

FIRE-MOOSE-CARIBOU INTERRELATIONSHIPS:
A REVIEW AND ASSESSMENT

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Abstract: Extirpation of caribou from the Kenai Peninsula in the early 1900's and the subsequent increase in moose numbers is frequently cited as a classic example of a faunal change that resulted from fire-initiated plant succession. A similar sequence has been observed recurrently throughout northern North America and is frequently cited as a causal relationship. Unfortunately, acceptance of this generalization resulted in the erroneous conclusion that the widespread burning of forests that accompanied settlement destroyed caribou winter range and precipitated the Nearctic decline of caribou. This attitude has precluded recognition of other factors that are limiting caribou and has created the belief that creating or increasing moose habitat by burning will automatically eliminate or displace caribou. We believe that the observed relationships were not necessarily causal, that factors other than fire were most likely responsible for past declines of caribou, and that creating or enhancing moose habitat by burning is not necessarily detrimental to caribou.

Extirpation of caribou (*Rangifer tarandus*) from the Kenai Peninsula in the early 1900's and the subsequent increase in moose (*Alces alces gigas*) numbers is frequently cited as a classic example of a faunal change that resulted from fire-initiated plant succession (Palmer 1933, Dufresne 1946). A similar sequence has been observed recurrently throughout northern North America and is frequently cited as a causal

relationship (Edwards 1954, Peterson 1955). In this paper we review and evaluate the validity of these observations as they apply to the cause and effect relationships inferred from them. We rely primarily upon the literature in evaluating the generalized North American observations and combine this with our personal experience in assessing Kenai Peninsula fire-moose-caribou interrelationships.

FIRE-MOOSE RELATIONSHIPS IN NORTH AMERICA

Fires can hardly be viewed as being other than beneficial to moose judging by the frequency that authors report the benefit of fire to moose (see reviews of moose distribution and habitats by Berg and Phillips 1974, Brassard et al. 1974, Dodds 1974, Kelsall and Telfer 1974, Kistchinski 1974, Krefting 1974, LeResche et al. 1974, Markgren 1974 and Peek 1974a). It is noteworthy that seven of these nine reviews of moose habitat and distribution, which encompassed all Nearctic moose ranges, repeatedly mentioned or implied that fire was a major force in the well-being of moose by favorably affecting habitat. In the remaining two (i.e. Peek and Markgren), fire was still mentioned or implied as being beneficial to moose in the respective situations. Perhaps even more noteworthy is that in all of the discussion contained in these reviews there were only a few qualified statements that fire was at all harmful to moose and their habitat. However, many authors specifically discuss the many variables that determine the overall benefit of a fire to habitat improvement.

The literature is replete with references to fire being of singular importance to moose abundance. For example, Krefting (1974) stated, "Because the moose is a fire-adapted species, there is a need to reintroduce

fire into the ecosystem," and, "Wildfire is the most important factor that has influenced moose distribution and habitat selection for at least several hundred years; historic fires that covered thousands of square kilometers created seral shrub stages needed by moose." From Dodds (1974), "Fire may kill game but, for moose, the fact that some animals are killed or forced to move is secondary to the long-term improvement in moose range that fire normally causes...(Pimlott 1961, Peterson 1955, Leopold and Darling 1953)." Brassard et al. (1974) stated, "...in northeastern Quebec, between 1963 and 1972, an extension of the moose range was correlated with disturbances caused by forest fires..." Kelsall and Telfer (1974) state, "Hatter (1950) concluded that a combination of extensive burning and lumbering created huge areas of young forest that permitted the invasion of much of British Columbia by moose in recent times." Also they cited Peterson (1955) as hypothesizing that logging and wildfire associated with opening up of the country north of Lake Superior led to the expansion of moose into that area. It is possible to continue ad nauseum with examples stating similar observations from throughout the Nearctic region.

Consideration of factors which commonly limit moose numbers should be instructive in ascertaining how fires benefit moose. In a recent review of the biogeography of moose in North America, Kelsall and Telfer (1974) discussed factors limiting moose. They concluded that moose distribution is limited in the north principally by an absence of woody food plants on the tundra; by a lack of woody plants and by excessive snow depths in many high altitude areas in the western cordillera; by combinations of excessive summer heat with absence of shade, water and

suitable food on the prairies and in the arid valleys of the south and west; and by neurologic disease in the southeast. Further, they concluded that moose populations everywhere fluctuate dynamically in response to environmental changes. In discussing adaptive and limiting factors they concluded that winter food profoundly influences distribution; that climatic factors including high temperatures and snow depth, density, hardness and duration restrict moose; certain parasites may restrict moose; and hunting can limit moose in certain instances. Of all these factors it appears that the principal limitation that fires would overcome is food limitation. Fire would probably be detrimental regarding the other limiting factors, directly or indirectly. Because moose frequently increase following fires, the benefit of additional food must generally outweigh the negative impacts of the fire.

The mechanism by which fires benefit moose appears straightforward and demonstrable: 1) increased edge, 2) increased forage quantity and 3) increased forage quality. The increased edge effect or interspersion between new growth and old growth cover types is described by Dodds (1955), LeResche et al. (1974), Krefting (1974) and others. The greatly increased abundance and availability of deciduous stems for browsing is mentioned repeatedly. Aldous and Krefting (1946) noted that a 1936 burn that covered 1/4 of Isle Royale 10 years later produced more browse than the rest of the Island. LeResche et al. (1974) reported that the 1947 Kenai burn supported 4 moose/km² in contrast to 0.08 moose/km² in similar unburned areas through a combination of high forage production, generally mild winters, abundant alternate foods (especially *V. vitis-idaea*), edge effect and adjoining upland ranges. Spencer and Hakala (1964) documented increased forage production after burning.

