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Analysis of ^{13}C and ^{15}N isotopes from Eurasian Quaternary fossils: Insights in diet, climate and ecology

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CHAPTER 3

**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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3.1 Introduction

3.1.1 The mammoth steppe ecosystem and its collapse

The woolly mammoth (*Mammuthus primigenius*) originated 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 biotope that occurred during its maximal expansion in a geographically extensive area stretching from western Europe, via northern Eurasia to northern America. This biotope is often referred to as ‘mammoth steppe’ (Guthrie, 1990; see also Chapter 1, section 1.1.1).

At the end of the Pleistocene, the mammoth steppe biotope started to collapse. The disintegration of the mammoth steppe biome did not occur simultaneously throughout its entire geographical range. *M. primigenius* changed its distribution range repeatedly during the Middle and Late Weichselian, often triggered by climatic and/or environmental changes. In general, its range increased in size during colder episodes (stadials) and decreased during most of the interstadials, and finally it 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 mammoths during the last 50,000 years (that is, the ^{14}C time scale) were obtained by analysing extensive datasets of ^{14}C dated remains from more than a thousand localities (Stuart, 2005; Nikolskiy *et al.*, 2011; Puzachenko *et al.*, 2017; Stuart *et al.*, 2019). 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 populations of (small-sized) mammoths survived longer on isolated islands.

On Wrangel Island, an island situated north of Chukotka mainland, the youngest dated woolly mammoth remains are found (3685 ± 60 ^{14}C 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.

3.1.2 Stable C and N isotope analysis of the mammoth steppe ecosystem

Stable isotope data from mammoth steppe mammals have been measured and investigated, in order to gain insights in different aspects of the mammoth steppe ecosystem. Significant variations through time and space are observed in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ records of Late Pleistocene and Holocene fossils of diverse mammoth steppe dwellers from Eurasia and Alaska (Iacumin *et al.*, 2000; Bocherens, 2003; Drucker *et al.*, 2003b, 2014; Richards and Hedges, 2003; Stevens and Hedges, 2004; Fox-Dobbs *et al.*, 2008; Szpak *et al.*, 2010). Mammal samples from North-eastern Siberia show, compared to the values in samples from Europe, and in particular compared to values in samples from Alaska, elevated $\delta^{15}\text{N}$ values and depleted $\delta^{13}\text{C}$ values (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 (Szpak *et al.*, 2010) and between Europe and Alaska (Rivals *et al.*, 2010) during the Late Pleistocene.

The diachronic isotope variations are observed in a number of species from North-western Europe and, although less pronounced, in species from 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, are 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 changing environmental circumstances include changes in atmospheric CO_2 concentration (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 are chronological hiatuses in 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 (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.

3.1.3 North-eastern Siberia

The area of North-eastern Siberia was more or less continuously inhabited by the woolly mammoth (Puzachenko *et al.*, 2017). Not only the numerous sites with woolly



Figure 3.1 Map of the study area. The locations of the fossil data are indicated with black open circles.

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 investigated 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 samples are mainly from Wrangel Island.

The study focuses on North-eastern Siberia (Fig. 3.1). A large number of new $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values have been analysed in order to track possible shifts within the woolly mammoth $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ record towards its time of extinction.

3.2 Material and methods

3.2.1 Material

The study presents $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from 109 woolly mammoth samples from an area located north of 70°N . The dataset includes new measurements ($n = 62$) and published data ($n = 47$, see Table SI Chapter 3.1: 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. 3.1): 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 new 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 (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 different material categories are comparable to each other. The $\delta^{13}\text{C}$ value of all samples was measured, and for 58 samples the $\delta^{15}\text{N}$ value has been determined as well.

The age of the samples is summarized in Table 3.1. It 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 ^{14}C yr BP (Table SI Chapter 3.1). Their age is not specified.

Table 3.1 Number of woolly mammoth samples from North-eastern Siberia, arranged per time interval relative to the LGM.

N	n (new)*	period	used abbreviation	¹⁴C age (yr BP)	cal yr BP**
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)				

*Numbers of newly provided samples by the current paper are shown between brackets

**cal yr BP = calendar ages relative to 1950

3.2.2 Methods

Chemical preparation, ¹⁴C dating, and stable isotope measurements of the new samples were performed at the Centre for Isotope Research in Groningen, the Netherlands, following the Groningen procedures as described in Chapter 2 (section 2.4).

General patterns in the dataset were visually examined using bivariate 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 $p\text{-value} < 0.05$. Normal distribution and homogeneity of variance were checked by applying 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.

