

## ABORIGINAL OVERKILL AND THE BIOGEOGRAPHY OF MOOSE IN WESTERN NORTH AMERICA

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**ABSTRACT:** At historical contact, moose (*Alces alces*) were rare or absent throughout much of western North America but since ca. 1900 moose have increased dramatically. Several hypotheses have been advanced to explain the historical distribution and recent spread of moose in western North America. These include, (1) European settlement modified the original climax forests, which were poor moose habitat, and created seral vegetation types moose prefer. (2) Predators such as wolves (*Canis lupus*) once limited moose but the near extermination of native carnivores allowed moose to extend their range. (3) Moose had insufficient time to colonize the areas since the last glaciation. (4) Climatic variation -- the Little Ice Age and associated severe winter weather limited moose populations ca. 1700-1880. And (5) disease once limited moose numbers. None of these hypotheses, though, is supported by the available evidence. Instead, I propose that moose biogeography was controlled primarily by native hunting. An Aboriginal Overkill hypothesis is presented and discussed. That analysis indicates that moose were extremely vulnerable to predation by Native Americans and that native peoples had no effective conservation practices. Native Americans were the ultimate keystone predator.

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At historical contact, moose were rare or absent throughout much of western North America. Early accounts indicate that moose were seldom seen in British Columbia except for the northeast portion of that province, and even there, moose were rare (Brooks 1928; McCabe and McCabe 1928; Hatter 1950a, 1950b; Hall 1964; MacGregor and Child 1981; Halter 1988; Spalding 1990). In Alaska, moose were rare or absent from southern coastal areas; the Alaska, Kenai, and Seward Peninsulas; and the North Slope (Lutz 1960, LeResche *et al.* 1974, Coady 1980, Yesner 1989). Early fur trappers encountered few or no moose in Idaho (Ritchie 1978), Wyoming (Houston 1968, 1982), Montana (Stevens 1970, 1971; Peek 1974a), Colorado (Bailey 1944), Utah (Durrant 1952, Durrant *et al.* 1955, Wilson 1971), or Washington state (Peterson 1955, Kelsall and Telfer 1974). Moose, though, were relatively more common in Alberta, the Yukon, and interior Alaska (Kelsall and Telfer 1974, Coady 1980,

Yesner 1989).

Kay (1990, 1995b) systematically summarized wildlife sightings, sign, and kills reported by early explorers in the Yellowstone Ecosystem. Between 1835 and 1876, 20 different expeditions spent 765 days on foot or horseback yet no one saw or killed even a single moose. Moose sign, primarily tracks, was seen on five occasions but those observations were confined to the area immediately south of Yellowstone Lake (Doane 1875:11; Norris 1880:620, 1881:807). In fact, during the early 1900s, George Shiras (1913) "discovered" the Shiras moose subspecies above Yellowstone Lake. According to Houston (1968, 1982), moose first appeared to the south in Jackson Hole and to the north on Yellowstone Park's northern range only after 1910. William Henry Jackson, who accompanied the 1872 Yellowstone survey, however, photographed three moose (a cow and two calves) that had been killed on the Teton River in eastern Idaho (Yellowstone

National Park Photo 65-249.7) and he also photographed a live-captured moose calf at the Pease's Ranch north of Yellowstone Park (National Archives Neg. No. 501, P and P Lot 3546).

Lewis and Clark (1893), the first Europeans to travel across Montana, Idaho, Washington, and Oregon, did not personally see a single moose (Moulton 1991:330), although the Nez Percés mentioned that moose could be found on the headwaters of Idaho's Salmon River (Moulton 1991:326) and one of their men, Reubin Fields, reported wounding a moose near the headwaters of Montana's Blackfoot River (Moulton 1993:95). Similarly, Peter Sekene Ogden (1950, 1961, 1972) led Hudson's Bay Company fur brigades through Montana, Wyoming, Utah, Idaho, Washington, Oregon, and Nevada from 1824 to 1829 yet he seldom saw a moose. When Ogden's (1950:73) men killed a cow and two calves near present-day Philipsburg, Montana in 1825, he noted that it was the first time any of his people had seen a moose despite having spent a total of nearly 300 man-years in the West during the early 1800s. Thus, there is no evidence to support Jacobs' (1991:118) and Rasker *et al.*'s (1991:63) claim that moose were abundant in the northern Rockies, numbering in the tens of thousands, until those animals were slaughtered by unregulated hunting (Kay 1995a).

Moose, though, were more frequently seen in the Canadian Rockies. Kay *et al.* (1994, submitted) and Kay and White (1995) systematically summarized wildlife observations in first-person accounts made between 1792 and 1872 from the U.S. border north to Jasper National Park. This included the Alberta Foothills, the main Canadian Cordillera, and the Columbia Valley or Rocky Mountain Trench. Between 1792 and 1863, 29 parties spent 212 days in the Alberta Foothills and reported moose 8 times, or once every 26.5 party-days. While in the main Rocky Mountains, 26 parties spent 369

days between 1792 and 1872 and saw moose 27 times, or once every 13.7 party-days. Further west in the Columbia Valley, 11 parties spent 161 days between 1807 and 1859 but reported seeing moose only twice, or once every 80.5 party days. Thus, moose were seen more frequently in the main Canadian Rockies than in the Alberta Foothills or in the Columbia Valley. In no instance, however, were moose abundant as judged by these sighting rates and similar kill data -- one moose killed per 23.6 days in the Foothills, one kill per 14.2 days in the main cordillera, and one kill per 161 days in the Columbia Valley.