Oldemeyer (1974) reviewed the requirements of good quality forage and gave definitions of quality by Dietz (1970), Reid et al. (1959) and Barnes (1965). Cowan et al. (1950) found that crude fiber increased in four of six moose forage species as forest age increased in British Columbia which suggests decreasing quality over time after disturbance. Cowan et al. (1950) and Tew (1970) found that fat and protein content, respectively, generally decreased as plants matured, and Dewitt and Derby (1955) and Lay (1957) reported that protein content in forage increases the first year or two after a fire, but decreases thereafter.

Traits of Good Burns

LeResche et al. (1974) list several factors determining the impact a fire-created successional community will have on moose populations: 1) species composition, 2) size of burn and per-area standing biomass and production of available browse, 3) rates at which forage attains a) above snow and b) above moose-reach heights and 4) extent and diversity of the resulting pattern of mature and seral communities.

The degree of interspersed communities, or amount of "edge effect," produced by a fire is very important in determining the fire's effect on moose populations (Krefting 1974, LeResche et al. 1974). Great discontinuity of burning is desirable because it provides cover close to feeding habitat, increased variety of alternate forage species and staggered maturation rates of individual stands. The forest edge ecotone allows moose to invade a heterogeneous burn sooner than a large homogeneous burn and to achieve higher year-round densities.

Negative Benefits of Fires to Moose

Repeated high temperature, deep burns may have destructive effects on shallow soils (Dodds 1974) which presumably could adversely affect moose. Dodds (1974) states, "Severe and repeated burning has produced a relatively stable sub-climax of ericaceous vegetation in portions of western Nova Scotia (Strang 1972) while in portions of central Newfoundland (Dodds 1955) and New Brunswick, past repeated burns have retarded succession favorable to moose." Several authors have stated that burns are used in early winter but as snow becomes deeper in late winter moose shift to more mature stands (see Coady 1974 for a review). If white-tailed deer (*Odocoileus virginianus*) have extended their range, as a consequence of fires, into areas where moose would exist without fires and restricted moose through transmission of the parasite *Parelaphostrongylus tenuis*, highly pathogenic to moose, then this is a negative impact (Kelsall and Telfer 1974).

FIRE-CARIBOU RELATIONSHIPS IN NORTH AMERICA

In contrast to the clear benefit that fires generally seem to contribute to moose, many biologists believe that fires have been clearly detrimental to caribou. As discussed above, scrutiny of all pertinent information concerning the correlation between observations of increased moose abundance following fires suggests that a cause and effect relationship exists. However, similar scrutiny of all the facts involved in the apparent correlation between caribou declines and burning of caribou habitat suggests there is not a cause and effect relationship (Bergerud 1974, Davis et al. 1978). Davis et al. (1978) recently reviewed the

effect of wildfire on caribou and their habitat and the following section is a paraphrased excerpt from that review.

General Effects of Fire on Caribou

Many observers and biologists have discussed the effects of wildfire on caribou populations. Wildfires, natural and man-caused, have commonly occurred for hundreds of years throughout most of the area inhabited by caribou in North America. Viereck (1973) commented on the occurrence of fire as follows: "Fire has always been a part of the Alaska taiga ecosystem; if it is totally excluded from the environment, some major ecological changes will result." Scotter (1964) stated, "Comments on forest fires in the journals of early explorers, and the presence of charcoal in soil profiles indicate that the relationship between forest fires and caribou is not a recent one." Scotter (1967, 1971a,b) reiterated that opinion and other authors (Lutz 1956, Skoog 1968) reached similar conclusions.

Many observers believe that caribou populations in North America began a general decline in numbers in the late 1800's and continued to decline through this century. Most early writers (Hind 1863, Pike 1892, Hornby 1934, Anderson 1938, Allen 1942, Manning 1946, deVos 1948, Rousseau 1951, Leopold and Darling 1953a, Banfield 1954, Edwards 1954, Moisan 1955, Lutz 1956, Cringan 1957, Kelsall 1957, Banfield and Tener 1958, Pruitt 1959, Scotter 1964, 1967, 1971a,b) believed that fire was detrimental to caribou. Many biologists and explorers have observed a strong direct correlation between increased forest fires (on a local scale) and declining caribou populations. Bergerud (1974) discussed this viewpoint as follows:

"The majority of northern biologists believe that man's destruction of caribou habitat was the primary cause of the Nearctic decline concurrent with settlement. For instance, Peterson (1966:334), in referring to caribou in eastern Canada, stated, '...it seems obvious that the deterioration of habitat by fire and human activity has been the most important fact in their decline.' Leopold and Darling (1953:67), 'Caribou have been...very much reduced in central and southern Alaska by burning over the winter range.' Again Scotter (1967:257) refers to the decline of barren-ground caribou in Canada: '...there can be little doubt that forest fires have been one of the principal causes of the decline.'"

Bergerud (1974) argued that wildfire was not the major factor responsible for the decline of caribou in Canada following settlement. He believed that caribou declined due to increased mortality from hunting augmented by increased predation and possibly disease. Bergerud (1974) stated the following:

"Recently, three long-term life history studies of caribou in North America have been completed. Two of those studies at opposite ends of the continent (Alaska and Newfoundland) concluded that caribou do not require lichens, and that range destruction was not a factor in the decline of caribou (Skoog 1968; Bergerud 1971a,b, 1972). In the third study in the Northwest Territories, Banfield (1954) and later Kelsall (1968) emphasized hunting mortality as the cause of the decline."

