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The Eurasian mammoth distribution during the second half of the Late Pleistocene and the Holocene: Regional aspects

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ABSTRACT

Based on geographic information (database PALEOFAUNA), in combination with ¹⁴C and other methods of paleo dating (1584 localities, 4033 dates, including 1501 direct dates), we first examined details of changes of mammoth distribution in Eurasia on the whole and in single parts of the range over the last 50ky. The analysis of regional features in the dynamics of mammoth range and the quantity of dated localities acknowledged a leading role of the climatic (environmental) factor in these processes. The maximum size of the Eurasian range, the largest number of remains of mammoths from dated localities and, probably, the maximum total number of population were established for the range of 38.2–8.6 cal ky BP (Denekamp interstadial = Bryansk interstadial). In Western and Central Europe, the increase of population was observed during Huneborg stadial (40.8–38.2 cal ky BP). In eastern Siberia, the maximum population growth occurred in the Last Glacial Maximum (28.6–22.5 cal ky BP), and in Western Siberia – during Deglaciation (22.5–14.7 cal ky BP). The population dynamics at the periphery of the range (Islands of Japan, British Isles, Northern Europe, Southern Siberia and Northern China, and, but to lesser extent, South-Eastern Europe) differs from the dynamics of its main part. The southernmost parts of the range – Southern Siberia and southeastern Europe experienced similar changes. Population dynamics in the Iberian Peninsula was much alike the changes in Western and Central Europe. We suggested that some peripheral populations could periodically be isolated from the populations of the main part of the range. Direct calibrated radiocarbon dates fixed upper boundary of extinction of this species in different parts of range within time interval from 21 (the Iberian Peninsula) to 4 (northeastern Siberia) thousands years BP. The hypotheses about the causes of the dynamics of the area and population of the mammoth in Eurasia, including those related to the extinction of certain genetic lines of a mammoth in the Late Pleistocene, are being discussed.

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1. Introduction

The woolly mammoth is one of the most significant Pleistocene species and is often used as a symbol indicating the Ice Age. Analyzing changes in the geographical distribution over time is a

productive way to obtain information about the biology and palaeoecology of the species, the significance of its remains for biostratigraphical and paleogeographical issues, and also various aspects of the evolution of the species, causes of extinction, and its relationship with humans and other mammalian species (Vereshchagin, 1979; Kahlke, 1994, 1999; Ukkonen et al., 1999; Garrut and Tikhonov, 2001; Lister and Sher, 2001; Stuart et al., 2002, 2004; Kuzmin et al., 2003; Tong and Patou-Mathis, 2003; Lister et al., 2005; Vereshchagin and Baryshnikov, 1985; Stuart,

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2005; Takahashi et al., 2006, 2007; Reumer, 2007; Vartanyan et al., 2008; Álvarez-Lao and García, 2010; Lorenzen et al., 2011; MacDonald et al., 2012; Ponomarev et al., 2012; Drucker et al., 2015; Stuart, 2015; and many others).

The PALEOFAUNA database created by the Institute of Geography RAS and Institute of plant and animal ecology UB RAS in Russia over the last 20 years contains information on more than 1500 mammoth geographical localities in Northern Eurasia and offers the ability to investigate the geographical history of the woolly mammoth.

Analysis of this database resulted in several publications, presenting data on the distribution of the mammoth in Europe during the last 50 kyrs for the different time intervals of the last glaciation and the Holocene (Markova et al., 1995, 2010, 2011, 2013; Markova and Puzachenko, 2007; Markova and van Kolfschoten, 2008). However, over the last several years, many new radiocarbon dates on mammoth bones have been obtained through joint projects supported by the Netherlands Organization on Scientific Research (NWO) and the Russian Foundation for Basic Research (RFBR). All of these dates gave new insights into the geographical distribution of mammoths during the interstadials and stadials of the Late Pleistocene and enhance our knowledge about the dynamic changes of the mammoth range over the entire territory of Eurasia and in its different parts, including stages of diminishing range at the end of the Pleistocene and the Holocene. The received information permits detailed study of the regional peculiarities of historical dynamics of mammoth range.

First, we studied the dynamics of the entire mammoth range along all Northern Eurasia. The principal characteristics of these dynamics in different parts of the mammoth range are presented in detail in the second part of this paper.

Besides radiocarbon-dated bones, Eurasian mammoth population dynamics have been investigated using ancient mtDNA. Such ancient mtDNA studies indicate that during the Late Pleistocene there were several woolly mammoth mtDNA haplogroups (a group of similar haplotypes that share a common ancestor having the same single nucleotide polymorphism (SNP) mutation) in Eurasia and North America organized in different clades (a group of similar haplogroups). In the current study, the results of radiocarbon dating are merged with recently obtained ancient mtDNA data (Barnes et al., 2007; Debruyne et al., 2008; Palkopoulou et al., 2013, 2015) to create an even more complete picture of dynamic changes of the geographical range of mammoth in Eurasia, including internal migration patterns.

2. Materials and methods

Detailed palaeoclimatic studies of the Late Pleistocene and early Holocene revealed the occurrence of a large number of climatic fluctuations. The Late Pleistocene Weichselian/Valdaian/Zyryanian Glaciation is divided into an Early, Middle and Late Weichselian or an Early, Middle and Late Valdaian. The study of the terrestrial Late Pleistocene geological and botanical record indicated that the Weichselian/Valdaian Glaciation encompasses a number of interstadials and stadials. The study of high-resolution records, such as deep-sea cores, lake cores and especially the Greenland GRIP, GISP2, and NGRIP ice cores, indicates the occurrence of major climatic oscillations (Svensson et al., 2006, 2008; Vinther et al., 2006). The $\delta^{18}\text{O}$ isotopic signal suggests a major increase in continental ice volumes during MIS 4 and in particular in MIS 2, and that the global ice volume was somewhat reduced during MIS 3 (Middle Weichselian/Middle Valdaian) (Lowe and Walker, 1997). The MIS 3 interval is characterized by a number of climatic fluctuations that have also been recognized in the continental record of Western and Central

