

Other papers



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Lichens, wildfire, and caribou on the taiga ecosystem of northcentral Canada

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Abstract: Terrestrial lichens are unique organisms that are pioneers on bare sand and rock, survive desiccation and reproduce both sexually and asexually. They compete poorly with dense, aggressive vascular flora. Wildfires require organic matter as fuels, are the driving force in perpetuation of the Taiga Ecosystem in a heterogeneous environment and, if left alone, are self-controlling. Caribou wintering on the Taiga are dependent on: (1) a terricolous lichen forage supply for most of the winter, (2) a heterogeneous environment to cope with predators and the changing nival environment, and (3) natural wildfires to supply these needs. Wildfire control on the Taiga winter range is not recommended as a management tool for barren-ground caribou.

Key words: caribou management, forage use, forest fire, *Rangifer*, snow cover, winter range.

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Introduction

Science is a search for truth, but it certainly has been difficult to identify what is fact and what is fiction in the controversial subject of forest fires, lichens, and wintering barren-ground caribou on the taiga of northcentral Canada (see Viereck & Schandelmier, 1980). There was nothing wrong with the original suggestion that forest fires on the taiga may have contributed to a rapid decline of caribou populations in northcentral Canada in the middle of the twentieth century (Banfield, 1954), and it certainly was proper to assign a range ecologist to the job of studying the relationship of forest fires on the taiga and the effect on declining caribou populations (Scotter, 1964; 1965; 1970). When Scotter reported an increase of forest fires in the taiga during the middle of the present century compared with the previous century, and its influence on the preferred lichen forage supply of caribou (Scotter 1964; 1966), there appeared to be a plausible cause for the population decline. However, it was later reported that Scotter's hypothesis was incorrect because the method used to age forest stands on the taiga winter range of the Beverly caribou population was biased to recent forest fires (Johnson & Rowe, 1975). Johnson & Rowe reported that forest fires in the winter range of the Beverly caribou population were mostly caused by lightning

and had not increased in recent years as a result of human caused fires, as proposed by Scotter (1964). They concluded that the carrying capacity of this winter range of the Beverly caribou population was much the same as it had been for centuries.

The barren-ground caribou populations in Canada continued to decline through the 1950s and had not shown any improvement by the middle of the 1960s despite an intense and costly wolf control program and a much reduced annual harvest of caribou by northern residents. In order to find some answers to why these caribou populations weren't responding to management efforts an intensive research program was initiated in 1966 on the Kaminuriak caribou population (renamed in 1989 the Qamanirjuaq caribou population). Four separate biological studies were conducted simultaneously and cooperatively between 1966 to 1969 on this one caribou population that calves in the vicinity of Kaminuriak Lake, Northwest Territories and usually winters in the taiga of northwestern Manitoba, northeastern Saskatchewan and southern Northwest Territories (Miller & Robertson, 1967). One of these four studies was on the taiga winter range relationships which revealed that caribou utilized a wide variety of habitats and winter forages associated with the changing winter seasons and nival characteristics on the taiga of northcentral Canada (Miller,

1974). Formosov (1946) and Nazimovich (1955) had reported similar nival characteristics on the taiga in Russia. Miller (1976a) reported that wildfires on the taiga were essential to maintain a heterogeneous environment (mosaic of environments in Heinselman, 1973) in which caribou could find suitable forage and escape habitat during any nival conditions they may be subjected to on the taiga during winter.

At the conclusion of the Kaminuriak caribou population study, Miller was given the assignment by his employer, the Canadian Wildlife Service, to study the taiga winter range relationships of the adjacent Beverly caribou population with emphasis on the influence of wildfires. This paper includes both the second taiga winter range study, which was reported as a dissertation (Miller, 1976b) and summarized at the second International Reindeer/Caribou Symposium (Miller, 1980); and the initial study of the Kaminuriak caribou population (Miller, 1974; 1976a). Essentially the results of these two winter range studies agreed with extensive studies in Alaska of barren-ground caribou (Skoog, 1968) and in Newfoundland of woodland caribou (Bergerud, 1971; 1972) that wildfires in the taiga did not appear to influence these particular caribou populations.

During the mid and late 1970s there were a number of important papers published on the incidence of forest fires and on the existing terricolous fruticose lichen flora in the taiga and adjacent transition zone (between taiga and tundra) in North America (Rowe & Scotter, 1973; Viereck, 1973; Johnson & Rowe, 1975; Makinow & Kershaw, 1976; Kershaw, 1977; Johnson, 1979, and others). A review paper by Kelsall *et al.* (1977) on the effects of fire made particular reference to northern Canada, and one by Viereck & Schandelmeier (1980) in Alaska and adjacent Canada. Klein (1982) in a review paper entitled, "Fire, Lichens and Caribou," concluded that there were long term benefits from fire on the taiga and short term consequences. Bunnell *et al.* (1975) reported on a computer simulation study involving Canadian Wildlife Service caribou biologists who had studied or were studying barren-ground caribou populations in northcentral Canada. They concluded that an increase of forest fires by five times the normal 1 percent per annum would have "little effect on the population."

In 1979, however, a reported 1 1/4 million hectares were burned in the taiga and adjacent transition zone of northcentral Canada and the caribou

users requested forest fire control to protect the barren-ground caribou's winter range (Thomas *et al.*, 1996). As a response to this request another study was initiated on the taiga winter range of the Beverly caribou population in 1982-1986. As a result of this study a forest fire control program was proposed specifically for the taiga and transition area winter range of the Beverly and Qamanirjuag caribou populations (Thomas, 1994).

The scorching of the large acreage on the taiga and the transition zone winter range of the Beverly caribou Population, as reported in 1979, is not unusual for this area (Johnson & Rowe, 1975). In some summers, practically nothing is burned in this particular winter range area and the combination of these light burn years with the large burns of other years, like in 1979, average out to about one percent scorched annually (Wein & MacLean, 1983).

