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Landscape, climate and mammoth food resources in the East European Plain during the Late Paleolithic epoch

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Abstract

Typical mammoth inhabited the East European Plain during the second half of the Late Pleistocene glaciation. Under conditions of extremely arid climate, periglacial, mostly open landscapes formed a vast hyperzone (cryohyperzone) that occupied the place of the modern tundra, forest and steppe zones. To assess the available foodstuffs for mammoth provision, data concerning productivity and nutritive value of modern herb and grass vegetation that may be considered as more or less close analogues of periglacial communities can be used. The central part of the Late Pleistocene periglacial hyperzone was most favorable for mammoths. Those regions were well endowed with water (in large rivers, as well as snow and ice) and presented the richest fodder base, because trees and bushes persisted in valleys, while higher watersheds were occupied by periglacial steppe.

Climate warming and consequent degradation of permafrost resulted in instability of the land surface, thermokarst, and expansion of wetlands. The snow thickness increased due to more abundant snowfall in winter and made grazing difficult for mammoths. The first interstadial warming affected the less hardy early mammoths, while the progressive warming towards the Holocene appeared fatal to the typical mammoth.

1. Introduction

Environmental reconstructions of mammoth habitats are among the principal lines of investigations aimed at gaining an insight into the mammoth phenomenon. In spite of long-term research along that line (for about a century), there is still no general agreement among scientists as to the environments most suitable for the mammoth population. Since the early studies of Sukachev (1914), it was accepted that mammoths existed under conditions of cryoarid climate and preferred open steppes, locally with trees and bushes (Sher, 1971; Velichko, 1973; Vereshchagin and Kuzmina, 1977; Tomirdiaro, 1980; Vereshchagin and Baryshnikov, 1980, 1985; Shilo et al., 1983; Ukraintseva et al., 1996). Other authors, however, hold to the idea that trees were much more important, and the climate, particularly in Siberia, was similar to the modern one or even warmer (Lazukov, 1973; Verkhovskaya, 1988).

There are various explanations for mammoth extinction. Most commonly, it is attributed to: (1) overkill by early humans; (2) food resource exhaustion by the mammoth population itself (as the phytomass produced by grass communities was insufficient for grazing); or (3) changes of climate and environments. The present diversity of opinion may be partly attributed to differences in the time interval considered.

2. Chronological limits of mammuthus primigenius (Blum.)

The mammutid group goes back to early Miocene (ca. 20 Ma BP). The *Mammuthus* genus appeared in subtropical Africa in the middle Pliocene, about 3–4 Ma BP (Haynes, 1993). In the Late Pliocene—earliest Pleistocene, the genus left Africa and became widespread in Eurasia. According to Haynes (1993), *Archidiskodon gromovi* belongs to this genus, although some specialists consider it to be an earlier form of *Archidiskodon* (or *Mammuthus*) *meridionalis*. The latter became adapted to the cold climate of Northern Asia, penetrated via Beringia into North America, and evolved into the tall *Mammuthus columbi*. A separate line is represented by wooly mammoths, namely

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Mammuthus primigenius, the Late Pleistocene species that inhabited periglacial Eurasia (Haynes, 1993).

This conclusion about the age of mammoths is supported by geological materials and radiocarbon dating of individual *Mammuthus primigenius* finds, such as mammoth carcasses in permafrost, bones embedded in various deposits, or remains at Paleolithic sites. It agrees well with earlier concepts (Velichko, 1973). It is still not quite clear, however, whether early type mammoths, dated to the second half of the middle Pleistocene, should be attributed to this group. The time of transition from the early type to typical *Mammuthus primigenius* (Blum.) also remains unknown. Some information on the subject has been obtained from Paleolithic campsites of the East European Plain. Chernysh (1982) reported finding early mammoth (the early form, according to Tatarinov, 1977) in Mousterian layers of the Molodovo-I site (Dniester River), whereas the Late Paleolithic layers of the same site yielded remains of late-type mammoth. Ivanova (1977) indicated that typical mammoth dated to the second half of the Late Pleistocene, as its bones were recovered from the Late Paleolithic cultural layers from the Korman' multi-layered site in the same region. The radiocarbon dates obtained indicate that the Mousterian people existed at least until 40 ka BP, and probably to 35 ka BP, when the earliest bearers of the Late Paleolithic cultures first appeared.

Distinctions, both chronological and paleontological, between late ("typical") mammoth and earlier forms have been considered in detail by Foronova (2001). Starting from relationships between enamel thickness, length of tooth lamellae (plates), and their number in 100 mm length of tooth, Foronova (2001) showed that late mammoths form a special group of Sartanian age, corresponding to the late Valdai in the East European chronostratigraphy.

3. Sequence of Late pleistocene events in the periglacial zone

The objective of the present paper is to consider environments and climates of the period when mammoths inhabited the East European Plain. The emphasis is on the time of typical mammoths, that is, on the second half of the Late Pleistocene glacial epoch.

At present, the sequence of the events in the Late Pleistocene has been adequately reconstructed from a wide assortment of evidence obtained in various regions of the plain, including geomorphology, chronostratigraphy (including radiocarbon dating), paleo-cryogenic features, paleosols, pollen spectra and mammal remains (e.g. Gubonina, 1975, 1977; Ivanova, 1977, 1982; Nechaev, 1980; Gurtovaya, 1981; Morozova, 1981; Grichuk, 1982; Velichko, 1982; Chichagova, 1985; Borisova and Gurtovaya, 1994; Bolikhovskaya, 1995; Gribchenko and Kurenkova, 1999; Agadjanian, 2001).

The initial wave of cooling, which marked the onset of the last (Valdai) glaciation, is recorded in periglacial regions as the early Smolensk phase. It separates the Salyn fossil soils of the Mezin soil complex attributed to the Mikulino (Eemian) interglacial (oxygen stage 5e) from the younger Krutitsa soil. There were cryogenic structures (primarily small-size polygons of earth-ice veins) developed during that rather short cold stage, but permafrost did not expand south of 52–53° N and soil temperatures were not very low.

This initial cooling was followed by the Krutitsa interstadial of the early Valdai. Judging from soil formation processes (there were chernozemic soils developed under conditions of extremely continental climate), it was longer and warmer than any of later interstadials. Pollen spectra suggest periglacial forest-steppe spread all over the East European Plain. Birch and pine woodlands occupied more area than during the previous cold interval (Borisova and Gurtovaya, 1994). Stratigraphic position of the Krutitsa soil (the upper profile in the Mezin soil complex) and its genetic type allow its correlation with the Brørup interstadial of Western Europe.

The Krutitsa interstadial was followed by the Khotylevo stadial. Its climate, though colder, was not extremely continental, as indicated by the low rate of loess accumulation (about 0.04 mm/yr), the relatively high proportion of clayey particles in the loess, and palynological data. That is also confirmed by the character of cryogenic deformations that disturb the Krutitsa soil. They are mostly of gelifluction and cryoturbation features, which require considerable soil moisture. The Khotylevo interval spans the whole post-Krutitsa stage of the early Valdai. Considering slope deposits in the Dniester valley, Ivanova (1982) identified weakly pronounced humified levels and correlated them with the Moershoofd and Poperinge of Western Europe.

Forests consisting of cold-tolerant taxa were not important in the periglacial vegetation. In steppe communities, proportions of xerophytes and halo-xerophytes grew gradually with increasing aridity, along with plants typical of disturbed or immature soils. Micro-thermal plants, such as *Betula nana, B. humilis, Alnaster fruticosus, Selaginella selaginoides,* and *Botrichium boreale* persisted on the East European Plain during the entire period.