Europe: the Glinde and Oerel interstadials during the first half of MIS 3 and the Moershoofd, Hengelo and Denekamp (the equivalent of the Bryansk interstadial) during the second half of MIS 3 (Behre, 1989) (Fig. 1, Table 1). The long Denekamp Interstadial was climatically heterogeneous. The ice core $\delta^{18}\text{O}$ signal reflects numerous climatic fluctuations, especially in the first half of the interstadial. A severe drop in temperature and a major increase of the continental ice sheet follow the Bryansk/Denekamp Interstadial: MIS 2 (Last Glacial Maximum – LGM or Pleniglacial). The end of the last cold stage is generally indicated as Deglaciation or as the Late Glacial Transition (LGT). The end of the Deglaciation period is marked by two interstadial episodes – Bølling and Allerød, separated by a stadial (Older Dryas) and followed by the Younger Dryas Stadial. Taking into account that the length of the Older Dryas is insignificant (only ~200 y) and considering the fact that the cooling, according to the $\delta^{18}\text{O}$ signal, was weak (Coope and Lemdahl, 1995), all data for these three intervals are merged in this study. The increase in temperature at the end of the Younger Dryas Stadial marks the Pleistocene/Holocene transition. The Greenland NorthGRIP (NGRIP) ice core contains a proxy climate record across the Pleistocene–Holocene boundary of unprecedented clarity and resolution (Walker et al., 2009). Khotinsky (1977) and Khotinsky and Klimanov (2002) reconstructed the climatic changes during the Holocene in Northern Eurasia using palynological data and identified 1) a Preboreal warming, which was characterized by the distribution of birch and pine forests in the northern, western and central parts of Europe, and 2) significant warming during the Boreal. The beginning of the Boreal shows a wide distribution of hazel. The second part of the Boreal shows a distribution of mixed broad-leaved (oak in the Europe) forests. The modern biomes of Northern Eurasia were formed during this time interval. During the Atlantic, the role of lime-tree and elm became less essential. It was the warmest and moistest period of the Holocene. In the next Subboreal period, the climate was generally dryer and slightly cooler than in the Atlantic. The last period of the Holocene, the Subatlantic, is characterized by an increasing influence of an oceanic climate (Khotinsky, 1977).

Table 1

Climate-stratigraphic units of the Late Pleistocene, the Holocene, and their durations. The ^{14}C dates are reported by convention in BP (Stuiver and Polach, 1977). The ^{14}C dates are calibrated into calendar ages using IntCal13 (Reimer et al., 2013). The calendar ages are reported in cal ky BP and correlated with cold phases (Greenland Stadials, GS) and warm phases (Greenland Interstadials, GI) (Shackleton, 1977; Hedges et al., 1998; Litt et al., 2001; Gibbard and van Kolfschoten, 2004; Andersen et al., 2006; Chabai and Uthmeier, 2006; Gerasimenko, 2006; Svensson et al., 2006, 2008; Mol, 2008; Velichko and Faustova, 2009; Rasmussen et al., 2014).

Climate-stratigraphic units and abbreviation	uncal ky BP	cal ky BP	Greenland interstadial/stadial
Subboreal (SB)	2.1–4.75	2.1–5.5	
Atlantic (AT)	4.75–8.0	5.5–8.9	
Boreal (BO)	8.0–9.0	8.9–10.2	
Preboreal warming (PB)	9.0–10.1	10.2–11.7	
Younger Dryas Stadial (YD)	10.1–11.0	11.7–12.9	GS 1
Bølling and Allerød interstadials ^a (BAIC)	11.0–12.5	12.9–14.7	GI 1
Late Glacial Transition (or Deglaciation) (LGT)	12.5–19.0	14.7–22.5	GS 2.1
Last Glacial Maximum (LGM)	19.0–24.6	22.5–28.6	GS 4 – GS 2.1
Denekamp (=Bryansk) Interstadial (DE)	24.6–33.6	28.6–38.2	GI 8 – GI 4
Huneborg Stadial (HUN)	33.6–36.1	38.2–40.8	GS 10 – GS 9
Hengelo Interstadial (HEN)	36.1–39.8	40.8–43.3 ^b	GI 11 – GI 10
Hasselo Stadial (HAS)	39.8–44.7	43.3–48.3	GS 13 – GS 12
Moershoofd Interstadial (MO)	>45.0	48.3–54.2	GI 14 – GI 13

^a separated by the Older Dryas cooling.

^b 36.0–38.6 uncal ky BP, 41.38–42.35 cal ky BP (Vandenberghe and Plicht, 2016).

For this study we used a large amount of published data on fossil mammoth remains from different parts of Eurasia (Vereshchagin, 1979; Vereshchagin and Baryshnikov, 1985; Musil, 1985; Kahlke, 1994, 2014, 2015; Vartanyan et al., 1995; Ukkonen et al., 1999, 2007; Garrut and Tikhonov, 2001; Foronova, 2001; Lister and Sher, 2001; Lougas et al., 2002; MacPhee et al., 2002; Stuart et al., 2002, 2004; Kuzmin et al., 2003; Kosintsev, 2003; Rustioni et al., 2003; Tong and Patou-Mathis, 2003; Kuzmin and Orlova, 2004; Sher et al., 2005; Stuart, 2005; Takahashi et al., 2007; Sommer and Benecke, 2009; Kuzmin, 2010, 2013; Lorenzen et al., 2011; Nikolskiy et al., 2011; and many others). The results presented in this paper are based on the dated mammoth localities spread over northern Eurasia (Table 2, Fig. S1). The strong correlation between the quantity of direct and indirect ^{14}C dates were estimated at 0.98. The correlations which were received by both U/Th disequilibrium and electron spin resonance (ESR) methods, optically stimulated luminescence (OSL) and thermoluminescence (TL) were 0.88 (direct) and 0.94 (indirect), 0.98 and 0.96, respectively. In addition, a strong correlation, 0.84, was revealed between the quantity of ^{14}C dates and indirect age definition of mammoth remains received by archaeological and biostratigraphical data (Table 2). Thus, all data concentrated in Table 2 can be used for study of mammoth range dynamics.

localities is 0.84 (Fig. S2), and indicates that the “accumulation” of the mammoth localities was more or less equable through time. The mean speed of localities’ accumulation in Eurasia was 41 units for the one thousand years. It is interesting that this dependence describes about 70% of the variation of number of localities from Table 2 (last column). So, as the principal indicator of “abundance” of mammoth we used the quantitative estimation of localities and the duration of the climatic-stratigraphical units in thousand cal years (cal kyrs) – the “average accumulation rate” (AAR). The significant difference between the absolute and relative (AAR) values of the number of mammoth localities on the territory of Northern Eurasia is shown in Fig. 2.

In this work, the mammoth distribution during the last 50 kyrs has been analyzed within Northern Eurasia as a whole and separately for nine geographical regions (Fig. S3): the Iberian Peninsula, the British Isles, Northern Europe, Western and Central Europe, Eastern Europe, Western Siberia, Eastern Siberia, Southern Siberia with Northern China, and Japan. Unfortunately, we have only single dated locality for the Apennine Peninsula (Settepolesini di Bondeno, HUN). Therefore, we are not able to examine the mammoth range dynamics for this region.

Table 2

The numbers of direct and indirect dates of mammoth remains used in work.

