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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.

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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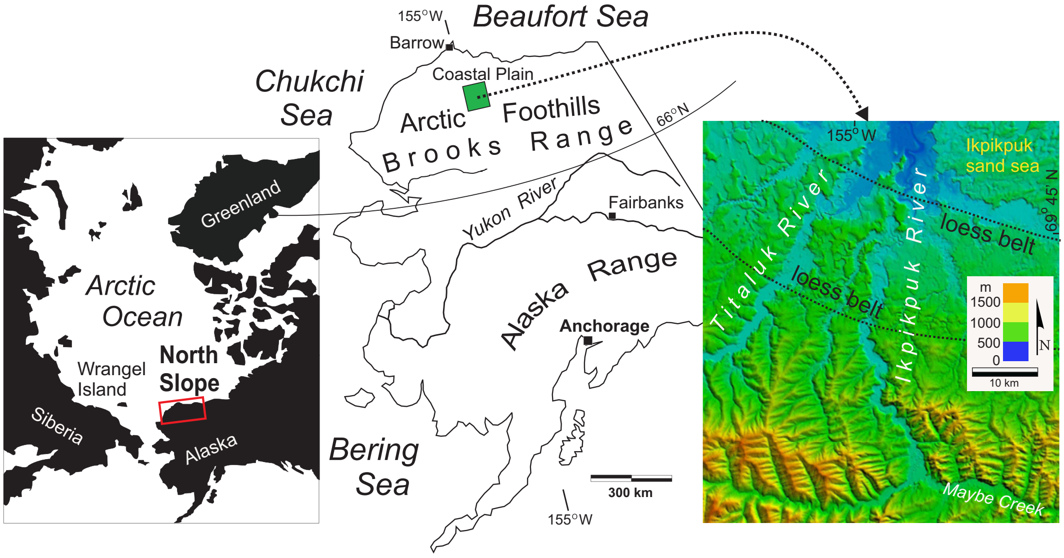

Fig. 1. Location map. The upper reaches of the Ikpikpuk and Titaluk Rivers are well-known for their accumulations of Pleistocene mammal bones. The loess belt borders the southern margin of the Ikpikpuk Sand Sea, a large dune field that was active in glacial times. Loess and sand sheet deposits exceed 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 (*Mammut 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}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* *antiquitatis*) in Eurasia. They think that a combination of climate change and human influences caused the extinction of steppe bison and horse in Eurasia. The most certain findings from the Lorenzen et al. (2011) study are that each megafauna species responded independently to environmental changes and interactions with humans, and that there is no way to predict which megafauna species became extinct based on their genetic characteristics (MacPhee et al., 2005) or the geographies of their ranges. These findings imply that chance played a major role in megafaunal extinctions in the Arctic, just as it does in many other ecological dynamics (Doak et al., 2008).

The most singular hypothesis for the cause of late Pleistocene extinctions of arctic megafauna was the suggestion by MacPhee and Marx (1997) that a disease epidemic wiped them out. These authors proposed that humans and their commensals introduced a deadly disease to previously naïve species, which then died in the resulting epidemic.

Nogués-Bravo et al. (2008) combined computer models of climate-determined geographic ranges with models of population dynamics to infer how the geographic range of woolly mammoth changed over time. They inferred that 90% of suitable mammoth habitat disappeared from Siberia between 42 and 6 cal ka BP. As their habitat shrank, mammoth populations declined, making them more vulnerable to human hunting. They see synergistic effects between human hunting and climate change as the cause of mammoth extinction in arctic Siberia. In a similar vein, MacDonald et al. (2012) mapped the shifting range of mammoth in Siberia after 40 cal ka BP and compared it to what is known about vegetation changes and the archaeological record. They concur with Guthrie's ideas about the importance of climate-driven changes in soils and vegetation being the proximate causes of mammoth extinction. Like Nogués-Bravo et al. (2008), they suggest humans were at most a synergistic factor in mammoth extinction in arctic Siberia.

Based on a large collection of dated mammoth bones from arctic Siberia, Nikolskiy et al. (2011) observed that mammoth populations fluctuated synchronously with global climate changes, increasing during interstadials and decreasing during the coldest times. They found that mammoths survived on mainland Siberia until 10.7 cal ka BP. Nikolskiy et al. (2011) suggest human hunting served as the *coup de grâce* for a species already pushed into extinction debt by unfavorable environmental changes during the early Holocene. "Extinction debt" is the persistence of individuals of a species after its habitat is no longer able to support a viable population of that species.

Ancient DNA reveals that lions underwent significant population fluctuations in the Arctic before human arrival, perhaps presaging the processes that would ultimately cause their extinction at the end of the Pleistocene (Barnett et al., 2009). In Eurasia, the cave lion, *P. spelaea*, became extinct in the interval 14–14.5 cal ka BP, probably in response to environmental changes affecting the abundance of its prey (Stuart and Lister, 2011). The role of humans in the extinction of arctic lions remains ambiguous.

DNA analyses of *Ursus arctos* (brown/grizzly bear) bones indicate that striking phylogeographic changes occurred within this species over the last 40,000 years in northwestern North America including eastern Beringia (Barnes et al., 2002). As with lions, muskoxen, and steppe bison, significant population bottlenecks and range shifts occurred in grizzly bears long before human entry into the New World.

In a magisterial review of the ^{14}C ages of a large collection of woolly rhinoceros bones from across Eurasia, Stuart and Lister (2012) find that the geographic range of this species contracted eastward starting ca 35 cal ka BP, and that final extinction occurred ca 14 cal ka BP in northeastern Siberia, the coldest, driest part of this species' range. They infer that woolly rhinoceros' extinction was caused by environmental changes, namely deeper snowpacks that interfered with wintertime foraging and a shift in vegetation to shrubs and trees.

In summary, previous studies show that arctic megafaunal species responded individualistically to environmental changes and human impacts at the end of the ice age. On the other hand, there is no escaping the fact that soils and vegetation form the bases of ecosystems and that the particular soils and vegetation that had once supported the Mammoth Steppe disappeared at the end of the Pleistocene. Which megafaunal species became extinct in the Arctic cannot be predicted based on their preexisting geographic ranges or genetic diversity. There is evidence that arctic megafauna populations experienced marked population bottlenecks during the period 30–50 cal ka BP, which in some parts of the Arctic was long before humans arrived. The occurrence of large fluctuations in megafauna populations during prehistoric times in the Arctic is consistent with the dynamics of caribou and muskox populations in historical times when extreme weather events and climate changes have caused local and even regional extirpations (Klein, 1991; Forchhammer and Boertmann, 1993; Post et al., 2009). As in other parts of the world (Barnosky et al., 2004), there was no universal agent of end-Pleistocene extinction in every sector of the Mammoth Steppe.

3. Regional setting

3.1. Physiography and geology

Alaska's North Slope lies between the Brooks Range and the Arctic Ocean (Fig. 1). It covers approximately 207,000 km^2, an area the size of the state of Nebraska. The North Slope has two physiographic units: the Arctic Foothills flanking the northern side of the Brooks Range and the Arctic Coastal Plain lying between the Arctic Foothills and the Arctic Ocean. Much of the North Slope has never been glaciated, and during the Last Glacial Maximum ca 19 cal ka BP glaciers terminated near the northern range front of the Brooks Range (Briner and Kaufman, 2008). North-flowing rivers have deposited extensive gravel deposits on the Arctic Coastal Plain and redistributed older, marine deposits left by Tertiary and Pleistocene sea-level high stands (Dinter et al., 1990). Intense periglacial activity in the form of ice-wedge polygons, pingos, and thermokarst lakes has reworked this unconsolidated sediment (Jorgenson and Shur, 2007). During dry intervals in the Pleistocene, sandy sediments on the Coastal Plain were incorporated into sand dunes forming the Ikpikpuk Sand Sea (Carter, 1981). Inactive today, this dune field was fully active in late Pleistocene times but had stabilized by ca 10 cal ka BP (Carter, 1993). A 30-km belt of thick loess and sand-sheet deposits borders the southern margin of the former sand sea (Carter, 1988), and both the Ikpikpuk and Titaluk Rivers pass through this loess belt upstream of their confluence (Fig. 1). Topography in the headwaters of the Titaluk and Ikpikpuk Rivers consists of rolling hills rising to 450 m asl. The underlying bedrock is predominately Cretaceous sandstone, which contains occasional bentonitic shales and silicified tuff beds (Mull et al., 2005).

3.2. Modern climate and permafrost

The North Slope is underlain by continuous permafrost hundreds of meters thick (Jorgenson et al., 2008). Active layers, the uppermost layers of the ground that freeze and thaw annually, are typically 15–40 cm thick (Bockheim and Hinkel, 2005). July is the warmest month, and July mean air temperature increases from 4 °C at Point Barrow on the coast to 12 °C at near the Brooks Range (Zhang et al., 1996). Mean annual precipitation also increases inland from 200 mm at Point Barrow to 320 mm near the range front.

About half this precipitation falls as snow that persists on the ground for 7–9 months.

3.3. *The rivers*

The upper reaches of the Ikpikpuk and Titaluk Rivers are well-known sources of Pleistocene mammal bones (Guthrie and Stoker, 1990). The channel reaches we surveyed lie within the Arctic Foothills, upstream of the Titaluk–Ikpikpuk confluence (Fig. 1). Both rivers are low-gradient, meandering streams whose headwaters lie 100 km north of the Brooks Range along the northern fringe of the Arctic Foothills (Mann et al., 2010). They have nival flow regimes in which the short-lived, breakup flood is the only significant high-water event during most years, and stream discharge drops steadily as the summer progresses. Both rivers have neutral to slightly basic pHs ranging between 6.5 and 7.6 in July and August, with the Titaluk being the more basic of the two. The upper Ikpikpuk River has a low gradient of 0.0003, and the Titaluk's gradient is even lower at 0.0002. The Ikpikpuk drainage basin upstream of the Titaluk confluence covers 4400 km^2, and the Titaluk drains an area of 2680 km^2. Hillslope water tracks flowing through peatlands (McNamara et al., 1999) cover large portions of the watersheds of both rivers. The Ikpikpuk and the Titaluk Rivers flow through sinuous, meandering channels lined by willow (*Salix* spp.) shrubs (Fig. 2). The Ikpikpuk carries a predominately sandy bedload with significant amounts of granule- and pebble gravel in its thalweg. The Titaluk River is finer grained with a predominately sandy bedload and significant amounts of suspended silt derived from the beds of former thaw lakes that the river has breached by lateral erosion. Base level in both rivers today is controlled by a series of bedrock knick points exposed in the valley floors. These bedrock highs are probably associated with anticlines that strike southeast–northwest across the area (Mull et al., 2005). In their upper reaches, both the Ikpikpuk and the Titaluk have now incised through their unconsolidated valley fills down to bedrock at multiple locations.

