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Woolly mammoth $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values remained amazingly stable throughout the last ~50,000 years in north-eastern Siberia

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ABSTRACT

The range of the woolly mammoth (*Mammuthus primigenius*) covered the northern circumpolar region, over time varying in size and space due to changes in regional climatic conditions. The species survived multiple glacial cycles, but got extinct around the end of the last glacial, between ~21,000 and 4000 years ago. Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) data of woolly mammoth fossils from western Eurasia and Alaska, show considerable variation during periods of global climatic change and towards time of regional extinction. In North-eastern Siberia, the woolly mammoth survived several millennia longer. The fossil record from North-eastern Siberia yields, therefore, crucial ecological information about the living conditions of the woolly mammoth and plays an important role in the debate about the cause of its extinction. The current dataset comprises an unprecedented amount of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data of directly radiocarbon-dated woolly mammoth skeletal samples from North-eastern Siberia, including numerous Holocene samples from Wrangel Island. This study shows that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the woolly mammoth remained amazingly stable in this region throughout the last ~50,000 years of its existence.

1. Introduction

1.1. The mammoth steppe ecosystem and its collapse

The woolly mammoth (*Mammuthus primigenius*), with its large size, long tusks and thick fur, became an icon for the last ice age (i.e., Weichselian) worldwide. It was present about 400,000 years ago in North-eastern Asia, and dispersed during the late Middle Pleistocene westwards (Lister and Sher, 2001, 2015; Lister et al., 2005). *M. primigenius* inhabited a biome that occurred in its maximal expansion in a geographically extensive area stretching from western Europe, via northern Eurasia to northern America. This biome represented a dry and highly productive environment with cold winters and warm summers (Guthrie, 1982, 1990, 2001). It is characterized by its non-analogue combination of plant and animal species. This former ‘tundra-steppe’ or ‘steppe-tundra’ consisted of mosaic-like biotopes dominated by grass and herbs communities, with patches of shrub-tundra and forest; a biome that is often referred to as ‘mammoth steppe’ (Guthrie, 1990), after its most famous dweller: the woolly mammoth.

At the end of the Pleistocene, around the Late Glacial, the mammoth steppe biotope started to collapse. Climatic ameliorations from cold and arid to warmer and wetter circumstances caused sea level rise and replacement of the original ‘mammoth steppe’ vegetation by less

productive mesic tundra in the north and (larch) forest further south (e.g. Andreev et al., 2011; Hoffecker and Elias, 2007; Lozhkin, 1993). The environmental alterations were critical for the geographical distribution of many plant and animal species. Several archetypal mammoth steppe faunal elements, including the woolly mammoth, became extinct (Guthrie, 2001; Lister and Stuart, 2008; Puzachenko et al., 2017; Stuart et al., 2002; Stuart, 2014).

The disintegration of the mammoth steppe biome did not occur simultaneously throughout its entire geographical span. *M. primigenius* changed its distribution range repeatedly during the Middle and Late Weichselian, often following climatic and/or environmental changes. Mostly, its range increased in size during stadials and decreased during most of the interstadials, and eventually fell apart into isolated patches (Puzachenko et al., 2017).

Woolly mammoth remains have been recovered abundantly throughout its distributional range. Insights into the dynamics of geographical distribution of the woolly mammoth during the last 50,000 years (i.e., the radiocarbon time scale) were obtained by analysing extensive datasets of radiocarbon-dated remains from more than a thousand localities (e.g. Stuart et al., 2004; Stuart, 2005; Nikolskiy et al., 2011; Puzachenko et al., 2017). In parts of its biome, *M. primigenius* went extinct as early as the Late Glacial (~21,000 years ago in Southwestern Europe, Puzachenko et al., 2017), whereas relict

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populations of (small-sized) mammoths persisted longer on isolated islands.

On Wrangel Island, an island situated north of Chukotka mainland, the youngest dated woolly mammoth remains are found (3685 ± 60 yr BP; Vartanyan et al., 2008). Hence, Wrangel Island plays an important role in the debate about the cause of the final extinction of the woolly mammoth and the nature of refugial areas.