Clim.- stratig.- units	Method						Total	Loca-lities
	$^{14}\text{C}^a$		U/Th and ESR ^a		OSL ^a	TL ^a		
	Direct	Indirect	Direct	Indirect		Archaeolo-gical and biostratigra-physical evidence		
SB	34						34	3
AT	71						71	7
BO	9						9	1
PB	16			1			17	14
YD	23	3		2		1	29	23
BAIC	84	79		5		10	178	74
LGT	282	340	7	3		15	658	280
LGM	292	437	13	7	4	1	792	300
DE	362	919	2	32	10	27	1354	398
HUN	75	142		9	3	13	244	145
HEN	73	115		7	2	9	206	109
HAS	123	199		11	5	9	353	172
MO	34	28	1	15	2	8	88	58
Total	1478	2262	23	92	26	93	4033	1584

^a Finite dates only.

In this article, we focus on the second half of the Late Pleistocene and the Holocene (MIS 3, MIS 2, MIS 1, covering the second half of the Last Glaciation, and the early, middle and the beginning of the late Holocene), a period that falls within the limitations of ^{14}C dating. The distribution of mammoths is discussed for the climate-stratigraphic units as described in Table 1. These climate-stratigraphic units are comparable to time windows used in previous papers discussing faunal changes during the Late Pleistocene and Holocene (Baryshnikov and Markova, 2002, 2009; Markova and Puzachenko, 2007; Markova and van Kolfschoten, 2008; Markova et al., 2010, 2011, 2013).

We calculated the number of geographical localities for every climatico-stratigraphical unit (Table 2). The correlation between the duration of climatic interval and the number of mammoth

3. The spatial and temporal distribution of woolly mammoth in Northern Eurasia

3.1. MIS 3

3.1.1. Moershoofd Interstadial (MO) (Fig. 3a)

The mammoth remains related to 54–49 ky BP can be assigned to the Moershoofd Interstadial: Rhinoceros Hole (British Isles), Güelga cave (Spain), Pecheurs (France), Peggauerwandhöhle (Austria), Kulna cave (Czech Republic), Jaroslaw-Garbarze (Poland), Pryima I (Ukraine), Kamenka (Transbaikalian region, Russia). During this interstadial, the dated mammoth localities are mainly distributed in three areas: 1) the British Isles and Central Europe; 2) sub-polar Eastern Siberian; 3) south of Western and Eastern Siberia (Fig. 3a). There are isolated localities in the Volga River basin, in the

Fig. 1. Geochronology of the second part of the Late Pleistocene and the Holocene.

Crimea and Japan (Hokkaido Island). To the south of 45°N , mammoth bones are found in Iberia (Álvarez-Lao et al., 2009; Álvarez-Lao and García, 2012), North China (Zhoujiayoufang (44.73°N) (Turvey, 2013) and Japan (Yuni (43.0°N)) (Iwase et al., 2012).

3.1.2. Hasselo stadial (HAS) (Fig. 3b)

A large number of mammoth finds are located in Central Europe, in the northern regions of Western and Eastern Europe and in Siberia. A few discoveries are located in the center of the Russian Plain, in the Ural Mountains, in the center of Western Siberia, in the south of Eastern Siberia, in the Far East, and on the Kamchatka Peninsula and on the Hokkaido Island. To the south of 45°N , mammoth bones are found in Iberia (Álvarez-Lao et al., 2009; Álvarez-Lao and García, 2012), in the Balkan Peninsula (Kozarnika

cave (43.65°N)) (Fernandez, 2009), in Northern Caucasus (Il'skaya cave (44.8°N)) (Baryshnikov, 2003), Russian Far East (Geographical Society Cave (43.33°N)) and in Japan (Hokkaido Is. (Churui (43.71°N)) (Iwase et al., 2012).

3.1.3. Hengelo Interstadial (HEN) (Fig. 3c)

The highest density of localities with mammoth remains is located in the north of Western Europe. The number of remains in Eastern Europe is increased. The mammoths existed in the mountainous areas of Southern Siberia and in Transbaikalia region, in the Far East and on the Hokkaido Island. To the south of 45°N , mammoth bones were found in Iberia (Álvarez-Lao et al., 2009; Álvarez-Lao and García, 2012), in the Balkan Peninsula (Kozarnika cave) (Fernandez, 2009), in Northern Caucasus (Il'skaya cave) (Baryshnikov, 2003), on Russian Far East (Geographical Society

Fig. 2. The time dynamic of the number of the Eurasian mammoth localities per climate-stratigraphic unit (a) and the "average accumulation rate" (AAR) – the number of localities per one thousand calibrated years (b). Dotted line marked of the average values of oxygen-isotope concentration ($\delta^{18}\text{O}$). Regression between $\delta^{18}\text{O}$ and number of localities with mammoth remains is presented.

Cave) and in Japan (Yuni, Rausu (43.97 °N)) (Takahashi et al., 2006; Iwase et al., 2012).

3.1.4. Huneborg Stadial (HUN) (Fig. 4a)

During the Huneborg Stadial, the mammoth range extended southwards both in the western and eastern part of its geographical distribution. The majority of finds are located in the center and north of Western Europe and in the coast of the Arctic Ocean in Western and Eastern Siberia. Mammoths also inhabited the mountains in Southern Siberia (Baikal region), in Kamchatka, on the New Siberian Islands and in the basin of the Indigirka River. There are discoveries on the south of Iberian Peninsula (Padul (37.02 °N) (Álvarez-Lao et al., 2009)), in the north of the Apennine Peninsula (Settepolesini di Bondeno (44.88 °N)) (Stuart et al., 2002), in South-Eastern Europe (Kozarnika cave), in Serbia (Baranika cave) (43.6 °N) (Pacher and Stuart, 2008) and in the Crimea (about 45 °N). Mammoth remains were found in the northeast of China (Mingyuegou, 43.11 °N) (Tong and Patou-Mathis, 2003; Lorenzen et al., 2011). We have not information about the dated mammoth remains from the Japan Islands for this interval.

3.1.5. Denekamp (= Bryansk) Interstadial (DE) (Fig. 4b)

The southernmost mammoth remains are still found in the south of Iberian Peninsula Figueira Brava cave (38.44 °N), Padul, Cueva de Los Casares (40.9 °N; this cave does not provide mammoth remains, but an engraving representing a mammoth only) (García, Arsuaga, 2003; Antunes and Cardoso, 1992). Many localities are situated in Southern Europe (Barma Grande, France), Kozarnika cave, the Balkans (Formicola et al., 2004) and in Western, Central, and Northern Europe. The nine localities were found in Scandinavia (Vastansjö, Pilgrimstad, Iijoki and others) (Ukkonen et al., 1999, 2007). Mammoth was widespread in Eastern Europe and in the Ural Mountains. The northernmost localities were found beyond the Arctic Circle and the southernmost ones in the Crimea. The highest density of localities is observed at the coasts and islands of the Arctic Ocean. A considerable number of finds was also discovered in the mountains of Southern Siberia, in the Baikal

region and Transbaikalia. Single finds are located in the Kamchatka, in the Far East and on the Hokkaido.