3.4. *Modern vegetation*

Today, the vegetation of the North Slope is a Low Arctic tundra mosaic encompassing Bioclimatic Subzones C, D, and E (CAVM Team, 2003; Walker et al., 2011). Sedge/grass and moss wetlands occupy the northern edge of the Coastal Plain, while sedge, moss, and dwarf-shrub wetlands are abundant further inland. A third main vegetation type, tussock-sedge dwarf-shrub moss tundra, covers much of the Arctic Foothills (Walker et al., 1994). Peat is widespread in the Arctic Foothills today, even on hillslopes. Occasional stands of *Populus balsamifera* (balsam poplar) trees occur in valleys (Bockheim et al., 2003). Of interest for the interpretation of bone isotopes is that the vast majority of grass species living in Alaska today are C3 species, and no C4 grasses are known from glacial times (Wooller et al., 2007; Gaglioti et al., 2011).

3.5. *Modern megafauna*

Mammals with body masses >44 kg that live on the North Slope today include moose, caribou, muskox, grizzly bear, and wolf. Polar bears (*Ursus maritimus*) rarely range inland from the coast, and wolverines (*Gulo gulo*) weigh <30 kg and so do not qualify as megafauna. Moose reach their northern range limit on the North Slope where they are restricted to gallery thickets of willow along rivers. The North Slope lies near the latitudinal midpoint of the geographic range of caribou, which extends poleward to Greenland. Muskoxen are the most arctic-obligate of the three large herbivores on the North Slope, which lies near the southern limit of their natural distribution today. Muskox became extinct on the North Slope in the mid-1800s as a result of climate change and, possibly, hunting (Lent, 1988). They were reintroduced to Alaska from Greenland in the 1930s and returned to the North Slope in the 1970s. The North Slope lies at the northern, geographical range limit of grizzly bears. Wolves are the most widely distributed of the surviving megafauna and live as far north as northern Greenland today.

Present-day population estimates for North Slope megafaunal species are problematic because of the remoteness of the region, the large fluctuations in their population sizes over decadal time scales, and the large home ranges of individuals of these species. Caribou are by far the most abundant species, with the Teshekpuk herd that sometimes occupies the headwaters of the Ikpikpuk and Titaluk Rivers estimated at 64,000 animals (ADNR, 2011). In some years, caribou from the much larger Western Arctic Herd cross into the Titaluk/Ikpikpuk basin. In 2011, caribou population density in Game Management Area 26A, the western half of the North Slope to the west of the lower Colville River, was estimated at 2.6 animals/

Fig. 2. A view of the upper Ikpikpuk River in late July 2011. The point bar in the foreground is about 40 m in width.

km^2 (US BLM, 2012). Moose numbers in the same region ca 2011 were approximately 0.01 animals/km^2, muskoxen 0.001/km^2, grizzly bears 0.01 km^2, and wolves 0.004/km^2 (US BLM, 2012; D. Yokel, pers. comm. 2013; P. Groves unpublished data).

4. Methods

4.1. Bone collections

We collected most megafauna bones from point bars and eroding bluffs along the upper 80 km of the Ikpikpuk and Titaluk Rivers and their tributaries (Fig. 1). A few come from other North Slope alluvial river valleys and from blowouts in the former sand sea. No data on archaeological bone material are presented here. Our collection technique was literally a random walk in which we traversed river point bars and the bases of river bluffs on foot and in canoes looking for bones and teeth. Occasionally we used masks and snorkels to collect bones from the river bottom. We collected megafaunal remains from the same river bars and bluffs along the upper Ikpikpuk annually since 1998. The Titaluk River was visited less regularly. We collected all the intact bones that we judged to be eventually identifiable, regardless of species, with the exception of mammoth tusk fragments, which we ignored.

It is important to note that both the collection of bones and the selection of specimens for ^{14}C dating are random processes as regards bone age. It is impossible to judge visually whether a bone is 100 years old or >43,000 years old. This is because of the sometimes exceptional preservation of bones that have been stored in frozen and/or anaerobic sediment in the floodplains of these rivers. MacPhee et al. (2002) reached a similar conclusion working with Pleistocene bones in northern Siberia. Our original goal was to date fifty bones each of mammoth, horse, caribou, muskox, and bison. Additional bones of these taxa were later dated when exceptional specimens (e.g., skulls, bones with soft tissue) were discovered. We dated most of the bones we found that belonged to rare taxa (moose, saiga, mastodon, lion, and bear).

The total collection consists of 4090 bones and teeth, all of which are either already stored in the University of Alaska Museum of the North or are in the process of being accessioned there. We identified bones to genus by comparison to reference collections at the University of Alaska Museum and using standard references. Unidentified specimens accounted for 5% of the total collection. A random subsample (n = 1145) of the collection was assessed for scavenger gnawing, root etching, and general weathering state (Behrensmeyer, 1978).

In addition to collecting bones, we also surveyed their concentrations on river bars to detect relationships with geological processes. This was done by conducting transects from the upstream to downstream ends of point bars. Transects were oriented parallel to the shoreline down the middle of each bar. We surveyed a 20-m wide swath, collecting every bone fragment encountered. Distances were estimated using the global positioning system. At the approximate center of each point bar, we recorded Wentworth-scale particle sizes at 5-m intervals along another transect oriented perpendicular to the shoreline and extending to the top of the bar.

To reconstruct the species composition of the fauna, we first assumed that each bone identified to species represented a separate individual. We then corrected the counts of each species by the percentage of the ^{14}C-dated bones of that species dating to between 43.5 and 10 cal ka BP.

4.2. Radiocarbon dating and stable isotopes

We ^{14}C-dated collagen from 496 bones that had definitive identifications and were in good condition (bone weathering stages 0, 1, and 2 of Behrensmeyer (1978)) using accelerator mass spectrometry (Appendix A). Collagen extraction was by the modified Longin method currently in use by Beta Analytic, Inc. An additional 67 dates for North Slope megafaunal bones were taken from the literature. Most of these came from prior collections by Dale Guthrie and Sam Stoker along the same reaches of the Ikpikpuk and Titaluk Rivers where we collected. In what follows in this report, we excluded bones from further consideration that had either infinite ages or finite ages >43.5 ^{14}C ka BP and/or standard deviations >750 years. This resulted in a subset of 245 bones. In cases where duplicate dates were obtained on the same bone, the average of the two dates was used. All dates were normalized for δ^{13}C. Published dates that lacked δ^{13}C values were normalized using standard procedures (http://calib.qub.ac.uk/calib/manual/chapter5.html) using average δ^{13}C values measured in bones of the same genus. All radiocarbon dates were calibrated using OXCAL 4.1 (http://c14.arch.ox.ac.uk/.html; Bronk Ramsey, 2009) and the IntCal 09 calibration curve (Reimer et al., 2009). Probability density distributions were generated in OXCAL 4.1.

Measurements of δ^{13}C and δ^{15}N in bone collagen were made using an Elemental Analyzer Isotope Ratio Mass Spectrometer. Typical errors in these measurements are ±0.5‰. Ordinations of bone isotopes were performed in Matlab (MathWorks, 2012). Our interpretations of stable isotope measurement rely on reviews by Högberg (1997), Heaton (1999), Ben-David et al. (2001), Hedges et al. (2005), Wooller et al. (2007), Koch et al. (2009), and Ben-David and Flaherty (2012).

Ultrafiltration techniques were not used in the ^{14}C dating of these bones. Because of the low amounts of ^{14}C remaining in old bones (<3% of modern at ca 30 cal ka BP), contamination of bone collagen by younger organics can be a critical issue in certain settings. Ultrafiltration techniques (Brown et al., 1988) can remove contamination and improve the accuracy of bone-collagen dates (Higham et al., 2012). As yet there has been no systematic comparison between ultrafiltered and non-ultrafiltered dates of the same bones sourced from permafrost environments. Although only a few were from permafrost environments, of five woolly rhinoceros bones dated by both methods, three returned older ages and two returned younger ages when re-dated using ultrafiltration (Stuart and Lister, 2012). In lieu of re-dating our entire collection using ultrafiltration techniques, we assume that contamination by younger carbon is minimal in the bones we dated since they have resided for much of their history either in permafrost or in anoxic sediments beneath river channels.

4.3. Estimating extinction times

An extinction time is when the last individual of some species died. Estimating extinction times is problematic because we will never discover and date the last surviving individual (Signor and Lipps, 1982) and because taphonomic processes can change over time. Also, megafaunal populations probably fluctuated in size over time, particularly at high latitudes and especially given the rapid tempo of climate changes during the ice age.

Despite the inherent complexity of extinction and taphonomy, several statistical approaches have been used to estimate extinction time. Solow's (1993, 2003) equation describes probability of extinction in relation to the number of sightings of a species over a given period. McInerny et al. (2006) modified Solow's equation to account for different lengths of sighting periods. Bradshaw et al. (2012) modified the McInerny approach by weighting sightings inversely according to time since last sighting under the assumption that sighting rates typically decline over time, so that the most recent sighting rate is the most informative. In the case of bones, this implies that the probability of preservation decreases with age and/or that animal populations decline to extinction along sigmoidal, linear, or exponential trajectories.

Many of the assumptions used in the statistical methods just described are debatable. When dealing with time scales of tens of millennia, it is particularly hazardous to assume that sightings are equally likely over time and that the intervals between these sightings conform to some theoretical distribution. It is likely that populations fluctuated and taphonomic/geological processes changed over such long time scales. Assumptions about the trajectories of population decline preceding extinction are also tenuous because the demographic trajectories of populations approaching extinction can vary widely. Familiar examples include the contrasting extinction trajectories of the passenger pigeon (*Ectopistes migratorius*) and California condor (*Gymnogyps californianus*). The ecological idiosyncrasies of extinction, the Signor-Lipps Effect, and the possibility of taphonomic nonstationarity undermine the credibility of even the most elegant statistical estimates of extinction times.

Our strategy for estimating extinction times emphasizes simplicity. We use OXCAL's simplest-case, "boundary" function because it accounts for the measurement and calibration uncertainties in ^{14}C dating. The "boundary" calculation assumes extinction occurred abruptly without a preceding decline in population size and that dated samples were uniformly sampled from the phase in question (Bronk Ramsey, 2009). A Bayesian approach similar to OXCAL's was used by Buck and Bard (2007) to estimate the extinction time of Alaskan Pleistocene horses. We also employ an empirical version of Solow's (1993) sighting-frequency method. This involves estimating the probabilities of time-since-last-sighting empirically from time series of dated bones. To do this, we first use OXCAL's "interval" function to estimate the duration of gaps between the 95% probability distributions of consecutive ^{14}C ages of bones of different taxa. Next, we group these age gaps into consecutive 100-year, age-gap bins. Finally, we calculate the probability of encountering an age gap within the fossil record that exceeds each of these 100-year intervals. This gap-probability method yields the probability of encountering absence-gaps of varying durations given that the species was still living on the landscape and given that taphonomic and population processes remained constant through time.