A way to track environmental changes that took place within this biome is by investigating stable isotope signals in fossil mammoth remains. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the bone collagen of a mammoth are related to the isotopic composition of the plants forming its diet, and in turn, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in these plants (and soils) are related to climatic and (local) environmental parameters (Kohn, 1999; Lee-Thorp, 2008).

1.2. Factors influencing C and N isotope values in the terrestrial biosphere

The stable carbon isotope composition in plants is primarily determined by the degree of exchange of CO_2 and moisture between the plant leaves and the atmosphere (so-called stomatal conductance; Marshall et al., 2007), which is consecutively affected by various factors. In the terrestrial biosphere, fractionation of $^{13}\text{C}/^{12}\text{C}$ is mainly governed by the type of photosynthetic pathway. In the mammoth steppe biome, plants used the C3 photosynthetic pathway (Blinnikov et al., 2011), usually having $\delta^{13}\text{C}$ values around -27‰ . The $\delta^{13}\text{C}$ values of C3 plants are mainly determined by (local) environmental factors, such as humidity, atmospheric CO_2 concentrations, and the occurrence of dense forest (e.g., Heaton, 1999; Polley et al., 1993; Tieszen, 1991).

Within the terrestrial biosphere, stable nitrogen isotope compositions in plants are determined by various biogeochemical processes within the plant and in the surrounding soil, including for instance nitrogen cycling, nutrient availability, and type of mycorrhizal fungi living in symbiosis with the plant (Nadelhoffer et al., 1996; Höglberg et al., 1996; Hobbie and Höglberg, 2012; Szpak, 2014). Most of these processes are linked to one another and relate to climatic conditions such as humidity and temperature.

1.3. Stable C and N isotope analysis of the mammoth steppe ecosystem

Significant variations through time and space are observed in the stable isotope records of Late Pleistocene and Holocene fossils of different mammoth steppe dwellers from Eurasia and Alaska (e.g. Iacumin et al., 2000; Bocherens, 2003; Drucker et al., 2003, 2014; Richards and Hedges, 2003; Fox-Dobbs et al., 2008; Stevens and Hedges, 2004; Szpak et al., 2010). Interregional variation was mainly observed as a distinctive pattern of elevated $\delta^{15}\text{N}$ values and depleted $\delta^{13}\text{C}$ values in mammal samples from North-eastern Siberia compared to the values in samples from Europe, and in particular Alaska (Bocherens, 2003; Szpak et al., 2010). These differences in values are linked to generally more arid conditions and lower temperatures in North-eastern Siberia throughout the Late-Pleistocene, opposed to more mesic components in the habitats of Alaska (Szpak et al., 2010). Other proxies, including palaeontomological data and dental wear patterns of ungulate species also point to ecological differences between respectively Alaska and North-eastern Siberia (e.g. Szpak et al., 2010) and between Europe and Alaska (e.g. Rivals et al., 2010) during the Late Pleistocene.

The diachronic isotope variations are in particular observed in a number of species from North-western Europe and, although less pronounced, in Alaska. The changing isotope compositions, predominantly reflected as a trend towards lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at the onset of the Late Glacial, have indeed been linked to changing environmental circumstances, especially those that were driven by major climatic deteriorations that took place around the Last Glacial Maximum (LGM) and the Pleistocene/Holocene transition. These include changes in atmospheric CO_2 concentrations (Richards and Hedges, 2003; Stevens

and Hedges, 2004), climatic variation on a local-scale including soil moisture conditions (Stevens and Hedges, 2004; Fox-Dobbs et al., 2008), and forest development (Drucker et al., 2008; Drucker and Bocherens, 2009).

Unfortunately, there is a lack of continuity of stable isotope records and/or low sampling density within parts of the mammoth steppe biome, hampering the data interpretation and the observation of possible trends in time (e.g., Fox-Dobbs et al., 2008). For instance, published $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ records of woolly mammoth samples with a post-LGM age and in particular with an LGM age are scarce.

