

Pleistocene megafauna from eastern Beringia: Paleoecological and paleoenvironmental interpretations of stable carbon and nitrogen isotope and radiocarbon records

Kena Fox-Dobbs^{a,b,*}, Jennifer A. Leonard^{a,c}, Paul L. Koch^b

^a Genetics Program/Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

^b Department of Earth and Planetary Sciences, University of California Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA

^c Department of Evolutionary Biology, Uppsala University, 75236 Uppsala, Sweden

Received 2 October 2007; received in revised form 18 December 2007; accepted 23 December 2007

Abstract

Late Pleistocene eastern Beringia is a model paleo-ecosystem for the study of potential and realized species interactions within a diverse mammalian fauna. Beringian paleontological records store a wealth of information that can be used to investigate how predator–prey and competitive interactions among consumers shifted in response to past episodes of environmental change. Two such recent periods of rapid climate change are the Last Glacial Maximum (LGM) and the end of glacial conditions at the beginning of the Holocene. Here we assemble carbon and nitrogen stable isotope, and AMS ¹⁴C data collected from bone collagen of late Pleistocene carnivores and megafaunal prey species from the interior of eastern Beringia (Alaska), and reconstruct the diets of ancient Alaskan carnivores and herbivores. We are able to account for the relative influences of diet versus changing environmental conditions on variances in consumer isotope values, to identify species hiatuses in the fossil record, and to draw conclusions about paleoenvironmental conditions from faunal chronologies.

Our isotopic results suggest that there was dietary niche overlap among some Beringian herbivore species, and partitioning among other species. We rely upon $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of modern Alaskan C₃ plant types to infer Beringian herbivore dietary niches. Horse, bison, yak, and mammoth primarily consumed grasses, sedges, and herbaceous plant species. Caribou and woodland muskox focused upon tundra plants, including lichen, fungi, and mosses. The network of Beringian carnivore interaction was complex and dynamic; some species (wolves) persisted for long periods of time, while others were only present during specific timeframes (large felids and ursids). Beringian carnivore diets included all measured herbivore species, although mammoth and muskox only appeared in carnivore diets during specific times in the late Pleistocene. We identified the potential presence of unmeasured diet sources that may have included forest-dwelling cervids and/or plant materials. None of the large-bodied carnivore species we analyzed (except short-faced bear) were specialized predators of a single prey species during the late Pleistocene. Differences in carnivore diet and dietary breadth between time periods either reflect changes in the relative abundances of prey on the Beringian landscape, or changes in competitive interactions among Beringian carnivore species.

© 2008 Elsevier B.V. All rights reserved.

Keywords: Paleoecology; Carnivore guild; Paleodietary reconstruction; *Panthera atrox*; *Canis lupus*; *Homotherium*; *Equus lambei*

1. Introduction

Twenty thousand years ago Beringia was a vast open ecosystem that extended from the Yukon in North America, across

the Bering Strait and through Siberia in Eurasia (Fig. 1). For much of the late Pleistocene Beringia hosted a productive mosaic of steppe, tundra, and shrub vegetation, and a diverse fauna of large-bodied mammals (Guthrie, 2001; Zazula et al., 2003). This ancient Beringian ecosystem was not analogous to any high-latitude ecosystems present on Earth today. Dynamic changes within the Beringian ecosystem over the past 50,000 yrs were largely driven by glacial–interglacial scale climate fluctuations, and biogeographic communication between continents via the

* Corresponding author. Department of Earth and Planetary Sciences, University of California Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA. Tel.: +1 831 459 5088; fax: +1 831 459 3074.

E-mail address: kena@pmc.ucsc.edu (K. Fox-Dobbs).



Fig. 1. Map showing western (Siberia) and eastern (Alaska and Yukon) Beringia. All specimens (except mammoth) in this study are from the Fairbanks area, Alaska. Dotted line designates the approximate extent of exposed land (Bering land bridge), and dashed line delineates the approximate edge of the Laurentide ice sheet, both at 18,000 ^{14}C yr BP (redrawn from the Paleoenvironmental Atlas of Beringia; available online at www.ncdc.noaa.gov/paleo/parcs/atlas/beringia/index.html). Note both the proximity of the Fairbanks area to the continental ice sheet, and isolation from coastal regions to the South and West during the Last Glacial Maximum.

Bering land bridge during the Last Glacial Maximum (LGM). The rapid reorganization of Beringian ecosystems at the end of the Pleistocene, which resulted in the establishment of modern tundra and boreal forest habitats, was associated with the extinction of most megafaunal species.

Our understanding of Beringian paleoenvironmental conditions and ecosystem dynamics during the late Pleistocene has blossomed in the past several years. We've gained new insight into the vegetation of eastern Beringia via studies of floral composition, isotopic and direct radiocarbon analyses of plant macrofossils (Wooller et al., 2007; Zazula et al., 2007), and analysis of spatio-temporal patterns in late Quaternary pollen data (Brubaker et al., 2005). Likewise, genetic and radiocarbon data extracted from fossils preserved in the permafrost shed light on the spatio-temporal dynamics of ancient mammal populations during the Pleistocene (e.g. Leonard et al., 2000; Shapiro et al., 2004; MacPhee et al., 2005; Guthrie, 2006; Barnes et al., 2007; Leonard et al., 2007). Yet, we still lack a detailed understanding of Beringian paleoecological connectivity, including food web organization.

Here we use stable-isotope ratios and AMS ^{14}C dates measured on ancient bone collagen to study the paleoecology of Pleistocene megafaunal carnivores and herbivores from eastern Beringia, as well as the paleoenvironment and paleocommunity in which they lived. We restrict the spatial scope of our study to only include predators and prey from the Fairbanks area, Alaska (Fig. 1). This allows us to eliminate potential isotopic variability among individuals due to spatial differences, and instead focus on interactions among animals that could have co-occurred on the Beringian landscape. Currently, there are few isotopic studies of North American late Pleistocene predator–prey systems,

and our knowledge is primarily defined by data collected from the La Brea tar pits in southern California (Coltrain et al., 2004a; Fox-Dobbs et al., 2007), and several sites in Europe (Fizet et al., 1995; Bocherens et al., 1999; Bocherens and Drucker, 2003) and Siberia (Bocherens et al., 1996).

We explore Beringian megafaunal isotope data in two contexts. First, we investigate patterns in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and ^{14}C records of megafaunal (>45 kg) carnivores [gray wolf (*Canis lupus*), American lion (*Panthera atrox*), scimitar-tooth sabercat (*Homotherium serum*)] and herbivores [caribou (*Rangifer tarandus*) and horse (*Equus lambei*)] from the Fairbanks area. The temporal trends within these $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ records illuminate changing paleoclimatic and paleoenvironmental conditions before, during, and after the LGM in eastern Beringia. Over this >40,000-year time interval Beringian climate transitioned from the relatively mild conditions of Marine Isotope Stage 3 [MIS3; >50,000 to 25,000 radiocarbon years before present (^{14}C yr BP)] to cold and dry during the peak of the LGM (ca. 18,000 ^{14}C yr BP), followed by rapid warming into the Holocene (for a review of Beringian paleoclimate see; Anderson and Lozhkin, 2001; Elias, 2001; Bigelow et al., 2003; Brigham-Grette et al., 2004). Extensive stable isotope and ^{14}C datasets collected from fossil bone collagen of Pleistocene herbivores in Europe and western Beringia (Siberia) have established that glacial-scale paleoenvironmental changes are reliably recorded in the biogeochemistry of fossil bone (e.g. Iacumin et al., 2000; Drucker et al., 2003a,b; Richards and Hedges, 2003; Stevens and Hedges, 2004). However no isotopic studies have used stable-isotope values of consumers at different trophic levels (carnivores and herbivores) to investigate paleoenvironmental changes during the LGM.

Second, we combine the wolf, felid, horse, and caribou data with additional $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data collected from bison (*Bison bison*), yak (*Bos grunniens*), and woodland muskox (*Symbos cavifrons*). We use these data, along with previously published $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and ^{14}C data for mammoth (*Mammuthus primigenius*), brown bear (*Ursus arctos*), and giant short-faced bear (*Arctodus simus*) to investigate species interactions among Beringian megafauna. Specifically, we examine patterns of niche partitioning and temporal overlap within the large-bodied carnivore guild. Was prey selection dependent upon size, abundance, and vulnerability of prey species, or upon interspecies interactions (e.g. resource competition, predation, territorial exclusion) among carnivores? We also use the herbivore $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ records to investigate habitat selection and foraging by Beringian herbivore species. Graham and Lundelius (1984) and Guthrie (1984, 2001) contend that strong niche partitioning among herbivores feeding in productive mosaic of vegetation allowed Pleistocene megafauna to simultaneously maximize available vegetation within a local area. There are no modern high-latitude faunas analogous to the ancient Beringian mammal community, thus our results provide new insight into a unique and extinct food web.

Carbon and nitrogen in collagen are derived from diet, thus the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of consumer collagen reflect the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of their diet (see review by Koch, 2007). Variation in plant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among different

habitats and plant types (e.g. Ehleringer, 1991; Nadelhoffer et al., 1996; Handley et al., 1999; Ben-David et al., 2001; Wooller et al., 2007) allow us to distinguish among Beringian herbivores with different foraging preferences and to estimate the relative contributions of prey species to the diets of Beringian carnivores. Isotopic analyses of ancient bone collagen are routinely used in archeological and paleoecological studies to reconstruct the diets of top consumers (humans and carnivores, respectively) (e.g. Bocherens et al., 2005; Fox-Dobbs et al., 2006). While fossil predator sample sizes are rarely large enough to investigate local population dynamics or long-term temporal patterns, Alaskan permafrost deposits are an exception; they are one of few Pleistocene depositional environments where both carnivore and herbivore fossil remains are abundant (Guthrie, 1968).

2. Methods

2.1. Sample collection

Fossil specimens were collected over the past century from placer mining gravel deposits within and around Fairbanks, Alaska. While the morphological and biogeochemical preservation of permafrost fossils are generally excellent, they have no stratigraphic context when found in gravel deposits. The specimens used in this study were curated at the American Museum of Natural History, New York and the Canadian Museum of Nature, Ottawa. We sampled wolf ($n=82$), lion ($n=8$), scimitar cat ($n=11$), horse ($n=32$), caribou ($n=10$), bison ($n=6$), yak ($n=5$), and woodland muskox ($n=10$) specimens. We sampled both cranial and postcranial bones that were morphologically diagnostic to the species-level.

2.2. Sample preparation and analysis

Cortical bone samples [~ 150 milligrams (mg)] were drilled from specimens with a handheld microdrill, and then crushed into a coarse powder in a mortar and pestle. Collagen extraction methods follow Brown et al. (1988). Samples were decalcified in 0.5 N HCl at 4 °C for 1–2 days, and then rinsed in 0.01M NaOH for 4–6 h to remove organic acid contamination. Samples were gelatinized in 0.01 N HCl at 58 °C for 12 h, and the gelatin solution was then passed across a 1.5 μm glass fiber filter. The filtrate was ultrafiltered (pre-cleaned Centriprep ultrafilters; Higham et al., 2006), with retention and lyophilization of the >30 kDa fraction. Collagen preservation was assessed with atomic C:N ratios, and all samples were between 2.2 and 2.8, which is well within the range for viable collagen (Ambrose, 1990).

For stable isotope analyses the collagen samples (1.0 mg) were weighed into tin capsules. Carbon and nitrogen stable-isotope ratios were measured using an elemental analyzer coupled with mass spectrometers at the University of California Davis Stable Isotope Facility, and the University of California Santa Cruz Stable Isotope Laboratory. Stable-isotope compositions are reported using the δ notation, and are referenced to Vienna PeeDee Belemnite and air for carbon and nitrogen,

respectively. The standard deviation for replicates of a gelatin standard was $<0.3\text{‰}$ for carbon and nitrogen for samples run at the Davis lab, and $<0.2\text{‰}$ for carbon and nitrogen for samples run at the Santa Cruz lab.

Ancient collagen samples analyzed for radiocarbon at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, were prepared with the method outlined above. Since there is no agreed upon calibration curve for dates $>26,000$ ^{14}C yr BP (Reimer et al., 2006), we present all specimen ages as uncalibrated ^{14}C dates.

2.3. Eastern Beringian carnivore dietary reconstructions

We reconstructed the diets of Beringian wolves, felids, and bears by comparing them to potential Fairbanks area megafaunal prey species. We used published isotope values for Fairbanks area Pleistocene brown bears ($n=16$) and short-faced bears ($n=4$) that were also ^{14}C dated (Matheus, 1995, 1997; Barnes et al., 2002). We excluded one Fairbanks area brown bear because the collagen analyzed was from tooth dentine, not bone, and this individual had anomalously high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Specimen F:AM 96612). In order to account for temporal differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values we group the dated carnivores and herbivores into three climatically relevant time periods. The groups are post-glacial (18,000 to 10,000 ^{14}C yr BP), full-glacial (23,000 to 18,000 ^{14}C yr BP), and pre-glacial ($>50,000$ to 23,000 ^{14}C yr BP). The post-glacial time period is characterized by the very rapid transition towards warmer, mesic conditions of the Holocene. The full-glacial is the 5000-year period when LGM conditions were the coldest and driest (Elias, 2001; Guthrie, 2001). The pre-glacial period encompasses mild conditions of MIS3 until $\sim 30,000$ ^{14}C yr BP, and the subsequent onset of LGM cooling.

For each time period we compared carnivore $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to those of ^{14}C dated horse and caribou individuals from the same time period, and to a range of bison, yak and woodland muskoxen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from undated specimens, which are represented by their means and standard deviations. Due to the small sample of full-glacial caribou ($n=1$), we calculated the full-glacial caribou mean and standard deviation (for carnivore dietary reconstructions) by combining the values of the full-glacial individual with those of the next older and next younger individuals (total $n=3$). We shifted carnivore $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values by -1.3‰ and -4.6‰ , respectively, to account for isotopic fractionations between consumers at different trophic levels (Fox-Dobbs et al., 2007). We also included means and standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for undated eastern Beringian (Alaska) mammoths ($n=5$) in the dietary reconstructions (Bocherens et al., 1994).