4.4. Estimates of animal numbers and biomasses

We make speculative estimates of the population sizes of ice-age species using caribou as a standard. As detailed in Section 6.3, the record of dated caribou bones suggests the population density of this species has remained roughly constant over the last 40,000 years. Knowing the population density of caribou in the region today (ADNR, 2011; US BLM, 2012), we use the abundances of the different megafaunal species in the bone collection relative to caribou to estimate the paleo-population densities of these other species. The body masses of different species used for biomass estimates come from Guthrie (1968).

5. Results

5.1. Post-mortem modification of bones

Only a few of the bones we collected were still articulated. Most occurred as single bones comingled with the bones and teeth of other species and other individuals. Some bones were modified by *post-mortem* processes, the most common ones being gnawing by scavengers, surface corrosion by plant roots (root etching), and general chemical and physical weathering. The latter category includes the interacting processes of bacterial decay, breakage by animal trampling and river ice, as well as damage caused by drying and cracking. Around 10% of the bones we collected still contained marrow and sometimes had bits of tissue attached. Despite their fresh appearance, some bones in this condition yielded infinite ^{14}C ages. About half of all bones fall into Weathering Stage 1 of Behrensmeyer (1978) in which there is some surface cracking on the bone (Fig. 3). Weathering Stage 3 bones that show extensive cracking, flaking, and dissolution pits account for only 10% of the total. Very few bones display gnawing by scavengers like fox, wolverine, wolf, or bear. Evidence of root etching is only slightly more frequent, suggesting that few of the bones spent time in the active layer of soils. We did not quantify bone breakage patterns. In summary, most bones were not scavenged before they were interred in sediment, and very few spent time exposed to plant roots in the active layer of a soil. Nonetheless, the majority of bones have spent long enough exposed to surface conditions to accumulate a slight degree of chemical and physical weathering.

5.2. Spatial distribution of bones

In the course of collecting bones, we noticed several distributional patterns, which at this stage remain anecdotal. The first is Andre Sher's rule: Pleistocene bones are most abundant on the first few point bars downstream of large eroding bluffs of Quaternary sediment. The second pattern is that bones tend to collect in channel thalwegs. Third, bones are most abundant on the upstream end of point bars where they are associated with the coarsest particle sizes (pebbles to coarse sand). We suspect this reflects a combination of steep gradients in current velocity at this location during break-up floods and the actions of ice floes that bulldoze sediment upwards onto the upstream edges of point bars. Fourth, bones are not randomly distributed within the valley fill below present river level. Rather they occur in widely separated *Konzentrat-Lagerstätten* (literally: "concentrated storage places", or colloquially: "bone closets"), which serve as source areas for many of the bones found on downstream river bars. These *Lagerstätten* are presently below river level and so are poorly exposed, but their dimensions and sediment characteristics are consistent with old channel fills lying near base level in the river valleys.

Detailed surveys of the concentration of bones on river bars indicate a lack of correlation with valley gradient in the Ikpikpuk, Titaluk, and Maybe Creek valleys (Fig. 4); however, bone

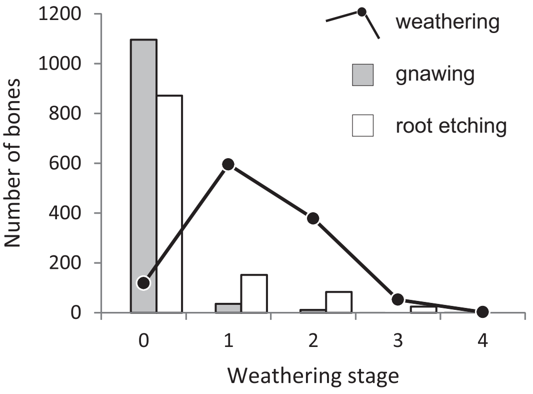

Fig. 3. Weathering characteristics of a random sample of 1145 bones. **General weathering state** (adapted from Behrensmeyer, 1978), Stage 0: no cracks or flakes, Stage 1: cracking parallel to fiber structure, Stage 2: outermost layers show thin flaking, Stage 3: surface has rough fibrous patches 1–1.5 mm deep, Stage 4: surface is rough and fibrous with loose splinters, Stage 5: bone falls apart *in situ*. **Root etching** Stage 0: no etching, Stage 1: <33% of surface etched, Stage 2: 33–66% of surface etched, Stage 3: >66% of surface etched. **Gnawing** Stage 0: no gnaw marks, Stage 1: single area of gnawing, Stage 2: multiple areas of gnawing; badly scarred.

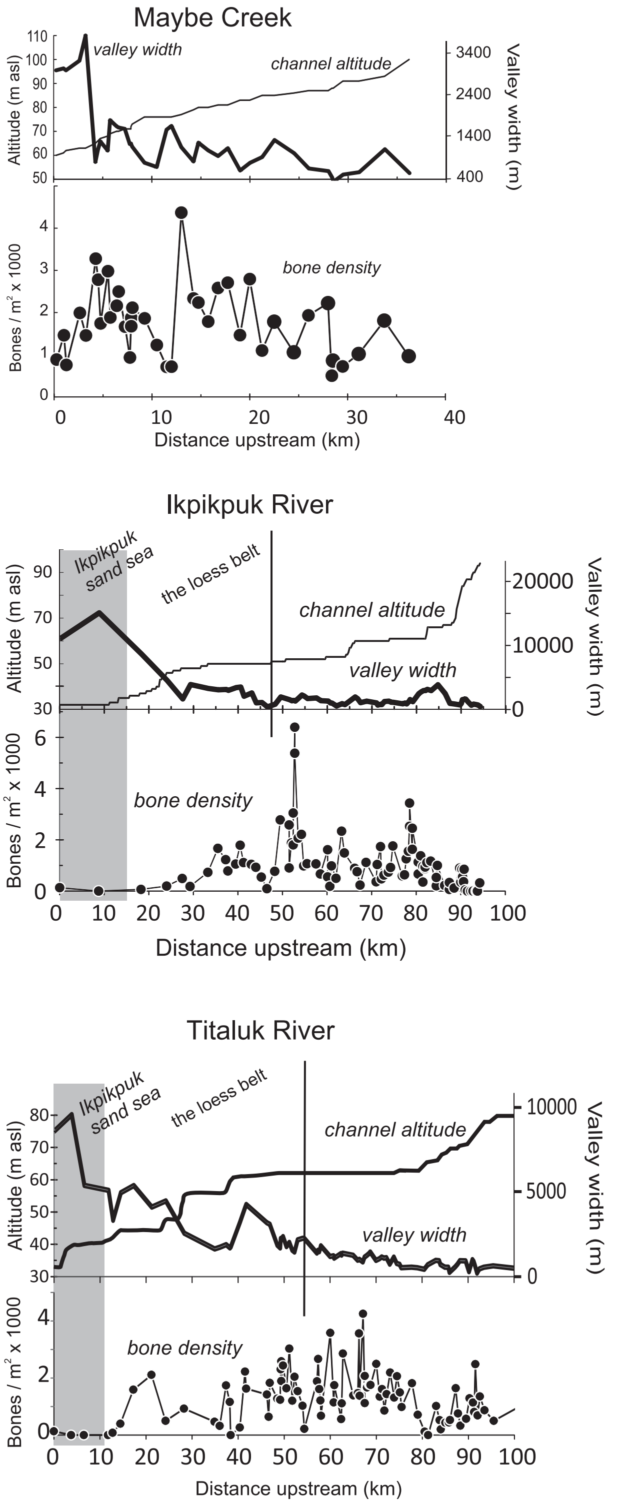

Fig. 4. Bone concentrations on river point bars compared to valley slope, valley width, and the location of the Ikpikpuk Sand Sea.

concentration does decline markedly where valleys widen. In the case of the Ikpikpuk and Titaluk valleys, bone concentration drops sharply where these rivers enter the former sand sea, at which point they lose any bedrock control over lateral channel position. The same is true for Maybe Creek where it debouches into the floodplain of the larger Ikpikpuk River (Fig. 4). As mentioned earlier, coarser particle size seems to be correlated with bone density at the upstream ends of point bars, but no relationship was found between particle size and bone occurrence at the scale of entire river valleys, except that the concentration of bones falls to zero where the Ikpikpuk and Titaluk enter the former sand sea and their sediment becomes entirely sand. The key inference from these observations is that bones are most abundant where paleochannels have been laterally constrained by bedrock-controlled valley walls.

5.3. *Relative abundances of different taxa*

In terms of individual animals, horses were the most abundant taxon on the North Slope between 43.5 and 10 cal ka BP (Fig. 5). Based on the lengths of their metacarpal bones, on the fact that hemionid horses became extinct in Alaska ca 34 cal ka BP (Guthrie, 2003; Weinstock et al., 2005), and on the identification of a partly mummified horse leg from the Titaluk River (Guthrie and Stoker, 1990), these were caballine horses belonging to the Eurasian species complex of *Equus ferus*. Steppe bison were the next most abundant taxon and comprised 23% of all identified bones, followed by caribou with 16%. Woolly mammoth and muskox each accounted for 9% of the collected bones. Predators (lion, bear, and wolf) together comprised approximately 2%. In terms of biomass, mammoth comprised an estimated 49% of the total (Fig. 5), followed by horse and bison, both at around 23%. Caribou and muskox comprised only about 3% of the total megafaunal biomass, and predators comprised $<$1%. Moose, which only arrived in the region ca 14 cal ka BP, also comprised $<$1%. The situation is radically different today when caribou comprise $>$97% of both the total number of megafauna on the North Slope and the total megafaunal biomass there. On the modern landscape, moose, muskox, wolf and bear each comprise $<$1% of the total number and biomass of the megafauna.

5.4. *Temporal patterns of species abundance*

The most striking difference in timing among the different taxa is that 95% of the dated horse bones ($n = 103$) and 78% of the lion bones ($n = 9$) are younger than 43.5 cal ka BP (Fig. 6, Table 1). In contrast, the majority of muskox and mammoth bones are $>$43.5 cal ka BP. Dated bones of all taxa exhibit a discontinuous, spikey distribution through time (Fig. 7). Because ^{14}C calibration causes distortions in these types of probability-density plots (Williams, 2012), and because the older part of the ^{14}C-calibration curve is currently being updated with new Lake Suigetsu varve data (Bronk Ramsey et al., 2012), we have postponed making detailed comparisons between these probability-density graphs and global climate events.

The youngest dates on extinct taxa provide limiting estimates on their extinction times (Fig. 8). The youngest horse and bison both lived ca 12.5 cal ka BP during the Younger Dryas chronozone. The two youngest horse bones in our collection (Beta-339279 and -331878) were found in blowouts within the Ikpikpuk Sand Sea 100 km distant from the upper Ikpikpuk basin. These new dates are approximately 1700 years younger than previous estimates of when horse became extinct in Alaska (Guthrie, 2003; Buck and Bard, 2007). Bison bones dating to ca 10.5 cal ka BP (Fig. 8) were excavated at the Engigstciak archaeological site 600 km east of the study area in the northwestern Yukon Territory (Cinq-Mars et al., 1991; MacNeish, 2000), though it is uncertain whether these bison represent *B. priscus* or *Bison occidentalis*.