3.3 Results

The atomic C/N ratio of the collagen 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 higher %C value (> 47 ; see the italic values in Table SI Chapter 3.1). 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 ¹⁴C dating (Mook and Streurman, 1983).

The results of the stable isotope measurements are shown in chronological order in Table SI Chapter 3.1. 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. 3.2. 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‰ to +12.1‰, with an average of +9.4‰ and a standard deviation of 1.2.

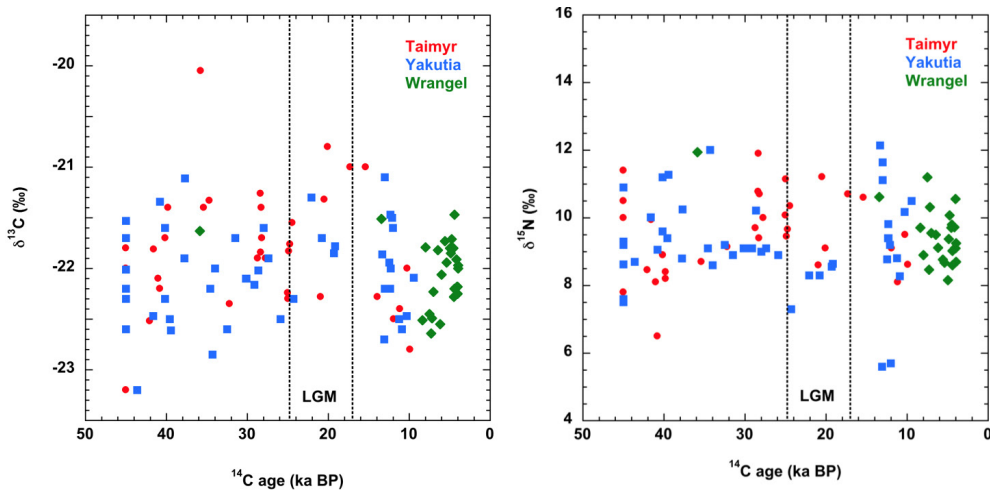


Figure 3.2 The $\delta^{13}\text{C}$ values (left) and $\delta^{15}\text{N}$ values (right) of samples from Taimyr Peninsula, Yakutia and Wrangel through time.

Table 3.2 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 (that is, Taimyr, Yakutia and Wrangel). It aggregates all data together and compares between regions irrespective of the age of the samples. Table 3.2 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, $p\text{-value} = 0.59$) of the regions. Therefore, the data are further discussed irrespective of the region of provenance of the samples.

Table 3.2 Averages and standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for different regions.

	$\delta^{13}\text{C}$ (‰)			$\delta^{15}\text{N}$ (‰)		
	mean	st dev	n	mean	st dev	n
Taimyr	-21.8	0.6	37	9.4	1.2	34
Yakutia	-22.1	0.5	46	9.3	1.4	46
Wrangel	-22	0.3	26	9.5	0.9	25
All areas	-22	0.5	109	9.4	1.2	105

Table 3.3 gives an overview of the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, 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 3.3 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.

