Moose (Alces alces) and Their Influence upon Terrestrial Ecology in the Copper River Watershed, Alaska

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INTRODUCTION

Climate and geology drive glacial, periglacial, and fluvial processes, controlling terrestrial and aquatic ecology in high latitude watersheds. In addition, uplift from earthquakes alter successional sequences, resulting in high variance, non-equilibrium habitat dynamics. The ecology of the Copper River watershed, and particularly the Copper River Delta, is directly linked to the dynamic geologic environment, influenced by earthquakes, glaciers and volcanic activity. Biotic factors can also exert a major influence on the ecology. The nutrient deposition and high productivity resulting from the carcasses of spawned out salmon (O*ncorhynchus* spp.) in the Copper River system is one example. Another example is the role of a large herbivorous mammal, the moose (*Alces alces*), in disturbing and therefore influencing terrestrial and aquatic ecosystems. Moose have been suggested by some to be a keystone herbivore that likely mediate the rates of nutrient cycling in northern ecosystems (Molvar et al. 1993), influence floral composition, and alter the rate of forest succession (Kielland and Bryant 1998). Their presence is especially important in the Copper River Delta, where they did not naturally colonize, but were introduced. This paper will provide background information on moose, including a physical description, and a discussion of distribution, introduction, life history, habitat and diet preferences. Also included is a review of the current scientific knowledge regarding the effects of moose on terrestrial ecology. While considerable research has been conducted on moose in the Copper River Delta, additional information comes from studies of moose in other parts of Alaska (i.e. Susitna River, Tanana River, etc.), and the world.

NATURAL HISTORY OF MOOSE

Physical Description

Moose (*Alces alces*) is the largest member of the deer family (Cervidae) in the world. The Alaskan race of moose (*Alces alces gigas*) is one of four recognized subspecies in North America, and is the largest of all moose. Moose (Fig. 1 and 3) are large even-toed mammals, with hooves, long legs, heavy bodies, a long drooping nose, a "bell" or dewlap under the chin, a hump at the shoulders, and a small tail (Rause and Gasaway 1994).

Moose vary in color, size and shape. Color varies depending on season and age. Young calves are often a light rusty color, and adult coloring ranges from golden brown to a dusty black. Moose height at the shoulder ranges between 2-2.3 m (6.5-7.5 ft). Bulls (male adult moose) in good condition can weigh 542 to 725 kg (1,200-1,600 lbs), while cows (female adult moose) range from 364 to 591 kg (800-1,300 lbs). Newborn calves weigh 13 to 16 kg (28 -35 lbs) but within five months of birth can grow to more than 136 kg (300 lbs) (Rause and Gasaway 1994). One Alaskan bull moose shot in 1897 holds the record for being the largest known modern deer, standing 2.34 m (7.7 ft) tall, weighing 816 kg (1,795 lbs), and having a rack (antlers) spread of 1.99 m (6.5 ft) (Baker 2002).

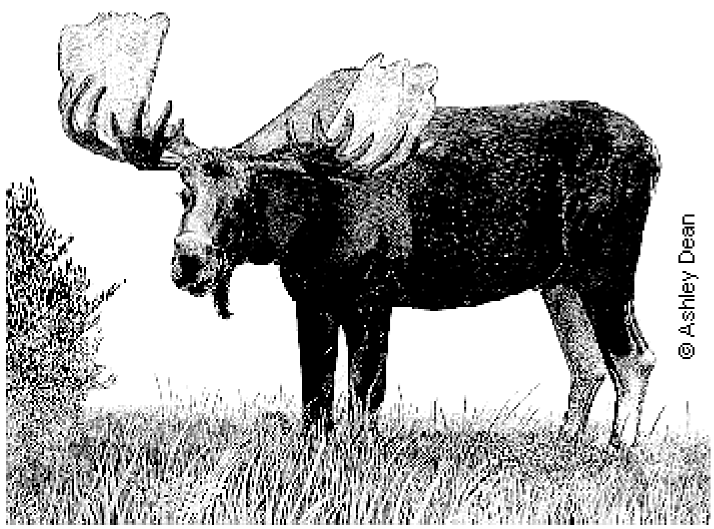

Figure 1. Artist's sketch of a bull moose. Notice large set of antlers and bell under the chin.