The most distinct horizon of the middle Valdai interval in the periglacial zone is the Bryansk fossil soil. Regarding its chronological boundaries, it is the upper limit that has been dated most reliably. A number of radiocarbon dates put its end at 24–25 ka BP. The time of its beginning is more uncertain. The earliest radiocarbon dates, 30–31 ka BP, were obtained for humic acids from the humus horizon of the Bryansk soils

(Chichagova, 1985). The soil processes recorded in humus horizons correspond to cold environments, the soil itself being diagnosed as pale cryogenic (Morozova, 1981). Pollen spectra recovered from the soil suggest vegetation similar to the modern middle taiga in West Siberia (Gurtovaya, 1981, 1985). Remains of arctic fox and lemming also indicate cold climate (Markova, 1992).

Quantitative reconstructions from the data show mean July and January temperatures to be 18–20°C and −16–20°C respectively, with total annual precipitation equal to 275 mm, forming a wet boreal climate (Markova, 1992). It is believed, however, that such conditions were not typical for the whole interval (although probably for the major part of it). Lithological studies revealed the mineral mass of the soil to be deeply weathered (Khalcheva, 1975). Grichuk (1982) also noted the presence of broadleaved species pollen in the spectra from the Bryansk soil. Fedorova (1963), when studying cultural layers of the Kostenki Paleolithic site on the Don River dated to about 32 ka BP, established a short phase of forests with broadleaved species. It is not inconceivable, therefore, to suggest that the Bryansk interval began earlier, at about 40–35 ka BP, at the time when the Mousterian culture was replaced by the Late Paleolithic and the earlier form of mammoth was superseded by the typical mammoth.

During the longer (and colder) phase of the Bryansk interval, the Desna drainage basin featured periglacial forest-steppe formations typical of cold and dry climates. According to Gubonina (1977), there were patches of pine-birch forests and open woodlands, some cryophytic bushes and periglacial steppe communities.

Pollen spectra from the Dubnov paleosol (analogous to the Bryansk soil in the Volyno-Podolia region) shows that the vegetation was not unlike that described in the Don River basin, although it included some mesophytes indicative of a wetter climate. Dwarf birch and periglacial steppe communities were widespread, along with forest formations (Gurtovaya, 1981, 1985).

The termination of the Bryansk interval was marked by a new wave of cryogenesis (Vladimir cryogenic horizon). The Bryansk soil was disturbed over large areas by unsorted cryogenic structures. This cold wave was the beginning of the main cold phase of the late Pleistocene cryogenic stage. At that stage most typical and thickest loess horizons were deposited (Desna and Altynovo). The deposition rate (0.4 mm/yr) was an order of magnitude higher than in the early Valdai. This cold phase lasted for about 10,000 years, 25 (23)–15 (13) ka BP, and was marked by extremely cold and dry climate. Ice wedge polygons (at present restricted to the arctic regions of permafrost) were widely distributed, and vegetation assemblages represented typical periglacial communities.

With some insignificant fluctuations, such as that recorded in the Trubchevsk level of soil formation, these conditions persisted until 15–13 ka BP. Later, towards the Late Pleistocene—Holocene transition, permafrost began to degrade. During warmer phases (Alleröd, Bölling), forests and open woodlands gained in importance. Those warmings alternated with episodes of colder climate. The most pronounced of the coolings was Dryas-3 (11–10.3 ka BP, uncalibrated age), when periglacial steppes were restored during a short wave of cryogenesis.

4. Reconstructions of environments at the time of typical mammoth

As most of the Late Paleolithic sites of typical mammoth are dated to the phase of the extremely severe climate, we will enlarge on spatial characteristics of periglacial environments of that time. Cryolithogenesis was an important constituent of the environments. The permafrost area expanded over the major part of the East European Plain, north of 48–49°N (Velichko, 1973; Nechaev, 1980; Velichko et al., 1996). There are two belts recognized within the permafrost area. The northern belt (north of 57–58°N) featured maximum thickness of frozen ground (up to 200 m) and dominance of polygonal ice wedges similar to those existing in north and northeast Siberia at present. The southern belt reached as far south as the coastal lowlands of the Black and Caspian seas (48–49°N), with permafrost decreasing in thickness southwards and becoming sporadic near its southern limit. It differed from the northern belt in having a greater diversity of paleocryogenic complexes, with somewhat reduced proportions of ice-wedge polygons. Cryogenic landforms are most diversified and best pronounced in the west of the plain due to better moisture supply than in the east. In the Dnieper drainage basin, there were hummocks and basins developed on lower terraces and polygonal microrelief with ice wedges on higher terraces and watersheds (especially on those mantled with loess). Thermokarst depressions were common (Fig. 1). Locally (e.g. along the right bank of the Desna and its tributary Sudost) the polygons were destroyed to a considerable degree by thermokarst. The Oka-Don Lowland featured polygons and thermokarst landforms (mostly in the north), though less developed than on the Dnieper Lowland. Farther east, in the Don basin, micro-depressions prevailed.

Similar attenuation of the cryogenic relief eastwards was found on elevated surfaces. The Central Russian Upland was marked by a distinctive fan-like pattern of deserption linear hollows on slopes and by chains of thermokarst depressions on watersheds. Those elements are present on the Provolzhskaya Upland, but they are

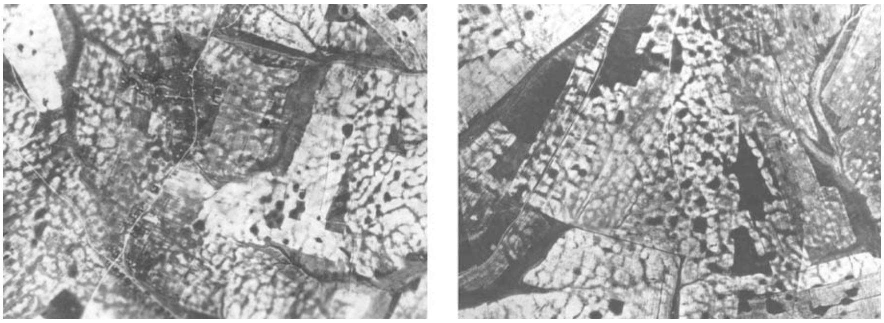


Fig. 1. Relict cryogenic landforms of the late Valdai glaciation on the modern surface at the center of the East European Plain (left—predominantly hummocky relief with thermokarst depressions, right—predominantly polygonal systems).

not so distinct, and farther eastward (east of the Volga) only isolated depressions are found.

Under extra-arid conditions, a vast hyperzone (cryohyperzone) of periglacial, primarily open landscapes was spread on the East European Plain in place of modern tundra, boreal forests and steppes (Fig. 2). The landscapes were slightly differentiated from north to south, with tundra elements conspicuous in the north, some elements of arboreal communities preserved in the middle part (mostly in valleys), and periglacial steppe dominant in the south.

According to reconstructions by Grichuk (1982), there was a certain spatial differentiation within the hyperzone. A narrow strip along the ice sheet margin, somewhat expanding in the north-east, was covered by periglacial tundra (or, more exactly, by periglacial forest–tundra). It was a complex combination of tundra and steppe-type herb communities, locally with open woodlands of birch and pine, with larch in the north-east. This type may be illustrated by the example of a palynologically studied section on the Puchka River near Kubenskoye Lake (59°N, 39°E). Pollen spectra from sediments about 21,000 yr old suggest an open woodland of birch, spruce and larch with cryophilic bushes (dwarf birch, *Alnaster*) in combination with tundra communities including typical tundra species such as *Dryas octopetala, Salix nummularia,* and *S. reticulata*, and periglacial-steppe communities with *Ephedra* and *Eurotia ceratoides*. The presence of *Selaginella selaginoides* suggests meadows (Grichuk, 1982). This is one of few sites on the East European Plain with definite evidence of tundra landscapes. The latter, however, were of a rather peculiar kind and differed considerably from modern tundra, as indicated by the presence of periglacial-steppe xerophytes.

