



## Ice-age megafauna in Arctic Alaska: extinction, invasion, survival

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## ABSTRACT

Radical restructuring of the terrestrial, large mammal fauna living in arctic Alaska occurred between 14,000 and 10,000 years ago at the end of the last ice age. Steppe bison, horse, and woolly mammoth became extinct, moose and humans invaded, while muskox and caribou persisted. The ice age megafauna was more diverse in species and possibly contained 6× more individual animals than live in the region today. Megafaunal biomass during the last ice age may have been 30× greater than present. Horse was the dominant species in terms of number of individuals. Lions, short-faced bears, wolves, and possibly grizzly bears comprised the predator/scavenger guild. The youngest mammoth so far discovered lived ca 13,800 years ago, while horses and bison persisted on the North Slope until at least 12,500 years ago during the Younger Dryas cold interval. The first people arrived on the North Slope ca 13,500 years ago. Bone-isotope measurements and foot-loading characteristics suggest megafaunal niches were segregated along a moisture gradient, with the surviving species (muskox and caribou) utilizing the warmer and moister portions of the vegetation mosaic. As the ice age ended, the moisture gradient shifted and eliminated habitats utilized by the dryland, grazing species (bison, horse, mammoth). The proximate cause for this change was regional paludification, the spread of organic soil horizons and peat. End-Pleistocene extinctions in arctic Alaska represent local, not global extinctions since the megafaunal species lost there persisted to later times elsewhere. Hunting seems unlikely as the cause of these extinctions, but it cannot be ruled out as the final blow to megafaunal populations that were already functionally extinct by the time humans arrived in the region.

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## 1. Introduction

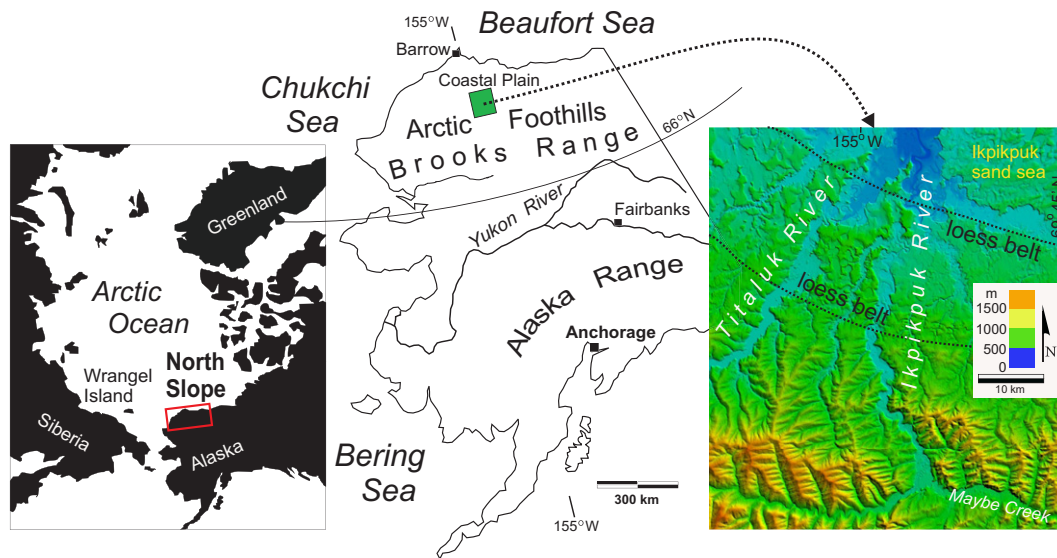
By understanding the causes of extinctions in the past, we may be better able to manage extinction threats in the future. In today's world, large herbivorous mammals are often keystone species in their ecosystems and many of them are threatened by extinction. Large numbers of megafaunal species (terrestrial mammals weighing >44 kg) became extinct at the end of the Pleistocene for reasons that remain controversial. End-Pleistocene extinctions of megafauna were regionally idiosyncratic (Barnosky et al., 2004), though many involved either overhunting by humans and/or loss of critical habitats. The main causes of habitat loss were climate changes, human activities, or a combination of both (Koch and Barnosky, 2006).

Some of the most accessible examples of prehistoric megafaunal extinctions occurred in the Arctic at the end of the last ice age (14,000–10,000 years ago). Climatic and environmental changes have been particularly large and abrupt at high latitudes (Miller et al., 2010), and megafaunal remains are often superbly preserved there in permafrost (perennially frozen ground). Moreover, humans were a late arrival to the North American Arctic and were never numerous there until late in the Holocene.

