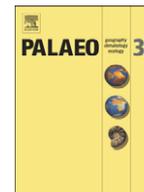




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Regional differences in bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Pleistocene mammoths: Implications for paleoecology of the mammoth steppe

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ABSTRACT

In this study, we present bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from a large set of Pleistocene woolly mammoths (*Mammuthus primigenius*) from Siberia, Alaska and Yukon. Overall, results for mammoth specimens from eastern Beringia (Alaska and Yukon) significantly differ, for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, from those from western Beringia (northeastern Siberia). In agreement with palynological, entomological, and physiographic data from the same regions, these isotopic differences strongly imply that the 'mammoth steppe,' the extensive ice-free region spanning northern Eurasia and northwestern North America, was ecologically variable along its east–west axis to a significant degree. Prior to the Last Glacial Maximum (LGM), the high-latitude portions of Siberia and the Russian Far East appear to have been colder and more arid than central Alaska and Yukon, which were ecologically more diverse. During the LGM itself, however, isotopic signatures of mammoths from eastern Beringia support the argument that this region also experienced an extremely cold and arid climate. In terms of overall temporal trend, Beringia thus went from a condition prior to the LGM of greater ecological variability in the east to one of uniformly cold and dry conditions during the LGM.

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1. Introduction

During the last glaciation, sea levels were considerably lower than at present, and Alaska and Siberia were connected by the exposed Bering Land Bridge (BLB). Beringia, the more extensive region of which the BLB was a part, extended from the Northwest Territories in northern Canada to the Kolyma River in northeastern Siberia (Hoffecker and Elias, 2007). Beringia was in turn a major component of the mammoth steppe, an even larger megacontinental biome initially described by Guthrie (1968) as stretching continuously from western Europe to North America.

The fauna of the Late Pleistocene mammoth steppe was markedly different than that of modern high-latitude ecosystems, with numerous large herbivores such as woolly mammoth (*Mammuthus primigenius*), bison (*Bison* sp.) and horse (*Equus* sp.) thriving across the

landscape (Guthrie, 1982; Guthrie, 1990). Faunal continuities suggest, but do not demonstrate, that the mammoth steppe was functionally similar across this vast area. Indeed, although low-growing herbaceous plants (grasses, sedges, forbs and sages) dominated the landscape of the mammoth steppe (Guthrie, 2001b), this biome was characterized by considerable regional variability in floral elements (Guthrie, 1990; Elias et al., 1997; Guthrie, 2001b; Zazula et al., 2007). More formally, Guthrie (1982) described the mammoth steppe as a mosaic of locally unique elements contributing to a series of related habitats, reflecting both the continuity of faunal elements and the variability in ecological conditions characteristic of this biome.

The existence of marked environmental differences between eastern and western Beringia during the Late Pleistocene is of considerable faunistic and ecological interest. Guthrie (2001b) posited that central Beringia acted as an ecological 'buckle' of more mesic climatic conditions that served as a strong filter or even a complete barrier to some steppe-adapted species. Arguably, this mesic buckle prevented the xeric-adapted Eurasian woolly rhinoceros (*Coelodonta antiquitatus*), whose range extended at least as far east as Chukotka, from migrating eastward across the Bering Isthmus toward the Americas. Similarly, the range of the Pleistocene North American

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camel (*Camelops hesternus*) continued into the valley of the Yukon River, but apparently no further.

In general, the area to the west of this proposed mesic zone has been reconstructed as cold and very dry during the interval leading up to the LGM, with the landscape dominated by herbaceous steppe-tundra. The Middle Valdai glacial period (50 ka–24 ka [thousand calendar years] BP) was characterized by relatively few major climatic oscillations, with a trend toward increasing aridity and decreasing temperature that apparently peaked during the LGM ca. 21.5 ka (Iacumin et al., 2000). Numerous lines of evidence, including pollen records (Lozhkin et al., 1993), macrobotanical remains (Schirmer et al., 2002), and invertebrate taxa (Kuzmina and Sher, 2006), support the argument that Western Beringia (northeastern Siberia) was extremely cold and arid during the LGM. Paleoenvironmental reconstructions from the Berelekh Site in the Allahovsk Region of the Sakha Republic (Yakutia) indicate a dry, steppe-tundra environment with herbaceous species (~90%) dominating pollen spectra after the LGM (Müller-Beck, 1982).

Further to the west, the Taimyr Peninsula was also characterized by cold and dry conditions before and during the LGM. Plant macrofossils from the northwest shore of Lake Taimyr dating to 34 ka, 31 ka and 20 ka BP indicate very dry conditions, with herb-steppe-tundra elements being most prevalent (Kienast et al., 2001). Pollen assemblages dating to the end of the Middle Valdai (30 ka–22 ka BP) from the Taimyr Peninsula also indicate cold steppe-tundra (Kienast et al., 1999). Although during the Middle Valdai the Taimyr Peninsula exhibited somewhat heterogeneous environmental conditions, with three warm and two cold stages, this area can still be characterized as cold and arid, with consistently low mean annual precipitation (400–450 mm annually) throughout the region (Drozov and Chekha, 2006).

Paleoecological data for the area to the east of the mid-isthmian mesic buckle (Alaska and Yukon) also imply the predominance of cryoxerophilous herb-tundra or steppe-tundra, though with a greater proportion of mesic habitats than western Beringia. Pollen data from western Alaska indicate the dominance of graminoid herb-tundra flourishing under cold, dry conditions prior to and during the LGM (Ager, 2003). Plant macrofossils from an *in situ* vegetated surface that was buried by volcanic ash on the Seward Peninsula confirms the presence of a xerophilous sedge dominated herb-tundra in western Alaska during the LGM (Goetcheus and Birks, 2001). Plant and insect macrofossils from a variety of contexts in central and northern Yukon and dating from 30 ka to 16 ka BP are indicative of cold, dry herbaceous steppe conditions at the regional scale (Zazula et al., 2003). LGM pollen data from northeastern Yukon suggest extreme conditions with sparse fell-field tundra (Kozhevnikov and Ukraintseva, 1997). Loess deposits in western and interior Alaska also signal the predominance of cold, arid conditions through the Late Pleistocene (Muhs et al., 2003).