This paper attempts to show that these wildfires are an essential component in terrestrial lichen dominance of the ground cover in much of the taiga. Also using data collected in the 1960s and early 1970s on the taiga of northcentral Canada, it shows how wildfires vary between years, what portion of areas within the margin of the burned areas actually was ignited, and what role wildfires play in the perpetuation of terrestrial lichens. Finally, also using field observations in the 1960s and early 1970s during the various winter seasons barren-ground caribou inhabit the taiga, it will be shown how caribou utilized both the burned and unburned habitats feeding on terrestrial lichens, arboreal lichen and non-lichen forage supplies in response to a continuously changing nival environment. The paper attempts to show how a successful wildfire control program in the taiga of northcentral Canada, as proposed by Thomas (1994), would ultimately reduce rather than increase the carrying capacity for wintering barren-ground caribou. And finally the paper concludes with a proposal that caribou managers need to monitor the effects of human population increase and activities in the taiga that can seriously threaten wintering caribou. Wildfire may briefly change how caribou use the taiga but people and their activities will eventually determine what portion of the taiga will be available for winter use by caribou.

Lichen Ecology

Lichens are unique organisms that dominate the ground flora in much of the taiga, especially on xeric, sandy soils. Most of the uplands in the taiga

and transition zone of northcentral Canada is composed of a xeric, well-drained, pure sand mantel. (Ritchie, 1962; Argus, 1966) They are pioneer organisms that are in a symbiotic relationship between a fungal (mycobiont) and one or more algal (photobiont) components (Hale, Jr., 1967; Nash, 1996). The primary characteristic of lichens that permits them to dominate the ground flora in the taiga is that they can survive severe desiccation which destroys vascular flora and most other bryophytes.

Lichens dominate the ground flora in much of the taiga until an accumulation of organic matter with its moisture retention characteristics occurs on the surface of the sandy soils. This retention of water in the accumulated organic matter permits vascular plants to become established and thrive at the expense of the lichen flora.

Lichen woodland is what has often been referred to as the sparsely treed taiga stands on upland sites of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*), either alone or in combinations, with a dominant ground cover of lichens. These are the lichen woodlands in the taiga that are important caribou feeding sites, in mid-winter especially. However, these are not the only sites where lichens grow in dense mats. They grow on hummocks in the lowland muskegs and also grow on the slopes and tops of eskers, which are often sparsely treed by white birch (*Betula papyrifera*). These esker sites may be fed on all winter, but especially the south exposed slopes and open tops are utilized by foraging caribou in late winter and spring when the sun begins to melt snow on exposed sites (Miller, 1974). Bare patches also appear in the snow cover on wind-swept openings and in feeding craters, previously excavated by caribou. The north and east slopes are usually still unavailable for foraging at this time because of deep, drifted snow.

How do terricolous, fruticose lichens recover from disturbances like caribou cratering, foraging and trampling activity? Lichens are well adapted to this kind of caribou activity in the presence of a snow cover because of their characteristic of growing new podogia when fragmented or dislodged (see Webb, 1998). This is exceedingly important because it permits lichens to not only survive caribou feeding activity in winter, and man's foot steps when the lichens are dry and brittle in summer, but to become established on favorable substrate when transported by wind and water or by mammals, birds and insects.

Another characteristic about lichens that is of major importance to caribou-besides taste, nutrition and abundance - is the species or groups of species available for foraging. This involves the successional sequence following disturbance, such as wildfire. There are many wildlife biologists, ecologists and lichenologists who have reported on this subject, and many are good for areas studied. The best general description of the lichen flora in my opinion is by Ahti (1977), who has numerous publications on caribou range in North America (Ahti, 1959a; b; 1964; Ahti & Hepburn, 1967) and reindeer ranges in Scandinavia (Ahti, 1961a; b; Ahti *et al.*, 1968). Following is his general sequence of this lichen succession in the "Boreal Coniferous Zone" (Ahti, 1977) or taiga. (Ahti does not accept *Cladina* as a true genus and therefore uses *Cladonia*):

1. Bare soil stage, 1-3 years after fire.
2. Crustose lichen stage, 3-10 years after fire; *Lecidea oligotropa*, *L. uliginosa* and *L. granulosa* dominant.
3. Cup lichen stage, 10-30 (-50) years after fire; *Cladonia* subgen. *Cladonia* dominant (e.g. *C. cornuta* var. *cornuta*, *C. gracilis* var. *dilata*, *C. crispata*, *C. gonecha*)
4. First reindeer lichen stage, 30 (-50) -80 (-120) years after fire; *Cladonia mitis*, *C. arbuscula*, *C. rangiferina* and *C. uncialis* dominant.
5. Second reindeer lichen stage 80 (120) or more years after fire; *Cladonia stellaris* dominant.

Since I have included this lichen successional sequence verbatim from Ahti (1977, p. 165), I must also give his following statement:

"It should be noted that the timetable of this succession is greatly dependent upon the moisture regime and the climatic position of the stand, and different rates of succession may be encountered side by side (Jalas & Valpas, 1962)."

He also comments on "somewhat mesic lichen forests (recognized by a thicker humus layer)" that "there may be a stage of very dense, young forest, when lichens are temporarily in decline and even absent, although they appear again when the climax is approached." Ahti also states, in the same publication, that there is "...a *Stereocaulon paschale* stage in some continental areas, such as western Lapland (Ahti, 1961a) and northern Manitoba (Ritchie, 1959), but its ecological background is not well understood." This lichen species is discussed later under the heading of Caribou, Lichen and Non-lichen Forage Relationships.

Table 1. Area burned during a 16-year interval in northcentral Saskatchewan and during 12 years in northwestern Manitoba as determined from colored aerial photographs compared with previous panchromatic aerial photographs.

	Hectares land surface interpreted	Hectares burned	Years of aerial photography (# of years)	Annual burn (%)	Number of fires
Saskatchewan	575 687	63 411	1955 & 1972 (16)	0.7	41
Manitoba	982 701	19 230	1955 & 1967 (12)	0.2	47

The only other characteristic of lichens that I want to discuss here is their dominance of the ground flora as long as the moisture holding capacity of the substrate remains poor. When moisture holding organic material accumulates on the ground surface and within the lichen community - with time-leaf drop, decayed branch litter, wind blown debris, and animal droppings - other bryophytes and vascular plants begin to invade and expand. Lichens lose their competitive advantage when the moisture holding capacity increases and usually do not again gain dominance until a major disturbance such as fire (wild or otherwise).