Antlers, found only on bulls, average 1.60 m (5.25 ft) across and 20 kg (44 lbs) in weight. On the antlers, several (up to 30) tines (spikes) are present with the antler shape differing from animal to animal (Baker 2002). Antlers are shed every year in November and December, and subsequently replaced with a new, larger pair. Even with such large bodies and antlers, moose are able to run at speeds of 55 km/h (34 mph) and are able to swim at a sustained speed of 10 km/h (6 mph) (Baker 2002). It is no wonder why on May 1, 1998 Governor Tony Knowles decreed moose the official land mammal of Alaska (ADCED 2002).

Distribution & Introduction To The Copper River Delta

Moose occur in northern forests of North America, Europe and Russia. In Alaska, moose are found in suitable habitats from the Stikine River in the Panhandle to the Colville River on the Arctic Slope. They are most abundant in recently burned areas containing willow and birch shrubs, on timberline plateaus and along the major rivers of south central and interior Alaska (Rause and Gasawau 1994). While moose are ubiquitous throughout south central Alaska, including the upper Copper River Watershed, they did not naturally colonize the Copper River Delta (MacCracken et al. 1997). Historical accounts show that moose were present in the Copper River Watershed, approximately 16-24 km north of the Copper River Delta, but they were absent or extremely rare in the Copper River Delta during the early 1900's (MacCracken et al. 1997). The narrow Copper River Canyon formed as the Copper River flows through the Chugach Mountain Range has been thought to be a dispersal barrier to moose immigration to the Copper River Delta (Klein 1965 in MacCracken et al. 1997). In 1949, "Kenai," a moose calf,