The distribution of fossil insect faunas indicates diverse ecological conditions throughout eastern Beringia in the Late Pleistocene. Aquatic beetles were found to be abundant in eastern Beringia, but almost entirely absent from its western end (Elias et al., 2000). Furthermore, it has been suggested that southwestern Alaska was a refugium for mesic and hygrophilous beetle species before, during and after the LGM, while northern and interior Alaska contained a much higher number of xeric and steppe-adapted species (Elias, 1992). In general, paleoecological reconstructions indicate a higher level of environmental variability to the east of the Bering Isthmus, with evidence of both mesic and xeric conditions; by contrast, mesic indicator species are lacking for all of the Late Pleistocene in Siberia.

2. Stable isotopes in bone collagen

Stable isotopes of bone collagen offer a direct way to analyze the diet and ecology of extinct and extant fauna. Because both carbon and

nitrogen in bone collagen are derived directly from the diet (Ambrose and Norr, 1993), the isotopic signatures recorded in these molecules are ideal for paleodietary and paleoecological studies.

A number of factors can influence the $\delta^{15}\text{N}$ values of bone collagen within a trophic level or a single taxon. It has been noted that species that excrete very concentrated urea in their urine tend to recycle nitrogen, which leads to elevated $\delta^{15}\text{N}$ values (Ambrose and DeNiro, 1986). This is likely related to drought tolerance, since in some mammalian species (including African elephants) there is a strong negative correlation between $\delta^{15}\text{N}$ values and local precipitation (Sealy et al., 1987; van der Merwe et al., 1990; Vogel et al., 1990; Gröcke et al., 1997; Schwarcz et al., 1999; Pate and Anson, 2008). An enrichment in plant $\delta^{15}\text{N}$ values at more arid locales has also been observed, although this relationship is not as strong as it is in animals (Heaton, 1987). In addition to drought stress, nutritional or protein stress may lead to elevated $\delta^{15}\text{N}$ values in animal tissues (Hobson et al., 1993; Fuller et al., 2005).

Bone collagen $\delta^{13}\text{C}$ values are informative with respect to the contribution of C_3 and C_4 forage to the diet (DeNiro and Epstein, 1978). Grazers and browsers can be differentiated on the basis of $\delta^{13}\text{C}$ values, with the former having tissues that are less depleted in ^{13}C than the latter (Ambrose and DeNiro, 1986). Moreover, because of the depletion in ^{13}C that is characteristic of plants in heavily forested areas (van der Merwe and Medina, 1991), animals living in forested and open environments can also be identified using $\delta^{13}\text{C}$ values in bones, teeth and other tissues (Cerling et al., 2004). With respect to plants, a negative correlation is thought to exist between annual rainfall and $\delta^{13}\text{C}$ values in some C_3 species (Stewart et al., 1995), but other studies have found only weak or no correlation (e.g. Swap et al., 2004). Low temperatures are also thought to produce more negative $\delta^{13}\text{C}$ values in plants due to reduced CO_2 uptake (Tieszen, 1991).

Previous isotopic data from woolly mammoth bone collagen suggest regional differences in carbon and nitrogen isotopic signatures (Koch, 1991; Bocherens et al., 1994; Bocherens et al., 1996; Iacumin et al., 2000; Fox-Dobbs et al., 2008). Specifically, mammoths from Siberia tend to be more depleted in ^{13}C and more enriched in ^{15}N than those from Alaska. These patterns are suggestive of climatic or environmental differences that may mirror the data obtained from other paleoecological indicators. Our aim in this study was to establish, from isotopic evidence, whether any ecological or dietary differences could be distinguished between mammoths living in eastern and western Beringia.

3. Methods

Bone collagen was extracted using a modified Longin method (Longin, 1971), as has been described previously (Szpak et al., 2009). Briefly, bone fragments (50–450 mg) were sampled using a hammer and chisel. Any visible foreign material was cleaned with a small brush and/or a brief treatment in an ultrasonic bath. Samples were soaked in chloroform-methanol (2:1 v:v, 4 ml) to remove lipids. Following cleaning and lipid extraction, samples were dried and reduced to fragments 1.0 mm to 2.0 mm in diameter.

Bone fragments were soaked in 0.50 M HCl at room temperature until the bone was completely demineralized. They were rinsed with MQ water and treated with 0.1 M NaOH for 30 min to remove humic acids. Samples were then neutralized with MQ water, rinsed with 0.25 M HCl and finally with MQ water, leaving the insoluble collagen residue in a slightly acidic solution. The solution containing the insoluble residue was heated in sealed glass tubes at $80 \pm 2^\circ\text{C}$ and then dried. The extracted collagen was then transferred into tin cups for isotopic analysis. Stable isotope values of bone collagen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and relative percentages of carbon and nitrogen were determined using a Thermo Finnigan Delta^{PLUS} XP continuous flow mass spectrometer coupled to a Costech elemental analyzer at McMaster University. Stable carbon and nitrogen isotope ratios are reported

versus VPDB and atmospheric nitrogen respectively. All samples were analyzed in at least duplicate and standard deviation was better than ± 0.1 for $\delta^{13}\text{C}$ and ± 0.2 for $\delta^{15}\text{N}$ measurements.

