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Prehistoric perspectives can help interpret the present: 14 000 years of moose (*Alces alces*) in the Western Arctic

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Abstract

Rapidly changing climate at high latitudes has triggered a search for bellwethers of ecological change there. If the initial signs of change can be identified, perhaps we can predict where these changes will lead. Large-bodied, terrestrial herbivores are potential candidates for bellwether taxa because of the key roles they play in some ecological communities. Here, we assembled historical, archaeological, and paleontological records of moose (*Alces alces* (Linnaeus, 1758)) from the western Arctic and subarctic. The results showed that rather than having recently invaded tundra regions in response to post Little Ice Age warming, moose have inhabited river corridors several hundred kilometres north of the closed, boreal forest since they first colonized North America across the Bering Land Bridge ca. 14 000 years ago. The combination of high mobility, fluctuation-prone metapopulations, and reliance on early successional vegetation makes changes in the northern range limits of moose undependable bellwethers for other biotic responses to changing climate. The history of moose at high latitudes illustrates how understanding what happened in prehistory is useful for correctly assigning significance and cause to present-day ecological changes.

Key words: *Alces alces*, moose, Arctic Alaska, megafauna, paleontology, archaeology

Résumé

Les changements rapides du climat à hautes latitudes se sont traduits par la quête de signaux annonciateurs de changements écologiques dans ces régions. Si des signaux des premiers changements peuvent être cernés, il pourrait être possible de prédire où mèneront ces changements. Les grands herbivores terrestres constituent de potentiels taxons annonciateurs en raison des rôles clés qu'ils jouent dans certaines communautés écologiques. Nous colligeons des cas de présence d'orignaux (*Alces alces* (Linnaeus, 1758)) dans des registres historiques, archéologiques et paléontologiques de régions arctique et subarctique occidentales. Les résultats révèlent que, plutôt que d'avoir envahi récemment les toundras en réponse au réchauffement qui a suivi le Petit Âge glaciaire, les orignaux ont, depuis leur colonisation initiale de l'Amérique du Nord par le pont continental de Behring il y a quelque 14 000 ans, occupé des couloirs fluviaux à plusieurs centaines de kilomètres au nord de la forêt boréale fermée. La combinaison de métapopulations d'une grande mobilité qui ont tendance à fluctuer et du recours à une végétation de début de succession fait en sorte que les variations des limites septentrionales de l'aire de répartition de l'orignal ne constituent pas des signaux annonciateurs fiables d'autres réponses biotiques aux changements climatiques. L'histoire des orignaux à hautes latitudes illustre l'utilité de comprendre ce qui s'est passé dans la préhistoire pour bien établir l'importance et les causes de changements écologiques actuels. [Traduit par la Rédaction]

Mots-clés : *Alces alces*, orignal, Alaska arctique, mégafaune, paléontologie, archéologie

Introduction

Earth's biogeography is rapidly shifting around us (Parmesan 2006; Chen et al. 2011; Davidson et al. 2017; Ratajczak et al. 2018). Effectively managing species within the present milieu of rapid environmental changes requires identifying the factors controlling their population sizes and geographic distributions. Human activities can drastically alter biogeography (Brook et al. 2008; Kolbert 2014), and this is especially true at high latitudes where the effects of global warming are amplified (Bhatt et al. 2017). Some of our most widespread impacts on terrestrial Arctic megafauna (terrestrial mammals weighing >40 kg) will happen indirectly through the impacts of global warming, which can take (Bhatt et al. 2017) diverse and subtle forms (Post and Stenseth 1998, 1999; Post et al. 2013). Because climate-change impacts are often indirect and collaborative (Turner et al. 2020), it can be difficult to attribute changes in the abundance and distribution of Arctic megafauna directly to climate (Cuyler 2007).

Historical perspectives are needed to judge the uniqueness of ongoing changes in population sizes and geographic distributions (Shuman 2012; Post and Høye 2013). Are recent range shifts unprecedented within the time spans of historical and prehistoric records? Gaining historical perspective is especially difficult in the Arctic because long-term records are often scarce. The resulting uncertainties make it easy to adopt a paradigm of catastrophism, when in fact the ongoing changes simply represent normal variation when viewed from the perspective of prehistory.

For example, Tape et al. (2016) hypothesized that an unprecedented range expansion of moose (*Alces alces* (Linnaeus, 1758)) occurred in tundra regions of northern Alaska at the end of the Little Ice Age (ca. CE 1850) in response to warmer summers that allowed willow shrubs to grow taller, which caused them to protrude above the winter snowpack and afforded moose a more dependable winter food supply. Based on their modelling study, Tape et al. (2016) asserted that this purported expansion of moose into tundra habitats coincided with a step-increase in high-latitude temperatures beginning in the 1920s (Morice et al. 2021), an increase that is generally attributed to greenhouse warming (Abram et al. 2016). Tape et al. (2016) concluded that this supposedly unprecedented expansion of moose into tundra areas of the North Slope was "…a bellwether for other boreal species…".

Here, we explored the alternative hypothesis that recent changes in moose populations at their northern range margins represent normal variability when viewed over timescales of centuries to millennia. After all, metapopulations inhabiting range margins are often smaller and more unstable than those occupying the core of a species' range (Gaston 2009; Sexton et al. 2009). We used paleontological, prehistoric (from archaeological sites), and historical records to establish a timeline for moose presence north of the closed boreal forest in the tundra biome of North America. Our focus was on the North Slope of Alaska, the region bordered by the Brooks Range to the south and the Beaufort and Chukchi seas to the north (Fig. 1). The results indicate that moose have inhabited shrub-lined, river corridors within this tundra region since they first crossed the Bering Land Bridge ca. 14 000 years ago. We argue that the complexity of factors controlling the range-edge metapopulations of large, Arctic mammals such as moose makes them poor bellwethers for ongoing ecosystem changes and urge other investigators to consider the usefulness of paleo records in detecting and attributing causation to ongoing ecological changes.

Background

Overview of moose biogeography and ecology

As the largest member of the deer family, moose are highly mobile and capable of dispersing long distances (Bowyer et al. 2003). Moose evolved in Eurasia and after surviving the ice ages in multiple refugia there (Dussex et al. 2020) crossed the Bering Land Bridge into North America ca. 14 000 calendar years before present (cal BP) (DeCesare et al. 2020), possibly at the same time the first humans and wapiti (*Cervus elaphus* Linnaeus, 1758) arrived (Guthrie 2006; Mann et al. 2013; Meiri et al. 2014). After reaching Alaska, moose dispersed across northern North America as deglaciation made new habitats available (Kelsall and Telfer 1974; Peterson 1978).

Moose's present circumboreal population of approximately two million animals (Hundertmark 2016) is composed of numerous regional metapopulations (Schmidt et al. 2009; DeCesare et al. 2020). Many of these local populations undergo short-term fluctuations driven by a hierarchy of causes, foremost among which are the density-dependent impacts of moose on their own food supplies, with some combination predation, human hunting, disease, and severe weather often being contributing factors (Bowyer et al. 2003).

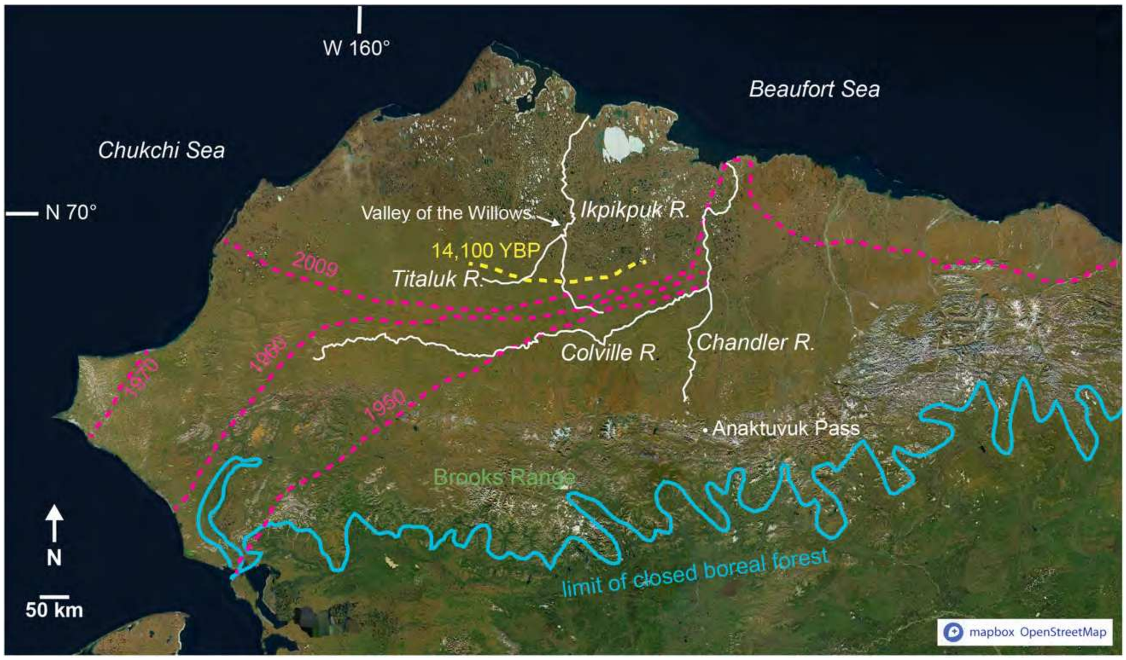
Moose populations can potentially increase rapidly (Bergerud and Elliot 1986; Schwartz 1998). Female moose with adequate nutrition typically bear their first calf around their second birthday (Bowyer et al. 2003), and cows can continue reproducing past 16 years of age (Dinneford 1988). Pregnancy rates can reach >80% within cow–moose populations (Boer 1992), and twins and even triplets occur under favorable conditions (Franzmann and Schwartz 1985), particularly in populations currently below carrying capacity (Gasaway et al. 1992).