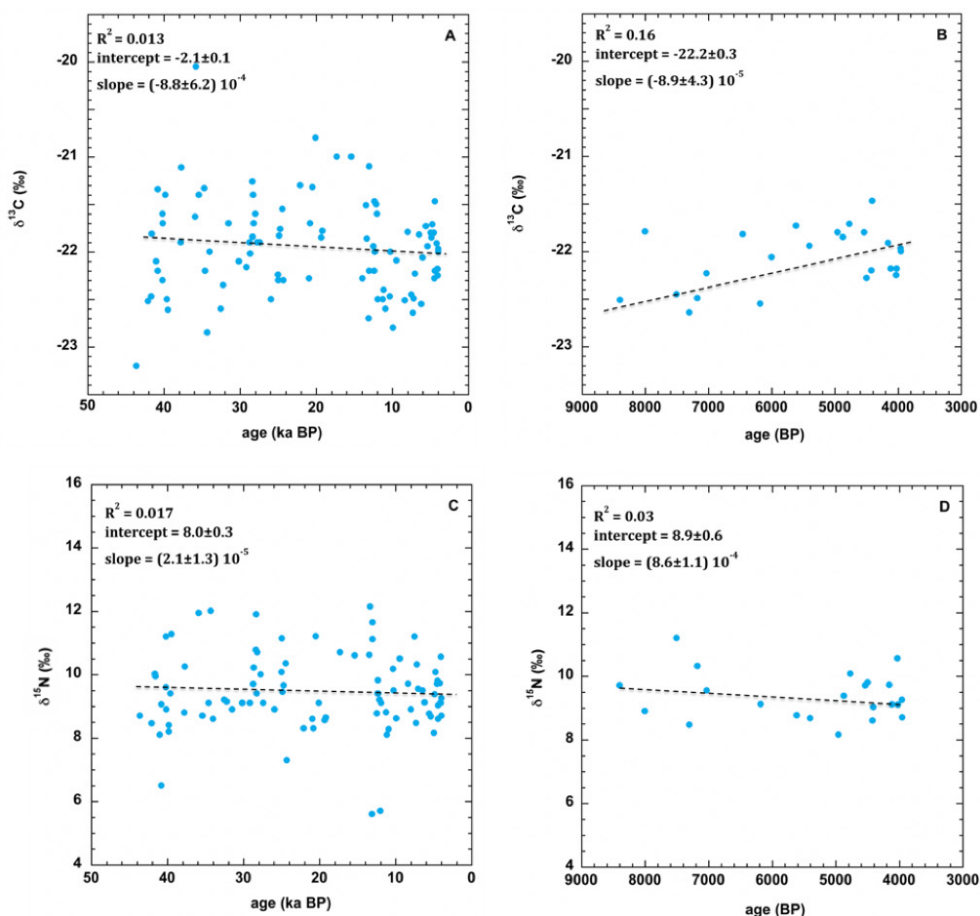


Figure 3.3 The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of samples with a finite age ($> 45,000$ ^{14}C yr BP) through time. A: $\delta^{13}\text{C}$ values of samples from North-eastern Siberia; B: $\delta^{13}\text{C}$ values of samples from Wrangel Island; C: $\delta^{15}\text{N}$ values of samples from North-eastern Siberia; D: $\delta^{15}\text{N}$ values of samples from Wrangel Island.

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. 3.3A) or in the $\delta^{15}\text{N}$ values ($p = 0.1$; Fig. 3.3C).

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, in particular considering the analytical uncertainty for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurement (see Chapter 2). It cannot be concluded at the 95% confidence level that there is a temporal trend in the $\delta^{13}\text{C}$ values ($p = 0.051$; Fig. 3.3B) or in the $\delta^{15}\text{N}$ values ($p = 0.43$; Fig. 3.3D). So, the values provide no evidence to reject the hypothesis that they remain constant. But even if there were a significant statistical correlation, an increase through time of $\sim 0.5\text{‰}$ is not very significant biologically and in terms of analytical precision.

Table 3.3 Averages and standard deviations of woolly mammoth $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for different time intervals.

	$\delta^{13}\text{C}$ (‰)		n	$\delta^{15}\text{N}$ (‰)		n
	mean	st dev		mean	st dev	
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

3.4 Discussion

3.4.1 Spatial and temporal distribution

Mainland

The current data set reveals stability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of woolly mammoth skeletal remains from North-eastern Siberia throughout the last part of the Late Pleistocene. This is even the case 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‰ and +5.7‰) relative to older samples. This depletion was attributed to higher precipitation rates during the post-LGM period (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, when compared to the newly obtained data from the present study and other recently published data, an exception for some unknown reason: all other samples from Yakutia with a post-LGM age ($n = 17$) have $\delta^{15}\text{N}$ values between +8.62‰ and +12.14‰, and are comparable to $\delta^{15}\text{N}$ values of samples with a pre-LGM and LGM age. 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).

Wrangel Island

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the Holocene woolly mammoth remains 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. Changes in habitat and/or diet at some point cannot be absolutely ruled out based on diachronic similarity of stable isotope data. But since $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ values of C3 plants are mainly determined by (local) environmental factors, such as humidity, temperature and atmospheric CO_2 concentration, some kind of change is to be expected in the tissues of the consumers of these plants in times of changing conditions. Especially, because other parts of the mammoth steppe did show significant changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from herbivore tissues following climatic and environmental changes.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of woolly mammoth samples from Wrangel Island (Fig. 3.3B and D) show less variation than the woolly mammoths which lived on the North-Siberian mainland (Fig. 3.3A 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 mainland counterparts.

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

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 living on Wrangel Island were feeding on resources with the same isotopic composition as their Late Pleistocene counterparts from the North-eastern Siberian mainland throughout their existence. The stable isotope data from Wrangel Island support the hypothesis 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.