4. Results

Mammoth samples were obtained primarily from three geographic regions (Fig. 1): eastern Beringia (central Alaska and Yukon), north-central Siberia (Taimyr Peninsula) and northeastern Siberia (Yakutia or Sakha Republic). Fifty-eight samples of woolly mammoth bone collagen were analyzed for stable carbon and nitrogen isotope ratios, forty-seven of which have been radiocarbon dated (Guthrie, 2006; Debruyne et al., 2008). The specimens were derived from a large temporal span, ranging in age from >51 ka–5 ka BP. All isotopic measurements, relative percentages of carbon and nitrogen and collagen yields are presented in Table 1.

It is generally accepted that the relative abundances of carbon and nitrogen (C:N ratio) of bone collagen can be used to determine whether postmortem alteration of the collagen has occurred. All samples analyzed had C:N ratios between 2.9 and 3.6 (see Table 1), which are typically assumed to be indicative of well-preserved collagen (DeNiro, 1985).

Mammoth $\delta^{13}\text{C}_{\text{coll}}$ values ranged from -23.2 to -20.3‰ , and $\delta^{15}\text{N}_{\text{coll}}$ ranged from 4.4 to 11.4‰. Siberian mammoths recorded $\delta^{13}\text{C}_{\text{coll}}$ values that are more ^{13}C depleted ($-21.9 \pm 0.5\text{‰}$, $N=32$) than mammoths from Alaska and Yukon ($-20.7 \pm 0.3\text{‰}$, $N=26$). Additionally, Siberian mammoths recorded more elevated $\delta^{15}\text{N}_{\text{coll}}$ values (9.3 ± 1.0) than Alaskan/Yukon mammoths ($7.2 \pm 1.3\text{‰}$). These differences are graphically illustrated in Fig. 2.

5. Discussion

5.1. Stable nitrogen isotopes in *Mammuthus primigenius*

The average $\delta^{15}\text{N}_{\text{coll}}$ values obtained for *Mammuthus primigenius* in this study ($8.4 \pm 1.6\text{‰}$) are relatively high for herbivores. Although no coeval species were analyzed in this study, data from previous analyses indicate that mammoths in general exhibit higher $\delta^{15}\text{N}_{\text{coll}}$ values than other herbivores (Bocherens et al., 1996; Iacumin et al., 2000). While a physiological explanation for the high $\delta^{15}\text{N}_{\text{coll}}$ values of Pleistocene mammoths has been suggested (Matheus et al.,

2003), the nature of this mechanism has yet to be satisfactorily explained.

Preserved stomach contents from frozen mammoth carcasses are dominated by high-fibre, low-protein forage (mainly graminoids), but also include the leaves of some other forbs, shrubs and a minor amount of moss (Ukrainitseva et al., 1996). On the basis of digestive physiology, Guthrie and Stoker (1990) noted that mammoths were capable of tolerating diets composed of extremely low quantities of protein as long as sufficient quantities of forage were available. Because $\delta^{15}\text{N}_{\text{coll}}$ values are affected by the quality of dietary intake, this general trend toward elevated $\delta^{15}\text{N}_{\text{coll}}$ values in mammoths might reflect a relatively nutrient-poor and/or protein-deficient diet. It has been noted that herbaceous vegetation tends to produce relatively high $\delta^{15}\text{N}$ values relative to woody vegetation (Delwiche et al., 1979). Modern Alaskan grasses in particular exhibit relatively high $\delta^{15}\text{N}$ values, possibly due to rooting depth and organic matter utilization (Schulze et al., 1994). As such, a diet composed mainly of low quality herbaceous and graminoid forage is likely an important factor contributing to the elevated $\delta^{15}\text{N}_{\text{coll}}$ values observed in mammoths.

Aside from generally high $\delta^{15}\text{N}_{\text{coll}}$ values in mammoths, a clear separation between Siberian and eastern Beringian mammoths was also evident and is statistically significant (Student's *t*-test; $\alpha=7.17$ for $v=56$, $p<0.0001$). By contrast, there were no significant differences between Alaskan and Yukon samples ($\alpha=1.34$ for $v=24$, $p=0.19$) or between samples from eastern Siberia and the Taimyr Peninsula ($\alpha=0.28$ for $v=29$, $p=0.78$). This is suggestive of different ecological conditions on either side of the Bering Isthmus, with (as explained below) western Beringia experiencing more arid conditions throughout the Late Pleistocene than eastern Beringia.

Water availability has been demonstrated to affect both plant and soil $\delta^{15}\text{N}$ values (Delwiche et al., 1979; Heaton, 1987). Soils and vegetation at drier sites lose relatively less ^{15}N and are characterized by more open cycling of nitrogen (Swap et al., 2004). Because the protein and nitrogen content of plants in arid environments tend to be lower than those in wetter regions, herbivores consuming these plants are more likely to recycle urea in order to conserve nitrogen, which would cause the tissues of these herbivores to be more enriched in ^{15}N (Sealy et al., 1987).

Recently, a strong negative correlation between $\delta^{15}\text{N}$ values and modern annual precipitation was found in woolly mammoth hair



Fig. 1. Map showing sample locations. (1) Taimyr Peninsula, (2) Yakutia, (3) Gydan Peninsula, (4) Wrangel Island, and (5) Central Alaska and Yukon.

Table 1
Isotopic and relevant contextual data for all analyzed woolly mammoths.