Particularly in the boreal forest and tundra, moose rely heavily on early successional habitats and the plant species growing there (Kielland and Bryant 1998; Bowyer et al. 2003). In the North American Arctic and subarctic, willow shrubs (species of the genus *Salix* L) are the mainstay of moose diet, particularly in winter (Peek 1974; Molvar et al. 1993). Ecological disturbances that create early successional communities rich in moose browse, particularly willow shrubs, can trigger localized increases in moose populations (Darimont et al. 2005; Nummi et al. 2019).

Perspectives from other northern ungulates

Causes of range shifts in the two megafaunal herbivore species that share moose's tundra habitats, muskox (*Ovibos moschatus* (Zimmermann, 1780)) and caribou (*Rangifer tarandus* (Linnaeus, 1758)), are better understood than for moose. The recent demographic histories of Arctic populations of muskoxen and caribou are characterized by decade- to century-scale cycles of local extirpation followed by recolonization and population re-establishment (Vibe 1967; Gunn et al. 1991; Forchhammer et al. 2002; Cuyler 2007). These cycles are driven by complex interactions between food resources, predation, parasite loads, disease organisms, and extreme weather events, all of which may or may not be affected by global climate changes (Cuyler et al. 2020; Schmelzer et al. 2020). The fluctuations in muskox and caribou numbers are most pronounced near their range margins where the animals are most vulnerable to environmental stresses and where population densities and reproduction rates are lowest (Caughley et al. 1988; Lawton 1993; Ruprecht 2016). Based on caribou and muskoxen, local extirpations followed by recolonizations via long-distance dispersal are characteristic of the natural histories of Arctic megafaunal herbivores (Meldgaard

Fig. 1. Locations of Ikpikpuk, Titaluk, Colville, and Chandler rivers (white lines) on Alaska's North Slope. Locations of Anaktuvuk Pass and Valley of the Willows are indicated. The blue line shows the approximate northern limit of continuous boreal forest today (CAVM 2003). The dashed pink lines show the approximate northern limits of moose (*Alces alces*) in different calendar year according to Tape et al.'s (2016) interpretation of the sparse literature concerning recent moose distribution in northern Alaska. The yellow line marks the northernmost occurrence of paleontological moose bones, which range from ca. 14 ka to present. Map uses WGS 84 geographic coordinate system. Map made with ExpertGPS (https://www.expertgps.com/) using ©Mapbox (https://www.mapbox.com/about/maps/) and ©OpenStreetMap (https://www.openstreetmap.org/copyright).



1986; Reynolds 1998; Harper and McCarthy 2015; Mallory and Boyce 2018).

Study area and methods

We compiled records of moose bones found in archaeological sites and historical records of extralimital moose sightings from the Western Arctic, roughly the region stretching from the western coast of Hudson Bay to the Chukchi and Bering Seas north of the boreal forest. Moose remains were collected in the course of a long-term study of Pleistocene megafauna (Mann et al. 2013, 2015) in the upper 50 km of the Ikpikpuk and Titaluk rivers in the National Petroleum Reserve Alaska (NPRA) on the North Slope of Alaska (Fig. 1). Both these rivers are low-gradient, meandering streams possessing nival flow regimes, which means that high water occurs once annually during ice breakup. Water levels are typically low during freeze-up, and consequently there is no ice on the floodplains when snowfall begins in autumn. The valleys of both the Ikpikpuk and Titaluk rivers are incised 10–40 m within thick terrace fills (Mann et al. 2010; Gaglioti et al. 2018). The resultant warm microclimate allows their floodplains to support dense thickets of willow shrubs (*Salix* spp.), some of which (e.g., feltleaf willow, *Salix alaxensis* (Andersson) Coville) grow to heights of 4 m.

We collected moose bones and antlers from point bars and eroding bluffs. All these remains occurred as disarticulated elements that had been reworked by the rivers to varying degrees (Mann et al. 2013). We revisited the same reaches of these rivers over 7 years, finding new moose bones and antlers during each visit. Identifications were made using a reference bone collection at the University of Alaska Fairbanks. No moose bones were found associated with archaeological sites. All these specimens are now archived in the Kunz Collection of NPRA bones in the University of Alaska Museum of the North.

We radiocarbon dated by accelerator mass spectrometry (AMS) collagen extracted from 14 of the best-preserved moose bones and antlers using a modified Longin protocol (Longin 1971) (Fig. 2). All radiocarbon dates were calibrated using OxCal 4.4 (Bronk Ramsey 2009) and the IntCal 20 calibration curve (Reimer et al. 2020) and are therefore expressed as calendar years before CE 1950 (cal BP). We used OxCal 4.4 to calculate probability density distributions and median calendar year ages. Measurements of δ^{13}C and δ^{15}N, which are indicators of diet, were obtained for most bone and antler samples. To check for dietary changes through time, we graphed isotopic values against estimates of median bone ages using OxCal 4.4. We used the AMS-^{14}C ages and isotopic data from an additional 20 moose bones we previously published in Mann et al. (2013). Finally, we compiled data from 14 caribou bones dating to the last 15 cal BP collected along the same rivers as the moose bones (Mann et al. 2013).

Fig. 2. Photos of some moose (*Alces alces*) elements dated for this study. Text in white boxes includes field ID followed by age (median cal YBP). Condition and weathering of elements do not always correlate with their age. [Color online.]

Results

^{14}C-dated moose bones from Alaska's North Slope

Radiocarbon dating reveals that only 1 (IK17-003) of the 34 dated moose bones and antlers is modern in age, where "modern" is defined as the calibrated age range that extends into the post-1900 period (Appendix A). Four other bones (MAY12-63, KIG05-4.1, IK08-129, and IK17-005) are possibly modern at the 2-sigma level; however, the older extremes of the probability distributions of these four "possibly modern" dates range from 260 to 350 years BP, where "BP" is conventionally defined as the year CE 1950. This means that these four "possibly modern" moose may have died during the last few centuries of the Little Ice Age, which ended ca. 1850. The oldest moose bone (IK99-472) dates to 12 245 ± 40 ^{14}C years, which equates to a median calibrated age of 14.1 cal BP. There is no evidence that any of these bones have been transported by human or natural agencies from the south, outside of the Ikpikpuk and Titaluk watersheds (Mann et al. 2013). Clearly, moose have inhabited the Ikpikpuk River and Titaluk River drainages at least intermittently for many millennia, including during the Little Ice Age (Fig. 3).

The probability-density distribution of the 29 pre-modern moose bones is skewed toward the last 3000 years (Fig. 3). This "rise to the present" is typical of many dated bone series and reflects taphonomic biases caused by a declining probability of preservation and the reduced likelihood of discovery as bones become older. What is not expected is the prominent gap in the occurrence of moose bones dating to the period 5–10 cal BP. The 14 caribou bones from the same region and dating to the last 14 000 years show a similar hiatus between ca. 5 and 10 cal BP (Fig. 4). Muskoxen, the only other large herbivore in the region during this period, also exhibits a similar

Fig. 3. Probability density graph of the ^{14}C ages of 33 moose (*Alces alces*) bones and antlers from the Titaluk River and Ikpikpuk River drainages on Alaska's North Slope. Pink/hatched bar indicates time span of Little Ice Age. [Color online.]

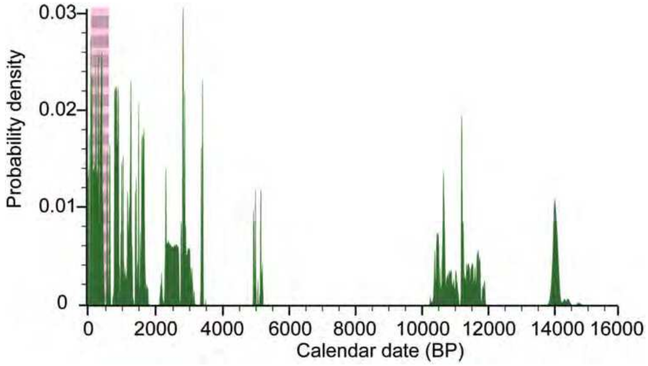


Fig. 4. Probability density graph of 14 caribou (*Rangifer tarandus*) bones from same area as the moose (*Alces alces*) bones in Fig. 3. [Color online.]

