Fire, Lichens, and Caribou

DAVID R. KLEIN

Abstract

Continental populations of caribou (Rangifer tarandus) usually winter in the northern taiga. Fire is a natural feature of the ecology of the taiga but its effect on the winter range of caribou has been the subject of conflicting reports in the literature. Lichens, which are an important component of the diet of caribou in winter, are associated with late successional stages in the post fire sequence; therefore their loss when old growth forests burn has been considered detrimental to caribou. On the other hand, several authors have suggested that lichens are not essential for caribou in winter and therefore their loss through forest fires does not seriously affect caribou. Recent nutritional investigations with reindeer and caribou have demonstrated the importance of lichens in their winter diet. Botanical studies have shown that fires are essential for the long-term productivity of the boreal forest and they account for much of the habitat diversity that characterizes caribou winter range. Extremely old forest stands show reduced lichen productivity. I conclude that, when viewed on a short-term basis of 50 years or less, fire may destroy lichens and other forage, thus reducing the taiga's potential to support caribou. Over long-time periods, often of a century or more, fire appears essential for maintaining ecological diversity and forage production for caribou.

Fire is a natural feature of the ecology of the taiga, a fact well documented in Scandinavia (Zackrisson 1977), the Soviet Union (Andreev 1977), and North America (Viereck 1973, Johnson and Rowe 1975, Kelsall et al. 1977). "Taiga" refers to the northern coniferous forest areas of Eurasia and North America and is synonomous in North America with the term "boreal forests." Only in Scandinavia has fire control technology been sufficiently effective to eliminate fire as an ecological agent in the taiga. In much of North America, increased government commitments to fire control now offer the potential to control the ecological influence of fire.

Caribou in North America and wild reindeer in Eurasia (both Rangifer tarandus) characteristically summer in alpine or arctic tundra areas and winter in adjacent forested areas or in the northern fringes of the taiga (Fig. 1), although variations from this pattern are found in the High Arctic and at the southern extremities of their distribution. Winter forage of caribou and reindeer in the taiga is usually composed of a high proportion of lichens, often dominated by species characteristic of old growth forest stands. From the earliest investigations of caribou and reindeer, biologists have consistently referred to the possible consequences of fire in caribou and reindeer ecology (Palmer 1926, Murie 1935, Govorukhin and Rabotnov 1937). Most of these authors have stressed the apparent destruction of lichen stands by fire and the long periods of time required for their regeneration. Inherent in the conclusion that fires are detrimental to caribou and reindeer range is the assumption that these animals are dependent upon lichens as winter forage. Several authors have suggested that declines in some caribou populations were the result of fires on their winter range

Manuscript received December 16, 1980.

(Palmer and Rouse 1945, Leopold and Darling 1953, Edwards 1954, Kelsall 1957, Scotter 1967). These views have contributed to efforts to control forest fires in Canada and Alaska especially in the 1960's and 1970's with the greater availability of government services. The increased fire control has also been based on the longstanding rationale that forest fires destroy valuable timber and threaten human settlements and property. In northern regions the destruction of furbearer habitat and associated trap lines is an additional effect of fire.

More recently, the general assumption that forest fires in northern ecosystems are largely destructive to the interests of mankind has been challenged. Several authors have pointed to the role of fire in the ecology of northern forests, emphasizing the importance of fire in recycling nutrients and in maintaining vegetative productivity (Scotter 1972, Viereck 1973, Johnson and Rowe 1975, Kelsall et al. 1977, Johnson 1981). Others have stressed the importance of fire in creating habitat for moose, snowshoe hares, and other wildlife dependent on early seral vegetation (Edwards 1954, Spencer and Hakala 1964, Grange 1965, Rowe and Scotter 1973). The case against indiscriminate fire control in the taiga has been strongly supported, especially in light of the increased acceptance of fire as a natural force in northern ecosystems and as a factor in the evolution of northern plant and animal species.

Fire and Caribou

Bergerud (1974) and Miller (1976) have both criticized what they consider to be overemphasis in the literature on the assumed detrimental impacts of fire on caribou range, stressing the long ecological association between caribou and fire. They imply that since caribou evolved with fire and are successful occupants of the taiga, they must have developed a compatibility or even a beneficial relationship with fire. They also cite recent botanical studies that show that periodic fire recycles soil nutrients, increases plant productivity, and maintains ecosystem diversity. The increased plant productivity as a result of the release of nutrients to the soil would be restricted to rooted vascular plants and not lichens. Even lichens, which are characteristic of later stages of forest succession, may decrease in productivity and abundance if fire is excluded from forests for 200 years or more (Skuncke 1969).