Sample #	Locality	Site	Latitude	Longitude	Age (years BP)	% collagen	%C	%N	C:N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	
AM 1114	Eastern Beringia (Alaska)	Ester Creek	64° 50'N	148° 00'W	59,583	13.2	40.5	14.9	3.2	-20.5	5.0	
AM 1208	Eastern Beringia (Alaska)	Sullivan Creek	65° 10'N	151°W	15,047	11.4	34.7	12.2	3.3	-20.8	5.9	
AM 2446	Eastern Beringia (Alaska)	Cripple Creek	64° 60'N	148°W	30,889	3.0	38.5	13.0	3.5	-20.8	6.4	
AM 523	Eastern Beringia (Alaska)	Cleary Creek	65° 10'N	147° 30'W	47,030	2.9	25.8	8.7	3.5	-20.8	4.4	
AM 8052	Eastern Beringia (Alaska)	Cleary Creek	65° 10'N	147° 30'W	22,019	19.8	36.9	13.6	3.2	-21.0	7.0	
NMC 42135	Eastern Beringia (Alaska)	Eldorado Creek	64° 50'N	147° 40'W	34,276	13.4	37.9	14.0	3.2	-20.7	7.8	
NMC 6746	Eastern Beringia (Alaska)	Tanana	65° 18'N	151° 54'W	27,745	14.5	35.8	13.4	3.1	-21.0	9.7	
NMC 42292	Eastern Beringia (Yukon)	Dawson	64° 03'N	139° 25'W	41,782	13.7	39.4	13.5	3.4	-20.6	7.9	
NMC 49562	Eastern Beringia (Yukon)	Paron's Lake	-	-	>50,867	23.3	40.2	14.0	3.4	-21.3	5.8	
NMC 49927	Eastern Beringia (Yukon)	Dawson	64° 03'N	139° 25'W	50,002	19.9	37.8	13.3	3.3	-20.4	8.7	
NMC 49928	Eastern Beringia (Yukon)	Dawson	64° 03'N	139° 25'W	>49,485	19.7	37.3	13.0	3.3	-20.3	6.9	
YU 130.2	Eastern Beringia (Yukon)	Quartz Creek	63° 49'N	139° 02'W	41,653	13.3	35.0	12.4	3.3	-20.5	6.6	
YU 133.18	Eastern Beringia (Yukon)	Whitman Gulch	63° 43'N	138° 38'W	36,537	17.8	39.5	14.8	3.1	-20.7	8.1	
YU 136.9	Eastern Beringia (Yukon)	Sulphur Creek	63° 44'N	138° 50'W	49,985	12.9	41.1	14.5	3.3	-20.8	7.5	
YU 137.3	Eastern Beringia (Yukon)	Whitman Gulch	63° 43'N	138° 38'W	43,724	13.0	31.0	11.0	3.3	-20.5	7.3	
YU 3.133	Eastern Beringia (Yukon)	Finning	63° 50'N	138° 15'W	33,495	22.8	38.5	13.6	3.3	-20.5	7.2	
YU 3.135	Eastern Beringia (Yukon)	Finning	63° 50'N	138° 15'W	49,709	16.5	39.7	13.8	3.4	-20.6	6.4	
YU 3.136	Eastern Beringia (Yukon)	Finning	63° 50'N	138° 15'W	33,598	18.6	30.3	10.8	3.3	-20.9	7.1	
YU 3.19	Eastern Beringia (Yukon)	Finning	63° 50'N	138° 15'W	48,491	19.5	38.3	13.5	3.3	-20.6	5.7	
YU 3.229	Eastern Beringia (Yukon)	Finning	63° 50'N	138° 15'W		22.9	37.4	13.3	3.3	-20.5	7.1	
YU 3.256	Eastern Beringia (Yukon)	Finning	63° 50'N	138° 15'W	33,436	10.4	39.7	14.0	3.3	-20.6	6.8	
YU 5.130	Eastern Beringia (Yukon)	Hunker Creek	63° 59'N	139° 02'W	36,990	14.5	33.5	12.5	3.1	-20.6	6.9	
YU 5.46	Eastern Beringia (Yukon)	Hunker Creek	63° 59'N	139° 02'W	27,098	11.4	37.7	13.3	3.3	-21.0	9.4	
YU 5.69	Eastern Beringia (Yukon)	Hunker Creek	63° 59'N	139° 02'W	>51,282	13.2	36.7	13.0	3.3	-20.7	9.0	
YU 52.36	Eastern Beringia (Yukon)	Indian River	63° 46'N	139° 19'W	34,944	12.0	36.8	13.3	3.2	-20.9	6.4	
YU 57.1	Eastern Beringia (Yukon)	VGFN Foot	68° 11'N	140° 32'W	>51,652	n.d.	36.7	13.9	3.1	-21.2	9.3	
	Eastern Beringia (N=26)										-20.7 ± 0.2	7.2 ± 1.3
2000/173	Western Beringia (Siberia)	Arilakh	74° 25'N	107° 45'E	13,795	10.7	38.2	14.2	3.1	-22.5	9.1	
2000/174	Western Beringia (Siberia)	Arilakh	74° 25'N	107° 45'E	32,640	14.7	39.1	14.5	3.1	-21.7	10.7	
2000/183	Western Beringia (Siberia)	Lake Taimyr	74° 30'N	100° 30'E	32,672	12.2	40.5	15.0	3.2	-21.4	9.4	
2000/198	Western Beringia (Siberia)	Cape Sablera	74° 35'N	100° 30'E	18,466	16.3	37.1	13.7	3.2	-21.0	10.6	
2001/412	Western Beringia (Siberia)	Ari Mas	72°N	101°E	>47,755	7.6	41.1	15.2	3.2	-21.8	10.5	
2002/472	Western Beringia (Siberia)	Arilakh	74° 25'N	107° 45'E	>52,803	22.4	38.2	13.4	3.3	-22.0	10.0	
2002/473	Western Beringia (Siberia)	Arilakh	74° 25'N	107° 45'E	51,013	24.0	38.8	14.5	3.1	-22.0	11.4	
2002/594	Western Beringia (Siberia)	Arilakh	74° 25'N	107° 45'E		15.2	39.8	12.8	3.6	-23.2	7.8	
2005/897	Western Beringia (Siberia)	Baikura-Turku	74° 15'N	101° 20'E	43,920	20.1	38.4	13.6	3.3	-21.7	8.9	
2005/900	Western Beringia (Siberia)	Lake Taimyr	-	-	33,169	17.2	36.6	12.9	3.3	-21.9	9.7	
2005/901	Western Beringia (Siberia)	Lake Taimyr	-	-	20,763	20.0	39.9	14.2	3.3	-21.0	10.7	
2005/907	Western Beringia (Siberia)	Taimyr Peninsula	-	-	44,649	22.3	35.0	12.2	3.3	-22.1	8.1	
2005/915	Western Beringia (Siberia)	Baikura-Turku	73° 45'N	102° 00'E	32,312	26.2	36.7	13.6	3.1	-21.9	10.0	
2005/916	Western Beringia (Siberia)	Baikura-Turku	73° 45'N	102° 00'E		17.9	38.2	13.5	3.3	-21.7	8.9	
2005/917	Western Beringia (Siberia)	Baikura-Turku	73° 45'N	102° 00'E	40,246	14.7	35.4	12.5	3.3	-21.4	8.7	
2005/928	Western Beringia (Siberia)	Soposhnaya	72° 30'N	108° 00'E		20.9	36.4	11.9	3.6	-22.4	8.0	
2005/945	Western Beringia (Siberia)	Cape Sablera	73° 24'N	101° 39'E	24,008	25.2	37.3	13.1	3.3	-20.8	9.1	
2005/988	Western Beringia (Siberia)	Popigay	72° 38'N	106° 40'E		23.8	36.8	13.2	3.3	-21.6	8.4	
2005/999	Western Beringia (Siberia)	Popigay	72° 38'N	106° 40'E	>54,260	23.4	32.0	11.1	3.4	-22.0	7.5	
2006/001	Western Beringia (Siberia)	Oymyakon	63° 30'N	142° 45'E	44,800	23.9	36.7	13.6	3.1	-21.7	8.1	
BER 11	Western Beringia (Siberia)	Berelekh	70° 33'N	149° 03'E		20.4	39.8	14.6	3.2	-21.9	9.5	
BER 12	Western Beringia (Siberia)	Berelekh	70° 33'N	149° 03'E	14,545	18.2	37.8	13.5	3.3	-22.2	9.4	
BER 13	Western Beringia (Siberia)	Berelekh	70° 33'N	149° 03'E		26.4	38.1	13.6	3.3	-22.0	9.9	
BER 16	Western Beringia (Siberia)	Berelekh	70° 33'N	149° 03'E	14,416	23.4	37.8	13.2	3.3	-22.0	9.4	
BER 20	Western Beringia (Siberia)	Berelekh	70° 33'N	149° 03'E		23.0	36.4	12.9	3.3	-22.1	9.1	
BER 28	Western Beringia (Siberia)	Berelekh	70° 33'N	149° 03'E	14,146	11.9	43.7	15.0	3.4	-21.5	9.2	
BER 5	Western Beringia (Siberia)	Berelekh	70° 33'N	149° 03'E		24.4	40.5	14.8	3.2	-21.9	8.9	
BER 7	Western Beringia (Siberia)	Berelekh	70° 33'N	149° 03'E		16.2	38.5	13.4	3.4	-22.4	8.9	
BER 9	Western Beringia (Siberia)	Berelekh	70° 33'N	149° 03'E		19.0	33.9	12.0	3.3	-22.2	9.0	
GDY1	Western Beringia (Siberia)	Cydan Peninsula	71°N 79°E	18,136	18,136	18.9	44.1	15.4	3.3	-21.1	9.8	
SYU 3	Western Beringia (Siberia)	Sanga-Yuriakh	71° 20'N	151°E	>51,652	18.6	35.9	12.6	3.3	-22.6	10.9	
WR2	Western Beringia (Siberia)	Wrangel Island	71°N	179°W	5007	15.5	37.9	13.6	3.3	-22.2	8.6	
	Western Beringia (N=32)										-21.9 ± 0.5	9.3 ± 1.0