2.4. Characterization of carnivore diets using *IsoSource* model results

In order to quantify the prey preferences of carnivore species from each time period we employed *IsoSource* 1.3.1, a multi-source stable-isotope mixing model, to estimate the relative contribution of megafaunal herbivore species (diet sources) to

carnivore diet (Phillips and Gregg, 2003). We ran the model for every individual wolf, lion, scimitar cat, brown bear, and short-faced bear, and included the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of caribou and horse from the appropriate time periods as well as undated bison, mammoth, woodland muskoxen, and yak as potential diet sources. Because we used two isotope systems ($n=2$), and greater than $n+1$ diet sources, there was no unique combination, or mixture, of diet sources to explain a given carnivore diet. Instead *IsoSource* output files reported all feasible diet source combinations in increments of 1%, as well as the mean, minimum, and maximum possible contributions of each diet source to an individual carnivore's diet. Dietary interpretations for some carnivores were complicated by the fact that both horse and bison had mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that were intermediate among the other four herbivore species. Specifically, it was impossible to distinguish between a carnivore diet comprised of only horse or bison, or a mixture of other herbivores.

We categorized an individual carnivore as a muskox, caribou, mammoth or yak 'specialist' if the *IsoSource* model results met both of the following criteria; the mean contribution (for all feasible solutions) of any one prey to the carnivore's diet was greater than or equal to 50%, and the minimum feasible contribution of that same prey to diet was greater than or equal to 33%. Carnivores were also assigned to one of the muskox, caribou, mammoth, and yak specialist categories if their values were within one standard deviation of the mean values of a single prey. We made an exception for two short-faced bears whose $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ values were higher than any measured diet sources, but were within two standard deviations of the mean caribou values (thus classified as caribou specialists). Carnivore individuals whose diet consisted of a range of prey (no diet source had a mean contribution greater than 50%) were classified as 'generalists' or 'horse/bison specialists', since we could not distinguish between these two categories.

We created a sixth carnivore dietary category, which included individuals that did not meet the criteria for any of the categories described above, or whose diet we interpreted based upon *a priori* knowledge. This category included pre-glacial wolves, and pre- and post-glacial brown bears, whose $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were lower than the measured herbivore values, suggesting the presence of an unmeasured diet source with relatively low $\delta^{15}\text{N}$ values. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of modern Alaskan closed-habitat (forest) cervids are low (Szepanski et al., 1999; Ben-David et al., 2001), and we suggest that moose, deer, and/or elk may have been in the diets of pre- and post-glacial carnivores. Closed-habitat cervids track the expansion of boreal forests in post-glacial Beringia (Guthrie, 2006), and may have inhabited forested areas of Beringia during MIS3. Small mammals such as rodents and lagomorphs are another unmeasured diet source, but we do not know of any empirical evidence that shows modern small mammals have systematically lower $\delta^{15}\text{N}$ values than co-occurring large herbivores. Alternatively, brown bears with relatively low $\delta^{15}\text{N}$ values may have had more omnivorous diets that included insects, leaves, berries and seeds (Hilderbrand et al., 1996; Hobson et al., 2000). In the dietary reconstructions we assume

all carnivore individuals were hypercarnivorous (pure-meat diet), and use corresponding isotopic trophic fractionations (Fox-Dobbs et al., 2007). Interspecies differences in digestive physiology and inter-individual dietary preferences (e.g. omnivory) may cause variation in carnivore trophic fractionations, but these factors are poorly characterized since bone collagen is rarely analyzed in carnivore feeding studies. Thus, variation in trophic fractionations may be a source of error in the dietary reconstructions. This sixth category also includes full- and post-glacial brown bears and lions that were classified as muskox specialists based upon the *IsoSource* model results. We obtained infinite ^{14}C dates for the two dated woodland muskox individuals, suggesting that woodland muskoxen may not have been abundant in the interior of Beringia during the full- and post-glacial. Therefore, it seems unlikely that these full- and

Table 1
Summary of megafaunal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰)

Taxon	Time period	<i>n</i>	$\delta^{13}\text{C}$ mean	$\delta^{13}\text{C}$ SD	$\delta^{15}\text{N}$ mean	$\delta^{15}\text{N}$ SD
Gray wolf (<i>Canis lupus</i>)	All	82	-19.3	0.6	7.8	1.1
	Post-glacial	9	-19.2	0.6	8.0	0.4
	Full-glacial	7	-19.2	0.5	9.8	1.4
	Pre-glacial ^a	23	-19.3	0.5	7.2	1.3
	Undated	43	-19.4	0.6	7.8	0.6
Scimitar cat (<i>Homotherium serum</i>)	All (Pre-glacial)	11	-19.3	0.6	8.0	1.4
American lion (<i>Panthera atrox</i>)	All	8	-19.0	0.4	7.8	0.7
	Post-glacial	5	-18.8	0.2	7.5	0.8
	Full-glacial	3	-19.3	0.6	8.2	0.2
Brown bear (<i>Ursus arctos</i>) ^b	All	16	-19.0	0.5	6.8	1.6
	Post-glacial	8	-18.7	0.4	7.0	1.3
	Full-glacial	2	-19.1	0.2	8.2	3.0
	Pre-glacial ^a	6	-19.5	0.4	6.1	1.5
Short-faced bear (<i>Arctodus simus</i>) ^b	All	4	-18.0	0.2	8.4	0.8
	Full-glacial	1	-17.8	-	8.0	-
	Pre-glacial	3	-18.1	0.2	8.6	0.9
Horse (<i>Equus lambei</i>)	All	32	-21.2	0.3	3.4	1.1
	Post-glacial	8	-21.0	0.2	3.5	1.1
	Full-glacial	14	-21.2	0.3	4.0	0.7
	Pre-glacial ^a	10	-21.2	0.4	2.7	1.2
Caribou (<i>Rangifer tarandus</i>)	All	10	-19.5	0.4	3.3	1.2
	Post-glacial	4	-19.4	0.5	3.5	1.4
	Full-glacial	1	-20.1	-	3.6	-
	Pre-glacial ^a	5	-19.4	0.2	3.1	1.2
Bison (<i>Bison bison</i>)	Undated	6	-20.5	0.6	4.3	0.9
Yak (<i>Bos grunniens</i>)	Undated	5	-21.6	1.5	3.2	2.7
Woodland muskox (<i>Symbos cavifrons</i>)	Undated	10	-20.0	0.9	1.2	1.7
Mammoth (<i>Mammuthus primigenius</i>) ^c	Undated	5	-21.1	0.2	7.4	1.0

Post-glacial: 18,000–10,000 ^{14}C yr BP, Full-glacial: 23,000–18,000 ^{14}C yr BP, Pre-glacial: >50,000–23,000 ^{14}C yr BP.

^a Pre-glacial time period includes individuals with infinite ^{14}C dates.

^b Fairbanks area short-faced and brown bear data reported in Matheus (1995) and Barnes et al. (2002).

^c Mammoth data reported in Bocherens et al. (1994).

Table 2
Eastern Beringian carnivore specimen ID's, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰), and ^{14}C dates

Genus	Dated Beringian carnivores						Time group	Undated Beringian wolves (<i>Canis lupus</i>)			
	Specimen ID	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	at. C:N	^{14}C yr BP	^{14}C Lab ID		Specimen ID	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	at. C:N
<i>Canis</i>	AMNH F:AM 30450	-19.4	5.6	2.2	7751±64	AA48695	Holocene	AMNH 42416	-19.8	6.6	2.3
<i>Canis</i>	AMNH F:AM 67165	-19.2	8.6	2.2	12,600±150	AA42317	Post-glacial	AMNH 42417	-18.9	6.8	2.3
<i>Canis</i>	AMNH F:AM 67157	-18.7	7.9	2.3	14,690±190	AA42315	Post-glacial	AMNH 42418	-19.0	7.8	2.3
<i>Canis</i>	AMNH F:AM 70944	-19.2	7.3	2.7	15,268±169	AA38449	Post-glacial	AMNH F:AM 142415	-19.1	6.5	2.3
<i>Canis</i>	AMNH F:AM 30447	-19.7	7.9	2.2	15,580±190	AA35223	Post-glacial	AMNH F:AM 30445	-19.0	8.1	2.3
<i>Canis</i>	AMNH F:AM 30451	-18.6	8.8	2.4	15,800±90	UCR3761	Post-glacial	AMNH F:AM 30454	-18.3	6.8	2.3
<i>Canis</i>	AMNH F:AM 67227	-18.9	7.9	2.3	15,870±190	AA35231	Post-glacial	AMNH F:AM 30458	-19.6	8.0	2.3
<i>Canis</i>	AMNH F:AM 68009-A	-18.9	8.0	2.8	16,800±210	AA35227	Post-glacial	AMNH F:AM 30477	-19.3	8.2	2.3
<i>Canis</i>	AMNH F:AM 67224	-19.0	7.8	2.2	17,640±240	AA35226	Post-glacial	AMNH F:AM 30478	-19.5	7.1	2.3
<i>Canis</i>	AMNH F:AM 30432	-20.5	8.1	2.4	17,670±230	AA48704	Post-glacial	AMNH F:AM 30480	-19.0	7.8	2.3
<i>Canis</i>	AMNH F:AM 30453	-18.3	9.3	2.4	19,210±260	AA48702	Full-glacial	AMNH F:AM 67158	-18.7	7.9	2.3
<i>Canis</i>	AMNH F:AM 70942	-19.8	9.3	2.3	20,150±110	CAMS115775	Full-glacial	AMNH F:AM 67164	-19.5	7.9	2.3
<i>Canis</i>	AMNH F:AM 67169	-19.3	10.3	2.3	20,305±385	AA35216A	Full-glacial	AMNH F:AM 67166	-20.2	6.8	2.3
<i>Canis</i>	AMNH F:AM 30452	-19.1	9.1	2.3	20,550±120	CAMS115769	Full-glacial	AMNH F:AM 67168	-19.5	8.4	2.3
<i>Canis</i>	CMN 9929	-19.3	12.7	2.2	20,910±70	UCR3764	Full-glacial	AMNH F:AM 67169	-19.2	8.1	2.3
<i>Canis</i>	AMNH F:AM 67231	-19.3	9.3	2.3	21,900±140	CAMS115774	Full-glacial	AMNH F:AM 67182	-19.3	7.5	2.4
<i>Canis</i>	AMNH F:AM 68008-G	-19.2	8.5	2.2	23,380±470	AA35222	Full-glacial	AMNH F:AM 67185	-19.6	8.4	2.3
<i>Canis</i>	AMNH F:AM 67170	-18.3	7.3	2.3	27,620±580	AA48694	Pre-glacial	AMNH F:AM 67201	-19.5	8.3	2.3
<i>Canis</i>	AMNH F:AM 30431	-19.1	8.6	2.3	28,500±300	CAMS115776	Pre-glacial	AMNH F:AM 67204	-19.3	7.4	2.2
<i>Canis</i>	AMNH F:AM 67248	-19.7	6.2	2.4	29,800±400	CAMS115773	Pre-glacial	AMNH F:AM 67205	-20.1	7.0	2.4
<i>Canis</i>	AMNH F:AM 67168	-19.0	9.2	2.4	31,200±450	CAMS115767	Pre-glacial	AMNH F:AM 67207	-19.1	7.8	2.3
<i>Canis</i>	AMNH F:AM 67163	-18.8	6.6	2.4	31,800	AA48693	Pre-glacial	AMNH F:AM 67209	-19.8	7.8	2.4
<i>Canis</i>	AMNH F:AM 67228	-19.4	7.0	2.3	32,100	AA42302	Pre-glacial	AMNH F:AM 67210	-20.5	8.4	2.2
<i>Canis</i>	CMN 42388	-18.5	8.5	2.6	33,900±1700	AA35221	Pre-glacial	AMNH F:AM 67211	-19.4	8.1	2.4
<i>Canis</i>	AMNH F:AM 67184	-20.2	6.2	2.4	34,600±700	CAMS115763	Pre-glacial	AMNH F:AM 67212	-19.5	6.4	2.3
<i>Canis</i>	AMNH F:AM 67159	-19.4	8.1	2.4	35,200±2300	AA48703	Pre-glacial	AMNH F:AM 67217	-19.1	7.9	2.3
<i>Canis</i>	AMNH F:AM 70958	-19.1	7.5	2.2	37,700±2600	AA37615	Pre-glacial	AMNH F:AM 67222	-20.3	7.3	2.4
<i>Canis</i>	AMNH F:AM 70945	-18.8	6.7	2.3	37,733±2633	AA38448	Pre-glacial	AMNH F:AM 67230	-20.4	6.5	2.3
<i>Canis</i>	AMNH F:AM 30440	-18.9	6.4	2.3	38,000	AA42314	Pre-glacial	AMNH F:AM 67239	-18.6	8.2	2.3
<i>Canis</i>	AMNH F:AM 67202	-19.2	6.8	2.4	38,000±2700	AA35224	Pre-glacial	AMNH F:AM 67253	-19.5	7.8	2.3
<i>Canis</i>	AMNH F:AM 67235	-19.8	5.8	2.3	38,000	AA42310	Pre-glacial	AMNH F:AM 67256	-18.6	8.0	2.4
<i>Canis</i>	AMNH F:AM 70946	-20.0	5.4	2.5	38,000	AA42313	Pre-glacial	AMNH F:AM 68006-E	-19.5	8.3	2.3
<i>Canis</i>	AMNH F:AM 67243	-20.1	6.2	2.3	38,500±1100	CAMS115772	Pre-glacial	AMNH F:AM 68006-F	-19.1	8.6	2.3
<i>Canis</i>	CMN 17311	-19.1	6.1	2.7	38,790±540	UCR3762	Pre-glacial	AMNH F:AM 68006-I	-18.9	8.6	2.2
<i>Canis</i>	AMNH F:AM 67197	-20.3	5.7	2.4	39,300±1230	CAMS115760	Pre-glacial	AMNH F:AM 68006-J	-19.5	7.4	2.3
<i>Canis</i>	AMNH F:AM 67208	-19.2	9.7	2.3	41,040±1530	CAMS115759	Pre-glacial	AMNH F:AM 68010	-17.9	8.3	2.2
<i>Canis</i>	AMNH F:AM 142410	-19.4	6.2	2.3	45,400	CAMS115762	Pre-glacial	AMNH F:AM 70935	-19.7	8.3	2.4
<i>Canis</i>	AMNH F:AM 30438	-19.4	6.4	2.3	45,500±2700	CAMS115778	Pre-glacial	AMNH F:AM 70938	-19.5	8.2	2.3
<i>Canis</i>	AMNH F:AM 67167	-19.0	9.2	2.3	45,800±2800	CAMS115768	Pre-glacial	AMNH F:AM 70943	-18.7	8.4	2.4
<i>Canis</i>	AMNH F:AM 142409	-19.4	8.6	2.3	48,130	CAMS115777	Pre-glacial	AMNH F:AM 70950	-19.1	8.4	2.3
<i>Panthera</i>	AMNH F:AM 69080	-18.8	6.7	2.4	12,990±70	CAMS131350	Post-glacial	AMNH F:AM 70951	-19.3	7.8	2.3
<i>Panthera</i>	AMNH F:AM 69053	-18.8	6.7	2.3	13,040±70	CAMS131348	Post-glacial	AMNH F:AM 70955	-20.8	8.3	2.3
<i>Panthera</i>	AMNH F:AM 69173	-19.0	7.5	2.3	14,050±80	CAMS131347	Post-glacial	AMNH F:AM 97079	-19.4	7.5	2.4
<i>Panthera</i>	AMNH F:AM 69126	-18.5	8.3	2.4	16,650±110	CAMS131346	Post-glacial				
<i>Panthera</i>	AMNH 69172	-19.0	8.3	2.5	17,140±110	CAMS131362	Post-glacial				
<i>Panthera</i>	AMNH F:AM 69078	-19.6	8.4	2.6	18,270±130	CAMS131349	Full-glacial				
<i>Panthera</i>	AMNH 69142	-19.6	8.2	2.6	18,590±130	CAMS131361	Full-glacial				
<i>Panthera</i>	AMNH 69140	-18.6	8.1	2.4	20,970±180	CAMS131360	Full-glacial				
<i>Homotherium</i>	AMNH F:AM 142490	-20.7	6.6	2.4	36,200±1300	CAMS131351	Pre-glacial				
<i>Homotherium</i>	AMNH F:AM 142494	-18.9	9.2	2.4	36,320±1270	CAMS131356	Pre-glacial				
<i>Homotherium</i>	AMNH F:AM 116840	-20.1	9.7	2.6	40,500	CAMS131363	Pre-glacial				
<i>Homotherium</i>	AMNH F:AM 128069	-18.3	5.5	2.4	41,000	CAMS131352	Pre-glacial				
<i>Homotherium</i>	AMNH F:AM 95567	-19.1	8.0	2.6	41,000±2300	CAMS131357	Pre-glacial				
<i>Homotherium</i>	AMNH F:AM 30770i	-19.2	9.2	2.5	41,900±2600	CAMS131353	Pre-glacial				
<i>Homotherium</i>	AMNH F:AM 142497	-19.0	8.2	2.4	42,500	CAMS131364	Pre-glacial				
<i>Homotherium</i>	AMNH F:AM 142496	-19.0	7.5	2.4	43,300	CAMS131359	Pre-glacial				
<i>Homotherium</i>	AMNH F:AM 142495	-19.7	9.0	2.4	43,400±3100	CAMS131358	Pre-glacial				
<i>Homotherium</i>	AMNH F:AM 142493	-19.4	5.9	2.5	44,200	CAMS131355	Pre-glacial				
<i>Homotherium</i>	AMNH F:AM 142492	-19.3	8.8	2.5	47,710±5270	CAMS131354	Pre-glacial				
<i>Ursus</i>	AMNH F:AM 95641	-18.4	4.8	na	11,940±100	OxA9798	Post-glacial				
<i>Ursus</i>	AMNH F:AM 95628	-18.5	7.5	na	12,310±65	OxA9828	Post-glacial				
<i>Ursus</i>	AMNH F:AM 95598	-18.2	7.1	na	12,320±90	OxA9799	Post-glacial				