Several authors have attempted to test the hypothesis that forest fire is detrimental to caribou by looking for a correlation between caribou population declines and the extent and sequence of fires on winter range. Miller (1976) and Johnson and Rowe (1975) found no correlation between forest fires and declines in the Kaminuriak and Beverley herds, and Scotter (1967) found no causal relationship between fires on winter range in northern Canada and the decline of caribou numbers throughout northern Canada during the 1950's. These findings are perhaps not surprising in view of the fact that forest fires in the taiga are a natural feature of the ecology; most of the land area burned within the taiga annually is the result of lightning (Barney 1971, Johnson 1979). Although certain areas are more prone to lightning fires, there may also be short-term variations in conditions favoring lightning fires, but over long periods the average area burned annually apparently has remained relatively constant. Bergerud (1974) also challenged and rejected the hypothesis that the decline of caribou in North America around the turn of the last century was related to the frequency or extent of forest fires. His reasoning was based on the assumptions that (1) caribou have catholic winter food habits which minimizes their

Author is Unit Leader, Alaska Cooperative Wildlife Research Unit, University of Alaska, Fairbanks 99701. The Alaska Cooperative Wildlife Research Unit is jointly sponsored by the Alaska Department of Fish and Game, the U.S. Fish and Wildlife Service, the University of Alaska, and the Wildlife Management Institute. This topic was first presented by the author as a discussion paper at a workshop on wildlife and wild fire in Whitehorse, Yukon Territory in November, 1979 and this paper benefits from the response of the workshop participants.

dependence on lichens, (2) lichens are poor winter forage at best, and (3) food supply has not been a factor influencing herd productivity among caribou in North America. He did note, however, that in southern caribou range predators had increased in disturbed forest areas.

Major obstacles to these efforts at ecosystem-level hypothesis testing have been the lack of accurate records of the frequency and extent of forest fires and of numbers of caribou in historical times and, more basically in my opinion, the untestability of the proposed hypotheses. Caribou populations in North America are under the influence of numerous environmental factors in addition to fire, including among others, predators, human harvest, winter snow conditions, parasites, and diseases. Unfortunately, the knowledge of the relative influence of each of these factors on any single caribou herd is sketchy at best. The influence of any one factor on a population potentially influenced by all of them cannot readily be isolated and accurately estimated, especially when the basis for this analysis is subjective accounts of caribou numbers and environmental conditions gleaned from the historical literature. Determination of the relative influence of environmental variables on caribou populations is rendered even more complex by the fact that the influence of each variable is not constant through time. For example, if food is limiting to any popluation it would only be expected to be operative at high population levels. The decline of the Nelchina Herd in central Alaska to about 12,000 was thought by Pegau (1975) to be at least partly related to the documented deterioration of the winter lichen range as the population approached a peak of over 60,000. The Western Arctic Herd in northwestern Alaska also showed symptoms of food limitation when it reached a peak of over 240,000 in 1970, before its decline to approximately 75,000 in 1976. In addition to poor over-winter calf survival coinciding with the high density, there was also a high frequency of lame animals, still births, and retained placentas among caribou on the calving grounds that were believed to be associated with brucellosis, which in turn is favored by poor nutrition (Doerr 1979). In both of these herds the drastic reduction was accelerated by heavy hunter harvest and most likely high levels of predation.

Patterns of range use by the Western Arctic Herd also point to the importance of lichens in their winter diet. In some years portions of the Western Artic Herd remain on the tundra coastal plain north of the Brooks Mountain Range throughout winter where lichens are poorly represented in the flora. This behavior, also observed among caribou of other large herds, has been cited as evidence that caribou do not require lichens during winter. However, recent observations by Davis et al. (1980) of high incidence of calf morbidity among caribou wintering on the coastal plain suggest that these animals are under greater nutritional stress than caribou on the traditional wintering grounds.

The hypothesis that food is the primary factor limiting most caribou populations in North America cannot be rejected, as Bergerud (1974) has suggested, on the basis of the lack of sufficient evidence to the contrary: it merely remains untested. There are, however, well-documented examples, in addition to those of reindeer introduced to islands (Klein 1968), of food-limited populations of caribou and wild reindeer in Greenland and Norway in the absence of predation (Thing 1980, Gaare and Skogland 1980).

