

Distribution and Habitats of Moose in Alaska

by

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ABSTRACT

Moose (Alces alces) have been present in Alaska since mid- to late Pleistocene times. They probably survived in relatively small, disjunct groups wherever suitable habitat could be found throughout this period, when a tundra-steppe community dominated much of the Alaska refugium. With the close of the glacial period, climatic warming, and proliferation of shrub and forest communities, they spread throughout much of Alaska. In more recent times riparian and subalpine willow communities have provided a means of maintaining minimal populations able to exploit new range produced by fire and other disturbances. This pattern persists today. Very recent extensions of moose distribution have occurred in the geographic extremes of Alaska: in Southeastern Alaska, where glacial recessions have allowed moose to expand along major river valleys crossing the coastal range, and in northwestern Alaska, where moose have become established on the western Seward Peninsula and north of the Noatak River. On the Arctic Slope moose seem to have been established for a longer time than on the western tundra areas, but are currently increasing in numbers. In most of Alaska, moose numbers have risen and declined dramatically in local areas over the last 150 years, largely in response to creation and maturation of fire-caused seral range. Historical accounts that moose were absent

from a particular locale most likely reflect only a period of very low moose numbers resulting from a prolonged absence of fires in that area. Extremely low densities of moose presently exist in some areas where extensive spruce stands are dominant. Thus in most of Alaska the purported variations in moose distribution have in reality been only variations in relative abundance. Moose numbers increased steadily through the 1950's and early 1960's throughout most of the state, largely in response to rather regular recurrence of extensive wildfires. In many areas numbers apparently exceeded severe winter carrying capacity. In much of Southcentral and Interior Alaska, moose numbers have stabilized or declined in recent years, primarily in response to a series of severe winters, complicated by deteriorating range conditions, changing hunting pressure, and predation.

The most important moose habitats in Alaska include both climax and subclimax communities. Moose are present in low densities throughout the climax taiga communities of the northern boreal forest. Climax upland birch - willow communities and lowland bog communities support greater densities of animals, as do continuously-renewed riparian seral communities and more transitional post-burn communities. Upland moose habitats are very important in many areas of the state. These habitats are timberline shrub communities characterized by birch and willow, with heath and

forb understories. These habitats are used most intensively in summer and autumn, but are year-round residences for moose in some areas. Lowland climax communities are many and diverse, occurring on the broad alluvial plains common south of the Brooks Range. These communities are especially important during spring and summer, and support tremendous concentrations of moose during calving. Riparian willow communities, although seral in nature, are consistently present because of constant renewal. They are key winter ranges in much of Alaska and are the only habitat consistently occupied by moose in Arctic areas. Fire created communities have been responsible for the greatest densities of moose achieved in Alaska, but are the least permanent of the habitats discussed. Species composition, size of burn, rate of growth, diversity of communities and ecotone created together determine the impact of a burn on moose populations. Moose are generally unable to alter the rate of post-burn succession, but may alter its course, by destroying some favored forage species. With the exception of burns man-made habitats have been negligible in Alaska as a whole, although local moose populations have been affected in recent times.

Moose (Alces alces) entered North America through Alaska and today remain distributed over most of the state, from the Arctic Ocean to the Alaska Peninsula and the Southeastern Panhandle. This review describes probable past distributions and known present distribution of moose in Alaska, and describes and discusses the major habitats important to moose in the state.

The Alaskan moose (Alces alces gigas Miller) (Hall and Kelson, 1959) has always impressed scientists and sportsmen alike with its considerable body and antler size. Earliest accounts of the size of Alaskan moose were those of hunters and collectors of trophy antlers who created small sensations with antlers approaching 2 m in greatest spread (Lutz, 1960). The type locality for A. a. gigas is the Kenai Peninsula; the area known, at the turn of the century, as the home of the "giant Kenai moose." Since that time trophy hunters have found moose to equal and exceed those of the Kenai throughout much of Alaska (Alberts, 1971).

Moose in most of Alaska as well as in adjacent portions of Canada are considered A. a. gigas, but intergradation with A. a. andersoni probably does occur in Southeastern Alaska (Klein, 1965).

DISTRIBUTION

Present distribution of moose in Alaska is shown in Figure 1. From recorded and recalled observations it is clear that moose distribution and abundance in Alaska ^{have} been and continues to be very dynamic. We will briefly review prehistoric records of moose and more fully comment on the probable processes leading to present conditions.

PLEISTOCENE DISTRIBUTION

Moose are Alaskan and North American residents of long standing. Flerow (1967) surmised that larger Pleistocene mammals originating in Eurasia crossed the Bering Land Bridge readily, perhaps as early as the Kansan glacial period. Moose remains have been identified from sediments of Illinoian age (100,000-175,000 years old) in central Alaska (Péwé and Hopkins, 1967). Repenning (1967) indicates Alces immigrated from Pale-arctica early in the Rancholabrean mammalian age (between the Illinoian and Wisconsin glaciations) and are known from an earlier period (Gunz glaciation) in northeastern Siberia. Later immigrations during the Wisconsin (10-35,000 years ago) glaciation are implicit in these observations, and probably contributed to development of subspecies among Alces. Klein (1965) recorded the relatively recent penetration of the Coast Range icefields of Southeastern Alaska by moose from the Alaska-Yukon refugium as far south as the Taku River, where they intergrade with A. a. andersoni. Progenitors of andersoni were likely earlier immigrants than those of gigas, for moose remains are known from the refugium south of the Continental ice sheet (Osburn 1921, cited by Klein 1965).

Hopkins (1967) characterized climatic changes produced by Illinoian and Wisconsin glaciations as "severe refrigerations" that resulted in a lowering of treeline by 400 m or more (Pewé 1965, Repenning et al. 1964) and produced a considerably dryer climate than exists today. On the basis of several lines of evidence various authors agree that Alaska and Beringia in general supported largely steppe and tundra during these glaciations (cf. Repenning 1967, McCulloch 1967, Colinvaux 1964a, 1964b, 1967). Repenning (1967) noted that most of the Rancholabrean immigrants to Alaska

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were boreal forms, already adapted to an arctic-subarctic environment. Guthrie (1968) studied data on collections of Pleistocene large mammal remains from four mining areas near Fairbanks in central Alaska. Sediments containing the remains were of Wisconsin age at three sites, and pre-Wisconsin at the fourth. Remains of grazing mammals predominated at all sites, and browsing mammals were very scarce. Moose comprised less than one percent of the remains except at one site, where they approached five percent. Guthrie concluded that the habitat of this mammalian complex was a grassland supporting a substantially larger biomass than the present vegetation complex, typical of Interior Alaska moose habitat.

RECENT PREHISTORIC DISTRIBUTION

On the basis of former forest extension with beaver (Castor spp.) present on the Seward Peninsula, and of glacial recession in the Brooks Range, McCulloch (1967) concludes an early Recent warming trend occurred in Northwestern Alaska 8000 to 10,000 years ago. A cooler period followed with reverse effects. Following this, McCulloch believes the Postglacial thermal maximum occurred in Alaska 3,000 to 6,000 years ago. Since then brief thermal fluctuations have occurred, with the most interesting note from our viewpoint that small glacial advances occurred in the Brooks Range about 1,000 to 1,500 years ago, and again during the first half of the 18th century (Porter 1964). During the last 200 years the climate has grown warmer.

Although there is little direct evidence of moose distribution from this period, it is clear from this brief summary that climatic trends were conducive to improved habitat conditions for moose. If beaver invaded

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western Seward Peninsula, it is very likely moose did also. Although both subsequently disappeared from that area, the response of forest and beaver to the early Recent warming is indicative of change that surely occurred in vegetation and in distribution of browsers such as moose as climatic warming ensued.

In summary, once moose immigrated to Nearctica they persisted, in Alaska at least, under marginal circumstances for several thousand years. During much of this time the environmental circumstances could hardly have been better than those to which Miller et al. (1972) attributed the death of a lone moose in the Keewatin District of Canada, concluding it had "overextended" its range.

During the last few thousand years, development of extensive shrub and forest communities favored increased moose densities throughout much of Alaska. As taiga developed, pioneering willow communities (in areas of glacial recession, unstable slopes and riparian situations) probably assumed increasing importance, since the taiga is basically incapable of supporting high densities of moose. Nevertheless, overall trends in plant communities undoubtedly favored moose.

EARLY HISTORIC DISTRIBUTION: 1800-1950

Post-Pleistocene moose remains and written records of moose distribution prior to 1800 are scarce. The record is little better since that time for many parts of the state because few people possessing written language travelled or lived in those areas. Some information has been gained from early explorers and archaeological work, and inferences can be made on the basis of native cultures.

Interior and Southern Alaska - Lutz (1960) reviewed early records from many sources on the occurrence of moose in Alaska, and concluded that moose have long been residents of most of Alaska. In view of the foregoing discussion of moose in Pleistocene times, and considering probable evolution of biotic communities (Hopkins 1967) since that time, no other conclusion seems tenable.

There is no need to repeat all of Lutz's comprehensive review, but a few references will serve to show that moose were present over much of Alaska in the 1800's, when Caucasian activity was increasing rapidly. LaPerouse (1797) observed a tanned moose hide at Lituya Bay (south of Cape Fairweather, Southeastern Alaska) in 1786. This hide was very likely obtained in trade, however. Wrangell (1839) noted that Indians of the Copper River used moose hides and sold them, and that moose occurred throughout the Copper River Basin, a large area in Southcentral Alaska. Zagoskin (1967) noted moose or their use by Indians along the Yukon, Kuskokwim, Innoko and Koyukuk Rivers of Interior Alaska in 1842 to 1844.