Forest Fires on the Taiga

The taiga winter range of caribou in northcentral Canada has evolved in the presence of lightning-caused wildfires. Johnson & Rowe (1975) in a study of fire on the subarctic wintering ground of the Beverly caribou population reported that 87% of the fires were started by lightning and burned 99% of the total area burned. They reported that the recent burn rate of about 1.0% annually (fire rotation period of 110 years) is similar to historical times, and that fire is necessary to maintain this fire-dependent ecosystem. Viereck (1973) had reported the same reason for a vegetation mosaic in the taiga of Alaska as resulting primarily from past wildfires in the taiga of Alaska, more populated than northcentral Canada. Viereck commented on a 30 year period of fires from 1940-1969 that less than 30% were caused by lightning, but 78% of the acreage burned were from lightning fires. Both Johnson &

Rowe (1975) and Viereck (1973) commented on the major acreage burned in the taiga as a result of a few large fire years that occur only occasionally over a span of low to moderate burn years.

In order to determine the actual area burned in a sample area of the taiga winter range of the Kaminuriak caribou population in northwestern Manitoba I had an area of 12 106 km² commercially photographed in 1967 with color positive film (Miller, 1976a). These colored aerial photographs were interpreted as stereo-pairs and compared with available black and white stereo-pairs photographed in 1955 (Table 1, from Miller, 1976b). A total of 19 230 hectares had burned in the 982 701 hectares, of land surface only, during the 12 year interval. The annual burn rate was slightly over 0.2%. This 12 year interval appeared to have covered a span of low fire years.

In a separate study of the taiga winter range, of the Beverly caribou population in northcentral Saskatchewan, I had a 7202 km² area commercially photographed in color and the stereo pairs were again interpreted and compared with the available 1955 black and white stereo pairs (Miller & Barnhard, 1973). The taiga in northcentral Saskatchewan included more upland portions compared with northwestern Manitoba (Table 2) and 63 411 hectares of the total land surface of 575 687 hectares had burned during the 16 year interval for an annual burn rate of 0.7 percent (Table 1). This burn rate, which only involves the land surface of the area photographed, agrees more closely to the burn rate of about 1.0 percent annually reported by

Table 2. Proportions of burns on uplands and lowlands relative to occurrence of these landforms in northcentral Saskatchewan and northwestern Manitoba as measured on colored aerial photographs.

	Uplands		Lowlands	
	Land surface %	Burned %	Land surface %	Burned %
Saskatchewan	80	78	20	22
Manitoba	55	67	45	33

Table 3. General caribou behavior and forage use relationships correlated with periodic changes in the snow cover on taiga ranges.

Season	Snow Condition	Movement*	Social behavior when foraging	Forage sites most used	Forage groups most utilized
Early winter	Shallow and soft, < 50 cm	M	Scattered in small bands, members (other than doe-fawn pairs) independent	River and lake shores Open canopy	Sedges, horsetails, lichens and shrubs
Mid-winter	Deep and soft, > 50 cm	M or S	Medium-sized bands, members dependent	Open conifer canopy close to treeless areas	Terrestrial lichens and evergreen shrubs
Late-winter	(a) Deep, sun crust	S	Large bands, members dependent	Open and closed conifer canopy close to treeless areas	Arboreal lichens and deciduous shrubs
	(b) Depth diminishing, alternate crust and no crust condition	S	Medium-sized bands, members dependent	Open canopy close to treeless areas	Terrestrial lichens and evergreen shrubs
Spring	Appearance of bare patches	M	Scattered in small bands, members independent	Open canopy on southern exposures	Terrestrial lichens and evergreen shrubs

* M=Mobile, bands migrating; S=Sedentary, bands not migrating.

that covered 38 404 hectares, included about 75% of the land area bounded by the periphery of the burn (Miller, 1980) and probably included some smaller areas that had burned between 1955 and 1972. This means that about 9601 hectares of land area within this 1970 burn remained as unburned islands (occlusions) within the periphery of the burn. These occlusions, which are a ready seed source for vegetation of the burned area and feeding sites of wintering caribou, are often included in the reported total area of the burn along with the water surface area when the periphery of the burn is used to calculate size of the burned area. In addition there is usually no distinction made in forest fire reports between upland and lowland areas burned. Lowland muskegs (bogs) and meadows (fens) often burn very superficially and are revegetated rapidly. The new growth of grass-like plants, forbs and shrubs on these burned sites is more nutritious forage, for a few years post fire, than the same forage plants on unburned sites. The favored mushroom forage of wintering caribou are also likely to be more abundant on recently burned than on unburned sites.

Caribou and Their Taiga Winter Range

The barren-ground caribou of northcentral Canada usually arrive on their taiga winter range in November or December and leave in late March or April (Kelsall, 1968). There is a complete snow cover on the taiga when they arrive and, except for portions of south-exposed banks and wind-swept esker and moraine ridge tops, there is a snow cover on their departure. During the early winter migration the caribou movements are not hindered by snow, they generally migrate over frozen lakes and rivers and freely move over treed and treeless terrain. As the snow depth reaches 50 centimeters (20 inches) in mid-winter the caribou mobility is restricted by snow (LaPerriere & Lent, 1977) and they travel more in single file when traveling inland from resting sites on frozen lakes and rivers to forage or move between lakes and rivers. Caribou forage in mid-winter close to their resting sites. As snow depths increase and drifts become deeper and more compact along lake and river shores caribou become more vulnerable to predation (Miller, 1975).

A sun crust forms in late winter, even in the major feeding sites of lichen woodlands, and caribou

forage on deciduous trees and shrubs and arboreal lichens above the snow cover as forage beneath the snow becomes unavailable (Table 3 from Miller, 1974: 753). Gradually, solar radiation during sunny days begins to expose bare ground, and forage plants on open south-facing banks, and windswept ridge tops as well as beneath the boles of exposed conifer trees. Caribou increasingly forage at these sites each sunny day. As the snow cover decreases and surface snow crusts soften with each sunny day, caribou start their migration from the taiga for their tundra calving grounds.