Estimates of extinction time come from two other sources as well. The “boundary” calculation in OXCAL suggests horse became extinct between 11 and 12.6 cal ka BP (Fig. 9). Similarly, bison’s estimated extinction occurred between 10 and 12.6 cal ka BP, and mammoth’s between about 11 and 14.2 cal ka BP.

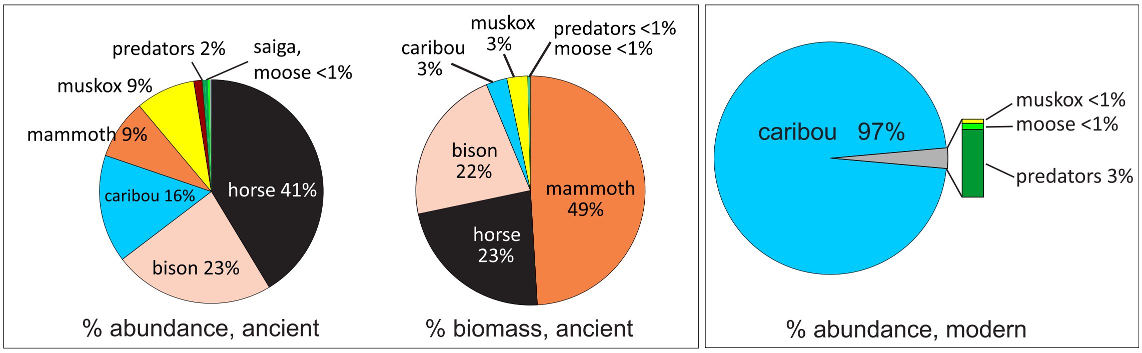

Fig. 5. Percentages of identifiable bones ($n = 1932$) dating to between 43.5 and 10 ^{14}C yr BP belonging to different taxa. For the ice age percentages, counts of identified bones are corrected using the percentage of the bones of that taxon dating to >10 and <43.5 ^{14}C yr BP. Biomass estimates are based on typical body masses listed in Table 1.

Analysis of the duration of dating gaps between the 95% probability density distributions of calibrated dates (Fig. 10) suggests in the case of horse ($n = 94$ age gaps) there is a >0.05 probability of finding a horse that is 0–1300 years younger than the youngest one we now have. This would postpone the extinction date for horse to ca 11.1 cal ka BP (Fig. 8). Similarly based on dating gaps there is a >0.05 probability of finding a bison as young as 10.6 and a mammoth as young as 11.8 cal ka BP in the study area.

Humans and moose arrived on the North Slope before horse, bison, and mammoth became extinct. The oldest date on archaeological charcoal comes from the Mesa Site (Kunz and Reanier, 1994; Mann et al., 2001) in the Arctic Foothills and dates to 13.5 cal ka BP (Fig. 8). OXCAL's "boundary" function estimates that humans may have first arrived on the North Slope ca 13.6 cal yr BP (Fig. 9). The oldest date for moose is 14.1 cal ka BP, and OXCAL estimates the lower (oldest) boundary of the "moose zone" at 16 cal ka BP.

5.5. Bone isotopes

Measurements of δ^{15}N and δ^{13}C reveal clear differences between megafaunal species. Known grazers (horse, mammoth, and bison) have δ^{15}N values centered between 4 and 9‰. Browsers like moose and mastodon, which are known to have subsisted largely on shrubs and trees, have δ^{15}N values between -1.0 and 3‰. δ^{13}C values vary less between species, but the combination of the two isotopes suggests separation between the diets of all species (Fig. 11). The species pairs showing the most overlap are steppe bison and muskox, moose and mastodon, and mammoth and horse. Of course, mastodon and moose were not contemporaries because mastodon probably became extinct at the end of the Last Interglacial (G. Zazula unpublished data).

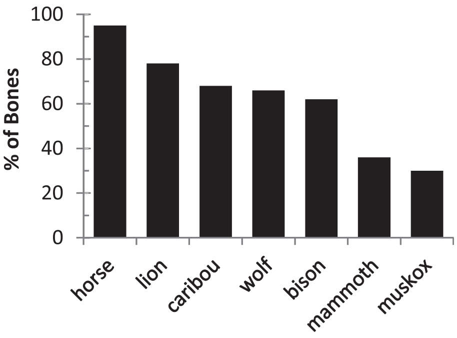

Fig. 6. Percentages of bones younger than 43.5 ^{14}C yr BP. Counts of the total number of identified bones of each taxon are adjusted by the percentage of the ^{14}C-dated bones of that taxon falling between 10 and 43.5 ^{14}C yr BP. Most horse and lion bones post-date 43.5 ^{14}C ka BP.

Measurements of δ^{13}C reveal shifts of 1–2‰ in all species after 43.5 cal ka BP (Fig. 12). δ^{15}N measurements show greater variability over time than δ^{13}C. Interestingly, the most striking changes in bone isotopes are not associated with the Pleistocene/Holocene boundary or the beginning of the Bølling–Allerød ca 14 cal ka BP but occurred earlier in time. Horse δ^{15}N decreased by 6‰ over a 3500-year period beginning ca 16 cal ka BP. A decline of similar magnitude in caribou bones began ca 20 cal ka BP, while bison δ^{15}N began a 3‰ decline beginning ca 25 cal ka BP (Fig. 12).

6. Discussion

6.1. Taphonomic pathways

The upper reaches of the Ikpikpuk and Titaluk are unusual among North Slope rivers in that their combination of low gradient, sand-dominated bedload, and nival flow regime favors the preservation of mammal bones. In contrast, streams with headwaters in the Brooks Range have subnival flow regimes involving frequent summer floods. They also possess steeper gradients and hence have higher flow velocities, and, with some exceptions, carry coarser bedloads that are less friendly to bones. We have descended most of the major rivers crossing the North Slope from the Brooks Range and found very few bones along any of them.

The processes responsible for incorporating bones into floodplain sediments and preserving them in the Ikpikpuk and Titaluk valleys differ from those operating in the uplands of Interior Alaska (Guthrie, 1990). There most carcasses were buried by mass movements, most of which involved slumps of loess-rich material at the foot of steep slopes. Bones later entered stream systems when they were exhumed by the lateral migration of channels. In the course of being carried downstream, bones tended to be concentrated (along with the gold) in the lowest levels of sediment overlying bedrock. This Interior-Alaska model predicts that more bones are preserved where more loess is present on the landscape. It also predicts that bones are most abundant where tributary streams enter larger valleys since these steeper tributary streams are carrying bones from their surrounding hillslopes. Neither of these patterns was observed in our study area.

Our conceptual model of how bones are preserved and concentrated in the Ikpikpuk and Titaluk incorporates some of the same processes just described and adds a few others (Fig. 13). The limited amount of *post-mortem* alteration suggests most bones were incorporated quickly – perhaps in <10 years – into sediment. There was little opportunity for scavengers to gnaw the bones or for roots to corrode them. Rapid burial is prerequisite to avoid

Table 1
Estimates of ice-age numbers of megafaunal population densities and biomasses.

Species	Body mass (kg)	Modern population density (indiv./km²)	Modern biomass (kg/km²)	% of total animals (inferred from bone counts)	Caribou relative abundance index	Ice-age population density (indiv./km²) this study	Ice-age population densities at Duvanniy Yar, Lena River, Siberia (Zimov et al., 2012) (indiv./km²)	Ice-age population densities, eastern Beringia (Matheus, 2003) (indiv./km²)	Ice-age population densities, Beringia (Redmann, 1982) (indiv./km²)	Ice-age population densities, Beringia (Bliss and Richards, 1982) (indiv./km²)	Ice-age biomass (kg/km²) this study	Ice-age biomass, eastern Beringia (Matheus, 2003) (kg/km²)
Muskox	180	0.001	0.2	9	0.56	**1.5**	–	–	–	0.7–1.4	**270**	–
Caribou	100	2.6	260	16	1	**2.6**	15	–	–	0.3–0.6	**260**	–
Horse	290	0	0	41	2.56	**6.7**	7.5	1	5.2	0.5–1.3	**1940**	180
Bison	500	0	0	23	1.43	**3.7**	5	0.6	3.1	0.2–0.5	**1850**	400
Mammoth	3000	0	0	9	0.56	**1.5**	1	0.08	0.4	0.02–0.04	**4500**	300
Carnivores (bear, wolf)	75 avg.	0.011	0.8	2	0.12	**0.3**	1.25 (lions + wolves)	–	–	–	**22**	–
Moose	360	0.007	2.5	<1	0.003	**0**	0	–	–	–	**0**	–
Totals	–	2.62	264	100%	–	**16.3**	29.75	1.7	8.7	1.7–3.8	**8840**	1000

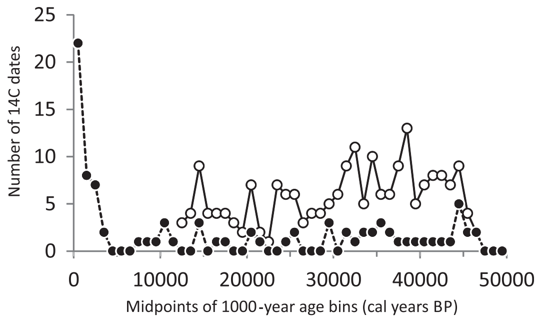

Fig. 7. Numbers of ^{14}C-dated bones <43.5 ^{14}C ka BP in 1000-year age bins. Open circles = extinct species (mammoth, horse, bison; $n = 203$). Solid dots = extant species (moose, caribou, muskox; $n = 88$).

scavengers. Other possible explanations for the limited evidence of carnivore gnawing are a predominance of winter kills and/or high prey abundance (Haynes, 1982, 1983); however, these alternatives seem unlikely because in the region today caribou carcasses are converted into broad scatters of gnawed and shattered bones within several years of death. Some of these bones may persist for decades on the ground surface, but they persist as gnawed fragments, and this is not the condition of the majority of Pleistocene bones we find.

The mixed nature of the bone assemblage in which bones of all species and all ages occur together on the same sand bar is consistent with the river repeatedly exhuming bones from the valley fill and then redepositing them. As in Guthrie's model for Interior Alaska, we think that bones are progressively elutriated downward in the valley fill by repeated episodes of erosion and redeposition. Elutriation occurs because of density differences between bones and the sandy matrix. Because the bedload of these rivers is fine grained and because the annual flood is a singular

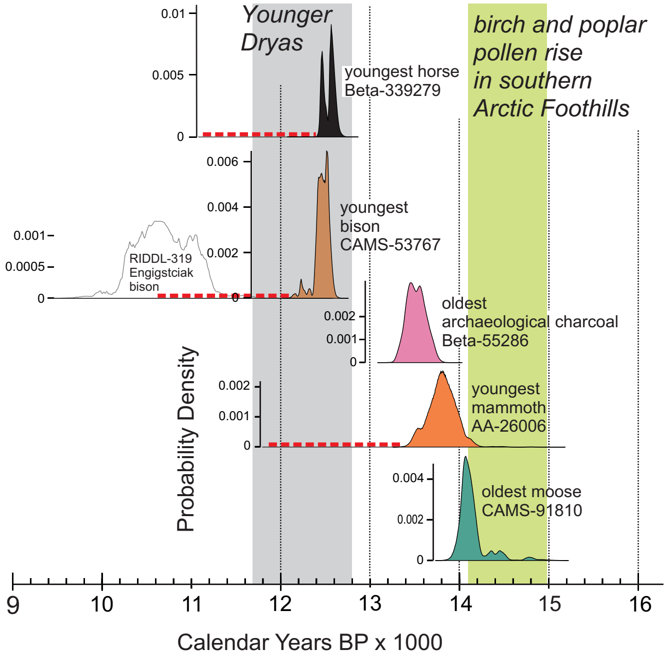

Fig. 8. Probability-density distributions of the youngest dates of extinct species and the oldest dates of humans and moose. The red dashed lines are period in which the probability of there being a time gap of this duration or longer is >0.05 (see Fig. 10). The bison from Engigstciak comes from 600 km east of the study areas and is not positively identified to species.