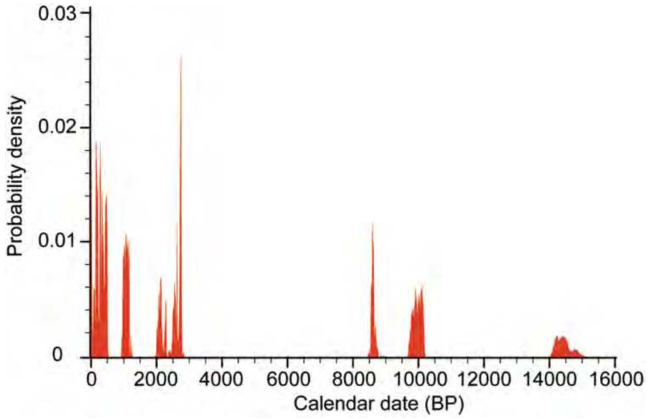
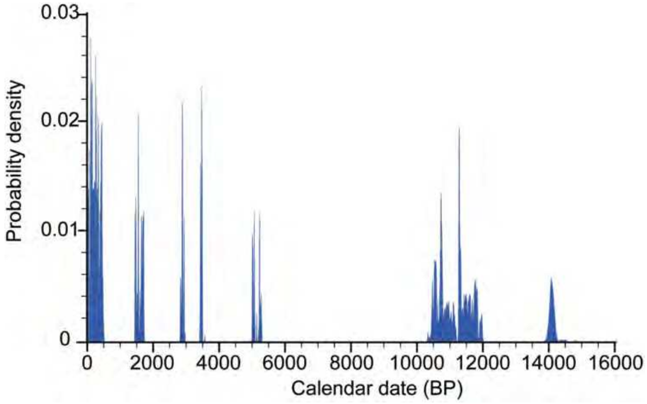


Fig. 5. Probability density graph of 18 cast moose (*Alces alces*) antlers, a subset of the 33 bone ages shown in Fig. 3. [Color online.]



hiatus (Mann et al. 2013). Because this hiatus is shared by multiple species, we suspect it has a taphonomic cause related to floodplain dynamics (Mann et al. 2010).

Of the 29 moose remains not in the "possibly modern" group, 18 are cast antlers (Fig. 5). Female moose lack antlers, and modern male moose cast their antlers between December and March (Peterson 1978). Assuming the timing of antler casting has remained constant over time, the presence of these antlers indicates that bull moose were not casual summer visitors to the Titaluk and Ikpikpuk drainages but instead overwintered there on multiple occasions during the past 14 000 years.

Bone isotope values

No significant trends occur in either the $\delta^{13}C$ or $\delta^{15}N$ content of moose bones dating to the last 14 000 years from the Ikpikpuk and Titaluk valleys (Fig. 6). There is more variability in $\delta^{13}C$ and $\delta^{15}N$ in the bones younger than 5000 years, but there are also more sampled bones from this younger period (25 vs. 8 samples for $\delta^{13}C$; 21 vs. 8 samples for $\delta^{15}N$). Only two of the pre-10 cal BP $\delta^{15}N$ values fall outside the range of younger values. Variations in $\delta^{13}C$ can be the result of minor changes in the proportions of shrubs, herbaceous plants, and aquatic plants in the diet, while the variation in $\delta^{15}N$ could relate to seasonal variations caused by negative energy balances in wintertime when food is limited (Ben-David et al. 2001). These data suggest there has been no significant change in the plant foods available to at least the older and younger groupings of moose in this study, which in turn suggests that the food available to moose remained more or less constant throughout.

Historical records of moose in Arctic Canada

The reports of early European visitors suggest that moose have been resident north of treeline in northern Canada since at least the early 1800s (Fig. 7; Appendix B). The Mackenzie River expedition of 1825–1827 encountered numerous moose on the Mackenzie River delta (Franklin and Richardson 1828). It has been suggested that moose were increasing along the lower Mackenzie River around 1908 in response to a declining human population there (Anderson 1924). Moose numbers declined again in 1920s when traders and trappers moved into the region and hunting increased (Kelsall 1972). Moose were reported to be common along the Anderson River at the edge of treeline prior to 1861 when Fort Anderson was established (MacFarlane 1905). In 1923, two bull moose were killed near Chesterfield Inlet, hundreds of kilometres beyond treeline on the west coast of Hudson Bay by Indigenous hunters who had never seen moose before (Anderson 1924) (Fig. 7).

Archaeological, oral, and historical records of moose in Alaska

Moose bones recovered from archaeological sites (Fig. 8; Appendix C) confirm the presence of the species in northern Alaska north of the Brooks Range dating between CE 1000 and 1800 (Giddings 1954, 1962; Hall 1973). These data suggest the species was at least intermittently present on the North Slope throughout the Little Ice Age (CE 1400–1850).

In northern Alaska, the oral traditions of Nunamiut people living at Anaktuvuk Pass in the Brooks Range (Fig. 1) suggest that major fluctuations have occurred in the moose population north of boreal treeline since the mid-late 1800s (Rausch 1951; Gubser 1965; LeResche et al. 1974; Coady 1980). According to elders in Anaktuvuk Pass, moose were rare north of the Brooks Range before ca. 1870 but beginning ca. 1880 they became locally abundant along the Colville River (Gubser 1965). After ca. 1900, Nunamiut hunters encountered increasing numbers of moose dispersing northward across the Brooks Range. They inferred these animals were dispersing because dense moose populations south of the range had degraded the habitat there (Gubser 1965, p. 284). In contrast to caribou, moose were never consistently hunted by the Nunamiut (Gubser 1965). Sporadic reports from non-Indigenous visitors (Figs. 7 and 8; Appendices B and C) confirm that moose have been locally present on the North Slope since at least 1900.

Discussion

Moose have a lengthy history in Arctic Alaska

The ^{14}C ages of moose remains from the North Slope of Alaska indicate that this species has been at least intermittently present several hundred kilometres north of boreal treeline over the past 14 000 years (Fig. 3). Only one of the moose bones we dated is definitely modern, and eight bone/antler dates fall within the time span of the Little Ice Age (Appendix A; Fig. 3). The 18 cast antlers we ^{14}C-dated (Fig. 5) indicate that moose spent winters as well as summers north of the Colville River and thus ranged 25–100 km north of the 2009 limit suggested by Tape et al. (2016) (Fig. 1).

Despite the lengthy history of moose on the North Slope, the records presently available from paleontological, archaeological, oral history, and explorer accounts suggest that they have never been abundant there, and that their populations have fluctuated in size over annual, decadal, and possibly millennial timescales. These observations are consistent with moose populations on the North Slope under-

Fig. 6. Isotopic values of moose (*Alces alces*) bones from North Slope Alaska graphed against their median radiocarbon ages. [Color online.]

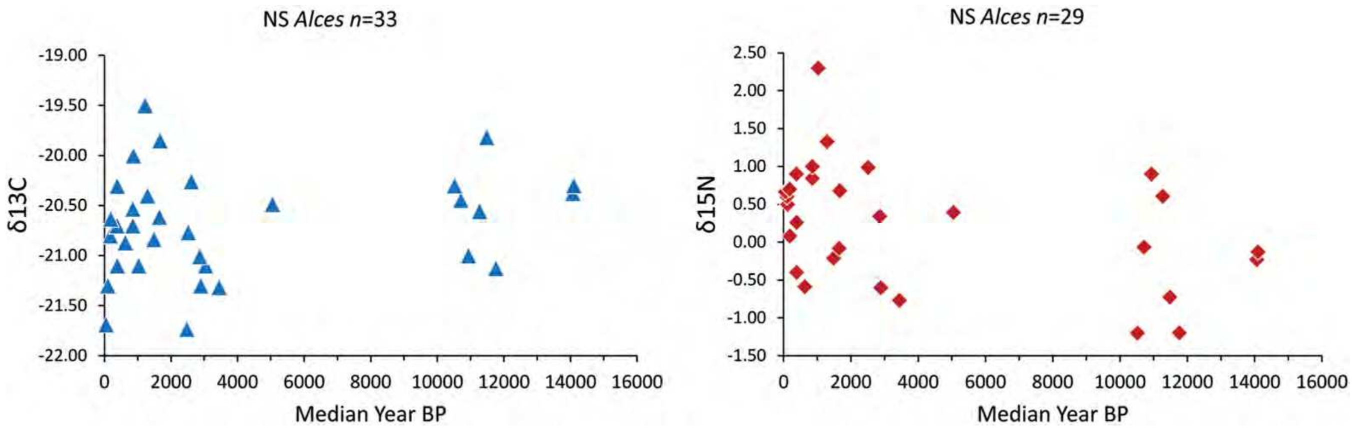
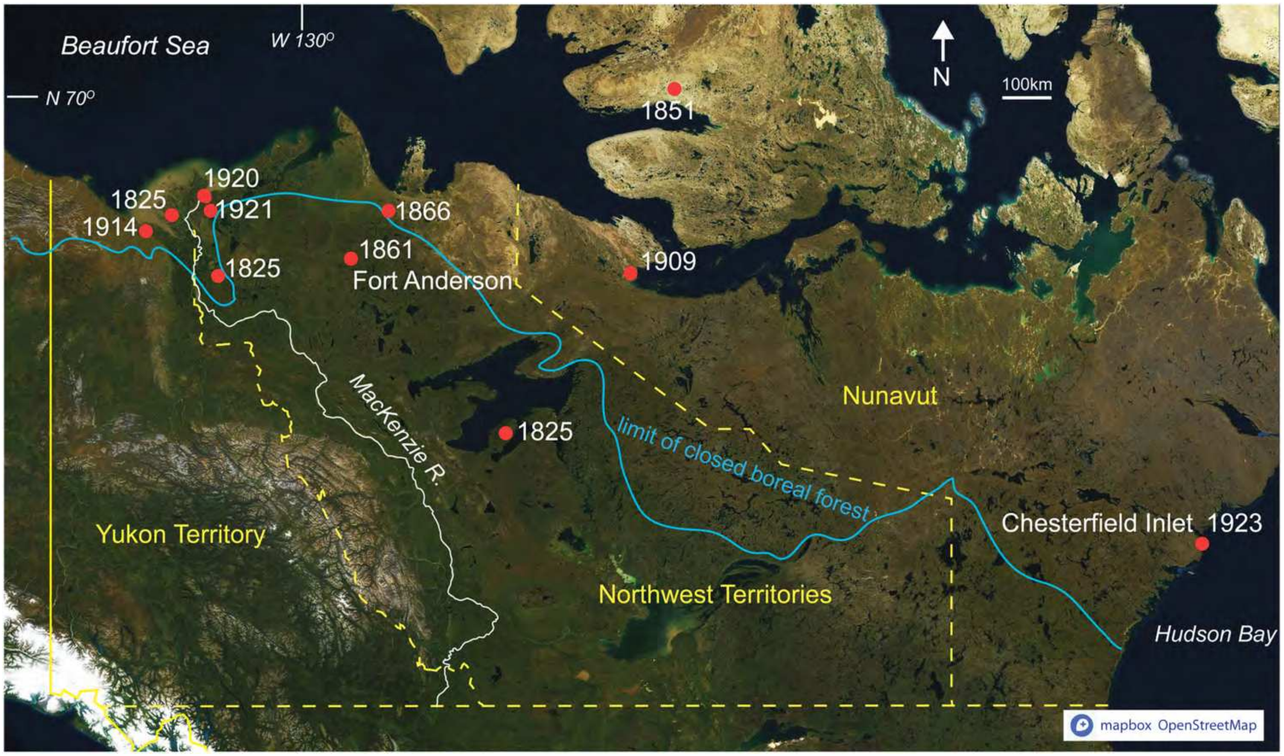