1.4. Current investigation

The area of North-eastern Siberia was more or less continuously inhabited the woolly mammoth (Puzachenko et al., 2017). Not only the numerous sites with woolly mammoth remains and the long-term survival of the woolly mammoth in that area, but also its geographical position and the fact that it was for a long period part of the Beringia Land Bridge - providing a corridor between continents for some species, but prohibiting crossing by others (Hopkins 1982; Guthrie, 2001; Elias and Crocker, 2008; Meiri et al., 2014)- makes this an attractive study area.

The current dataset comprises an unprecedented amount of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of directly dated woolly mammoth samples from North-eastern Siberia, including many samples dating to the post-LGM and a number to the LGM. The majority of the samples date to the Late-Pleistocene, but also a relatively large number have a Holocene age. The latter are mainly from Wrangel Island.

This study focuses on North-eastern Siberia (Fig. 1), and adds a large number of new $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of woolly mammoth fossils from that area. The data are studied in order to track possible shifts within the woolly mammoth stable carbon and nitrogen record towards its time of extinction, coinciding with global climatic changes; features that are observed in other parts of the mammoth steppe biome.

2. Material and methods

2.1. Material

This study presents $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of 109 woolly mammoth samples from northern territories, north of 70° N. The dataset includes new measurements ($n = 62$) and published data ($n = 47$, see Table S1: Bocherens et al., 1996; Iacumin et al., 2000, 2010; Szpak et al., 2010). Geographically, the samples can roughly be divided into three regions of provenance (Fig. 1): from west to east - Taimyr Peninsula, Yakutia (predominantly Lena River Delta, New Siberian Archipelago and Yana-Indigirka Lowland), and Wrangel Island (specifically Gusinaya River in the west of the island, Peak in the centre, and Mamontovaya River in the southwest).

Samples were taken from different skeletal parts. Samples from tusks form the majority of the unpublished data, ($n = 42$), the rest of the samples is bone ($n = 16$) or molar dentine ($n = 3$). For one sample the material was not specified, but it is highly probable that it was taken from either bone or tusk. In tusks, seasonal variation in isotope signals can be recorded (e.g., Rountrey et al., 2007). However, the tusk samples used for the present study are bulk samples, in which the isotope signal of several seasons is averaged. The current analysis assumes that the stable isotope signals of the collagen from these three material categories are comparable to each other. The $\delta^{13}\text{C}$ value of all samples was measured, and for 58 of these the $\delta^{15}\text{N}$ value has been determined as well.

The age of the samples is summarized in Table 1, which shows the number of records per period relative to the LGM. Most samples ($n = 98$) date to the last part of the Late Pleistocene or to the succeeding Holocene. Eleven samples have ‘infinite ^{14}C ages’, which means they are older than 45,000 yr BP (Table S1). Their age is not specified.

Fig. 1. Map of the study area. The approximate locations of the fossil data are indicated with black open circles.

2.2. Methods

Chemical preparation, radiocarbon dating, and stable isotope measurements of the new samples were performed at the Centre for Isotope Research in Groningen, the Netherlands, following standard procedures (Dee et al. forthcoming). Samples underwent standard chemical cleaning and collagen extraction following an improved version of the method developed by Longin (Longin, 1971). In short, the bone samples are decalcified over at least a 24-h period using weak acid (HCl, 4% w/vol). When CO₂ release has ceased and the fragments have become soft and pliable they are rinsed thoroughly with distilled water (DW). Following the demineralisation, the samples were soaked into NaOH (1%, > 30 min) to eliminate humic acids, rinsed to neutrality and treated once more with acid (HCl, 4% w/vol, 15 min). The raw collagen fraction is then denatured to gelatine in acidified DW (pH 3) at 90 °C for 18 h. Before drying, the dissolved gelatine is filtered through a 50 µm mesh to eliminate any remaining foreign particulates. The collagen is combusted to obtain CO₂ using an Elemental Analyser (Isocube, Elementar) connected to an Isotope Ratio Mass Spectrometer (Isoprime 100, Elementar), providing the stable isotope ratios ¹³C/¹²C and ¹⁵N/¹⁴N.