The middle belt of the hyperzone (periglacial forest-steppe subzone) included drainage basins of the Pripyat, Dnieper (middle reaches) and Desna, Oka, upper and middle Volga, and Vyatka rivers. The data obtained from this area (in particular, from comprehensively studied loess sections along the Desna and middle Dnieper rivers) indicate complex vegetation, with patches of forests and open woodlands of birch and pine, with admixtures of spruce, *Pinus sibirica*, and larch on the lower topographic elements (Fig. 3). Cold-tolerant shrubs (*Betula nana, B, humilis, Alnaster fruticosus*) occurred in the shrub layer in the tree communities, as well as forming communities of their own. Flat interfluves were dominated by periglacial steppe vegetation including grass. Commonly occurring on disturbed or immature soils were pioneer plant communities (*Chenopodium album, Ch. botrys, Ch. rubrum, Fagopyrum sagittatum, F. tataricum*). Meadow occurred in wetter habitats, as determined from the presence of pollen and spores of meadow species, such as cryophilic *Selaginella selaginoides, Botrychium boreale, Thalictrum contortum,* as well as *Lycopodium inundatum* and *Polemonium coeruleum*. Grasses were also present. Halophytes and halo-xerophytes were restricted to saline soils.

River valleys presented protected habitats for plants with higher environmental requirements. Currant and large mesophytic herbs (*Thalictrum* and *Impatiens noli-tangere)* pollen were found in loess of that age. There were spruce and *Pinus sibirica* in forest communities.

Vegetation of the southern periglacial steppe portion of the hyperzone in the south of the East European Plain differed from that of the periglacial forest steppe subzone by the lesser presence of trees, even in river valleys. Some plants, such as *Scabiosa,* typical of meadow steppe, and *Dipsacus*, found in valleys in the steppe zone, are unknown farther to the north.

During the second half of the Late Valdai glaciation, the vegetation on the East European Plain was much the same as at the maximum stage. Only the Late Glacial was marked by essential changes. During the Alleröd Interstadial, open woodlands of spruce (in the middle part of the plain) and pine became the principal zonal vegetation over the major part of the plain. Some new plants appeared (*Helianthemum, Pleurospermum, Hippophae rhamnoides*) which were rare or absent during the glacial time. Periglacial steppe communities lost its dominance, although were still preserved in the vegetation. During the new cold wave of the Younger Dryas,

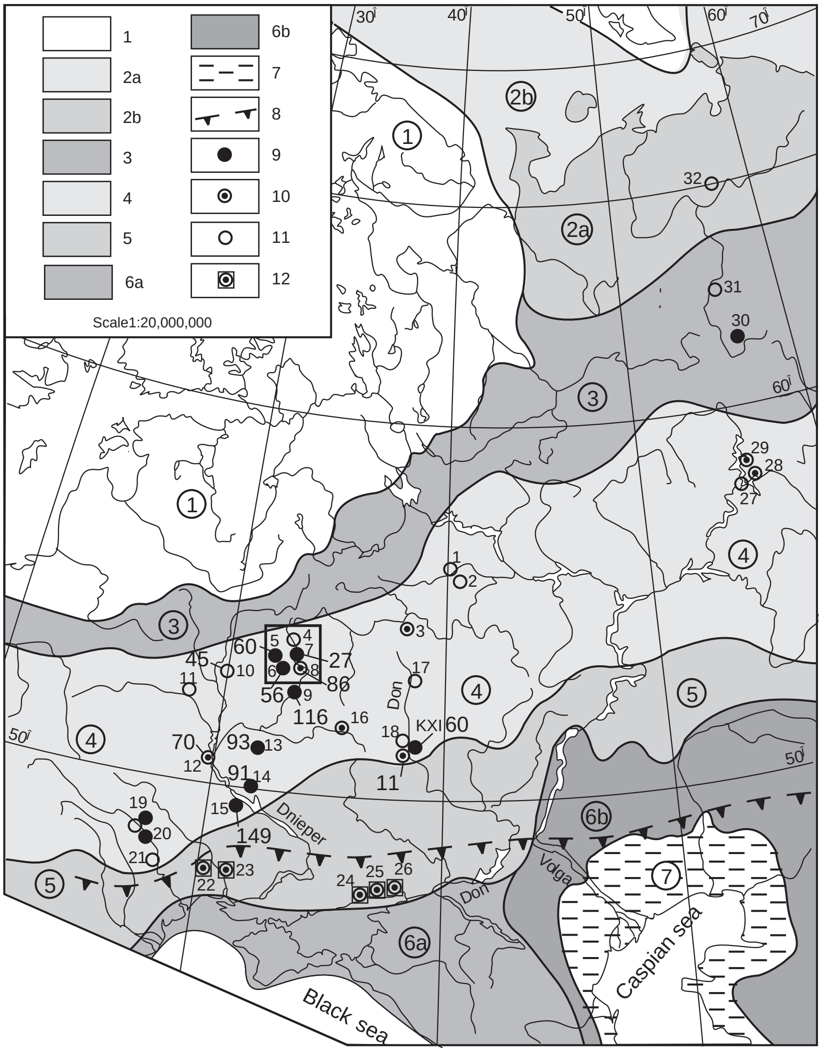


Fig. 2. Environments of Late Valdai epoch in the East European Plain and upper Paleolithic sites with and without mammoth bones. 1—ice sheet; 2–6—vegetation subdivisions (from Grichuk, 1982, modified): 2a—arctic deserts and moss and shrub tundra, 2b—the same on the emerged shelf, 3—tundra and steppe communities with patches of woodland, 4—periglacial steppe with halophytes and open woodlands in river valleys, 5—periglacial steppe, 6a—grass–herb steppe, 6b—sage-brush steppe; 7—area flooded by transgression of Caspian Sea; 8—southern limit of permafrost; 9–11—Paleolithic sites with mammoth bones: 9—younger than 19 ka BP, 10—23–19 ka BP, 11—older than 23 ka BP; 12—Paleolithic sites without mammoth bones. Numbers 1–32 near the site symbols correspond to the list of sites given below. Amount of mammoth individuals recovered from a site shown in bold italics (Soffer, 1985, with additions). Upper Paleolithic sites: 1—Sungir, 2—Rusanikha, 3—Zaraisk, 4—Khotylevo, 5—Eliseevichi, 6—Yudinovo, 7—Timonovka, 8—Pushkari, 9—Mezin, 10—Berdyzh, 11—Jurovichi, 12—Kirillovskaya, 13—Gontsy, 14—Dobranichevka, 15—Mezhirich, 16—Avdeevo, 17—Gagarino, 18—Kostenki, 19—Molodovo, 20—Korman', 21—Kossoutsy, 22—Anetovka, 23—Sagaidak, 24—Amvroissievka, 25—Muralovka, 26—Zolotovka, 27—Zaozerie, 28—Garchi I, 29—Talitskogo, 30—Medvezhia, 31—Byzovaya, 32—Mamontovaya Kuria. Rectangle in the central part of the map shows the region for which calculations of herd number has been made for cold and warm seasons.

the conditions became unsuitable for forests, and the latter were replaced by periglacial steppe formations. Dryas-3 (11–10.3 ka BP, uncalibrated ^{14}C age) was the last stage of the periglacial steppe existence on the East-European Plain.

Paleoclimatic reconstructions suggest a drop in precipitation at the LGM in the East European periglacial area (Velichko, 1984). The mean annual precipitation was reduced by 250 mm (to about 350 mm/yr) in the west of the region and by 400 mm (to ~250 mm/yr) in the central part. Temperatures dropped considerably, winter ones in particular to −35°C, 10–15° below the present-day values in the north and by 20–22° in the south. Summer temperatures were also lower than at present by 5–7° in the north and by 4–to 5° in the south.