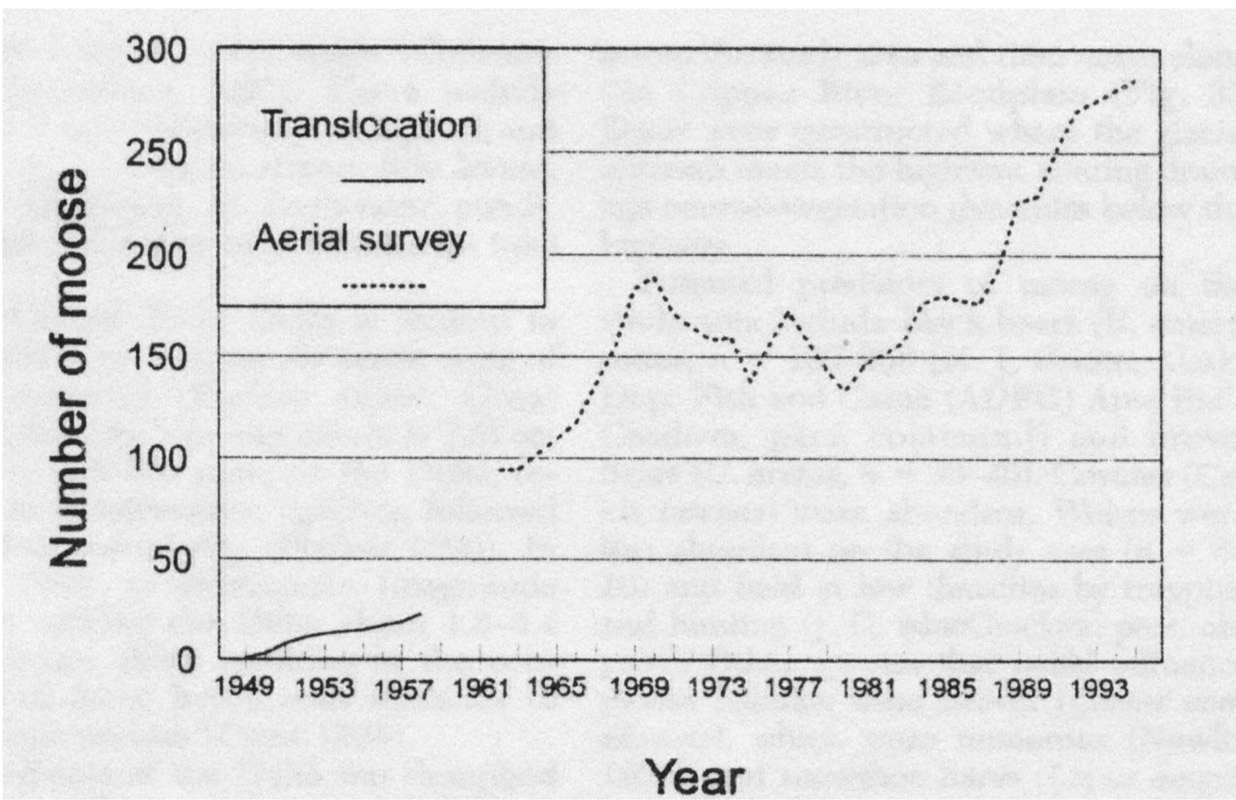

Figure 2. Moose population trends on the west Copper River Delta, Alaska, from 1949 to 1994. The solid line shows cumulative numbers that were translocated to the Delta during 1949-58. Estimates during 1962-95 (dotted line) were from annual aerial herd composition counts (Alaska Dept. Fish and Game, Cordova, unpublished data). A 3-year moving average was used for the aerial survey counts. Figure taken from MacCracken et al. 1997.

was introduced to the Copper River Delta (MacCracken et al. 1997). In the period that followed from 1949 to 1958, 22 additional calves, 8 male and 14 female, and one yearling female were released in the Copper River Delta (MacCracken et al. 1997). This translocation of moose was one of the most successful ever conducted in Alaska; the population grew rapidly (Fig. 2), and is currently maintained at about 250-300 individuals through tightly regulated hunting (MacCracken et al. 1997).

Reproduction and Mortality

Cow moose can breed as young as 16 months, but generally begin breeding at 28 months. Calves are born between mid May and early June after a gestation of 230 days. Calves begin on solid food a few days after birth and are defended rigorously by the mother. This maternal bond lasts until the calves are a year old, at which point the mother aggressively chases her offspring away just before she again gives birth. Moose breed in the fall with the peak of the "rut" activities arriving in late September and early October. Adult males joust during the rut, using their antlers to win the opportunity to mate with the female. While serious battles are rare, moose occasionally receive puncture wounds and can die from these activities (Rause and Gasaway 1994).

In the wild, moose rarely live more than 16 years (Rause and Gasaway 1994). While wolves (*Canis lupus*) and brown and black bears (*Ursus* spp.) are natural predators of the moose, hunting by man has a major influence upon moose populations in Alaska. Currently, 6,000 to 8,000 moose are annually harvested throughout the state, producing a total of ~3.5 million lbs of meat. A study conducted in the Copper River Delta found 91% of adult deaths were due to hunting, with the remaining percentages attributed to accidents, starvation, and unknown causes (MacCracken et al. 1997). No instances of wolf or bear predation on adult moose were recorded during the three-year period 1987-1989; however calf mortality due to predation by brown bears was noted (MacCracken et al. 1997).

Severe winters exert strong pressure on moose populations. High snow levels reduce available forage abundance and increase energy expenditures when travelling. While moose populations in the Copper River Delta are currently maintained below 300 individuals, MacCracken (1997) estimates the carrying capacity of the west Delta to be 380 moose for a severe winter, 1,347 for a moderate winter, and 1,424 for a mild winter. In theory, this indicates that the population of moose in the Delta could be allowed to expand beyond its current size.

Figure 3. Photograph of a bull moose grazing on aquatic plants. (Baker 2002)

Diet

Moose are herbivorous ruminants (any of various hoofed, even-toed, usually horned mammals of the suborder Ruminantia, such as cattle, sheep, goats, deer, and giraffes, characteristically having a stomach divided into four compartments and chewing a cud consisting of regurgitated, partially digested food). Moose diets vary from season to season based upon the availability of suitable forage. The average daily intake of moose is considerably higher in summer than in winter (Persson et al. 2000). Moose both graze (feed on growing grasses and herbage) and browse (feed on young twigs, leaves, and shoots of trees). Diet preferences of moose in Alaska and specifically in the Copper River Delta have been identified and quantified through a variety of techniques such as browse surveys, and indirectly from stomach and fecal samples (MacCracken et al. 1993a).

A study conducted in the Copper River Delta found willow (*Salix* spp.) dominated the diet of moose throughout the year, as it does in other parts of the Copper River Watershed and Alaska (MacCracken et al. 1997, Rause and Gasaway 1994). However,seasonal diets differed in the amount of other items such as sweetgale (*Myrica gale*), Sitka alder (*Alnus sinuata*), and emergent aquatic plants like marsh fivefinger (*Potentilla palustris*), horsetails (*Equisetum* Spp.), and others (MacCracken et al. 1997). Please refer to Table 1 for a comparison of seasonal dietary items. During the spring-summer period, moose take advantage of aquatic habitats to feed on aquatic plants. Some researchers (Botkin et al. 1973 in MacCracken et al. 1993b) have suggested that the consumption of submergent and emergent aquatic plants is linked to sodium hunger. Other researchers suggest that the aquatic plants are a more efficient food source for moose because these aquatic habitats produce roughly four times more forage than terrestrial habitats (MacCracken et al. 1993b). The aquatic plants are more digestible and have higher concentrations of minerals than terrestrial browse, allowing moose to intake forage at higher rates in aquatic habitats (MacCracken et al. 1993b).