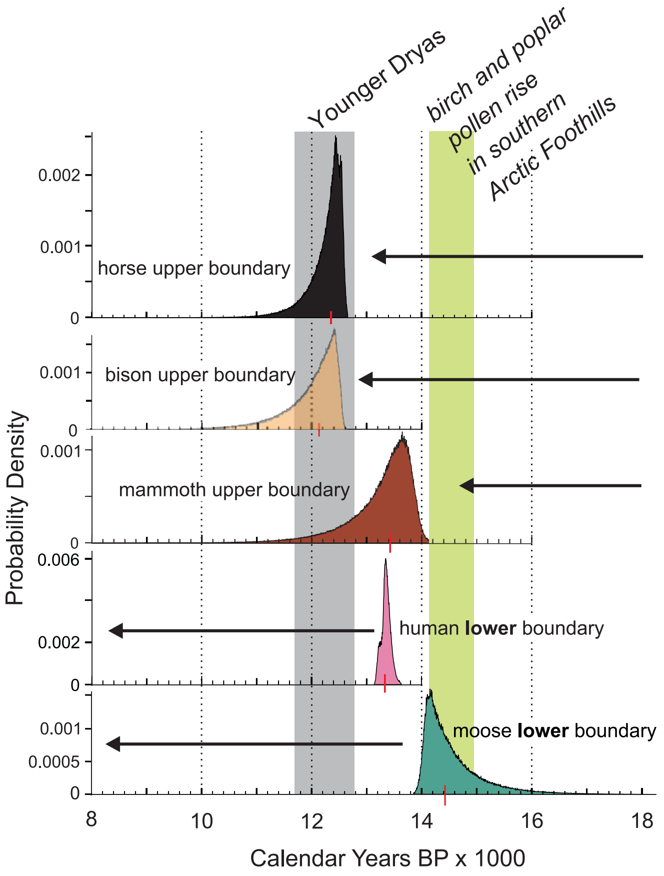

Fig. 9. OXCAL-estimated upper (youngest) boundaries for extinct species and lower (oldest) boundaries for humans and moose.

event, this exhumation and redeposition process is relatively gentle.

We think that bones enter the valley fills of the Titaluk and Ikpikpuk through two different routes. The first involves animals dying on upland surfaces near the river and being rapidly buried by loess or sand sheet sediment there (Fig. 13). We are uncertain how exactly this burial occurred before scavengers and weathering altered the bones. Perhaps animals died in thermokarst hollows (Boeskorov et al., 2011) or in ravines that drifted over with snow, sand, and/or loess during the winter. At the few places where the rivers are eroding old upland surfaces today, bones sequestered via this first pathway are tumbling into the river channel where they are concentrated in the channel thalweg and join bones arriving via the second taphonomic pathway.

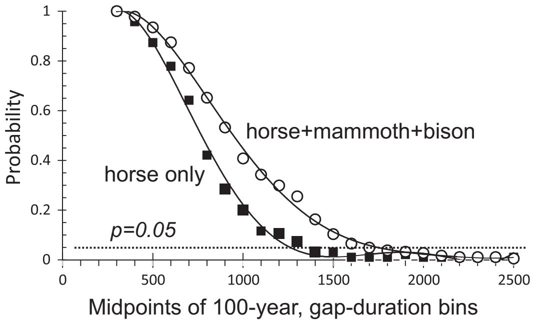

Fig. 10. Probability of encountering gaps between calibrated ages at 95% probability. Open circles show the duration of gaps between the 95% probability distributions of consecutive dated bones of combined mammoth, horse, and bison ($n = 184$, $R^2 = 0.998$). Black squares = consecutive gaps between horse dates only ($n = 94$, $R^2 = 0.995$).

The second pathway involves animals dying on the floodplain where they were quickly buried by fluvial sediment. Repeated bouts of exhumation and reburial mix the bones of different carcasses. Progressive elutriation during repeated episodes of valley-fill incision (Mann et al., 2010) concentrates the bones in abandoned channel fills at progressively deeper levels in the valley fills. Laterally, these channel fills are concentrated where the valley walls are narrowest. Vertically, they become concentrated in valley reaches that are immediately upstream of bedrock knick points on the valley floor. Observations consistent with this pathway are a) concentrations of bones in the thalweg at the base of bluffs that are shedding bones into the river, b) the influence of valley width on bone density (Fig. 4), and c) the fact that most of the bones we collected originated upstream of the loess belt (Figs. 1 and 4).

What were the relative contributions of these two different taphonomic pathways? There is only one situation where we are able to associate particular bones with the sedimentary units where they were initially deposited. This is at cutbanks on the lower Titaluk River located within the loess belt. At these locations (the Russian and Carter sections), 5–10 m of fluvial sand and gravel are overlain by 15–40 m of sand sheet and loess (Guthrie and Stoker, 1990; Mann et al., unpublished data). We have obtained multiple ^{14}C dates on these fluvial and aeolian units, so we know when they were deposited. At the same sections, we have dated seven megafauna bones, and by knowing their ages we can assign them an origin in either the fluvial or aeolian unit. Three of these seven have ages consistent with deposition in the fluvial unit, and the other four have ages requiring they originated from the overlying aeolian unit. A fifth undated specimen consists of the shattered skull of a mammoth calf encountered while excavating a buried soil in the loess unit. This one example confirms the existence of the two taphonomic pathways; however, keep in mind that most dated bones (>75%) come from upstream of the loess belt, implying that most entered through the floodplain-first pathway.

To summarize, there are two pathways for interring bones in the valley fills of these rivers. The first pathway involves megafauna dying in the uplands and being rapidly buried by aeolian sedimentation. Bones initially deposited in the uplands later fall into the channel when the rivers erode laterally into these deposits of loess and sand sheets. The second pathway starts on the floodplain where dead animals are quickly buried by fluvial sedimentation. These bones are mixed downstream with those entering via the upland path and are similarly elutriated downward in the valley fills. We think that the second, floodplain pathway is the main one because the majority of the bones we collected came from upstream of the loess belt.

6.2. *Implications of taphonomic processes for the fossil record*

Bones entering the valley fill via the upland-loess pathway are much less likely to do so at times when rates of loess and sand-sheet deposition are low. The Ikpikpuk Sand Sea probably stabilized ca 10,000 cal yr BP (Carter, 1993) and as it revegetated, the supply of aeolian sediment to adjacent areas ceased. So the upland-loess pathway probably operated only during the late Pleistocene, and even then its intensity would have varied episodically according to the activity of the dune field.

In contrast, the floodplain pathway has probably operated continuously. Even today when the rivers are in a state of maximum incision compared to their levels during the Lateglacial and early Holocene (Mann et al., 2010), channels continue to migrate, bluffs erode, and overbank deposition occurs. This pathway has probably

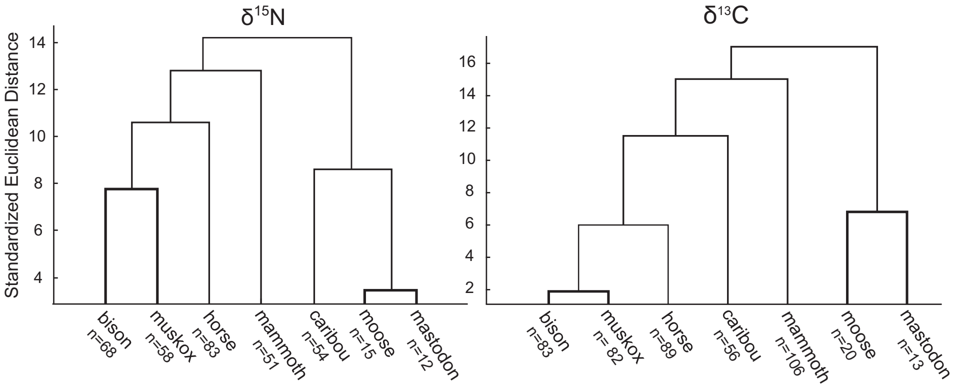

Fig. 11. Ordination of $\delta^{13}C$ and $\delta^{15}N$ describe similarities in diet. Bones of all ages are included here. Euclidean distance to population mean is a measure of departure from central tendency in isotopic niche.

sampled the extant megafauna at about the same rate throughout the last 40,000 years. Because most of the bones we dated came from upstream of the loess belt, we think that shifts in taphonomy had minimal influence over the rate at which bones have been incorporated into the fossil record. In what follows, taphonomic processes are assumed to have been constant over the last 40,000 years.

Once incorporated in the valley fill, bones have an extremely low probability of loss. Several observations support this interpretation: a) This is an arctic environment where the ice-free season during which the rivers flow and bones are vulnerable to physical and chemical weathering is brief: 3–5 months at most. b) The channel-fill deposits where we think many bones eventually are stored are the geologically most stable sites on this landscape. This is because they are situated at low levels in the valley fills where they are protected from most river erosion by bedrock sills. c) If bones are exhumed by the river, they have a high probability of being rapidly reburied. Even if they spend several months exposed at the surface of a point bar, the combination of low current velocities and an arctic climate mean they will probably survive intact until reburial. Quantitative evidence for a decreasing probability of bone loss through time is described in the next section.