The stable isotope values of the samples are expressed in delta (δ) values, which are defined as the deviation (expressed in per mil) of the rare to abundant isotope ratio from that of a reference material:

$$\delta^{13}C = \frac{(^{13}C/^{12}C)_{sample}}{(^{13}C/^{12}C)_{reference}} - 1 \left(\times 1000 \text{‰} \right)$$
(1)

$$\delta^{15}N = \frac{(^{15}N/^{14}N)_{sample}}{(^{15}N/^{14}N)_{reference}} - 1 \left(\times 1000 \text{‰} \right)$$
(2)

The absolute isotope contents of the reference materials have been measured very accurately (Mook, 2006 and references therein). For carbon, the reference material is belemnite carbonate (V-PDB; NBS 18, NBS 19 and LSVEC are the international standards used to calibrate by two-point normalisation relative to V-PDB). For nitrogen, the reference is ambient air (AIR; IAEA-N1 and IAEA-N2 are the international standards used to calibrate relative to AIR). The combined uncertainty is about 0.3‰ for δ¹³C and 0.2‰ for δ¹⁵N. To monitor analytical accuracy and precision, (internal) normalisation standards and control references were used. For δ¹³C, these are oxalic acid (−17.6‰), caffeine (−38.2‰), CaN (caffeine mixed with δ¹⁵N-enriched caffeine, +0.61‰) and collagen (−19.87‰); for δ¹⁵N, these are CaN (+19.04‰), caffeine (−6.61‰) and collagen (+10.07‰).

For ¹⁴C, the CO₂ was cryogenically trapped using an automatic collection device. Next, the CO₂ was transformed into graphite by reduction with H₂ using Fe as catalyst. The routine graphitization procedure at the CIO has been operational for over 20 years (Wijma et al., 1996; Aerts-Bijma et al., 1997), with only minor, mainly mechanical, adjustments being required over this time. The ¹⁴C/¹²C ratio in the graphite was measured by Accelerator Mass Spectrometry (AMS) relative to the international Oxalic Acid standard, and reported by a convention including correction for isotopic fractionation using the stable isotope ratio ¹³C/¹²C to δ¹³C = −25‰, and using a half-life value of 5568 years (Mook and van der Plicht, 1999; van der Plicht et al., 2000). The AMS was based on a 2.5 MV Tandatron manufactured by HVEE (High Voltage Engineering Europa).

Table 1
Number of woolly mammoth samples from North-eastern Siberia, ordered per time interval relative to the LGM.

n	n (new) ^a	period	used abbreviation	¹⁴ C yr BP	cal yr BP ^b
54	(21)	Pre-Last Glacial Maximum	Pre-LGM	> 45,000–24,600	> 50,000–28,660
10	(5)	Last Glacial Maximum	LGM	24,600–17,000	28,660–20,520
45	(36)	Post-Last Glacial Maximum	Post-LGM	< 17,000	< 20,520
109	(62)				

^a Numbers of newly provided samples by the current paper are shown between brackets.
^b Cal yr BP = calendar ages relative to 1950.

General patterns in the dataset were visually examined using bi-variate plots. Further, differences in the means and trends were tested for by statistical modelling. Differences in the means of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were examined by using One-way ANOVA: a parametric statistical test at the 95% confidence level, with H_0 = all means are the same and H_0 is rejected when p -value < 0.05 . Normal distribution and homogeneity of variance was checked by using the Shapiro-Wilk test and Bartlett test, respectively. A linear regression model was used to test if $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values show a linear trend with time.