Caribou-Wildfire Interrelationships

Caribou use of recently burned sites differs from pre-burn use in response to changes in forage potential, cover and snow characteristics. During early winter, caribou migrate across these sites single file. In mid-winter, during deep, soft snow conditions, relatively sedentary bands use burns as treeless escape cover and as access to forage in adjacent unburned stands, probably in response to wolf harassment (Miller, 1975). It was apparent during my field work that unburned islands within burns also attract caribou as feeding sites in mid-winter and occasionally caribou feed in recent burns. Use of burned sites increases with time and vegetative recovery as these sites become more useful as food sources. The rate at which terricolous lichens recover on burned sites varies according to many factors, such as severity of the burn, site characteristics, and weather, but generally good lichen standing crops appear in 30 to 40 years after the burn. Scotter (1968) showed that the appearance of usable stands of lichen standing crops was greatest between 31 to 50 years on his four taiga study areas in northcentral Canada. Bergerud (1971) reported that grazed lichen stands in Newfoundland were usually in stands 25 to 80 years after fire. I found that caribou had fed intensively on lichens in stands aged 35 to 166 years in northwestern Manitoba and northeastern Saskatchewan and 46 to 148 years in northcentral Saskatchewan (Miller, 1976a; b).

Caribou forage primarily on terricolous lichens on taiga winter ranges in northcentral Canada consuming living and dead portions of podetia, both primary and secondary thalli of certain species, fruticose and foliose forms, and climax and sub-climax species. Large standing crop reserves of lichens are found on the taiga range of northwestern Manitoba and caribou damage to these reserves during a single winter are light (Miller, 1976a). Caribou and

reindeer damage to terricolous lichen forage supplies occurs primarily through the action of trampling and pawing (Skoog, 1968; Pegau, 1968). Use of different portions of the taiga during a single winter (Miller, 1974) and between winters (Kelsall, 1968; Skoog, 1968) results in a form of natural rotation. Since light cropping of lichen pastures does not maintain lichen productivity (Skuncke, 1969), a fairly high stocking rate of caribou is desirable. Changes of snow depth, hardness and density (Pruitt, 1959), along with fluctuating ambient temperatures and wind velocities, help to disperse caribou over much of the taiga range within and between most winters. Even with high caribou stocking rates, it is unlikely that terricolous lichens could continue to dominate upland treed ranges without periodic disturbance by wildfires.

Under the present rate of wildfire occurrence, there is no justification for fire prevention and control for the expressed purpose of caribou management. *Cladonia mitis*, probably the most important single lichen species utilized by caribou on the taiga of northcentral Canada, (Thomas *et al.*, 1996) is especially fire dependent (Ahti, 1959a).

Caribou, Lichen and Non-lichen Forage Relationships

Food habit studies of cratered sites, individual craters and analyses of rumens collected during early, mid and late winter (Miller, 1976a) had shown that terrestrial lichens are an important forage of caribou on the taiga winter range, but lichens are by no means the only source of forage. Caribou can thrive without a winter forage supply of lichens according to reports in Alaska (Palmer, 1926; Murie, 1935; Skoog, 1968) and wild reindeer in Russia (Syroechkovskii, 1986). The use of non-lichen forage probably increases the digestibility of lichens (Scotter, 1964). Lichens alone have been listed repeatedly to be an insufficient forage to sustain caribou and reindeer for long periods of time (Druri, 1960; Ahti & Hepburn, 1967) although under protected conditions reindeer have been reported to do well on lichens alone (Palmer, 1926; Poijärvi, 1945). However, if for no other reason than abundance and availability, terrestrial lichens were the most predominant single source of forage utilized during the winter by both the Kaminuriak and Beverly caribou populations in northcentral Canada (Miller, 1976a; b). Thomas & Hervieux (1996) also reported terricolous lichens to be the most important forage item of wintering barren-ground caribou from their rumen and crater samples collected

during March in Northwest Territories and adjacent Saskatchewan. Russel *et al.* (1993) reported that terrestrial fruticose lichens also predominated in the winter diet of the Porcupine caribou herd in Canada.

Lichens of the *Cladina* group made up the bulk of the winter rumen contents and were also the most abundant found in the taiga winter range (Miller, 1976a; b). *C. mitis* and *C. stellaris* were the most abundant species in this branched group found at the study plots in northwestern Manitoba. Of the two species, *C. mitis* appears to be the most important as caribou forage (Scotter, 1965; Thomas *et al.*, 1996). Ahti (1959b) found this species in Newfoundland to be "a most abundant species owing to its rapid regeneration" and he believed it "to be the most important food-lichen of the caribou". *C. stellaris* on the other hand, is considered questionable as a preferred reindeer forage in Scandinavia and northwestern Manitoba (Scotter, 1965) while in certain areas of Russia (Kareev, 1968) it is "reindeer's main lichen fodder during winter".

There is a suggestion that *Stereocaulon* is a preferred caribou forage next to the *Cladina* branched group on the basis of its abundance in the winter rumen samples and low occurrence on the taiga winter range. Although there is a possible bias in the rumen sample analysis data, in so far as *Stereocaulon* is easily recognized, the crater observations in April at Hara Lake, Saskatchewan, support the idea that it is an important late winter forage (Miller, 1976a). *Stereocaulon* recovers rapidly from caribou utilization or mechanical disturbance at favorable sites. This lichen has a much higher protein content than *Cladonia* and *Cladina*. Kareev (1968) states that *Stereocaulon paschale* in Russia "is considered as a good fodder for young animals and, in certain cases, included among the fattening varieties of fodder plants".