Fig. 7. Historical records of moose (*Alces alces*) in northwestern Canada. Numbers are dates in years CE. The blue line is the approximate northern limit of the closed boreal forest (CAVM 2003). The solid yellow line is international border with the USA. Details of these records are given in Appendix B. Map uses WGS 84 geographic coordinate system. Map made with ExpertGPS (https://www.expertgps.com/) using ©Mapbox (https://www.mapbox.com/about/maps/) and ©OpenStreetMap (https://www.openstreetmap.org/copyright).



going multiple, local extirpations followed by long-distance recolonizations. As is the case for caribou and muskoxen at the northern edges of their ranges (Meldgaard 1986; Cuyler 2007), extirpations and recolonizations of moose in Arctic Alaska were probably driven by a variety of causes, including changing predation pressures, anomalous weather events, changes in climate, and changes in vegetation. In many cases, these drivers probably acted collaboratively rather than separately.

Ecological interactions with taxa other than willow shrubs have the potential to influence the northern range limits of moose. Ecological engineering by beavers (*Castor canadensis* Kuhl, 1820) has the potential to enlarge moose-favorable habitats (Tape et al. 2018; Nummi et al. 2019; Larsen et al. 2021); however, beavers have been absent from the study area during the 14 000 years when moose inhabited the Titaluk and Ikpikpuk watersheds. Despite the presence of large quantities of well-preserved willow and poplar logs and sticks of

Fig. 8. Records of moose (*Alces alces*) on Alaska's North Slope based on historical (red, $n = 30$), archaeological (blue, $n = 5$), and paleontological (green, $n = 33$) sources. Numbers by red and blue sites are the calendar dates of sightings in years CE. Details of these records are given in Appendices A and C. See Appendix A for the ages of the paleontological samples. The blue line is the approximate northern limit of the closed boreal forest (CAVM 2003). Map uses WGS 84 geographic coordinate system. Map made with ExpertGPS (https://www.expertgps.com/) using ©Mapbox (https://www.mapbox.com/about/maps/) and ©OpenStreetMap (https://www.openstreetmap.org/copyright).

multiple ages older than 40 000 cal year BP (e.g., Mann et al. 2010), careful search has failed to find the distinctive chew marks left by beavers.

Was human predation important?

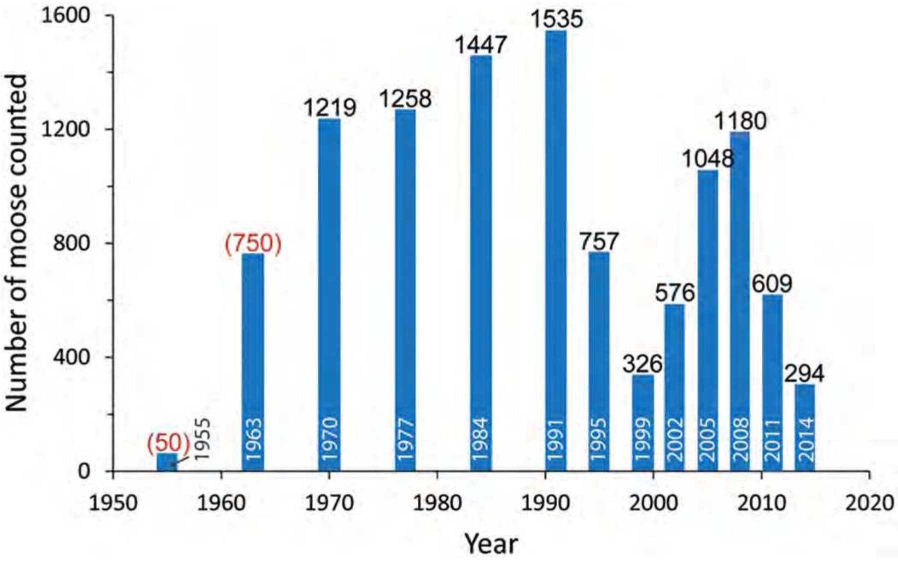
As in the case of the extirpation of muskoxen on the North Slope in the late 1800s (Allen 1912), it is unclear what effect, if any, human predation had on moose populations in Arctic Alaska. The archaeological record is sparse, and Yesner (1989) speculated that archaeological remains underestimate the abundance of this species because moose bones are too large for hunters to transport to camp sites. LeResche et al. (1974) speculated that intensive hunting by Indigenous people limited the moose population along the Colville River until these people moved north to the coast in the 1920s. Accounts from northwest Canada suggest that moose numbers there were also locally reduced by hunting (Porsild 1945; Coady 1980). Kay (1997) speculated that predation by people and wolves kept moose populations low on the North Slope until ca. 1900, despite suitable moose habitat existing there for thousands of years. He suggested that after the Nunamiut population declined following European contact in the late 1800s, hunting pressure on moose also declined, allowing moose populations to rebound. Because early human hunters supposedly killed mostly breeding-age females (Wolfe 1987; Kay 1995), hunting might have been effective in controlling moose populations, but only if it occurred with sufficient intensity. On the North Slope, this seems unlikely because human populations have always been sparse there (Brown 2007). The settlement at Anaktuvuk Pass, the only permanently occupied village in the interior of the region, was only established in 1947 (Gubser 1965). Clearly, there is much we have yet to discover about human–moose interactions in Arctic Alaska.

Did post Little Ice Age warming trigger an unprecedented northward expansion of moose in Alaska?

The ^{14}C chronology of moose remains from the Ikpikpuk and Titaluk rivers is not consistent with the assertion of Tape et al. (2016) that the presence of moose in tundra regions of Arctic Alaska today is a historically unusual occurrence. A close look at the model used by Tape et al. (2016) exposes serious weaknesses in the assumptions it is based upon.

Out of the wide range of influences that climate can have on the ecology and distribution of Arctic moose, Tape et al. (2016) hypothesize that willow height is key. They suggest that as climate warmed at the end of the Little Ice Age, willow shrubs, the critical winter food of moose, grew tall enough to

Fig. 9. Moose (*Alces alces*) counts from Game Management Unit 26A in northern Alaska (Carroll 2014). Numbers above bars are the actual estimates; those in red and parentheses are from estimates made prior to late-winter aerial surveys. Rotated numbers are the calendar years of the counts. Counts more recent than 2014 have not yet been released. [Color online.]



protrude far enough above the winter snowpack for moose to eat them. To test this idea, they used Walker's (1987) measurements of willow heights along a latitudinal transect across the North Slope to predict how the stature of willow shrubs might have responded to changes in summer climate. Their modelling results suggested that willow shrubs growing in river valleys on the North Slope responded to warmer air temperatures by increasing their average height from 1.10 m in CE 1860 to 1.97 m in 2009. They hypothesized this increase in willow height caused a significant increase in the amount of food available to moose, which then "…allowed moose to colonize tundra regions of Alaska hundreds of kilometres north and west of previous distribution limits." (Tape et al. 2016).

A key assumption of the Tape et al. (2016) model is of "…a variable but trendless end-of-winter snow cover despite increasingly shrub height". However, even if shrub height did increase in response to warming summers after 1850, the increase in snow depth caused by snow drifting around these taller willows (Sturm et al. 2001) could have negated any beneficial effects for moose. It is also likely that snowpacks deepened as post Little Ice Age winters warmed (Danco et al. 2016). Moreover, it is important to remember that snowfall varies markedly across northern Alaska today. Late-winter snowpacks are significantly deeper at the northern front of the Brooks Range than near the Beaufort Sea coast (Zhang et al. 1996). Thus, even during the coldest parts of the Little Ice Age, numerous willow shrubs probably protruded above the snowpack in the northern sector of the North Slope despite having an overall shorter stature there. Compounding the challenge of accurately modelling willow responses to climate is the fact that moose habitat on the North Slope of Alaska is located in valley bottoms whose microclimates are difficult to simulate using the climate models that Tape et al. (2016) relied upon.