Three assumptions are involved in the theory that increased wildfires reduced the absolute abundance of lichens which caused the caribou

population declines. The first assumption is that fires increased following settlement. The second is that quality and/or quantity of caribou range were reduced because of wildfire. The third is that lichen requirements of caribou are sufficiently high that reduction in absolute abundance can cause a major reduction in the caribou population.

Frequency of Fires in the Canadian North and Alaska

Investigators in Canada do not agree that fire increased following settlement in the North. Kelsall et al. (1977) presented an excellent review of the history of fire in northern Canada.

In Alaska, however, records indicate that burning of wildlands increased during periods of early white settlement and mining activities (Lutz 1956, Hardy and Franks 1963, Skoog 1968). Lutz (1956) stated:

"The tempo of forest destruction in Alaska was substantially increased after gold was discovered in the Klondike in 1896. The fabulous stampede that followed brought thousands of people to Yukon and to Alaska.... With the advent of white man in the Territory near the end of the 19th century, fires became even more widespread than previously. Particularly affected were those districts where gold placer deposits were discovered. A map of the Fortymile Quadrangle prepared by Barnard (9) shows that at that time (1900) only 3.6 percent (54 of 1,481 square miles) of the forest land had been burned over. Barnard wrote, 'The entire area of this quadrangle is fairly well timbered to an altitude of 3,000 feet, save some areas which have

been burned over....' Since then most of the region has been burned."

Lutz (1956) also stated that 1915 was one of the worst fire years recorded. Viereck (1973) mentioned, "With the appearance of contemporary man in the northern areas, fire activity increased, especially during the Gold Rush at the turn of the century."

Wildfire, Lichens and Caribou

The second and third assumptions are related; reduction of range quality by removal of the climax species of lichens is based on the assumption that lichens are important to caribou. These assumptions are an essential part of the theory that fire has a detrimental effect on caribou populations. Leopold and Darling (1953a) wrote: "To ignore range limitation for caribou is to ignore the crux of the problem. One fire could undo the work of decades in protecting a local caribou population from men and wolves." They further state that "...fire has played so dominant a part in destroying the lichen range that we feel quite safe in attaching to that one factor the major blame for caribou decrease." Scotter (1967) concluded, "More prevention and control of forest fires would seem desirable in light of the small caribou population and the long-term destruction of winter range by fire." Edwards (1954) concluded:

"It appears that fire is the major cause of caribou decline in Wells Gray Park. The northward march of the decline through the province is suggestive of the same cause, since the trend of first human influence upon wilderness lands in British Columbia had progressed generally from south to north. In

Alaska (Murie 1951, p. 278), western Ontario (deVos 1948) and other areas where caribou declines or exterminations were followed by increases in deer or moose there is ample evidence to suspect fire."

The general rule that survival of caribou depends on the abundance of lichens is not valid (Bonner 1958, Skoog 1968, Bergerud 1974, Klein 1974). Feeding studies have shown that caribou almost invariably lose weight on an ad libitum diet of only lichen (Courtright 1959, Kelsall 1968, Bergerud 1974, Cameron et al. 1976). In fact there is some evidence that some members of the genus *Rangifer* may fare better on a reduced lichen diet. Klein (1974) described a situation in Siberia as follows:

"One study involved the comparison of feeding behavior of the Hargin reindeer from the Chukotsk region (Chukchi Peninsula) and the Evenki reindeer typical of the region. The Hargin deer are well known for their thriftiness in existing on ranges with little or no lichens present. In the study, carried out in winter, groups of Hargin and Evenki deer were kept in adjacent large enclosures with similar forage available to each group. The Evenki deer used 70 percent lichens and 30 percent nonlichens and gave a meat yield of 50 kg per 100 kg of live weight. The Hargin deer used 30 percent lichens and 70 percent nonlichens and were able to obtain their forage needs on a smaller area per animal than the Evenki deer. Meat yield from the Hargin deer averaged 65 kg per 100 kg live weight."

In many areas lichens form only a minor portion of the diet or are completely lacking (for food habits see Murie 1935, Cringan 1956, Bonner

1958, Courtwright 1959, Kelsall 1968, Klein 1968, Skoog 1968, Bergerud 1972). Skoog (1968:352) stated: "...all who have discussed caribou-range relationships have implied that lichens are required by caribou and that the relative abundance of these plants sets the carrying capacity of the range. There seems to be adequate information available to dispute this idea." Furthermore, investigators have shown that certain lichens are highly digestible, high in carbohydrates, but low in nitrogen (Cameron et al. 1976, Pegau et al. 1973, Miller 1976).

Fire may in fact improve the quality of caribou range. Ahti and Hepburn (1967) and Rowe and Scotter (1973) concluded that because fire destroys thick carpets of bryophytes in the southern part of barren-ground caribou range in Canada it makes the forest more productive of lichens and other forage plants.

Courtwright (1959) believed that small fires would be beneficial to caribou range by returning nutrients to the soil. Similarly, Bergerud (1971a) concluded "...forest fires in the past have increased the extent of winter range by altering closed-canopy forests to lichen woodlands or shrub-barrens, and prostrate subalpine spruce-fir thickets to lichen shrub barrens."

Miller (1976) conducted the most recent intensive investigation of caribou-taiga winter range relationships and concluded as follows:

"In particular forest fires are beneficial in that they increase the heterogeneity of the plant cover and favour the growth of some lichens which occur in early successional stages. There is a plentiful supply of forage in the area despite caribou use and fires. Snow cover rather than scarcity of forage limits the capacity of the taiga to support caribou."