3. Results

The atomic C/N ratio of the collagen of the samples is 2.9–3.6 (%C = 37.7–50.1 and %N = 13.4–18.4). These percentages indicate good quality collagen (Ambrose, 1990). Eight samples have a somewhat high %C value (> 47 ; see the italic values in Table S1). These samples are included in the current investigations since the %C values fall between 45 and 50, a range that is regarded as indicative for good quality collagen suitable for radiocarbon dating (e.g. Mook and Streurman, 1983).

The results of the stable isotope measurements are shown in chronological order in Table S1. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of samples from Taimyr Peninsula, Yakutia and Wrangel are plotted relative to time in Fig. 2 and Fig. 3, respectively. The $\delta^{13}\text{C}$ values range from -23.2‰ to -20.1‰ , with an average of -22.0‰ and a standard deviation of 0.5. The $\delta^{15}\text{N}$ values range from $+5.6\text{‰}$ to $+12.1\text{‰}$, with an average of $+9.4\text{‰}$ and a standard deviation of 1.2.

Table 2 gives an overview of the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, standard deviations and number of available samples for the different regions (i.e., Taimyr, Yakutia and Wrangel). It aggregates all data together and compares between regions irrespective of the age of the samples. Table 2 shows that both the mean $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values of the samples from the three regions are very similar ($< 0.3\text{‰}$ difference). No statistically significant difference was found at the 95% confidence level between the mean $\delta^{13}\text{C}$ values (ANOVA, $p = 0.13$) and $\delta^{15}\text{N}$ values (ANOVA, p -value = 0.59) of the regions. Therefore, the data are further discussed irrespective of the region of provenance of the samples.

Table 3 gives an overview of the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values,

Fig. 2. The $\delta^{13}\text{C}$ values of samples from Taimyr Peninsula, Yakutia and Wrangel through time.

Fig. 3. The $\delta^{15}\text{N}$ values of samples from Taimyr Peninsula, Yakutia and Wrangel through time.

Table 2

Averages and standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for different regions.

	$\delta^{13}\text{C}$ (‰)	st dev	n	$\delta^{15}\text{N}$ (‰)	st dev	n
	mean			mean		
Taimyr	-21.8	0.6	37	9.4	1.2	34
Yakutia	-22.1	0.5	46	9.3	1.4	46
Wrangel	-22.0	0.3	26	9.5	0.9	25
All areas	-22.0	0.5	109	9.4	1.2	105

Table 3

Averages and standard deviations of woolly mammoth $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for different time intervals.

	$\delta^{13}\text{C}$ (‰)	st dev	n	$\delta^{15}\text{N}$ (‰)	st dev	n
	mean			mean		
Pre-LGM	-22.0	0.5	54	9.5	1.2	52
LGM	-21.6	0.5	10	9.1	1.2	10
Post-LGM	-22.1	0.4	45	9.4	1.2	43
Pleistocene	-21.9	0.5	80	9.4	1.3	77
Holocene	-22.1	0.3	29	9.4	0.7	28

standard deviations and number of samples for different time slices relative to the LGM, and for the Pleistocene and Holocene ($> 11,000$ ^{14}C yr BP). Table 3 shows that both the mean $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values of the samples are very similar throughout the different periods. Indeed, we cannot conclude at the 95% significance level that there is a temporal trend in the $\delta^{13}\text{C}$ values ($p = 0.157$; Fig. 4A) or in the $\delta^{15}\text{N}$ values ($p = 0.1$; Fig. 4C). Also, in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of woolly mammoths from Wrangel Island no significant temporal correlation is observed. The variation through time is on average very small.

We cannot conclude at the 95% confidence level that there is a temporal trend in the $\delta^{13}\text{C}$ values ($p = 0.051$; Fig. 4B) or in the $\delta^{15}\text{N}$ values ($p = 0.43$; Fig. 4D).