In winter, powerful anticyclonal systems were dominant (due to growth of the North Siberian anticyclone and another one formed above the Scandinavian ice sheet). That favored mostly cloudless weather during the cold season. In summer the anticyclonic influence was reduced and air masses from the Atlantic penetrated into East Europe bringing some rainfall. The moisture content, however, was much lower (50–70%) than at

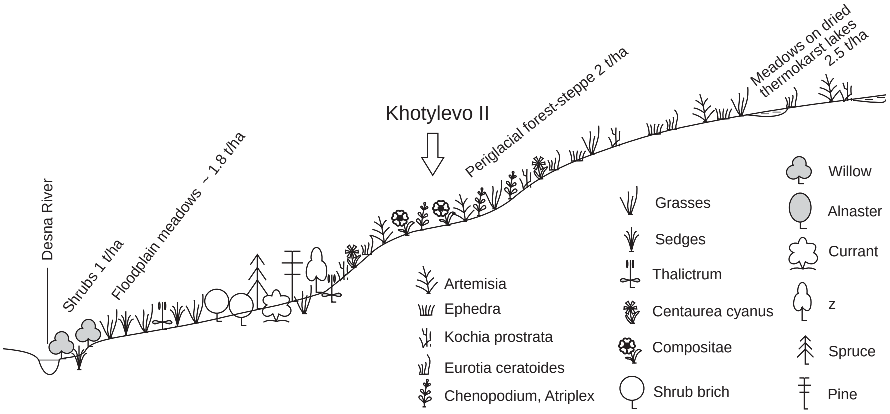


Fig. 3. Reconstructed vegetation along a cross profile (from watershed to the Desna river floodplain (Late Paleolithic site Khotylevo II).

present, as the ocean was ice-covered in high and even in middle latitudes for a considerable part of the year.

The climate and weather in periglacial zone were greatly influenced by air masses moving down the ice sheet surface. They were most active in summer, when vertical air convection was particularly intensive outside the ice sheet. Heated adiabatically during their descent from the glacier, cold air masses became increasingly dry and penetrated into the periglacial zone for 200–300 km, bringing about dust storms.

5. Mammoth existence in periglacial environments

Descriptions of mammoth, an animal typical of severe periglacial environments, may be found in many publications, including a number of overviews (Garutt, 1965; Sher, 1971; Velichko, 1973; Vereshchagin and Kuzmina, 1977; Guthrie, 1982; Soffer, 1985; Haynes, 1993; Ukraintseva et al., 1996; Velichko et al., 1997). An adult mammoth was about 3–3.5 m high and weighed as much as 4000–5000 kg. Hair cover up to 10–15 cm thick preserved the body temperature at 36–37°C. A herd of mammoths included 10–30 individuals on average. Taking only one example, remains of 33 or 34 mammoths are found in the Sevsk site, in the Desna drainage basin, with 55% mature individuals (Mashchenko, 2001). Average estimates based on data from the Kostenki-Borshchev campsites suggest a somewhat higher proportion of mature mammoths (Vereshchagin and Kuzmina, 1977).

When discussing mammoth population, elephant herds are used as possible analogs. The grazing area of an elephant herd is usually about 100–120 km in diameter (Haynes, 1993). However, as follows from observations in Africa, a herd may move over a larger area, 200–300 km. Mammoth herds presumably migrated over a vast territory much in the same way, because of the specific conditions of the periglacial environments. By analogy with present-day elephants, it seems reasonable to suggest that the daily need of one adult mammoth amounted to about 175–200 kg of vegetable mass, mostly grass and herbs with some coarser twigs. During the dry season, elephants also feed on tree branches, especially young sprouts.

To estimate the provision of foodstuffs, data concerning productivity and nutritive value of herb and grass communities which may be considered as analogous to periglacial communities can be used. Assuming that mammoths grazed on habitats similar to modern floodplain meadows, the data collected by Nomokonov (1978) for Siberian valley meadows is applicable (Table 1).

Productivity of steppe meadows (more closely resembling communities of river valleys in the periglacial zone) was about 800–1700 kg/ha (Nomokonov, 1978). The nutritive value of 1 ton of dry weight for meadow grasses is about 500–700 fodder units (Kormovye rasteniya Senokosov i pastbishch SSR, 1950).

Meadow communities similar to modern ones could exist only on valley bottoms (floodplains). On higher terraces and watersheds, besides grasses, there were also xerophytes and halophytes (Chenopodiaceae family), such as *Atriplex tatarica, Eurotia ceratoides, Kochia prostrata,* and *Chenopodium album.* Nutritive value of those plants is close to that of grasses: 470–500 fodder units per 1 ton of dry weight on the average, sometimes as much as 660–750 units (Kormovye rasteniya Senokosov I pastbishch SSR, 1950). Xerophytes of periglacial steppes show similar protein content: perennial grasses—19.8% of dry weight, halophytes of solonchaks and meadow on saline soils—26.0%, mesic grasses—18.0%, and Chenopodiaceae family—15% on average.

It follows from the above that herb and grass of periglacial areas were comparable in their nutritive value with modern floodplain meadows (though the latter have denser plant cover). Productivity of modern steppe meadows which are closest to periglacial communities in

Table 1
Average productivity of meadow on floodplains of Siberian Rivers (ton/ha) and protein contents (in % of absolutely dry weight

Meadows	Ob R.	Enisei R.	Lena R.	Amur R.	Protein content
Typical meadow	1.8–2.6	1.7–3.3	0.8–2.3	1.0–1.9	13.5–15
Steppe meadow	1.6	1.6–1.7	0.8	0.9–1.0	8–13
Wet meadow	2.8–3.5	3.3–3.65	1.8–21.5	1.8–2.6	6–13
Peaty meadow	2.1–2.2	2.5	2.0	1.6–1.7	6–10

Table 2
Food resources for mammoth population in periglacial zone

Productivity of modern vegetation units similar to periglacial ones
  Steppe and floodplain meadows ~0.8–1.7 ton/ha
  Grass and sedge meadows on dry thermokarst lakes ~2.5 ton/ha
Assumed productivity of periglacial steppe vegetation ~1.5–2 ton/ha
Daily diet for one adult mammoth ~0.15–0.2 ton
Average herd consists of about 30 mammoths (55–60% of them are adult)
Food needed for a herd is taken as needed for 20 adult mammoths

Estimation of food supply during the warm period
Food and grazing area needed for the herd
  Daily ~4 ton and ~2–2.5 ha of net grazing area
  Monthly ~120 ton and 60–80 ha (0.7 km^2) of net grazing area
Taking into account landscape structure (steep slopes, lakes, bogs, ravines and rivers) the grazing area should be taken at least about twice as great, ~1.5–2 km^2 monthly
Duration of warm period—about 5 month
Grazing area needed for 1 herd during the warm period— ~10 km^2/

Estimation of food supply during the cold period
Main source of food—shrubs and meadows in large and small valleys
Productivity of modern floodplain shrubs—0.9—1.1 ton/ha
  Herb and grass meadows—0.8—1.2 ton/ha
  Amount of fodder preserved in winter ~0.5 ton/ha
Assumed daily *diet* minimum for 1 adult mammoth ~0.125 ton
Minimum food and grazing area required for 1 herd (enough for survival during the cold period)
  Daily ~2.5 ton and 0.5 ha of net grazing area
  Monthly ~75 ton and 150 ha of net grazing area
Duration of cold period—7 months
Food required ~530–550 ton, net grazing area—~1050 ha, 10,5 km^2
Considering scarcity and discontinuity of pastures in winter, required total grazing area may be increased to ~20–50 km^2

composition is 0.8–1.7 ton/ha (1.2 ton/ha on average). This estimate of periglacial steppe productivity, however, seems low, at least for the western province of the East European periglacial area. Thermokarst lakes were typical elements of the cryogenic complex. Those lakes are periodically dried, and highly productive pastures develop on their bottom (Tomirdiaro, 1980). Herb-grass and sedge meadow communities on dry lake floors may be as high as 2.5 ton/ha (Ustinov, 1978), that is, 1.5–2 times more than common meadows. On the whole, productivity and nutritive value of the periglacial steppe communities within the limits of thermokarst cryogenic complex were not less than those of typical floodplain meadows, and probably exceeded the latter.