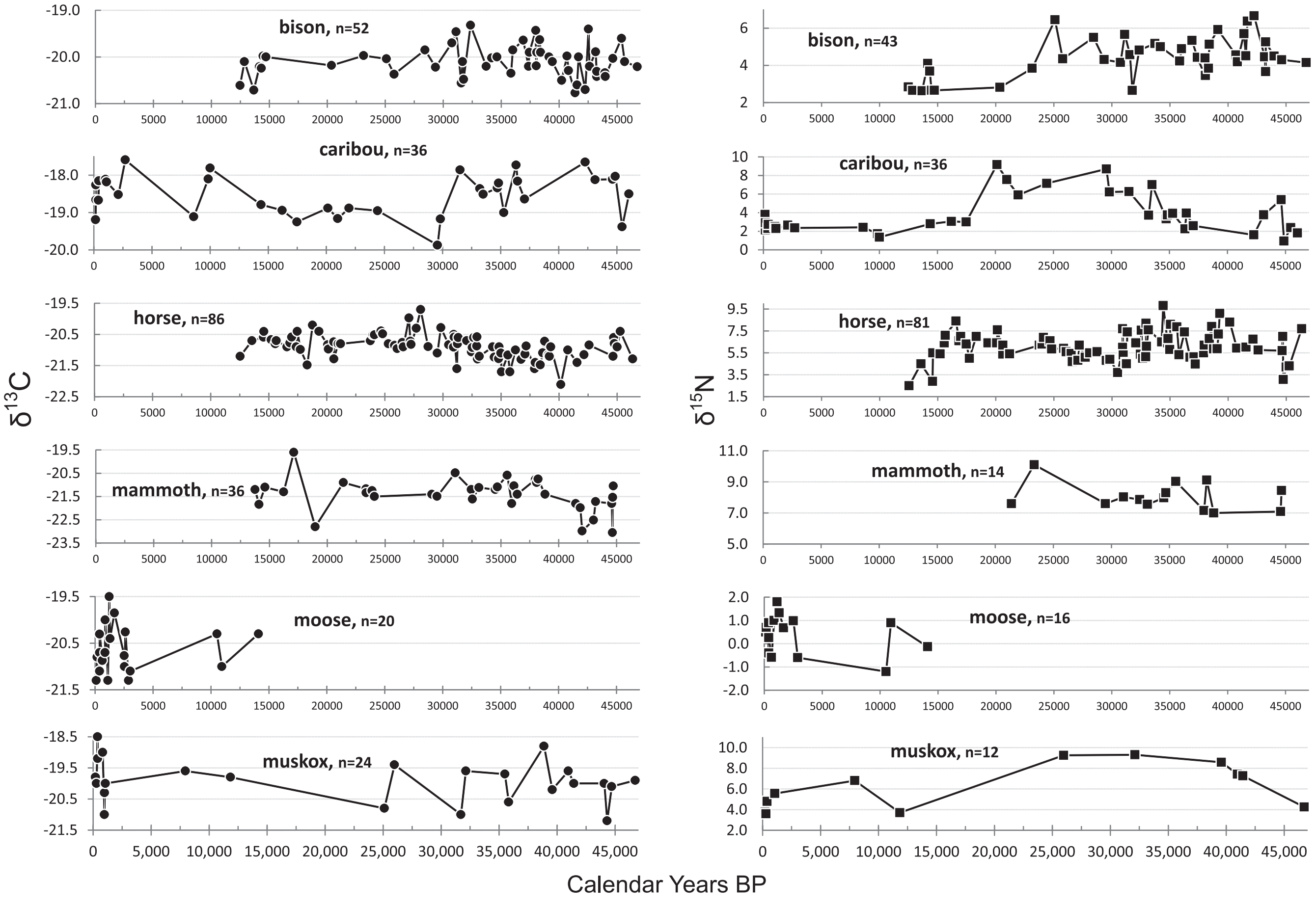

Fig. 12. Changing $\delta^{13}C$ and $\delta^{15}N$ values in dated bones through time.

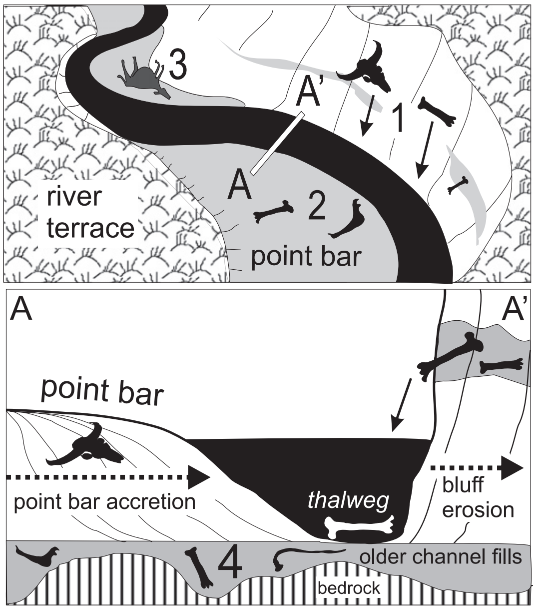

Fig. 13. Conceptual model of taphonomic processes operating in the study area. Bones enter flood-plain deposits via two pathways. In the first, bones buried by aeolian sediment on uplands in the loess belt (1) are eroded from cutbanks and concentrated in channel thalweg. Break-up floods carry some bones onto point bars (2), where they are reworked back into sandy sediments. The second pathway involves animals dying on the active floodplain (3), where their bones are dispersed, rapidly buried, and mingled with bones from the first pathway. Once in the floodplain, bones are gradually elutriated from the sandy matrix and concentrated in channel fills upstream of bedrock outcrops (4).

6.3. *How many megafauna were there?*

We can estimate the population densities of the extinct megafauna between 45 and 10 cal ka BP by accepting the conceptual model just described for the dynamics of bones in the study area and making several assumptions about how caribou population density changed over time. We use caribou as the standard to estimate the numbers of other species because many more caribou were dated than muskoxen, and unlike moose, caribou are present throughout the record. Assuming that taphonomic processes have remained constant, the distribution of bone ages through time is a function of changing population sizes. Probability of discovery typically increases toward the present day because taphonomic loss increases into the past. This rise-to-present curve links paleopopulation sizes to modern ones. There is no rise to the present in the ^{14}C-dates of the extinct species, but the frequency of dated bones of the extant species (moose, muskox, and caribou) increases greatly after 4–5 cal ka BP. We combined the ^{14}C ages of bones of these three species to get a clearer description of the shape of the rise-to-present curve. Similar patterns result from using the caribou dates alone (Fig. 14). The Surovell equation fitted to these data describes the rise to present of geological deposits (Surovell et al., 2009; Williams, 2012).

Both the Surovell equation and the moose/caribou/muskox power law underestimate the number of pre-10 cal ka BP caribou dates (Fig. 14), suggesting that the actual taphonomic loss rate declines to near-zero values for bones >10,000 years old. This is consistent with the taphonomic model described earlier. Alternatively, there were more caribou during the ice age than there are today. Since our goal is to use these curves to estimate paleopopulation sizes, the conservative approach is to assume a zero-loss rate for bones >10,000 years old. The taphonomic-loss relationship that best describes both the observed rise to the present and the pre-10 cal ka BP distribution of caribou ages is an "L"-shaped one that follows a power law equation back to ca 10 cal ka BP and a flat line before then (Fig. 14).

Assuming that caribou populations were similar in the early Holocene as they are today, and assuming that taphonomic loss "flat-lines" in the years prior to 10 cal ka BP, and by knowing what population densities of caribou are today, we can use the relative abundances of the bones of the different taxa (Fig. 5) to estimate the population densities of the extinct taxa on the ice-age landscape (Table 1). Today, there are approximately 2.6 caribou/km^2 on the North Slope west of the lower Colville River. Based on the assumptions just stated, caribou numbers during the ice age were *at least* 2.6 animals/km^2. Among the ice-age bones, caribou are 1.8× *more* abundant than muskox and mammoth, 1.4× *less* abundant than bison, and 2.6× *less* abundant than horse (Fig. 5a, Table 1). If caribou were present on the ice-age landscape at a density of 2.6 individuals/km^2, then there would have been 1.5 muskox, 1.5 mammoth/km^2, 3.7 bison/km^2, and 6.7 horse/km^2 during that same period. The total number of megafaunal animals would have been 16/km^2. Today, there are approximately 2.6 megafauna/km^2 in the region, which means that megafauna of all species combined were approximately 6× more numerous during the ice age than today. Based on these estimates, biomass during the ice age was approximately 8800 kg/km^2, which was about 30× greater than today (Table 1). In comparison, grassland and savannah ecosystems in East and Central Africa in recent times have supported megafaunal biomasses ranging from 4000 to 20,000 kg/km^2 (Kruuk, 1972; Schaller, 1972; Coe et al., 1976; Redmann, 1982).

Previous estimates have been made of megafaunal population densities and biomasses in the Mammoth Steppe of eastern Beringia during the ice age. Redmann (1982) and Bliss and Richards (1982) combined estimates of the carrying capacities of lower

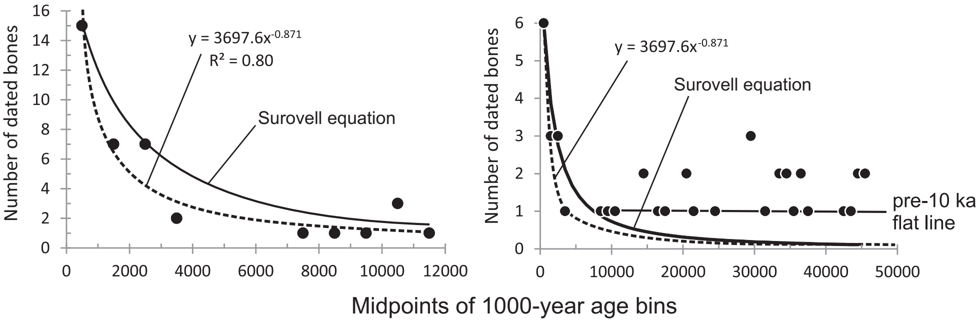

Fig. 14. LEFT: The Rise to Present of ^{14}C-dated moose, muskoxen, and caribou ($n = 38$). Zero values have been dropped. Not included here are eight muskox specimens collected from possible archaeological contexts north of the study area. The dashed line is a power law fitted to these data. The solid line is the fitted Surovell equation originally derived from the taphonomic loss of volcanic ash deposits in terrestrial environments. **RIGHT**: The number of ^{14}C-dated muskoxen ($n = 25$) and caribou ($n = 42$) compared to the equations fitted in the left-hand panel.

latitude grasslands and high latitude ecosystems to calculate how many megafauna could have been supported. Redmann's (1982) estimates are somewhat similar to ours, while those of Bliss and Richards (1982) are roughly an order of magnitude lower. Matheus (2003) arrived at values similar to Bliss and Richards (1982).

Zimov et al. (2012) arrived at population estimates similar to our's for the interval 40–10 cal ka BP along the lower Lena River in northeastern Siberia (Table 1). Working with bones eroding out of the valley-fill deposit exposed at Duvanniy Yar (Strauss et al., 2012), Zimov calculated the number of animal carcasses per volume of sediment, divided by the total age of the deposit. Muskox bones are absent at Duvanniy Yar, and caribou bones are more abundant there than on the North Slope, but the relative abundances of the other taxa are similar. Zimov et al. (2012) assert that other Quaternary bone beds in northern Siberia evidence megafauna population densities similar to those at Duvanniy Yar.