Lichens and Caribou

The question of the relative value or importance of lichens to caribou also requires clarification. This issue has become confused by frequent references in the literature to the low forage value of lichens, based on their low protein content and the failure of animals fed lichens *ad libitum* in winter to maintain their body weight (Kelsall 1968, Jacobsen and Skjenneberg 1975). All northern cervids studied to date characteristically show a growth plateau in winter even when offered a high quality diet, and this corresponds with the period when plant nutrients required for proliferation of body tissues are in short supply (Wood et al. 1962, McEwan 1970). They also store fat during the summer period of vegetative growth to compensate for the period of low quality and quantity of available forage in winter when loss of body weight is a normal consequence (Nieminen et al. 1977). Adult males are somewhat of an exception as they use much of their stored fat during the rut.

Holleman et al. (1979) have demonstrated the importance of lichens in the winter diet of free-ranging caribou of the Porcupine Herd through the use of the fallout radiocesium method. They found an average lichen intake rate of 4.9 kg per day (dry weight) for an 80 kg caribou in late winter. In studies of lichen intake with penned reindeer fed lichens ad libitum, and free-foraging, esophageal-fistulated reindeer, these authors found much lower lichen intake rates (1.3-2.5 kg per day) which they associated with the lower metabolic requirements of the penned or restrained reindeer. On the basis of estimated metabolic requirements of free-ranging caribou and the experimental reindeer, they conclude that although the reindeer were not consuming enough lichens in the experiments to meet daily energy requirements and therefore would lose weight if continued on these lichen diets, the freeranging caribou were consuming 9.1 Mcal/day of lichens while expending an estimated 8.6 Mcal/day. On this basis the caribou would be in a positive energy balance.

Citing examples in the literature of free-ranging reindeer fattening under optimum winter feeding conditions where lichens were abundant (Steen 1966, Westerling 1970), Holleman et al. pointed out that, both reindeer and caribou, when feeding heavily on lichens, also select for other forage plants high in nitrogen and other minerals when they are available.

Jacobsen and Skjenneberg (1975) in Norway also found that reindeer on an ad libitum lichen diet increased their lichen intake if supplemental protein and minerals were offered. We have made observations of forage selection by caribou in northwestern Alaska in early winter which show that although lichens make up a major portion of the diet, there is active selection for such "winter-green" vascular plants as Hippuris vulgaris, Carex aquatilis, Equisetum variegatum, Arctophylla fulva rhizomes, and even the "pushups" of submerged aquatic vegetation on the ice of shallow lakes that are made by muskrats, which was also observed by Skoog (1968). These foods are usually in limited supply and are most frequently found along lake margins and in marsh areas. These green components of caribou forage contain much higher concentrations of protein and phosphorus than are present in the major lichen forage species and they also have high digestibility in contrast to other vascular plants that are available but little used (Klein unpublished). Skoog (1968) reported similar feeding behavior of caribou in Alaska and concluded that caribou were not dependent upon lichens in winter. His conclusions, however, were based primarily on early winter observations of feeding caribou and rumen samples showing relatively high proportions of vascular plants in contrast to lichens. Our subsequent observations of caribou feeding selectivity in Alaska show a shift to greater use of lichens as the winter progresses even when vascular plants remain available. This trend is also reported in the Soviet literature for wild reindeer (Andreev 1975). The standard rumen analysis techniques and field examination of rumens upon which Skoog relied have been shown to greatly underrepresent lichens in the diet (Gaare et al. 1977) and this was likely a factor leading to Skoog's conclusions.

Caribou appear to "balance" the low protein content in the *Cladonia* and *Cetraria* species that normally make up the major portion of lichens consumed by also including in their diet a portion of the nitrogen-fixing lichens of the genera *Stereocaulon* and *Peltigera* which have relatively high protein content (Klein unpublished), even though in feeding trials these forms have a lower preference rating (Holleman and Luick 1977). It seems apparent that direct extrapolation from feeding trials with captive animals fed exclusively lichens in which weight loss occurred to free-ranging caribou in which selective feeding is possible is unjustified.

Lichens, although perhaps inadequate by themselves to allow caribou to maintain body weight in winter, are rarely an exclusive diet. They are, however, high in digestible carbohydrates mostly in



Fig. 1. Caribou feeding in craters dug into the snow with their hoofs in early winter in northwestern Alaska. Lichens are a major component of the winter diet, increasing in proportion to vascular plants as the winter progresses.

the form of complex starches and are therefore a good source of energy. Their relatively high digestibility (55-75%-Cameron 1972, Jacobsen and Skjenneberg 1975, Pearson et al. 1975) is not due solely to the nature of the lichens, since they are poorly digested by most other herbivores, but is apparently due largely to evolutionary adaptation which allows caribou and reindeer to digest lichens more efficiently than other ruminants (Nordfeldt et al. 1961). A factor which should not be overlooked is that lichens constitute the plant biomass in northern ecosystems that enables the existence of large herds of both wild and domestic Rangifer throughout most of the circumpolar region. Andreev (1974) has pointed out that in the southern portions of Siberia where lichens are sparse, reindeer herding becomes an inefficient form of meat production; herds of horses are replacing reindeer in these areas for the production of meat. According to Andreev, however, reindeer, either domestic or wild, are the only ungulates that can make efficient use of the lichen ranges in the north.