These low sighting and kill rates occurred even though most parties were living off the land, or at least attempting to, and were constantly searching for game. Many expeditions split into smaller groups and several sent out hunters ahead of their line of march but those smaller groups were no more successful at seeing or killing game than were the larger parties. In addition, many expeditions traversed areas where large numbers of moose can be found today yet they saw or killed few animals (Kay 1990, 1995b; Kay *et al.* 1994, submitted). If moose were as common in the past as they are today, there is no logical reason why early explorers would have not seen and killed a great many moose. In addition, these accounts note that the early parties were often short of food or even starving. For instance, in the Yellowstone journals discussed above, there are 45 references to a shortage of food or a lack of game (Kay 1990, 1995b) while in the main Canadian Cordillera, early travelers made 17 references to food shortages or a general absence of game (Kay *et al.* 1994, submitted).

Archaeological evidence indicates that moose were rare in pre-Columbian times, as well. Kay (1990, 1994a) summarized archaeologically recovered ungulate faunal remains unearthed at over 200 sites in Montana, Washington, Idaho, Oregon, Wyoming,

Utah, and Nevada. Of more than 52,000 ungulate bones, only one was identified as moose. Spalding (1990) reported that moose bones were also rare from archaeological sites in British Columbia while Yesner (1989) reported a similar pattern for archaeological sites in Alaska and the Yukon. Kay *et al.* (1994) summarized ungulate faunal remains unearthed in the Alberta Foothills, the main Canadian Rockies, and the Columbia Valley. Less than one percent of the identified ungulate bones found in the Alberta Foothill or the Canadian Cordillera were from moose and no moose bones have been recovered from the Columbia Valley.

Excavation at Jasper House, a ca. 1830-1884 Hudson's Bay Company trading post, however, uncovered a relatively large number of moose bones. Jasper House is located in the Athabasca Valley near the east boundary of Jasper National Park (Pickard 1985, Pickard and D'Amour 1987). Of 1,382 ungulate bones identified to species, 441 or 32% were moose and of the total number of ungulates present, 16 of 70 or 23% were moose (Kay *et al.* 1994). While these percentages are higher than those found in archaeological sites, they do not necessarily imply that moose were abundant. Instead, post journals and other first-hand accounts indicate that game was scarce and that post inhabitants were often starving or short of food (Kay *et al.* 1994, submitted). In fact, as discussed elsewhere, first-person historical accounts and archaeological data indicate that all species of ungulates were rare in intermountain western North America ca. 10,000 BP (before present) - 1900 (Kay 1994a, 1995a).

After ca. 1900, however, moose extended their range and/or became much more abundant (Kelsall 1987). Moose spread across Montana (Stevens 1971, Peek 1974a) and south into Wyoming, Idaho, Utah, and even Colorado (Kelsall and Telfer 1974). Moose have recently extended their range in Alaska

and are now common in southcentral forests; on the Seward, Kenai, and Alaska Peninsulas; and on the North Slope (LeResche 1974, Coady 1980, Yesner 1989). Moose presently occupy most of British Columbia where they have established high density populations (Hatler 1988, Spalding 1990). Today, there are more than 500,000 moose in western North America with an annual harvest of approximately 35,000 animals -- Alaska 155,000; Alberta 100,000; British Columbia 175,000; Colorado 425; Idaho 5,500; Montana 4,000; Utah 2,700; Washington 200; Wyoming 12,600, and the Yukon 50,000 (Kelsall 1987, Timmermann and Buss 1995) -- and populations may have been even higher during the 1950s and 1960s especially in western Canada and Alaska (Gasaway *et al.* 1983a, 1983b; Hatler 1988).

This raises the question of why moose were rare or absent in the past and why they have increased so dramatically during the 1900s. Moreover, these changes have been synchronous throughout the region (Karns 1987). At least five hypothesis have been advanced to explain the biogeography of moose in western North America (Kelsall and Telfer 1974). These include, (1) moose had insufficient time to colonize the areas since the last glaciation. (2) Climatic variation -- the Little Ice Age and associated severe winter weather limited moose populations ca. 1700-1800. (3) Disease once limited moose numbers. (4) European settlement modified the original climax forests, which were poor moose habitat, and created seral vegetation types that moose prefer. And (5) predators once limited moose but the near extermination of native carnivores allowed moose to extend their range and expand their populations. Of course, different factors may have influenced moose populations in different areas, but any hypothesis that could explain the entire spectrum of moose biogeography would be the most robust.

#### INSUFFICIENT TIME

This hypothesis maintains that moose did not have sufficient time to colonize parts of western North America since the last major glaciation. If this is a valid paradigm then, (a) moose colonization should have followed glacial retreat in a progressive manner and, (b) moose should have very low rates of dispersal since the entire area was ice-free for the last 7,000-10,000 years (Pielou 1991). There are, though, two schools of thought on how moose colonized North America.