Howard (1868) noted deer (caribou, Rangifer tarandus) and moose on the Alaska Peninsula, and that moose meat was the main food at Ft. Yukon, far up the Yukon River. Raymond (1871) stated moose were numerous on the upper Yukon in 1869, and in 1873 reported that moose occurred on the Arvik River, Tanana River, and Porcupine River, all tributaries of the Yukon River. Turner (1886) reported that moose were abundant at the headwaters of the Tanana, Kuskokwim and Nushagak Rivers. Wickersham (1938) noted the presence of moose along the Yukon River between Eagle and Circle near the Canadian border in 1901-1902, and abundant moose along the Kantishna River north of McKinley Park in 1903. Sheldon (1930) commented on numerous

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sightings of moose in McKinley Park in 1904. Osgood (1909) found moose locally abundant between Eagle and Circle on the Yukon River, and noted market hunting was heavy adjacent to these settlements. Lutz (1960) gives many references to show that moose were known on the Kenai Peninsula since the early 1800's, and in fact were present in archaeological sites dated to about 750 B.C. He concluded that the often repeated story that moose were absent from the Kenai prior to 1870-1900 had no basis in fact.

Murie (1959) cites Osgood's (1904) report that moose were reported in several local areas on the Alaska Peninsula between 1901 and 1903, including a report from as far west as Port Moller. Chatelain (1952) reported that residents felt moose had "invaded" the Alaska Peninsula about 1923 or 1924. However, it is most likely that moose numbers were rapidly recovering from effects of the last major volcanic eruption of Mt. Katmai in 1912 (Alaska Department of Fish and Game 1973). Vegetation over a considerable portion of the upper Alaska Peninsula was damaged or killed by ash from this eruption.

Thus it appears that moose were present throughout most of Interior and Southcentral Alaska in the 1800's. In some areas they apparently were abundant. Athabascan Indians of Alaska developed a tradition of dependence on moose for a substantial proportion of their food and clothing, particularly during winter when moose tended to congregate in riparian willow stands.

Still, numerous early accounts exist of moose being absent from a particular area, or of having recently moved into a locale; we believe moose were present in most of these areas, but their numbers may have been extremely low at various times.

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Arctic Alaska - In the Brooks Range, on the Arctic Slope, and on the tundra of northern and western Alaska moose were apparently very scarce at the turn of the 20th Century. Leopold and Darling (1953a) suggest moose were rare on the North Slope in the early 1900's because most travellers on the Colville River failed to mention moose or their signs. Moose did not inhabit the Colville River Delta until about 1890 to 1910, were seen rarely through about 1930, and became common by the early 1950's, based on our interpretation of events reported by Bee and Hall (1956). Bee and Hall also cite Stone's (1903) observation of a moose on the upper Colville River in 1900.

The Nunamiut Eskimo of Anaktuvuk Pass formerly ranged throughout the central Brooks Range, Arctic Slope, and down to the Arctic coast. Robert O. Stephenson (vive voce) summarizes the Nunamiut's collective observations thus: moose were rare, essentially absent, from the central Brooks Range and Arctic Slope from around 1900 to about 1930. At least in the early 1930's moose were still essentially absent on the middle Colville River. A few moose were seen in the late 1930's, and they were common in some places along the Colville. During the late 1930's and 1940's moose slowly became more abundant, and they were quite common in the 1950's. Stephenson feels that intensive native hunting along the well-traveled Colville River may have retarded growth of the moose population prior to 1920. Most of the Nunamiut moved to the coast in the 1920's and early 1930's, removing much of whatever hunting pressure they had applied, and the moose population subsequently increased. Wolves may well have contributed to control of moose until the late 1940's and early 1950's when extensive predator control work was done on the Arctic Slope.

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Trends in moose numbers followed a similar pattern south of the Brooks Range in the upper Koyukuk River drainage. Observations gathered from older residents of the Koyukuk by Stephenson indicate moose were first seen around Wiseman (upper Koyukuk River) in 1922 to 1924, after virtual absence for perhaps 20 years. Further down the Koyukuk River at Huslia, moose became noticeably common about 1925 (R. A. Rausch, vive voce, from Jack Sackett of Huslia). James Tobuk, Anaktuvuk Pass (vive voce), felt that the influx of miners in the early 1900's substantially depressed moose numbers along the Koyukuk River.

In summary, available records for the Brooks Range and Arctic Slope indicate few moose about 1900, with a very slow increase resulting in moose becoming common, and in some locations abundant, by the early 1950's. Moose numbers seem to have increased in similar fashion on the south side of the central Brooks Range.

Western Alaska - Along the northwestern and western coast of Alaska moose seem to have been essentially absent beyond treeline at the turn of the century, but few records exist. Hadleigh-West (1966) found no moose remains in archaeological excavations of two houses at Ogotoruk Creek, near Cape Thompson on the northwest coast. The houses had been occupied from about 1880-1900 until recently. Remains of various other terrestrial and marine animals were abundant. What accounts are available concerning the Noatak and Kobuk Rivers suggest a gradual increase in moose numbers similar to that in the central Brooks Range. On much of the Seward Peninsula moose were absent until perhaps as recently as the last 30 years. South of the Seward Peninsula moose probably occurred in small, disjunct groups along streams flowing into Norton Sound where treeline extends to

the coast along many streams. Moose have evidently been residents for some time, because in the local Eskimo dialect there is a specific word for moose. By comparison, the local Eskimo word for moose on the Seward Peninsula is a modification of the word for caribou (John J. Burns, vive voce). Nelson (1887) noted that a few years prior to 1881 a moose was killed on the Yukon Delta quite near the Bering Sea, which suggests moose occasionally wandered west from better habitat along the Yukon River, much as they do today.

To the best of our knowledge the Yukon-Kuskokwim Delta has never supported more than the occasional wandering moose.

CONTEMPORARY DISTRIBUTION: 1950-1972

Efforts to document distribution and relative abundance of moose throughout the state have increased considerably within the last 30 years. Several transplants of moose have also been made, which extended the distribution of moose in Southeastern Alaska. In general, moose appear to be increasing and extending their distribution in extreme northern and western Alaska and in local Southeastern areas, while in much of Southcentral and Interior Alaska current population trends are stable or downward.

Southeast Alaska - Moose naturally invaded Southeastern Alaska (the area south of Cape Fairweather) via the Chilkat, Taku, Stikine, Unuk, and Alsek Rivers from Canada (Klein 1965). A small natural population also exists at Thompson Bay, north of the Stikine River. It is apparently dependent on secondary succession following clearcutting of timber (Alaska Department of Fish and Game 1973). Timing of moose invasions in the Chilkat,

Taku and Unuk Rivers is not known, but they must have occurred well before 1900. Small populations limited by restricted habitat have persisted.

Moose probably invaded the Yakutat area by the Alsek River valley 40 to 50 years ago, following recession of glaciers that previously blocked access (Klein 1965). Since then the population has grown rapidly, and may have approached 4000 to 5000 (Alaska Department of Fish and Game 1973) prior to the winter of 1971-72, when substantial losses occurred due to deep snow. The Icy Cape-Yakutaga area north of Yakutat may have been colonized by moose from Yakutat, or from the Copper River Delta population.

Moose apparently became established in the Stikine River valley between 1875 and 1900 (Klein 1965). Habitat is limited, but a small population thrives there. Twenty-one moose calves were transplanted to Berner's Bay, 34 miles north of Juneau, in 1958 and 1960 (Burris 1965). This population grew rapidly and needs control by continued sport hunting to avoid over-use of its range (Alaska Department of Fish and Game 1973).

Fourteen moose calves were released at Chickamin River on the east side of Behm Canal, east of Ketchikan, in 1963 and 1964 (Burris 1965). Moose have been observed there since that time, but the population does not seem to be increasing. Moose persist at low densities in the Unuk River valley (Robert Wood vive voce).

With the exception of Yakutat, none of the Southeastern areas can sustain large populations of moose, but all populations do support limited sport hunting. Habitat is limited to relatively small areas in and adjacent to river valleys, where coastal and interior influences mingle.

Southcentral Alaska - For discussion purposes, Southcentral Alaska includes the area south of the Alaska Range, the Bristol Bay drainages, and the Alaska Peninsula. It includes a striking diversity of ecotypes, ranging from coastal rain forest in Prince William Sound, to taiga south of the Alaska Range, to coastal tundra on the Alaska Peninsula.

Prince William Sound - Moose were probably effectively isolated from Prince William Sound by glaciation and by Miles Canyon on the Copper River (Klein 1965). The largest extant population was established on the Copper River Delta by a series of transplants between 1948 and 1958 (Burris 1965). This population is largely dependent upon riparian willow communities, and now occupies essentially all available range (Alaska Department of Fish and Game 1973).

A few moose inhabit the Valdez area, and they occasionally reach western Prince William Sound via the Nellie Juan River (Ronald Somerville, vive voce).

Kenai Peninsula - Moose are absent from much of the southern coast of the Kenai Peninsula, which is isolated by the Kenai Mountains and the Harding Icefield. The eastern portion of the Kenai Peninsula is mountainous, available habitat is limited, and in many areas browse is decadent. Moose numbers have declined here since the late 1950's, although distribution has probably changed little.

Chatelain (1952) stated moose numbers on the Kenai Peninsula probably peaked in 1925, and had declined somewhat by 1950. He cited major fires in 1871, 1891, and 1910 as the probable cause for subsequent moose increase. His comments do not relate directly to the eastern Kenai

Moose have been seen as far west as Port Moller and Pavlof Bay (Murie 1959, Alaska Department of Fish and Game 1973).

Upper Bristol Bay Drainages - The status of moose populations in this area is poorly known. General observations indicate similar distribution but lower densities than on the Alaska Peninsula.