Three localities were found southward from 45 °N in North-Eastern China: Ji'nan (Jinan) (36.66 °N), Mingyuegou, Zhoujiayoufang (44.7 °N) (Takahashi et al., 2007).

On the whole, during MIS 3 the mammoth range occupied a huge area and spread northward till the 76 °N (Zhohov Island, East Siberian Sea) and southward till 36.7 °N (North-Eastern China). Its western boundary was located on –9.1 °W (South-West of Iberian Peninsula) and the eastern boundary on 180 °E (Wrangel Island).

3.2. MIS 2

3.2.1. The Last Glacial Maximum (LGM) (Fig. 4c)

During the maximum cooling of the Valdai Glaciation (= Weichselian) the mammoth occurred in Western, Central and Northern Europe, in Western Siberia, in the sub-polar regions of Siberia, in the mountains of Southern Siberia, Kamchatka and Japan Islands.

The northern limit of mammoth range was located on 79.5 °N (October Revolution Island from Severnaya Zemlya group) in Eastern Siberia. A significant number of Northern European mammoth localities distributed in the zone of Scandinavian ice-sheet (Favang = Fevang, Lohtaja, Munke Bjergby, Turženų, Topsa) (Aaris-Sørensen et al., 1990; Vasil'chuk et al., 1997; Ukkonen et al., 1999; Arppe, 2009; Ponomarev et al., 2012; and others). In an addition to published data for this region we can indicate one new mammoth locality: Likhnevschina (Arkhangelsk Oblast, Russia, Northern Dvina River; 63.141 °N, 42.079 °E) 20 450 ± 110 y. BP (GrA-42214: material – tooth, M2 ?; 95.4% of confidence data is 25 030–24 259 cal y BP).

Comparably to Denekamp interstadial the southern limit of mammoth range in LGM shifted northward in Iberian Peninsula. On the other part of the territory, the configuration of the mammoth range changed inconsiderably. Several sites were located southward from 45 °N: Grotte de la Rainaude (43.3 °N) in the southern France (Crégut-Bonnoure, 1995), Kozarnika cave and Baranika cave on the Balkans, Shaitan-Koba (44.8 °N) at the Crimean Peninsula

Fig. 3. Mammoth localities correlated with the Moershoofd interstadial (a), the Hasselo stadial (b), the Hengelo Interstadial (c).

(Bonch-Osmolovskii, 1930), Kasozhskaya cave (44.27 °N) on the North Caucasus (Mashchenko and Kalmykov, 2005).

Mammoth remains were found as well as on the north of Japan Islands (Hokkaido Island), so on the south on the Honshu Island

(Onsentsu, 35.28 °N) (Iwase et al., 2012). However mammoth was not spread so far southward in China during LGM as it was during Denekamp Interstadial (Dabusu, 44.73 °N, Mudanjiang, 44.63 °N) (Tang et al., 2003).

Fig. 4. Mammoth localities correlated with a – the Huneborg stadial (a), the Denekamp interstadial (b), the LGM (c).

3.2.2. Late Glacial transition (or Deglaciation) (LGT) (Fig. 5a)

On a whole, the LGT mammoth range was similar to LGM time. Mammoth survived along the coast and at the drained continental shelf of the Arctic Ocean (Severnaya Zemlya Islands, the New

Siberian Islands and the Wrangel Island), in the Urals region, in southern Siberia, Chukotka and Kamchatka, and on Hokkaido Island. Mammoths still inhabited the southern part of Europe: Las Caldas (Cueva de las Hienas) (43.34 °N) (Domingo et al., 2005;

Fig. 5. Mammoth localities, correlated with the Late Glacial transition (a), Bølling – Allerød interstadial complex (b), the Younger Dryas stadial (c).

Álvarez-Lao and García, 2010, 2012), Arene Candide Cave (I) (44.15 °N) (Cassoli and Tagliacozzo, 1994). LGT was probably the last period when mammoth reached south-west of the Iberian Peninsula (Grotte de Joao Ramos, 39.5 °N) (Antunes and Cardoso, 1992).

In the beginning of LGT mammoth lived also in Crimea (Shaitan-Koba (Bodrak)). The southernmost site in Asian part of the range (Khorol, Russia) is located at 44.15 °N (Vasilevsky, 2007). LGT finds are the last in Trans-Baikalia (Tamir, 50.3 °N),

northeastern China (Xiaonanshan, 46.78 °N) (Orlova et al., 2006), Kamchatka (Ushki I, Kamchatka River (Dikov, 1979; Sulerzhitsky, 1995)) and Hokkaido Island (Yubari, 43.08 °N) (Iwase et al., 2012).

3.2.3. The Bølling and Allerød interstadials separated by the Older Dryas cooling (BAIC) (Fig. 5b)

For this time slice, the density of mammoth localities is sharply decreased. They are distributed very irregularly. A drastic contraction and fragmentation of the mammoth range happened in Siberia. Some single finds are known from southern Europe: Grotte de Combe Saunière (45.2 °N) (Marquet, 1989), Zupanov Spodmol (45.74 °N) (Pohar, 1997). The Severnaya Zemlya Islands, Wrangel Island, and the New Siberian Islands yielded finds that dated to the BAIC interval. The species entirely disappeared from southern Siberia and Far East. In the north of Europe mammoth range also reduced. The overwhelming majority of the mammoth sites are located in an area between 45 °N and 60 °N with the highest density in Western-Central Europe, the Urals Mountains, Taimyr Peninsula, and in the upper reach of Yana and Indigirka Rivers (north of Eastern Siberia).

3.2.4. Younger Dryas Stadial (YD) (Fig. 5c)

The short distinct cooling event known as the Younger Dryas is well expressed in ice core $\delta^{18}\text{O}$ signal (Rasmussen et al., 2014). There are only 23 dated mammoth localities for this interval (Table 2). During this time, the last mammoths lived on British Isles (Cathole Cave (Cat Hole) (Nash, 2011)) and in the west of Europe (Le Buisson Capin, Grand Canton (Bignon, 2006), Oelknitz (Musil, 1985)). The data suggest an abrupt collapse of the mammoth range and its disintegration into isolated parts. The mammoth survived only in isolated refuges with steppe vegetation particularly in the basin of the Dniester River and in the upper Elbe River; in Siberia on the Yamal and Taimyr Peninsulas, along the mouth of the Indigirka River, on the New Siberian Islands and Wrangel Island. The data show a continuation of the contraction of the mammoth range that started in BAIC and during the Younger Dryas.