from northern Siberia (Iacumin et al., 2006). We suggest that the findings of this study are indicative of a similar pattern in Pleistocene mammoths on a larger scale, with the high $\delta^{15}\text{N}_{\text{coll}}$ values observed west of the Bering Isthmus being characteristic of drier steppe-tundra environments. Conversely, lower $\delta^{15}\text{N}_{\text{coll}}$ values of mammoths inhabiting eastern Beringia suggest that this area was more ecologically variable, containing more mesic habitats.

On the basis of the dimensions of glaciers and ice sheets, as well as their equilibrium line altitudes, western Beringia was likely more arid or colder (or both) than eastern Beringia in the Late Pleistocene (Elias

et al., 2000). Zazula et al. (2007) examined paleoecological proxies dating to ~28 ka BP from central Yukon and found that it was characterized by a high degree of local level ecological heterogeneity within a regional environment dominated by xeric steppe-tundra. Steppe-indicator beetle species were ubiquitous in Late Pleistocene assemblages from Siberia, even during interglacials, while this is not the case for eastern Beringia (Elias and Kuzmina, 2008). This suggests that northern Siberia was drier than eastern Beringia throughout much of the Late Pleistocene, which fits well with the elevated $\delta^{15}\text{N}_{\text{coll}}$ values observed for Siberian mammoths in this study. This does not