To estimate the area needed for a mammoth herd, the productivity of periglacial herb and grass communities was taken as 2000 kg/ha, and daily food requirements for an adult mammoth—200 kg (though it could be in fact 150 or 175 kg under unfavorable conditions), and an average number of animals in a herd equal to 30 (of which about 55% are mature, and the rest are young animals). Total vegetable mass daily consumed by the herd is taken as equivalent to that eaten by 20 adult animals (Table 2).

Therefore, the daily demand of the herd for vegetable mass may be estimated at 4000 kg. That amount may be obtained from 2 to 2.5 ha of grazing area. Accordingly, the herd would require 60–80 ha of grazing area per month, and about 7 km^2/yr. This value assumes that productivity was uniform all over the territory, if only during the warm season. Actually, it was not so.

Geomorphologically, the area inhabited by mammoths was not uniform, both at macro- and mesoscale. It included river valleys with floodplain and terraces, higher slopes and flat watersheds dissected by gullies. This resulted in variations in productivity. As well, individual landforms were differently used according to season. In summer, floodplains with ice-wedge polygons were too wet (due to floods and melting of seasonally frozen soils) and could not carry mammoths which had a great weight (3–5 tons) and rather small feet. The load exceeded the permissible limit for the floodplain soil, about 3–5 kg/cm^2. At that time the herds would prefer dry sites on high interfluves covered with loess. Mammoths were presumably grazing on drier areas between thermokarst depressions. The latter were inaccessible because of cryogenic features, with the exception of their rims covered with shrubs attractive for mammoths and producing 0.9–1.1 ton/ha of dry weight. Besides, the rims were rich in halophytes and could partly satisfy the mammoth need for salt. Patches of shrubs and trees occurred also on gully slopes and river terraces. When estimating the required grazing area, even in summer, when the animals could forage over vast interfluvial plains, part of the area was difficult to access. The necessary grazing area must be considered as at least twice, and more probably three to four times greater than the value given above.

In winter mammoth herds preferred other topographic elements. In river valleys, frozen floodplains were accessible for mammoths which could easily feed on the grass and bushes grown during summer, especially as snow cover was usually thin. The last factor was vital for mammoth existence in winter (Sher, 1971; Velichko, 1973; Shilo et al., 1983). Interfluvial areas could be partly used for grazing, but the biomass was exhausted there during the summer and therefore was insufficient. Large and small valleys were preferable, as they provided protection against cold winds (though they might be locally colder because of temperature inversions).

No less important reason for the seasonal changes of habitats (from watersheds in summer to valley floors in winter) was access to water. Even in winter, at low temperatures, one mammoth would require about 150 l (Krause, 1997), and a herd would require 20 times as much. Partly the demand for water could be satisfied by snow (according to Krause, 3 m^3 are equivalent to 150 l of water), but it seems hardly probable under conditions of low precipitation in winter. Stable sources of water could be icings in river channels, as well as groundwater seeping at the base of scarps and on valley slopes. Salt often occurs on icing surfaces. At present, dimensions of salt patches may be up to 30 m in diameter and 5 cm thick (Glossary of Glaciology, 1984). The conclusion that the river valleys were the principal source of food for mammoth in winter has been corroborated by Vereshchagin and Kuzmina (1982). An analysis of age groups of mammoth remains recovered from the Kostenki sites led those authors to conclude that mammoths migrated into the Don valley in winter.

Shallow lakes on watersheds were frozen to the bottom and could not be used as water supplies. Drinking of cold water (below 10°C) and consumption of snow could result in considerable stress. Haynes (1993) mentioned observations by F.Benedict on the behavior of a female Indian elephant: upon drinking water at 23°C she began to tremble all over and showed discomfort. To raise the water temperature by 20–25°C, a mammoth would need 3000–4000 kcal. In compensating for spent energy, besides additional food, the thick hair cover was essential.

6. General pattern in the mammoth distribution and early humans

The outlines of area inhabited by a mammoth herd varied essentially according to season. In summer, when mammoth were grazing on higher open watersheds, it was relatively isometric. In winter, the grazing area was elongated along rivers, where mammoth herds gathered from vast adjoining territories. That resulted in increased load on food resources in valleys which were nonrenewable in winter time. The fact that African elephants migrate repeatedly during one season over a distance of 100 km and more in search of fresh vegetation (Haynes, 1993) lends support to the validity of Soffer's (1985) idea that the mammoth herds migrated along valleys across the periglacial zone from south to north and back.

The area required for a conventional mammoth herd of 20 adult individuals and some young animals can be estimated (Table 3). By analogy with elephants (which are known to reduce their daily amount of food under unfavorable conditions), it may be assumed that a mammoth could consume merely 100 kg of vegetable mass per day. For floodplain shrubs, eatable mass is estimated at 0.9–1.1 ton/ha (dry weight), and for herb and grass meadow, 0.8–1.2 ton/ha (Ustinov, 1978). In winter the mass was probably only half of its summer amount, about 0.5 ton/ha. It follows that a mammoth herd consuming daily about 2.5 ton of plant matter needed about 5 ha of grazing area per day, about 10.5 km^2 for the whole cold season (about 7 months). Making allowance for unproductive areas (the river channel, oxbow lakes, point bars, and sites heavily disturbed by cryogenic fissures), the needed area may be increased by an order of magnitude, up to 100 km^2. Observations on river floodplains within the modern permafrost zone (Protasyeva, 1967) indicate that their surfaces are broken by polygonal fissures, often forming concave polygons with elevated rims. About 70–80% of the polygon area is covered with water in summer and with ice in winter. Thermokarst depressions are common on higher surfaces within the valleys. Taking the width of floodplain and lower terraces to be 2–5 km, a herd in winter would require a section of valley about 30–40 km long. That is probably an overestimation, as areas of tributary valleys have not been taken into account.

Table 3
Estimates of number of mammoth herds within the model area (middle Desna drainage basin) depending on a season

	Season	
Area, food supply and productivity	Warm (5)	Cold (7 months)
Total area of herds migration	15,000 km^2	~1,600 km^2 (total length of Desna and Sudost valley—320 km, valley floor width—2–5 km)
Daily diet of one adult mammoth	0.15–0.2 ton	0.15–0.125 ton
Food needed for a herd of 20 adult mammoths during the season	15–20 ton	21–17.5 ton
Grazing area productivity	2 ton/ha	0.5 ton/ha
Area needed for one herd during the season	10 km^2	~40–50 km^2 considering mosaic structure of the landscape
Possible number of herds	A few hundreds	~20–30