The manner in which the terrestrial lichen forage is utilized by caribou is extremely important. Some investigators (Andreev, 1954; Scotter, 1964; Skoog, 1968; Pegau, 1968) suggest that the living portions of terrestrial lichens are nipped off by caribou and that the recovery from this utilization depends on the percent of the lichen tips removed. My observations do not agree with this (Miller, 1976a). During the early and mid-winter periods the entire lichen podetium, with the exception of the jelly-like layer, is plucked from the lichen community and ingested. This method of feeding on terrestrial lichens by

caribou was observed at craters and was supported by rumen analysis findings. The dead portion of the lichen podetium and particularly the black portion of *C. rangiferina* is common in the rumens. Even the primary thallus, which is the portion of the lichen that is attached to the substrate, is common in the winter rumens. By utilizing the dead portion of the lichen podetium, as well as the living portion, the potential caribou lichen forage supply would increase by 100% (Scotter, 1963). During the latter part of the late winter period, however, caribou crop the top portions of lichens that are no longer protected by a snow cover and each night the exposed lichens become frozen to the substrate. Foraging at the snow free sites during early morning of sunny days permits caribou to remove the supple upper portions of lichen communities.

Arboreal lichens are also an important source of winter forage in the taiga winter range. In fact, in periods of extremely hard snow conditions during the early stages of the late winter period arboreal lichens may be very important. A number of investigators have reported that arboreal lichens are an important forage for caribou (Hustich, 1951; Banfield, 1954; Cringan, 1957; Scotter, 1971). Besides being more nutritious than the *Cladina* terrestrial lichens the arboreal lichens no doubt help to retain a balanced rumen environment for the microorganisms during the period when terrestrial lichens are inaccessible. Scotter (1965) found arboreal lichens to be relatively abundant in the taiga winter range of northwestern Manitoba.

Grass-like plants are the major non-lichen forage utilized in the taiga winter range during the early winter period and are utilized during the late winter and spring as snow depths decrease. *Carex aquatilis* and *Equisetum fluviatile* are the primary grass-like plants utilized in northwestern Manitoba (Miller, 1974). *C. aquatilis* is the most abundant sedge in the "marshlands" of the area (Baldwin, 1953). This plant provides the richest reserves of "undersnow" green vegetation for reindeer in parts of Russia (Kareev, 1968) and is also considered especially important to caribou in Alaska (Skoog, 1968). *Equisetum* was reported as heavily utilized by wintering caribou at a site in northern Manitoba by Loughrey (1952), it is considered as heavily utilized in Alaska at all times of the year (Skoog, 1968) and as a good winter forage in parts of Russia (Aleksandrova & Andreev, 1964) where it is eaten when green as well as brown (Kareev, 1968). Russell *et al.* (1993) also reported caribou use of

horsetails in certain habitats of wintering Porcupine caribou in Canada. Concerning the nutritious substances in *Equisetum* Aleksandrova & Andreev (1964) stated that "The ash is very rich in calcium, potassium, phosphorus and other elements of mineral nutrition". Baldwin (1953) listed *E. fluviatile* "as common and abundant on alluvium of the Cochrane River and silted bays of the larger lakes" in northwestern Manitoba.

In mid-winter and more often in late winter the major non-lichen forage items include evergreen leaves and deciduous stems. The leaves of *Vaccinium vitis-idaea* are the most utilized although large amounts of *V. myrtelloides*, *V. uliginosum* and *Ledum* spp. are also consumed. Scotter (1965) observed that the leaves were stripped from *V. vitis-idaea* in northern Saskatchewan and he thought that this may be an important source of protein in that caribou winter range. Skuncke (1963) attaches high significance to this plant as a winter forage for reindeer. Baldwin (1953) found *V. vitis-idaea* as one of the most common plants in the area he examined in northwestern Manitoba. Argus (1966) reported this plant as abundant in the area he studied in northeastern Saskatchewan. Kelsall (1960) believed that *Ledum groenlandicum* was actively sought by barren-ground caribou and Simkin (1965) reported that *L. groenlandicum* leaves were the most heavily used of the vascular plants in cratets dug by woodland caribou in Ontario. This plant is considered as "ubiquitous" in the taiga winter range by Scotter (1964; 1965) although I found that it was uncommon on well-drained, sandy soils with little or no humus layer.

Deciduous stems make up a large portion of the non-lichen material found in rumens although differential digestion rates exaggerate the abundance of this forage (Bergerud & Russell, 1964). White birch and willow are browsed occasionally all winter but especially during the period in late winter when a hard snow crust covers much of the inhabited range. Stems of *Salix* and *Betula* are listed as winter forage stems for caribou (Skoog, 1968) and reindeer (Herre, 1956; Andreev, 1954). Simkin (1965) listed that *Salix* sp. and *Alnus crispa* are utilized by woodland caribou in Ontario.

Mushrooms are another non-lichen winter forage which may be important in years of abundance. Entire, small mushrooms have been found in April caribou rumens and up to 10% of the contents in November rumens have been comprised of mushrooms (Miller, 1976a). Kareev (1968) states that

reindeer in Russia "unerringly detect and dig out the snow covered shrunken and frozen mushrooms". He listed mushrooms as a valuable, nutritive and vitamin-rich fodder. Although mushrooms are not consumed by caribou in large quantities during the winter their high nutritional value (Larin, 1951) may be a very valuable supplement to a predominantly protein scarce, terrestrial lichen diet.

Discussion

I have attempted to show a relationship between wildfires and terrestrial lichen communities in the taiga ecosystem of northcentral Canada and how wintering barren-ground caribou benefit from each. It seemed from my data and observations that attempt to suppress wildfires on this taiga winter range as a caribou management tool (Thomas, 1994) was unwise. However, Thomas and BQCMB (1996: 345) explained "There is no justification for fire suppression based on the natural ecosystem, fire suppression capabilities, or caribou conservation," and that this proposed fire suppression model was "based strictly on the food and socio-economic requirements of local communities." This would appear to be a risky approach since Kelsall (1968) emphasized hunting mortality as the cause for the decline of barren-ground caribou in the middle of the present century, especially since the populations of indigenous people (caribou users) are increasing and expanding (Thomas, 1994). Perhaps a more long range approach would be to encompass the entire ecosystem instead of attempting to maximize a single species.