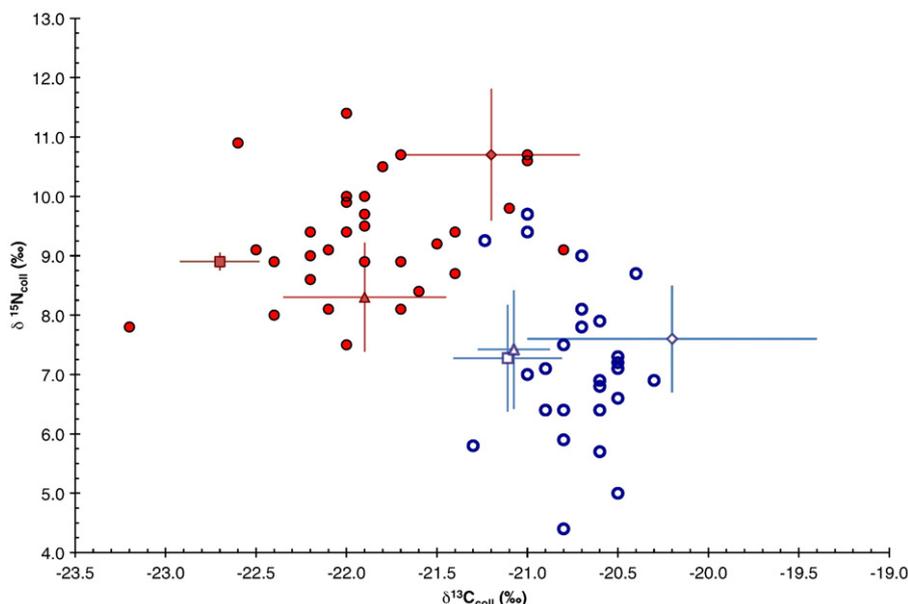


Fig. 2. Plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for mammoth bone collagen. Closed circles represent samples from Siberia, open circles represent samples from eastern Beringia (Alaska and Yukon). Additional data from Alaska (open diamond – Koch, 1991; open triangle – Fox-Dobbs et al., 2008; open square – Bocherens et al., 1994), Yakutia (closed diamond – Iacumin et al., 2000; closed square – Bocherens et al., 1996) and the Taimyr Peninsula (closed triangle – Iacumin et al., 2000) are shown \pm one standard deviation.

suggest that dry conditions and steppe-tundra were absent from eastern Beringia, but that moister habitats, characterized by more mesic vegetation, were more common than they were throughout Siberia. Thus, mammoths in eastern Beringia would have been more likely to encounter and feed in these mesic zones, which is reflected in the isotopic composition of their tissues.

5.2. Stable carbon isotopes in *Mammuthus primigenius*

The $\delta^{13}\text{C}_{\text{coll}}$ values for mammoths in this study are indicative of a diet based entirely on C_3 vegetation, which is consistent with paleobotanical reconstructions based on pollen and plant macrofossils from the region (Wooller et al., 2007). While the specimens analyzed in this study showed a very limited range in $\delta^{13}\text{C}_{\text{coll}}$ values, a clear distinction between mammoths on either side of the Bering Isthmus was observed, with Siberian mammoths being more depleted in ^{13}C than eastern Beringian mammoths. A Student's t -test confirms that this difference is statistically significant ($\alpha = 10.68$ for $v = 56$, $p < 0.0001$). Again, there was no significant difference between Alaskan and Yukon samples ($\alpha = 0.98$ for $v = 24$, $p = 0.34$) or between samples from eastern Siberia and the Taimyr Peninsula ($\alpha = 1.49$ for $v = 29$, $p = 0.15$).

The fact that the Siberian samples recorded more ^{13}C -depleted values was surprising since it has generally been noted that plant $\delta^{13}\text{C}$ values are positively correlated with aridity (Stewart et al., 1995). In addition to this, Wooller et al. (2007) examined $\delta^{13}\text{C}$ values of plants from eastern Beringia and found that plants inhabiting more arid environments exhibited higher $\delta^{13}\text{C}$ values than plants from wetter environments. Therefore, given the observed difference and interpretation in $\delta^{15}\text{N}_{\text{coll}}$ values, we would expect to see higher $\delta^{13}\text{C}_{\text{coll}}$ values in Siberian mammoths (i.e., those with the highest $\delta^{15}\text{N}_{\text{coll}}$ values). In this case, however, the exact opposite was observed.

There are likely several factors that combine to produce these seemingly conflicting values obtained for mammoth $\delta^{15}\text{N}_{\text{coll}}$ and $\delta^{13}\text{C}_{\text{coll}}$. While the data and interpretation of Wooller et al. (2007) suggest a positive correlation between $\delta^{13}\text{C}$ and aridity, they could only distinguish between wet and dry locations when the plant $\delta^{13}\text{C}$ value was $< -28\%$. Based on typical carbon isotope enrichment factors for mammalian herbivores (following Bocherens and Drucker, 2003), mammoths would have been consuming plants with $\delta^{13}\text{C}$

values between -25% and -20% . Thus, based on the model of Wooller et al. (2007) the $\delta^{13}\text{C}_{\text{coll}}$ values observed in this study are not likely to be indicative of either dry or wet conditions.

A large number of studies from a diverse geographical area have examined $\delta^{13}\text{C}$ values in tree rings and found positive correlations between $\delta^{13}\text{C}$ and temperature, although the basis for this relationship is not known (Heaton, 1999). Nikolaev et al. (2004) analyzed modern woody and herbaceous plants from Yakutia (Siberia) and found weak or no correlation between plant $\delta^{13}\text{C}$ and precipitation/relative humidity. Instead, they suggested that temperature was the controlling factor with respect to plant $\delta^{13}\text{C}$ values rather than moisture availability.

Because of atmospheric circulation and topography, temperatures in Siberia are generally much colder than are locations in Alaska and Yukon at similar latitudes. In the northern hemisphere, weather is strongly influenced by the two centers of semi-permanent atmospheric circulation: the Siberian High and Aleutian Low. The Siberian High produces extremely low temperatures in northeast Asia, including Siberia (Elias et al., 2000), while the Aleutian Low has a moderating effect on North American temperatures, bringing warm Pacific air masses into Alaska (Hoffecker and Elias, 2007). Furthermore, the Brooks and Richardson mountain ranges in the far north of North America act as barriers against cold Arctic air masses in the interior of Alaska and Yukon. Continental northeast Asia is directly exposed to these Arctic air masses and as a result, temperatures are significantly lower in Siberia (Elias et al., 2000). The atmospheric circulation affecting Late Pleistocene Beringia was likely similar to that of the present day (Alfimov and Berman, 2001). If the assertion that temperature affects $\delta^{13}\text{C}$ values in high-latitude plants, the $\delta^{13}\text{C}$ values observed for mammoths in this study may be a reflection of regional differences in mean annual temperature. The factors affecting $\delta^{13}\text{C}$ values in Arctic plants are, however, not well understood. Additional data from North America, Europe and Asia need to be collected to document potential environmental influences on high-latitude plant $\delta^{13}\text{C}$ values. In addition, isotopic analysis of plant macrofossils preserved in frozen carcasses of megafauna would greatly aid in the understanding of carbon cycling in Arctic plants throughout the Late Pleistocene.