Lichens, that are of major importance to caribou and reindeer on continental ranges, are often of minor importance in the High Arctic or among introduced island populations under maritime climatic influence. If the premise is accepted that *Rangifer* evolved to fill a lichen-based northern food niche essentially unoccupied by other herbivores, this apparent anomaly raises a perplexing question.

The examples of High Arctic *Rangifer* populations existing without dependence on lichens require close examination. Floral diversity is extremely limited in the High Arctic, with the absence of many forage species of importance further south. The vascular plants that are the primary winter food base for these *Rangifer* are, however, noted for their "winter-green" character and relatively high nutritive value (Kiskchinskii 1971, Klein unpublished). High Arctic *Rangifer* retain a preference for foliose lichens in their winter diet, but the climatic and substrate conditions there do not favor their growth. Where present, even in small amounts, they are utilized but they are not usually a major component of the winter diet.

The food-energetic relationships of High Arctic *Rangifer* in the absence of lichens are perhaps better understood in the context of several conditions that are unique to the High Arctic. Harassment by insects is frequently absent or is an infrequent occurrence in the High Arctic thus allowing undisturbed feeding by reindeer and

caribou during the summer vegetative growth period, an advantage denied to their more southern relatives. Where predators are absent the need for flight is also eliminated, thus allowing the accumulation of thick blankets of subcutaneous fat (Parker 1975, Ringberg 1979). The absence of both insects and predators also minimizes the need for seasonal migration common to continental *Rangifer*. This further conservation of energy also contributes to greater efficiency of summer forage utilization. On Svalbard, where predators are absent reindeer show reduced gregariousness and are relatively inactive during winter which conserves energy and reduces forage requirements.

On oceanic islands, such as the Aleutians and South Georgia, introduced reindeer have prospered in the relative absence of lichens, but only when vascular plants of high nutritive value were available throughout the winter. The maritime climatic influence is an important factor in moderating the severity and duration of winter conditions on these islands (Klein 1968, Leader-Williams 1978). On St. Matthew Island, north of the Aleutians and in the zone of seasonal sea ice and harsher winter conditions, introduced reindeer crashed to extinction following their elimination of lichens at the peak of population numbers (Klein 1968).

The existence of *Rangifer* populations that do not depend on lichens clearly does not preclude the premise that the evolution of *Rangifer* was in relation to lichens, nor that *Rangifer* depend on lichens under most range conditions. This premise is also supported by paleoecological evidence from interior Alaska which indicates that caribou, although present, were relatively uncommon during the late Pleistocene when a grass-sedge steppe prevailed and the typical graminivores, the bison and horse, dominated the large mammalian fauna (Guthrie 1968).

The assumption that caribou in the taiga can turn to alternative food sources in winter when lichen ranges have burned is not verified. The quality of most matured and dried sedges, grasses, and forbs in winter is normally very low. This is because by the onset of winter most of the aboveground growth of these plants has senesced and died. Nitrogen and other soluble plant nutrients have, for the most part, been retranslocated to the roots and other living tissues of the plants. There losses from the aboveground tissue, as well as those from leaching, result in the remaining aboveground dead material consisting largely of the structural components, cellulose, hemicellulose and lignin (Chapin et al. 1975). Lignin is virtually indigestible by ruminants and cellulose and hemicellulose are very poorly digested. It is significant, however, that the digestibility of cellulose and hemicellulose is enhanced if a high proportion of carbohydrates in a readily digestible form is also present in the diet (Gibbons et al. 1955). Similarly, rumen microorganisms also require a source of nitrogen for their growth, either recycled through the saliva or from a direct dietary source (Klein 1970). Caribou, therefore, while incapable of subsisting exclusively on the dead vascular plant material of low quality that is available on most winter ranges, can make efficient use of small portions of it when lichens are readily available as a source of highly digestible carbohydrates and some forage of at least moderate nitrogen levels is available. In this latter category is the "winter-green" vegetation mentioned above, largely around lake margins and in marsh areas, but since the total amount available is normally small it can serve little more than a dietary supplement, although an important one, under moderate range stocking levels.