Modelling aside, there is no convincing evidence from paleontological records, Indigenous oral traditions, explorer accounts, or recent wildlife surveys that a significant expansion of the moose population occurred on Alaska's North Slope in response to enhanced willow growth after the end of the Little Ice Age. The post-1880 increase in moose numbers recounted by elders at Anaktuvuk Pass (Gubser 1965) precedes by some 40 years the time that Tape et al. (2016) predicts willows would have become tall enough to provide abundant winter forage. Nunamiut hunters believed that the post-1880 increase in moose on the North Slope was caused by habitat changes south of the Brooks Range rather than by ecological changes on the North Slope (Gubser 1965).

The sole historical record pertaining specifically to the height of willow shrubs on the North Slope during the late 1800s further contradicts the model-based inferences of Tape et al. (2016). U.S. Navy Ensign W.L. Howard (Howard 1886) descended the Ikpikpuk River to the Beaufort Sea in the spring of 1886 (Hall 1978). Howard describes willows >3 m in height near the now-abandoned village of Kigalik (69°26.70′N, 154°53.32′W) in what came to be known as the Valley of the Willows (Howard 1886) (Fig. 1). While waiting at Kigalik for the river ice to break up, Howard wrote in his log book: "Sunday May 23… There is plenty of brush growing as large as my wrist, and in some instances ten to twelve feet high…". Willows in this region typically require several decades of growth to achieve heights >2 m. The Indigenous people with whom Howard traveled routinely camped in the Valley of the Willows probably because it was sheltered from the wind and possessed abundant firewood. These observations suggest that in addition to abundant firewood, suitable moose browse was present north of the Colville River certainly prior to 1900 and most likely before the end of the Little Ice Age.

Tundra moose as bellwethers of ecological change

Arctic moose make poor “climate-change canaries” for several reasons. First, their populations can fluctuate widely at annual to decadal timescales, even without the involvement of climate change. Recent fluctuations in moose abundance at high latitudes have been triggered by extreme storm events, wildland fires, deteriorating range conditions, and changes in predation pressure (LeResche et al. 1974; Solberg et al. 1999; Karns 2007). The moose population in Game Management Unit 26A in northwestern Alaska fluctuated markedly between 1950 and 2015 (Carroll 2014) (Fig. 9), despite the increased supply of willow browse suggested in the region by the Tape et al. (2016) model. Between 1999 and 2014, fluctuations of similar magnitudes were also observed in Game Units 26B and 26C in northeastern Alaska (Lenart 2018). Our own sightings of moose in the Titaluk and Ikpikpuk drainages reflect similar volatility in population size. In the early 2000s, we regularly encountered moose, sometimes cows with calves of the year while traveling the same river stretches annually. Their fresh sign was widespread along river reaches supporting willow gallery thickets. Then, beginning in 2009, moose became rare along the Titaluk and Ikpikpuk Rivers (P. Groves and D. Mann, personal observation).

Additional reasons why it is difficult to attribute changes in abundance and (or) distribution of Arctic moose to recent changes in climate relate to their high mobility and the wide-ranging nature of the plants they rely on for winter food. Moose are highly vagile; they were able to cross the Bering Land Bridge during the Pleistocene/Holocene transition and then expand their range across much of northern North America (Kelsall and Telfer 1974; Peterson 1978; Meiri et al. 2014). Historical records document vagrant moose hundreds of kilometres beyond their generally accepted range limits (Figs. 7 and 8). Coupled with their high vagility is the wide distribution of their preferred winter food, the genus *Salix*, whose diverse species specialize in colonizing the recently disturbed soils of floodplains. Because willow communities are associated with geomorphic disturbances, many willow species are azonally distributed in the sense of occupying multiple biomes with minimal conformance to climatic zonation at a regional scale. Within Alaska, willows are abundant on newly disturbed ground in biomes ranging from temperate rainforest to boreal forest, to tundra. In pursuit of their preferred food, the past and present range distributions of moose span these same biomes in a similarly azonal fashion.

Conclusions

Viewed at decadal and millennial timescales, the current presence of moose in shrubland habitats in the tundra biome of North America is unremarkable and is not a unique biogeographic event. Moose is a highly mobile species with a diffuse northern range limit that extends into tundra along river corridors where willow shrubs are abundant. Paleontological and historical records indicate moose have inhabited the same river corridors in Arctic Alaska at least intermittently since first colonizing North America across the Bering Land Bridge ca. 14 000 years ago. Isotopic ratios in moose bones from Alaska’s North Slope suggest that no significant changes in moose diet have occurred over this period, implying that sufficient willow browse has been continuously available. Indigenous oral accounts suggest that moose became more abundant on the North Slope after ca. 1870, but correlating this increase with increased willow growth caused by warming climate remains an intriguing but speculative idea. The combination of high vagility, fluctuation-prone populations, and a transbiome food resource consisting of early successional willow shrubs makes changes in the northern range limit of moose an undependable bellwether for other biotic responses to changing climate. The history of moose in Arctic Alaska illustrates how understanding what happened in the past is a prerequisite for correctly identifying, judging the significance of, and attributing causation to present-day ecological changes.

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The authors report that there are no competing interests to declare.

References

Abram, N.J., McGregor, H.V., Tierney, J.E., Evans, M.N., McKay, N.P., and Kaufman, D.S. 2016. Early onset of industrial-era warming across the oceans and continents. Nature, **536**(7617): 411–418. doi:10.1038/nature19082.

Allen, J. 1912. The probable recent extinction of the muskox in Alaska. Science, **36**(934): 720–722. doi:10.1126/science.36.934.720.

Anderson, R.M. 1924. Range of the moose extending northward. Can. Field-Nat. **38**: 27–29.

Bee, J.W., and Hall, E.R. 1956. Mammals of northern Alaska on the Arctic slope. Museum of Natural History, University of Kansas, Lawrence, KS.

Ben-David, M., Shochat, E., and Adams, L.G. 2001. Utility of stable isotope analysis in studying foraging ecology of herbivores: examples from moose and caribou. Alces, **37**: 421–434.

Bergerud, A., and Elliot, J. 1986. Dynamics of caribou and wolves in northern British Columbia. Can. J. Zool. **64**(7): 1515–1529. doi:10.1139/z86-226.

Bhatt, U.S., Walker, D.A., Raynolds, M.K., Bieniek, P.A., Epstein, H.E., Comiso, J.C., et al. 2017. Changing seasonality of panarctic tundra vegetation in relationship to climatic variables. Environ. Res. Lett. **12**(5): 055003. doi:10.1088/1748-9326/aa6b0b.

Boer, A.H. 1992. Fecundity of North American moose (*Alces alces*): a review. Alces, **1**: 1–10.

Bowyer, R., Ballenberghe, V.V., and Kie, J. 2003. Moose (*Alces alces*). *In* Wildlife mammals of North America: biology, management, and conservation. *Edited by* G. Feldhammer, B. Thompson and J. Chapman. Johns Hopkins University Press, Baltimore, MD. pp. 931–964.

Bronk Ramsey, C. 2009. Bayesian analysis of radiocarbon dates. Radiocarbon, **51**(1): 337–360. doi:10.1017/S0033822200033865.

Brook, B.W., Sodhi, N.S., and Bradshaw, C.J.A. 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. **23**(8): 453–460. doi:10.1016/j.tree.2008.03.011.

Brown, W.E. 2007. The history of the central Brooks Range: gaunt beauty, tenuous life. University of Alaska Press, Fairbanks, AK.

Carroll, G. 2014. Unit 26A moose management report. ADF&G, Juneau, AK.

Caughley, G., Grice, D., Barker, R., and Brown, B. 1988. The edge of the range. J. Anim. Ecol. **57**: 771–785. doi:10.2307/5092.

CAVM. 2003. Circumpolar Arctic Vegetation Map. (1:7,500,000 scale), Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, AK.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., and Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. Science, **333**(6045): 1024–1026. doi:10.1126/science.1206432.

Coady, J. 1980. History of moose in northern Alaska and adjacent regions. Can. Field Nat. **94**(1): 61–68.

Cuyler, C. 2007. West Greenland caribou explosion: what happened? What about the future? Rangifer, **17**: 219–226. doi:10.7557/2.27.4.347.

Cuyler, C., Rowell, J., Adamczewski, J., Anderson, M., Blake, J., Bretten, T., et al. 2020. Muskox status, recent variation, and uncertain future. Ambio, **49**(3): 805–819. doi:10.1007/s13280-019-01205-x.

Danco, J.F., DeAngelis, A.M., Raney, B.K., and Broccoli, A.J. 2016. Effects of a warming climate on daily snowfall events in the Northern Hemisphere. J. Clim. **29**(17): 6295–6318. doi:10.1175/Jcli-D-15-0687.1.

Darimont, C.T., Paquet, P.C., Reimchen, T., and Crichton, V. 2005. Range expansion by moose into coastal temperate rainforests of British Columbia, Canada. Divers. Distrib. **11**(3): 235–239. doi:10.1111/j.1366-9516.2005.00135.x.