Effects of Fires Other Than Reducing Lichens

Although no cause-and-effect relationship between increased wildfires and caribou population declines has been demonstrated, the correlation between these two events suggests that wildfire may have direct or indirect effects other than destroying lichens. Because caribou are mobile and can avoid a wildfire, and because they are usually in tundra habitat during the taiga fire season, they would rarely be killed by the fire itself.

Indirect adverse effects of fire have been postulated by several authors but most conclusions are speculative. Banfield (1954) and Scotter (1971a) speculated that fire could create physical barriers (e.g. downed timber) and Banfield (1954) observed caribou avoiding recent burns during migrations. Kelsall (1957) and Scotter (1967) found that caribou avoid areas in young successional stages and frequented more open forests of spruce or jack pine. They also observed that snow conditions, low forage production and windfallen trees made recent burns unattractive to caribou.

Bergerud (1974) has discussed extensively the increases in predator populations and exposure of caribou to parasites which occurred following increases in fires resulting in seral habitat. Seral habitat allowed increases in different "buffer species" of prey, which in turn allowed predator populations to increase. He discussed Edwards' (1954) data from Wells Gray Park, and concluded that increased predation rather than a shortage of lichen habitat was responsible for the caribou population decline noted there. Bergerud reviewed observations from other Canadian studies, and reached similar conclusions for these populations. Seral

habitat may have resulted in faunal changes which subjected caribou to a wider array of diseases and parasites. Bergerud (1974) presents circumstantial evidence that range extension by white-tailed deer into caribou habitat possibly resulted in a decline in caribou populations following infection by the meningeal worm (*Parelaphostrongylus tenuis*) which is highly pathogenic in species other than white-tailed deer.

MOOSE-FIRE RELATIONSHIPS ON THE KENAI PENINSULA

References to fires benefiting moose on Alaska's Kenai Peninsula are abundant (Lucas 1932; Palmer 1933, 1938; Dufresne 1946; Leopold and Darling 1953a,b; Lutz 1956, 1960; Spencer and Chatelain 1953; Spencer and Hakala 1964; LeResche et al. 1974). Little was known of the Kenai Peninsula's biological characteristics before 1875, but moose were apparently scarce prior to the 1890's.

The idea that moose were absent from the Kenai Peninsula prior to about 1871 is of Indian origin. Lucas (1932) states, "Native tradition indicates that the Western Kenai country was quite extensively burned over and the moose appeared shortly thereafter." We can find a specific day for that appearance in a quote of Andrew Berg presented in Palmer (1938), "...the first moose landed on Point Possession [on the north side of the Kenai Peninsula, at the entrance to Turnagain Arm]...on October 10, 1871." Lutz (1960) cited 15 similar references to moose arriving sometime around 1880. It is surprising that the misconception of moose not being present on the Kenai until the late 1800's has persisted because Lutz (1960) presented convincing evidence that moose were never absent since earliest recorded times (Spencer and Hakala



1964, Klein 1965, LeResche et al. 1974). Lutz (1960) cites numerous reports by Russian and other travelers which document moose presence from the late 1700's, the language of the early Kenai Indians included words for moose and archeological work has located moose bones from the period when they were supposedly absent. Lutz (1960) summarizes by saying, "...that moose first made their appearance on the Kenai Peninsula in 1871, or later, is untenable. Fluctuations in the moose population certainly occurred and it may be that local scarcity, or absence, led to reports of scarcity or absence on the Peninsula as a whole."

Further, Lutz (1960) stated,

"Although the written record of forest fires on the Kenai Peninsula is scanty (the first written record of a fire being 1851), evidence of past burning may be seen...today...charcoal can be found in the soil of practically every upland forest site.... It is likely that forest fires have occurred on the Kenai Peninsula ever since there have been forests. If fire were essential to set the stage for the appearance of moose...there is every reason to believe that the stage was already set, centuries ago."

LeResche et al. (1974) list the various types of climax and seral habitats present on the Kenai Peninsula. There is no reason to believe that the climax or non-fire created winter ranges have not always supported moose since moose first colonized the Kenai after the Pleistocene. Spencer and Chatelain (1953) stated that in 1953 the Kenai had an aggregate of 2072 km² of wintering areas capable of supporting more than two moose per square mile. Of this, 388 km² were natural wintering areas such as

stream drainages, flood plains, timberline areas and flats below receding glaciers. Spencer and Hakala (1964) concluded that within recorded history the largest impetus to the production of moose populations was through widespread fires occurring about 1870 to 1900. Although many moose capes and antlers were exported from the Kenai Peninsula in the late 1800's the first records of very large populations were in 1913 and 1916, followed by other peaks in 1922-1923, 1936, 1945 (Spencer and Chatelain 1953) and in the 1960's. The extent and pattern of former burns, the probable vegetative development in these burns, and evidence of past heavy browsing indicates that moose populations during the past 75 years were probably lower than numbers present in 1964 (Spencer and Hakala 1964).

The 1947 Kenai Burn

The largest fire that has occurred on the Kenai Peninsula during recorded history was a 125,455 ha fire started from road construction on 3 June 1947 that burned relatively unimpeded for 6 weeks and covered the heart of the 7,770 km² (770,013 ha) Kenai lowlands (Spencer and Hakala 1964). The nature of vegetative growth within the 1947 burn indicates that no fire had occurred there for more than 50 years. All types of the interior forest are represented with a large number of relicts remaining--tracts unburned by reason of topography, ground fuel or fire behavior. These include pure stands of birch and aspen and some mature white spruce-birch forests located on ridges.