Under some circumstances following fire, new growth vegetation, stimulated by the release of minerals from the burned organic matter, may remain in the active growth phase until the onset of winter, thus providing another source of high quality "wintergreen" forage. This phenomenon, however, is largely confined to the growth season following fire. When mid-summer tundra fires occurred in the winter range of the Western Arctic Herd near Kotzebue Sound, Alaska, in 1977, late summer regrowth of *Eriophorum vaginatum* remained green into the winter and we observed caribou using this forage as they moved through the burned areas in late October. This forage proved to be relatively high in protein content and digestibility.

In British Columbia, Edwards (1954) investigated alternation of animal species following fire in Wells Gray Park and demonstrated the vulnerability to fire of the forested winter range of mountain caribou through a pronounced reduction in caribou numbers and their replacement by an expanding moose population. Scotter (1967) found similar patterns of use by caribou and moose of burned areas in northern Canada. By counting winter fecal pellet groups he determined that moose made heaviest use of forest areas within 11–30 years following fire whereas caribou made greatest use of forest stands over 50 years of age. Palmer (1941) attributed the abandonment by caribou of range areas in the vicinity of Fairbanks, Alaska, after 1928 to the extensive burning of the forests during intensive mining activities. He estimated that at least 75% of the area formerly used by caribou near Fairbanks had burned at least once between 1900 and 1941.

In view of the high dependence of most large mainland North American caribou herds on lichens as the primary component of their winter diet, it seems obvious that any fire that burns a significant portion of lichen range will have potential short-term detrimental consequences for the caribou. Whether these consequences are realized will depend on the seasonal range use patterns of the caribou, their range stocking levels and the availability of alternative unburned lichen ranges.

Short-term vs. Long-term Effects of Fire

A major problem in assessing the relationship between fire and caribou ecology has been the failure to distinguish between short-term versus long-term effects. *Short-term*, as used here, refers to the immediate and often direct post fire effects of vegetative destruction and the resulting stimulation of early successional plant communities which usually encompasses the first 50 to 70 years following fire. *Long-term* effects can be considered those related to the timing of the return of climax vegetation following fire and the associated patterning of the landscape with varying-age plant communities as a result of fire. Long-term effects will therefore usually extend for a century or more. The distinction between short-term and long-term consequences of fire is exemplified in the following classification of fire effects on caribou range:

Short Term Effects

Destruction of forage lichens and other forage species: Degree and duration of effect relates to size, intensity and completeness of burn; previous vegetation types present and their seral stages; and, for caribou, to availability of alternative feeding areas.

Influence on caribou movements:

The literature is conflicting. Miller (1976) reported that recently burned areas are used as avenues of travel by caribou or to escape predators. Pruitt (1959) observed that snow conditions in recent burns may interfere with movements of caribou to unburned winter range. Condition of the forest prior to the fire is apparently a major factor as windfalls and fire-felled trees may make such areas virtually impassable.

Reduced availability and quality of forage in post-fire areas: Few lichens are present on recently burned areas. Early successional stage vegetation is not used significantly by caribou in winter. Thick second growth vegetation may impede movements.

Low intensity burns may improve forage quality:

Fires of moderate to low intensity may release nutrients and remove insulative plant material without killing most graminoids and shrubs, thus stimulating regrowth of plant material of high nutritive value. This effect is largely lost after 1 to 2 years following fire.

Long-Term Effects

Maintain diversity in vegetation types:

Fire in association with landform is the major element maintaining plant successional sequences in the taiga; the interspersion of young, intermediate and old growth forest stands; and availability and productivity of lichen stands.

Rejuvenate old forest stands with declining lichen productivity:

Lichen productivity and quality declines in very old forest stands. Very low intensity fires have been observed to stimulate regrowth of lichens (Skuncke 1969); hot fires return land to early successional stages.

Can create extensive monotypes under certain conditions: Under drought conditions in uniform terrain fire may burn vast areas, leading to uniformity of vegetation type, thus creating long term irregularity in productivity and availability of forage lichens (*i.e.*, vast areas of early seral vegetation poor in lichens, followed by maturing vegetation ultimately rich in lichens).

Replacement of forests with grasslands:

Repeated frequent burning may favor the establishment of grasses thus delaying the return of forests and their associated lichens.

Depression of tree line:

Fires may replace tree line forests with tundra, creating a drier microclimate less favorable for lichens.