Table 2 (continued)

Genus	Dated Beringian carnivores						Time group	Undated Beringian wolves (<i>Canis lupus</i>)			
	Specimen ID	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	at. C:N	^{14}C yr BP	^{14}C Lab ID		Specimen ID	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	at. C:N
<i>Ursus</i>	AMNH F:AM 95659	-18.5	8.0	na	13,415±70	OxA9709	Post-glacial				
<i>Ursus</i>	AMNH F:AM 95642	-18.5	8.3	na	14,150±90	OxA9262	Post-glacial				
<i>Ursus</i>	AMNH F:AM 95599	-19.1	6.5	na	14,310±100	OxA9801	Post-glacial				
<i>Ursus</i>	AMNH F:AM 95632	-18.6	8.4	na	14,810±80	OxA9830	Post-glacial				
<i>Ursus</i>	AMNH F:AM 95670	-19.4	5.4	na	15,830±100	OxA9263	Post-glacial				
<i>Ursus</i>	AMNH 30422	-19.2	10.3	na	19,027±132	AA17507	Full-glacial				
<i>Ursus</i>	AMNH F:AM 95671	-18.9	6.1	na	20,820±120	OxA9796	Full-glacial				
<i>Ursus</i>	AMNH F:AM 95601	-20.0	3.3	na	36,137±783	AA17509	Pre-glacial				
<i>Ursus</i>	AMNH F:AM 95666	-19.5	6.3	na	47,100±3100	OxA9260	Pre-glacial				
<i>Ursus</i>	AMNH F:AM 95609	-19.2	7.7	na	50,800±1900	OxA9767	Pre-glacial				
<i>Ursus</i>	AMNH F:AM 95640	-19.6	6.4	na	53,900	OxA9861	Pre-glacial				
<i>Ursus</i>	AMNH F:AM 95639	-19.0	6.8	na	56,900	OxA9797	Pre-glacial				
<i>Ursus</i>	AMNH F:AM 95681	-19.4	6.0	na	59,000	OxA9829	Pre-glacial				
<i>Arctodus</i>	AMNH F:AM 30492	-17.8	8.0	na	20,524±180	AA17511	Full-glacial				
<i>Arctodus</i>	AMNH F:AM 30494	-17.8	7.7	na	25,496±224	AA17512	Pre-glacial				
<i>Arctodus</i>	AMNH A-37-10	-18.3	9.5	na	27,511±279	AA17513	Pre-glacial				
<i>Arctodus</i>	AMNH 99209	-18.1	8.5	na	39,565±1126	AA17514	Pre-glacial				

na — Not available.

at. C:N — Atomic C:N.

Museum Abbreviations: AMNH — American Museum of Natural History; CMN — Canadian Museum of Nature.

^{14}C Lab Abbreviations: CAMS — Center for Accelerator Mass Spectrometry, Lawrence Livermore National Lab; AA — NSF Arizona Accelerator Mass Spectrometry Lab UCR — Radiocarbon Lab, University of California, Riverside; OxA — Oxford Radiocarbon Accelerator Unit.

Post-glacial: 18,000–10,000 ^{14}C yr BP, Full-glacial: 23,000–18,000 ^{14}C yr BP, Pre-glacial: >50,000–23,000 ^{14}C yr BP, Infinite: minimum age given.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and ^{14}C dates for a subset of wolves ($n=40$) are reported in Leonard et al. (2007).

Fairbanks area *Ursus* and *Arctodus* data reported in Matheus (1995) and Barnes et al. (2002).

post-glacial carnivores were muskox specialists, and instead may have consumed forest cervids, or had a more omnivorous diet (for brown bears only).

We do not use *IsoSource* to reconstruct the diets of Beringian herbivores because few stable-isotope data have been collected from Beringian plant macrofossils. Wide ranges in modern plant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values would complicate dietary interpretations drawn from *IsoSource* results based on modern plant isotopic data. Future isotopic analyses of Beringian plant macrofossils may allow us to explore the diets of ancient herbivores further.

3. Results

The means and standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for all carnivore and herbivore species are included in Table 1, and a full list of specimens, stable-isotope data, and ^{14}C dates are presented in Tables 2 and 3. We divided the wolf, felid, bear, horse and caribou $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values into post-, full-, and pre-glacial time periods. There are no differences in the means (MANOVA – F -test; $p>0.05$) and variances (Levene's test; $p>0.05$) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of wolf, horse and caribou with finite versus infinite ^{14}C dates >23,000 ^{14}C yr BP, thus we treat all individuals with dates >23,000 ^{14}C yr BP as one group (hereafter called pre-glacial). Because most lions and scimitar cats fell into single time groups (post-glacial and pre-glacial, respectively), we did not look for temporal trends within the felid $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data. Due to a small sample size we did not include the short-faced bears in the statistical analyses.

3.1. Temporal trends in Eastern Beringian megafaunal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ records

We found significant differences in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of wolves from the three time periods (MANOVA – Pillai's Trace Test; approximate $F_{4,72}=5.3$, $p=0.0009$). Post-hoc pairwise comparisons among groups revealed that full-glacial wolves were highly significantly different than the pre-glacial aged wolves (F -test; $F_{2,35}=14.2$, $p\leq 0.0001$), and significantly different than post-glacial wolves (F -test; $F_{2,35}=4.9$, $p=0.013$). Pre-glacial and post-glacial wolves were not different (F -test; $p>0.5$). We note that the differences among wolf groups were primarily driven by differences in $\delta^{15}\text{N}$ values (one-way ANOVA; $F_{2,36}=14.1$, $p<0.0001$), whereas the mean $\delta^{13}\text{C}$ values of all groups were within 0.1‰ of each other (one-way ANOVA; $p>0.05$). Leonard et al. (2007) previously showed that there were no significant temporal differences in the variances of wolf $\delta^{13}\text{C}$ values, but there were differences in $\delta^{15}\text{N}$ values. In summary, we found that post-glacial wolves had significantly less variable $\delta^{15}\text{N}$ values than wolves from the earlier time periods, and the pre-glacial wolves had the highest level of variance. The undated wolf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were significantly different than pre-glacial (MANOVA – F -test; $F_{2,63}=4.2$, $p=0.02$) and full-glacial (MANOVA – F -test; $F_{2,47}=20.8$, $p<0.0001$) wolves, but not post-glacial wolves.

There were significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of horses from pre-glacial, full-glacial and post-glacial time periods (MANOVA – Pillai's Trace Test; approximate $F_{4,58}=$

Table 3
 Eastern Beringian herbivore specimen ID's, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰), and ^{14}C dates