Food Item		Season		
		Winter	Spring-summer	Summer-fall
Shrub and tree				
Willow	*Salix* spp.	80	61	93
Sitka Alder	*Alnus sinuata*	3	3	2
Sweetgale	*Myrica gale*	7	10	1
Black Cottonwood	*Populus trichocarpa*	1	1	<1
	total	92	75	96
Forbs				
Horsetails	*Equisetum* spp.	<1	9	<1
Buckbean	*Menyanthes trifoliata*	1	4	1
Marsh fivefinger	*Potentilla palustris*	2	10	1
	total	6	23	3
Graminoids				
Reedgrass	*Calamagrostis* spp.	1	1	1
Sedge	*Carex* spp.	1	1	<1
	total	2	2	1

Table 1. Mean percent relative density of plant fragments identified in moose feces collected monthly from July 1987 to September 1989 on the west Copper River Delta, Alaska. Note the dominance of willow in each season and the increased consumption of aquatic plants like horsetails, marsh fivefinger and buckbean during the spring-summer season. Table partially reproduced from MacCracken et al. 1997.

Habitat Preferences And Movement

Moose habitat preference appears to be determined by the activity in which the moose is engaged. When feeding, moose prefer areas with higher densities of their preferred food item, found in stands in the early shrub stages of succession [refer to (Trowbridge 2002) for more detail], which are often dominated by various willow species (*Salix* spp.). However, when resting, moose prefer Alder (*Alnus* spp.) and young Poplar (*Populus* spp.) forests indicative of an intermediate stage of forest succession, presumably because this environment provides better cover than the early shrub stands, and are successionally and spatially adjacent to the early shrub stands. In addition, during the spring, moose are often found in mature White Spruce (*Picea glauca*) stands during sunny days (Collins and Helm 1997). Moose make seasonal movements associated with calving, rutting, and wintering. These movements can range from a few to 100 km (62 miles). The average home range of radio-collared individuals in the Copper River Delta was found to be 59 km^2 (23 mi^2) (MacCracken et al. 1997). Non-vegetated areas including dry sloughs and frozen river channels, tend to have less snow accumulation and are preferentially used by moose for travel during periods of deep snow (Collins and Helm 1997).

DISTURBANCES AND TERRESTRIAL ECOLOGY

As moose inhabit a region, they alter it through their presence, resource utilization, and contributions. These alterations can be viewed as disturbances upon the landscape. Types of disturbances exerted by moose include feeding, trampling, defecation and urination. These disturbances affect many elements of the landscape, including the species composition, canopy structure, rate of succession, soil parameters, fungal interaction, and biogeochemistry (Persson et al 2000). While the Copper River Delta has been relatively unaffected by human activities, the US Forest Service lists the introduction of moose as significant in altering natural processes like vegetation succession (Christensen et al. 2000). The long-term effect of browsing appears to be the replacement of palatable deciduous species with long- lived unpalatable evergreens (Pastor et al 1988). In the short term (<30 yr) however, herbivory strongly affects many structural and functional properties of these successional ecosystems and will be discussed further below (Kielland and Bryant 1998).