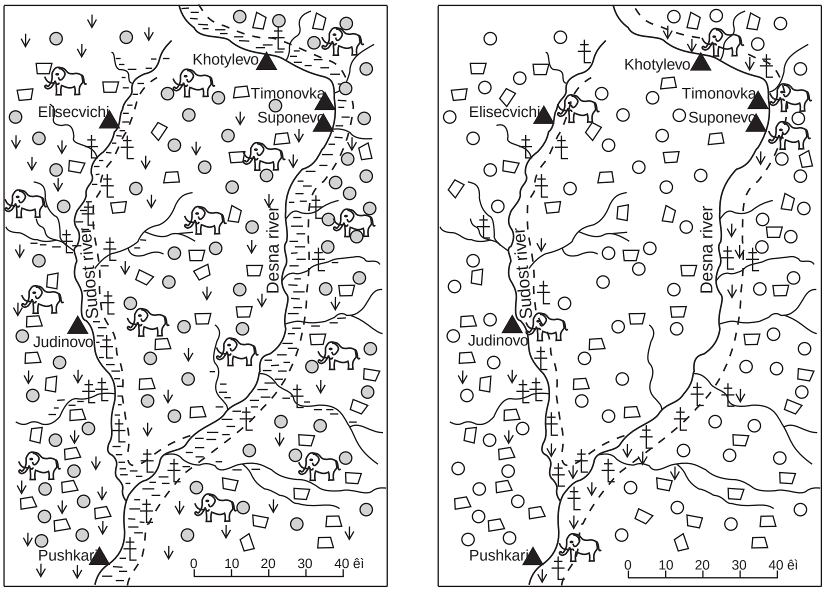
A consequence from the above is that the food supply, and therefore potential abundance of mammoths, varied considerably from warm to cold season within the same region. Summer pastures could provide for many more herds than could winter ones. To estimate a range of those variations, the drainage basin of the middle Desna and its tributary Sudost can be taken as a model (Fig. 4, Table 3). The region is known for its Late Paleolithic sites (from the Khotylevo II site 20 km upstream of Bryansk to Mezin site 30 km downstream of Novgorod-Seversky). That area, about 20,000 to 25,000 km^2, could support a few hundred mammoth herds in summer, while only 20–25 herds could survive through winter, when the grazing area was restricted to the valley floor about 320 km long. Evidently, such a drastic reduction in food resources during cold seasons put a limitation on mammoth population in the periglacial regions.

Such a situation during the cold season could affect the mode of living of the Late Paleolithic hunters. Numerous mammoth herds could easily feed in the warm season. In the cold season, however, the herd number far exceeded the fodder producing capacity of the area in valleys. As a result, part of the herds died out.

In addition, mammoth herds could not migrate all over the area of the East European hyperzone. In the south their migrations were limited by the transition from the middle subzone (with patches of trees and shrubs) to the southern subzone of purely periglacial steppes with drastically reduced food supply. As a consequence, many animals could die near the ecotone. This may be confirmed by the fact that extremely abundant mammoth remains are concentrated at the early human sites within the southern part of the forest-steppe subzone. The latter acted as a barrier of a kind which limited the southward migration. Soffer (1993) provided further evidence, as practically every Paleolithic site within this belt contained mammoth remains belonging to dozens of individuals (Kirillovskaya site in the Dnieper basin—70, Dobranichevka—91, Mezhirich—as many as 149).

The presence of such a barrier is clearly seen in the data from the middle reaches of the Don River. The Kostenki-Borshevo Paleolithic region (located near the southern margin of the forest-steppe subzone of the periglacial hyperzone) is distinctive in the mammoth remain abundance in the later cultural layers. For example, about 60 mammoth remains have been recovered from the Kostenki 11 site (Vereshchagin and Kuzmina, 1982). Farther south, however, along the same right bank of the Don River, there is a gap in the mammal remains, in spite of the quite similar topographic position of the Late Paleolithic sites. South of Kostenki, the paleoenvironmental features seemingly give an insight into this unusual phenomenon: the periglacial steppe with its poor fodder supply hindered mammoth migrations south of Kostenki, and consequently interfered with human dispersal southwards.

Judging from the environmental requirements of mammoth, it may be concluded that the entire territory of the East European Plain was not equally suitable for mammoths. The great majority of the Late Pleistocene mammoth sites is limited by the permafrost boundary (Velichko and Kurenkova, 1990). This hardly may be attributed to the state of surfaces, which could support those heavy animals throughout the year. Periglacial steppes south of the permafrost featured even harder surfaces. More likely, water resources were the limiting



Warm season

Cold season

Fig. 4. Schemes of mammoth herd distribution during warm and cold seasons in the middle Desna drainage basin (see also Fig. 2).

factor. There was a considerable amount of water stored as ground ice in the cryolithozone, while farther south rivers were the only source of water besides the rather scarce snow cover. Food resources were also limited. Productivity of periglacial steppe was lower than that of modern chernozemic steppe 0.5–0.8 t/ha, and 2–3 times below that of the cryolithozone.

When the vast periglacial area is considered, there are certain variations in mammoth life conditions within it. In particular, mammoth remains are much rarer in the northern part. In addition to less comfortable climate in this zone, with frequent cold winds from the ice sheet and dust storms, this could be due to rather poor fodder base. In modern tundra covered with sedge and cottongrass, as well as in bush tundra, the dry weight of vegetable mass varies from 0.7–1.35 ton/ha (Ustinov, 1978), half as much as food resources father south.

Therefore, the most comfortable environments for mammoth were those of the middle part of the Late Pleistocene periglacial hyperzone (which corresponded to the southern part of the cryolithozone). Those latitudes featured sufficient water, both in rivers and stored in the cryogenic complex (ground ice). As well, periglacial vegetation was the richest there, with steppe communities on watersheds and trees and shrubs persisting in large and small valleys.

There are, however, variations in concentration of mammoth findings even within this latitudinal belt. A scheme of mammal remains recovered from Late Paleolithic campsites (Velichko and Kurenkova, 1990) shows that the mammoth findings are mostly concentrated in the western province. Fossil remains decrease in abundance eastward and are practically absent east of the Oka-Don lowland. Such a trend is probably attributable to drier climate (as indicated, in particular, by the essential reduction of ground ice content towards the east). The periglacial vegetation, accordingly, became scarcer and less productive, with trees and shrubs disappearing first. Such environments and climate could not encourage mammoth occupation of the region.

The analysis can shed light on the problem of Late Paleolithic human distribution in Eastern Europe: why the human sites are concentrated in the west of the plain and were scarce in the east. Studies of mammal remains found on the sites indicate that mammoth was an important source of food for Late Paleolithic humans at the time of maximum cooling and predominantly periglacial environments (Velichko et al., 1997), and man would follow mammoth over the East European Plain. Thus, in the east of periglacial zone environments were unsuitable for mammoth, and this region practically lacks Paleolithic campsites.

Such a conclusion may be true not only at a macroregional scale, but also at a mesoscale. It seems reasonable to conclude that early humans gravitated towards river valleys because mammoth herds concentrated there in cold seasons. All the Late Paleolithic sites in the Dnieper, Desna, Dniester and Don rivers show that the human dwellings (mostly of mammoth bones) and the character of economy were adjusted to those environments.

Taking into account the bonds which existed between mammoth and human towards the end of the Late Paleolithic, it can be said with confidence that the Paleolithic campsites concentrated within those areas in river valleys which were attractive for mammoth herds (such as icings convenient as watering places, or thickets of trees and bush). Other sites could be located near places of mammoth deaths and their carcass conservation in permafrost. It is conceivable that the same group of people could be wandering after mammoth herds to new grazing areas and form new campsites. It is quite understandable, considering that utilization, and more so acquisition of mammoth carcasses after a hunt or excavation from permafrost, was a hard and labor-consuming job. Large parts of the animal carcasses (some of them were used for construction) hardly could be transported for a considerable distance. A mammoth skull exceeded 100 kg, and a tusk exceeded 200 kg (Soffer, 1985).

Two conclusions may be tentatively inferred from the above. First, the same groups of hunters could establish several campsites of nearly the same age, which now may be erroneously attributed to different groups of people. Second, some places of choice for mammoths within valleys (such as watering places), as well as those places where mammoth carcasses were preserved in permafrost, could be constant places of attraction for different generations of Paleolithic men who visited them repeatedly at different time. It is not inconceivable, that essential discrepancies in dates obtained for one and the same Paleolithic site may be partly attributed to this circumstance (Table 4).

7. Causes of mammoth extinction

As has been argued (Velichko, 1973), mammoth was adapted to a rather narrow range of climatic characteristics and certain type of landscapes (extremely continental arid climate with a small amount of solid precipitation; firm soil; dominance of open plant communities (herb, grass and low shrubs), locally with trees). Changes in the environments were usually unfavorable for the mammoth's existence, as has been shown by many specialists.