Genus	Specimen ID	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	at. C:N	^{14}C yr BP	^{14}C Lab ID	Time group
<i>Equus</i>	AMNH F:AM 142429	-21.28	4.29	2.4	12,310±45	CAMS119982	Post-glacial
<i>Equus</i>	AMNH F:AM 142423	-20.90	3.85	2.4	12,560±50	CAMS119976	Post-glacial
<i>Equus</i>	AMNH F:AM 60025	-21.19	4.65	2.3	13,710±60	CAMS120061	Post-glacial
<i>Equus</i>	AMNH F:AM 60005	-21.29	1.64	2.3	14,630±60	CAMS119969	Post-glacial
<i>Equus</i>	AMNH F:AM 142421	-20.95	4.79	2.4	14,860±60	CAMS119974	Post-glacial
<i>Equus</i>	AMNH F:AM 142424	-20.70	2.94	2.4	15,460±70	CAMS119977	Post-glacial
<i>Equus</i>	AMNH F:AM 60032	-20.89	2.54	2.4	15,850±70	CAMS120068	Post-glacial
<i>Equus</i>	AMNH F:AM 60004	-20.93	3.08	2.4	16,370±80	CAMS119968	Post-glacial
<i>Equus</i>	AMNH F:AM 60044	-20.85	3.47	2.4	18,630±100	CAMS119970	Full-glacial
<i>Equus</i>	AMNH F:AM 60023	-21.45	2.53	2.5	19,000±100	CAMS120058	Full-glacial
<i>Equus</i>	AMNH F:AM 60027	-20.81	3.60	2.4	19,590±110	CAMS120059	Full-glacial
<i>Equus</i>	AMNH F:AM 142420	-21.23	4.96	2.5	19,870±110	CAMS119973	Full-glacial
<i>Equus</i>	AMNH F:AM 142430	-21.40	3.23	2.4	19,950±110	CAMS119983	Full-glacial
<i>Equus</i>	AMNH F:AM 60020	-21.25	3.99	2.4	19,950±120	CAMS120062	Full-glacial
<i>Equus</i>	AMNH F:AM 142427	-21.05	4.73	2.4	19,960±110	CAMS119980	Full-glacial
<i>Equus</i>	AMNH F:AM 142426	-21.20	5.07	2.4	20,300±120	CAMS119979	Full-glacial
<i>Equus</i>	AMNH F:AM 142425	-20.76	4.23	2.4	20,440±120	CAMS119978	Full-glacial
<i>Equus</i>	AMNH F:AM 142419	-21.07	4.52	2.4	20,520±120	CAMS119971	Full-glacial
<i>Equus</i>	AMNH F:AM 142428	-21.03	3.74	2.4	21,280±130	CAMS119981	Full-glacial
<i>Equus</i>	AMNH F:AM 60026	-21.32	3.96	2.4	21,310±140	CAMS120060	Full-glacial
<i>Equus</i>	AMNH F:AM 142435	-21.87	3.82	2.4	21,840±140	CAMS119989	Full-glacial
<i>Equus</i>	AMNH F:AM 142434	-20.97	3.76	2.4	22,610±150	CAMS119988	Full-glacial
<i>Equus</i>	AMNH F:AM 60003	-21.25	1.41	2.3	24,260±200	CAMS120077	Pre-glacial
<i>Equus</i>	AMNH F:AM 142431	-21.09	3.94	2.4	25,710±230	CAMS119985	Pre-glacial
<i>Equus</i>	AMNH F:AM 142433	-20.70	2.85	2.4	25,960±240	CAMS119987	Pre-glacial
<i>Equus</i>	AMNH F:AM 60033	-20.87	2.64	2.4	39,910±1330	CAMS120069	Pre-glacial
<i>Equus</i>	AMNH F:AM 60017	-21.58	3.58	2.4	41,000±1500	CAMS119972	Pre-glacial
<i>Equus</i>	AMNH F:AM 60221	-21.70	0.74	2.3	43,700±2000	CAMS120067	Pre-glacial
<i>Equus</i>	AMNH F:AM 60028	-20.63	4.43	2.4	48,400	CAMS120064	Pre-glacial
<i>Equus</i>	AMNH F:AM 142422	-21.50	2.98	2.3	48,500	CAMS119975	Pre-glacial
<i>Equus</i>	AMNH F:AM 60019	-21.50	1.65	2.4	48,500	CAMS119984	Pre-glacial
<i>Equus</i>	AMNH F:AM 142432	-21.48	2.47	2.3	48,500	CAMS119986	Pre-glacial
<i>Rangifer</i>	AMNH F:AM 142443	-19.21	3.26	2.4	16,000±190	AA48686	Post-glacial
<i>Rangifer</i>	AMNH F:AM 142444	-18.99	3.13	2.4	16,400±202	AA48687	Post-glacial
<i>Rangifer</i>	AMNH F:AM 142440	-19.45	1.97	2.3	16,700±207	AA48682	Post-glacial
<i>Rangifer</i>	AMNH F:AM 142441	-20.07	5.43	2.5	17,300±222	AA48683	Post-glacial
<i>Rangifer</i>	AMNH F:AM 142438	-20.08	3.63	2.3	21,000±361	AA48680	Full-glacial
<i>Rangifer</i>	AMNH F:AM 142446	-19.31	3.13	2.4	29,640±370	CAMS120070	Pre-glacial
<i>Rangifer</i>	AMNH F:AM 142439	-19.43	4.67	2.4	40,700	AA48681	Pre-glacial
<i>Rangifer</i>	AMNH F:AM 142442	-19.27	2.13	2.4	40,700	AA48685	Pre-glacial
<i>Rangifer</i>	AMNH F:AM 142445	-19.72	3.65	2.3	41,100	AA48688	Pre-glacial
<i>Rangifer</i>	AMNH F:AM 142447	-19.19	1.69	2.5	45,200	CAMS120071	Pre-glacial
<i>Bison</i>	AMNH F:AM 5092	-20.08	4.38	2.4			
<i>Bison</i>	AMNH F:AM 46555	-20.10	5.21	2.4			
<i>Bison</i>	AMNH F:AM 46858	-20.88	3.73	2.3			
<i>Bison</i>	AMNH F:AM 46856	-19.77	2.93	2.5			
<i>Bison</i>	AMNH F:AM 3135	-20.51	5.22	2.4			
<i>Bison</i>	AMNH F:AM 1636	-21.34	4.38	2.6			
<i>Bos</i>	AMNH F:AM 142448	-20.73	2.65	2.3			
<i>Bos</i>	AMNH F:AM 142449	-24.16	0.47	2.3			
<i>Bos</i>	AMNH F:AM 142450	-20.38	0.98	2.4			
<i>Bos</i>	AMNH F:AM 142451	-21.68	4.77	2.3			
<i>Bos</i>	AMNH F:AM 30657	-21.26	7.03	2.4			
<i>Symbos</i>	AMNH F:AM 142452	-20.32	0.80	2.5			
<i>Symbos</i>	AMNH F:AM 142453	-20.19	0.01	2.4			
<i>Symbos</i>	AMNH F:AM 142454	-19.96	-0.40	2.4			
<i>Symbos</i>	AMNH F:AM 142455	-19.71	-0.24	2.5			
<i>Symbos</i>	AMNH F:AM 142456	-20.94	1.16	2.4			
<i>Symbos</i>	AMNH F:AM 142457	-19.92	-0.26	2.4			
<i>Symbos</i>	AMNH F:AM 142458	-19.89	0.09	2.4	41,200±1500	CAMS120072	Pre-glacial
<i>Symbos</i>	AMNH F:AM 142459	-20.36	3.33	2.4	48,800	CAMS120073	Pre-glacial
<i>Symbos</i>	AMNH F:AM 142460	-20.72	3.20	2.4			
<i>Symbos</i>	AMNH F:AM 142461	-17.51	3.96	2.4			
<i>Mammuthus</i>	V-54-1 367 ^a	-20.80	6.80	na			

Table 3 (continued)

Genus	Specimen ID	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	at. C:N	^{14}C yr BP	^{14}C Lab ID	Time group
<i>Mammuthus</i>	V-74-2 ^a	−21.00	6.40	na			
<i>Mammuthus</i>	V-78-1 ^b	−21.30	6.85	na			
<i>Mammuthus</i>	AK-170-V-1 ^a	−21.20	8.50	na			
<i>Mammuthus</i>	AK-171-V-1 ^a	−21.10	8.30	na			

na — Not available.

at. C:N — Atomic C:N.

Refer to Table 2 for museum and ^{14}C lab abbreviations, and time group definitions.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and ^{14}C dates for all herbivore specimens are reported in Leonard et al. (2007).

We report ^{14}C dates here for two *Symbos* specimens.

Mammuthus data reported in Bocherens et al. (1994).

^a Collagen extracted from tooth dentine.

^b Collagen extracted from tusk dentine, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are averages of samples taken from tip and base of tusk.

2.9, $p=0.03$). Post-hoc pairwise comparisons revealed full- and pre-glacial horse were different (F -test; $F_{2,28}=5.3$, $p=0.012$). Again, this difference among horse groups was largely driven by their $\delta^{15}\text{N}$ values (one-way ANOVA; $F_{2,29}=5.3$, $p=0.011$), and not their $\delta^{13}\text{C}$ values (one-way ANOVA; $p>0.05$). Due to the limited number of full-glacial caribou and brown bears, we only tested for a difference between pre- and post-glacial $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for these species. We found no difference between the values of pre- and post-glacial caribou (MANOVA – F -test; $p>0.05$). There was a significant difference between pre- and post-glacial brown bear $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (MANOVA – F -test; $F_{2,11}=7.8$, $p=0.008$), driven by a difference in their $\delta^{13}\text{C}$ values (one-way ANOVA; $F_{1,12}=15.4$, $p=0.002$), and not their $\delta^{15}\text{N}$ values (one-way ANOVA; $p>0.05$). The levels of variance in bear, horse and caribou $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values did not change through time (Levene's test; $p>0.05$).

3.2. Eastern Beringian herbivore $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

Our interspecies comparison (time independent) of herbivore (horse, caribou, bison, yak, woodland muskoxen, mammoth) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values found significant differences (MANOVA – Pillai's Trace Test; approximate $F_{10, 124}=15.1$, $p<0.0001$) among taxa. Post-hoc comparisons showed that all species were distinct (F -test; $p<0.05$), except for horse and yak, which had overlapping distributions of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. We made additional (time dependent) comparisons between the two herbivore species with abundant ^{14}C dates (horse and caribou), although we were unable to make a full-glacial comparison because there was only one caribou in this time period. The difference between horse and caribou persisted though the late Pleistocene; in both the pre-glacial and post-glacial time periods their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were different (MANOVA – F -test: Pre-glacial; $F_{2,12}=52.0$, $p<0.0001$ and Post-glacial; $F_{2,9}=31.0$, $p<0.0001$). The differences between horse and caribou were primarily driven by their $\delta^{13}\text{C}$ values.

3.3. Eastern Beringian carnivore $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

In the post-glacial there were weak interspecies differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among carnivores (wolf, brown bear,

lion) (MANOVA – Pillai's Trace Test; approximate $F_{4,38}=2.6$, $p=0.05$); post-hoc pairwise comparisons revealed that only wolves and brown bears were significantly different (F -test; $F_{2,18}=6.5$, $p=0.008$). There were no differences among carnivores during the other time periods. Among carnivore species brown bears had the most variable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in each time period. We tested for equal variances in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among species from each time period, and found the only significant difference was between bear and wolf $\delta^{15}\text{N}$ values during the post-glacial (Levene's test; $F_{1,15}=9.3$, $p=0.008$).

4. Discussion

4.1. Eastern Beringian paleoenvironmental context

Eastern Beringia experienced large shifts in temperature and moisture associated with the climate fluctuations of the late Pleistocene. Beringian LGM paleoclimate was strongly affected by growth and proximity of the Laurentide ice sheet, exposure of the Bering land bridge, and a southward migration of the jet stream (Bartlein et al., 1998; Edwards et al., 2001; Elias, 2001). A range of proxy data from eastern Beringia provides evidence of these climatic changes over the past 40,000 yrs. Pollen records (Ager and Brubaker, 1985; Bigelow and Edwards, 2001), plant macrofossil assemblages (Zazula et al., 2003; Wooller et al., 2007; Zazula et al., 2007), lake sediments (Barber and Finney, 2000), ice-cores (Alley, 2000), ocean sediment cores (Phillips and Grantz, 2001), insect abundances (Elias, 2001), and mammal abundances (Guthrie, 2006) are among the physical and biotic records used to reconstruct former Beringian climate conditions. These records suggest that; 1) the interior of eastern Beringia was cold and arid during the LGM relative to pre- and post-glacial conditions, and 2) large, rapid shifts in temperature and moisture regimes were associated with the transitions into, and out of, the LGM (reviews in Elias, 2001; Guthrie, 2001; Brigham-Grette et al., 2004).

The ramifications of these climate shifts are not well understood at the ecosystem-level, but fossil pollen and plant macrofossil assemblages shed light on first-order patterns of vegetation distribution and composition. In general, the milder

condition of MIS3 corresponded to the presence of both forested and open biomes in eastern Beringia (Anderson and Lozhkin, 2001). Forests were absent in Alaska during the LGM; instead vegetation was characterized by a productive ‘steppe-tundra’ biome that included grasses, herbs, shrubs, and sedges

(Anderson et al., 1989; Edwards and Barker, 1994; Walker et al., 2001). Beringian vegetation responded quickly to post-glacial warming and increases in precipitation, and by ~12,000 ¹⁴C yr BP the ‘steppe-tundra’ biome was fully replaced by tundra and boreal forests (Ager and Brubaker, 1985; Lozhkin

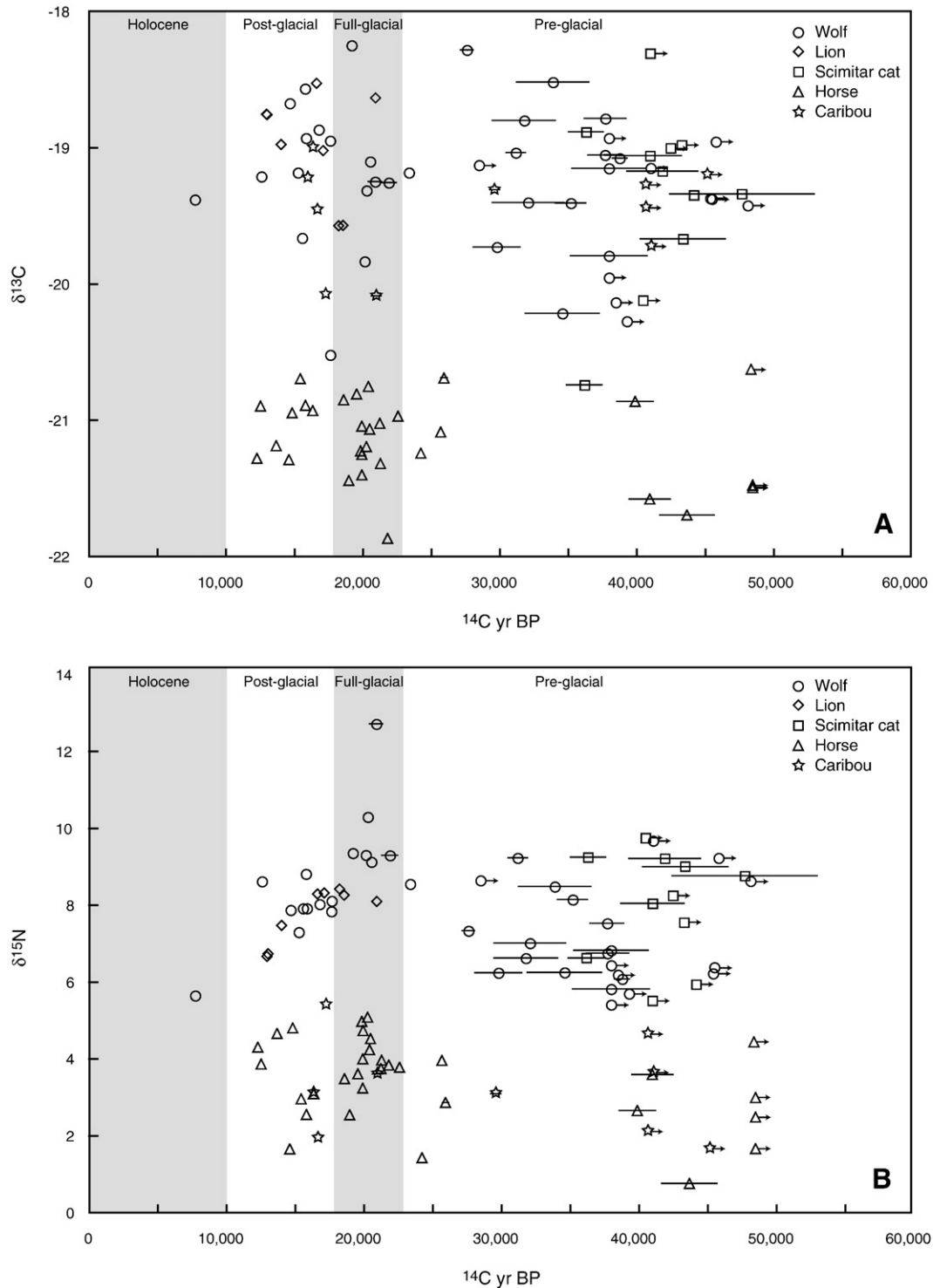


Fig. 2. Temporal records of gray wolf, lion, scimitar cat, horse and caribou δ¹³C (A), and δ¹⁵N (B) values. Records are divided into four time periods with gray shading. Lines through symbols indicate the error (±1 standard deviation) associated with each ¹⁴C date, and empty symbols indicate that the error is ≤ the size of the symbol. Symbols with an arrow designate the minimum ¹⁴C age of a specimen with an infinite date.

et al., 1993; Anderson and Brubaker, 1994; Brubaker et al., 2005).