Although the vegetative environment on the taiga of northcentral Canada is relatively unchanged from what it has been for centuries there are indications that wintering caribou are being restricted from utilizing large portions of their former winter range by expanding human populations and activities in the taiga. In northern Manitoba, in particular, there has been a considerable amount of human activity since the late 1950s. Two modern mining communities have emerged, in the more southern portion of the caribou's former winter range at Lynn Lake and Thompson. In the more northern part of Manitoba, in the core area of the caribou's early winter migration, two settlements of indigenous people have appeared prior to 1982 at Lac Brochet and Tadoule Lake. The populations in the "user communities are doubling in 16-20 years" (Thomas, 1994) within the entire range of these barren-ground cari-

bou populations. The influence of these human communities and activities in northern Manitoba, located in the path of early wintering caribou herd movements, may influence where these caribou spend the major portion of the winter.

Large wintering caribou populations require large units of uninterrupted range. Ordinarily these herds are on the move all winter and they are not known to utilize the same taiga range in successive winters. Some portions of the taiga are used infrequently, but this does not mean these ranges are less important to the population than more frequently used areas. In an excellent publication on "Sensitive Habitats of the Porcupine caribou herd" (IPCB, 1993), the criteria used to assess the sensitive habitats was based on frequency of use. Therefore, this aspect of identifying critical, but little used habitats was not discussed. During unusual weather conditions, as occurred in the interior of Alaska in 1992 (Valkenberg *et al.*, 1996) two caribou populations wintered outside their normal range in black spruce north of Fairbanks. These occasionally-used portions of winter range may be essential to caribou populations.

The future challenge to caribou management and wildlife biologists is not how to increase the sustained yield of caribou (Thomas, 1994) or to favor optimal use of the range by caribou (Klein, 1982), but to identify and minimize the spatial conflicts between human and caribou populations. We need to recognize if and how caribou movements are being deflected and how best to harmonize human and caribou spatial needs within both the caribou's winter and summer ranges. A start in this direction is to read and digest Harrington (1996), who wrote about the human impacts on the George River caribou population. I would suggest, however, that Harrington's subsistence hunting comments need to be adjusted for taiga residents of northcentral Canada where communication, transportation and meat storage conditions have improved to both favor and encourage subsistence hunting. This means that some of Harrington's comments on commercial hunting need to be applied to existing conditions in northcentral Canada instead of his conclusion about subsistence hunting. Hopefully with a long term perspective and recognition of these dangers, caribou can be maintained both as a national resource and to meet the various needs of the resident indigenous people.

References

- Ahti, T. 1959a. Macrolichens and their zonal distribution in boreal and arctic Ontario, Canada. – *Ann. Bot. Fennici* 1 (1): 1–35.
- Ahti, T. 1959b. Studies on the caribou lichen stands of Newfoundland. – *Annals Bot. Soc. Zool.-Bot. Fenn. Vanamo* 30 (4): 1–44.
- Ahti, T. 1961a. Open boreal woodland subzone and its relation to reindeer husbandry. – *Arch. Soc. Zool.-Bot. Fenn. Vanamo* 16 (suppl.): 91–93.
- Ahti, T. 1961b. Taxonomic studies on reindeer lichens (*Cladonia* subgenus *Cladina*) – *Annls. Bot. Soc. Zool. – Bot. Fenn. Vanamo* 32 (1): 1–160.
- Ahti, T. 1964. Macrolichens and their zonal distribution in boreal and arctic Ontario Canada. – *Annals Bot. Fenn.* 1: 1–35.
- Ahti, T. 1977. Lichens of the Boreal Coniferous Zone. – *In: Seaward, M. R. D. (ed.). Lichen Ecology.* Academic Press. New York, pp. 145–181.
- Ahti, T., Hamer-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. – *Ann. Bot. Fenn.* 5: 169–211.
- Ahti, T. & Hepburn, R. L. 1967. Preliminary studies on woodland caribou range, especially on lichen stands, in Ontario. – *Ont. Dept. Lands Forests Res. Rep. (Wildl.)* 74: 1–134.
- Aleksandrova, V. D. & Andreev, V. N. 1964. *Forage characteristics of the plants in the far north of the USSR.* Izdatel'stvo Nanka. Can. Wildl. Serv. transl.
- Andreev, V. N. 1954. The growth of forage lichens and the methods for their regulation. – *Geobotanika* 9: 11–74.
- Argus, G. W. 1966. Botanical investigations in north-eastern Saskatchewan: the subarctic Patterson-Hasbala Lakes region. – *Can. F. Nat.* 80: 119–143.
- Baldwin, W. K. W. 1953. Botanical investigations in the Reindeer-Nueltin lakes area, Manitoba. – *Nat. Mus. Can. Bull.* 128: 110–142.
- Banfield, A. W. F. 1954. Preliminary investigation of the barren-ground caribou. Part 1 and 2. – *Can. Wildl. Serv. Wildl. Manage. Bull. Ser. 1.*
- Bergerud, A. T. 1971. Abundance of forage on the winter range of Newfoundland caribou. – *Can. Field Nat.* 85: 39–52.
- Bergerud, A. T. 1972. Food habits of Newfoundland caribou. – *J. Wildl. Manage.* 38: 757–770.
- Bergerud, A. T. 1974. Decline of caribou in North America following settlement. – *J. Wildl. Manage.* 38: 757–770.
- Bergerud, A. T. & Russell, L. 1964. Evaluation of rumen food analysis for Newfoundland caribou. – *J. Wildl. Mgmt.* 24 (4): 809–814.
- Bunnell, F., Dauphine, D. C., Hilborn, R., Miller, D. R., Miller, F. L., McEwen, E. H., Parker, G. R., Pererman, R., Scotter, G. W. & Walters, C. J.