3.3. MIS 1

3.3.1. Preboreal (PB) and Boreal (BO) (Fig. 6a)

There are only limited data for these two intervals of the Holocene; that is why they are merged in our analysis. There are only 14 PB localities and 1 BO locality; almost all are located to the north of 58 °N. During the early Holocene mammoth lived in the territory of the Baltic region (Nikonov and Nikonova, 1965; Lougas et al., 2002), northwestern Russia (Stuart et al., 2002), in Yamal (Arslanov et al., 1982), Taimyr (MacPhee et al., 2002), Gydan, on the New Siberian Islands (New Siberia Island) (Stuart et al., 2004; Sher et al., 2005), and on Wrangel Island (Vartanyan et al., 1995).

3.3.2. Atlantic (AT) and Subboreal (SB) (Fig. 6b)

The maximum warming of the Holocene is known as the Atlantic period. The significant differentiation and increase of complexity of the vegetation communities and the expansion of forest biome to the south and to the north took place during this period. Later, during the Subboreal period the climate became generally some cooler, but it was heterogeneous during the different intervals of this period. During the middle and the late Holocene, the last Eurasian mammoth populations survived on Wrangel Island and on one of the Pribilof Islands in the Bering Sea (Qagnax Cave, St. Paul Island (Guthrie, 2004); 5630 ± 40 yrs BP (Yesner et al., 2005)). The youngest mammoth date is obtained on materials from Wrangel Island –

3685 ± 60 yrs BP (4225–3854 cal yrs BP) (Kuzmin and Orlova, 2004; Vartanyan et al., 2008).

4. The spatial and temporal distribution of woolly mammoth in the different parts of Eurasia

4.1. Iberian Peninsula

This territory was the SW mammoth range boarder in Eurasia. The quantities of mammoth localities for all studied intervals are 33 (Table S1). The correlation of AAR with $\delta^{18}\text{O}$ is -0.69 .

The maximum value of AAR was obtained for Huneborg stadial (Fig. 7) and the maximum number of localities was revealed for Denekamp (MIS 3) (Álvarez-Lao, 2014). It is possible, that mammoth absolutely disappeared from the Iberian Peninsula during LGT.

4.2. British Isles

The British Isles were the part of the Eurasian continent during the last glaciation and here the western part of the mammoth range was located. The AAR has the low correlation with $\delta^{18}\text{O}$ ($r = -0.53$) (Fig. 7). Herewith, the total number of dated localities is twice more than on the Iberian Peninsula (Table S1).

The maximum values of AAR were obtained for HEN and HUN, the minimum – for LGM and LGT (Fig. 7). The most northern localities related to the Hasselo stadial (Oxbow, 53.77 °N (Gaunt et al., 1970)), and to Hengelo and Denekamp interglacial (Ash Tree Cave, Pin Hole Cave Robin Hood's Cave). Possibly, the decreasing of mammoth population in LGM was negatively influenced by the ice-sheet (Hughes et al., 2011). The high value of BAIC AAR could be partly explained by mammoth migration from the more southern regions of Western Europe. This hypothesis is based on the fact that the number of the BAIC mammoth localities is higher than of LGT (Table S1). Finally, mammoth disappeared no earlier than the end of the BAIC from the British Isles (Hedges et al., 1991), but it could possibly survived until the Younger Dryas (Cathole Cave (Nash, 2011)).

4.3. Northern Europe

This region is a “core” of the Scandinavian ice sheet during the Last Glaciation and the northern peripheries of mammoth range in Europe.

In spite of this obstacle we received the high negative correlation between AAR and $\delta^{18}\text{O}$ for this region ($r = -0.71$). The maximum rate of localities accumulation was in Denekamp (Fig. 7). The first dated locality in this region is related to Hasselo stadial (Table S1; Ramsele, 64.07 °N) (Ukkonen et al., 2007). The maximum population existed in Denekamp Interstadial (Ukkonen et al., 1999, 2007). Fourteen localities are correlated with the LGM. These localities were found on the territory covered by the ice-sheet according to the modern reconstructions (Fig. 4c). The youngest localities are situated on the Baltics (Kunda, 59.48 °N; Puurmani, 58.57 °N) and related to the early Holocene (PBO) (Nikonov and Nikonova, 1965; Lougas et al., 2002).

4.4. Southeastern Europe

This region is the southeastern periphery of the mammoth range in Europe. The mammoth expansion to this territory is linked with cool intervals (correlation between AAR and $\delta^{18}\text{O}$ -0.76 , Fig. 7). The earliest locality situated on the far northeast of this region is correlated with the MO interstadial (Fig. 3a, Ripiceni-Izvor, 47.97 °N) (Ichim and Costas, 2011). The

maximum number of localities is related to the LGM (Table S1). The youngest indirect dates correlate with the first half of LGT (Szeged-Othalom, 46.26 °N) (Kovacs, 2001), (Ceahlau-Podis, 47.03 °N) (Ichim and Costas, 2011).

4.5. Western and Central Europe

The mammoth constantly habituated here during MIS 3 – MIS 2. The average speed of mammoth localities' accumulation is

Fig. 6. Mammoth localities correlated with the Holocene Preboreal-Boreal (a), Atlantic-Subboreal (b), and full set of mammoth localities for the MIS3 – MIS1 (c).

Fig. 7. Time dynamic of the “average accumulation rate” (AAR) – the number of mammoths localities per one thousand calibrated years for different parts of Eurasian range (Fig. S3). Dotted line marked of the average values of oxygen-isotope concentration ($\delta^{18}\text{O}$).

strongly correlated with $\delta^{18}\text{O}$ ($r = -0.81$). The maximum value of this parameter falls on the HUN stadial (Fig. 7); maximum density of localities (126 localities, Table S1) and possibly the quantity of the populations are related to the Denekamp. During the LGM, cold stage the quantity of localities twice decreased (73 localities). The mammoth extinction and the degradation of its range began during LGM, lasted mainly during BAIC interstadial and completed in Younger Dryas and in the beginning of the Holocene (Figs. 5c and 6a) (Arppe, 2009; Wiśniewski et al., 2009; Musil, 2010).

4.6. Eastern Europe

Unlike Western and Central Europe, in Eastern Europe maximum AAR is revealed not for Denekamp but for LGM stadial (Fig. 7). The highest density of localities in the region (totally 74 sites) is also observed in LGM (Table S1). In the LGT, the range and density of localities did not change considerably; intensive extinction occurred during BAIC only. The last mammoth finds in Eastern Europe dated YD and the Early Holocene (PBO): Berezn-6 (51.0 °N), Zhidikhovo Peatbog (59.16 °N) (Stuart et al., 2002; Lisitzin, 2010).