Davidson, A.D., Shoemaker, K.T., Weinstein, B., Costa, G.C., Brooks, T.M., Ceballos, G., et al. 2017. Geography of current and future global mammal extinction risk. PLoS ONE, **12**(11): e0186934. doi:10.1371/journal.pone.0186934.

DeCesare, N.J., Weckworth, B.V., Pilgrim, K.L., Walker, A.B., Bergman, E.J., Colson, K.E., et al. 2020. Phylogeography of moose in western North America. J. Mammal. **101**(1): 10–23. doi:10.1093/jmammal/gyz163.

Dinneford, B. 1988. Moose colonization of post-glacial sites in southeastern Alaska. *In* Proceedings of the Second Glacier Bay Science Symposium. 19–22 September 1988, Glacier Bay Lodge, Alaska.

Dussex, N., Alberti, F., Heino, M.T., Olsen, R.-A., van der Valk, T., Ryman, N., et al. 2020. Moose genomes reveal past glacial demography and the origin of modern lineages. BMC Genomics, **21**(1): 1–13. doi:10.1186/s12864-020-07208-3.

Forchhammer, M.C., Post, E., Stenseth, N.C., and Boertmann, D.M. 2002. Long-term responses in Arctic ungulate dynamics to changes in climatic and trophic processes. Popul. Ecol. **44**(2): 113–120. doi:10.1007/s101440200013.

Franklin, J., and Richardson, J. 1828. Narrative of a Second Expedition to the Shores of the Polar Sea, in the Years 1825, 1826, and 1827. John Murray.

Franzmann, A.W., and Schwartz, C.C. 1985. Moose twinning rates: a possible population condition assessment. J. Wildl. Manage. **49**(2): 394–396. doi:10.2307/3801540.

Gaglioti, B.V., Mann, D.H., Groves, P., Kunz, M.L., Farquharson, L.M., Reanier, R.E., et al. 2018. Aeolian stratigraphy describes ice-age paleoenvironments in unglaciated Arctic Alaska. Quat. Sci. Rev. **182**: 175–190. doi:10.1016/j.quascirev.2018.01.002.

Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kelleyhouse, D.G., Stephenson, R.O., and Larsen, D.G. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildl. Monogr. **120**: 3–59.

Gaston, K.J. 2009. Geographic range limits of species. Proc. R. Soc. Lond. B Biol. Sci. **276**: 1391–1393.

Giddings, J.L. 1954. The tenuous Beaufort Sea archeology. Sci. Alaska, **5**: 94–99.

Giddings, J.L. 1962. Onion portage and other flint sites of the Kobuk River. Arct. Anthropol. **1**(1): 6–27.

Giddings, J.L. 1967. Ancient men of the Arctic. Alfred Knopf, New York.

Gubser, N.J. 1965. The Nunamiut eskimos: hunters of Caribou. Yale University Press, New Haven.

Gunn, A., Shank, C., and McLean, B. 1991. The history, status and management of muskoxen on Banks Island. Arctic, **44**: 188–195. doi:10.14430/arctic1538.

Guthrie, R.D. 2006. New carbon dates link climatic change with human colonization and pleistocene extinctions. Nature, **441**(7090): 207–209. doi:10.1038/nature04604.

Hall, E.S. 1973. Archaeological and recent evidence for expansion of moose range in northern Alaska. J. Mammal. **54**(1): 294–295. doi:10.2307/1378902.

Hall, E.S. 1978. William Lauriston Howard and the first crossing of Interior Northern Alaska. Brockport, NY. pp. 1–90.

Harper, P., and McCarthy, L. 2015. Muskox management report of survey-inventory activities 1 July 2012–30 June 2014. Alaska Department of Fish and Game, Division of Wildlife Conservation, Species Management ReportADF&G/DWC/SMR-2015-2, Juneau, AK.

Howard, W.L. 1886. William Lauriston Howard Point Barrow Expedition Diaries, Harvard University, Houghton Library, Cambridge, MA. pp. 1885–1886.

Hundertmark, K. 2016. *Alces alces*. The IUCN Red List of Threatened Species 2016: e.T56003281A22157381.doi:10.2305/IUCN.UK.2016-1.RLTS.T56003281A22157381.en.

Karns, P.D. 2007. Population distribution, density and trends. *In* Ecology and management of the North American moose. *Edited by* A. Franzmann and C. Schwartz. University Press of Colorado, Boulder, CO. pp. 125–140.

Kay, C.E. 1995. Aboriginal overkill and native burning: implications for modern ecosystem management. West. J. Appl. For. **10**(4): 121–126. doi:doi: 10.1093/wjaf/10.4.121.

Kay, C.E. 1997. Aboriginal overkill and the biogeography of moose in western North America. Alces, **33**: 141–164.

Kelsall, J.P. 1972. The northern limits of moose (*Alces alces*) in western Canada. J. Mammal. **53**(1): 129–138. doi:doi: 10.2307/1378833.

Kelsall, J.P., and Telfer, E. 1974. Biogeography of moose with particular reference to western North America. Nat. Can. **101**: 117.

Kielland, K., and Bryant, J.P. 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. Oikos, **82**: 377–383. doi:10.2307/3546979.

Kolbert, E. 2014. The sixth extinction: an unnatural history. Henry Holt & Co., New York. p. 319.

Larsen, A., Larsen, J.R., and Lane, S.N. 2021. Dam builders and their works: beaver influences on the structure and function of river corridor hydrology, geomorphology, biogeochemistry and ecosystems. Earth-Sci. Rev. **218**: 103623. doi:10.1016/j.earscirev.2021.103623.

Lawton, J.H. 1993. Range, population abundance and conservation. Trends Ecol. Evol. **8**(11): 409–413. doi:10.1016/0169-5347(93)90043-O.

Lenart, E.A. 2018. Moose Management Report and Plan, Game Management Units 26B and 26C. Alaska Department of Fish and Game, Species Management Report and Plan, Juneau.

LeResche, R.E., Bishop, R.H., and Coady, J.W. 1974. Distribution and habitats of moose in Alaska. Nat. Can. **101**: 143–178.

Longin, R. 1971. New method of collagen extraction for radiocarbon dating. Nat. Insects, **230**: 241–242.

MacFarlane, R. 1905. Notes on mammals collected and observed in the northern Mackenzie River District, Northwest Territories of Canada, with remarks on explorers and explorations of the far north. Proc. U.S. Natl. Mus. **28**: 673–764. doi:10.5479/si.00963801.28-1405.673.

Mallory, C.D., and Boyce, M.S. 2018. Observed and predicted effects of climate change on Arctic caribou and reindeer. Environ. Rev. **26**(1): 13–25. doi:10.1139/er-2017-0032.

Mann, D.H., Groves, P., Reanier, R.E., and Kunz, M.L. 2010. Floodplains, permafrost, cottonwood trees, and peat: what happened the last time climate warmed suddenly in Arctic Alaska? Quat. Sci. Rev. **29**(27–28): 3812–3830. doi:10.1016/j.quascirev.2010.09.002.

Mann, D.H., Groves, P., Kunz, M.L., Reanier, R.E., and Gaglioti, B.V. 2013. Ice-age megafauna in Arctic Alaska: extinction, invasion, survival. Quat. Sci. Rev. **70**(0): 91–108. doi:10.1016/j.quascirev.2013.03.015.

Mann, D.H., Groves, P., Reanier, R.E., Gaglioti, B.V., Kunz, M.L., and Shapiro, B. 2015. Life and extinction of megafauna in the ice-age Arctic. Proc. Natl. Acad. Sci. U.S.A. **112**(46): 14301–14306. doi:10.1073/pnas.1516573112.

Meiri, M., Lister, A.M., Collins, M.J., Tuross, N., Goebel, T., Blockley, S., et al. 2014. Faunal record identifies Bering isthmus conditions as constraint to end-Pleistocene migration to the new world. Proc. R. Soc. B. Biol. Sci. **281**(1776): 20132167. doi:10.1098/rspb.2013.2167.

Meldgaard, M. 1986. The Greenland caribou: zoogeography, taxonomy, and population dynamics. Meddelelser Grønland Bioscience, **20**: 1–88.

Molvar, E.M., Bowyer, R.T., and Van Ballenberghe, V. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia, **94**(4): 472–479. doi:10.1007/BF00566961.

Morice, C.P., Kennedy, J.J., Rayner, N.A., Winn, J., Hogan, E., Killick, R., et al. 2021. An updated assessment of near-surface temperature change from 1850: the HadCRUT5 data set. J. Geophys. Res. Atmos. **126**(3): e2019JD032361. doi:10.1029/2019JD032361.

Nummi, P., Liao, W., Huet, O., Scarpulla, E., and Sundell, J. 2019. The beaver facilitates species richness and abundance of terrestrial and semi-aquatic mammals. Glob. Ecol. Conserv. **20**: e00701. doi:10.1016/j.gecco.2019.e00701.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. **37**: 637–669. doi:10.1146/annurev.ecolsys.37.091305.110100.

Peek, J. 1974. A review of moose food habits studies in North America. Nat. Can. **101**: 195–215.

Peterson, R.L. 1978. North American moose. University of Toronto Press, Toronto.