1975. Preliminary report on computer simulation of barren-ground caribou management. – In: Luick, J. R., Lent, P. L., Klein, D. R. & White, R. G. (eds.). *Proc. First International Reindeer and Caribou Symposium*, pp. 189–193.
- Cringan, A. T. 1957. History, food habits and range requirements of the woodland caribou of continental North America. – *N. Am. Wildl. Conf.* 22: 485–501.
- Edwards, R. Y. & Ritcey, R. W. 1960. Foods of caribou in Wells Gray Park, British Columbia. – *Can. F. Nat.* 74 (1): 3–7.
- Druri, L. M. 1960. *Changes with age and season in live weight of reindeer*. A. N. Severtsov Inst. of Animal Morphology Issue No. 31.
- Formosov, A. N. 1946. *Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds*. Materials for fauna and flora of the USSR. Moscow Society of Naturalists, New Series, Zoology 5: 1–152.
- Hale, M. E., Jr. 1967. *The Biology of Lichens*. Edward Arnold, Ltd., London. 176 pp.
- Harrington, F. H. 1996. Human impacts on George River caribou: An Overview. – *Rangifer Special Issue No. 9*: 277–278.
- Heinselman, M. L. 1973. Fire in the Virgin Forests of the Boundary Waters Canoe Area, Minnesota. – *Quat. Res.* 3: 329–382.
- Herre, W. 1956. *Rentiere*. Die neye Brehm-Bucherei. A. Ziemsen Verlag, Wittenberg.
- Hustich, J. 1951. The lichen woodlands in Labrador and their importance as winter pastures for domesticated reindeer. – *Acta Geogr.* 12 (1): 1–48.
- International Porcupine Caribou Board. 1993. *Sensitive Habitats of the Porcupine Caribou herd*. Report accepted by the International Porcupine Caribou Board from the Porcupine Caribou Technical Committee, January 1993.
- Jalas, J. & Valpas, A. 1962. Flechtenheide oher Heide-wald Analyse eines Grenzfalls. – *Arch. Soc. Zool.-Bot. Fenn. Vanamo*. 16: 67–74.
- Johnson, E. A. 1979. Fire recurrence in the subarctic and its implications for vegetation composition. – *Can. J. Bot.* 57: 1374–1379.
- Johnson, E. A. & Rowe, J. S. 1975. Fire in the subarctic wintering ground of the Beverly caribou herd. – *The Am. Mid. Nat.* 94: 1–14.
- Kareev, G. T. 1968. Reindeer fodder resources. Chap. 4. – In: Zhigunov, P.S. (ed.). *Reindeer Husbandry*, pp. 129–176.
- Kelsall, J. P. 1960. *Cooperative studies of barren-ground caribou 1957–58*. Can. Wildl. Serv. Wildl. Mgmt. Bull. Ser. 1. No. 15. 145 pp.
- Kelsall, J. P. 1968. *The migratory barren-ground caribou*. Can. Wildl. Serv. Monogr. 3. Queen's Printer, Ottawa.
- Kelsall, J. P., Telfer, E. S. & Wright, T. D. 1977. *The effects of fire on the ecology of the Boreal Forest. With particular reference to the Canadian north: a review and selected bibliography*. Can. Wildl. Serv. Occas. Pap. No. 32. 56 pp.
- Kershaw, K. A. 1977. Studies on lichen-dominated systems. XX. An examination of some aspects of the northern boreal lichen woodlands in Canada. – *Can. J. Bot.* 55: 393–410.
- Klein, D. R. 1982. Fire lichens and caribou. – *J. Range Manage.* 35: 390–395.
- LaPerriere, A. J. & Lent, P. C. 1977. Caribou feeding sites in relation to snow cover characteristics in north-eastern Alaska. – *Arctic* 30: 101–108.
- Larin, L. V. 1951. *Forage plants of the meadow and pasture lands of the U.S.S.R.* All-Union Research Institute of Forage Plants, State Agri. Publ. House. Moscow. Vol. 2. 648 pp.
- Loughrey, A. G. 1952. *Caribou winter range study 1951–52*. Unpubl. Rept. in files of Can. Wildl. Serv., Ottawa. 30 pp.
- Makinow, E. & Kershaw, K. A. 1976. Studies on lichen dominated systems. XIX. The postfire recovery sequence of black spruce - lichen woodland in the Abitau Lake Region, N. W. T. – *Can. J. Bot.* 54: 2679–2689.
- Miller, D. R. 1974. Seasonal changes in the feeding behavior of barren-ground caribou on the taiga winter range. – In: Geist, V. & Walther, F. (eds.). *Proc. The Behavior of Ungulates and its relation to management*. Vol. 2, pp. 744–755.
- Miller, D. R. 1975. Observations of wolf predation on barren-ground caribou in the winter. – In: Luick, J.R., Lent, P., Klein, D. R. & White, R. G. (eds.). *Proc. First International Reindeer and Caribou Symposium*, pp. 209–220.
- Miller, D. R. 1976a. *Biology of the Kaminuriak Population of barren-ground caribou. Part 3: Taiga winter range relationships and diet*. Can. Wildl. Serv. Rep. Ser. 36. 41 pp.
- Miller, D. R. 1976b. *Wildfire and caribou on the taiga ecosystem of northcentral Canada*. Ph. D. Dissertation. U. of Idaho. Moscow, Idaho. 131 pp.
- Miller, D. R. 1980. Wildfire effects on barren-ground caribou wintering on the taiga of northcentral Canada. – In: Reimers, E., Gaare, E. & Skjenneberg, S. (eds.). *Proc. 2nd Int. Reindeer/Caribou Symp., Røros, Norway*. 1979, pp. 84–98.
- Miller, D. R. & Barnhard, H. W. 1973. Colour aerial photography as an aid to study of taiga as caribou winter range. Paper presented at workshop: Color aerial photography in the plant sciences and related fields – *Amer. Soc. of Photogrammatry*. Orono, ME, July 10–12.
- Miller, D. R. & Robertson, J. 1967. Results of tagging caribou at Little Duck Lake, Manitoba. – *J. Wildl. Manage.* 31: 150–159.
- Murie, O. J. 1935. *Alaska-Yukon caribou*. N. Am. Fauna 54. U. S. Gov't. Print. Off., Wash. D. C. 94 pp.