4.2. Megafaunal $\delta^{13}\text{C}$ records through time

The $\delta^{13}\text{C}$ values of wolves, felids, horses, and caribou remained constant through the late Pleistocene (Fig. 2A, Table 1). A similar pattern was observed in the $\delta^{13}\text{C}$ values of late Pleistocene mammoth and caribou from western Beringia (Russia and Siberia) (Iacumin et al., 2000). Both the eastern and western Beringian megafaunal isotope records are sparse after 15,000 ^{14}C yr BP, and end at approximately 12,500 ^{14}C yr BP (Iacumin et al., 2000). Thus, the combined eastern and western Beringian $\delta^{13}\text{C}$ datasets record neither; 1) the well-documented decrease in herbivore $\delta^{13}\text{C}$ values that occurred after 13,500 ^{14}C yr BP in Europe (Drucker et al., 2003b; Richards and Hedges, 2003; Hedges et al., 2004; Stevens and Hedges, 2004), and between 15,000 and 12,000 ^{14}C yr BP in southern California (Coltrain et al., 2004a), nor 2) the significant increase in the $\delta^{13}\text{C}$ values of Fairbanks area grass macrofossils between 31,200 and 14,300 ^{14}C yr BP (Wooller et al., 2007).

The decrease in megafaunal collagen $\delta^{13}\text{C}$ values has been attributed to changes in plant $\delta^{13}\text{C}$ values due to either a transition from an open to forested environment (e.g. canopy effect) (Drucker et al., 2003b), or plant ecophysiological response to changing atmospheric CO_2 concentrations (Richards and Hedges, 2003; Stevens and Hedges, 2004; Ward et al., 2005). Stevens and Hedges (2004) compared their 40,000 yr records of horse $\delta^{13}\text{C}$ values to $\delta^{13}\text{C}$ records collected from wood cellulose, plant leaves, and bulk organic lake sediments and found that all showed a decrease in $\delta^{13}\text{C}$ values at roughly the same time. Furthermore, when aligned with an ice-core derived record of CO_2 concentration over the same time interval the decrease in $\delta^{13}\text{C}$ values of organic records (herbivore, plant, lake sediment) is coeval with the increase in atmospheric CO_2 concentration (Richards and Hedges, 2003; Stevens and Hedges, 2004). The paucity of latest Pleistocene (12,000 to 10,000 ^{14}C yr BP) Beringian megafaunal samples precludes comparison with European megafaunal $\delta^{13}\text{C}$ data from that time period. Wooller et al. (2007) correlated the increase in Fairbanks area grass $\delta^{13}\text{C}$ values from 31,200 to 14,300 ^{14}C yr BP to higher aridity associated with the LGM. The pre- and full-glacial Beringian megafaunal $\delta^{13}\text{C}$ datasets are robust, and yet do not reflect the contemporaneous rise in Beringian grass $\delta^{13}\text{C}$ values ($\sim 2\%$). While grass tissues represent both a temporal and spatial snapshot of environmental conditions, the megafaunal bone collagen $\delta^{13}\text{C}$ values reflect several years of an animals' diet and movement. From these results we conclude that changes in moisture availability affecting grass isotope values were very local, affected habitats that herbivores did not use, and/or did not affect all plants similarly.

4.3. Megafaunal $\delta^{15}\text{N}$ records through time

There are two significant shifts in Beringian megafaunal bone collagen $\delta^{15}\text{N}$ values; an increase between the pre- and full-glacial time periods, and a subsequent decrease between

full- and post-glacial time periods (Fig. 2B, Table 1). The timings of the shifts are similar in Fairbanks area horses, wolves, brown bears, and lions, but the magnitude of the shifts differs among species. The caribou, short-faced bear and scimitar cat $\delta^{15}\text{N}$ records are difficult to interpret because of low temporal resolution. There are several ways, and even combinations of ways, to account for temporal patterns in consumer $\delta^{15}\text{N}$ values. Changes in carnivore $\delta^{15}\text{N}$ values can either reflect shifts in consumption of prey with different $\delta^{15}\text{N}$ values, or variation in the $\delta^{15}\text{N}$ values of a constant diet (specific type of prey). In turn, herbivore $\delta^{15}\text{N}$ values record both changes in diet (e.g. grass versus shrub), and environmentally-mediated changes in the $\delta^{15}\text{N}$ values of plants.

Our results suggest that either all species changed diets synchronously, or that portions of the shifts in the megafaunal isotope values are food web-wide and therefore climate-driven. Horses feed on a mix of grass, herbs, and shrubs (Berger, 1986; Hoppe et al., 2004), so it is possible that shifts in the consumption of different plant types could account for the observed pattern in their $\delta^{15}\text{N}$ values. Yet, the coeval changes in wolf, lion and bear $\delta^{15}\text{N}$ values, none of which were horse-specialists, suggest that the $\delta^{15}\text{N}$ values of other Beringian herbivore species also shifted, pointing to a bottom-up, climate-driven factor. The magnitude of the shift in carnivore $\delta^{15}\text{N}$ values is greater than the shift in horse values, and likely reflects both environmental and dietary (prey selection) changes. For example, a greater reliance on mammoth versus muskox in the full- versus pre-glacial can account for the fraction of the shift in wolf $\delta^{15}\text{N}$ values that is greater than the increase in horse $\delta^{15}\text{N}$ values. Carnivore diets are discussed in more detail below.

If the changes, or some fraction of the changes, in megafaunal $\delta^{15}\text{N}$ values were environmentally-mediated, then the higher average $\delta^{15}\text{N}$ values during the full-glacial may reflect increased aridity in the interior of eastern Beringia during the LGM. Modern studies have identified a significant inverse correlation between $\delta^{15}\text{N}$ values of terrestrial ecosystems and mean annual rainfall (Heaton, 1987; Handley et al., 1999; Swap et al., 2004). In each of these studies the authors found that mean annual rainfall accounted for nearly 50% of the variability in plant $\delta^{15}\text{N}$ values. In the few modern (non-Arctic) regions where it has been tested, taxon-specific collagen nitrogen isotope values are inversely correlated with moisture-related climate variables (Heaton et al., 1986; Sealy et al., 1987; Cormie and Schwarcz, 1994; Gröcke et al., 1997). Megafaunal $\delta^{15}\text{N}$ values likely also reflect changes in the types of vegetation present between interglacial and glacial periods. The occurrences of low consumer $\delta^{15}\text{N}$ values in the pre-glacial and post-glacial may record the presence of forest habitats, as well as generally moister conditions. The relative influences of diet and environment on megafaunal $\delta^{15}\text{N}$ values may become clearer as additional isotopic and radiocarbon datasets are collected from Beringian fossils.

For comparison, large temporal shifts in Pleistocene European herbivore $\delta^{15}\text{N}$ values are neither synchronous between European regions, nor congruent with the pattern we observe in eastern Beringian fauna. Herbivores from northwestern Europe and the United Kingdom have post-glacial $\delta^{15}\text{N}$ values that are $\sim 5\%$

lower than pre-glacial values (Richards and Hedges, 2003; Stevens and Hedges, 2004). The data from this region are sparse during the LGM, making it difficult to determine if the decrease in

$\delta^{15}\text{N}$ values was initiated during, or after the LGM. Post-glacial $\delta^{15}\text{N}$ values remain low until 13,000 ^{14}C yr BP, and then rebound to pre-glacial levels by 10,000 ^{14}C yr BP (Richards and Hedges, 2003; Stevens and Hedges, 2004). A similar ^{15}N -depletion ($\sim 3\text{‰}$) is evident in herbivore records from southwestern France (Drucker et al., 2003a). Stevens and Hedges (2004) highlight the potential effects of temperature on ecosystem $\delta^{15}\text{N}$ values at the glacial–interglacial scale, and suggest that low post-glacial $\delta^{15}\text{N}$ values in Europe may have persisted even as temperatures warmed due to increased moisture availability associated with permafrost melting.

4.4. *Herbivore habitat use*

Recent molecular and radiocarbon studies have shown that Beringian herbivore populations were not spatially or evolutionarily static during the last 50,000 yrs of the Pleistocene (Shapiro et al., 2004; Drummond et al., 2005; MacPhee et al., 2005; Barnes et al., 2007). Of the herbivore species we analyzed for this study only caribou are present in Alaska today. Horses went extinct in the region between 12,000 and 11,000 ^{14}C yr BP, coincident with a severe decrease in bison abundance, followed by the extinction of bison at approximately 9000 ^{14}C yr BP (Guthrie, 2006). In the $\sim 10,000$ yrs prior to their extinction it appears that horses underwent a reduction in body size, a response in mammals that can be driven by extended resource limitation (Guthrie, 2003) or a more direct response to climatic warming. Population dynamics of other herbivore species were also changing during this interval; mammoths went extinct in interior Alaska at approximately 11,000 ^{14}C yr BP, and moose appeared and elk became abundant in the fossil record between 13,000 and 12,000 ^{14}C yr BP (Guthrie, 2006). However, the most important faunal change at this time in eastern Beringia may have been the arrival of humans. Untangling the relative impacts of climate-driven environmental change and human predation upon herbivore population sizes in the latest Pleistocene has proven difficult (Barnosky et al., 2004). In their review of current evidence Koch and Barnosky (2006) conclude that the megafaunal extinction in eastern Beringia was likely caused by climate-driven changes to the paleoenvironment, exacerbated near the end by the arrival of

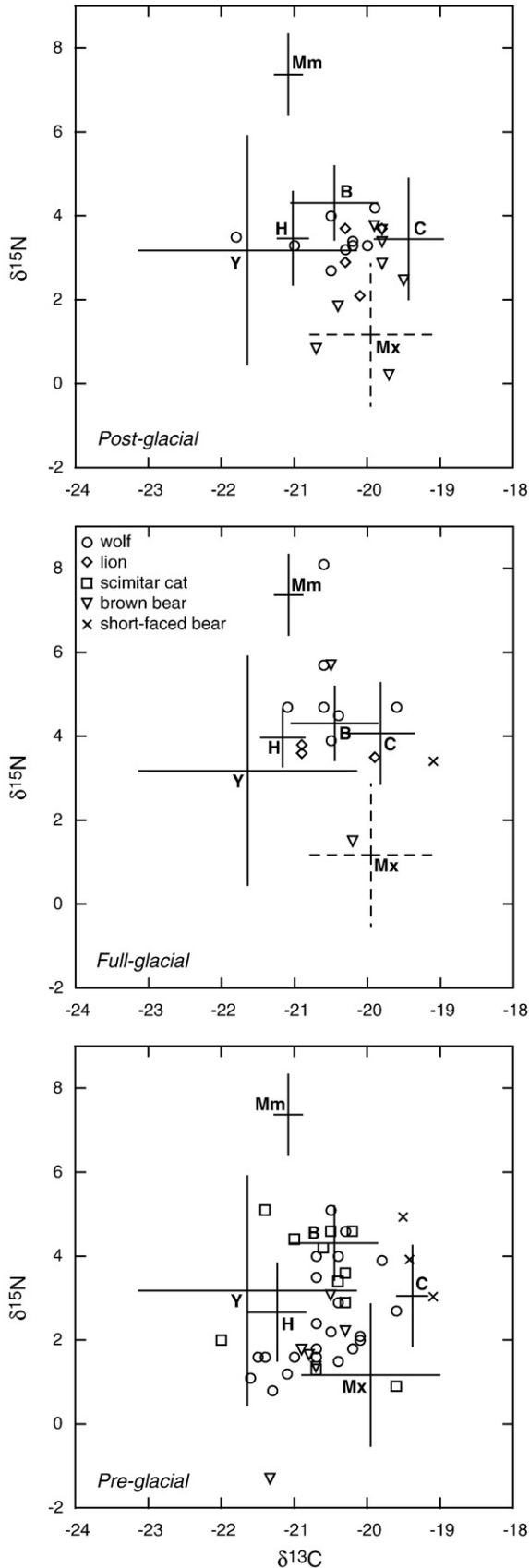


Fig. 3. Dietary reconstructions for ^{14}C dated late Pleistocene Fairbanks area gray wolves, lions, scimitar cats, brown bears, and short-faced bears from three time periods during the late Pleistocene (as in Fig. 2). Brown bear and short-faced bear data are from Matheus (1995, 1997) and Barnes et al. (2002). In each reconstruction the carnivore $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values have been corrected for trophic level isotopic fractionations (-1.3‰ for $\delta^{13}\text{C}$ and -4.6‰ for $\delta^{15}\text{N}$; Fox-Dobbs et al., 2007), and are compared to isotope values of megafaunal prey species from the Fairbanks area (except for mammoth, which are from sites throughout Alaska; Bocherens et al., 1994). Horse and caribou individuals are ^{14}C dated, and isotopic values are included for individuals from each time period. Bison, yak, muskox, and mammoth are not ^{14}C dated, and the same ranges of isotopic values (means \pm standard deviations) are included for each time period. Dashed lines that delineate the muskox range of values in the full- and post-glacial indicate that muskoxen were included in the dietary reconstructions, but probably were not present in the Fairbanks area during these times periods. B — Bison, C — caribou, H — horse, Mm — mammoth, Mx — woodland muskox, Y — yak.

humans. They cite as evidence the lack of synchrony in the timing of extinction among megafaunal species, and the magnitude of ecosystem change (e.g. steppe-tundra to boreal forest) in Beringia (Koch and Barnosky, 2006). In contrast, the megafaunal extinction in North America south of the LGM ice sheets was highly synchronous among species, suggesting that humans had a larger role in the extinction (Barnosky et al., 2004).