Porsild, A.E. 1945. Mammals of the Mackenzie delta. Can. Field Nat. **59**: 4–22.

Post, E., and Høye, T.T. 2013. Advancing the long view of ecological change in tundra systems. Philos. Trans. R. Soc. B, **368**: 20120477. doi:10.1098/rstb.2012.0477.

Post, E., and Stenseth, N.C. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. J. Anim. Ecol. **67**(4): 537–543. doi:10.1046/j.1365-2656.1998.00216.x.

Post, E., and Stenseth, N.C. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology, **80**(4): 1322–1339. doi:10.1890/0012-9658(1999)080[1322:CVPPAN]2.0.CO;2.

Post, E., Bhatt, U.S., Bitz, C.M., Brodie, J.F., Fulton, T.L., Hebblewhite, M., et al. 2013. Ecological consequences of sea-ice decline. Science, **341**: 519–524. doi:10.1126/science.1235225.

Ratajczak, Z., Carpenter, S.R., Ives, A.R., Kucharik, C.J., Ramiadantsoa, T., Stegner, M.A., et al. 2018. Abrupt change in ecological systems: inference and diagnosis. Trends Ecol. Evol. **33**(7): 513–526. doi:10.1016/j.tree.2018.04.013.

Rausch, R.L. 1951. Notes on the Nunamiut Eskimo and mammals of the Anaktuvuk Pass region, Brooks Range, Alaska. Arctic, **4**: 147–195. doi:10.14430/arctic3943.

Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., et al. 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). Radiocarbon, **62**(4): 725–757. doi:10.1017/RDC.2020.41.

Reynolds, P.E. 1998. Dynamics and range expansion of a reestablished muskox population. J. Wildl. Manage. **62**: 734–744. doi:10.2307/3802350.

Ruprecht, J.S. 2016. The demography and determinants of population growth in Utah moose (Alces alces shirasi). MS thesis, Ecology, Utah State University.

Schmelzer, I., Lewis, K.P., Jacobs, J.D., and McCarthy, S.C. 2020. Boreal caribou survival in a warming climate, Labrador, Canada 1996–2014. Glob. Ecol. Conserv. **23**: e01038. doi:10.1016/j.gecco.2020.e01038.

Schmidt, J.I., Hundertmark, K.J., Bowyer, R.T., and McCracken, K.G. 2009. Population structure and genetic diversity of moose in Alaska. J. Hered. **100**(2): 170–180. doi:10.1093/jhered/esn076.

Schwartz, C. 1998. Reproduction, natality, and growth *In* Ecology and management of the North American moose. *Edited by* A.W. Franzmann and C.C. Schwartz. Smithsonian Institution Press, Washington, DC. pp. 141–171.

Sexton, J.P., McIntyre, P.J., Angert, A.L., and Rice, K.J. 2009. Evolution and ecology of species range limits. Annu. Rev. Ecol. Evol. Syst. **40**(1): 415–436. doi:10.1146/annurev.ecolsys.110308.120317.

Shuman, B. 2012. Patterns, processes, and impacts of abrupt climate change in a warm world: the past 11,700 years. Wiley Interdiscip. Rev. Clim. Change, **3**(1): 19–43. doi:10.1002/wcc.152.

Solberg, E.J., Saether, B.E., Strand, O., and Loison, A. 1999. Dynamics of a harvested moose population in a variable environment. J. Anim. Ecol. **68**(1): 186–204. doi:10.1046/j.1365-2656.1999.00275.x.

Stone, A.J. 1903. The moose, where it lives and how it lives. *In* The deer family. *Edited by* T. Roosevelt, T.S. van Dyke, D.G. Elliot and A.J. Stone. McMillan Company, New York. pp. 291–325.

Sturm, M., Holmgren, J., McFadden, J.P., Liston, G.E., , Chapin, F.S., III, and Racine, C.H. 2001. Snow–shrub interactions in Arctic tundra: a hypothesis with climatic implications. J. Clim. **14**(3): 336–344. doi:10.1175/1520-0442(2001)014%3C0336:SSIIAT%3E2.0.CO;2.

Tape, K.D., Gustine, D.D., Ruess, R.W., Adams, L.G., and Clark, J.A. 2016. Range expansion of moose in Arctic Alaska linked to warming and increased shrub habitat. PLoS ONE, **11**(4): e0152636. doi:10.1371/journal.pone.0160049.

Tape, K.D., Jones, B.M., Arp, C.D., Nitze, I., and Grosse, G. 2018. Tundra be dammed: beaver colonization of the Arctic. Glob. Change Biol. **24**(10): 4478–4488. doi:doi: 10.1111/gcb.14332.

Turner, M.G., Calder, W.J., Cumming, G.S., Hughes, T.P., Jentsch, A., LaDeau, S.L., et al. 2020. Climate change, ecosystems and abrupt change: science priorities. Philos. Trans. R. Soc. B, **375**(1794): 20190105. doi:10.1098/rstb.2019.0105.

Vibe, C. 1967. Arctic animals in relation to climatic fluctuations. Meddel. Gronland, **170**: 1–227.

Walker, D. 1987. Height and growth rings of *Salix lanata* ssp. *richardsonii* along the coastal temperature gradient of northern Alaska. Can. J. Bot. **65**(5): 988–993. doi:10.1139/b87-136.

Wolfe, M. 1987. An overview of the socio economics of moose in North America. Swed. Wildl. Res. (Sweden), **1**: 659–675.

Yesner, D.R. 1989. Moose hunters of the boreal forest? A re-examination of subsistence patterns in the western subarctic. Arctic, **42**(2): 97–108. doi:doi: 10.14430/arctic1646.

Zhang, T., Osterkamp, T.E., and Stamnes, K. 1996. Some characteristics of the climate in northern Alaska, U.S.A. Arct. Alp. Res. **28**(4): 509–518. doi:10.1080/00040851.1996.12003204.

Appendix A. North Slope dated paleontological moose (*Alces alces*).

						^{14}C date reported (years BP)						
Field ID	UAMES #	Latitude (N)	Longitude (W)	Skeletal element	AMS Lab #	^{14}C date	SD	δ^{13}C (‰; VPDP)	δ^{15}N (‰; AIR)	95.4% calibrated range (cal YBP)	Median cal YBP	Source
IK17-003	42546	69°19.37′	154°40.03′	Mandible	UCIAMS-199206	Modern	na	−21.69	0.67	46 – 54	50	This study
KIG05-4.1	30186	69°19.74′	154°40.28′	**Antler**	Beta-339266	107	0.3	−23.40	0.50	31 – 255	122	Mann et al. 2013
MAY12-63	30187	69°17.34′	154°34.37′	**Antler**	Beta-339275	116	0.3	−21.30	0.60	29 – 260	104	Mann et al. 2013
IK17-005	42548	69°19.33′	154°41.12′	**Antler**	UCIAMS-199208	155	15	−20.63	0.08	5 – 283	189	This study
IK08-129	30181	69°24.61′	154°46.78′	**Antler**	Beta-339280	210	30	−20.80	0.70	na – 305	179	Mann et al. 2013
TIT10-58	30188	69°39.06′	155°24.33′	**Antler**	Beta-339271	290	30	−20.70	0.90	288 – 458	384	Mann et al. 2013
IK12-094	30184	69°21.87′	154°40.71′	**Antler**	Beta-339281	310	30	−21.10	−0.40	301 – 465	387	Mann et al. 2013
IK02-210	10355	69°35.57′	154°56.64′	Mandible	CAMS-91966	320	35	−20.30	0.26	304 – 474	388	Mann et al. 2013
IK01-404	11844	69°27.58′	154°51.81′	Mandible	CAMS-92094	665	35	−20.87	−0.59	556 – 678	629	Mann et al. 2013
IK16-03	38515	69°37.62′	154°54.14′	Cranium	UCIAMS-183469	920	20	−20.53	0.84	789 – 912	856	This study
IK12-077	30183	69°20.53′	154°38.37′	Skull	Beta-339274	950	30	−20.70	1.00	795 – 926	854	Mann et al. 2013
IK99-229	10691	69°22.31′	154°40.77′	Mandible	CAMS-64459	980	40	−20.00	8.56	795 – 959	872	Mann et al. 2013
IK18-12	51671	69°28.48′	154°50.55′	Mandible	UCIAMS-210925	1 145	20	−21.10	2.30	978 – 1 173	1 036	This study
IK99-393	30189	69°03.48′	152°51.78′	Metatarsal	Beta-134225	1 280	40	−19.50	na	1 086 – 1 294	1 225	Mann et al. 2013
IK99-776	11066	69°49.29′	154°44.11′	Mandible	CAMS-64474	1 370	40	−20.40	1.33	1 186 – 1 351	1 294	Mann et al. 2013
IK17-009	42552	69°30.60′	154°50.32′	**Antler**	UCIAMS-199212	1 610	15	−20.84	−0.21	1 416 – 1 553	1 494	This study
IK17-004	42547	69°18.74′	154°42.16′	**Antler**	UCIAMS-199207	1 730	15	−20.61	−0.08	1 570 – 1 700	1 653	This study