Fig. 4. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of samples with a finite age ($> 45,000$ ^{14}C yr BP) through time. A: $\delta^{13}\text{C}$ values of samples from North-eastern Siberia; B: $\delta^{13}\text{C}$ values of samples from Wrangel Island; C: $\delta^{15}\text{N}$ values of samples from North-eastern Siberia; D: $\delta^{15}\text{N}$ values of samples from Wrangel Island.

4. Discussion

4.1. Spatial and temporal distribution

4.1.1. Mainland

The current data set reveals stability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of woolly mammoth skeletal remains throughout the last part of the Late Pleistocene in North-eastern Siberia. Even in periods in which in other regions the stable isotope values change considerably. The post-LGM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from North-eastern Siberia are similar to those of the pre-LGM, and even fairly similar to those of the LGM.

The dataset of a previous study by Iacumin et al. (2010) comprised two woolly mammoth samples from Yakutia dating to post-LGM, which appeared to have low $\delta^{15}\text{N}$ values ($+5.6\text{‰}$ and $+5.7\text{‰}$) relative to older samples. This depletion was attributed to higher precipitation rates after the LGM (Iacumin et al., 2010), and seemed to be part of a trend towards lower $\delta^{15}\text{N}$ values after the LGM. However, the two samples with low values form an exception when compared to the newly obtained data from the present study and other recently published data: all other samples from Yakutia with a post-LGM age

($n = 17$) have $\delta^{15}\text{N}$ values between $+8.62\text{‰}$ and $+12.14\text{‰}$, and are comparable to $\delta^{15}\text{N}$ values of samples from pre-LGM and LGM. Hence, the current data are consistent with information revealed from other ecological proxies such as pollen and entomological data from Taimyr and Yakutia, which indicate that after the LGM but pre-dating the start of the Holocene, climatic and environmental conditions resembled those during pre-LGM times (Nikolskiy et al., 2011).

At the start of the Holocene, temperatures started to rise in different regions inhabited by the woolly mammoth, including Taimyr and Yakutia; a temperature rise that resulted in, amongst others, a rise in sea level. A marked paludification is recorded in palynological, macrobotanical and insect assemblages (Nikolskiy et al., 2011). Around that time, the woolly mammoths went extinct on the North-eastern Siberian mainland (Nikolskiy et al., 2011; Puzachenko et al., 2017).

4.1.2. Wrangel Island

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the Holocene woolly mammoths from Wrangel Island are well within the range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the Late-Pleistocene mammoths from the North-eastern Siberian mainland. Moreover, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from Wrangel Island remain

consistent through time.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of woolly mammoth samples from Wrangel Island (Fig. 4B and D) show less variation than the woolly mammoths which lived on the North-Siberian mainland (Fig. 4A and C). This might partly be explained by the fact that the woolly mammoths on Wrangel Island exploited a much more restricted and likely more uniform area –despite the supposed local variation in vegetation cover on the island–over a much shorter time span than their Late Pleistocene counterparts.

Different hypotheses/models are launched to explain the disappearance of the woolly mammoth: the ‘overkill’ model (Haynes, 2007; Martin, 1984) or ‘Blitzkrieg’ model (Martin, 1984) in which mainly human hunters are held responsible, models in which climate change played a major role (e.g. Cooper et al., 2015; Koch and Barnosky, 2006; Nikolskiy et al., 2011), pandemic theories, and models which involve (a combination of) ecological changes, habitat reduction, and reduction of genetic diversity (e.g. Graham et al., 2016; Palkopoulou et al., 2015).

The stable isotope data do not give direct information about the extinction of the woolly mammoth on Wrangel Island. But the consistency in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values through time implies that Holocene mammoths were feeding on resources with the same isotopic composition as their Late Pleistocene counterparts from the North-eastern Siberian mainland throughout their existence on Wrangel Island. Therefore, stable isotope data from Wrangel Island are consistent with the suggestion that climate change was not the (main) cause of the ultimate extinction of the woolly mammoth. These results are in line with conclusions from Fox et al. (2007): climate signals recorded in oxygen isotope values in serially sampled tusks from North-eastern Eurasia, including Holocene tusks from Wrangel Island do not point to climate change that could be regarded as the direct cause of the woolly mammoth extinction (Fox-Dobbs et al., 2008).