Quantification Of Various Disturbance Types

A recent study estimated quantities for each of the disturbances listed above, based upon the available literature of moose populations internationally (Persson et al. 2000). By taking the average hoof size, length of stride and annual distance traveled, they calculated that one moose tramples roughly 9,324 m^2 (100,000 ft^2) or 0.9 ha (2.2 ac) annually. To support their large body size on plant material alone, they must consume very large quantities of food. The study calculated an estimate of yearly consumption to be 7, 200 - 9,000 kg (15,400 – 19,800 lbs) of fresh mass or 2,700 kg (5,940 lbs) of dry matter per moose. For fecal deposition, the study estimated 860 kg (1,890 lbs) of dry mass each year with an average of 5.7 kg (12.5 lbs) of Nitrogen (N) in the winter and 10.5 kg (23.1 lbs) of N in the summer. In this study the year was only divided into two periods, summer and winter. In addition, they estimated that each moose discharges 2,360 l (623 gal.) of urine, contributing 12.1 kg (26.6 lbs) of N each summer (Persson et al. 2000). No data were available on moose urination during the winter months. It is important to remember that this study used data from moose studies conducted across the world, to calculate these estimates of annual averages. However, if we multiply these numbers by a population estimate of moose in the western Copper River Delta, of 275 individuals (275,000,000 ft^2 trampled, ~5,445,000 lbs consumed, ~520,000 lbs defecated) we begin to see the magnitude of each of the various disturbances, which in turn affect the terrestrial and aquatic environment.

Rate Of Forest Succession

Temporally, moose affect plant species dominance and nutrient availability, which impact the rate of forest succession. One simplified conceptual model of the successional sequence (Fig. 4) shows barren land, colonized by early shrub species, which improve the environment and facilitate succession by Alder (*Alnus*), and then Poplar (*Populus*), succeeded eventually by Spruce (*Picea*) and Birch (*Betula*) [refer to (Trowbridge 2002) in this volume for more details] (Helm and Collins 1997). Moose prefer willow as a food item throughout the year (see Table 1). As moose browse on various plant parts, they slow the vegetation development by reducing heights of many shrubs (primarily willows) in earlier stages, consequently allowing alder (*Alnus* spp.) to dominate more rapidly (Helm and Collins 1997). Alder is a nitrogen fixing species, which suggests that an increased dominance by alder would increase available soil nitrogen and increase primary productivity, essentially accelerating this phase of early succession.

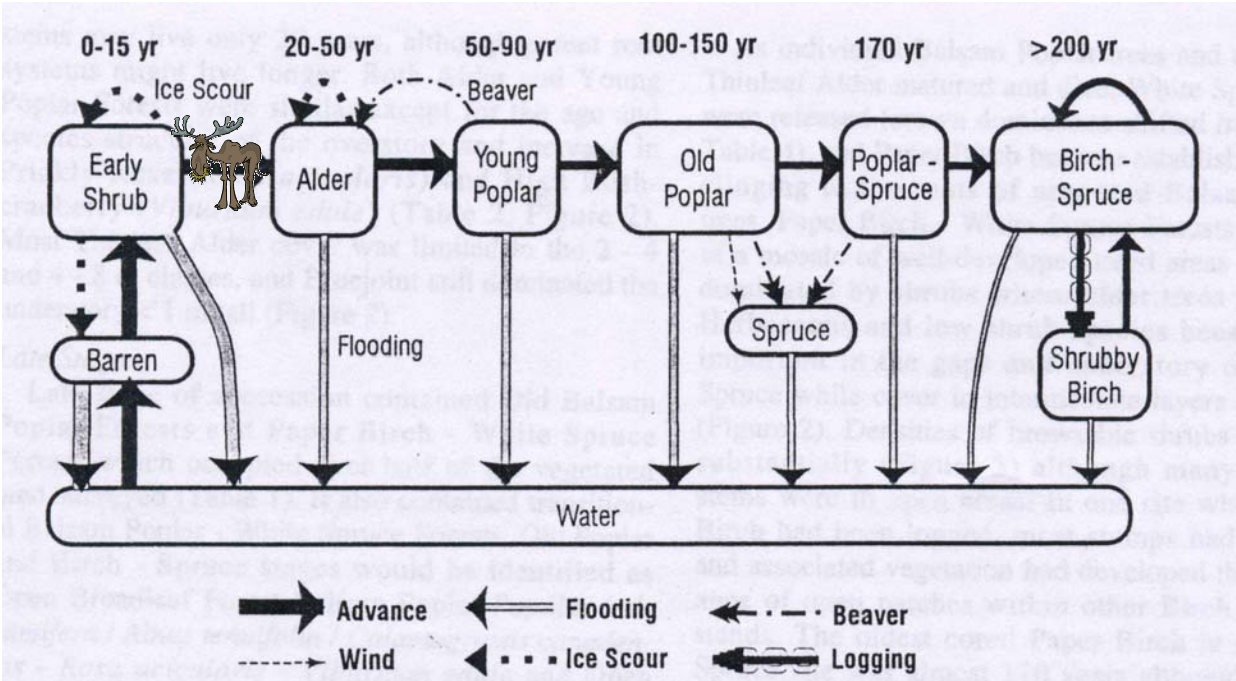

Figure 4. Conceptual model of succesional pathways along the Susitna River and their controlling factors. Width of arrows represents relative importance of the pathway. Moose accelerate the rate of forest succession from Early Shrub to Alder dominated vegetation communities. Figure taken from Helm and Collins 1997, moose added by author.