Our isotopic results suggest that in the 30,000 yrs leading up to the late Pleistocene extinction there was dietary niche overlap among some Beringian herbivore species, and partitioning among most species (Table 1, Fig. 3). We rely upon $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of modern Alaskan C_3 plant types presented in Fig. 4 to infer Beringian herbivore dietary niches. We do not directly compare the vegetation and faunal isotope values, but rather use the relative position of different plants and herbivores in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ space to estimate herbivore habitat use and diet qualitatively. The range in grass and sedge $\delta^{15}\text{N}$ values is not wholly empirical, but instead is inferred from the range of values for herbaceous plants (herbs), and sedge values (Nadelhoffer et al., 1996). We assume that the wide range in herb $\delta^{15}\text{N}$ values captures the potential range in grass and sedge $\delta^{15}\text{N}$ values.

The $\delta^{13}\text{C}$ values of the Beringian herbivores are all within the range of values expected for animals feeding within an environment dominated by C_3 plants (Cerling et al., 1997). At the regional scale $\delta^{13}\text{C}$ values vary amongst C_3 plants due to ecophysiological differences, and local aridity and soil moisture conditions, with higher $\delta^{13}\text{C}$ values correlated to higher plant water-use efficiency and drier environments (Ehleringer, 1991;

Ehleringer and Monson, 1993; Wooller et al., 2007). This has been observed in modern interior Alaskan grasses and sedges collected from wet and dry environments, and we indicate in Fig. 4 the $\delta^{13}\text{C}$ value half-way between the dry and wet mean values (Wooller et al., 2007). Variation in $\delta^{13}\text{C}$ values among herbivores likely reflects both the relative contribution of lichens and fungi (tundra vegetation) to diet, and the water-use efficiency of other types of vegetation.

As mentioned previously, plant $\delta^{15}\text{N}$ values can vary due to a range of ecophysiological and environmental parameters. The variation in $\delta^{15}\text{N}$ values between Beringian herbivores may reflect the contribution of different plant types to diet, with fungi and grasses/sedges having relatively higher $\delta^{15}\text{N}$ values than lichens, mosses and shrubs/trees (Nadelhoffer et al., 1996; Ben-David et al., 2001). Herbivores consuming similar plant types in areas with varying soil moisture conditions may also have different $\delta^{15}\text{N}$ values, with higher moisture levels generally corresponding to lower plant $\delta^{15}\text{N}$ values (Handley et al., 1999). Differing animal physiologies or dietary quality may also contribute to inter-individual variance in $\delta^{15}\text{N}$ values. For example, the protein content of herbivore forage can influence the magnitude of the isotopic fractionation that occurs during the assimilation of dietary macromolecules into herbivore bone collagen (Sponheimer et al., 2003). As such, a horse feeding primarily on grass (low protein forage) may have a lower collagen $\delta^{15}\text{N}$ value than a herbivore feeding on shrubs (high protein forage), even when the two types of vegetation have identical $\delta^{15}\text{N}$ values. Finally, there may be taxon-specific differences among herbivores, such as the high $\delta^{15}\text{N}$ values of mammoths (Koch, 1991; Bocherens et al., 1994; Iacumin et al.,

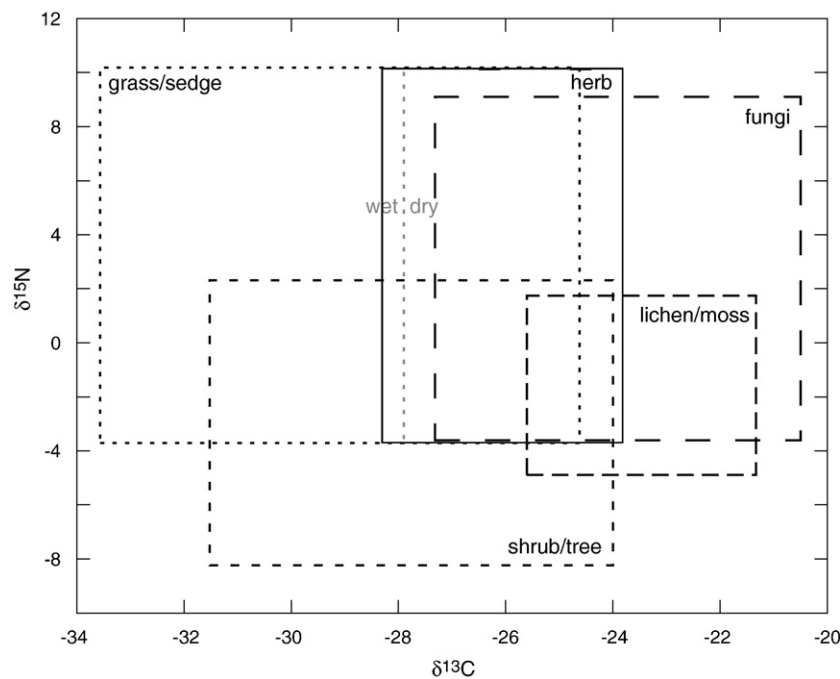


Fig. 4. Theoretical figure demonstrating the range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for Beringian plant and habitat types, based upon published values for modern Alaskan vegetation. Boxes for each plant type encompass the means and standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Grass/sedge values are from Wooller et al. (2007) and Nadelhoffer et al. (1996), herb and fungi values are from Ben-David et al. (2001), shrub/tree and lichen/moss values are from Ben-David et al. (2001) and Nadelhoffer et al. (1996). See text for a description of how the grass/sedge box is defined.

2000). While the differences in $\delta^{15}\text{N}$ values of fungi versus lichen, and plants growing in wet versus dry soils have been measured in modern ecosystems, there is no conclusive evidence for why mammoths consistently have higher $\delta^{15}\text{N}$ values than contemporaneous grazing species.

Horse and yak had overlapping distributions of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, indicating similar diets that were potentially comprised of grasses, sedges, and herbs (Fig. 4). The exact amount of dietary overlap is difficult to determine with carbon and nitrogen isotopes alone, since C_3 grasses, sedges and herbs from the same area can have identical isotopic values (Cerling et al., 1997). Modern bison are obligate grazers (Coppedge et al., 1998), and the slightly higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Beringian bison compared to horse and yak during the pre- and post-glacial may correspond to pure-grass diet, versus a mixed grass and shrub/tree diet. Paleocologic interpretations drawn from dental wear patterns and ^{14}C records provide additional insight into Beringian herbivore habitat use. Specifically, mesowear and microwear patterns on Beringian bison and horse teeth show comparable levels of abrasion, indicative of a graminoid-rich diet for both (Solounias et al., 2004). Likewise, Guthrie (2006) cited the disappearance of Beringian horses at 11,000 ^{14}C yr BP and the subsequent abundance of bison in the radiocarbon record as potential evidence for direct competition between grazing species. Our isotopic results do not demonstrate complete dietary overlap between horse and bison, and instead suggest that Beringian bison, yak, and horse foraged on grasses, sedges, and herbs in the same open, steppe-tundra environment, but had slightly different dietary preferences.

We are able to conclude from the caribou and woodland muskoxen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data that the two species occupied separate dietary niches from each other, and from the yak/horse/bison niche. Historic arctic caribou and muskoxen (*Ovibos moschatus*) also have different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Coltrain et al., 2004b), and modern co-existing populations of muskoxen and caribou are known to consume different plant types (Ihl and Klein, 2001). Caribou select lichens, and muskoxen select mosses and sedges. Beringian caribou have relatively high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and using Fig. 4 as a guide, we infer that caribou diet was lichen/moss- and fungi-rich. Woodland muskoxen also have relatively high $\delta^{13}\text{C}$ values, but unlike caribou they have very low $\delta^{15}\text{N}$ values. We propose that ancient woodland muskoxen foraged on sedges in wetter lowland habitats, lichen-rich tundra vegetation, or some combination of the two types of vegetation. As with $\delta^{15}\text{N}$, the magnitude of the $\delta^{13}\text{C}$ trophic fractionation between the proteinaceous tissues of a herbivore and its diet can vary (on the order of 0.5‰) depending upon the protein content of the plants consumed (protein-rich = larger fractionation; Ayliffe et al., 2004). In modern arctic regions lichens are protein-poor compared to grasses, herbs and shrubs (Larter and Nagy, 2001). Variation in trophic fractionations contributes to the error associated with our interpretations of herbivore habitat use. A potential consequence is the difference between the $\delta^{13}\text{C}$ values of Beringian grazers (horse/bison/yak) and tundra browsers (caribou/muskox) underestimates of the actual isotopic difference between Beringian forage types.

The relative isotopic differences among eastern Beringian horse, bison, and caribou have been observed in other Pleistocene locations (e.g. Iacumin et al., 2000; Drucker et al., 2003a; Richards and Hedges, 2003; Bocherens et al., 2005). Pleistocene Alaskan caribou dental mesowear and microwear patterns are similar to bison and horse, indicating a grass-rich diet (Solounias et al., 2004). The discrepancy in caribou dietary interpretations drawn from the isotopic and dental wear data may be due to the high abrasiveness of grasses relative to lichens. Even a modest amount of grass in caribou diet could account for a disproportionate fraction of dental wear. When we combine the paleodietary information gleaned from caribou isotope values and dental wear patterns we surmise that Pleistocene caribou had a mixed diet of grasses, and fungi- and lichen-rich tundra vegetation. Modern barren-ground caribou seasonally alternate between a winter diet dominated by lichen and mosses, and a summer diet of herbaceous species (Wilson and Ruff, 1999). Our study expands the geographic scope of the existing understanding of late Pleistocene megafaunal community dynamics. The relative spacing among late Pleistocene herbivore $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values appears to have been remarkably conserved across continents, and through time, which implies an impressive fidelity to dietary niche partitioning among megafaunal species.

4.5. Temporal patterns of carnivore presence and absence

Previous genetic, radiocarbon and isotopic research on Beringian wolves, brown bears, and short-faced bears illuminated dramatic changes within the carnivore guild during, and at the end of the late Pleistocene (Leonard et al., 2000; Barnes et al., 2002; Leonard et al., 2007). Our compilation of new and

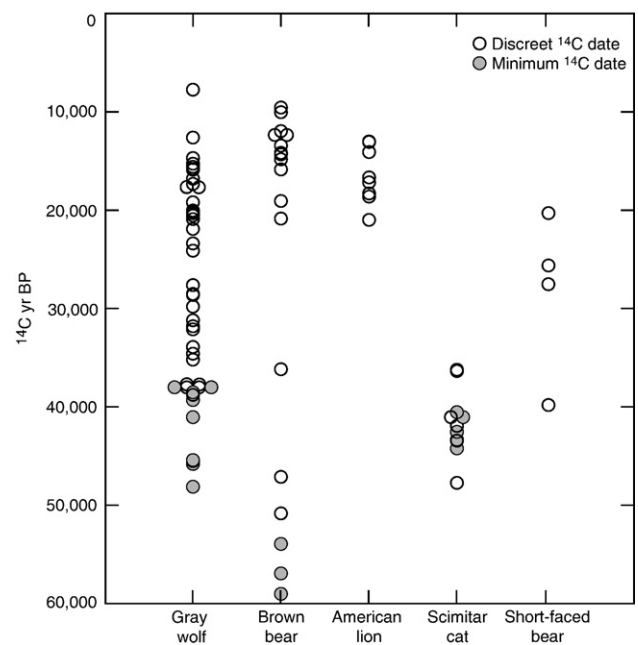


Fig. 5. Fairbanks area megafaunal carnivore ages in radiocarbon years. Open symbols represent discreet ^{14}C dates, and filled symbols represent minimum ^{14}C dates. Brown and short-faced bear dates are from Matheus (1997) and Barnes et al. (2002).

existing geochemical data gives further insight into how and when the members of the Beringian large-bodied carnivore guild co-existed on the landscape (Fig. 5). The temporal patterns of species presence and absence are compelling; of the five carnivores discussed here, we only found evidence for the persistence of gray wolves through the entire late Pleistocene. Furthermore, during most of the late Pleistocene only two or three of the five carnivore species were present, and therefore potentially interacting. Barnes et al. (2002) highlighted the staggered presence of bear species in eastern Beringia, and the different diets of brown bears that did, and did not, co-occur with short-faced bears. Felids (scimitar cats and lions) also had non-overlapping chronologies, and both were rare in the Fairbanks area during the time when short-faced bears were present (40,000 to 20,500 ^{14}C yr BP). Thus, short-faced bears either dictated which carnivore species were present, or were able to persist locally while other species were absent.

Isotopic results presented below suggest that both competition for resources and changing environmental conditions could have contributed to patterns of carnivore presence/absence, although we emphasize that species interactions between ancient animals can only be inferred, not defined, from geochemical records. Importantly, reconstructions of the Beringian steppe-tundra megafaunal community must be revised to reflect the dynamic patterns of predator presence and absence during the late Pleistocene.

4.6. Carnivore dietary reconstructions

Based upon our isotopic dietary reconstructions from pre-, full-, and post-glacial time periods we conclude that Beringian wolves, felids, and bears consumed a range of prey throughout the late Pleistocene. Yet when we compare dietary patterns revealed by visual assessment of the data (Fig. 3), and the *IsoSource* model results (Fig. 6) from each time period, there are some subtle differences in prey selection. Short-faced bears were the most specialized carnivore species; all individuals were caribou specialists, including the one full-glacial individual. Except for two wolf individuals, no other carnivore species were caribou specialists in the pre-glacial. In contrast, lions, brown bears and wolves all preyed upon caribou during the full- and post-glacial. By combining isotope and presence/absence data, we infer that short-faced bears excluded brown bears and scimitar cats from caribou in the pre-glacial.