An alternative, but related, explanation for this distinction in $\delta^{13}\text{C}_{\text{coll}}$ values in mammoths concerns variable reliance on seasonal fat

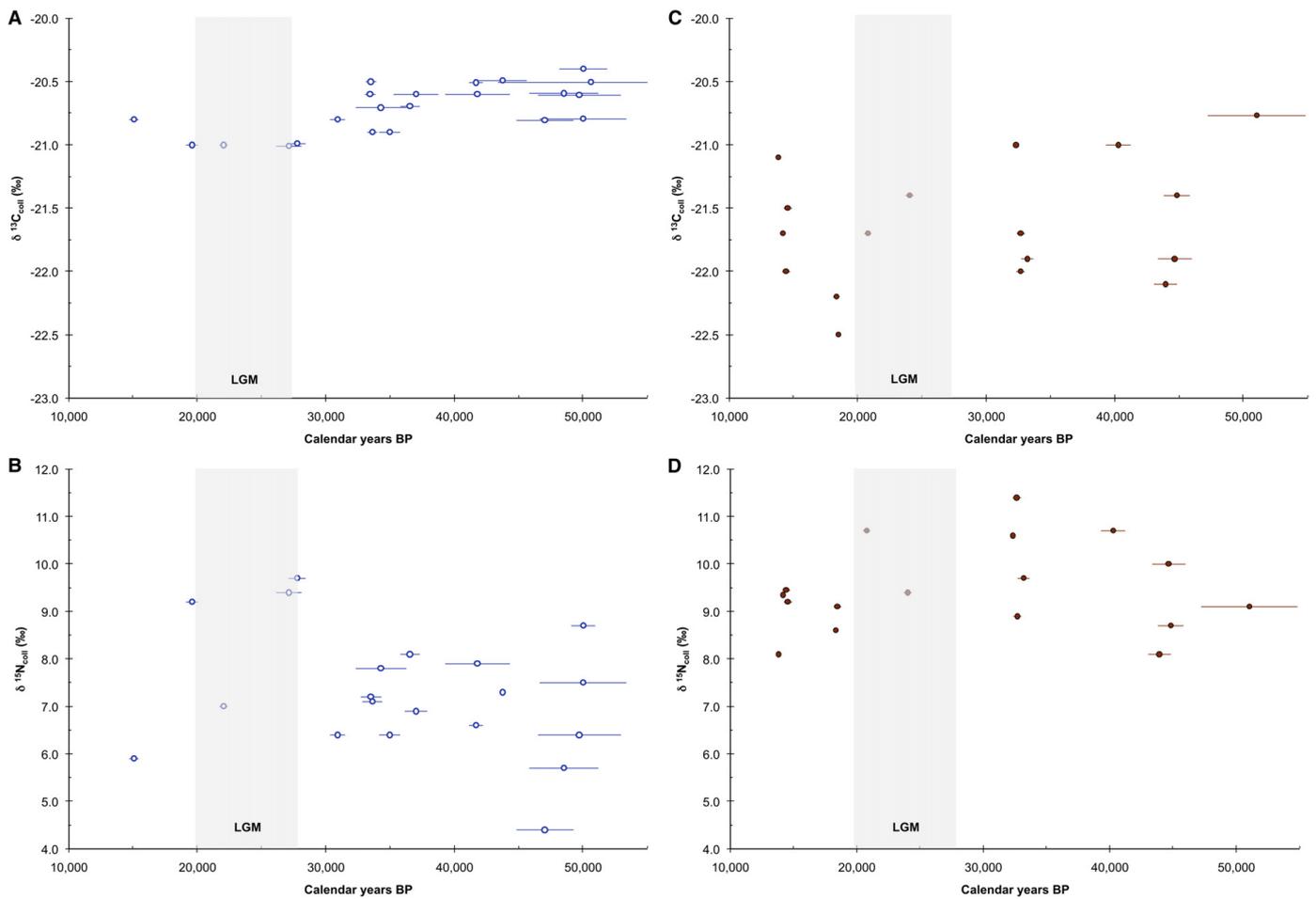


Fig. 3. Mammoth $\delta^{13}\text{C}_{\text{coll}}$ plotted against time for Beringian mammoths (A) and western Beringian mammoths (C). Mammoth $\delta^{15}\text{N}_{\text{coll}}$ plotted against time for eastern Beringian mammoths (B) and western Beringian mammoths (D).

stores. Mammoths generally tend to exhibit slightly more ^{13}C -depleted $\delta^{13}\text{C}_{\text{coll}}$ values than do coeval herbivores. Because fat is more depleted in ^{13}C than bone collagen (Ambrose and Norr, 1993), the more negative $\delta^{13}\text{C}_{\text{coll}}$ values in mammoths relative to other herbivores could be the result of the metabolism of stored fat during the winter (Bocherens et al., 1996; Bocherens, 2003).