The traditional view of moose subspeciation holds that North America was first colonized by *Alces* during the late Wisconsin and that subsequent glacial events isolated moose in Alaska (*A.a. gigas*) from those south of the continental ice-sheet -- *A.a. shirasi* in the West, *A.a. andersoni* in the Midwest, and *A.a. americana* in the East (Peterson 1955, Kelsall and Telfer 1974, Bowyer *et al.* 1991). Recently, however, it has been postulated that moose first arrived in North America much later and colonized only after the development of an ice-free corridor down the eastslope of the Rockies ca. 14,000 BP (Geist 1987a, 1987b; Bowyer *et al.* 1991:15-16). DNA evidence appears to support the latter interpretation (Bowyer 1991:15, Cronin 1991), but in either case, there is little correlation between local dates of deglaciation and whether or not moose were present or common at historical contact.

In Yellowstone, for instance, moose were first reported above Yellowstone Lake instead of from low elevation areas where moose are common today (see above). Those low-elevation ranges were ice-free sooner, however, than the area around Yellowstone Lake which is at higher elevation (Baker 1981); i.e., moose were first reported in a more recently deglaciated portion of the ecosystem, the exact opposite of the pattern predicted by the insufficient time hypothesis. Similarly, as described earlier, moose were seen more frequently ca. 1800-1870 in the

Canadian Rockies, where glaciers remained longer, than in British Columbia or the Alberta Foothills which were deglaciated earlier.

Moreover, moose have relatively high dispersal rates (LeResche 1974). Pimlott (1953) reported that after introduction in Newfoundland, moose spread at 8-10 km/yr until they occupied the entire province. Moose naturally entering Labrador spread at 13-24 km/yr (Mercer and Kitchen 1968), while moose colonized central British Columbia at 17 km/yr (Hall 1964:17; but see Spalding 1990). Even in established populations, moose have dispersal rates sufficient to colonize all of western North America in a few hundred years (LeResche 1974, Lynch 1976, Gasaway *et al.* 1980, Hauge and Keith 1981, Crete and Jolicoeur 1985). Furthermore, in some populations, moose make seasonal migrations of 40-80 km (Edwards and Ritcey 1956, Gillingham and Klein 1992, Van Ballenberghe 1992). Moose are also great wanderers often traveling 100-200 km beyond their normal ranges (Kelsall 1987:3).

Thus, the insufficient time hypothesis is not supported by available ecological data. If moose could colonize much of their present range as they did in the last 100 years, it is highly unlikely that time alone prevented them from doing so during the previous millennia. So, some other factor(s) must have inhibited their spread and/or abundance in earlier times.

### CLIMATIC CHANGE

According to this hypothesis, severe winter weather associated with the Little Ice Age limited moose populations ca. 1700-1880 (Hatler 1988:11). There are four variations of this theme. (a) Prolonged deep snow caused widespread starvation that limited moose. (b) Cool wet weather reduced vegetation production adversely effecting moose populations. (c) Cool wet weather reduced fire frequencies which in turn limited the

formation of seral plant communities favorable to moose. (d) Increased snowfall allowed wolves to kill more animals which limited moose numbers and prevented population expansion (Kelsall and Telfer 1974, Coady 1980, Hatler 1988, Spalding 1990).

First, while deep snow can have a negative effect on moose populations (Edwards 1956, Coady 1974), there is no evidence that severe winter weather has ever eliminated moose from large areas. Moreover, moose are adapted to low temperatures (Kelsall and Telfer 1974) and moose also have a competitive advantage as snow depths increase (Kelsall and Telfer 1971, Parker *et al.* 1984, Telfer and Kelsall 1984, Dailey and Hobbs 1989). Thus, if Little Ice Age induced climatic variation was a major factor limiting ungulate populations ca. 1700-1880, there is no reason why moose should have been affected to a greater degree than other ungulates. As bighorn sheep (*Ovis canadensis*), deer (*Odocoileus hemionus* and *O. virginianus*), and elk (*Cervus elaphus*) were reported more frequently by historical observers than moose and since archaeological data show the same pattern (Kay 1990; Kay *et al.* 1994, submitted; Kay and White 1995), it is highly unlikely that severe winter weather had a drastic effect on moose but not on other ungulates. In addition, it is not clear why winter weather would have had a greater impact in places where moose were not found ca. 1870 than where they occurred. Finally, climatic changes associated with the Little Ice Age were relatively small compared to the range of environmental conditions faced by moose today making it doubtful that cooler-wetter conditions ca. 1700-1870 had any significant impact on moose numbers or distribution (Coady 1980).

Second, there is no evidence that weather ca. 1700-1870 adversely affected moose populations to any major extent by either reducing plant production or by reducing fire frequency (see below for additional discus-

sion of the vegetation change hypothesis). In fact, Luckman and Seed (1995:98-99) questioned traditional interpretations of the Little Ice Age. "In the Canadian Rockies the pattern of climate variation prevailing during the 18th and 19th centuries appears to extend back to at least 1300 A.D. ... over the last several hundred years, there appear to have been several warmer and cooler periods, often no more than 30-50 years duration and there is no extended period that, on climatic grounds, could be identified as a cooler/wetter Little Ice Age that continued for several hundred years. Neither do these records show a major shift during the 18th century that could be defined as the inception of the Little Ice Age ... The Little Ice Age is named for, and identified as, a glacier event not a climatic event. Although glaciers clearly respond to changes in climate the nature of this response varies from region to region. The paleo-environmental records ... developed for the Canadian Rockies to date do not show a distinctive, prolonged period of cooler/wetter conditions that extended from ca 1700-1850s ... The significance of this record in terms of fire frequency studies is that, despite citations of our work to support it, it is very difficult to argue that the marked difference in reconstructed fire regimes using Time-Since-Fire analyses can be attributed to a change in climate conditions at the onset of the Little Ice Age. The reconstructed climatic history using glacier fluctuations and tree-rings does not coincide with the hypothesized 'shifts' in fire regime determined from these analyses." Others have concluded that time-since-fire-analysis derived fire-frequency shifts ca. 1600-1800 are most likely due to inappropriate use of the negative exponential model, normal statistical variation, or changes in aboriginal burning due to epidemic events, not climatic change, especially since the fire-frequency shifts are largely asynchronous (Kay *et al.* 1994, Kay and White 1995, Wierzchowski

1995, Rogeau 1996).