Indeed, the local extinction of the woolly mammoth often co-occurred with environmental changes and habitat expansion of humans. However, the interference of early man is not likely to have driven the mammoths on Wrangel Island to extinction, since there is no clear evidence that humans occupied the island before the mammoth's disappearance (Nikolskiy et al., 2011). The absence of humans and other predators allowed the woolly mammoths to reduce in size, which is a well-known phenomenon for islands. Pleistocene bones from Wrangel all belong to normal-sized mammoths, but between 8000 and 6000 BP, the mammoths started to reduce in size. After 6000 BP, all mammoths were small-sized (Vartanyan et al., 1993).

Recent investigation on the genome of one of the last surviving Wrangel mammoths (dated to about 4300 yr BP) demonstrates reduced genetic variation (Palkopoulou et al., 2015). In the course of the Holocene, the reduced genetic variation was probably harmful for the reproductive success of the Wrangel mammoths and might have contributed to their extinction (Palkopoulou et al., 2015).

Late Pleistocene fossils from woolly mammoth, horse, and woolly rhinoceros indicate that Wrangel Island was inhabited by a mammalian assemblage comparable to that of Late Pleistocene Yakutia and Taimyr (Zimov et al., 2012). In contrast, except for one bison fossil with an Early Holocene age, the woolly mammoths remained in the Holocene the only large herbivore species on the island. Based on the number of radiocarbon-dated fossils, the woolly mammoth population even seems to have increased in number compared to the Late Pleistocene population living on Wrangel (Zimov et al., 2012).

First, the continued existence of woolly mammoths on the one hand and the extinction of many other species on the island on the other hand, indicates a high degree of ‘resilience’ of the woolly mammoth to changing conditions. Second, it indicates that conditions which disallowed survival of other large species on the island, did not (negatively) affect the habitats which were suitable for the woolly mammoth. This is supported by the current stable isotope results, since the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Holocene woolly mammoth samples from Wrangel

Island are similar to these of Late Pleistocene North-eastern Siberia mainland and remain the same throughout the Holocene.

Since woolly mammoths were virtually the only large herbivore species that lived on Wrangel Island during the Holocene, niche competition did not play a role (Zimov et al., 2012). It was hypothesized by Zimov et al. (2012) that woolly mammoths might have occupied the ecological niches of bison and horse which became available in the Holocene. Indications for niche change are found in the isotope record of Pleistocene woolly mammoths from Mezhyrich (Drucker et al., 2014). Late-Glacial samples of woolly mammoth samples from this Ukrainian site show $\delta^{15}\text{N}$ values similar to those of horses from the same spatiotemporal range. These overlapping $\delta^{15}\text{N}$ values of woolly mammoth and horses were associated with niche partitioning (Drucker et al., 2014). The lack of other large herbivores prohibits comparison of isotope data of the woolly mammoth with such species on Wrangel. However, Drucker et al. (2014) observed significantly higher $\delta^{15}\text{N}$ values prior to the Late Glacial, in the bone collagen of the woolly mammoths from Mezhyrich. Such a shift in $\delta^{15}\text{N}$ values pointing to a change of the ecological niche is not observed in the isotope data of the woolly mammoth from Wrangel Island.