Warming and related degradation of permafrost resulted in the surface instability, and development of thermokarst and wetlands. A whole herd of mammoths could perish in thermokarst depression, as seen in the

Table 4
Radiocarbon dates of upper Paleolithic sites on the East-European Plain

Sites	Dates	Lab. No.	Material
Sites with mammoth bones			
Yudinovo	12 300±200	OxA-696	Charred bone
Yudinovo	13 300±200	OxA-695	Charred bone
Yudinovo	13 650± 200	LU-153	Bone
Yudinovo	13 720±210	LE-3303	Bone
Yudinovo	13 830±850	LU-103	Charred bone
Yudinovo	13 980±110	ISGS-2085	Bone
Yudinovo	14 300±110	ISGS-2084	Bone
Yudinovo	14 470±160	AA-4801	Charred bone
Yudinovo	14 500±200	GIN-5588	Charred bone
Yudinovo	14 610±60	GIN-5661	Charred bone
Yudinovo	14 650±105	AA-4802	Charred bone
Yudinovo	15 660±180	LU-127	Bone
Yudinovo	15 790±320	LE-3301	Bone
Yudinovo	17 800±810	LE-3302	Charred bone
Yudinovo	18 630±320	LE-3401	Charred bone
Eliseevichi I	12 630±360	GIN-4137	Mammoth tooth
Eliseevichi I	12 970±140	LU-102	Charred bone
Eliseevichi I	14 080±70	GIN-4135	Charred bone
Eliseevichi I	14 100±400	GIN-4139	Mammoth tooth
Eliseevichi I	14 240±120	GIN-5475	Charred bone
Eliseevichi I	14 470±100	LU-126	Mammoth tooth
Eliseevichi I	14 590±140	GIN-4186	Mammoth tooth
Eliseevichi I	16 850±120	GIN-4138	Mammoth tooth
Eliseevichi I	17 340±170	LU-360	Mammoth tooth
Eliseevichi I	15 600±1350	QC-889	Charred bone
Eliseevichi II	15 620±200	IGAN-556	Mammoth tooth
Khotylevo II	23 660±400	JIY-359	Mammoth tooth
Khotylevo II	27 024±960	IGAN-73	Mammoth tooth
Timonovka I	12 200±300	IGAN-86	Mammoth tooth
Timonovka I	14 530±120	GIN-8414	Mammoth tooth
Timonovka I	14 750±120	GIN-120	Mammoth tooth
Timonovka II	15 300±700	GIN-2003	Bone
Timonovka II	15 110±530	LU-358	Mammoth tooth
Suponevo	13 500±100	GIN-3381	Bone
Suponevo	14 260±120	GIN-3719	Bone
Pushkari I	16 775±605	QC-899	Bone
Pushkari I	19 010±220	AA-1389	Bone
Pushkari I	20 600±1300	GIN-8529	Mammoth tooth
Pushkari I	20 700±500	GIN-8529A	Mammoth tooth
Mezin	15 100±200	OxA-719	Mammoth tooth
Mezin	21 600±2200	GIN-4	Mammoth tooth
Berdyzh	15 100±250	OxA-716	Mammoth tooth
Berdyzh	23 430±190	LU-104	Mammoth tooth
Yurovichi	26 470±420	LU-125	Mammoth tooth
Radomyshl	19 000±300	OxA-716	Mammoth tooth
Gontsy	13 200±270	ISGS-1740	Bone
Gontsy	13 400±180	QC-898	Mammoth tooth
Gontsy	14 350±190	ISGS-1739	Bone
Gontsy	14 600±200	OxA-717	Mammoth tooth
Dobranichevka	12 700±200	OxA-700	Mammoth tooth
Kirillovskaya	19 200±250	OxA-718	Mammoth tooth
Mezhirich	12 900±200	OxA-709	Mammoth tooth
Mezhirich	14 300±300	GIN-2596	Bone
Mezhirich	14 320±270	QC-897	Mammoth tooth
Mezhirich	14 400±250	OxA-712	Mammoth tooth
Mezhirich	14 420±190	AA-1317	Mammoth tooth
Mezhirich	14 530±300	GIN-2595	Bone
Mezhirich	14 700±500	GIN-2593	Mammoth tooth
Mezhirich	15 245±1080	QC-900	Mammoth tooth
Mezhirich	17 355±950	KI-1054	Bone
Mezhirich	18 020±600	KI-1055	Mammoth tooth
Mezhirich	18 470±550	KI-1056	Bone
Mezhirich	19 280±600	KI-1058	Bone
Avdeevo	16 565±270	QC-621	Bone
Avdeevo	16 960±420	QC-886	Bone
Avdeevo	17 200±1800	GIN-1571A	Charred bone
Avdeevo	19 800±1200	GIN-1570	Bone
Avdeevo	20 100±500	GIN-1746	Bone
Avdeevo	20 800±200	GIN-1747	Bone
Avdeevo	21 000±200	GIN-1748	Bone
Avdeevo	21 200±200	GIN-1569	Bone
Avdeevo	22 200±700	GIN-1970	Bone
Avdeevo	22 400±600	GIN-1969	Bone
Avdeevo	22 700±700	GIN-1571	Bone
Gagarino	17 930±100	LE-1432A	Bone
Gagarino	20 150±300	LE-1432Б	Bone
Gagarino	20 620±300	LE-1432В	Bone
Gagarino	21 800±300	GIN-1872	Bone
Gagarino	30 000±1900	IGAN-83	Charred bone
Kostenki I (layer 1)	18 230±620	LE-3280	Charred bone
Kostenki I (layer 1)	19 010±120	LE-2950	Charred bone
Kostenki I (layer 1)	19 540±580	LE-3292	Charred bone
Kostenki I (layer 1)	19 860±200	LE-2949	Mammoth tooth
Kostenki I (layer 1)	20 100±680	LE-3277	Charred bone
Kostenki I (layer 1)	20 315±200	AA-4800	Charred bone
Kostenki I (layer 1)	20 855±260	AA-4799	Charred bone
Kostenki I (layer 1)	21 330±400	GIN-2534	Charred bone
Kostenki I (layer 1)	21 680±700	LE-3279	Charred bone
Kostenki I (layer 1)	22 020±310	LE-3282	Mammoth tooth
Kostenki I (layer 1)	22 300±230	GIN-1870	Charred bone
Kostenki I (layer 1)	22 300±200	GIN-2533	Charred bone
Kostenki I (layer 1)	22 700±250	LE-2969	Mammoth tooth
Kostenki I (layer 1)	22 760±250	LE-2800	Mammoth tooth
Kostenki I (layer 1)	22 800±200	GIN-2530	Charred bone
Kostenki I (layer 1)	23 000±500	GIN-2528	Charred bone
Kostenki I (layer 1)	23 010±300	LE-3276	Mammoth tooth
Kostenki I (layer 1)	23 260±680	LE-3289	Mammoth tooth
Kostenki I (layer 1)	23 500±200	GIN-2527	Charred bone
Kostenki I (layer 1)	23 640±920	LE-3283	Tusks
Kostenki I (layer 1)	23 770±200	LE-2951	Mammoth tooth
Kostenki I (layer 1)	24 100±500	GIN-2529	Charred bone
Kostenki I (layer 3)	24 500±1300	GIN-4850	Charcoal
Kostenki I (layer 3)	25 600±1000	Gin-4852	Charcoal
Kostenki I (layer 3)	25 730±1800	LE-3541	Charcoal
Kostenki I (layer 3)	25 900±2200	GIN-4899	Cultural layer
Kostenki I (layer 3)	26 200±1500	GIN-4885	Charcoal
Kostenki I (layer 3)	38 080±5460	AA-5590	Wood charcoal