- Nash, T. H., III. 1996. Introduction. – In: Nash, T. H., III. (ed.). *Lichen Biology*. Cambridge University Press. pp. 1–8.
- Nazimovich, A. A. 1955. *The role of snow conditions in the life of ungulates in the USSR*. Unedited translation by Can. Wildl. Serv. On file at Nat. Sci. Library, Translation Unit, Nat. Res. Council, Ottawa.
- Palmer, L. J. 1926. *Progress of reindeer grazing investigations in Alaska*. U. S. Dept. Agr. Bull. 1423. 37 pp.
- Parker, G. E. 1971. *Biology of the Paminuriak population of barren-ground caribou*. Part 1. Total numbers, mortality, recruitment, and season distribution. Can. Wildl. Serv. Rep Ser. 20. 95 pp.
- Pegau, R. E. 1968. Growth notes of important reindeer forage lichens on the Seward Peninsula, Alaska. – *Arctic* 21 (4): 255–259.
- Poiijärvi, I. 1945. The consumption of lichens by reindeer kept on lichen feed from autumn to spring. – *State Agr. Exp. Activity Bull.* 205. Helsinki, Finland. 10 pp.
- Pruitt, W. O., Jr. 1959. Snow as a factor in the winter ecology of the barren-ground caribou (*Rangifer arcticus*). – *Arctic* 12: 158–179.
- Ritchie, J. C. 1959. The vegetation of northern Manitoba. III. Studies in the Subarctic. – *Tech. Rep. Arch. Inst. N. Am.* 3: 1–56.
- Ritchie, J. C., 1962. A geobotanical survey of northern Manitoba. – *Arctic Inst. N. Amer. Tech. Paper* 9: 48 pp.
- Rowe, J. S. & Scotter, G. W. 1973. Fire in the boreal forest. – *Quaternary Research* 3: 444–464.
- Russell, D. C., Martell, A. M. & Nixon, W. A. C. 1993. Range ecology of the Porcupine caribou herd in Canada – *Rangifer* Special Issue No. 8: 167 pp.
- Scotter, G. W. 1963. Growth rates of *Cladonia alpestris*, *C. mitis* and *C. rangiferina* in the Talston River region, N. W. T., – *Can. J. Botany* 41: 1199–1202.
- Scotter, G. W. 1964. Effects of forest fires on the winter range of barren-ground caribou in northern Saskatchewan. – *Can. Wildl. Serv., Wildl. Manage. Bull. Ser. 1.* 18: 111 pp.
- Scotter, G. W. 1965. Study of the winter range of barren-ground caribou with special reference to the effects of forest fires. *Can. Wildl. Serv. Prog. Rep.* No. 3. 81 pp.
- Scotter, G. W. 1967. The winter diet of barren-ground caribou in northern Canada. – *Can. Field-Nat.* 81: 33–39.
- Scotter, G. W. 1968. *Effects of forest fires on the lichen winter ranges of barren-ground caribou in Northern Canada*. Ph. D. Dissertation. Utah State Univ. at Logan. 120 pp.
- Scotter, G. W. 1970. Wildfires in relation to the habitat of barren-ground caribou relations in northern Canada. – *Proc. Tall Timbers Fire Ecol. Conf.* 10: 85–104.
- Scotter, G. W. 1971. Fire, vegetation, soil and barren-ground caribou relations in northern Canada. – In: Slaughter, P. L., Barney, P. J., & Hansen, G. M. (eds.). *Fire in the Northern Environment*. USDA For. Serv., Pacific Northwest For. and Range Exp. Stn., pp. 209–230.
- Simkin, D. W. 1965. *A preliminary report of the woodland caribou study in Ontario*. Section Report (Wildl.) No. 59. 75 pp.
- Skoog, R. O. 1968. *Ecology of the caribou (Rangifer tarandus granti) in Alaska*. Ph. D. Dissertation, Univ. of Cal., Berkeley. 699 pp.
- Skunke, F. 1963. Renbetet marklavarna och skogsbruket – *Lappvasendent-Renforskningen* No. 8: 149–262.
- Skuncke, F. 1969. Reindeer ecology and management in Sweden. – *Biol. Pap. Univ. of Alaska* 8: 1–81.
- Syroechkovskii, E. E. 1986. *Wild Reindeer*. Agropromized at Publishers Moscow, 1986 (Translated to English 1995, Oxonian Press Pvt. Ltd., New Delhi). Smithsonian Inst. Lib., Washington D. C. 290 pp.
- Thomas, D. C. 1994. *A review of Fire Management on Forested Range of the Beverly and Qamanirjuag herd of Caribou*. The Beverly and Qamanirjuag Caribou Management Board. Technical Report 1. 64 pp.
- Thomas, D. C. & Hervieux, D.P. 1986. The late winter diets of barren-ground caribou in north-central Canada. – *Rangifer* Special Issue No. 1: 305–310.
- Thomas, D. C., Barry, S. J. & Alaie, G. M. 1996. Fire-caribou-winter range relationships in northern Canada. The Second International Ungulate Conference. – *Rangifer* 16: 57–67.
- Thomas, D. C. & The Beverly and Qamanirjuag Caribou Management Board 1996. A fire suppression model of the Beverly and Qamanirjuag herds of caribou. – *Rangifer* Special Issue No.: 343–349.
- Valkenburg, P., Davis, J. L., VerHoef, J. M., Boertje, R. D., McNay, M. E., Eagan, R. M., Reed, D. J., Gardner, C. L. & Tobey, R. W. 1996. Population decline in the Delta caribou herd with reference to other Alaskan herds. – *Rangifer* Special Issue No. 9: 53–62.
- Viereck, L. A. 1973. Wildfire in the taiga of Alaska. – *J. of Quaternary Research* 3: 465–495.
- Viereck, L. A. and L. A. Schandelmeier. 1980. *Effects of fire in Alaska and adjacent Canada - a literature review*. Tech. Report. 6. Bureau of Land Manage., U.S. Dept. of the Interior. 124 pp.
- Webb, E. T. 1998. Survival, persistence and regeneration of the reindeer lichens, *Cladonia stellaris*, *C. rangiferina* and *C. mitis* following clearcut logging and forest fire in northwestern Ontario. – *Rangifer* Special Issue No. 10: 41–47.
- Wein, R. W. & MacLean, D. A. 1983. An overview of fire in northern ecosystems. – In: Wein, R. W. & MacLean, D. A. (eds.). *The Role of Fire in Northern Circumpolar Ecosystems*. John Wiley and Sons Ltd, pp. 1–18.