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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 ^{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 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.

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 $\delta^{18}O$ 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 $\delta^{18}O$ 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 $\delta^{18}O$ 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-leafed (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).