. There is no evidence that only 20% of winter range is available today compared with 1950. The 1973 fire season, when 9.8% of non-water land surface was burned (Robertson 1977), can be considered highly atypical and seven or eight such seasons would be necessary in one 10-30-year period to reduce the capacity of range by 80% relative to 1950.

In conclusion, winter range in northern Manitoba likely is capable of maintaining 200 000 to 500 000 caribou indefinitely at the average burn rate since 1956. Herd size has fluctuated but populations of barren-ground caribou probably were substantially higher than estimated to date. Harvest data, also underestimated, indicates that population size must have been much higher than estimated. Populations of the Beverly and Kaminuriak populations are unlikely to have fallen below 100 000 in the last 50 years.

3. At present rate of burning, what population can winter range support?

We can not estimate maximum carrying capacity for several reasons. We do not know if winter range ever becomes limiting in terms of quantity and quality of food. This would be difficult to assess by measuring and monitoring forage supplies.

Caribou can overuse parts of their range and other parts remain unused. Monitoring of over-winter condition probably is the best measure of winter range condition. Secondly, rates of burning over the last 20-40 years may not continue over the next few decades. Caribou use tundra range when snow conditions permit it but we do not know what affect this use has on tundra range or what it says about the state of winter range. Finally, we do not have a fire history of forested winter range. We do not know how much of the forested winter range is old enough to support caribou.

4. What rate of burning is optimal to yield optimum winter habitat for caribou? We do not know the answer to this question. It can not be estimated until we learn more about relative use of winter range by caribou at various time periods after fire. Theoretical estimates can be made if we know what constitutes winter diet and production of such forage at various successional periods after fire.

Still, we may not be able to do much about variability in areal extent of burning and generally should live within what nature provides. There is some scope for suppressing fire in important hunting areas around communities if little suitable range remains. On the other hand, use of snowmobiles and aircraft permits hunters to quickly range out to where caribou are located.

Management of fire for a single species in taiga and boreal forest is contrary to ecosystem management, where all species must be considered (Kelsall et al. 1977). Fire creates vegetation diversity, which results in a wide array of fauna. The only justification for fire suppression is to correct for human activities that have reduced the capacity of the natural system to sustain caribou. There would have to be a shortage of caribou or evidence of range degradation. In some years, there is a shortage of caribou in the vicinity of communities but the herds are sufficiently large to provide for community needs at a subsistence level. The influence of human activities on rate of burning is unknown.

9. CONCLUSIONS

1. The size of caribou herds are poorly known as numbers undoubtedly were underestimated by a factor of 1.5-4 and little can be said about trends except that numbers declined in the 1950s to about 1958 because recruitment was poor.

2. Locations of calving grounds are well known but location of wintering areas is only known in a general way from tag returns. Herd identity of some groups on the tundra in winter and in areas of overlap in the forest can only be guessed at.

3. Between the 1920s-1940s and 1970s, there was a progressive withdrawal by caribou from about 54-55°N latitude in Manitoba and Saskatchewan to about 59°N. Reasons for this retraction are speculative.

4. Succession of vegetation after fire is known in general terms but more needs to be known about changes of individual plant species, particularly in old stands. Does biomass of lichen species preferred by caribou decline in old forests?

5. More information is needed on relative use by caribou of various age classes and cover types.

6. Winter diet of caribou and forage digestibilities are known in general qualitative terms but little is known about requirements for specific nutrients including whether lack of protein in winter is a nutritional problem for caribou.

7. The rate at which the landscape has burned is only known for short periods of time in certain study areas and there is a need to determine areas burned in the past 40-50 years throughout winter range of caribou herds.

8. Knowledge of the relative importance of limiting factors (hunting, predation, malnutrition, and parasites/diseases) for caribou is poorly known as is information about sustained carrying capacity of winter and summer range.

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Appendix 1. Percent cover of plants in age classes after fire on drumlinoid ridges at Carleton Lake, NWT. (Data reworked from Kershaw et al. 1975).

Age of burn (yr)	3	12	23	32	47-52	67-70
Bare ground	91.4	43.4	1.8	4.0	4.8	2.1
Biatora granulosa		9.1	8.1	1.7	4.6	0.3
Cetraria islandica		0.1	0.2	2.6	3.7	2.5
Cetraria nivalis			0.5	33.6	4.1	8.9
Cladina alpestris		0.1	1.1	26.5	32.5	31.1
Cladonia uncialis	1.0		0.4	13.4	13.5	14.0
Cladonia amaurocrea			0.2	11.0	2.7	7.3
Cladonia botrytes		0.3	3.0	0.1		0.1
Cladonia coccifera		0.4	0.7	1.0	1.3	0.8
Cladonia cornuta		0.1	1.1	1.2	4.3	2.2
Cladonia crispata			0.3	0.9	4.0	4.5
Cladonia cristatella		2.2	1.4	0.1	0.3	
Cladonia gonecha			1.6	1.3	1.9	0.2
Cladonia gracilis			1.2	1.1	9.1	3.5
Cladonia macroptera		0.3	0.5	0.5	0.9	0.1
Cladonia subulata			0.4	0.1	0.3	
Stereocaulon paschale				3.6	0.7	20.8
Lecidea uliginosa		2.5	7.6	1.4	0.6	0.5
Ledum groenlandicum	0.7	1.4	4.5	1.0	3.7	
Vaccinium myrtiloides		2.4	1.0			
Vaccinium uliginosum	5.5	5.8	1.8	0.4	1.4	0.5
Vaccinium vitis-idaea	0.6	2.3	7.9	12.7	13.2	11.7
Carex leporina	0.2	1.7	0.1			
Polytrichum juniperinum		4.4	3.4	0.1	0.8	
Polytrichum piliferum		31.8	58.4	0.2	3.8	4.6

Appendix 2. Percent cover of plants at phases after fire on drumlinoid ridges at Carleton Lake, NWT. (Data summarized from Kershaw et al. 1975).

Phase ---->	1A	1	2	3
Age of burn ---->	3	12 & 23	32 - 49	52 - 70
Bare ground	91.4	8.7	4.0	3.8
Biatora granulosa		9.8	3.0	2.7
Cetraria islandica		0.2	3.3	2.9
Cetratia nivalis		0.4	14.1	7.7
Cladina alpestris		0.9	30.5	31.4
Cladonia uncialis	1.0	0.3	14.3	11.9
Cladonia amaurocrea		0.1	5.7	5.8
Cladonia botrytes		2.6	0.1	0.1
Cladonia coccifera		0.6	1.2	0.8
Cladonia cornuta		1.0	3.4	2.2
Cladonia crispata		0.2	3.3	3.6
Cladonia cristatella		1.5	0.2	0.1
Cladonia gonecha		1.3	1.8	0.5
Cladonia gracilis		1.0	5.4	7.5
Cladonia macroptera		0.4	0.8	0.2
Cladonia subulata		0.3	0.2	0.1
Stereocaulon paschale			1.7	16.7
Lecidea uliginosa		6.7	0.9	0.4
Ledum groenlandicum	0.7	3.9	3.0	0.1
Vaccinium myrtiloides		1.2	<0.1	
Vaccinium uliginosum	5.5	2.5	0.6	1.8
Vaccinium vitis-idaea	0.6	6.9	13.4	11.1
Carex leporina	0.2	0.4		
Polytrichum juniperinum		3.6	0.4	0.5
Polytrichum piliferum		54.2	1.1	8.1