Here we examine patterns of change in populations of megafauna over the last 40,000 years on North Slope of Alaska, the tundra region north of the Brooks Range (Fig. 1). During the last ice age between ca 43 cal ka BP and 10 cal ka BP (calendar years before AD 1950 × 1000), twelve megafauna species inhabited the North Slope of Alaska. Two of these, moose (*Alces alces*) and humans, first arrived after 14 cal ka BP, and four species (caribou, *Rangifer tarandus*; muskox, *Ovibos moschatus*; wolf, *Canis lupus*; and grizzly bear, *Ursus arctos*) survived the end of the ice age apparently *in situ*. The other six megafauna species (steppe bison, *Bison priscus*; horse,

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**Fig. 1.** Location map. The upper reaches of the Ikpikuk and Titaluk Rivers are well-known for their accumulations of Pleistocene mammal bones. The loess belt borders the southern margin of the Ikpikuk Sand Sea, a large dune field that was active in glacial times. Loess and sand sheet deposits exceed about 5 m thickness on upland surfaces in this loess belt.

*Equus* sp.; woolly mammoth, *Mammuthus primigenius*; saiga antelope, *Saiga tatarica*; lion, *Panthera spelaea*; and short-faced bear, *Arctodus simus*) all disappeared from the North Slope before 10 cal ka BP. A thirteenth megafauna species, mastodon (*Mammuth americanum*), probably became extinct in the region long before, perhaps at the end of the Last Interglacial (Marine Isotope Stage 5e) (G. Zazula, unpublished data).

Our goals in this paper are to present a new series of  $^{14}\text{C}$ -dated megafauna bones, to estimate extinction times for various taxa, to describe the taphonomic processes at work on this landscape, to infer faunal composition during the last ice age (here considered 43.5–10 cal ka BP), to estimate animal numbers and biomass, and to infer dietary differences between megafaunal species based on the carbon and nitrogen isotopes in their bones. We conclude with an assessment of the probable causes of end-Pleistocene extinction in this particular region.

## 2. Background: end-Pleistocene extinctions on the Mammoth Steppe

During the ice ages, Alaska's North Slope was part of the Mammoth Steppe, the now-vanished biome that intermittently extended from northwest Europe to the Yukon Territory (Guthrie, 1990; Yurtsev, 2001). Megafaunal extinctions in the Mammoth Steppe have been assigned several different causes. In this brief review, we focus first on Alaska and the Yukon and then widen the scope to Eurasia.

Guthrie et al. (2001) blamed the demise of the Mammoth Steppe on the moistening of continental interiors. As sea level rose in post-glacial times, maritime air masses invaded northern Alaska more frequently, transforming summer climate from sunny, dry, and warm to its present state of cloudy, damp, and relatively cold (Mann et al., 2001). Paleoenvironmental records from arctic Alaska lend support to Guthrie's ideas in the form of evidence for sweeping changes in hillslope erosion, floodplain dynamics, and vegetation – all triggered by increases in effective moisture during the Pleistocene–Holocene transition (Mann et al., 2002, 2010). Mesic–hydric vegetation dominated by sedges and shrubs spread across the region early in post-glacial times (Oswald et al., 1999), replacing the formerly dominant graminoids and forbs (Zazula et al., 2006,

2011), and probably lowering soil temperatures (Blok et al., 2010). Shrubs tend to be better defended by anti-herbivory compounds against mammalian herbivores than are grasses and forbs, so range quality for grazers would have declined as moist tundra spread (Guthrie, 2006). The same moistening of summer climate at the end of the Pleistocene that caused the vegetation to change also stabilized dune fields and restricted loess deposition (Carter, 1993). This permitted soil acidification to proceed unhindered by the inputs of unweathered mineral material in the form of loess and blowing sand (Walker et al., 2001). Lower soil pH and enhanced production of hard-to-decompose plant litter contributed to the development of peat, which among its other disadvantages for megafauna made locomotion difficult for species adapted for running across firm ground (Guthrie, 1990).

Unlike Guthrie's emphasis on the factors responsible for causing the collapse of an entire megafaunal ecosystem, Stuart et al. (2004) stress the importance of autecological factors driving the extinction of individual species in Eurasia. They point out that both woolly mammoth and Irish elk (*Megaloceros giganteus*) were highly mobile and responded to post-glacial climate change by shifting their ranges over great distances. These range shifts allowed survival of these two species into Holocene times.

In a study that pioneered the use of ancient DNA to infer the causes of Pleistocene extinction at high latitudes, Shapiro et al. (2004) correlated megafaunal population sizes with genetic diversity in dated bones and concluded that *B. priscus* underwent marked population fluctuations at high latitudes before humans were present there. From this they concluded environmental changes were more important than human impacts in causing extinctions. Similarly, Campos et al. (2010) studied changes in the genetic diversity of muskoxen using bones from the Arctic. They found that major bottlenecks in genetic diversity, which they interpreted as reflecting bottlenecks in population size, were not correlated with the arrival dates of humans. On this basis, they argued that muskox population dynamics are better explained by environmental changes than by hunting.

By comparing dates of extinction, genetic changes, and human arrival in different regions, Lorenzen et al. (2011) inferred that environmental changes driven by shifts in climate caused the extinctions of muskox and the woolly rhinoceros (*Coelodonta*

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