Matanuska and Lower Susitna Valleys - This broad area forms an arc surrounding upper Cook Inlet, and originally supported mainly taiga vegetation. Agriculture, other development, and associated fires beginning in the 1920's and 1930's prompted substantial production of browse species in much of the Matanuska Valley and adjacent Susitna Valley (Hatter 1948, Chatelain 1952, Alaska Department of Fish and Game 1973). In remote areas west of the Susitna River, riparian and subalpine willow communities, old burns and glacial outwash areas provide prime moose habitat. Moose populations reached historic highs over much of the area in the late 1950's. Maturation of browse communities and continued human development have since impinged on available moose winter range, particularly in the immediate Anchorage area. Numbers of moose have declined in certain areas and stabilized in others as a result. Moose numbers are still high, however, with an estimated 15,000 moose east of the Susitna River, and unknown but substantial numbers to the west (Alaska Department of Fish and Game 1973). Primary wintering and calving areas are on lowlands, and migrations to adjacent highlands occur in summer and fall. Distribution and movement patterns have not changed significantly in the last 20 years, although redistribution of wintering moose has occurred in response to maturation of range and development.

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Peninsula, but rather to the foothills and broad flats extending west from the Kenai Mountains. Large fires in 1947 and 1969 have resulted in a current peak of moose densities in this area.

Moose are found throughout the western portion of the Kenai Peninsula. They exhibit strong seasonal movement patterns (LeResche 1973a and this volume) in which substantial numbers alternately use upland willow communities and lowland birch-spruce second growth. General distribution and movement patterns probably have changed little since 1950, but succession following fire has undoubtedly produced spatial readjustments in seasonal use patterns as well as an increase in moose numbers.

On the southwestern portion of the Kenai seasonal distribution and movements have probably changed little in the last 20 years. However, certain winter ranges are currently very decadent and little used. Fires have been rare in the area. Total moose population on the Kenai probably exceeds 15,000.

Six moose were released on Kalgin Island in Cook Inlet near the Kenai Peninsula between 1958 and 1960 (Burris 1965). A small population persists there.

Alaska Peninsula - Chatelain (1952) noted moose numbers were increasing on the Alaska Peninsula through the late 1940's. The increase continued in certain areas, principally south of Mother Goose Lake, through the early 1960's (Alaska Department of Fish and Game 1973). Greatest densities of moose presently are associated with willow communities on and adjacent to drainages from King Salmon River to Meshik River. An estimated 7,500 moose inhabit the area (Alaska Department of Fish and Game 1973). Chatelain (1952) ventured to say that moose populations would not reach great numbers on the Alaska Peninsula, but in fact they have.

Copper River and Upper Susitna River - This vast area lies between summits of the Alaska Range on the north and west, the Chugach Mountains on the south, and the Wrangell Mountains on the east. Much of the area lies above timberline, but considerable area supports predominantly taiga. Moose are found wherever suitable habitat is available, in plant communities ranging from subalpine willow to old burns and riparian communities. Greatest concentrations of moose occur in sub-alpine climax willow communities in October and November, and in lowland riparian willow communities later in winter. Substantial numbers of moose occur at low densities throughout areas supporting predominantly spruce, but with willows, birch and other shrubs comprising a sparse understory.

Chatelain (1952) observed that moose were increasing rapidly in this general area in response to extensive fires over the preceding 30 years. Additional factors that may have contributed to marked increases were cessation of market hunting and virtual elimination of wolves in much of the area, (Alaska Department of Fish and Game 1973). An estimated 25,000 to 30,000 moose occupied the western and northern two-thirds of this area in 1965. Since then, a considerable decline has occurred for various reasons. Deterioration of range quality and quantity is most likely, but predation, combined with heavy hunting pressure in certain areas, may also have contributed to the decline. Range conditions may have been affected by high moose populations, and in some areas high snowshoe hare (Lepus americanus) populations in 1963-1964 did kill substantial numbers of willows (Alaska Department of Fish and Game 1973). Although wildfire has been of only local and limited importance in creating moose range, the acreage burned in the last 15 to 20 years (Barney 1969) has declined

to near zero, and therefore has made virtually no contribution to support of moose.

Interior Alaska - Interior Alaska comprises the drainages of the Yukon and Kuskokwim Rivers. In contrast to the Copper River-upper Susitna River area discussed above, a large proportion of Interior Alaska is below timberline (Viereck and Little 1972, Warhaftig 1965). Moose inhabit all of the Interior except alpine areas.

Populations are probably more closely attuned to the frequency and extent of wildfires here than in any other part of the state. Extensive and important ranges of both subalpine and riparian willows exist throughout the Interior, but fire-caused seral range undoubtedly determines the upper limit of carrying capacity. The warm, dry summers of the Interior are conducive to lightning storms and to excellent burning conditions.

In the broadest sense, Interior Alaska moose distribution has changed little in the last 20 years; that is, no previously unoccupied range has been occupied. Changes in abundance have occurred, however. During the late 1950's moose numbers appeared to be rising throughout much of Interior Alaska (U. S. Fish and Wildlife Service, Alaska Department of Fish and Game unpublished reports, and Alaska Department of Fish and Game 1973). Quantities of additional seral range were created through relatively regular and extensive wildfires (Hardy and Franks 1963, Lutz 1956, Barney 1969).

Because the quantity of climax alpine and riparian winter range is relatively constant, seral range created by disturbance is the major agent for increase in carrying capacity. As Geist (1971) succinctly states, climax-type ranges support a nucleus population from which individuals can rapidly colonize newly created transient (seral) habitat. In Interior Alaska, fire is the chief disturbance.

Many of the Interior Alaska areas most heavily used by moose in fall and early winter are burns that date from 1957, when an estimated 5 million acres burned in Alaska (Hardy and Franks 1963). Local distribution of moose is materially affected by the prevalence and successional stage of fire site vegetation dating from that year. Annual concentrations of moose in old burns occur usually from October into December.

Similar effects occur on a broader scale. Chatelain (1952) reported low numbers of moose along the Kuskokwim River in the taiga zone. Today, moose are abundant, although areas of abundance are discontinuous. In contrast, moose in the Big Delta area south of Fairbanks have declined from the abundance reported by Chatelain largely in response to successional changes in seral range.

The importance of snow characteristics must be emphasized in any discussion of moose distribution or abundance (Coady, this volume). Rapid accumulation of snow on higher seral and sub-alpine ranges appears to accelerate movement to lowland seral and riparian ranges. Deep snow for extended periods can substantially lower productivity, calf survival, and adult survival (Bishop 1969).

In summary, general distribution of moose in Interior Alaska has not changed materially in the last 20 years, but local distribution and abundance have been substantially affected by creation and maturation of primarily fire-caused seral ranges. In addition, a series of relatively severe winters (in terms of snow depth and temperature) has recently caused reductions of moose numbers in much of the Interior.

Western and Arctic Coastal Alaska - The only area where moose have significantly extended their range in the past two decades appears to be

northwestern coastal Alaska, including the Seward Peninsula north to the vicinity of Point Hope.

Moose have occurred commonly in and near the limit of timberline on the eastern Seward Peninsula for an indefinite but long period (Alaska Department of Fish and Game 1973). Within the last 20 to 30 years, however, they have gradually become common on the western, treeless portion of the Peninsula. Brooks (1953) reported shooting a bull moose near Cape Prince of Wales in 1948, one of the earliest documented occurrences of moose on the Seward Peninsula. Chatelain (1952) commented that a few moose were found on the Seward Peninsula. Although densities are low compared to Interior Alaska populations, moose are now permanent residents throughout most of the Peninsula. Beyond treeline, moose depend upon upland willow communities for much of their summer range, and upon riparian willow communities in winter.

In the Kobuk and Noatak River drainages to the north moose were apparently scarce or absent until 50 to 75 years ago (Alaska Department of Fish and Game 1973). In coastal areas north of the Noatak River moose were definitely absent as noted earlier. They have reached the Point Hope area only within the last five years (Alaska Department of Fish and Game 1973). Beyond treeline they concentrate in riparian willow habitat during winter.

Thus, the western Seward Peninsula and the northwest coastal areas of Alaska are the only actual extensions of moose distribution that have occurred in the last 20 to 30 years in Alaska.

Although moose have increased in number on the Arctic Slope over the last 20 years, their distribution has changed little. Within the last 5

years, many more sightings of moose have been reported, largely because of increased activities related to the developing oil fields. On the basis of these various reports, limited surveys by the Alaska Department of Fish and Game, and reconnaissance by Renewable Resources Consulting Services Ltd., moose population densities appear highest from the Colville River east to the Canning River. Moose do occur outside of this area along essentially all major streams. Records are fewer from the west, but Chesemore (1968) recorded several sightings from the Barrowvicinity and Meade River for the period 1958-1963.

Yukon-Kuskokwim Delta - Moose distribution apparently has not changed appreciably over the last 20 to 30 years in the Yukon-Kuskokwim Delta area, where occasional wanderers are the rule, nor in Norton Sound, where moose regularly approach the coast along timbered valleys.

HABITATS

Because moose occupy perhaps 1,350,000 km² of Alaska's 1,518,000 km² of very diverse wild land, it is necessary to generalize considerably in this discussion of their habitats in the state. The most important of these habitats can most simply be considered as being composed of four major "types" occurring relatively distinctly or intergraded. Each "type" represents a continuum of rather similar communities. Climax communities utilized are (1) upland willow (Salix spp.) or birch (Betula spp.) dominated communities and (2) lowland bog areas; seral communities include those created by (3) fire and by (4) glacial or fluvial action. This discussion will deal with these four types, but it must be emphasized that the types are seldom discrete are very often mixed and are sometimes

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hybridized with each other or with the coniferous, mature deciduous, or tundra types also abundant in the state. Further, although these four types are differentially important to moose in various parts of the state, many moose populations migrate between two or more types annually. In contrast, some populations exist entirely within a sometimes very small area of only one type community, and survive year-round on it. In addition to these four types, other taiga communities are very widespread, but support only low densities of moose wherever they occur.