Stand Structure And Nutrient Cycling

Browsing reduces plant height and twig density, which creates a more open canopy causing changes to the physical environment. For example, higher light intensity results in higher soil temperatures, lower relative humidity and lower soil moisture (Persson et al. 2000). The selective browsing of moose often causes a shift in canopy composition towards dominance by unbrowsed species, like Alder (Persson et al. 2000). This in turn alters the quality of litter (leaves, and other plant parts), which falls to the forest floor. Browsing has been shown to increase litter quality and decomposition, accelerating the soil organic matter turnover rates and increasing habitat productivity (Keilland and Bryant 1998). In addition to biogeochemical changes associated with changes in litter fall, moose affect biogeochemical nutrient cycling through the contribution of plant nutrients from feces and urine (Persson et al. 2000). While these inputs would be trivial were they distributed evenly over the home range of an animal, they are often concentrated in feeding areas, and are substantial. The contribution to the soil nitrogen from urine and feces can be a considerable proportion of the total aboveground nitrogen input in early successional stages (Persson et al. 2000).

Mycorrhizal Interactions

The symbiosis between plants and mycorrhizal fungi are one of the most important biotic interactions affecting the functioning of plant communities and ecosystems (Harley 1971 in Rossow et al. 1997). Mycorrhizal fungi provide nutrients to plant roots in exchange for carbon from the plant. Browsing by moose on tree shoots and leaves has been shown to have a significant effect upon soil fungal communities (Rossow et al. 1997). In an exclusion experiment, the effect of moose browsing on mycorrhizal infection was investigated in the willow stage of primary succession in a taiga ecosystem along the Tanana River. The study found that mycorrhizae infection of fine roots of various willow species (*Salix* spp.) and Balsam Poplar (*Populus balsamifera*), was reduced in browsed areas by about 16%, as compared to a similar regions where moose were excluded with fencing (Rossow et al 1997).

Presumably, the mechanism driving this reduction is the supply of soluble carbohydrate needed by mycorrhizae. Browsing by moose and snowshoe hare can reduce the supply of soluble carbohydrate to the roots, thereby reducing the supply of carbohydrates available to the mycorrhizae, and as a consequence, reduce mycorrhizal infection of the fine roots of willows. In addition, large inputs of moose fecal nitrogen may also enhance the flux of soil inorganic nitrogen resulting in a lowered ectomycorrhizal infection. This is relevant, because successful infection of fine roots by mycorrhizae is very important to the competitive ability of woody plants, and especially woody plants growing in nutrient deficient soils (Allen and Allen 1990, and Allen 1991 in Russow et al. 1997). Therefore, the browsing and reduced mycorrhizal infection may reduce the ability of browse species to compete with alder (*Alnus* spp.), a species that is rarely browsed upon. This reduced competitive ability could contribute to the replacement of willow by alder during the primary stage of succession in floodplain taiga ecosystems.

CONCLUSION

The distribution and abundance of organisms, in other words, the ecology of a region, is controlled by both abiotic and biotic factors. In high latitude watersheds such as the Copper River, climate and geology create glacial, periglacial, and fluvial processes, which create a habitat template for terrestrial and aquatic environments. With this template created, biotic elements begin to influence the resulting ecology. Examples include nutrient deposition and near stream soil enrichment from anadromous runs of fish, facilitation observed in successional sequences of vegetation communities, and the influence of moose upon the environments they occupy. Moose inhabitation has been shown to affect nutrient cycling and geochemistry, floral and fauna species composition and dominance, stand structure, fungal interactions, and the rate of forest succession. The magnitude of disturbance resulting from moose occupation has lead some to suggest moose are a keystone herbivore in northern ecosystems (Molvar et al. 1993). The role of moose as a keystone herbivore is especially important in the Copper River Delta where moose were introduced and are altering vegetation communities through their presence. While the landscape of the Copper River watershed is driven by glacial and periglacial processes, and punctuated by large magnitude earthquakes and ice dam breakouts, moose still leave their mark.

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