The felids and brown bears consumed all the types of prey we analyzed. Most scimitar cats were generalists and/or horse and bison specialists, and had high dietary overlap with pre-glacial wolves. The abrupt disappearance of scimitar cats at $\sim 36,000$ ^{14}C yr BP could be related to changing predator guild dynamics (e.g. the recent appearance of short-faced bears) and/or environmental shifts that occurred at the end of MIS3. Without data for scimitar cats from other eastern Beringian locations we cannot know if their disappearance represents a local, or regional extinction. Lions were less isotopically variable than the scimitar cats, and their patterns of prey preference were similar to full- and post-glacial wolves. Two post-glacial lions with low $\delta^{15}\text{N}$ values were classified as forest cervid

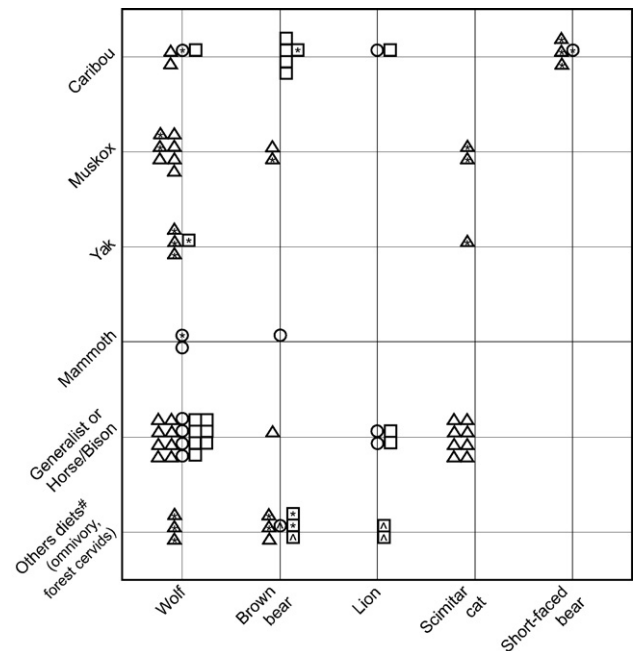


Fig. 6. Carnivore dietary categories, based upon *IsoSource* stable-isotope mixing model output. Symbols represent different time periods; Δ — pre-glacial, O — full-glacial, \square — post-glacial. Empty symbols indicate carnivore dietary categorization derived from *IsoSource* results, using criteria described in the text. Symbols with * indicate individuals whose dietary categories were inferred from graphical assessment, because their $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ values fell outside the dietary mixing polygon and *IsoSource* could not generate feasible diet source solutions. Symbols with ^ indicate individuals that met the criteria for muskox specialists, but were reinterpreted as omnivores and/or predators of forest cervids (moose/elk/deer). Woodland muskoxen may not have been present in the Fairbanks area in the full- and post-glacial.

specialists, which may indicate foraging in closed habitats just prior to extinction. Brown bears fall into two main categories; post-glacial caribou specialists, and individuals from all time periods that have an omnivorous diet, which included plant food sources (lower $\delta^{15}\text{N}$), muskox, and/or consumption of forest cervids. The one full-glacial individual classified as a mammoth specialist was most likely a scavenger, and not a mammoth predator.

Almost 50% of wolves were specialists on tundra herbivores (muskox and caribou) in the pre-glacial, whereas the other 50% were generalists and/or horse and bison specialists, or were feeding on forest cervids. In each time period wolves consumed the widest range of prey among the carnivores, matched only by lions in the post-glacial. Two full-glacial wolves were mammoth specialists, although as with the brown bears we cannot know if this represents scavenging or predation. Mammoth did not contribute significantly to the diets of felids and short-faced bears, the only other Beringian carnivores large enough to kill a mammoth. Thus, the mammoths consumed by wolves and brown bears either died of natural causes, or were killed by one of these two carnivores. Regardless of the mechanism, it is interesting that mammoth was so rare in the diets of Beringian carnivores.

While we have established that Beringian wolves consumed a range of prey we are unable to determine with isotopes alone

whether they were mainly generalist predators, or scavengers. A similar interpretation of Beringian gray wolf foraging behavior was drawn from morphologic analyses of various craniodental features (Leonard et al., 2007). The craniodental morphology in Beringian gray wolves was more hypercarnivorous, and patterns of tooth wear and fracture more extreme than modern wolves, suggesting that they ate more bone and perhaps took down larger prey than living wolves do (Leonard et al., 2007). All morphologic indices do indicate heavy carcass utilization, regardless of foraging mode. If Beringian wolves were scavengers it might explain why they persisted continuously for thousands of years while populations of other hypercarnivores in the Fairbanks area waxed and waned through time, although they also go extinct. The one early Holocene wolf (not included in dietary reconstruction) had a lower $\delta^{15}\text{N}$ value than the post-glacial wolves, indicating a diet of forest cervid.

Our interpretations of the eastern Beringian carnivore dietary reconstructions can be summarized by three points: 1) none of the large-bodied carnivores we analyzed (except short-faced bear) were specialized predators of a single prey species during the late Pleistocene; 2) Beringian carnivore diets included all measured herbivore species, and an unmeasured diet source(s) of forest cervids and/or plant materials; and 3) differences in carnivore diet and dietary breadth between time periods either reflect changes in the relative abundances of prey on the Beringian landscape, or changes in competitive interactions among Beringian carnivore species.

Ideally we would compare the foraging ecology of eastern Beringian predators to other late Pleistocene populations, but isotopic records for fossil carnivores are sparse. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of isolated gray wolf and felid individuals from late Pleistocene sites in Europe and Siberia correspond to mixed diets of the abundant herbivore megafauna at each site (Bocherens et al., 1996; Bocherens and Drucker, 2003; Bocherens et al., 2005). It is notable that the only prey not common in the western Beringian wolf diet is mammoth (Bocherens et al., 1996). There are robust isotopic records for carnivores and megafaunal herbivores from the La Brea tar pits in southern California. Isotopic data suggest that La Brea dire wolf (*Canis dirus*), lion, and saber-toothed cat (*Smilodon fatalis*) diets were variable, and included all measured herbivore species (horse, bison, camel, sloth, and mastodon) (Coltrain et al., 2004a; Fox-Dobbs et al., 2007).

5. Conclusions

Biogeochemical records collected from Fairbanks area megafaunal fossils shed light on paleoecological interactions among predators and their prey during changing paleoenvironmental conditions of the late Pleistocene. Faunal $\delta^{13}\text{C}$ chronologies were relatively invariant, while faunal $\delta^{15}\text{N}$ chronologies were more dynamic and reflected dietary and environmental changes. We found evidence that there was both dietary overlap, and resource partitioning, among co-occurring Beringian herbivores feeding upon steppe and tundra vegetation. We combined megafaunal radiocarbon records with carnivore dietary reconstructions and showed that carnivore presence/absence were likely dictated by

competitive and predator–prey interactions. In general, Fairbanks area carnivores had surprising dietary breadth, indicative of high connectivity within the megafaunal food web.

Acknowledgements

We thank Richard Harington at the Canadian Museum of Nature, and Richard Teford at the American Museum of Natural History for providing access to museum specimens. We thank Tom Guilderson and Paula Zermeno at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory for assistance with radiocarbon dating. We thank Cristie Boone, Brooke Crowley, Andrew Marcus, and Justin Yeakel for help with sample preparation and analysis. We thank Mark Clementz, Blaire Van Valkenburgh, Robert Wayne, and Matthew Wooller for thoughtful input and discussion. Logistical support was provided by the Genetic Program, Smithsonian Institution. Funding for this project provided by a NSF grant to J. A.L. and P.L.K. (OPP-0352634).

References

- Ager, T.A., Brubaker, L., 1985. Quaternary palynology and vegetational history of Alaska. In: Bryant, V.M., Holloway, R.G. (Eds.), *Pollen Records of Late Quaternary North American sediments*. American Association of Stratigraphic Palynologists, Dallas, TX, pp. 353–384.
- Alley, R.B., 2000. Ice-core evidence of abrupt climate changes. *Proceedings of the National Academy of Sciences* 97, 1331–1334.
- Ambrose, S.H., 1990. Preparation and characterization of bone and tooth collagen for isotopic analysis. *Journal of Archaeological Science* 17, 431–451.
- Anderson, P.M., Brubaker, L.B., 1994. Vegetation history of northcentral Alaska: a mapped summary of Late-Quaternary pollen data. *Quaternary Science Reviews* 13, 71–92.
- Anderson, P.M., Lozhkin, A.V., 2001. The Stage 3 interstadial complex (Karginiskii/middle Wisconsinan interval) of Beringia: variations in paleoenvironments and implications for paleoclimatic interpretations. *Quaternary Science Reviews* 20, 93–125.
- Anderson, P.M., Bartlein, P.J., Brubaker, L.B., Gajewski, K., Ritchie, J.C., 1989. Modern analogues of late-Quaternary pollen spectra from the western interior of North America. *Journal of Biogeography* 16, 273–291.
- Ayliffe, L.K., Cerling, T.E., Robinson, T., West, A.G., Sponheimer, M., Passey, B.H., Hammer, J., Roeder, B., Dearing, M.D., Ehleringer, J.R., 2004. Turnover of carbon isotopes in tail hair and breath CO_2 of horses fed an isotopically varied diet. *Oecologia* 139, 11–22.
- Barber, V.A., Finney, B.P., 2000. Late Quaternary paleoclimatic reconstructions for interior Alaska based on paleolake-level data and hydrologic models. *Journal of Paleolimnology* 24, 29–41.
- Barnes, I., Matheus, P., Shapiro, B., Jensen, D., Cooper, A., 2002. Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science* 295, 2267–2270.
- Barnes, I., Shapiro, B., Lister, A., Kuznetsova, T., Sher, A., Guthrie, D., Thomas, M.G., 2007. Genetic structure and extinction of the Woolly mammoth, *Mammuthus primigenius*. *Current Biology* 17, 1072–1075.
- Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L., Shabel, A.B., 2004. Assessing the causes of late Pleistocene extinctions on the continents. *Science* 306, 70–75.
- Bartlein, P.J., Anderson, P.M., Anderson, K.H., Edwards, M.E., Thompson, R.S., Webb, R.S., Webb III, T., Whitlock, C., 1998. Paleoclimate simulations for North America for the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. *Quaternary Science Reviews* 17, 549–585.
- Ben-David, M., Shochat, E., Adams, L., 2001. Utility of stable isotope analysis in studying foraging ecology of herbivores: examples from moose and caribou. *Alces* 37, 421–434.