UPLAND CLIMAX COMMUNITIES

These communities have been little studied but are of great importance throughout the Alaska and Seward Peninsula, Southcentral Alaska (including the Kenai Peninsula and Matanuska highlands) and southern Interior Alaska, as well as on the south slopes of the Brooks Range. They are essentially timberline shrub complexes containing both birch (predominately Betula glandulosa and B. Nana) and several species of willow mixed with heaths and forbs, and often intergraded with coniferous taiga communities growing at lower elevations.

These communities occur on relatively well-drained uplands, generally commencing at 600m or more elevation, but also occurring as low as sea level in some areas. The type extends to elevations of 1200-2000m, depending upon local timberline. Upland streamsides usually support the most dense and tallest willow shrub stands, with birch dominated communities being more common in the drier sites between. The upland shrub type most often intergrades with alpine tundra or heath-dryas

communities at higher elevations, and with spruce (Picea spp.)-birch taiga below. The upland shrub communities often contain scattered white spruce (Picea glauca) at their lower reaches.

Hanson (1951) likened the birch shrub type ("scrub birch") to communities described in Norway by Nordhagen (1943) as "dwarf heath shrub on lime - poor rock" and to communities in northern Siberia and northwestern Manchuria called "jernik" or "shrub tundra" by Imaniski (1950). Birch shrub communities may be created by repeated fires in spruce-paper birch (Betula papyrifera) stands, or by peculiarities of topography and elevation alone. Upland willow stands along streams are the rule in areas both with and without recent fire history and are primarily products of topography, soils and elevation.

Tables 1 and 2 list floristic characteristics of upland willow and shrub birch stands from Interior and Southcentral Alaska. These communities are often interwoven along stream-cut rolling hills and upland plateaus. Forb species present vary considerably by area of the state and specific site, but the woody shrub and heath species listed are representative of most upland moose habitat in Alaska.

Willow Communities - These communities are concentrated at streamsides above timberline or in low coastal tundra areas. Shrubs may be decumbent, at higher elevations, growing no more than 20-30 cm tall. In the more lush stands at lower elevations, willow species are tree-shrubs, often more than 1.5 m tall. Density of willows generally decreases with increased elevation, but very high densities occur in the lushest stands (Table 1).

Shrub Birch Communities - These communities also occur at and just below timberline, but on drier sites than upland willow stands. Shrub height

Table 1. Composition and some characteristics of two upland willow communities in Interior Alaska; modified from Milke 1969.

Location	Elevation	Dominant Species Present	\bar{X} Ht. (cm)	\bar{X} Stems/hectare
Mt. Fairplay (63°46'N 142°13'W)	1690m	<u>Salix pulchra</u>	95	23,709
		<u>S. glauca</u>	71	13,600
		<u>S. arbusculoides</u>		
		<u>S. alaxensis</u>		
		<u>S. depressa</u>		
		<u>S. scouleriana</u>		
		<u>Betula nana</u>		
		<u>Vaccinium uliginosum</u>		
		<u>V. vitis-idaea</u>		
		<u>Calamagrostis sp.</u>		
Wood River (63°45'N 147°45'W)	1100- 1450m	<u>Salix alaxensis</u>	141.5	7,022
		<u>S. glauca</u>	113.8	10,823
		<u>S. arbusculoides</u>	121.2	6,178
		<u>S. lanata</u>	68.2	20,287
		<u>S. hastata</u>	44.8	34,619
		<u>S. barclayi</u>	56.5	11,105
		<u>S. pulchra</u>	58.9	8,070
		<u>Picea glauca</u>		
		<u>Populus trichocarpa</u>		
		<u>Betula nana</u>		
		<u>Vaccinium uliginosum</u>		
		<u>Shepherdia canadensis</u>		

Table 2. Mean composition and cover of 10 upland shrub ("shrub birch") stands measured in the Nelchina Basin, Alaska by Hanson in 1957 and 1958: modified from Pegau, 1972. Average cover was measured by the modified Hult-Sernander scale.

	Average Cover	Frequency of Occurrence in 100-lm ² Quad- rats	Frequency of Occurrence in 10 Stands
<u>Betula glandulosa</u>	2.5	92	100%
<u>Salix arctica</u>	0.2	11	40%
<u>S. pulchra</u>	0.5	26	70%
<u>S. glauca</u>	0.2	6	20%
<u>Vaccinium uliginosum</u>	1.5	73	100%
<u>V. vitis-idaea</u>	1.6	99	100%
<u>Empetrum nigrum</u>	1.6	74	100%
<u>Ledum decumbens</u>	1.1	57	90%
<u>Diapensia lapponica</u>	0.1	8	30%
<u>Arctostaphylos alpina</u>	0.1	2	10%
<u>Dryas octopetala</u>	0.2	8	30%
<u>Loiseleuria procumbens</u>	0.0	1	10%
<u>Rubus chamaemorus</u>	0.1	6	20%
<u>Spiraea beauverdiana</u>	0.1	6	10%
<u>Calamagrostis canadensis</u>	0.6	61	90%
<u>Festuca altaica</u>	0.4	33	60%
<u>Hierochloe alpina</u>	0.6	50	80%
<u>Arctagrostis latifolia</u>	0.0	1	10%
<u>Carex bigelowii</u>	0.7	48	70%
<u>C. montanensis</u>	0.1	8	10%
<u>C. podocarpa</u>	0.0	1	10%
<u>Anemone narcissiflora</u>	0.4	31	60%
<u>Artemisia arctica</u>	0.2	17	50%
<u>Pedicularis spp.</u>	0.1	13	50%
<u>Polygonum bistorta</u>	0.4	33	60%
<u>Cornus canadensis</u>	0.0	3	20%
<u>Lycepodium annotinum</u>	0.0	1	10%
<u>Antennaria monocephala</u>	0.0	4	20%
<u>Arnica lessingii</u>	0.0	2	10%
<u>Gentiana glauca</u>	0.1	5	20%
<u>Stellaria laeta</u>	0.0	1	10%
Mosses	3.9	99	100%
Lichens	4.4	100	100%

may vary from 20-30 cm to over 2m, depending upon location and elevation. Densities of shrubs within the type are quite variable, but generally decrease with increased elevation. Dominant and characteristic species include Betula glandulosa, Vaccinum uliginosum, V. vitis-idaea, Ledum decumbens, Empetrum nigrum, Salix pulchra, Calamagrostis spp. and Festuca spp. Mosses and lichens are the typical understory plants. Forbs and grass species vary with the site.

Moose Use - Most upland shrub communities are important to moose in summer and autumn; however, in some areas of light snowpack they support moose throughout the year. In the Kenai Peninsula and Matanuska Valley and many areas of Interior Alaska, moose migrate to these areas in June and July, breed in these communities or slightly below in mixed shrub birch-white spruce stands, and return to upland shrub areas until driven out by snow in November or later. Mature bulls and cows without calves are most characteristic of these upland areas, for cows with calves and young bulls tend to remain in lowland areas throughout the summer (LeResche 1973a and this volume). In contrast, in some Interior Alaska areas moose desert lowland summering areas and move upward to shrub communities in winter (LeResche 1973b).

With the exception of temporary aggregations, moose density seldom reaches extreme levels on upland ranges, but densities of 0.8-1.6 moose per km² are not uncommon over vast upland areas. As a result, and because the range is seldom occupied throughout the year, we know of no major instances where upland shrub communities have been over-utilized by moose. One such case possibly exists in the Nelchina Basin, south of the Alaska

Range, where moose populations have decreased drastically since 1965. A series of severe winters has occurred, along with a general drying trend, and many upland shrub stands are in low vigor today (Pegau 1972). Specific moose-habitat relationships in the area remain unclear, however.

Upland ranges are permanent refugia for moose populations, and are among the most luxurious in Alaska. Due to their topography they have seldom been encroached upon by man, and the limited use receive relative to standing biomass insures their continued high-quality. Upland ranges are very extensive in some areas. Skoog (1968) estimated that shrub birch and willow communities made up 18.7% of the 44,800 km² of moose and caribou range he studied in the Nelchina Basin. Only a few moose winter in these ranges in normal years. During years of light snowfall, moose remain in upland areas well into winter, thereby relieving pressure on heavily used lowland wintering areas (LeResche 1973b).

Forage quality on upland ranges is sometimes superior to that in fire-created seral winter range. Washed rumen contents from eight moose collected from upland shrub ranges on the Kenai Peninsula in November, 1970 (LeResche and Davis, unpubl.) had higher protein (6.5 vs 6.1 g%), caloric value (245 vs 230 cal/100g) and digestible dry matter (16.3 vs 15.2% in bovine rumina) than those from six moose collected on adjacent seral birch ranges 30 km away. Identified rumina on the upland range were 59% Salix spp., 33% Betula spp., 3% Aspen (Populus tremuloides) and 5% forbs by volume. On the seral range, identified plant particles were 39% Salix spp., 36% Betula spp., 6% aspen, 14% Vaccinium vitis-idaea and 3% dried leaves.

LOWLAND CLIMAX COMMUNITIES

This habitat type contains a broad spectrum of communities particularly important to moose during summer. In addition, all the major calving concentrations we know of in Alaska occur in boggy lowland climax communities. These communities are an integral part of taiga vegetational complexes throughout Interior and Southcentral Alaska.

Extensive lowlands, locally referred to as "flats" or "muskeg," occur on broad alluvial plains from the south slopes of the Brooks Range to the southern coastal forests, and from the Alaska-Canada border nearly to the Bering and Chukchi Seas (Wahrhaftig 1965, Johnson and Hartman 1969). Approximately 30 percent of this area is forested, while the remaining land consists of bogs, shrub thickets, and alpine tundra (Viereck, ms). Surface vegetation patterns are closely related to topography, drainage, presence or absence of permafrost, and past fire history.