So how many megafauna were there on the Mammoth Steppe? Keeping in mind that this biome had a continental extent and that climate changed in a complex fashion over the tens of thousands of years during which it existed, the estimates in Table 1 agree that the Mammoth Steppe supported a significantly larger biomass of megafauna than live in the same regions today. Our data and those of Zimov et al. (2012), which are the only "hard" data relevant to this question, both indicate megafaunal animals were 6–12× more abundant than today, at least in certain parts of the Arctic and at certain times during the ice age. They also suggest that total megafaunal biomass may have been 30× greater. At these high animal densities, feedbacks between the herbivorous megafauna and the rangeland ecology (McNaughton, 1984) would be inevitable (Zimov et al., 1995, 2012).

Possible errors in our estimates of megafauna numbers and biomasses fall into four categories: instability of modern caribou populations, changing taphonomic processes, misinterpretation of the species composition of the bone fauna, and fluctuating populations during the ice age.

1) **Caribou populations fluctuate so much today that it is difficult to assign a typical, Holocene population density,** and this could undermine their usefulness as a standard for estimating the prehistoric population sizes of other megafauna. Since record-keeping started 50 years ago, the sizes of the Teshekpuk and Western Arctic herds have fluctuated by nearly an order of magnitude (Vors and Boyce, 2009; US BLM, 2012). Due to the brevity of records, there is no way to know how typical these rapid shifts are.
2) **Taphonomic processes have changed.** It could be that bone deposition has been less likely during the Holocene than during the ice age. Certainly the loess-upland pathway of bone sequestration and storage has not operated for much of the Holocene, and perhaps the floodplain pathway captured and stored more bones while in an ice-age state than during the current interglacial. If this is true, then we are overestimating animal populations during the ice age.
3) **The relative abundances of species were different than how we reconstructed them.** In calculating the relative abundances of different species in the bone fauna (Fig. 5), we make no allowances for interspecific differences in the sizes of bones, their preservation potentials, or the differing behaviors of the various species that could influence the likelihood of their bones of being preserved. Size-biasing can affect the representation of bone assemblages (Behrensmeyer et al., 1979) particularly for species weighing <100 kg; however, for animals larger than caribou, size-biasing is probably not an important issue (Western and Behrensmeyer, 2009; Miller, 2011). That said, mammoths are probably overrepresented in the collection by virtue of their large bones, their tusks, and their large and breakage-resistant teeth. But even if we halve the number of mammoth to 0.75 individuals/km^2 during the ice age, this reduces the numbers of megafauna only slightly and lowers total megafauna biomass by only 25%.
4) **The "ice age" was not a period of uniform climate.** The equable climates of the present interglacial have created long-term, ecological stases that are unusual from the perspective of the last 100,000 years. The millennial-scale effects of the Dansgaard–Oeschger cycles and Heinrich Events that are so prominent in the Greenland ice-core records affected places as distant as Lake Baikal (Prokopenko et al., 2001), Yakutia (Müller et al., 2010), the Sea of Okhotsk (Gorbarenko et al., 2007), and Peru (Kanner et al., 2012). These short-lived bouts of rapid climate change undoubtedly affected northern Alaska as well. It could be that the greater abundances of megafauna that we infer during the ice age represent short-lived peaks in megafauna abundance. The "spike-iness" of the probability density distributions of megafaunal ages (Fig. 7) is consistent with this idea. It is probably deceptive to cite what may be short-lived, maximum animal densities as representative of the entire ice age.

6.4. Implications of isotopes

Comparisons of δ^{15}N and δ^{13}C between species and over time provide information about their diets and clues about why some species became extinct. Species that are known from their current natural history (moose) and their dental morphology (mastodon) to be dedicated browsers have the most similar isotope values of any species pair (Fig. 11). The next closest pair is composed of muskox and bison. Today, muskoxen have a diverse diet of forbs, graminoids, and shrubs. Bison, who are often considered to be obligate grazers (Fox-Dobbs et al., 2008, 2012), in fact subsist on a mixed diet of grass, sedge, forbs, and shrubs in parts of Interior Alaska today (Gardner et al., 2007). Like muskox, steppe bison's descendant species, *Bison bison*, has been a fugitive species in northern Alaska during post-glacial times. It was intermittently present south of the Brooks Range during the Holocene (Stephenson et al., 2001), and several herds of introduced *B. bison* persist on outwash plains in the region today. It seems that the bison–muskox niche is still present in the region but only in widely scattered patches.

The δ^{13}C and δ^{15}N values of caribou and muskox bones indicate that during the ice age these species occupied one end of the dietary phase space defined by these isotopes (Fig. 15). This was the case prior to 14 cal ka BP and became even more pronounced afterward. The isotopic values of a plant are controlled by complex interactions between its physiology, soil moisture, temperature, soil fertility, and atmospheric CO_2 levels (Heaton, 1999; Stevens and Hedges, 2004; Koch et al., 2009). Although trophic fractionation means that plant and bone isotope values do not match exactly, measurements of modern plants from northern Alaska indicate that graminoids tend to be enriched in ^{15}N and depleted in ^{13}C compared to forbs, lichens, and shrubs (Nadelhoffer et al., 1996; Ben-David et al., 2001; Wooller et al., 2007; Fox-Dobbs et al., 2008). When considered together, the isotopic values of modern plants and the bone-isotope values are consistent with the interpretation that on the ice-age landscape muskoxen and caribou were eating plant taxa that today are associated with moist acidic tundra. The further depletion in δ^{15}N after ca 14 cal ka BP (Fig. 15) suggests muskox and caribou diet shifted even closer toward values characteristic of moist acidic tundra. Additional support for the idea that during the ice age muskoxen and caribou fed in the plant

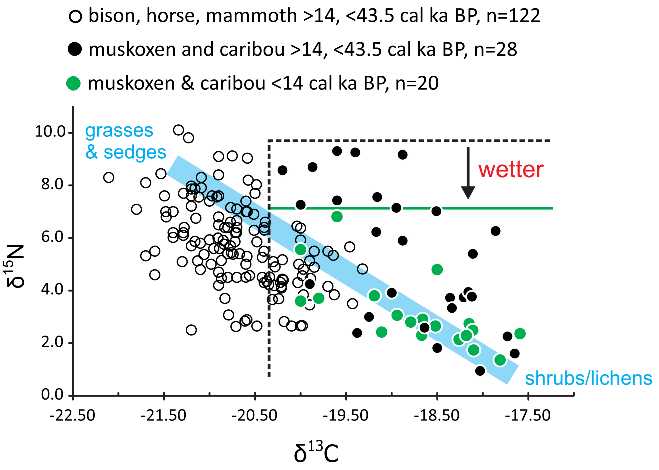

Fig. 15. Shifts in bone-isotope values after 14 cal ka BP. During the ice age, the diets of muskoxen and caribou occupied the part of the δ^{15}N/δ^{13}C phase space corresponding to plants growing in warmer/wetter habitats and most resembling the isotopic values of moist acidic tundra that today covers much of the Arctic Foothills today. In post-glacial times, the diets of these species shifted even further toward moist values. The blue diagonal line illustrates the relative gradient in present day isotopic values of arctic plant taxa.

communities most similar to the ones dominating the landscape today comes from the inverse correlation between δ^{15}N and mean annual precipitation (Heaton, 1999; Hedges et al., 2005) and the positive correlation between mean annual temperature and δ^{13}C that exists in some regions (Van Klinken et al., 1994; Heaton, 1999; Iacumin et al., 2006). As to why more enriched bone δ^{13}C values are associated with moister vegetation types, as opposed to more depleted ones as would be predicted by global patterns of δ^{13}C and precipitation (Diefendorf et al., 2010; Kohn, 2010), we can only point out that isotope fractionation occurs through multiple interacting processes and that the patterns exhibited in local vegetation trump global trends when interpreting bone isotopes. The lower pH and nutrient levels found in moist acidic tundra compared to well-drained, graminoid-dominated vegetation (Heaton, 1999) might have contributed to the higher δ^{13}C values found in the bones of caribou and muskoxen exploiting the moister, warmer parts of the ice-age vegetation mosaic. Also, some of the enrichment in ^{13}C in caribou and muskox bones after 14 cal ka BP was probably due to increasing levels of CO_2 in atmosphere (Stevens and Hedges, 2004; Iacumin et al., 2006).

Decreasing δ^{15}N values in muskoxen and caribou bones after 14 cal ka BP (Fig. 15) probably reflect the impacts of regional paludification, the spread of peat and organic soils across previously well-drained mineral soils. Paludification would have closed the open nitrogen cycle that formerly operated in warmer, better drained mineral soils and intensified the recycling of N from organic compounds and therefore its fractionation (Stevens and Hedges, 2004). The spread of organic soils was accompanied by the replacement of grass- and forb-dominated vegetation by moisture-loving sedges, mosses, lichens, and shrubs, all of which have lower δ^{15}N values (Nadelhoffer et al., 1996; Fox-Dobbs et al., 2008). A decline in δ^{15}N is also consistent with the spread of colder, more stable soils with shallower rooting depths (Nadelhoffer et al., 1996), all of which are features of a paludified landscape.

Additional evidence for the effects of regional paludification may come from the δ^{15}N record in horse bones, the taxon with the most dated bones (Fig. 12). Beginning ca 16 cal ka BP, δ^{15}N declined rapidly, falling about 6‰ over 4000 years. A similar decline in δ^{15}N over the same period occurred in horses in northwest Europe where it is attributed to the combined effects of changing water availability, temperature, soil processes, and mycorrhizal associations (Stevens and Hedges, 2004). All these processes are involved in paludification, which causes soils to cool, soil moisture to increase, rooting depths to decrease, and overall vegetation to change drastically. The size reduction in Alaskan horses that started ca 25 cal ka BP and culminated at their extinction (Guthrie, 2003) could be related to declines in range quality caused by paludification.

In bison and caribou from the North Slope, directional shifts in δ^{15}N started before regional paludification did (Fig. 12). A striking decline in the δ^{15}N of caribou bones began ca 20 cal ka BP, 4000 years before the decline in horse δ^{15}N began. Bison began a unidirectional shift to lower δ^{15}N values earlier still at ca 25 cal ka BP. These successive declines in δ^{15}N could reflect the idiosyncratic physiological responses of the different species to the same changes in aridity, soils, and vegetation as the North Slope moved into the full glacial conditions and then out again. But it is unclear why these changes were unidirectional toward less positive δ^{15}N values. The non-synchroneity of δ^{15}N in different megafaunal species on the North Slope contrasts with the synchroneity observed in Interior Alaska, where they are attributed to shifts in vegetation driven by regional climate change (Fox-Dobbs et al., 2008). Compared to δ^{15}N, δ^{13}C values from North Slope bones are relatively stable through time. As Fox-Dobbs et al. (2008) found for megafauna in Interior Alaska, North Slope δ^{13}C values do not show the pronounced decline that occurred after ca 15 cal ka BP in Europe (Stevens and Hedges, 2004).