4.7. Western Siberia

Changes of mammoth range in Western Siberia are very peculiar (Fig. 8). Maximum value of AAR as well as the highest density of localities was found here in LGT (Table S1). Correlation between AAR and $\delta^{18}\text{O}$ is -0.88 .

The extinction of mammoth in the region occurred relatively fast during BAIC. The last mammoths lived in the north of Western Siberia until the YD and the PBO (the Holocene) on the Yamal (68.92 °N) and Gydan (70.3 °N) Peninsulas (Figs. 5c and 6a) (Evseev et al., 1982; Vartanyan et al., 1995).

4.8. Eastern Siberia

Mammoth inhabited Eastern Siberia during MIS 3, MIS 2, and MIS 1 till the extinction that ended in Subboreal interval of the Holocene on Wrangel Island (see above). The influence of climate to mammoth populations is high ($r = 0.82$). Maximum AAR was observed for Huneborg and LGM stadials. Relatively high AAR was also found for BAIC (Fig. 8). Maximum density of localities and the broadest range was noted for Denekamp interstadial (Table S1). Mammoth range contracted from south to north. In the southern part (54 °N – 55 °N) terminal stage of extinction occurred in BAIC

Fig. 8. Time dynamic of the “average accumulation rate” (AAR) – the number of localities with mammoth remains per one thousand calibrated years for different parts of Eurasian range (Fig. S3). Dotted line marked of the average values of oxygen-isotope concentration ($\delta^{18}\text{O}$).

(Tseitlin, 1979; Akimova et al., 2005). In the northern part there are some sparse mammoth finds along Enisey (55.3 °N) and Lena (55.6 °N – 59.3 °N) Rivers, but already in Younger Dryas mammoth remains are found only in the high Arctic to the north of 73 °N in the Taymyr Peninsula, on Severnaya Zemlya and New Siberian Islands (Figs. 5b, c). Mammoth finds on Wrangel Island dated from $43\,299 \pm 2162$ cal y BP to 4024 ± 86 cal y BP, but the majority of dates are from 10 to 4.5 cal ky BP (Vartanyan et al., 2008; Nikolskiy et al., 2011). Taking into account that mammoths of the same age were not yet found on the continent in northeastern Siberia, we can suppose that the last island population was isolated not earlier than the Early Holocene.

4.9. Southern Siberia and northern China

Mammoth inhabited southern part of Siberia and northern China during MIS 3, MIS 2, from MO to BAIC. Maximum AAR was obtained from Hasselo and Huneborg stadials (Fig. 8). The broadest range and highest density of localities was noted for Hasselo and Denekamp (Table S1). The abrupt reduction of density of localities twice compared to Denekamp occurred already in the LGM. The youngest direct date related to the end of LGT was made on mammoth remains from China (46.78 °N) (Kuzmin and Orlova, 2004). The last indirect date of mammoth (BAIC) in the region is

known from Nizhnaja Dzhilinda I locality (55.63 °N) (Vetrov et al., 1993).

4.10. Islands of Japan

Islands of Japan were the southeastern periphery of mammoth range in Asia. There is no correlation between abundance of mammoth and climate ($r = -0.54$, Fig. 8). The most numerous finds are known for Hengelo and LGM (Table S1). The majority of remains are found on the northern island (Hokkaido). The only one dated case of mammoth inhabiting southern island of Honshu was in the beginning of LGM ($28\,033 \pm 915$ cal yrs BP (Iwase et al., 2012)). There are two possible ways of species migration to archipelago – via the territory of modern Sakhalin Island and via the Korean Peninsula. It is possible that Hokkaido population was isolated from the continent for a long time because no mammoth finds dated to the last 50 kyrs are so far known from Sakhalin. Mammoth died out on Hokkaido (43.08 °N) in the beginning of LGT (Iwase et al., 2012).

Thus, the extinction process was more detailed revealed in the north of Eurasia. Direct dates on mammoth remains from the southern part of the range are not numerous, and sometimes they are not related to the latest history of species in the region (they are rather old). The extinction of the species went asynchronously in different parts of the range (Table 3).

Table 3

The youngest direct dates of mammoth remains in different parts of its range: radiocarbon age and calibrated age (within brackets).

Region	Climate-stratigraphic units					References
	SB	PBO	YD	BAIC	LGM-LGT	
Iberian Peninsula					17050 ± 290 (20604 ± 377)	1
British Isles				11650 ± 50 (13484 ± 53)		2
Western and Central Europe			10510 ± 70 (12437 ± 130)			3
Northern Europe		10100 ± 100 (11684 ± 240)				4
Eastern Europe		9760 ± 50 (11184 ± 61)				5
Western Siberia		9600 ± 300 (11000 ± 457)				6
Eastern Siberia	3685 ± 60 (4024 ± 86)	9470 ± 40 (10739 ± 116)		11980 ± 55 (13844 ± 86)		7
Southern Siberia and Northern China					12900 ± 410 (15338 ± 666)	8
Islands of Japan					16250 ± 90 (19630 ± 137)	9

References: 1 – Domingo et al. (2005), Álvarez-Lao and García (2010, 2012); 2 – Hedges et al. (1991); 3 – Arppe (2009); 4 – Lougas et al. (2002); 5 – Stuart et al. (2002); 6 – Evseev et al. (1982); 7 – Vartanyan et al. (2008); Nikolskiy et al. (2011); Akimova et al. (2005); 8 – Kuzmin and Orlova (2004); 9 – Iwase et al. (2012).

5. Discussion

Based on the geographical information, combined with the radiocarbon data, a correlation has been revealed between the observed shifts in mammoth range and the climatic changes that occurred during the last 50,000 y. During the Late Pleistocene *M. primigenius* inhabited a vast area in Eurasia. Mammoth range changed repeatedly during the Middle and Late Valdai (Veishelian) Glaciation. The general trend of changes in woolly mammoth range in Eurasia is shown in Figs. 2b, 3–6, and his survival/extinction pattern in the different parts of the continent is shown in Figs. 7 and 8.

We first examined details of changes of mammoth Eurasian range on the whole and in its single parts. This allowed revealing the general regularities of range pulsation following the climatic events during the last 50 kyrs. Dynamics of the range was well correlated in general with climate changes (dynamics of $\delta^{18}\text{O}$ GICC05, Fig. 1). The expansion of the range increased during the stadial intervals and decreased during the most of the interstadials, excluding the Denekamp. The maximum expansion of mammoth range in Eurasia is related to the Denekamp Interstadial. This long interval (38.2–28.6 cal kyBP) comprised five sharp warm peaks and four deep drops of temperature down to the levels typical for LGM (Fig. 1). It is possible that such combination of environmental conditions have led to the situation when during warm periods the mammoth range expanded to the north, and during cold periods – to the south. In the result for the entire interval, this creates a pattern of maximum range expansion to the south and to the north (Fig. 4b). This suggestion can be verified by more detailed study of mammoth range dynamics during Denekamp interstadial. Later, after the Denekamp interstadial, the range of mammoth contracted and, it should be noted, that this process started before the end of the LGM.