Surface features in lowland areas frequently include extensive flood plains with little relief, meander scars and oxbow lakes, terraces, and alluvial outwash deposits (Black 1958, Wahrhaftig 1965). Loess, sand, and outwash of Quaternary age, organic deposits formed in bogs, and recently deposited alluvium frequently overlay a micaceous schist bedrock (Dutro and Payne 1957, Viereck, ms). Forest soils are generally shallow with poorly developed profiles. Piedmont streams, many of glacial origin, change from braided to tightly meandering tributaries as they enter lower elevations.

Permafrost, or permanently frozen ground, is a widespread phenomenon throughout much of the Alaskan taiga. Between the Alaska Range and the Brooks Range permafrost occurs in all areas except south facing slopes and recently deposited alluvium. South of the Alaska Range permafrost is sporadic in occurrence, and is found only in bogs and on north facing slopes (Viereck, ms). Permafrost affects vegetation patterns by preventing lateral movement and downward percolation of soil water (Benninghoff 1952). Thus, permafrost results in saturated soils or standing water throughout much of the taiga.

Regional distribution of vegetation types and permafrost in lowland areas are closely interrelated. Insulation provided by black spruce (Picea mariana) and bog vegetation prevents melting of permafrost during summer months, and permafrost governs climax vegetation during the course of succession (Benninghoff 1952, Drury 1956). Disjunct stands of shrubs and deciduous trees scattered throughout Alaskan lowlands are frequently due to burning of climax vegetation, which results in lowering of permafrost tables and formation of a substrate temporarily favorable to sub-climax vegetation (Viereck, personal communication).

Geologically and vegetatively the flats of Interior Alaska consist of treeless or nearly treeless bogs and more or less forested areas surrounding or occurring within the bogs. Drury (1956) and Viereck (1970a, 1970b) have discussed lowland forest succession and origin of bogs along braided or meandering streams in Interior Alaska. Freshly deposited alluvium is first colonized by willow or alder (Alnus spp.), and later by balsam poplar (Populus balsamifera). An understory of low shrubs, horsetails (Equisetum spp.) and white spruce seedlings may develop beneath

the poplars. As the white spruce mature, an organic ground layer of mosses, herbs, and low shrubs develops, permafrost forms and after 200 to 300 years, the substrate becomes more favorable to black spruce than to white spruce.

Local disturbance of the insulating organic layer in black spruce forests may result in shallow thawing of the permafrost, water accumulation, and bog formation (Benninghoff 1952, Drury 1956). Development and expansion of bogs is frequently indicated by angular growth of trees due to soil instability. The resulting vegetation over extensive lowland areas becomes an intricate mosaic of black spruce forests, bogs, shrubs, and sub-climax hardwood communities, as well as numerous intermediate stages.

Characteristics - Floristics of northern lowlands have been reported by Ritchie (1959) and Larsen (1965) in subarctic Canada, Hanson (1951, 1953) in western Alaska, Drury (1956) in the upper Kuskokwim River region of Alaska, and Johnson and Vogel (1966) in the Yukon Flats of Alaska. In addition, Anderson (1959), Hulten (1968), and Viereck and Little (1972) have described the circumpolar distribution of trees, shrubs, and herbs found in Alaska.

Recent alluvial deposits on lowland floodplains throughout Interior Alaska are generally colonized first by horsetails (Equisetum arvense), grasses (Calamagrostis canadensis), willows (Salix alaxensis, S. arbusculoides, S. bebbiana), and alder (Alnus tenuifolia).

As balsam poplar and later, white spruce or mixed white spruce-paper birch become established, herbs such as wintergreen (Pyrola secunda) and fireweed (Epilobium angustifolium), and low shrubs such as rose (Rosa acicularis), currant (Ribes triste), and highbush cranberry (Viburnum edule) appear.

Accompanying the replacement of white spruce and birch by black spruce is a gradual increase in the sphagnum moss (Sphagnum capillaceum, S. girgensobnii, S. fuscus, and S. rubellum) cover and growth of a dense shrub layer of blueberry (Vaccinium uliginosum), Labrador tea (Ledum groenlandicum, L. decumbens) and birch (B. glandulosa, B. nana).

A dense ground cover of sphagnum and low shrubs, along with willow thickets (S. pulchra, S. bebbiana), and widely spaced paper birch, black spruce, or tamarack (Larix laricina) may replace stands of black spruce. The recurring process of bog formation and subsequent reforestation has been described in detail by Drury (1956).

All stages of bog development, from open water to black spruce forest, are found in Alaska lowlands. Sphagnum mosses, sedges (Carex spp. and Eriophorum spp.) and pond lilies (Nyphar polysepalum and Nymphaea tetragona) are common in open water, while other sedges (C. aquatilis) and horsetails (E. fluviatile, E. palustre) are found along margins of ponds and shallow flowing water. Bog shrubs, such as bog rosemary (Andromeda polifolia), Labrador tea, bog blueberry (Vaccinium uliginosum), swamp cranberry (Oxycoccus microcarpus), leather-leaf (Chamaedaphne calyculata), cloud-berry (Rubus chamaemorus), dwarf birch (Betula nana) and shrub birch (B. glandulosa), along with sphagnum mosses, are common on moist ground.

Tanana Flats, Interior Alaska - The vegetation of the Tanana Flats, a 7200 km² alluvial lowland lying immediately south of Fairbanks, Alaska, has been recently studied (Coady and Simpson, unpubl.). The area is bounded on the south by the rugged Alaska Range, on the north and east by the glacial Tanana River, and on the west by the glacial Wood River, and is part of the much larger Tanana-Kuskokwim physiographic province described by Wahrhaftig (1965).

Surface deposits from glacial streams flowing into the Tanana Flats on the south form a belt of broad coalescing fans that grade from coarse sand and gravel near the mountains to fine sand and silt at lower elevations. Material mantling the eastern and northern portion of the Flats has been deposited by the Tanana River (Andreasen, et al., 1964). Except for scattered low hills of granite, ultramafic rocks, and possibly Precambrian schist, the Flats are an area of little relief (Andreasen, et al. 1964). The entire region is underlain by permafrost (Black 1958, Wahrhaftig 1965), and drainage is poor, resulting in numerous small, shallow ponds, extensive bogs, and meander scars.

A vegetation type map of the Tanana Flats based on black and white aerial photographs (scale 1":1320') was completed in spring 1972 (Figure 2). Five major types were identified: herbaceous bog, heath bog, tall shrub, deciduous tree, and conifer tree.

Herbaceous bogs occur primarily in the northern portion of the Flats and cover approximately 7 percent of the area. Vegetation is dominated by emergent species, and live trees and shrubs are totally absent (Table 3). Stagnant or slowly flowing water depths vary seasonally, ranging from several cm to several m after spring run-off. Bog bottoms consist of a meter or more of dead and decaying vegetation, and permafrost depths are presumably well below the upper surface of organic material.

Heath bogs occupy approximately 40 percent of the land. Dominant vegetation consists of mosses and shrubs, although scattered trees and various herbs rooting on precipitous sedge hummocks are common (Table 4). Both mineral soil and permafrost tables occur within a meter of the surface,

although seasonal thaw may extend to greater depths in some areas. Soil

the Flats but are most frequent along rivers, streams, sloughs and along margins of ponds and meander scars. Recently burned areas may also support tall shrub communities. Vegetation ranges from pure to mixed stands of willow and alder with a dense understory of mosses, herbs, and low shrubs in poorly drained sites (Table 5). Exposed mineral soil, low moisture content, and absence of permafrost are common on recent alluvial deposits, while a thick organic layer, impeded drainage, and high permafrost tables are found in other areas.

Discontinuous pure or mixed stands of paper birch, aspen, or balsam poplar occur on approximately 8 percent of the Flats, particularly on slightly elevated land and on coarse river alluvium. Understory vegetation ranges from a dense herbaceous cover in cottonwood (Populus balsamifera) stands to mixed herbs and low shrubs in aspen and birch stands. Scattered willows and alders are common among cottonwood communities (Table 6). Well-drained mineral soil lies close to the surface and permafrost tables are deep or non-existent.

Scattered conifer stands in the western portion and extensive low, dense black spruce and occasional tamarack forests in the southern area cover approximately 35 percent of the Flats. Mature white spruce forests with a ground vegetation of low shrubs and mosses are common on elevated areas near streams. Black spruce forests underlain by a dense mat of moss, herbs, and low shrubs grow in poorly drained areas (Table 7). Soil organic layer, moisture content, and permafrost tables range from low in young white spruce stands to high in black spruce and tamarack stands.

Moose Use - The seasonal importance to moose of local flatlands south of the Brooks Range is variable. Lowland areas, by virtue of their abundant herbaceous vegetation, are generally important summer ranges for moose of all sex and age groups. Furthermore, interspersions of escape cover with prime feeding habitat create favorable calving areas for large numbers of moose (Rausch and Bratlie 1965, Bishop 1969).

In the Tanana Flats moose commonly feed in herbaceous bogs from spring thaw to late summer. However, greatest use of this habitat appears to be during early to mid-summer. During late summer moose may feed more frequently on herbaceous and woody browse in heath bog and tall shrub communities.

Generally, the Tanana Flats do not seem to be good winter moose range, and there is large scale emigration of animals during fall and early winter. Although several species of willows are widely scattered throughout portions of the Flats, most plants are old and extremely decadent. Apparently, changes in local edaphic factors (eg. soil temperature, moisture, and organic content) due to the dynamic nature of bog formation frequently create substrates unfavorable to continued growth of tall shrub and other sub-climax communities. However, vigorous growth of shrubs occurs in burned areas and on well drained recent deposits along some streams, and these areas do support modest numbers of moose during winter.