LeResche et al. (1974) presented a thorough discussion of the characteristics of the 1947 Kenai burn. The optimum amount of edge and/or the optimum size and shape of individual burned stands in Alaska

is difficult to determine because moose densities depend upon so many variables. However, the 1947 burn was nearly ideal as it represented one of the largest known areas of productive moose habitat.

LeResche et al. (1974) concluded that of the 260 km² area affected by the 1947 burn, over 60,000 separate stands having more than 11,000 km of ecotone and 128,000 ha of new shrub communities were created. And they concluded that it is not surprising that moose densities achieved such a high level as a result of the fire. The mature stands which comprised 46 percent of the burn sampled were extremely segmented.

Other Burns

Although numerous small spot fires have occurred on the Kenai during recorded history, relatively few were ecologically significant. A brief summary of each of the fires of presumed significance follows, as expanded from Spencer and Hakala (1964):

Funny River Plateau: This 8,000 ha benchland, about 305 m in elevation, burned most recently about 1885 to 1890 and probably covered a previous burn. The area continues to support a heavy growth of willow, hedged by browsing to 1.2 to 1.5 m high. Invasion by spruce has been slow but is increasing in recent years.

Chickaloon River: This poorly drained tract of 800 ha burned around 1900. It revegetated to a pure dense stand of black spruce and apparently never supported significant hardwood browse.

Bedlam Lake: A 4,000 ha white spruce-birch stand burned in 1915 to 1920. It revegetated to dense birch with sparse stocking of spruce and provided a significant wintering site during the 1930's and 1940's.

However, much of the birch stand grew out of reach and the area no longer produces much available browse.

Kasilof area: Approximately 4,000 ha to 4,800 ha in a settled area has repeatedly burned, most recently in 1926. Since 1920 it has supported high wintering populations of moose over much of the period; this has resulted in a hedge-like growth of birch and willow about 1.5 m high. Although much of this range is badly deteriorated due to overuse, much forage is still produced. Invasion of spruce has been slow.

Slikok area: A tract of white spruce of approximately 1,600 ha burned in 1926. Revegetation resulted in dense, even-aged stands of spruce which matured in the early 1940's. Concurrently, a good stand of willow, birch and aspen developed and was heavily used until 1950. The stand became decadent, but recent removal of spruce from the entire area by mechanical means has increased growth of browse species.

Engineer Lake: One-hundred sixty ha of the 1947 burn were reburned in July 1963 by a hot fire which removed all windfalls and moderately heavy spruce reproduction. At the end of the summer birch and willow rootstock showed regeneration by basal sprouting.

Swanson River: In 1969, 34,400 ha burned in the area east of the city of Kenai. This burn did not produce significant browse to attract many wintering moose until 5-10 years after the fire. However, the timing and location of this fire was critical because it now provides habitat for relatively large numbers of moose at various times throughout the year.

Russian River: In 1969 about 1,080 ha of spruce timber burned in the area west of the Russian River and immediately south of the Kenai River. Significant browse production is now occurring.

Mystery Creek: In 1974 about 1,520 ha were burned on lower Mystery Creek. The area was primarily mature black spruce.

The abundance of moose on the Kenai Peninsula has been or will be greatly influenced by these fires. The Kenai Peninsula first became famous for its moose population early in the 1900's following the occurrence of fires in the late 1800's. Of these the Funny River Plateau fire was most significant. By 1910 a rapidly expanding moose population was evident and it peaked in 1922-1923 and again at a higher level in the late 1960's or early 1970's (Spencer and Hakala 1964, LeResche et al. 1974).

The benefit of the 1947 burn to moose is best documented. Spencer and Hakala (1964) reported that no fire had occurred in the area of the 1947 burn for at least 50 years. Available winter forage for moose was scarce and in spite of a 15-year hunting closure the area supported a small moose population. In January 1950, 140 wintering moose were counted in the area. By 1959, 2,500 moose were wintering there. Empirical evidence suggests a corresponding benefit to moose from many of the other burns.

These major fires, smaller fires and limited mechanical disturbance of climax vegetation accounted for the great increase in the Kenai Peninsula moose population. The density increased from general scarcity in the 1870's to one of the highest levels ever recorded in the late 1960's and early 1970's (LeResche et al. 1974).

CARIBOU FIRE RELATIONSHIPS ON THE KENAI PENINSULA

Spencer and Hakala (1964) state that the Kenai Peninsula was evidently inhabited by Stone caribou, *Rangifer arcticus stonei*, Allen, until the 1890's following which they disappeared about 1913, presumably because of unfavorable forage changes (destruction of lichen range), blockage of migration routes and hunting of remnant populations.

This reference to hunting of remnant populations and blockage of migration routes suggest that factors other than destruction of lichen range may have been involved in the disappearance of the Kenai caribou. We were unable to find any documentation of migration route blockage, but reference to over-exploitation by humans is plentiful.

Early abundance of caribou on the Kenai Peninsula remains conjectural as no good reference to early abundance is available. However, Porter (1893, cited in Lutz 1960) in discussing the Kenai Peninsula for the Eleventh Census in 1890 wrote, "The open uplands and the swampy valleys and poplar thickets are still frequented by droves of moose and caribou...."

Seton-Karr (1887, cited in Lutz 1960) stated that Lieutenant Doroshin in 1850 and Ivan Petroff (no date) ascended the Kenai River and found reindeer (i.e. caribou) plentiful. Additional suggestion that caribou were reasonably abundant for some time on the Kenai is that the local natives had a name for caribou (Schiefner 1874, cited in Lutz 1960).