Fire Adaptation

Early caribou literature stresses the presumed short-term detrimental effects of fires on caribou ecology through the direct destruction of lichens (Palmer 1941, Murie 1935). More recently, botanical studies of fire effects in the taiga have brought into sharper perspective the long-term ecological consequences of fire. Johnson and Rowe (1975), Miller (1980) and Johnson (1981) have now placed strong, and seemingly justified, emphasis on the ecological consequences of fire in maintaining vegetative heterogeneity and in renewing plant succession which, viewed over a long-time scale, may be beneficial to caribou. This conclusion, along with the acceptance of fire as a natural element of the ecology of the taiga, unfortunately has led to the unwarranted assumption

that caribou, having evolved with fire, must be fire-adapted and therefore beneficially affected by fire. Fire adaption in caribou may be reflected in their yearly variations in patterns of winter range use to compensate for the temporary loss of portions of winter range through fire. Nevertheless, long-term benefits to the species in an evolutionary or ecological sense may be disproportionate to the short-term detrimental effects on herds or populations. A species may be considered fire adapted if it has evolved specific responses to fire; serotinous cones in black spruce (Picea mariana) and lodgepole pine (Pinus contorta) for example. The mere existence of a species in a fire-dominated ecosystem, however, does not necessarily imply fire adaptation. Johnson (1979) has suggested alternative strategies in fire adaptation for plants that conceivably could also apply to animals such as moose, snowshoe hares, caribou, and marten. He pointed out that those plants living on sites with short intervals between reburning will likely be r-selected and therefore tend to have short life expectancies and a high investment in reproductive effort. On sites with long intervals between fires, that is with a low fire hazard, plants will be K-selected and will be long-lived and with a low reproductive effort. Presumably lichens would fall in the latter category, as would the animals that depend upon them. Caribou lack the reproductive plasticity of moose that can vary the number of offspring per year from one to three and can be considered fire-adapted. There, caribou might be more correctly considered to be fire-influenced rather than fire-adapted.

Implications for Management

Even if it is conceded that caribou are adapted to fire-dominated ecosystems, the fact remains that wild fires are catastrophic events that vary in frequency and extent in relation to long term variations in weather patterns and therefore cannot be counted on to burn in patterns, in sequences, and in extent that favor optimal use of the range by caribou. Short-term losses of portions of rangelands due to fire may therefore lead to wide variations in rangeland potential to support caribou. It seems apparant that as long as caribou populations are substantially below the optimum carrying capacity of their winter ranges, fires will not cause population reductions, although the potential for future increases will be lowered. On the other hand, population reductions will inevitably occur if ranges are stocked to capacity when significant portions of them burn. The wide population fluctuations that have characterized major caribou herds in North America since records have been available may be the normal pattern for the species, thus complicating assessment of the effects of range fires. Long-term monitoring of the responses of varying types of range vegetation to fires of differing intensities clearly should be a high priority of government agencies responsible for management of caribou range lands.

Literature Cited

- Andreev, V.N. 1974. Horse pasturage in northeastern Yakutia. (In Russian). Institute of Biology, Siberian Affiliate Academy of Science of USSR. Yakutsk. 246 p.
- Andreev, V.N. 1975. The state of food supply for reindeer herding and problems of the wild reindeer range use. p. 68-79. In: E.E. Syroechkovsky (ed.), Wild Northern Reindeer in the USSR. Central Research Lab. on Wildlife Management and Nature Preserves. Moscow. 317 p. (In Russian).
- Andreev, V.N. 1977. Reindeer pastures in the subarctice territories of the USSR. p. 275-313. In: Krause (ed.), Handbook of Vegetation Science. Part XIII Application of vegetation science to grassland husbandry. Dr. W. Junk B.V., The Hague.
- Barney, R.J. 1971. Wildfires in Alaska-some historical and projected effects and aspects. p. 51-59. In: Fire in the Northern Environment, A Symposium. Pacific Northwest Forest and Range Exp. Sta., Portland, Ore.
- Bergerud, A.T. 1974. Decline of caribou in North America following settlement. J. Wildl. Manage. 38:757-770.
- Cameron, R.D. 1972. Water metabolism by reindeer (Rangifer tarandus). Ph.D. Thesis, Univ. Alaska. 98 p.
- Chapin, F.S., K. Van Cleve, and L.L. Tieszen. 1975. Seasonal nutrient

dynamics of vegetation at Barrow, Alaska. Arctic and Alpine Res. 7:209-226.