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). However, during the Early Holocene the woolly mammoth was by far the most dominant large herbivore species. Only one bison fossil with an Holocene age, has been discovered so far. Based on the number of ^{14}C dated fossils, the Wrangel woolly mammoth population even seems to have increased in number compared to the Late Pleistocene population (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

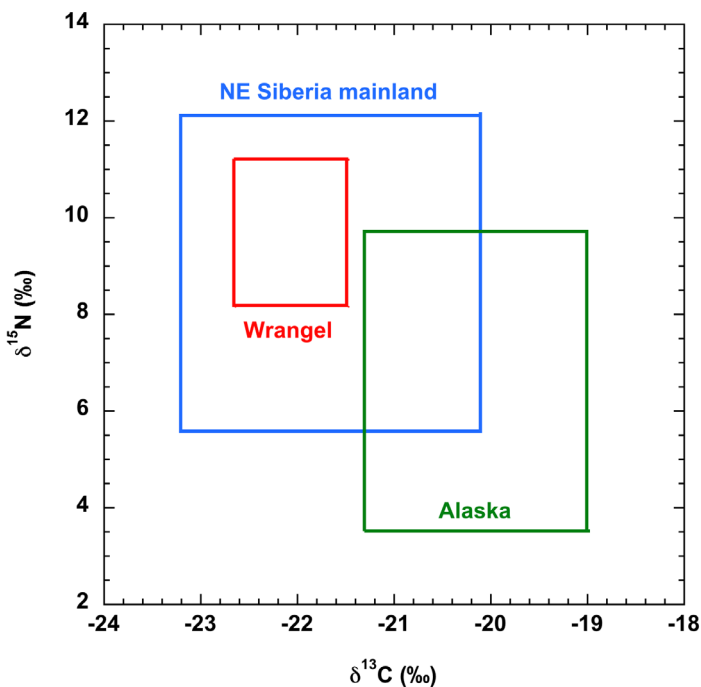


Figure 3.4 The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges of woolly mammoth samples from Wrangel Island (in red), compared to these from North-eastern Siberia mainland (in blue) and from Alaska (green; Debruyne *et al.*, 2008; Szpak *et al.*, 2010; Graham *et al.*, 2016; see Table SI Chapter 3.2 for raw data).

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 the woolly mammoth was 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 mammoths 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 mammoths and horses were associated with niche competition (Drucker *et al.*, 2014). However, the Wrangel data differ. The lack of other large herbivores on Wrangel prohibits comparison of isotope data of the woolly mammoth with such species. 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.

Beringia

By including data from Wrangel Island, the current study presents crucial stable isotope data from the border region between Siberia and Alaska. Wrangel Island is, geopolitically part of Siberia, but it is geographically closer to Alaska (Fig. 3.1). Wrangel is nowadays an island in the Arctic Ocean, but it was connected to the mainland until about 12,000 ^{14}C yr BP (Keighwin *et al.*, 2006; Vartanyan *et al.*, 2008). From the onset of the Holocene to about 6000 years ago, the Long Strait (that is, 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. The conditions in Central Beringia are supposed to have been much more mesic than at either side of the land bridge, that is, West Beringia/North-eastern Siberia and East Beringia/Alaska (Guthrie, 2001; Elias and Crocker, 2008).

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. 3.4) 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 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 Wrangel Island and Central Beringia

and Alaska is also observed in the mammalian fauna, 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 that prevented this xerophilic species to migrate to East Beringia (Elias and Crocker, 2008).

3.4.2 Comparison with other species from North-eastern Siberia

It is interesting to compare the results of our analyses 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 Pleistocene and Holocene musk oxen samples 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 values. The authors explain the observed differences in the muskoxen from Canada by an increase in precipitation during the Holocene, and conclude that Canada might have experienced a more pronounced increase in precipitation during the Holocene than Taymir (Raghavan *et al.*, 2014).

From North-eastern Siberia, the number of ^{14}C 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 Taimyr, whilst change at the Pleistocene/Holocene transition is observed in other parts of their biome (Raghavan *et al.*, 2014), corresponds to the results of the current study.

3.5 Conclusion

The 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 of woolly mammoths and other large herbivores from Europe and Alaska, which revealed significant changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values; changes that are related to climatic fluctuations during and/or after the LGM.

Even more remarkable, 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 of woolly mammoth samples from Alaska, despite the fact that both regions are geographically rather close.

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.



North Sea, photo: M. Kuitens