Pedersen (1976) states that caribou were plentiful and there were some moose on the Kenai Peninsula at the time the Russians arrived in 1786. Also, in describing the Kenai natives she wrote, "Caribou skin provided their clothing...long shirts of caribou fell to the knees...loose boots of caribou...."

Palmer (1938) wrote, "...Mr. Berg reports that there were practically no moose in the Kenai area when he arrived in 1890, but the woodland caribou were plentiful and wolves numerous."

On the other hand caribou must have been getting scarce in the late 1800's and there is ample evidence that overhunting was a major factor because reference to market hunting is abundant. Traffic in moose heads from Cook Inlet country in the 1890's was heavy. Burnham (1899, cited in Lutz 1960) reported that Wm. W. Hart and Co. received a remarkable shipment of heads from Cook's Inlet country including heads, horns and scalps of 22 bulls all very old and unusually massive. Lee (1898, cited in Lutz 1956) states, "...the game is wantonly killed by market hunters every winter...."

Elliott (1902) observed,

"On the Kenai Peninsula and surrounding districts head hunters, both white and red, have nearly exterminated the species [caribou] and the increased means of transportation to and through their country, the large number of hunters, greatly added to annually, and the improved firearms, would seem to foretell the extinction in a brief period of this fine animal in the regions where he is accessible."

Allen (1901) quoted Stone as follows: "Caribou...are already very scarce on the Kenai Peninsula, and will doubtless soon be exterminated, the region being greatly frequented by visiting sportsmen, while native hunters kill the moose and caribou for their heads, disposing of them at good prices for shipment to San Francisco." Phillips (1925, cited in Lutz 1956) remarked that caribou on the Kenai Peninsula "vanished as rapidly as the buffalo when modern rifles were sold to the natives by

enterprising American traders." Lee (1898, cited in Lutz 1956) reportedly killed three caribou between Kachemak Bay and Tustumena Lake.

Leopold and Darling (1953a) even mention in a general context that hunting of Kenai caribou may have been excessive when they state, "...uncontrolled killing of big game was likely worst in the period of widely dispersed trapper-pro prospector population. This was also the period when native Indians and Eskimos obtained general access to modern firearms and ammunition. For many years both moose and caribou were indiscriminantly overshot." This would seemingly apply to the Kenai Peninsula in the late 1800's.

Apparently market hunting continued through the period when caribou became extinct. Lucas (1932) states, "Market hunting was greatly curtailed from 1918 to 1925 when, with the passage of the Alaska Game Law, it was brought under almost complete control and now there is none."

Grant (1903) wrote, "The caribou of the Kenai Peninsula...was described in May 1901 by D. Allen.... As yet only three specimens are known. On the peninsula itself this fine animal seems to be on the verge of extinction, being now limited to one small herd."

Caribou-fire relationships on the Kenai Peninsula were initially discussed by Palmer (1933):

"The occurrence of fire on the Skilak-Tustumena Lakes area in about 1880 destroyed the climax cover and permitted establishment of subclimax dominants. This, as furnishing an abundance of suitable forage, provided for the income and establishment of moose. By destruction of lichens, however, the fire undoubtedly resulted in the disappearance

of caribou, last reported on the area in 1903. Moose appeared on the area 15 years following the fire and became abundant about 30 years after the fire."

Dufresne (1946) stated,

"In the year of 1883 a forest fire raged for months on the Kenai Peninsula. Shortly thereafter the caribou herds vanished. Coincident with this rapid passing of the caribou appeared the moose which were practically unknown on the Kenai before the big fire. Today not a single caribou exists on the Peninsula, but the place is world famous for its moose herds."

Leopold and Darling (1953a) state that their observations on the Kenai Peninsula suggest that there was insufficient lichen for caribou to find a meal through the snow in winter.

Buckley (1958) repeated the theme: "For those species, such as caribou, that require climax conditions, fire has undoubtedly reduced the quality of the range, and has contributed to the decline of caribou in Alaska noted during the first half of the century. With other species, such as moose, the result has been quite the opposite." Klein (1965) stated, "Changing habitat, possibly accelerated by fires started by man, may have caused the extinction of the caribou on the Kenai Peninsula before 1900."

Lutz (1956) stated,

"The problem of fires and caribou is in a category wholly different from that of fires and moose. Unlike the moose, which prefers pioneer plant communities or at least

vegetation representing early stages of successional development, the barren-ground caribou normally lives in environments characterized by climax plant communities, tundra and forest tundra transition."

He offers the summary statement that the effects of most fires on moose are generally favorable, but caribou are adversely affected by fires.

Leopold and Darling (1953a) stated, "The status of caribou, therefore, seems to be intimately associated with the presence of undisturbed climax vegetation of which the lichen share a prominent part. The caribou itself, then, can be thought of as a member of a climax biota."

Leopold and Darling (1953b) stated,

"The caribou, then, may be looked upon as a member of a climax biota.... The quickened rhythm of fire has encouraged the spread and local increase of moose, at the same time eliminating or greatly reducing the winter range usable for caribou. For example, caribou have been extirpated from the Kenai Peninsula and in fact from all the lowlands adjoining Cook Inlet...."

It is difficult to analyze what actually happened in the past, whether the Kenai caribou became extinct because of hunting and/or fires, or even other factors. However, we feel that over-exploitation is a more probable proximate cause of the extermination than fires. It should be noted that wolves were apparently extirpated through shooting and poisoning within 10 years following the 1896 gold rush, allegedly prompted by a rabies scare (Rolf Peterson, pers. comm.).

Fires eliminate much of the lichen forage in spruce forests for considerable periods, thereby reducing the potential carrying capacity

of a total range. However, on much of the Kenai Peninsula the irregular topography and the interspersed fire barriers permit many areas containing abundant winter forage to escape destruction by fire.