GLACIAL AND RIPARIAN SERAL COMMUNITIES

These predominately willow communities are key winter ranges in much of Alaska and are the only habitat consistently occupied by moose on the North Slope and Arctic coastal plain. They differ from fire-created

seral communities in that many are constantly renewed by erosion, flooding and/or ice scouring. Thus they provide relatively permanent (if dynamic) moose range.

Most large Interior and Southcentral Alaska rivers create many square miles of riparian willow communities. The Yukon, Kuskokwim, Tanana, Porcupine, Kobuk, Koyukuk, Chandalar, Susitna, Copper and scores of smaller drainages are all lined with these communities. Arctic rivers, notably the Colville, Chandler, Anaktuvuk, Sagavanirktok and Canning, likewise have created riparian willow stands which have allowed moose to disperse to the Arctic Ocean. Glacially scoured and still active deltas and outwash plains such as at Yakutat, Redoubt Bay and Cordova support similar communities (cf: Cooper 1942, Crocker and Dickson 1957, Crow 1968) and sustain substantial moose populations.

Throughout Alaska, glacial-riparian stands occur on predominately coarse gravel substrate on riverine and glacial flood plains. Salix alaxensis is the dominant shrub species, and is associated with several willow species, most notably S. arbusculoides, and occasionally with Alnus crispa or Populus balsamifera (in Interior and Southcentral Alaska). Herbs and grasses form the understory. Adjoining these communities on more poorly drained soils further from the river in tundra areas are Salix pulchra, S. glauca, S. lanata dominated stands, similar to those described as upland shrub types. Hanson (1951) describes such communities from the Seward Peninsula, and we have studied them on the Arctic Coastal Plain and in the Interior. Willow heights in these stands vary from 1-7m, depending upon the site.

In the Interior, riparian willow stands commonly grade into Balsam poplar and white spruce communities (Viereck 1970a); whereas, in tundra areas willow stands typically adjoin terraced heath or dwarf shrub communities (Spetzman 1959).

Characteristics - Tables 8-10 present floristic and other characteristics of riparian willow stands in Interior and Arctic Alaska. The Tanana River stand (Table 8) is on an alluvial island in a broad, braided glacial river, and is representative of these dense stands along all major Interior rivers which may flood and ice-scour annually. The Chena River stand (Table 9) is on a gravel bank on the upper reaches of a smaller, clear stream, and represents a less extreme situation where flooding is less persistent.

The Kongakut River stand, on the eastern Arctic north slope (Figure 3; Table 10), is representative of the clumped feltleaf (S. alaxensis) communities found on coarse gravel bars of these clear braided streams as they flow onto the Arctic coastal plain. These streams normally flood only in spring, and many produce considerable aufeis in most years. Bliss and Cantlon (1957) describe intergrading young and decadent feltleaf willow communities occurring between gravel bar herb communities and terrace communities. The chief differences are height and vigor of the dominant S. alaxensis plants (1-1.6m in young communities; up to 7m, with many dead stems, in decadent communities) and a shift from herb (typically Lupinus arcticus, and Deschampsia caespitosa) to moss understory.

Moose Use - Riparian willow communities are the year-round habitats of moose at the edges of their range, (in the Arctic, for example) and are important winter habitats wherever they occur. In addition, they serve

Table 8. Shrub characteristics of a riparian willow community on an island in the Tanana River, Interior, Alaska (64° 47'N 147° 45'W; elevation 140m). Modified from Milke, 1969.

Species	\bar{X} Height (cm)	Stems/ hectare	Oven-dried wt. "available browse"* (g/hectare)
<u>Salix alaxensis</u>	131.3	1,497	36,850
<u>S. lasiandra</u>	52.5	499	--
<u>S. interior</u>	69.3	8,485	19,980
<u>S. myrtillifolia</u>	77.3	3,244	15,100
<u>S. niphoclada</u>	70.0	14,725	131,870
Total Available Browse:			203,900

* All twigs above minimum browsed height were clipped at mean browsed diameter for the species.

Table 9. Characteristics of a riparian willow stand on the Chena River, Interior Alaska (approx. 64°55'N147°W; elevation 200m). Modified from Viereck, 1970z.

	Frequency of Occurrence (%)	\bar{X} Cover (%)	Stems/hectare
<u>Salix alaxensis</u>	60	15	1,220
<u>S. pseudocordata</u>	10	1	40
<u>Rosa acicularis</u>	40	3	
<u>Alnus incana</u>	10	6	540
<u>Viburnum edule</u>	10	2	
<u>Rubus idaeus</u>	10	1	
<u>Populus balsamifera</u> (3.8cm)			420
<u>Picea glauca</u> (3.8cm)			40
<u>Populus balsamifera</u> (3.8cm)			7,280
<u>Picea glauca</u> (3.8cm)			10,660
<u>Betula papyrifera</u> (3.8cm)			540
<u>Gatium boreale</u>	40	3	
<u>Poa alpina</u>	40	2	
<u>Epilobium angustifolium</u>	40	2	
<u>Artemisia tilesii</u>	40	1	
<u>Agrostis scabra</u>	20	1	
<u>Agropyron macrourum</u>	10	1	
<u>Stellaria laeta</u>	10	1	
<u>Wilkelmsia physodes</u>	10	1	
<u>Arabis lyrata</u>	10	1	
<u>Mertensia</u>	10	1	
<u>Calamagrostis canadensis</u>	10	1	
Mosses and lichens	10-80	21	

Table 10. Characteristics of a riparian willow stand on the Kongakut River, Arctic North Slope, Alaska (69°25'N141°30'W; elevation 300m).

	\bar{X} Cover (%)	
<u>Salix alaxensis</u>	5	(mean height ca. 2m)
<u>S. myrtiliflora</u>	1	
<u>S. reticulata</u>	1	
<u>S. glauca</u>	28	
<u>Arctostaphylos alpinus</u>	48	
<u>Astragalus</u> spp.	5	
<u>Equisetum variegata</u>	4	
<u>Solidago multiradiata</u>	1	
<u>Calamagrostis</u> spp.	2	
<u>Dryas integrifolia</u>	2	
<u>Ranunculus</u> sp.	5	
<u>Pyrola grandiflora</u>	1	
<u>Pedicularis capitata</u>	1	
<u>Achillea borealis</u>	1	
<u>Festuca altica</u>	2	
<u>Lupinus arcticus</u>	1	
<u>Polemonium</u> spp.	1	
Mosses	60	

as calving and summering areas for moose in Interior Alaska. Since these stands are relatively permanent features, they serve as reservoirs from which moose populations can expand into newly-burned areas and as avenues for dispersal into new range.

Movement into riparian willow habitats from upland and lowland summer ranges usually occurs in November or later, apparently depending upon snow characteristics. During harsh winters, river "bottoms" become yarding areas for high densities of moose. When deep snow persists, overbrowsing may occur, and these areas have been the scenes of the most spectacular moose die-offs recorded in Alaska. Where extensive burned areas are lacking, riparian communities are the habitat of last resort for wintering moose. Their extent and vigor ultimately determine at what level moose populations will persist in the area.

FIRE CREATED SERAL COMMUNITIES

Fire-mediated habitats are the most ephemeral of Alaskan moose habitats; yet, they support the greatest population explosions and among greatest densities of moose in the state. The earliest specific publications concerning moose management in Alaska (Spencer and Chatelain 1953, Leopold and Darling 1953a and b, Chatelain 1951, 1952) correctly stressed the correlation between dense moose populations and forest fires.

The ecological effects of fires in Alaska are extremely complex (cf. Lutz 1956, Slaughter et al. 1971, Viereck ms) and cannot be considered in detail here. Lutz (1956) presented a diagrammatic representation of normal courses of post-fire succession in Alaskan taiga. Viereck (ms) modified the chart and we reproduce his chart here (Figure 4). The

course of succession and the seral community's value to moose are determined by a multitude of site (soils, temperature, moisture, slope and exposure), fire (severity, mode of travel, duration) and miscellaneous (natural reseeding sources, size of openings created) factors. The general successional courses producing maximum benefits to moose populations are those involving paper birch-willow-aspen shrub thickets.

Fires have probably always been common in Alaska, but have increased in frequency and area burned since modern settlement (Hardy and Franks 1963). Viereck (ms) maintains there are very few Interior forests that survive burning long enough to reach what can be considered climax stage. Barney (1971) suggests that 600,000 to 1,000,000 ha burned annually from 1900-1940. Even with modern fire control, a mean of approximately 400,000 ha annually have burned between 1940-1969 (Barney 1971). The general trend in the past three decades has been toward an increase in numbers of fires (1,138 in the 1940's, 2,583 in the 1950's and 2,380 in the 1960's in Interior Alaska) but a decrease in the total area burned (5,018,000 ha in the 1940's, 4,330,000 ha in the 1950's, 2,590,000 ha in the 1960's) and the area burned per fire. Increased fire control capabilities have thus perhaps decreased the benefits of civilization to moose.

Characteristics - Several factors determine 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) rate of attaining a) above snow and b) above moose-reach heights and (4) amount and distribution of mature communities

remaining, diversity of seral communities created and distribution of mature communities remaining (e.g.: "edge effect" created).

Composition - The species re-invading burned areas in Alaska most often tend to be the same species present before the fire (Figure 4). This results from re-sprouting or growth of root suckers (Spencer and Hakala 1964, Viereck ms). Stands are often nearly monotypic in shrub species (cf. Table 11), with birch or aspen (on the warmest, driest sites) predominating. Spruce encroachment occurs usually slowly (Viereck ms) in the Interior, but sometimes almost immediately (e.g.: on some stands on the Kenai Peninsula). Although willows are often among the first recolonizers, they generally do not achieve great numbers or production, perhaps because of consistent utilization by moose. Aspen may be similarly affected. Spencer and Hakala (1964) described how moose and plant competition had altered the proportion of aspen in the Kenai (1947) burn. It apparently decreased from 96.5 percent of the standing shrub biomass in 1952 (Spencer and Chatelain 1953) to less than one percent in 1967 (Table 11). Wet lowland and permafrost sites are usually less thoroughly burned (Viereck ms) and thus may rapidly recover by vegetative reproduction to a composition similar to that existing before the fire. Willows, blueberry and dwarf birch tend to be more numerous in these stands.