We also found particular regional features of range dynamics in the European part, and in the Asian part of the range. Differences between them were in the AAR index. We suggested that AAR indirectly reflects the population number. In Western Europe absolute maximum of AAR index was observed in Huneborg stadial (40.8–38.2 cal kyBP), while in Western and Eastern Siberia this index slightly varied (population number more or less stable, probably) for period after the Moershoofd Interstadial. Despite the total growth of number of mammoth localities in Denekamp

interstadial in Europe, the index value here was essentially lower than for the previous Stadial (Fig. 7). We interpret this as an indirect evidence of the tendency towards the lower population density, which is possibly linked with climatic fluctuations during Denekamp. During the same time, analogous process probably affected the population of Eastern Europe, although there was no population decline in Western and Eastern Siberia. The population dynamics in the Russian plain was of intermediate character between the dynamics of Western Europe and Asia: the Huneborg peak was expressed here but maximum AAR was observed for LGM like in Eastern Siberia.

The population dynamics at the periphery of the range was also affected by the climate changes but it demonstrated essential differences from the range dynamics of the main part of the range. These differences were specific for any given territory except for the Iberian Peninsula. We assumed that populations inhabited Island of Japan (Hokkaido) and possible the British Isles were periodically isolated from the main part of the range (but see Stuart (1995)).

During the Huneborg Stadial, the expansion of the mammoth range is connected with a general cooling and aridization of the climate accompanied with an expansion of open periglacial steppe landscapes to the south. Except for the most western part, no mammoth remains were found on the Scandinavian Peninsula. This might indicate the existence of a Scandinavian ice sheet during this interval.

Fluctuations of this Scandinavian ice sheet might also account for the expansion of the mammoth range into Scandinavia during the climatically heterogeneous Denekamp Interstadial.

During the LGM, the Scandinavian Ice Sheet had its maximum extent in Europe reaching 55 °N. There were only mountain glaciations in Siberia and the Ural Mountains. There are some, very intriguing, dated mammoth remains found in areas of which it was assumed that they were covered by the Scandinavian Ice sheet during the LGM. Finnish researchers, however, state that these finds indicate that some areas remained ice-free even in Scandinavia (Ukkonen et al., 1999, 2007).

The severe conditions during the LGM with widespread periglacial steppe, periglacial forest-steppe and tundra-steppe landscapes seem to have been relatively favorable for mammoth (Markova and van Kolfschoten, 2008). It should be mentioned, however, that the southern limit of the distribution of mammoths moved northwards in some places during this period.

The data at least suggest if not indicate that the mammoth range decreased dramatically during the LGT and that the population of the species declined in number during this transitional period throughout the range, but except the Western Siberia, where was population increased.

The Pleistocene/Holocene transition is characterized by an increase in humidity, cloudiness and a related decrease of incoming solar radiation. The considerable mammoth' range-size reduction, which continued during the BAIC, probably occurred first because the specific periglacial biome ("hyperzone" according to Velichko (1973)) became degraded at the end of the Pleistocene. This biome was characterized by the wide distribution of open landscapes with highly productive grassland vegetation. According to Reumer (2007), natural habitat fragmentation led to isolated populations, which thereafter were unstable, vulnerable, and highly sensitive to random unfavorable factors including human hunters.

Mammoths had specific food niche in relation to other large herbivores of "mammoth fauna": graminoids (cyperaceous and cereals), for the most part (Geel et al., 2011; Kirillova et al., 2015), and forbs (Willerslev et al., 2014). In addition, this conclusion is based on studies of the isotopic composition of different mammoth' remains, particularly the variations in carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes (Bocherens, 2003; Drucker et al., 2015; Wißing et al., 2015). The vegetation and landscapes of Northern Eurasia dramatically changed at the end of the Pleistocene. Mammoths were forced to feed on plants growing in more wet biotopes, which contained fewer amounts of nutrients and minerals than food plants from drier biotopes (Ukrainitseva, 1991; Zimov et al., 2012). The changes in the food source are one of the decisive factors that caused the range contraction of this large herbivorous mammoth (Kirillova et al., 2015). According to Leshchinskiy (Leshchinskiy, 2015), at the end of the Pleistocene, mammoth experienced a powerful geochemical stress which would manifest as mass destructive changes of bones due to enzootic diseases caused by mineral deficiency. In addition, the distribution patterns observed during the PB and BO indicate that the contraction of the mammoth range occurred under the influence of climate warming and the changes of vegetation. As a result, mammoth survived only in small isolated, "insular" populations. Progressive warming started from the end of the Pleistocene onwards resulted in dramatic changes in the environment that appeared to be critical for the distribution of not only this animal, but also the whole "Mammuthus-Coelodonta" Faunal Complex in Eurasia, and its megafaunal component, especially (Stuart and Lister, 2007; Kahlke, 2014; Cooper et al., 2015).

Thus, mammoth distribution variations in Eurasia should probably be linked to climatic changes and coinciding alterations of e.g. vegetation, ice sheet extensions and landscape. Late Paleolithic and Mesolithic hunters (modern human) might have some additionally affected the mammoth population in Eurasia (but see for discussion: Koch and Barnosky, 2006; Prescott et al., 2012; Sandom et al., 2014). Their impact was probably particularly higher when the species were close to extinction.

The studies of the ancient DNA of the mammoths from Wrangel Island and Chukotka region (Nyström et al., 2010, 2012; Thomas, 2012; Pečnerová et al., 2016) have shown significant decrease in genetic diversity before isolation, during the Pleistocene/Holocene transition. The further isolation on Wrangel Island during six thousand years led to a decline in genetic diversity by 20% in autosomal heterozygosity and about 37% in allelic richness as the result of inbreeding and genetic drift when an estimated mean effective population size was about 326 individuals (Nyström et al., 2012; Palkopoulou et al., 2015; Pečnerová et al., 2016). It should be emphasized that the current evidences do not point directly at reduction of genetic diversity as the root cause of the extinction of mammoths on the Wrangel Island in the Subboreal time.