Third, increased snow can make moose more vulnerable to wolf predation (Mech *et al.* 1971, 1987; Peterson and Allen 1974) but there is little evidence that wolves or other carnivores can take moose populations to the exceedingly low levels seen at historic contact (see below). In addition, increased snow depths make other smaller ungulates relatively more vulnerable to wolf predation than moose. So if this was an important factor, wolf predation would have been relatively more intense on other species ca. 1700-1870, but as we have seen, other ungulates were more common than moose during that period.

Finally, if moose populations declined or if moose contracted their range due to the Little Ice Age, then that should be reflected in the archaeological record. That is to say, moose should have been relatively more abundant prior to ca. 1700 and less abundant thereafter. That pattern, however, is not found in the archaeological record. Instead, moose became more common relative to other ungulate species 400-500 BP (Yesner 1989) which does not correspond with any climatic pattern. Thus, available evidence does not support the climatic change hypothesis.

### DISEASE

It has also been suggested that disease and/or parasites might be important in moose biogeography. Most often mentioned is the meningeal worm (*Parelaphostrongylus tenuis*), which produces only occasional mild symptoms in its principal host, white-tailed deer (*O. virginianus*), but which can cause heavy mortality in moose (Anderson 1972; Anderson and Lankester 1974; Kelsall and Telfer 1974; Clark and Bowyer 1986; Geist 1987a; Lankester 1987; Thomas and Dodds 1988; Nudds 1990, 1992; Gilbert 1992; Schmitz and Nudds 1994). It is thought that white-tailed populations infected with *P. tenuis* have a negative impact on moose by

restricting the latter's numbers and distribution. White-tailed deer infected with meningeal worms are thought to limit the spread of moose and as white-tailed deer have expanded their range, moose are thought to have declined.

This may be a concern in the eastern U.S. and Canada but it is not true in the West because there *P. tenuis* is absent. White-tailed deer and moose are conspecific in Alberta, British Columbia, Idaho, Washington, Montana, and Wyoming but those white-tails are not infected with *P. tenuis* (Anderson 1972, Anderson and Lankester 1974, Prescott 1974, Lankester 1987). Moreover, neither whitetails nor *P. tenuis* are found in the Yukon or Alaska (Prescott 1974, Coady 1980). So, meningeal worms have not played a part in the biogeography of moose in western North America.

Furthermore, there is no evidence that any other parasite or disease has been important in moose biogeography over a large scale and certainly none that could have created the pattern of moose numbers and distribution seen at historic contact or since (Anderson and Lankester 1974, Lankester 1987). There is also no evidence that European introduced livestock diseases or parasites have had a major impact on moose (Anderson and Lankester 1974, Tessaro 1986, Lankester 1987, Northern Diseased Bison Environmental Assessment Panel 1990, Carbyn *et al.* 1993).

### VEGETATION CHANGE

Of all the hypotheses advanced to explain moose biogeography, vegetation change has received the most attention. Proponents of this view contend that moose populations were historically low because much of western North America was originally covered with virgin forests and moose only increased after European settlement created seral habitats that could support moose (Hatter 1950a, 1950b; Hall 1964; Kelsall and Telfer 1974;

Spalding 1990). According to this thesis, (a) moose cannot live in mature forests, (b) old-growth forests blanketed most of western North America in pre-Columbian times, (c) Europeans burned-off the original climax forests, i.e. fires were rare prior to European arrival, and (d) the spread of moose and/or the increase of moose populations closely followed forest destruction. In addition, this hypothesis implies that moose numbers and distribution are determined primarily by habitat and/or food which means that all suitable moose habitat should have been occupied in historic times. In other words, if there were large areas of suitable moose habitat historically but those areas were unoccupied, that would falsify this hypothesis.

First, there was no forest primeval. In fact, prior to European influence there was little old-growth forest anywhere in western North America, regardless of how old-growth is defined (Johnson *et al.* 1995, Kay 1995b, Kay and White 1995). Instead, disturbance was the rule. Fires were common and structured most forest communities (Lutz 1959; Wright and Bailey 1982; Parminter 1983a, 1983b, 1984; Johnson 1992; Bunnell 1995; Telfer 1995). Many montane and subalpine forests had fire-return intervals of 100 years or less, and in the boreal forest, one percent of the area burned each year, on average (Johnson 1992, Telfer 1995). "Thus, a substantial percentage of the vast boreal moose range was always in food-producing stands under primitive conditions" (Telfer 1984:172). Even in forests with 200-300 year fire-return intervals, there was little old-growth (Johnson *et al.* 1995).