6.5. What caused megafaunal extinctions on the North Slope?

The disappearance of mammoth, horse, and bison from the North Slope between 14 and 11 cal ka BP were local, not global extinctions. With the possible exception of short-faced bear, whose fossil record is exceedingly sparse, all of these species survived to more recent times somewhere else. Mammoth survived to ca 6.6 cal ka BP on St. Paul Island in the Bering Sea (Guthrie, 2004; Veltre et al., 2008) and to ca 4 cal ka BP on Wrangel Island in northern Siberia (Vartanyan et al., 2008). *B. priscus* underwent phylogenetic extinction, and its descendants survive in Eurasia and North America (Shapiro et al., 2004; Wilson et al., 2008). Both saiga antelope and caballine horses survive today in Asia. Not all the North Slope's megafauna departed. Caribou, muskoxen, and grizzly bears survived in place, while moose and humans immigrated to the region about the same time mammoth, bison, and horse disappeared. The local extinction of some megafaunal species and the arrival of new ones – including humans – indicates the end of the Pleistocene was a period of extensive range adjustments in arctic Alaska. What caused these range adjustments?

The simplest interpretation of the shifting ranges of megafauna at the end of the Pleistocene on the North Slope is that they were responses to a unidirectional shift in the same, major axis of environmental variation that had differentiated between megafaunal niches within the ice-age landscape. As Guthrie (2001) suggested, this critical niche axis was moisture, which is intimately connected to air temperature as described by the Clausius–Clapeyron relationship. The moisture niches of present and former North Slope megafauna are delineated by their diets and the ratios between their body masses and foot surface areas.

Diet can be inferred from bone isotopes (Fig. 15), tooth anatomy, and natural history. The arid extreme of the moisture gradient was shared by horse, bison, saiga, and mammoth, with muskoxen and caribou in the middle, and moose, humans, and mastodon (potentially anyway) at the extreme wet end where shrubs and trees grow. While human diet was only indirectly dependent on moisture, it was highly dependent on summer temperatures being warm enough (>10–12 °C in summer) to permit the large shrubs and trees needed for firewood to grow on the North Slope (Guthrie, 2006). In the Arctic, this wood-dependence allies people closely with mastodon and moose at the moist end of the gradient.

Based on foot loading (Guthrie, 1990), bison, horse, and saiga occupied the extreme arid end of the moisture gradient because of their small foot sizes relative to their body masses, which would have greatly impeded their locomotion over the water-saturated, peaty landscapes that became widespread in post-glacial times. Living elephants possess foot-loading values only slightly less than horses. Muskoxen are significantly lighter on their feet than any of the above species, and caribou have the lowest foot-loading of all. Moose have higher foot-loading values than muskoxen but unlike the latter are adept at extracting their feet from deep mud and at transferring their weight onto their dewclaws and forelimbs.

When the regional moisture gradient shifted from dry to wet at the end of the ice age, the dryland-specialists (horse, bison, and mammoth) lost their niches, while the mesic specialists (caribou and muskox) retained theirs. The spread of moist, wood-rich habitats allowed the hydric specialists (moose and humans) to invade the region. At a landscape scale, this radical shift in the moisture–niche axis was manifested as paludification. In this sense, paludification was the proximate cause megafaunal extinctions on the North Slope. This was Guthrie's (1990, 2001) basic hypothesis, and it fits with how post-glacial changes in climate affected the biophysical processes that he asserts were important in maintaining the Mammoth Steppe. We know that paludification began on the North Slope ca 16 cal ka BP (Jones and Yu, 2010) and that the present-day tundra vegetation types were in place, at least in the Arctic Foothills, by 9–10.5 cal ka BP (Mann et al., 2002). This chronology is consistent with the estimated extinction dates of horse, bison, and mammoth on the North Slope (Figs. 8 and 9), with the decrease in δ^{15}N in horses that began ca 16 cal ka BP (Fig. 11), and with the arrival of moose and humans between 13.5 and 14.5 cal ka BP (Figs. 8 and 9).

6.6. *A role for humans?*

People arrived in arctic Alaska only recently compared to the Eurasian Arctic, where they first appeared >34,000 years ago (Pitulko et al., 2004; Slimak et al., 2011). The earliest archaeological date from the North Slope has a 2σ range of 13.7–13.3 cal ka BP (Kunz and Reanier, 1994; Mann et al., 2001) (Fig. 8). We have only a vague idea of what animal species were hunted by these early people. Most archaeological sites pre-dating 10 cal ka BP occur along the northern front of the Brooks Range in places where caribou concentrate today during migration (Rasic, 2011). There are only two known associations between megafaunal remains and early humans in the region. The first is near the U.S.–Canada border where human-modified bones of bison of uncertain species date between 12 and 10.6 cal ka BP (Cinq-Mars et al., 1991). The second is on the Kivalina River at the western end of the Brooks Range where Paleoindian artifacts and associated caribou bones date between 13.1 and 11.1 cal ka BP (Hedman and Rasic, *unpublished data*). At the time of European contact, caribou were a staple food for people in the interior of northern Alaska, and human population sizes closely tracked caribou abundance (Burch, 1972, 1980; Lent, 1988).

The population density of aboriginal people on the North Slope in the mid-19th century provides a limiting estimate of how many people might have lived there during the late Pleistocene. In AD 1840, approximately 3000 Iñupiat people lived north of the Brooks Range and west of the Colville River mouth (Burch, 1980). If we add 500 more people to account for those living along the less productive coastline east of the Colville River, human population density on the North Slope around the time of European contact would have been about 0.02 persons/km^2 (1 person/50 km^2). In AD 1840, people were concentrated in coastal areas where they exploited the rich marine mammal resource. Population densities at the end of the Pleistocene were probably much lower than in 1840 because systematic hunting of marine mammals in arctic Alaska only began ca 5 cal ka BP (Ackerman, 1998). Ethnographic records from arctic Alaska and Canada suggest caribou-dependent, inland groups had significantly lower population densities of <0.01 persons/km^2 (<1 person/100 km^2) (Burch, 1972), which is similar to the densities of wolves and bears on the landscape today (Table 1). Human ecology in northern Alaska during the Pleistocene–Holocene transition was probably much more like the caribou-reliant, inland Iñupiat lifestyle than it was like the coastal one ca 1840, and, judging from the scarcity of archaeological sites dating to the Pleistocene–Holocene transition and early Holocene, it is likely that the North Slope lay near the northern range limit of humans at this time. There are no ethnographic records of ecosystem modification by burning caused by humans in arctic Alaska, and there are no indications that human predation ever had a significant effect on caribou population density there.

In summary, there is no direct evidence that humans played a role in the extinction of megafauna on the North Slope. In fact, humans coexisted with horse and bison for 1000 years before these species became extinct. During this time, people were probably rare visitors north of the Brooks Range. Mammoth is the only megafauna species whose youngest dated remains coincide with the first arrival of humans, and, based on the age-gap analyses (Fig. 8), we anticipate finding younger mammoth bones eventually.

7. Conclusions

Taphonomy: Bones become incorporated into the valley fills of the Ikpikpuk and Titaluk rivers via two different pathways. The first involves rapid burial of bones by aeolian sediment on upland surfaces within about 30 km of the active Ikpikpuk Sand Sea. Migrating river channels later eroded these bones out of the sand sheet and loess deposits. This pathway accounts for a minority of the bones we collected. The second, more frequent pathway involved animals dying on river floodplains and being rapidly buried by fluvial sediment. In both pathways, bones are disarticulated and mixed with those of other species and of other ages during multiple episodes of reworking by these low-gradient, sandy rivers. As the lighter sand is carried downstream, bones are elutriated downwards into the valley fills until they come to rest in channel-fill deposits above bedrock strath terraces. If a bone survives the first 4000 years, it has likely been deeply buried within the valley fill and will survive indefinitely.

Timing of extinction: New dates postpone the demise of the Mammoth Steppe in northern Alaska several thousand years later than previously thought (Guthrie, 2003; Buck and Bard, 2007). Horse and bison persisted until at least 12.5 cal yr BP, which coincides with the early part of the Younger Dryas chronozone. By way of reference, flooding of the Bering Strait was complete by ca 12 cal ka BP (Keigwin et al., 2006). Bison and horse may have been the last survivors of the Mammoth Steppe megafauna on the North Slope, though there may still be a >5% chance of discovering a mammoth dating to as young as 12 cal ka BP. The age of the youngest dated lion is ca 13.2 cal ka BP, indicating an intact megafaunal food chain persisted to at least that time. Humans were hunting along the northern front of the Brooks Range by at least 13.5 cal ka BP, so they potentially interacted with bison and horse, and possibly with mammoth, for ca 1000 years.

Composition of the ice-age megafauna: In terms of numbers of individuals, horse was the dominant megafaunal species on the

North Slope between ca 40 and 12 cal ka BP. Bison and caribou were less abundant than horse while mammoth and muskox were comparatively scarce, and saiga were rare. Lion, short-faced bear, wolf, and grizzly bear comprised the megafaunal predator/scavenger guild. The fact that the majority of horse and lion bones postdate 40 cal ka BP suggest horse became much more abundant after ca 40 cal ka BP and that lion populations tracked horse abundance. Moose arrived ca14 cal ka BP, slightly before people did. Mastodon has probably been absent from the North Slope since the end of the Last Interglacial.

Animal Numbers and Biomasses: The ice age fauna was more diverse than today with five abundant herbivore species living in the region as compared to a single abundant herbivore species (caribou) and two much less abundant species (muskox and moose) living there today. There were many more megafaunal individuals living on the North Slope during the ice age than today. Conservatively, there were 6× more of them, and they comprised 30× more megafaunal biomass than present today. These ice-age estimates probably represent short-lived, peak populations that occurred only during particularly favorable times.

Isotopes suggest changes in moisture were important: Changing values of $\delta^{13}C$ and $\delta^{15}N$ in bones suggest that during the ice age the surviving megafaunal species (muskox and caribou) utilized the warmer, wetter portions of the regional vegetation mosaic most like the moist acidic tundra vegetation that is widespread in the region today, while horse, bison, and mammoth were dryland specialists. Shifts in $\delta^{15}N$ values through time are consistent with the idea that paludification progressively degraded range conditions for horse, perhaps the most grass-dependent taxon, starting ca 16 cal ka BP.

Causes of extinction: The disappearance of bison, horse, mammoth, saiga, and lion from northern Alaska at the end of the ice age represent local, not global extinctions since all these taxa survived later elsewhere. The most important driver of these range shifts was probably a change in moisture availability that manifested itself as regional paludification. Dryland specialists (bison, horse, and mammoth) were forced out as climate shifted toward wetter/warmer conditions, which favored the invasion of moose, humans, and the shrubbery both these species depended upon. Muskox and caribou, which isotope measurements suggest utilized the mesic portion of the moisture gradient during the ice age, were able to persist in the region during post-glacial times. The fact that the terminal dates of horse and bison coincide with the Younger Dryas suggest that rapid climate changes during this period may have been involved in the extinctions of these two species. It is unlikely humans played a role in megafaunal extinctions in this particular part of the world for two reasons. First, they were a rare species on the North Slope at the end of the Pleistocene. Second, they coexisted with horse and bison for at least 1000 years before these species disappeared. On the other hand, humans may have been the last straw for megafaunal species already in states of extinction debt.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2013.03.015.

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