Seasonal reliance on fat reserves in mammoths has been widely discussed (Guthrie, 1990; Guthrie, 2001a; Guthrie, 2001b). Forage available during winter months would have been far below even maintenance levels, which suggests that winter forage would act only as a buffer to stave off rapid burning of fat reserves (Guthrie, 2001b). A mummified mammoth recently recovered from Yakutia possessed a very large fat storage area extending from the base of the skull into the region between the scapulae and onto either side of the body (Boeskorov et al., 2007). Long seasonal migrations by mammoths has been suggested to account for the lack of forage available during the winter months (e.g. Churcher, 1980; Colvinaux and West, 1984), but evidence for this is lacking (but see Sharp et al., 2003). On the basis of dental evidence for winter deaths and the extraordinarily high metabolic costs for migrations in mammoths due to biomechanical limitations, Guthrie (1990) suggests that mammoths did not undertake seasonal migrations. Given these conflicting interpretations, it is difficult to determine whether and to what extent mammoths may have migrated, seasonally or otherwise. Regardless, fat storage would have been of particular importance for mammoths during the winter months when forage was in short supply.

Even during periods of winter hibernation, the bone of polar bears and grizzly bears undergoes active remodeling (Lennox and Goodship, 2008; McGee et al., 2008). As such, it is reasonable to suggest that the bone of mammoths was also remodeled during winter months; this process would have required the routing of carbon from stored fat into bone. This would in turn lead to more ^{13}C -depleted values in animals that relied more heavily on stored fat during the winter. Because the turnover rate for bone collagen is ten years (Stenhouse and Baxter, 1979) or more (Hedges et al., 2007), we would expect to see several seasons worth of metabolized fats represented in the isotopic composition of this tissue. In the Late Pleistocene, Siberian winters were colder and summers were warmer than they are today (Kienast et al., 2005). Therefore, the fact that Siberian mammoths exhibited significantly more negative $\delta^{13}\text{C}_{\text{coll}}$ values suggests that this may be the result of a higher reliance on stored fat during winter relative to eastern Beringian mammoths.

Iacumin et al. (2005) performed incremental $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses of mammoth hairs and observed regular negative peaks in $\delta^{13}\text{C}$, which they attribute to the consumption of different types of plants. Interestingly, these negative peaks are also narrower than the positive peaks, suggesting that they represent periods of restricted hair growth. In modern large arctic grazers, such as the musk ox (*Ovibos moschatus*), hair growth is significantly restricted during the winter months (Flood et al., 1989). The pattern observed in the mammoth hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ presented by Iacumin et al. (2005) can also be explained as a result of an increased reliance on ^{13}C -depleted fat during the winter.

5.3. Temporal variability in *Mammuthus primigenius* $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$

When interpreting isotopic data, it is important to keep in mind that temporal trends are regionally specific (Fox-Dobbs et al., 2008). Furthermore, different taxa likely have variable physiological responses to environmental stresses (e.g. Levin et al., 2006), and trends should only be examined within a species and a region.

According to the large dataset presented by Richards and Hedges (2003), the most significant changes in stable carbon isotope values of mammalian bone collagen appear to have occurred following the LGM. The $\delta^{13}\text{C}_{\text{coll}}$ values exhibited little variability prior to 15 ka BP,

following atmospheric CO_2 concentrations, which also show relative stability. With respect to mammoths in particular, Iacumin et al. (2000) examined stable carbon and nitrogen isotopes in mammoth bone collagen (Siberia and the Russian plain) and found that $\delta^{15}\text{N}_{\text{coll}}$ values shifted around 14 ka BP, probably due to a marked increase in precipitation and associated vegetation changes. The dataset contains large temporal gaps for any given region (e.g. Yakutia, Taimyr Peninsula, Russian Plain), making interpretation difficult. Although data for mammoth bone collagen are omitted by Richards and Hedges (2003), they suggest that their data are in general agreement with those of Iacumin et al. (2000).

When data are examined with respect to time, it is apparent that the separation in both $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ between Siberian and eastern Beringian mammoths is temporally consistent (see Fig. 3). On this basis, we suggest that Siberia was on average colder and more arid than central Alaska and Yukon prior to the LGM. It is difficult to assess the scale of this difference in Siberia during the LGM because relevant samples are lacking. By contrast, in eastern Beringia, for which we have better temporal coverage, the most negative $\delta^{13}\text{C}_{\text{coll}}$ and most elevated $\delta^{15}\text{N}_{\text{coll}}$ values are associated with the LGM (see Fig. 3). Indeed, it is only for the period of the LGM that the pattern of isotopic results for eastern Beringia strongly converges with that of western Beringia. Although limited, our data are in agreement with the argument, noted previously, that interior Alaska and Yukon had to have been extremely cold and dry at this time (Goetcheus and Birks, 2001; Hoffecker and Elias, 2007).

Although only one of our analyzed samples postdates the LGM, $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values closely correspond to those observed for samples from eastern Beringia prior to the LGM. While not statistically significant, this result does suggest that mammoths responded relatively well to the extreme conditions of the LGM. This is in agreement with phylogeographic data from the same mammoth samples published by Debruyne et al. (2008), which show that the LGM had only a very limited impact on the overall genetic diversity of mammoths living at high latitudes in both Eurasia and North America.

6. Conclusion

This study demonstrates the utility of isotopic analysis of mammalian bone collagen for the study of regional and temporal environmental variability. Many lines of evidence establish that ecologically variable conditions prevailed across the mammoth steppe during the Pleistocene, with substantial regional differences in precipitation and temperature. According to the data presented here, Siberia was colder and more arid than central Alaska and Yukon prior to the LGM; however, following the onset of the LGM, eastern Beringia likewise became much cooler and drier. Environmental change at this time was not fatal to the mammoths of either region; they persisted, evidently unscathed at least in terms of their genetic diversity, until the time of the Pleistocene/Holocene transition.

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Contributions: DRG, HNP and RDM designed the project. PS performed the research. HNP and RDM collected and contributed samples. PS and DRG analyzed the data. PS, DRG, HNP, RD, WPP and RDM wrote the paper. GDZ, RDG and DF provided critical assessment of the palaeoecological interpretation.

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