4.1.3. Beringia

By including data from Wrangel Island, the current study presents crucial stable isotope data from the border region between Siberia and Alaska. Formally, the island is part of Siberia, but geographically the island is located also close to Alaska (Fig. 1). Wrangel is nowadays an island in the Arctic Ocean, but it was connected to the mainland until about 12,000 ^{14}C yr BP (Keigwin et al., 2006; Vartanyan et al., 2008). From the onset of the Holocene to about 6000 years ago, the Long Strait (i.e. the water body that separates Wrangel from the Siberian mainland) was so narrow that mammoths might still have crossed the strait during winter. During the Weichselian, the Beringia Land Bridge connected North-eastern Siberia and Alaska. Conditions in Central Beringia are supposed to have been much more mesic than on either side of the land bridge, i.e. West Beringia/North-eastern Siberia and East Beringia/Alaska (Elias and Crocker, 2008; Guthrie, 2001).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of samples from Wrangel Island fall entirely within the range of values from North-eastern Siberia (Fig. 5) and hardly overlap with the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from Alaska. Hence, the stable isotope data suggest that the stable isotope composition of the vegetation on Wrangel Island was similar to that of other parts of West-Beringia and not to that in Alaska, despite the proximity to Central Beringia and Alaska. A remarkable difference between the environmental conditions between Wrangel Island and Central Beringia and Alaska is also observed in the occurrence of the woolly rhinoceros. The woolly rhinoceros (*Coelodonta antiquitatis*) inhabited Wrangel during the Pleistocene (Vartanyan et al., 2008) but fossils of this species have never been recovered at the east side of the Bering Land Bridge. Central Beringia might have acted as ecological barrier in keeping this xerophilic species from entering East Beringia (Elias and Crocker, 2008).

4.2. Comparison with other species from north-eastern Siberia

It is interesting to compare the results with data of other mammalian species from North-eastern Siberia. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of musk oxen are well documented, in particular in a publication by Raghavan et al. (2014). They analysed the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of 160 samples of Pleistocene and Holocene musk oxen from across the Holarctic, and observed similarity in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between Holocene and Pleistocene musk oxen from Taimyr ($n = 52$). In contrast to the samples from Taimyr, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Canadian musk oxen are lower during the Holocene compared to the Pleistocene. The authors explain the observed differences in musk oxen from Canada by an increase in precipitation during the Holocene (N.B. the authors use 10,000 yr BP as onset of the Holocene, instead of 11,000 yr BP used in the current study), and conclude that Canada might have experienced a

Fig. 5. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges of woolly mammoth samples from Wrangel Island (in red), compared to these from North-eastern Siberia mainland (in blue) and from Alaska (green; Szpak et al., 2010; Debruyne et al., 2008; Graham et al., 2016; see Table S2 for raw data). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

more pronounced increase in precipitation during the Holocene than Taymir (Raghavan et al., 2014).

From North-eastern Siberia, the number of radiocarbon-dated samples of mammalian species other than mammoth and musk oxen of which the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are published are scarce. Making statements about temporal variations based on these few samples is not justified, because of lack of continuity of relevant data through time. However, the observed continuity through time in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of musk oxen from Taymir, whilst change is observed in other parts of their biome at the Pleistocene/Holocene transition (Raghavan et al., 2014), corresponds to the results of the current study.

5. Conclusion

The current data set reveals a remarkable stability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of woolly mammoth skeletal remains throughout the last part of the Late Pleistocene in North-eastern Siberia. Minor differences are observed in samples with an LGM age, but the post-LGM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from North-eastern Siberia are similar to those pre-dating the LGM. This continuity or recovery of stable isotope values sharply contrasts to published data from samples of woolly mammoths and other large herbivores from Europe and Alaska, which revealed significant changes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values related to climatic fluctuations during and/or after the LGM.

Even more, woolly mammoths maintained similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values throughout their Holocene existence, as demonstrated by results of woolly mammoth fossils from the legendary Wrangel Island, where they survived until around 2100 BCE. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the Holocene woolly mammoths from Wrangel Island are similar to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the Late Pleistocene mammoths from the North-eastern Siberian mainland. They diverge from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from woolly mammoth fossils from Alaska, despite the proximity of both regions.

The stable isotope data indicate that Holocene mammoths from Wrangel Island were feeding on isotopically the same resources as they

did on the North-eastern Siberian mainland throughout the last part of the Late Pleistocene, and suggest, at least in broad sense, that these mammoths were able to maintain the same diet throughout their whole existence on the island.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quaint.2019.03.001>.

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