Moreover, aboriginal burning was common and may have been more important than lightning-started fires in structuring plant communities (Lewis 1977, 1985; Pyne 1993, 1994, 1995a, 1995b; Kay 1995a; Kay and White 1995). Even in the wetter parts of British Columbia, aboriginal burning was widespread (Turner 1991, Gottesfeld 1994).

In addition, fire-history studies indicate that there was no increase in the area burned with European settlement (Tande 1979; Johnson and Fryer 1987; Masters 1990; Johnson *et al.* 1990, 1995; Kay *et al.* 1994). Europeans did start many fires but those only substituted for aboriginal and lightning-caused fires. So, large areas of seral habitat were always available to moose in western North America, yet those areas were largely unoccupied or populations were exceedingly low. Furthermore, Hall (1964) noted that there were large forest fires in central British Columbia during the early 1800's, but moose did not become common until the early to mid 1900s; i.e., the spread of moose was not closely related to area burned.

Second, research has shown that moose can live in climax forests (LeResche *et al.* 1974, Pierce 1983, 1984; Pierce and Peek 1984; Matchett 1985; Peek *et al.* 1987; Costain 1989; Costain and Matchett 1992; Tyers and Irby 1995). Even in old-growth forests there are always understory shrubs and stringers of riparian vegetation that can support moose, albeit at low densities. In fact, Geist (1971:121-123, 1974; Telfer 1984:164) proposed the concept of permanent and transient moose habitat. Moose could survive in mature forests and associated permanent habitat such as alluvial floodplains and riparian communities. Then, when the forests periodically burned, moose could increase by taking advantage of newly created seral vegetation. Thus, moose numbers might vary in time and space, but large areas would not be devoid of moose nor would moose populations be exceedingly low, as occurred at historical contact.

Third, in much of Montana, Wyoming, Idaho, and Utah, streamside willow (*Salix* spp.) communities provide prime moose habitat in summer and critical moose habitat during winter (Denniston 1956; Knowlton 1960; Peek 1963, 1974a, 1974b; Stevens 1970, 1971; Wilson 1971; Ritchie 1978;

Telfer 1984; Emmerich 1989; Van Dyke *et al.* 1995). Aspen (*Populus tremuloides*) is also an important vegetation type for moose in the Intermountain West (Peek 1974a, 1974b). Yet these habitats were common in historic and pre-Columbian times, and have actually decreased since European settlement. Overgrazing, irrigation withdrawals, and impoundments have reduced riparian areas by 90% or more in many areas of the western U.S. (Dobyns 1981, General Accounting Office 1988, Platts 1991, Kay 1994b) and aspen has declined precipitously due to overgrazing and an absence of fire (DeByle and Winokur 1985, Kay 1990). Similarly, in Alaska many moose populations depend on extensive willow stands but those habitats have been common for thousand of years even in places where moose were rare or absent until ca. 1920 such as the Kenai, Steward, and Alaska Peninsulas, and on the North Slope (LeResche *et al.* 1974, Coady 1980, Ritchie 1987).

Fourth, by creating and maintaining riparian communities beaver (*Castor canadensis*) often improve habitat for moose (Denniston 1956, Kelsall 1987, Kay 1994b). Moose numbers may even be linked with beaver populations -- the more beaver there are, the more riparian habitat there is, the more moose present (Flook 1964, Kelsall 1987). Early fur trappers and homesteaders, however, eradicated or severely reduced beaver throughout western North America (Johnson and Chance 1974, Ray 1975, Dobyns 1981, Kay 1994b). Thus, beaver-produced moose habitat was declining while moose were expanding their range and numbers -- the exact opposite of the predicted pattern. This is another indication that habitat was not limiting pre-European moose populations.

So in summary, suitable moose habitat was available over much of western North America well before ca. 1900 population expansions and increases. Paleo-environ-

mental studies also indicate that moose habitat was widespread in pre-Columbian times (LeResche *et al.* 1974; Peek 1974a, 1974b; Coady 1980; Vance *et al.* 1983; Telfer 1984; Hills *et al.* 1985; Mathewes 1985; Barnosky *et al.* 1987; Ritchie 1987; Pielou 1991). Yet, as discussed above, moose had been rare or absent for the previous 10,000 years. This suggests that something besides habitat availability must have limited moose populations in earlier times. One such factor could have been carnivore predation (Coady 1980, Spalding 1990).

### CARNIVORE PREDATION

Recent research in Alaska, British Columbia, Yukon, Alberta, and other Canadian provinces indicates that wolves and other carnivores, more often than not, limit moose and other ungulates (Gasaway *et al.* 1983a, 1983b, 1992; Messier 1989, 1991, 1994, 1995; Seip 1989, 1992a, 1992b; Bergerud 1990, 1992; Ballard 1991, 1992; Carbyn *et al.* 1993; Boertje *et al.* 1996; Kay 1996a). These studies can be summarized as follows. (1) In many situations, wolves and other carnivores limit moose populations below the level set by food resources; that is, moose are not resource limited or "naturally regulated" (i.e., Houston 1976) and any compensatory response of the moose population to predators is not enough to offset predation losses. (2) Human predation and carnivore predation on moose populations are additive, not compensatory. (3) If grizzly (*Ursus arctos*) or black bears (*U. americanus*) are present, they often prey heavily on newborn and, to a lesser degree, adult moose. Wolf and bear predation are additive, not compensatory, and together they can have a major impact on moose numbers. In some areas, grizzlies kill more moose than wolves (Gasaway *et al.* 1992). (4) If moose populations have been reduced by severe weather, human hunting, or other causes, wolves and other carnivores can drive moose



numbers even lower and maintain them at that level. As Alaskan biologists have noted, "prey populations can reach extremely low densities under natural conditions, contrary to the 'balance of nature' concept" (Gasaway *et al.* 1983a:6). Today, moose populations across much of western Canada and Alaska are being kept at low levels by the combined actions of carnivorous predators even in areas where moose are not hunted; i.e., national parks.