Skoog (1968) states, "The fact that Alaska caribou are not dependent upon lichen growth in spruce forest and can utilize the extensive sedge forage on the tundra, alpine meadows, bogs, and lake shores greatly mitigates the losses due to fire." As pointed out by LeResche et al. (1974) and Oldemeyer (1974), the extensive 1947 burn (the largest ever recorded on the Kenai Peninsula) encompassed 125,455 ha but only 53 percent of the vegetation was burned. About 37 percent of the area consisting of mixed mature white spruce-hardwoods or mature hardwoods was not burned and 10 percent of the area is low lying water, sedge, grass, or spruce-*Ledum* communities. Moreover, there is no evidence to suggest that a high percentage of the Kenai Peninsula was ever in a recent post-burn condition. Although fires have regularly occurred at least as early as 1851 (Lutz 1960), much of the Kenai apparently continued as poor moose habitat from old growth vegetation.

A more convincing argument that much suitable foraging area was present even immediately following the greatest period of burning was presented by Davis et al. (1978). The essence of their analysis is as follows:

"Caribou from the Nelchina herd were transplanted to the Kenai Peninsula in 1965 and 1966 and are presently well established (Burris and McKnight 1973). There are two distinct groups and both utilize winter range that was not affected by fires in the past. We interpret this fact as

suggesting that this habitat was also present at the time that caribou were eliminated, supposedly due to habitat destruction. A herd of 300 animals (maintained at that number by hunting) presently inhabits an alpine area in the Kenai Mountains, south of Hope. These animals attain large body and antler size, and the herd as a whole has excellent initial production. The herd uses an alpine area that has presumably been little affected by fire throughout the years.

A smaller herd (65-80 animals in 1976) occupies a black spruce muskeg habitat in the Kenai lowlands on the Moose River Flats and the vicinity of the Kenai Airport. The Moose River Flats area is inside the perimeter of the 1947 burn, but was likely little affected by that fire. The animals appear to feed mainly in sedge areas, but they may also be feeding on lichen in the sparse black spruce ecotype. Stands of climax white spruce forest are located to the east and to the north of this muskeg wintering area, but they apparently receive no caribou use, suggesting that habitat loss because of fire likely was not the sole reason for extinction of the Kenai caribou.

Apparently there is suitable caribou habitat in at least two other locations. The alpine benchland country between Tustumena and Skilak Lakes, and a more marginal area in the Caribou Hills. These areas of potential caribou habitat were probably never greatly affected by

fire. The Tustumena-Skilak Lakes area may be an exception. However, even here it is probable that sufficient winter range to support a sizable caribou population remained around the lakes and in the alpine area south of the Funny River Plateau burn."

Figure 1 delineates apparently suitable caribou habitat, present distribution of caribou and the distribution of known major fires on the Kenai Peninsula. Since much suitable potential habitat is outside of the area burned by the major fires, extermination of caribou because of fire seems a less tenable argument than over-exploitation.

To summarize, we believe that Bergerud's (1974) argument that North American caribou populations declined following settlement primarily because of over-exploitation applies to the extirpation of caribou from the Kenai Peninsula.

Mediating influences may have been involved as advanced by Skoog (1968):

"The presence of caribou on the Kenai Peninsula during this early period also might have been an indicator of a former high population farther to the north. This area, as well as the Chugach Mountains on the north through which the animals would have had to pass in order to reach the Kenai, can be considered as marginal habitat for caribou, because of the precipitous terrain, deep snows in the mountains, and rather limited suitable areas above timberline (i.e. extensive sedge-meadow and/or heath-lichen stands). There is no record indicating that caribou were ever