Ancient mtDNA studies indicate that during the Late Pleistocene, there were five woolly mammoth haplogroups in Eurasia and North America organized in three clades (Debruyne et al., 2008; Palkopoulou et al., 2013): clade I – autochthonous North American haplogroup C, and Siberian haplogroups D and E; clade II – Central and East Siberian haplogroup A; clade III – European haplogroup B. The split between the North American and Eurasian populations within clade I took place at about 66 cal kyrs BP (Palkopoulou et al., 2013) (MIS 4, Transitional Cooling, GS-19.1 (Rasmussen et al., 2014)). The Central and East Siberian clade II probably became extinct around 45 cal kyrs BP (MIS 3, GI-12c) or some later (MacDonald et al., 2012). The mammoths from the clade I (haplogroup C) replaced the old Siberian haplogroup A in the North-East of Siberia, partially mixed with haplogroups B and E, and then expanded to the west in Europe where they replaced the autochthonous haplogroup B (clade III). Clade III disappeared at about 34 cal kyrs BP and Clade I reached the Grate Russian Plain at about 32 cal kyrs BP (Palkopoulou et al., 2013). At present, we have new data about the complicated history of the Clade I and haplogroup C (Enk et al., 2016). The evidences of the interbreeding between woolly mammoths and American Columbian mammoth (*M. columbi* (Falconer, 1857)) are especially intriguing.

Genetic hypothesis about the degradation of European mammoth population was indirectly supported by the results of analysis of collagen stable isotopes ^{13}C and ^{15}N ratio (Drucker et al., 2015). Authors hypothesized that, as applied to population occupied the southwestern France during the Aurignacian and Gravettian time, the ecological niche of mammoth was intact but it was not occupied by mammoths due to a decline in their population. It was supposed that one the factors influencing the decay or full extinction of mammoth of clade III in Europe was a hunting of Gravettian people (Palkopoulou et al., 2013; Drucker et al., 2015). New reconstruction the dietary ecology of Neanderthals from Belgium (North-Western Europe) suggests, probable, the direct hunting of a mammoth for earlier time interval, 45.7–40.5 cal kyrs BP (Wißing et al., 2015).

However, it remains unclear how could Siberian mammoths occupy Europe so quickly and lived there for more than 15 cal kyrs.

Using our ARR parameters, we tried to detect the signals from the events found in the genetic (ancient mtDNA) history of the Eurasian mammoth population. This indicator indirectly confirms the decline of mammoth population only in Western and Central Europe during Denekamp, 38.2–28.6 cal ky BP (Fig. 7). The decrease of the population number in this part of the range probably continued later during the LGM – LGT. In Eastern Europe, the population probably declined during Denekamp but it grew up at the LGM (Fig. 7). The pattern of population changes in Western Siberia showed an increase of population number in LGM and most of all in LGT (Fig. 8). In addition, in Eastern Siberia we did not find significant fluctuations in AAR before the LGT time. Nonetheless, there are general correlations between regional patterns of Eastern Europe, Western, and Eastern Siberia (Fig. 9); we can propose that this correlation is a "track" of a migration wave from the East to the West.

However, if take into consideration a relatively strong correlation of mammoth dynamics with climate changes, it is difficult to explain the population growth in Eastern Europe during the LGM by immigration from Eastern Siberia only. Thus, our results do not contradict to the conclusions obtained from the study of ancient mtDNA but they do not provide direct evidences for extinction of any particular genetic clades. The work provides a more detailed pattern of mammoth evolution in the Late Pleistocene. However, in spite of the presence of very many dates, direct evidences are still not enough for studying several important aspects of dynamics of some regional populations, such as population changes during the

Fig. 9. The UPGMA classification tree of different regions of Eurasian mammoth' range. The distances between regions calculated as $1 - r$, where r is correlation coefficient. See details in the text.

complex Denekamp interstadial or the extinction process at the southern periphery of the range.

6. Conclusion

Based on geographic information (database PALEOFAUNA), in combination with ^{14}C and other methods of paleo dating (1584 localities, 4033 dates, including 1501 direct dates), we first examined details of changes of mammoth distribution in Eurasia on the whole and in single parts of the range over the last 50 000 years.

The liner negative correlation of AAR with $\delta^{18}\text{O}$ was revealed for the materials from the Huneborg to LGT, which indicates the negative correlation with climatic changes. We can interpret this fact as the indirect evidence of increasing of population number or population density during the stadials and its decreasing during interstadials.

During the Hasselo stadial (GS 13–GS 12), the maximum value of AAR, and possibly the mammoth density was revealed. In the previous Moershoofd Interstadial, this value was very low.

During Huneborg – LGM the mammoth range in Eurasia was rather stable. However, its southern limit southward of the 45°N changed repeatedly. The northern limit of mammoth range also changed in Northern Europe depending on the fluctuation of the Scandinavian ice-sheet.

Mammoth range reached its maximum size during Denekamp. In this time, range was as large as it could potentially be judging by the all known environmental data for MIS 3 – MIS 1. Some differences between the modeled and real range was revealed only for Apennine Peninsula and Sakhalin (single find).

It is interesting that the climatic model predicts the significantly stronger decreasing of mammoth range during BAIC, than it was revealed in reality. The number of GI1 localities significantly decreased comparing to the LGT ones. However, they are located around the same borders in Europe as in the previous period. The mammoth range decreased more pronounced in Asia in this interval.

The model predicts relative reconstruction of range during the Younger Dryas. However, this range reconstruction did not happen possibly because the interval (GS1) was short or because of irreversible degradation of local mammoth populations and significant transformation of mammoth steppe as a main Eurasian ecosystem.

Our analysis of regional features in the dynamics of mammoth range and the quantity of dated localities acknowledged a leading role of the climatic factor in these processes. At the background of

the general distribution pattern, the regional particular features were found that might indicate the existence of different mammoth “local” populations. Thus, changes of the range in Eastern Europe and Russian plain were essentially different from alterations in Western and Central Europe. The dynamics at the periphery of main enormous Eurasian range also has its particular features.

We used AAR for classification of regions. Dendrogram (Fig. 9) reflects, first, differences in population dynamics between Western and Central Europe, and eastern, Asian part of the range including Eastern Europe. The population dynamics at the periphery of the range (Islands of Japan, British Isles, Northern Europe, Southern Siberia and Northern China, and, but to lesser extent, South-Eastern Europe) differs from the dynamics of its main part. The southernmost parts of the range – Southern Siberia and southeastern Europe experienced similar changes. Population dynamics in the Iberian Peninsula was much alike the changes in Western and Central Europe. Our results allow suggesting the existence, at least during MIS 3, 2 groups of mammoths inhabiting eastern and western parts of Eurasia respectively.

The second suggestion is that some peripheral populations could periodically be isolated from the populations of the main part of the range. The extinction of the mammoths went asynchronously in different parts of the range.

In recent years, some complex hypothesis raised about the population dynamics of mammoth in the Late Quaternary based on the studies of ancient DNA and isotopic composition of fossil bones. In the future palaeontological data will allow testing these hypotheses on the huge amount of data.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quaint.2016.05.019>.

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