The question, however, is not whether wolves and bears can keep moose populations at low levels, but if carnivore predation could have created the distribution and abundance patterns seen at historical contact (Coady 1980). If wolves once limited the distribution of moose, as has been proposed (Spalding 1990), then it follows that moose should be extremely vulnerable to wolf predation. In addition, this hypothesis predicts that in a multi-ungulate system, wolves should prey disproportionately on moose. Furthermore, moose should not be able to extend their range in the face of wolf predation.

None of these predictions, however, is supported by available evidence. Moose, for instance, are less susceptible to wolf predation than are smaller ungulates and in many systems, wolves actually appear to avoid moose when other prey are present (Bergerud *et al.* 1984; Bergerud and Elliot 1986; Seip 1989, 1992b; Bergerud 1990, 1992; Weaver *et al.* 1992; Weaver 1994). On Coronation Island off the Alaskan coast, introduced wolves killed-off all the deer before the last wolf starved to death (Merriam 1964, Klein 1970), but moose on Isle Royale have done well despite over 40 years of wolf predation (Peterson 1995). So, this plus the fact that smaller ungulates were more common historically and prehistorically than moose, would suggest that carnivore predation was not the over-riding factor in moose biogeography. Moreover, while predator-prey stud-

ies indicate that wolves and other carnivores can limit moose populations, in none of those studies have moose become as rare as they were in earlier times nor has wolf predation eradicated moose from large areas -- like what was seen at historical contact.

Similarly, when moose populations expanded during the 1900s, they often did so despite carnivore predation. When moose spread throughout Alaska, for instance, they moved into areas with established wolf packs and bear populations -- wolves that were preying on other species before moose arrived (Coady 1980). In fact, the addition of moose into these systems actually allowed the number of wolves to increase, which then exerted additional predation pressure on the smaller ungulate species causing those populations to decline (Bergerud 1990, 1992; Seip 1992b). Although it may seem counter intuitive, multi-ungulate species systems appear to be less resilient than simpler predator-prey systems (Taylor 1984).

So if carnivore predation was not responsible and if the insufficient time, climatic change, disease, and vegetation change hypotheses cannot be sustained, as I have argued, how then is the biogeography of moose in western North America to be explained? I believe that the observed patterns were the result of native hunting. While I am not the first to suggest that native hunting limited moose (McCabe and McCabe 1928:4, Hatter 1950b:48-50, Coady 1980), I have formulated a comprehensive Aboriginal Overkill hypothesis (Kay 1994a, 1995a, 1995b). While this hypothesis was originally developed to explain the scarcity of elk in the historical and archaeological record (Kay 1990, Kay *et al.* 1994, Kay and White 1995), I believe that it is also applicable to moose.

#### ABORIGINAL OVERKILL

The age of their respective kills indicates that Native Americans were more efficient predators than wolves (Temple 1987). The

more difficult it is for a predator to capture a particular prey, the more that predator will take substandard individuals and young. So, if two or more predators are preying upon the same species, the least efficient predator will tend to kill fewer prime-age animals (Okarma 1984). While wolves and other carnivores kill primarily young-of-the-year and old animals, Native Americans killed mostly prime-age ungulates (Kay 1995a:123).

Since ungulates recovered from Intermountain archaeological sites invariably exhibit mortality profiles dominated by prime-age animals, this suggests that Native Americans were more efficient predators than wolves or other carnivores. Killing mostly prime-age animals, though, runs contrary to any maximum sustained-yield strategy (Hastings 1983, 1984) and indicates that Native Americans could have had a major impact on pre-Columbian ungulate populations. This is even more true when one considers that Native Americans killed mostly females (Kay 1994a).

As I have presented my Aboriginal Overkill hypothesis elsewhere (Kay 1994a, 1995, in press), I will not elaborate on its details except to note that Native American preferences for prime-age females runs counter to any conservation strategy. It is often claimed, however, that Native Americans' religious belief systems prevented those peoples from over-utilizing their resources (e.g., Nelson 1982, 1983). Native Americans tended to view wildlife as their spiritual kin where success in the hunt was obtained by following prescribed rituals and atonement after the kill (Feit 1987). A scarcity of animals or failure in the hunt were not viewed as biological or ecological phenomena, but rather as a spiritual consequence of social events or circumstances. If a Native American could not find any game, it was not because his people had overharvested the resource, but because he had done something to displease his gods. Since Native Americans saw no connection

between their hunting and game numbers, their system of religious beliefs actually fostered the over-exploitation of ungulate populations. Religious respect for animals does not equal conservation.