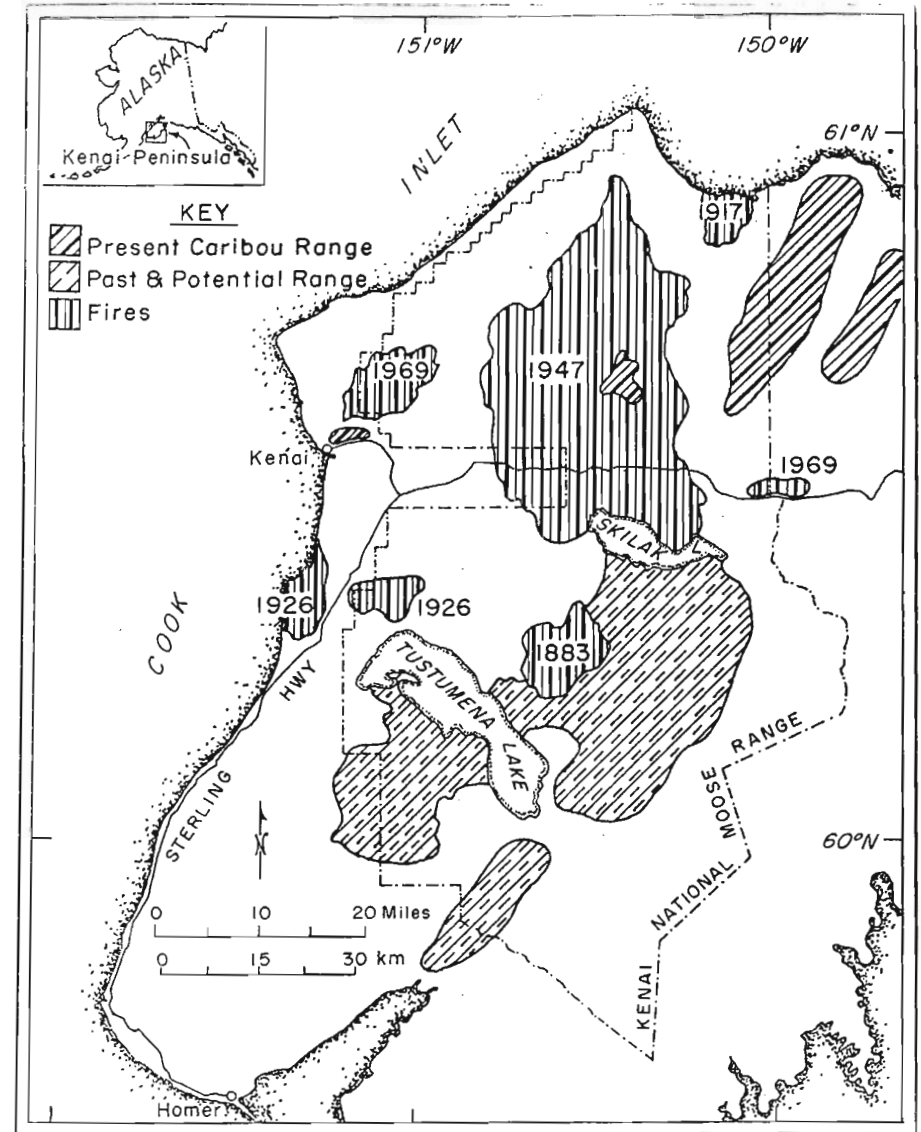


FIGURE 1. Caribou range and major fires on the Kenai Peninsula, Alaska.

particularly abundant on the Kenai. Petrov (1881:38) mentioned the natives there hunted caribou in the interior, but from this comment it would appear that moose and fish provided most of the protein food.... I concur more with O. J. Murie's (1935:77) statement, however, that, "The Kenai Peninsula seems to be simply an overflow area that probably often received an influx of caribou from unusual migratory movements of interior herds." In this respect, then, the Kenai Peninsula, like the Chitina River Valley mentioned earlier, would be utilized only as a result of high population pressures at the center of habitation."

MOOSE-CARIBOU INTERACTIONS

The literature is surprisingly lacking in information regarding interactions between moose and caribou. In Wolfe's (1974) review of moose coactions with other animals no mention was made of caribou. The three major life history summaries of North American caribou (i.e. Kelsall 1968, Skoog 1968, Bergerud 1971b) provide no information on the subject.

Peterson (1955) commented briefly on the subject, "So little is known of the ecology of woodland caribou that it is difficult to evaluate the relationships of the species with moose. In general it appears that direct competition is not a primary factor affecting the decline of the caribou. The introduction of moose to Newfoundland has apparently had little detrimental effect on the native caribou herds...." This also applies to several Alaskan situations. Moose and caribou increased simultaneously in the 1950's and early 1960's in the Nelchina Basin, in

the Fortymile area and in the Tanana Flats and associated uplands. This would imply that direct competition must not be of paramount importance.

A comparison of food habits of moose (Peek 1974b) and caribou (Courtwright 1959, Skoog 1968, Kelsall 1968, Bergerud 1972) shows that both utilize a great number of plant species and that both use many of the same species including browse. From this it could be concluded that direct competition may at times be significant. However, close inspection of the proportion of diet each plant species comprises and the seasonal preference for specific species and plant parts suggests that forage competition rarely occurs.

Moose and caribou may serve as reservoirs of disease and parasites for one another but to date only a few of these relationships have been documented (K. Neiland and R. Zarnke, pers. comm.). Agonistic encounters occur between the species but likely do not result in the exclusion of either from extensive areas.

SUMMARY AND CONCLUSIONS

Most northern biologists believe that fire is generally beneficial to moose although they acknowledge that the benefit depends on many variables. Further, moose numbers have repeatedly increased following alteration of vegetation by disturbance such as fires and logging. There is no evidence to suggest that the observed relationship is other than cause and effect. The mechanism for the increase in moose numbers can be demonstrated through an increase in available, palatable forage and perhaps increased quality of vegetation.

In contrast, the generalized observation that caribou populations declined throughout North America following settlement is apparently

valid. While many biologists have concluded that fires and logging destroyed lichen range which precipitated the declines, the conclusion does not appear tenable. We concur with Bergerud (1974) who states that two long-term studies of caribou life history (Skoog 1968 in Alaska and Bergerud 1971a, 1971b and 1972 in Newfoundland) concluded that caribou do not require lichens, and that range destruction was not a major factor in the decline of caribou in the early 1900's, and a third study in Northwest Territories (Banfield 1954 and Kelsall 1968) emphasized hunting mortality as the cause of the decline. We believe the following statement by Bergerud (1974) is most appropriate:

"Various ungulate species of North America declined in the 1800's and early 1900's. The generally accepted explanation of these declines was that the various species were overhunted when effective firearms came into general use. It seems paradoxical that caribou, which are probably more vulnerable to hunting than most ungulate species, should be considered the exception...."

The observation that moose numbers repeatedly increased on the Kenai Peninsula following fires, as in many other areas, seems to have been a cause and effect relationship. However, we believe two common conclusions regarding fire-moose-caribou relationships on the Kenai Peninsula are unwarranted. The common conclusion that moose are comparatively late arrivals on the Kenai Peninsula, first having appeared around 1871 or later, is totally unfounded (Lutz 1960). The conclusion that caribou were exterminated from the Kenai Peninsula as a result of forest fires appears likewise untenable. Although fires may have decreased the theoretical carrying capacity of caribou range on the Kenai, we are

confident that sufficient suitable habitat was always available for remnant populations.

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