The exact composition of species recolonizing a burn may depend upon the timing of the fire relative to plant phenology (Viereck ms). Willow species produce seeds that are viable for only a matter of weeks, and various species produce seeds at different times of year. Further, some species (paper birch, white spruce) produce "bumper" seed crops only once in several years, (Viereck ms) and the year the burn occurs might thus affect species composition of the resulting seral community.

Table 11. Characteristics of shrub standing crop and production on Kenai Burn twenty years after the 1947 fire. Modified from Seemel 1969.

Species	Community	Stems/ hectare	Annual Production g/hectare
<u>Betula papyrifera</u>	Dense Birch	80,046	479,348
" "	Medium Birch	47,221	315,987
" "	Thin Birch	34,381	249,316
" "	Spruce-birch	19,296	118,118
" "	Spruce Regrowth	6,775	35,226
<u>Populus tremuloides</u>	Dense Birch	237	202
" "	Medium Birch	339	348
" "	Thin Birch	541	875
" "	Spruce-birch	200	224
" "	Spruce Regrowth	168	224
<u>Viburnum edule</u>	Dense Birch	114	101
" "	Spruce-birch	89	90
<u>Salix spp.</u>	Dense Birch	1,641	9,233
" "	Medium Birch	1,196	6,193
" "	Thin Birch	692	3,747
" "	Spruce-birch	469	2,255
" "	Spruce Regrowth	652	2,109
<u>Alnus crispa</u>	Thin Birch	319	713
<u>Betula nana</u>	Spruce Regrowth	8,772	9,008
Totals:	Dense Birch	82,038	488,884
	Medium Birch	48,756	322,328
	Thin Birch	35,933	254,656
	Spruce-birch	20,054	120,687
	Spruce Regrowth	16,367	46,567

There is little detailed information directly relating species composition of burn regrowth to subsequent moose population densities. However, observations suggest that the higher the proportion of first, willow, and second, birch shrubs produced, the greater the moose densities that will result during early years of succession.

Production - Biomass production of shrubs can be prodigious following burns in Alaska. Seemel's (1969) studies 21 years after the Kenai (1947) burn indicate annual production of nearly 500 kg/ha in the densest shrub B. papyrifera stands (Table 11). Standing crop is also large, with 82,000 shrub stems/ha estimated in the most dense stands. Both production and standing crop, as well as composition, vary considerably with individual stand (cf.: Table 11), and thus the proportions of various communities and variously-productive stands in a burn also influence moose numbers.

Productivity and quantity of available browse are seldom limiting factors to moose densities in large burns in Alaska. In the Kenai (1947) burn of 127,600 ha, Seemel (1969) estimated that more than 8 moose/km² in a 2.6 km² enclosure used only 18.3 - 22.8% of the estimated annual shrub production, depending upon community. Spencer and Chatelain (1953) in contrast, had estimated that utilization by only 1.7 moose per km² on the same burn in 1952 was 45 percent of the annual production of aspen, then virtually the only shrub present. Since then plant production has exceeded moose production in relative terms, even though moose densities achieved the highest level ever recorded. Spencer and Hakala (1964) suggested that adequate densities of moose might retard succession in seral shrub habitats under certain conditions. We feel that these densities are seldom reached and never persist. Although moose may alter relative

abundance of species in seral communities, we know of no instance where they have retarded succession over a large burned area. In the case of the Kenai burn, moose populations appeared to peak at the very high level of 4-6 moose/km² in the most productive habitat, at about the same time Seemel made his estimates. Within four 2.6 km² enclosures, populations remained relatively static at 4.6 - 5.4 moose/km² (before calving) over a three-year period, and utilization probably did not exceed Seemel's estimate (LeResche and Davis 1971).

Isolated smaller burns serving as winter concentration areas for moose are sometimes retarded in succession and, on occasion, "over-utilized" by immigrant moose. Succession on the 1320 ha Kenai Lake burn (1959) has been effectively retarded by wintering moose, with most shrubs being browsed to snowline annually. This burn is unusual in that it is situated in the midst of nearly-mature range that wintered many moose until the late 1950's, and is about 20 km from the nearest edge of the larger Kenai burn (1947). Because fires are frequent throughout most of Alaska, small burns are often near other burns of various ages, and are therefore not subjected to intensive use by large concentrations of moose from a vast area. Furthermore, small isolated burns do not produce widespread moose population explosions sufficient to alter succession. Thus, in most cases, post-burn succession in large burned areas seems to proceed at a rate little different from what it would in the absence of moose. The course of succession may well be altered, however.

Rate of Growth - The sooner recolonizing shrubs achieve a height that makes them available to moose during winter, the sooner moose population explosions occur. Conversely, the more rapidly shrubs mature into

trees, the shorter is the productive life of the burn. Spencer and Chatelain (1953) estimated that the Kenai burn (1947) produced significant browse by 1950, and that by 1953 moose had increased four-fold. Moose densities peaked on the burn about 1967-1969, and may have experienced the first stages of a decline in the winter of 1971-1972; however, they remain very high today.

Rates of growth differ between burns and within large burns, depending upon species present and site and climatological variables. Within the Kenai (1947) burn, heights of B. papyrifera plants in adjacent stands ranged from 1m to almost 7m in 1970. We do not know whether some sites were recolonized by paper birch later than others or whether growth rates alone account for the differences.

Hakala, et al. (1971) predicted that browse would "continue to improve" on areas burned on the Kenai Peninsula (1969) for 23-25 years after the burn, as has been the case with the 1947 Kenai burn area. Moose densities could be expected to remain high for this period, and then decline as happened after a series of fires in the 1880's and 1920's (Spencer and Hakala 1964). The limited information available, then, suggests that the "useful life" of a burn as moose habitat in Alaska is usually less than 50 years, and that moose densities peak 20-25 years after the burn.

Shape of Burn, Diversity and "Edge Effect" - The degree of inter-spersion of communities, or amount of "edge effect", produced by a fire is very important in determining the fire's effect on moose populations. Great discontinuity of burning is desirable because it provides, (1) cover (mature) habitat close to feeding habitat, (2) increased variety of alternate forage species and (3) staggered maturation rates of individual stands.

The forest edge ecotone allows moose both to invade a heterogeneous burn sooner than a large homogeneous burn and to achieve higher year-round densities. The distance a moose will continually move from cover into open feeding areas likely varies with season, age, sex, reproductive status, snow characteristics and a multitude of other factors. It appears certain, however, that increased mature forest edge will hasten establishment of moose in a new burn. The rate of moose increase on the Kenai (1947) burn, described by Spencer and Chatelain (1953) as 400% in 5 years, was probably near the maximum attainable because of the tremendous amount of edge created. It is problematical whether immigration from nearby areas had a significant effect (LeResche 1973b).

Once the moose population is established, small stands of mature timber (30-40m tall birch, white spruce and aspen in the 1947 Kenai burn) provide year-round escape cover and winter refugia from deep snow. In addition, these stands provide alternate food sources that may be of considerable importance to the maintenance of high moose densities. LeResche and Davis (1973) showed that Vaccinium vitis-idaea plants were important to moose in winter and remained available more consistently in mature stands than in adjacent seral stands on the Kenai.

Shrub-forest ecotones are not the only important edges created by fires. Shrub-sedge and shrub-aquatic ecotones are also important at various times of year. Brush bordering summer feeding bogs, for example, can be excellent cover habitat for young calves (LeResche 1966). Dense shrubs bordering small, drying potholes is preferred habitat for adults in late fall, when they dig craters in snow to feed on cured sedge leaves.

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. The Kenai burn (1947), however, appears to represent, if not the ideal, at least the most productive large area of moose habitat known to us. Densities of moose exceeding $4/\text{km}^2$ have been achieved over most of the burn (vs densities of ca $0.08/\text{km}^2$ in similar unburned areas (Spencer and Chatelain 1953) through a combination of high forage production, generally mild winters, abundant alternate foods (especially V. vitis-idaea), edge effect, and adjoining upland ranges.

The fire burned 127,600 ha of approximately 260,000 ha, and has regenerated into several paper birch and birch-spruce communities (Table 11). The entire burn has not been analyzed, but detailed type maps have been constructed of the reasonably-representative 1024 ha enclosed by the Kenai Moose Research Center¹ enclosures.

A map of 254 ha of this mixed habitat, prepared 20 years after the burn, (Figure 5) was analyzed for sizes of individual stands and amount of ecotone between each of the 11 communities distinguished (Tables 12-13). A "stand" was defined as a contiguous area of one community, regardless of shape, and ecotone was simply taken as the length of mapped margin between stands.

The 254 ha contains 624 individual stands ranging in size from .02 ha to 18.4 ha (Table 13). Mean stand size is 0.41 ha, and 86% of all stands are less than 0.5 ha in area; only 8% of the stands are larger than 1 ha, and only 2% larger than 5 ha. Remnant mature stands comprise 118 ha, or 46% of the area. This mature forest is extremely segmented, comprising 411 stands distributed throughout the area.

¹ A joint project of Alaska Department of Fish and Game and U. S. Fish and Wildlife Service.

Table 12: Sizes of 624 stands of 11 communities in 254 ha of the Kenai, Alaska (1947) burn, mapped in 1967, Kenai Moose Research Center, Pen 4.