- Berger, J., 1986. Horses of the Great Basin. University of Chicago Press, Chicago, Illinois.
- Bigelow, N.H., Edwards, M.E., 2001. A 14,000-yr paleoenvironmental record from Windmill Lake, central Alaska: late-glacial and Holocene vegetation in the Alaska Range. *Quaternary Science Reviews* 20, 203–215.
- Bigelow, N.H., Brubaker, L.B., Edwards, M.E., Harrison, S.P., et al., 2003. Climate change and Arctic ecosystems I. Vegetation changes north of 55degN between the last glacial maximum, mid-Holocene and present. *Journal of Geophysical Research* 108, 11–25.
- Bocherens, H., Drucker, D., 2003. Trophic level isotopic enrichment of carbon and nitrogen in bone collagen: case studies from recent and ancient terrestrial ecosystems. *International Journal of Osteoarchaeology* 13, 46–53.
- Bocherens, H., Fizet, M., Mariotti, A., Gangloff, R.A., Burns, J.A., 1994. Contribution of isotopic biogeochemistry (^{13}C , ^{15}N , ^{18}O) to the paleoecology of mammoths (*Mammuthus primigenius*). *Historical Biology* 7, 187–202.
- Bocherens, H., Pacaud, G., Lazarev, P.A., Mariotti, A., 1996. Stable isotope abundances (^{13}C and ^{15}N) in collagen and soft tissues from Pleistocene mammals from Yakutia: implications for the palaeobiology of the Mammoth Steppe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 126, 31–44.
- Bocherens, H., Billiou, D., Mariotti, A., 1999. Palaeoenvironmental and palaeodietary implications of isotopic biogeochemistry of last interglacial Neanderthal and mammal bones in Scladina Cave (Belgium). *Journal of Archaeological Science* 26, 599–607.
- Bocherens, H., Drucker, D.G., Billiou, D., Patou-Mathis, M., Vandermeersch, B., 2005. Isotopic evidence for diet and subsistence pattern of the Saint-Césaire I Neanderthal: review and use of a multi-source mixing model. *Journal of Human Evolution* 49, 71–87.
- Brigham-Grette, J., Lozhkin, A.V., Anderson, P.M., Glushkova, O.Y., 2004. Paleoenvironmental Conditions in Western Beringia before and during the Last Glacial Maximum. In: Madsen, D.B. (Ed.), *Entering America: Entering America: Northeast Asia and Beringia Before the Last Glacial Maximum*. University of Utah Press, Salt Lake City, Utah, pp. 29–61.
- Brown, T.A., Nelson, D.E., Vogel, J.S., Southon, J.R., 1988. Improved collagen extraction by modified Longin method. *Radiocarbon* 30, 171–177.
- Brubaker, L.B., Anderson, P.M., Edwards, M.E., Lozhkin, A.V., 2005. Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data. *Journal of Biogeography* 32, 833–848.
- Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Erlinger, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389, 153–158.
- Coltrain, J.B., Harris, J.M., Cerling, T.E., Ehleringer, J.R., Dearing, M., Ward, J., Allen, J., 2004a. Rancho La Brea stable isotope biogeochemistry and its implications for the palaeoecology of late Pleistocene coastal California. *Palaeogeography, Palaeoclimatology, Palaeoecology* 205, 199–219.
- Coltrain, J.B., Hayes, M.G., O'Rourke, D.H., 2004b. Sealing, whaling, and caribou: the skeletal isotope chemistry of Eastern Arctic foragers. *Journal of Archaeological Science* 31, 39–57.
- Coppedge, B.R., Leslie Jr., D.M., Shaw, J.H., 1998. Botanical composition of bison on tallgrass prairie in Oklahoma. *Journal of Range Management* 51, 379–382.
- Cormie, A.B., Schwarcz, H.P., 1994. Stable isotopes of nitrogen and carbon of North American white-tailed deer and implications for paleodietary and other food web studies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107, 227–241.
- Drucker, D., Bocherens, H., Bridault, A., Billiou, D., 2003a. Carbon and nitrogen isotopic composition of red deer (*Cervus elaphus*) collagen as a tool for tracking palaeoenvironmental change during Lateglacial and Early Holocene in northern Jura (France). *Palaeogeography, Palaeoclimatology, Palaeoecology* 195, 375–388.
- Drucker, D.G., Bocherens, H., Billiou, D., 2003b. Evidence for shifting environmental conditions in Southwestern France from 33,000 to 15,000 years ago derived from carbon-13 and nitrogen-15 natural abundances in collagen of large herbivores. *Earth and Planetary Science Letters* 216, 163–173.
- Drummond, A.J., Rambaut, A., Shapiro, B., Pybus, O.G., 2005. Bayesian coalescent inference of past population dynamics from molecular sequences. *Molecular Biology and Evolution* 22, 1185–1192.
- Edwards, M.E., Barker, E.D., 1994. Climate and vegetation in northeastern Alaska 18,000 yr B.P.–Present. *Palaeogeography, Palaeoclimatology, Palaeoecology* 109, 127–135.
- Edwards, M.E., Mock, C.J., Finney, B.P., Barber, V.A., Bartlein, P.J., 2001. Modern-climate analogues for paleoclimatic variations in eastern interior Alaska during the past 14,000 years: atmospheric-circulation controls of regional temperature and moisture responses. *Quaternary Science Reviews* 20, 189–202.
- Ehleringer, J.R., 1991. $^{13}\text{C}/^{12}\text{C}$ Fractionation and its utility in terrestrial plant studies. In: Coleman, D.C., Fry, B. (Eds.), *Carbon Isotope Techniques*. Academic Press Inc, pp. 187–200.
- Ehleringer, J.R., Monson, R.K., 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. *Annual Review of Ecology and Systematics* 24, 411–439.
- Elias, S.A., 2001. Beringian paleoecology: results from the 1997 workshop. *Quaternary Science Reviews* 20, 7–13.
- Fizet, M., Mariotti, A., Bocherens, H., Lange-Badre, B., Vandermeersch, B., Borel, J.B., Bellon, G., 1995. Effect of diet, physiology and climate on carbon and nitrogen stable isotopes of collagen in a late Pleistocene anthropic paleoecosystem: Marillac, Charente, France. *Journal of Archaeological Science* 22, 67–79.
- Fox-Dobbs, K., Stidham, T.A., Bowen, G.J., Emslie, S.D., Koch, P.L., 2006. Dietary controls on extinction versus survival among avian megafauna in the late Pleistocene. *Geology* 34, 685–688.
- Fox-Dobbs, K., Bump, J.K., Peterson, R.O., Fox, D.L., Koch, P.L., 2007. Carnivore-specific stable isotope variables and variation in the foraging ecology of past and present wolf populations: case studies from Isle Royale, Minnesota and La Brea. *Canadian Journal of Zoology* 85, 458–471.
- Graham, R.W., Lundelius, E.L., 1984. Coevolutionary disequilibrium and Pleistocene extinctions. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions: A Prehistoric Revolution*. The University of Arizona Press, Tucson, Arizona, pp. 223–249.
- Gröcke, D.R., Bocherens, H., Mariotti, A., 1997. Annual rainfall and nitrogen-isotope correlation in macropod collagen: applications as a paleoprecipitation indicator. *Earth and Planetary Science Letters* 160, 279–285.
- Guthrie, R.D., 1968. Palaeoecology of the large-mammal community in interior Alaska during the late Pleistocene. *American Midland Naturalist* 70, 346–363.
- Guthrie, R.D., 1984. Mosaics, allelochemicals, and nutrients: an ecological theory of late Pleistocene megafaunal extinctions. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions*. University of Arizona Press, Tucson, Arizona, pp. 259–298.
- Guthrie, R.D., 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews* 20, 549–574.
- Guthrie, R.D., 2003. Rapid body size decline in Alaskan Pleistocene horses before extinction. *Nature* 426, 169–171.
- Guthrie, R.D., 2006. New carbon dates link climatic change with human colonization and Pleistocene extinctions. *Nature* 44, 207–209.
- Handley, L.L., Austin, A.T., Robinson, D., Scrimgeour, C.M., Raven, J.A., Heaton, T.H.E., Schmidt, S., Stewart, G.R., 1999. The ^{15}N natural abundance of ($\delta^{15}\text{N}$) of ecosystem samples reflects measures of water availability. *Australian Journal of Plant Physiology* 26, 185–199.
- Heaton, T.H.E., 1987. The $^{15}\text{N}/^{14}\text{N}$ ratios of plants in South Africa and Namibia: relationship to climate and coastal/saline environments. *Oecologia* 74, 236–246.
- Heaton, T.H.E., Vogel, J.C., von la Chevallerie, G., Collett, G., 1986. Climatic influence on the isotopic composition of bone nitrogen. *Nature* 322, 822–823.
- Hedges, R.E.M., Stevens, R.E., Richards, M.P., 2004. Bone as a stable isotope archive for local climatic information. *Quaternary Science Reviews* 23, 959–965.
- Higham, T.F.G., Jacobi, R.M., Ramsey, C.B., 2006. AMS radiocarbon dating of ancient bone using ultrafiltration. *Radiocarbon* 48, 179–195.
- Hilderbrand, G.V., Farley, S.D., Robbins, C.T., Hanley, T.A., Titus, K., Servheen, C., 1996. Use of stable isotopes to determine diets of living and extinct bears. *Canadian Journal of Zoology* 74, 2080–2088.
- Hobson, K.A., McLellan, B.N., Woods, J.G., 2000. Using stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River basin, British Columbia. *Canadian Journal of Zoology* 78, 1332–1339.
- Hoppe, K.A., Amundson, R., Vavra, M., McClaran, M.P., Anderson, D.L., 2004. Isotopic analysis of tooth enamel carbonate from modern North American

- feral horses: implications for paleoenvironmental reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 203, 299–311.
- Iacumin, P., Nikolaev, V., Ramigni, M., 2000. C and N stable isotope measurements on Eurasian fossil mammals, 40,000 to 10,000 years BP: herbivore physiologies and paleoenvironmental reconstruction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 163, 33–47.
- Ihl, C., Klein, D.R., 2001. Habitat and diet selection by muskoxen and reindeer in western Alaska. *Journal of Wildlife Management* 65, 964–972.
- Koch, P.L., 1991. The isotopic ecology of Pleistocene proboscideans. *Journal of Vertebrate Paleontology* 11, 40A.
- Koch, P.L., 2007. Isotopic study of the biology of modern and fossil vertebrates. In: Lajtha, K., Michener, B. (Eds.), *Stable Isotopes in Ecology and Environmental Science*. Blackwell Scientific Publication, Boston, Massachusetts.
- Koch, P.L., Barnosky, A.D., 2006. Late Quaternary extinctions: state of the debate. *Annual Review of Ecology, Evolution, and Systematics* 37, 215–250.
- Larter, N.C., Nagy, J.A., 2001. Seasonal and annual variability in the quality of important forage plants on Banks Island, Canadian High Arctic. *Applied Vegetation Science* 4, 115–128.
- Leonard, J.A., Wayne, R.K., Cooper, A., 2000. Population genetics of Ice Age brown bears. *Proceedings of the National Academy of Sciences* 97, 1651–1654.
- Leonard, J.A., Vila, C., Fox-Dobbs, K., Koch, P.L., Wayne, R.K., Van Valkenburgh, B., 2007. Cryptic extinction of Pleistocene Alaskan wolves: evidence from genetics, isotopes, and morphology. *Current Biology* 17, 1146–1150.
- Lozhkin, A.V., Anderson, P.M., Eisner, W.R., Ravako, L.G., Hopkins, D.M., Brubaker, L.B., Colinvaux, P.A., Miller, M.C., 1993. Late quaternary lacustrine pollen records from Southwestern Beringia. *Quaternary Research* 39, 314–332.
- MacPhee, R.D.E., Tikhonov, A.N., Mol, D., Greenwood, A.D., 2005. Late Quaternary loss of genetic diversity in muskox (*Ovibos*). *BMC Evolutionary Biology* 49, 1–13.
- Matheus, P.E., 1995. Diet and co-ecology of Pleistocene short-faced bears and brown bears in eastern Beringia. *Quaternary Research* 44, 447–453.
- Matheus, P.E., 1997. Paleoecology and ecomorphology of the giant short-faced bear in eastern Beringia. Ph.D. Thesis. University of Alaska, Fairbanks.
- Nadelhoffer, K., Shaver, G., Fry, B., Giblin, A., Johnson, L., McKane, R., 1996. ^{15}N natural abundances and N use by tundra plants. *Oecologia* 107, 386–394.
- Phillips, R.L., Grantz, A., 2001. Regional variations in provenance and abundance of ice-rafted clasts in Arctic Ocean sediments: implications for the configuration of late Quaternary oceanic and atmospheric circulation in the Arctic. *Marine Geology* 172, 91–115.
- Phillips, D.L., Gregg, J.W., 2003. Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136, 261–269.
- Reimer, P.J., Baillie, M.G.L., Bard, E., Beck, J.W., Blackwell, P.G., Buck, C.E., Burr, G.S., Edwards, R.L., Guilderson, T.P., Hogg, A.G., Hughen, K.A., Kromer, B., McCormac, G., Manning, S., Reimer, R.W., Southon, J.R., Stuiver, M., van der Plicht, J., Weyhenmeyer, C.E., 2006. Comment on “Radiocarbon calibration curve spanning 0 to 50,000 years b.p. based on paired $^{230}\text{Th}/^{234}\text{U}/^{238}\text{U}$ and ^{14}C dates on pristine corals” by R.G. Fairbanks, R.A. Mortlock, T.-C. Chiu, L. Cao, A. Kaplan, T.P. Guilderson, T.W. Fairbanks, A.L. Bloom, P.M. Grootes, and M.-J. Nadeau and “Extending the radiocarbon calibration beyond 26,000 years before present using fossil corals” by T.-C. Chiu, R.G. Fairbanks, R.A. Mortlock, and A.L. Bloom. *Quaternary Science Reviews* 25, 855–862.
- Richards, M.P., Hedges, R.E.M., 2003. Variations in bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in fauna from northwestern Europe over the last 40,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* 193, 261–267.
- Sealy, J.C., Van Der Merwe, N.J., Lee Thorpe, J.A., Lanham, J.L., 1987. Nitrogen isotopic ecology in southern Africa: implications for environmental and dietary tracing. *Geochimica et Cosmochimica Acta* 51, 2707–2717.
- Shapiro, B., Drummond, A.J., Rambaut, A., Wilson, M.C., Matheus, P.E., Sher, A.V., Pybus, O.G., Gilbert, M.T.P., Barnes, I., Binladen, J., Willerslev, E., Hansen, A.J., Baryshnikov, G.F., Burns, J.A., Davydov, S., Driver, J.C., Froese, D.G., Harington, C.R., Keddie, G., Kosintsev, P., Kunz, M.L., Martin, L.D., Stephenson, R.O., Storer, J., Tedford, R., Zimov, S., Cooper, A., 2004. Rise and fall of the Beringian steppe bison. *Science* 306, 1561–1565.
- Solounias, N., Muhlbacher, M., Rivals, F., Blondel, C., Guthrie, D., 2004. Evaluation of diet in mammoths and other late Pleistocene and early Holocene ungulates from Alaska. *Journal of Vertebrate Paleontology* 24, 116A.
- Sponheimer, M., Robinson, T., Ayliffe, L., Roeder, B., Hammer, J., Passey, B., West, A., Cerling, T., Dearing, D., Ehleringer, J.R., 2003. Nitrogen isotopes in mammalian herbivores: hair $\delta^{15}\text{N}$ values from a controlled feeding study. *International Journal of Osteoarchaeology* 13, 80–87.
- Stevens, R.E., Hedges, R.E.M., 2004. Carbon and nitrogen stable isotope analysis of Northwest European horse bone and tooth collagen, 40,000 BP–present. *Quaternary Science Reviews* 23, 977–991.
- Swap, R.J., Aranibar, J.N., Dowty, P.R., Gilhooly III, W.P., Macko, S.A., 2004. Natural abundance of ^{13}C and ^{15}N in C_3 and C_4 vegetation of southern Africa: patterns and implications. *Global Change Biology* 10, 350–358.
- Szepanski, M.M., Ben-David, M., Van Ballenberghe, V., 1999. Assessment of anadromous salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis. *Oecologia* 120, 327–335.
- Walker, D.A., Bockheim, J.G., Chapin, F.S., Eugster, W., Nelson, F.E., Ping, C.L., 2001. Calcium-rich tundra, wildlife and the “Mammoth Steppe”. *Quaternary Science Reviews* 20, 149–163.
- Ward, J.K., Harris, J.M., Cerling, T.E., Wiedenhoef, A., Lott, M.J., Dearing, M.D., Coltrain, J.B., Ehleringer, J.R., 2005. Carbon starvation in glacial trees recovered from the La Brea tar pits, southern California. *Proceedings of the National Academy of Sciences* 102, 690–694.
- Wilson, D.E., Ruff, S. (Eds.), 1999. *The Smithsonian Book of North American Mammals*. Smithsonian Institution Press, Washington D.C.
- Wooller, M.J., Zazula, G., Edwards, M., Froese, D., Boone, R., Parker, C., Bennett, B., 2007. Stable carbon isotope compositions of Eastern Beringian grasses and sedges: investigating their potential as paleoenvironmental indicators. *Arctic, Antarctic, and Alpine Research* 39, 318–331.
- Zazula, G.D., Froese, D.G., Schweger, C.E., Mathewes, R.W., Beaudoin, A.B., Telka, A.M., Harington, C.R., Westgate, J.A., 2003. Ice age steppe vegetation in east Beringia. *Nature* 423, 603.
- Zazula, G.D., Froese, D.G., Elias, S.A., Kuzmina, S., Mathewes, R.W., 2007. Arctic ground squirrels of the mammoth-steppe: paleoecology of Late Pleistocene middens (~24000–29450 ^{14}C yr BP), Yukon Territory, Canada. *Quaternary Science Reviews* 26, 979–1003.