Instead, native hunters are essentially opportunistic and tend to take high-ranking ungulates regardless of the size of the prey populations or the likelihood of those animals becoming extinct (Winterhalder 1981a, Smith 1983). Native Americans had no concept of maximum sustained yield and did not manage ungulate populations to produce the greatest offtake. In addition, human predation and predation by carnivores are additive and work in concert to reduce ungulate numbers (Walters *et al.* 1981, Kay 1994a, Kay and White 1995). Moreover, competition from carnivores tended to negate any possible conservation practices (Kay 1994a). Because Native Americans could prey-switch to small animals, vegetal foods, and fish, they could take their preferred ungulate prey to low levels or extinction without having any adverse effect on human populations. In fact, once Native Americans killed off all the ungulates, human populations actually rose (Hawkes 1991, 1992, 1993).

There are, however, exceptions to Aboriginal Overkill. According to predator-prey theory, prey populations will increase if they have a refugium where they are safe from predation (Taylor 1984). So, ungulates that could escape aboriginal hunters in time or in space were more abundant. Moreover, refugia do not have to be complete to be effective. Partial refugia will also enable prey populations to survive. This explains why there were larger numbers of ungulates on the Great Plains and in the Arctic. By undertaking long-distance migrations, bison (*Bison bison*) and caribou (*Rangifer tarandus*) were able to outdistance most of their human and carnivorous predators (Kay 1994a, Kay 1996b). Ungulates were also able to survive in buffer zones between tribes that were

locked in mortal combat (Hickerson 1965, Kay 1996b). Lewis and Clark (1893:1197), for instance, noted that, "With regard to game in general, we observe that the greatest quantities of wild animals are usually found in the country lying between nations at war."

Moreover, the idea that North America was a "wilderness" untouched by the hand of man prior to 1492 is a myth, a myth created, in part, to justify appropriation of aboriginal lands and the genocide that befell native peoples (Denevan 1992, Gomez-Pompa and Kaus 1992, Simms 1992, Cronon 1995). North America was not a "wilderness" waiting to be "discovered," but instead was home to as many as 100 million Native Americans before European-introduced diseases decimated their numbers (Stannard 1992). In addition, by being transmitted from native group to native group, diseases such as smallpox decimated aboriginal populations 100-200 years before direct European contact (Dobyns 1983, Ramenofsky 1987, Campbell 1990). That is to say, depopulation of western North America began ca. 1550-1600.

Although the demonstrated lack of moose in archaeological sites may at first appear to negate my Aboriginal Overkill hypothesis, in fact, the opposite is true. Optimal-foraging theory (Smith 1983, Stephens and Krebs 1986) predicts that high-ranked items, like moose and other ungulates, are more susceptible to overexploitation than low-ranked items, such as vegetal foods, small mammals, or fish. According to optimal-foraging models, high-ranked items will seldom appear in the diet if they are being overexploited. So, ungulate species unearthed with the lowest frequency in archaeological sites, such as moose and elk, were probably subjected to extreme overexploitation (Kay 1994a). Moreover, the small proportion of large mammals in Intermountain aboriginal diets, both historically and prehistorically, as well as the highly fragmented nature of archaeologically recovered bone suggest that all species of

ungulates were relatively rare for the past 10,000 years (Kay 1994a, Kay *et al.* 1994, Kay and White 1995). Contrary to prevailing beliefs that native diets were primarily meat (McCabe and McCabe 1984:28), 80%-90% of aboriginal diets in western North America were vegetal foods or fish, except for Inuit, Aleut, and perhaps plains tribes (Kay 1994a).

Aboriginal peoples' ability to kill ungulates depended not only on their behavior but also on the prey's. For instance, moose that stand and hold their ground when tested by wolves have a higher probability of survival than individuals that attempt to flee (Mech 1970; Peterson 1977, 1995; Bubenik 1987). This behavioral strategy, evolved through eons of coevolution, may be adaptive when moose encounter wolves, but the same strategy is fatal when moose are hunted by Native Americans who kill at a distance. Aboriginal peoples used dogs to bay moose in order to take full advantage of this situation. In addition, Bubenik (1987:339) noted that moose do "not fear any other species including man." This combination of factors made killing moose extremely easy, despite those animals' large size.

Most native groups used dogs to hunt moose, especially during winter (McKenna 1959; Nelson 1973, 1983; Smith 1984; Feit 1987). Father Nicolas Point, who lived with various tribes in western Montana during the 1840s, made a watercolor drawing of a dog being used to hunt moose (Donnelly 1967:148). In Russia, where dogs are still used to hunt moose, dogs greatly increase hunter productivity and kill rates (Baskin and Lebedera 1987). Because of its effectiveness, the practice of using dogs to hunt moose and other ungulates has been banned throughout western North America since the inception of modern game management.

Native Americans also used snowshoes to run down moose in winter (McKenna 1959, Nelson 1973, Feit 1987). Ethnohistoric accounts indicate that Native Americans com-

monly ran down all species of ungulates (Anell 1969). Carrier (1984) has even suggested that humans evolved as long-distance endurance predators. Where there is a differential accumulation of snow in western mountains, Native Americans on snowshoes could simply run ungulates uphill into deeper and deeper snow where they were able to kill the floundering animals, including moose, often with no more than handaxes or clubs. Native Americans also preferred to kill female moose (Wolfe 1987) because of their higher fat content and better hides (Nelson 1983, Kay 1994a).