- Davis, J.L., P. Valkenburg, and H.V. Reynolds. 1980. Population dynamics of Alaska's Western Arctic Caribou Herd. Proc. Second Int. Reindeer/Caribou Symposium. Røros, Norway. Sept. 1979.
- Doerr, J. 1979. Population analysis and modeling of the Western Arctic Caribou Herd with comparisons to other Alaskan Rangifer populations. M.S. Thesis, Univ. Alaska. 341 p.
- Edwards, R.Y. 1954. Fire and the decline of a mountain caribou herd. J. Wildl. Manage. 18:521-526.
- Gaare, E., and T. Skogland. 1980. The lichen-reindeer interaction studied in a simple case model. Proc. Second Internat. Reindeer/Caribou Symposium. Røros, Norway. Sept. 1979.
- Gaare, E.A. Sørensen, and R.G. White. 1977. Are rumen samples representative of the diet? Oikos. 29:390-395.
- Gibbons, R.J., R.N. Doetsch, and J.C. Shaw. 1955. Further studies on polysaccharide production by bovine rumen bacteria. J. Dairy Sci. 38:1147-1154
- Govorukhin, V.S., and T.A. Rabotonov. 1937. Lichens. In: I.V. Larin (ed.). 1937. Forage Plants of the Meadow and Pasture Lands of the U.S.S.R. Publ. House Lenin Acad. Agr. Sci., Leningrad, 994 p.
- Grange, W.B. 1965. Fire and tree growth relationships to snowshoe rabbits. Proc. Tall. Timbers Ecol. Conf. 4:110-125.
- Guthrie, R.D. 1968. Paleoecology of the large-mammal community in interior Alaska during the late Pleistocene. Amer. Midland Natur. 79:346-363.
- Holleman, D.F., and J.R. Luick. 1977. Lichen species preference by reindeer. Can. J. Zool. 55:1368-1369.
- Holleman, D.F., J.R. Luick, and R.G. White. 1979. Lichen intake estimates for reindeer and caribou during winter. J. Wildl. Manage. 43:192-201.
- Jacobsen, E., and S. Skjenneberg. 1975. Some results from feeding experiments with reindeer. 95:107. In: J.R. Luick, P.C. Lent, D.R. Klein and R.G. White, (eds). Proc. First Internat. Reindeer and Caribou Symp., Biological Papers of the Univ. Alaska. SR1, Fairbanks, Ala. 551 p.
- Johnson, E.A. 1979. Fire recurrence in the subarctic and its implications for vegetation composition. Can. J. Bot. 57:1374-1379.
- Johnson, E.A. 1981. Vegetation organization and dynamics of lichen woodland communities in the Northwest Territories, Canada. Ecology 62:200-215.
- Johnson, E.A., and J.S. Rowe. 1975. Fire in the subarctic wintering ground of the Beverely Caribou Herd. Amer. Midland Natur. 94:1-14.
- Kelsall, J.P. 1957. Forest fire on caribou winter ranges. Can. Wildl. Serv. (type. rep.) 5 p.
- Kelsall, J.P. 1968. The imigratory barren-ground caribou of Canada. Can. Wildl. Serv. Monogr. Ser. No. 3, Ottawa, 340 p.
- Kelsall, J.P., E.S. Telfer, and T.D. Wright. 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. Occ. Pap. No. 32, 58 p.
- Kiskchinskii, A.A. 1971. The modern state of the wild reindeer population on the Novosibersky Islands. Zool. J. USSR Acad. Sci. 50:117-125 (Trans. from Russian).
- Klein, D.R. 1968. The introduction increase, and crash of reindeer on St. Matthew Island. J. Wildl. Manage. 32:350-367.
- Klein, D.R., and F. Schønheyder. 1970. Variation in rumen nitrogen levels among some cervidae. Can. J. Zool. 48:1437-1442.
- Leader-Williams, N. 1978. The history of the introduced reindeer of South Georgia. Deer 4:256-261.
- Leopold, A.S., and F.F. Darling. 1953. Wildlife in Alaska. The Ronald Press, N.Y. 129 p.
- McEwan, E.H. 1970. Energy metabolism of barren-ground caribou (Rangifer tarandus). Can. J. Zool. 48:391-392.
- Miller, D.R. 1976. Wildfire and caribou on the taiga ecosystem of northcentral Canada. Ph.D. Diss. U. of Idaho, Moscow. 131 p.
- Miller, D.R. 1980. Wildfire effects on barren-ground caribou wintering on the taiga of northcentral Canada: A reassessment. Paper presented at Second Internat. Reindeer/Caribou Sympossium Røros, Norway. Sept. 1979.
- Murie, O.J. 1935. Alaska-Yukon caribou. North American Fauna. 54:1-93.
- Nieminen, M.P. Väyrynen, and R. Väyrynen. 1977. Poron ravitsemusfysio-

logiasta. (Finnish with English summary). Suomen Luouto. 36:98-101. Nordfeldt, S., W. Cagell, and M. Nordkvist. 1961. Smältbarhetsförsök med

- renar. Üjebyn 1957-60. Statens Husdjurskförsök. Sartryck ock förhandsmeddelauden. 151:1-12.
- Palmer, L.J. 1926. Progress of reindeer grazing investigations in Alaska. U.S. Dep. Agr. Bull. 1423. 32 p.