Community	Number Stands	Total area ha	\bar{x} area/ stand-ha	range ha/stand	No. Stands of Area					
					.5ha	.5-1.0ha	1.1-2.0ha	2.1-5ha	5-10ha	10ha
Dense Mature Hardwoods	22	43.07	1.96	.05-12.9	9	5	2	3	2	1
Thin Mature Hardwoods	383	70.69	0.18	.02-18.4	368	7	4	1	1	2
Mature Spruce	6	4.54	0.76	.02- 3.9	5				1	
Spruce Regrowth	10	19.29	1.93	.14-11.6	4	2	2	1		1
Spruce-Birch Regrowth	33	17.83	0.54	.02-2.3	22	5	5	1		
Spruce-Ledum	6	5.39	0.90	.23- 2.5	3	1	1	1		
Dense Shrub Birch	23	7.30	0.32	.21- 1.3	20	1	2			
Medium Shrub Birch	40	41.16	1.04	.03- 8.9	24	7	4	2	3	
Thin Shrub Birch	77	31.28	0.41	.02- 6.2	62	7	5	2	1	
Grass	19	1.82	0.10	.02- 0.4	19					
Sedge	5	12.05	2.41	.07-10.2	3	1	0			1
Totals	624	254.42	0.41	.02-18.4	539	36	25	11	8	5
Percent of total stands					86%	6%	4%	2%	1%	1%

Table 13. Amount of ecotone (in meters) between 11 plant communities in 254 ha of the Kenai, Alaska (1947) burn mapped in 1967, Kenai Moose Research Center, Pen 4. (Figure).

	Dense Mature Hardwoods	Thin Mature Hardwoods	Mature Spruce Spruce Regrowth	Spruce- Birch Regrowth	Spruce Ledum	Dense Shrub Birch	Medium Shrub Birch	Thin Shrub Birch	Grass	Sedge	Water	
Community												
Dense Mature Hardwoods		17,581	325	206	356	-	711	1,728	2,642	51	-	-
Thin Mature Hardwoods			305	2,541	2,795	-	3,150	22,764	22,967	508	178	-
Mature Spruce				-	-	76	203	1,016	406	-	76	-
Spruce Regrowth					3,455	1,524	305	457	1,524	661	356	-
Spruce-Birch Regrowth						203	1,067	4,522	4,472	813	102	-
Spruce-Ledum							-	102	280	-	1,931	-
Dense Shrub Birch								3,303	1,016	-	-	-
Medium Shrub Birch									3,303	457	508	-
Thin Shrub Birch										457	102	-
Grass												152
Sedge												356
	23,600	72,789	2,407	11,029	17,785	4,116	9,755	38,167	37,169	3,099	3,609	508

Total Edge = $\frac{224,033 \text{ m}}{2}$ = 112.0 km

The large number of stands and their irregular shapes have produced tremendous amounts of ecotone (Table 14) --112 km in the 2.5km² area. Mature communities have about 99 km of "edge", sharing 59 km of this with the various seral shrub communities. Shrub communities themselves are surrounded by about 103 km of ecotone, bordering on mature forest and on other seral communities.

This 2.5 km² area by no means represents an extreme case, but rather is a fair sampling of the entire 260 km² area affected by the burn. By extrapolation, then, the Kenai Burn (1947) produced over 60,000 separate stands more than 11,000 km of ecotone and 128,000 ha of new shrub communities. It is not surprising that moose densities achieved such a high level as a result of this fire.

Moose Use - Seral burn habitats are extremely important wintering ranges once growth is sufficient to provide available browse above the snow. Some burns (the Kenai burn [1947], for example) receive an influx of moose from upland ranges in early winter, and support very dense wintering concentrations. Others (in the upper Little Chena drainage near Fairbanks, for example) support moose during late summer and fall, but may be virtually deserted when moose move down into denser forests and riparian stands in November and December. The most diversified burns (Kenai 1947) also support significant densities of moose during calving, summer and rutting periods and have relatively high resident populations throughout the year.

ANTHROPOGENIC HABITATS AND EFFECTS OF DEVELOPMENT

The greatest part of man-caused moose habitat in Alaska has been, and continues to be, created through accidental fires. From 1940 through

1969, 70% of the fires in Alaska were man-caused, and these fires accounted for 22% of the area burned (Viereck ms). This amounts to a mean of approximately 88,000 ha of largely seral brush moose habitat created annually by man in the last three decades. Other human activities, by comparison, today have little effect on available moose habitat in Alaska.

Two short-lived activities of man, mining and homesteading, have been of some importance to moose in the last century. Both increased man-caused fires, and both created habitat by physical disruption of forests. Placer mining from 1900 to as recently as 1965, although it destroyed some riparian habitat, created a much greater area of dense, productive seral shrub communities along stream courses in many parts of the Interior. This disturbance had an especially great effect on moose distribution because it occurred in many areas where there were low densities of moose before mining. The Kuskokwim Mountains and Yukon-Tanana highlands are two regions where mining probably contributed significantly to increased moose densities. Dredged "tailing" piles near Fairbanks still support stands of birch and willow shrubs important to wintering moose.

Settlement of the Matanuska Valley by homesteaders from the 1910's to 1950's resulted in much clearing and burning of then-maturing forests, which probably contributed significantly to the dense moose populations present there from the 1960's to the present time. In addition, availability of farm and garden crops surely did the moose no harm. Other smaller areas of concentrated agriculturally-oriented settlement in the Tanana Valley and on the Kenai Peninsula probably contributed similarly to moose populations. In all these cases, resulting fires probably had the greatest effect upon moose habitat, however.

Several thousand acres of maturing spruce forest have recently been cleared mechanically on the Kenai National Moose Range. This program has resulted in increased moose winter range, and may be expanded (Hakala et al. 1971).

Most land clearing in Alaska today is for road and building construction and oil exploration. Seismological trails have been bulldozed through many forests of the state and provide some shrub-forest ecotone. Because the actual area cleared is small, impact on moose populations is slight. Road and building construction, similarly, create some new brush communities. Depending upon their location, they may also remove productive moose habitat.

Perhaps the greatest effect of these activities on moose is to increase accidental mortality by attracting them to areas occupied by motor vehicles, trains, and occasionally aircraft. In some years, moose mortalities from such collisions may exceed 750-1000 animals.

With these exceptions, developmental activities have as yet had little effect on Alaska moose distribution and habitat. The proposed Prudhoe Bay - Valdez oil pipeline and a possible Prudhoe Bay - Mackenzie River gas pipeline would both pass through forested areas. Their effects on habitat will likely be minimal due to the small area actually disturbed, but if they restrict free passage of moose they could significantly affect moose movements and distribution.

OTHER HABITATS

The northern boreal forests in Alaska, referred to by the general term "taiga," consist primarily of low elevation open-growing spruce forests, occasional stands of well developed spruce and hardwoods, and frequent

tracts of treeless or sparsely treed bogs. On south facing slopes and well drained sites the forest consists of white spruce and hardwood stands of mature aspen and paper birch; on cool north facing slopes and poorly drained lowlands climax vegetation is generally black spruce and bogs.

Most of forested Alaska north of the Gulf of Alaska consists of a matrix of taiga communities within which most other habitats discussed earlier have developed, each due to a particular set of special circumstances. Because the taiga is so extensive, it supports substantial numbers of moose even though densities are very low. In many areas, moose densities may not exceed one moose each 5-10 km², but some animals are generally present.

The most important taiga habitats, in addition to the bog communities discussed above, are those bordering upon riparian or upland shrub habitats or interspersed with seral fire-created communities. These areas provide cover and some food for moose spending most of the year on more preferred habitats.

SUMMARY

The moose is an opportunistic species, well adapted to expand rapidly into new habitat and to persist at low levels in restricted habitat (Geist 1971, Cole 1971, Mercer and Kitchen 1968, Pulliainen, this volume). Moose populations and distribution in Alaska have fluctuated in response to habitat changes in prehistoric and historic times.

Moose have been present in Alaska since mid- to late Pleistocene times. They probably survived in relatively small, disjunct groups wherever suitable habitat could be found throughout this period, when a tundra-steppe

community dominated much of the Alaska refugium. With the close of the glacial period, climatic warming, and proliferation of shrub and forest communities, they spread throughout much of Alaska. In more recent times riparian and subalpine willow communities have provided a means of maintaining minimal populations able to exploit new range produced by fire and other disturbances. This pattern persists today.

Very recent extensions of moose distribution have occurred in the geographic extremes of Alaska: in Southeastern Alaska, where glacial recessions have allowed moose to expand along major river valleys crossing the coastal range, and in northwestern Alaska, where moose have become established on the western Seward Peninsula and north of the Noatak River.

On the Arctic Slope moose seem to have been established for a longer time than on the western tundra areas, but are currently increasing in numbers.

In most of Alaska, moose numbers have risen and declined dramatically in local areas over the last 150 years, largely in response to creation and maturation of fire-caused seral range. Historical accounts that moose were absent from a particular locale most likely reflect only a period of very low moose numbers resulting from a prolonged absence of fires in that area. Extremely low densities of moose presently exist in some areas where extensive spruce stands are dominant. Thus in most of Alaska the purported variations in moose distribution have in reality been only variations in relative abundance.

Moose numbers increased steadily through the 1950's and early 1960's throughout most of the state, largely in response to rather regular recurrence of extensive wildfires. In many areas numbers apparently exceeded

severe winter carrying capacity. In much of Southcentral and Interior Alaska, moose numbers have stabilized or declined in recent years, primarily in response to a series of severe winters, complicated by deteriorating range conditions, changing hunting pressure, and predation.

ACKNOWLEDGMENTS

Robert A. Rausch contributed many ideas to this review and read the manuscript. R. O. Guthrie, D. C. McKingit and L. A. Viereck read the manuscript. L. McManus, C. Rhody, D. Simpson and J. Trent assisted in manuscript preparation. We are pleased to acknowledge these contributions.

Data presented here were gathered under Federal Aid in Wildlife Restoration projects W-17 (Alaska).

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