Appendix A. Continued

Field ID	UAMES #	Latitude (N)	Longitude (W)	Skeletal element	AMS Lab #	^{14}C date reported (years BP)		δ^{13}C (‰; VPDP)	δ^{15}N (‰; AIR)	95.4% calibrated range (cal YBP)	Median cal YBP	Source
						^{14}C date	SD					
IK99-556	10996	69°20.36′	154°40.85′	Mandible	CAMS-64467	1 760	40	−19.85	0.68	1 566 – 1 810	1 668	Mann et al. 2013
GAAR-7846*	na	68°50.61′	153°25.33′	Metatarsal	Avg of 3 rep dates*	2 427	43	−21.73	na	2 352 – 2 703	2 478	Mann et al. 2013
IK01-023	12022	69°20.68′	154°39.97′	Mandible	CAMS-92076	2 450	35	−20.77	0.99	2 360 – 2 705	2 528	Mann et al. 2013
IK98-0888	3288	69°32.36′	154°55.82′	Mandible	CAMS-64418	2 540	50	−20.26	na	2 464 – 2 756	2 613	Mann et al. 2013
IK16-01	38513	69°35.27′	154°56.98′	**Antler**	UCIAMS-183467	2 770	15	−21.01	0.34	2 795 – 2 924	2 862	This study
IK12-096	30185	69°20.53′	154°38.37′	Antler broken	Beta-339282	2 790	30	−21.30	−0.60	2 795 – 2 960	2 890	Mann et al. 2013
KIG09-02	32882	69°19.37′	154°39.78′	Skull	Beta-263035	2 900	40	−21.10	na	2 925 – 3 165	3 036	Mann et al. 2013
IK17-008	42551	69°32.79′	154°56.23′	**Antler**	UCIAMS-199211	3 230	15	−21.32	−0.77	3 397 – 3 479	3 444	This study
IK16-02	38514	69°24.74′	154°48.04′	**Antler**	UCIAMS-183468	4 450	15	−20.49	0.39	4 972 – 5 273	5 048	This study
TIT12-35	30191	69°31.50′	155°47.31′	**Antler**	Beta-339283	9 310	40	−20.30	−1.20	10 303 – 10 654	10 518	Mann et al. 2013
TIT16-001	38516	69°33.43′	155°36.09′	**Antler**	UCIAMS-183471	9 470	25	−20.45	−0.06	10 592 – 10 784	10 710	This study
IK09-70	30182	69°21.09′	154°40.27′	**Antler base**	Beta-339270	9 610	40	−21.00	0.90	10 775 – 11 161	10 937	Mann et al. 2013
TIT16-003	38518	69°29.64′	155°54.63′	**Antler**	UCIAMS-183473	9 890	25	−20.56	0.61	11 230 – 11 349	11 268	This study
IK17-006	42549	69°18.74′	154°42.16′	**Antler**	UCIAMS-199209	10 010	25	−19.82	−0.72	11 327 – 11 690	11 485	This study
IK17-007	42550	69°19.98′	154°38.82′	**Antler**	UCIAMS-199210	10 120	25	−21.13	−1.20	11 615 – 11 978	11 757	This study
TIT16-002	38517	69°32.89′	155°36.42′	**Antler**	UCIAMS-183472	12 220	35	−20.38	−0.23	13 992 – 14 243	14 113	This study
IK99-472	10922	69°27.00′	154°52.14′	Tooth	CAMS-91810	12 245	40	−20.30	−0.13	14 000 – 14 314	14 143	Mann et al. 2013

Note: UAMES # refers to University of Alaska Museum Earth Sciences accession number. AMS refers to accelerator mass spectrometry. Skeletal elements in boldface type are from a cast antler. Rep dates refer to the average of 3 dates on this bone (Beta-130571: 2330 +/- 50, CAMS-58093: 2490 +/- 40 and CAMS-58096: 2460 +/- 40). na, not available.

Appendix B. Northern Canada historical moose (*Alces alces*) observations.

Year obs.	Location	Latitude (N)	Longitude (W)	Comment	Source	Type
1825	Mackenzie River Delta	69°03.8′	135°45.1′	Cow and calf hunter killed	Franklin and Richardson 1828	Historical
1825	Mackenzie River Delta	68°15.8′	134°20.7	Tracks seen along river	Franklin and Richardson 1828	Historical
1825	Great Bear Lake	65°11.2′	120°54.67′	Hunter killed 2 moose	Franklin and Richardson 1828	Historical
1851	Prince of Wales Strait	71°00.0′	114°00.0′	Three moose reported by Captain McClure	MacFarlane 1905	Historical
1861	Fort Anderson	68°30.0′	128°00.0′	Moose numerous prior to this	MacFarlane 1905	Historical
1866	Horton River	69°00.0′	126°30.0′	Tracks and feces seen	MacFarlane 1905	Historical
1909	Mouth of Rae River	67°56.0′	115°31.5′	Observed 2 males	Anderson 1924	Historical
1914	Blow River Delta	68°56.0′	137°05.9′	Hunter killed	Anderson 1924	Historical
1920	Mackenzie River Delta	69°19.6′	134°26.2′	Hunter killed	Anderson 1924	Historical
1921	Mackenzie River Delta	69°09.2′	134°35.0′	Hunter killed	Anderson 1924	Historical
1923	Chesterfield Inlet	63°20.8′	90°44.2′	Hunter killed 2 males	Anderson 1924	Historical

Appendix C. North Slope Alaska archaeological and historical moose (*Alces alces*) records.

Year obs.	Location	Latitude (N)	Longitude (W)	Comment	Sources	Type
1903	Headwaters Colville River	68°56.5′	157°33.7′	Reportedly seen	Stone 1903	Historical
1924	Colville River	69°59.0′	151°40.0′	Tracks seen	Bee and Hall 1956	Historical
1929	Sagavanirktok River	69°27.5′	148°30.0′	Hunter killed	Bee and Hall 1956	Historical
1931	Mouth of Kuparak River	70°23.8′	148°07.2′	Hunter killed	Bee and Hall 1956	Historical
1935	Colville River	70°18.0′	150°52.0′	Seen	Bee and Hall 1956	Historical
1936	Sagavanirktok River	69°17.5′	148°04.0′	Hunter killed	Bee and Hall 1956	Historical
1942	West Kuparuk River	69°51.5′	149°37.0′	Group of 5 seen	Bee and Hall 1956	Historical
1942	Canning River	69°37.5′	146°16.0′	Greatest congregation	Bee and Hall 1956	Historical
1942	East Fork Shaviovik	69°34.0′	146°41.0′	Congregation	Bee and Hall 1956	Historical
1942	West Kuparuk River	69°17.5′	150°15.0′	10–15 seen	Bee and Hall 1956	Historical
1945	Killik River	68°12.3′	153°02.0′	Seen	Bee and Hall 1956	Historical
1946	Umiat	69°22.0′	152°08.6′	Seen	Bee and Hall 1956	Historical
1949	Maybe Creek	69°21.6′	154°36.2′	Seen	Bee and Hall 1956	Historical
1950	Colville River	68°50.7′	156°08.8′	One per mile	Bee and Hall 1956	Historical
1950	Tolugak Lake	68°24.0′	151°26.0′	Skull	Rausch 1951	Historical
1951	Fish Creek	70°22.3′	151°20.2′	Calf = less cow seen	Bee and Hall 1956	Historical
1951	Colville River	70°03.5′	151°13.0′	Seen	Bee and Hall 1956	Historical
1951	Shaviovik River	69°20.0′	147°11.8′	Herds up to 20 seen	Rausch 1951	Historical
1952	Colville River	70°19.5′	150°50.2′	Seen	Bee and Hall 1956	Historical
1952	Gavia Lake	69°35.0′	150°00.0′	Seen	Bee and Hall 1956	Historical
1952	Canning River	69°35.0′	146°23.0′	Seen	Bee and Hall 1956	Historical
1952	East of Lake Schrader	69°24.5′	145°08.0′	Tracks and feces seen	Bee and Hall 1956	Historical
1952	Awuna River	69°02.0′	155°32.0′	Seen	Bee and Hall 1956	Historical
1952	Grandstand	68°58.0′	151°59.0′	Seen	Bee and Hall 1956	Historical

Appendix C. Continued

Year obs.	Location	Latitude (N)	Longitude (W)	Comment	Sources	Type
1958	Noatak	67°34.3′	162°57.9′	Observed	Hall 1973	Historical
1962	Point Hope	68°20.9′	166°48.5′	Hunter killed	Hall 1973	Historical
1973	Cape Krusenstern	67°07.7′	163°44.7′	Seen	Hall 1973	Historical
1973	Cape Thompson	68°08.6′	165°58.7′	Seen	Hall 1973	Historical
1973	Point Lay	69°45.5′	163°03.1′	Seen	Hall 1973	Historical
1973	Point Barrow	71°23.3′	156°28.9′	Seen	Hall 1973	Historical
1000	Cape Krusenstern	67°07.7′	163°44.7′	>12 moose bones at site	Giddings 1967; Hall 1973	Archaeological
1400	Camden Bay	70°01.0′	144°51.5′	Moose tibia at site	Hall 1973	Archaeological
1450	Onion Portage Site, Kobuk River	67°06.4′	158°16.2′	Moose bones at site	Hall 1973	Archaeological
1578*	Kangiguksuk Site, Noatak	67°58.0′	161°50.0′	Maxilla, teeth, phalanges	Hall 1973	Archaeological
1800	Tukuto Lake	68°30.1′	157°01.8′	Moose bones at site	Hall 1973	Archaeological

*Based on dendrochronological date from site.