- Palmer, L.J. 1941. Caribou versus fire in interior Alaska. (A study of burned over lichen ranges). U.S. Fish and Wildlife Service (typed report). L.J. Palmer Collection, Univ. of Alaska, Fairbanks. 14 p.
- Palmer, L.J., and C.H. Rouse. 1945. Study of the Alaska tundra with reference to its reactions to reindeer and other grazing. U.S. Fish & Wildlife Service Res. Rep. 10:1-48.
- Parker, G.R. 1975. An investigation of caribou range on Southampton Island, Northwest Territories. Can. Wildl. Serv. Report Series 33:83 p.
- Pegau, R.E. 1975. Analysis of the Nelchina caribou range. Pages 316-323. In: J.R. Luick, P.C. Lent, D.R. Klein and R.G. White, (eds). Proc. First International Reindeer and Caribou Symp. Biol. Papers of the Univ. of Alaska. SR1. Fairbanks, Alaska, 551 p.
- Person, S.J., R.G. White, and J.R. Luick. 1975. In vitro digestibility of forages utilized by *Rangifer tarandus. In: J.R. Luick*, P.C. Lent, D.R. Klein and R.G. White (eds.) Proc. First International Reindeer and Caribou Symp. Biol. Papers of the Univ. of Alaska. SR1, Fairbanks, AK. 551 p.
- Pruitt, W.O., Jr. 1959. Snow as a factor in the ecology of the barren-ground caribou. Arctic 12:159-179.
- Ringberg, T. 1979. The Spitzbergen reindeer-a winter dormant ungulate? Acta Physiol. Scand. 105:268.
- Rowe, J.S., and G.W. Scotter. 1973. Fire in the Boreal Forest. Quaternary Rev. 3:444-465.
- Scotter, G.W. 1967. Effects of fire on barren-ground caribou and their forest habitat in northern Canada. Trans. N. American Wildl. Conf. 32:243-254.

- Scotter, G.W. 1972. Fire as an ecological factor in boreal forest ecosystems of Canada. *In:* Fire in the Environment, Symposium Proc. Denver, Colo. U.S. Forest Ser. FS-276:15-24.
- Skoog, R.O. 1968. Ecology of the caribou (*Rangifer tarandus grantii*) in Alaska. Ph.D. dissertation. Univ. Calif. Berkeley, Berkeley, California. 699 p.
- Skuncke, F. 1969. Reindeer ecology and management in Sweden. Biological Papers of the Univ. of Alaska. 8:1-82 p.
- Spencer, D.L., and J.B. Hakala. 1964. Moose and fire on the Kenai. Proc. Tall Timbers Fire Ecol. Conf. 3:11-13.
- Steen, E. 1966. The biology of reindeer pasture. Considerations about the report on reindeer pasture ranges. Swedish Gov. Off. Rep., Stockholm. 12:1-22.
- Thing, H. 1980. Preliminary studies of habitat use and food selectivity of West Greenland caribou. Proc. Second Int. Reindeer/Caribou Symposium. Røros, Norway. Sept. 1979.
- Viereck, L.A. 1973. Wildfire in the taiga of Alaska. Quatern. Res. 3:465-495.
- Westerling, B. 1970. Rumen ciliate fauna of semi-domestic reindeer (*Rangifer tarandus* L.) in Finland: composition, volume and some seasonal variations. Acta. Zool. Fenn. 127:1-76 p.
- Wood, A.J., I. McT. Cowan, and H.C. Nordan. 1962. Periodicity of growth in ungulates as shown by deer of the genus *Odocoileus*. Can. J. Zool. 40:593-603.
- Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. Oikos 29:22-23.

THE UNIVERSITY OF BRITISH COLUMBIA—FACULTY OF FORESTRY

Position:	Assistant Professor
Qualifications:	Ph.D.in Range-related Research. Minimum 1 degree in Forestry with specialization in range management. Prefer- ence to be given to candidate with teaching and research background. In accordance with Canadian immigration requirements, priority will be given to Canadian citizens and permanent residents of Canada.
Duties:	Report to Acting Head of Dept. of Forest Resources Man- agement and hold joint appointment with Dept. of Plant Science both in teaching and research.
Date of Employment:	September 1, 1982 (preferable)
Salary:	Commensurate with training and experience.
Deadline:	August 1, 1982 or when position filled.
Forward curriculum v	vitae and 3 letters of reference to:
	Dr. J.H.G. Smith, Acting Head
	Department of Forest Resources Management
	Faculty of Forestry
	University of British Columbia
	Vancouver, B.C. V6T 1W5