Nelson (1973, 1982, 1983) and Feit (1987), among others (e.g. Child 1988, Spalding 1990), contend that Native Americans were conservationists who had little impact on moose numbers. Their data, however, show that moose were hunted when they were most vulnerable with little regard for conservation. For instance, Nelson (1983:165) recounted that when moose were rare, "men often tracked a moose for days on snowshoes before they managed to overtake and kill it." With this hunting strategy, it is easy to see how aboriginal peoples could have had a major impact on moose. Because of their extremely high return rates, 10,000-95,000 kcal/hr (Winterhalder 1981b, Feit 1987), it is easy to understand how moose could have been overexploited.

Recall, that moose were exceedingly rare or absent from most of British Columbia except for the northeast portion of the province (see Hatter 1950b:35 -- figure 4). I suggest that this pattern reflects the amount of alternative foods available to native people. Where Native Americans had access to salmon and plentiful vegetal resources, there were few or no moose, but where salmon and other foods were scarce or absent, moose were relatively more abundant. In areas with few alternative foods, native people were less likely to take moose to low levels or extinction because human populations were

lower and starvation would have checked the hunters before the few remaining moose could be found. In my opinion, this explains why moose were more common historically farther from coastal areas -- fewer salmon and marine mammals, and in the far north -- less vegetal foods and fewer ungulate species.

In Alaska, for instance, moose were historically rare or absent within 100-200 km of the ocean where salmon, marine mammals, and sea birds were more available than further inland. Moose were absent from the North Slope for similar reasons, plus the lack of tree cover made moose extremely vulnerable to aboriginal hunters. Moose were relatively more common historically in central Alaska, central Yukon (Yesner 1989), and Alberta because in those areas there were fewer alternative foods for native peoples. Similarly, moose were rare or absent from most of the western U.S. because vegetal foods were more common, especially root crops which were heavily used by native peoples, and in some locations salmon were also abundant. Even in areas without salmon, however, there were other species of ungulates not available in northern Canada or Alaska. Again, multi-ungulate species prey bases are less persistent than simpler predator-prey systems, and in a multi-ungulate system, the predator will take the more vulnerable ungulates to low levels or extinction because it can survive on the other animals. Of all the ungulates in North America, I believe that moose were the easiest for Native Americans to kill (Kay 1994a).

In fact, moose survived in the western U.S. only where they had partial refugia in thick coniferous forests far removed from areas of native activity. This is why historically there were a few moose on the headwaters of the Yellowstone River. The area had fewer vegetal foods than lower-elevation habitats and native people did not winter in that high mountain valley (Wright 1984). This does not mean that the headwaters of the

Yellowstone were not hunted, for they were, but they were hunted less frequently and less intensively than surrounding areas. When moose or other populations are exceedingly low, it is not efficient for hunters to search just for that species. Instead, natives adopt a generalized hunting strategy but when they encounter a moose track, they are then likely to follow that animal until it is killed.

Several authors have noted that during the early 1800s, moose were common along the Canoe River in eastern British Columbia (Hall 1964:35, Spalding 1990). David Thompson, the first European to explore that area, wintered at the junction of the Canoe and Columbia Rivers in 1810 where he and his party subsisted largely on moose (Kay *et al.* 1994, submitted). Salmon do come up the Columbia past this point, so why were moose found here but not in other areas of southeastern British Columbia? I suggest that moose were relatively abundant in this portion of the Columbia Valley because, at that time, it was a buffer or boundary zone between warring tribes -- the Kootenay to the south and the Beaver to the north. During their 1810 winter stay, David Thompson's party was not visited by, nor did they see, any native people -- something very unusual in western North America during that era.

Similarly at historical contact, game, including moose, was common along the Peace River in eastern British Columbia and western Alberta because the area was a boundary zone between the Beaver on the west and the Cree who were moving in from the east. As the Cree gained control, hunting pressure increased and wildlife populations declined. The same was true on the Alberta side of the southern and central Canadian Rockies. At historical contact, the Piegan kept the Kootenay west of the continental divide by force of arms (Kay *et al.* 1994, submitted). Prior to expansion of the Blackfoot confederation in the 1700s, the Kootenay may have permanently resided east of the divide. Early

explorers to the Canadian Cordillera encountered few native people, and correspondingly moose and other ungulates were seen more frequently (Kay *et al.* 1994, submitted).

The impact of native hunting can even be observed in the archaeological record. If my Aboriginal Overkill hypothesis is correct and if Dobyns' (1983) disease hypothesis is correct, that is European-introduced diseases decimated native populations ca. 1550-1600, then as native peoples declined, moose populations would have increased and moose should become relatively more common in archaeological sites. This, in fact, is the pattern Yesner (1989:133) reported for Alaska and the Yukon, and that I have found for other ungulates (Kay 1994a).

Once native people were driven from their lands by repeated disease epidemics, European settlement, or conquest, only then did moose populations throughout western North America increase to unprecedented levels. Government programs that resettled native people in permanent villages for administrative purposes also contributed to this trend (Coady 1980). In my opinion, native hunting is also the reason large herds of ungulates never populated the Columbia Basin or other areas of the West (Kay 1994a). Only where the prey had refugia, or where there were few alternative human foods, were ungulates able to survive (Kay 1996b). Instead of being "Ecologically Noble Savages" (Alvard 1993), Native Americans were the ultimate keystone predator that structured ungulate communities throughout western North America.

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