Table 4 (*continued*)

Sites	Dates	Lab. No.	Material
Kostenki I (layer 4)	27 390±300	LE-2030	Mammoth tooth
Kostenki 2	11 000±200	GIN-93	Bone
Kostenki 2	16 190±150	LE-1599	Bone
Kostenki 8	27 700±750	LE-1509	Wood charcoal
Kostenki 8	27 700±750	GrN-10509	Charcoal
Kostenki XI (layer 1a)	12 000±100	LE-1403	Bone
Kostenki XI (layer 1a)	14 610±120	LE-1637	Bone
Kostenki XI (layer 1a)	17 310±220	LU-1704Б	Bone
Kostenki XI (layer 1a)	19 900±350	GIN-2532	Charred bone
Kostenki XI (layer 2)	21 800±200	GIN-2531	Bone
Kostenki XI (layer 3)	22 760±340	LE-1638	Bone
Kostenki XII	20 900±390	TA-157	Bone
Kostenki XII	23 060±300	GIN-89	Bone
Kostenki XII	30 240±400	LE-1428B	Mammoth tooth
Kostenki XII	31 900±200	LE-1428G	Bone
Kostenki XII	32 700±700	GrN-7758	Charcoal
Kostenki XIV	22 780±250	OxA-4114	Bone
Kostenki XIV	25 909±310	LE-1400	Bone
Kostenki XIV	26 400±660	LU-59A	Bone
Kostenki XIV	28 380±220	GrN-12598	Charcoal
Kostenki XIV	28 200±700	LU-59B	Bone
Kostenki XIV	28 580±420	OxA	Bone
Kostenki XV	21 720±570	LE-1430	Bone
Kostenki XVI	25 100±150	LE-1431	Bone
Kostenki XVII	26 750±700	LE-10511	Charcoal
Kostenki XVII	32 200±2000	GrN-10512	Charcoal
Kostenki XVII	32 780±300	LE-1436	Bone
Kostenki XVII	36 400±1700	GrN-12596	
Kostenki XIX	17 420±150	LE-1705A	Bone
Kostenki XIX	18 900±300	LE-1705Б	Bone
Kostenki XXI	20 250±100	LE-1437Б	Bone
Kostenki XXI	22 270±150	LE-7363	Wood charcoal
Kostenki XXI	22 900±150	LE-1437B	Wood charcoal
Molodova V (1a)	10 590±230	GIN-7	Bone
Molodova V (1a)	10 940±150	GIN-54	Charcoal
Molodova V (layer 2)	11 900±230	GIN-8	Bone
Molodova V (layer 2)	12 300±140	GIN-56	Charcoal
Molodova V (layer 3)	13 370±540	GIN-9	Charcoal
Molodova V (layer 3)	17 100±1400	GIN-147	Charcoal
Molodova V (layer 7)	23 000±800	MO-11	Wood charcoal
Molodova V (layer 7)	23 700±320	GIN-10	Soil
Molodova V (layer 9)	29 650±1320	LG –15	Charcoal
Korman' IV	24 500±500	GIN-1099	Wood charcoal
Korman' IV	27 500±100	GIN-832	Soil
Sungir	21 800±1000	GIN-326A	Charcoal
Sungir	22 500±600	GIN-326Б	Charcoal
Sungir	24 430±400	GrN-5446	Charcoal
Sungir	25 500±200	GrN-5425	Bone
Sungir	27 700±500	GIN-5880	Bone
Rusanikha	27 180±340	IGAN-555	Mammoth tooth
Zaraisk	15 600±300	GIN-6095	Charred bone
Zaraisk	16 200±1000	GIN-2487	Charred bone
Zaraisk	18 300±200	GIN-3727	Mammoth tooth
Zaraisk	19 000±200	GIN-8975	Charred bone
Zaraisk	19 100±260	GIN-8397	Charred bone
Zaraisk	19 100±200	GIN-8396	Charred bone
Zaraisk	19 200±300	GIN-8486	Charred bone
Zaraisk	19 900±260	GIN-8484	Bone

Table 4 (*continued*)

Sites	Dates	Lab. No.	Material
Zaraisk	21 000±430	GIN-8975	Bone
Zaraisk	21 400±500	GIN-8488	Charred bone
Zaraisk	22 300±300	GIN-3998	Mammoth tooth
Byzovaya	18 320±280	TA-121A	Bone
Byzovaya	25 450±380	TA-121Б	Bone
Byzovaya	25 740±500	LE-3047	Bone
Medvezh'ya	16 130±150	LE-3060	Bone
Talitskogo	18 700±200	GIN-1997	Mammoth tooth
Mamontovaya Kuria	34 655±570	Tua-3524	Mammoth tusk
Mamontovaya Kuria	37 360±630	LU-4001	Mammoth bone
Zaozerie	31 000±700	GIN-11501	Bone
Zaozerie	31 000±500	GIN-11500	Bone
Zaozerie	31 000±400	GIN-11499	Bone
Zaozerie	31 500±500	GIN-11497	Bone
Sites without mammoth bones			
Amvrosievka	15 250±150	LE-1637	Bone
Amvrosievka	20 620±150	LE-1805	Bone
Amvrosievka	21 500±340	LE-3403	Bone
AnetovkaII	19 170±120	LE-2947	Bone
AnetovkaII	18 040±150	LE-2424	Bone
AnetovkaII	18 265±1650	LE-4066	Bone
AnetovkaII	19 090±980	LE-4610	Bone
AnetovkaII	24 600±150	LE-2624	Bone
Muralovka	18 780±300	LE-1438	Bone
Muralovka	19 630±200	LE-1601	Bone
Sagaidak	20 300±200	LE-1602Б	Cultural layer
Sagaidak	21 240±200	LE-1602A	Cultural layer
Zolotovka	17 400±150	GIN-1938	Bone
Leski	19 200±200	LE-200	Cultural layer
Leski	23 770±1540	LE-4456	Cultural layer

Sevsk site dated to the Late Glacial warm phase (about 14 ka BP).

Warmer phases at the end of the last glaciation were also wetter. An increase in winter precipitation and therefore in thickness of snow cover made difficult grazing during cold seasons. Snowfalls with alternating thaws and frosts affected mammoth's hair.

The above considerations are confirmed by the radiocarbon dates obtained for mammoth bones (Sulerzhitsky, 1997). A majority of dates fall into two intervals: about 45 (40)–30 (25) ka BP and about 15–10 ka BP. The first interval corresponds to the middle Valdai mega-interstadial, the second one to the Late Glacial warming.

As has been noted above, it was during the mega-interstadial that the early mammoth was replaced by the typical mammoth. It may be well supposed that the early mammoth had less endurance, so it could not survive an interstadial warming, while the progressive warming resulting in heat and moisture supply of the modern (interglacial) rank put an end to the typical mammoth *Mammuthus primigenius*.

8. Conclusion

The period of the typical (late) mammoth existence (*Mammuthus primigånius* Blum., late form) corresponds to the Late Valdai—Sartan—Late Weichselian glacial epoch. The coldest interval, from 24–23 to 17–16 ka BP, was exemplified by the periglacial environments at their fullest, with maximum expansion of permafrost and hyperzonal structure of lansdcapes all over the east European Plain.

An analysis of vegetation in various habitats revealed that the middle belt of the periglacial hyperzone was best supplied with fodder suitable for mammoth grazing. The southern boundary of this belt (ecotone) put a limit to further southward migrations of mammoths, as the periglacial steppe farther south could not provide them with the needed amount of food.

The southern boundary of permafrost was positioned close to this ecotone. Within the permafrost area the animals were much better supplied with water from thermokarst lakes, icings and taliks in river valleys.

On the whole, the annual cycle of climate and landscape variations would have a profound impact on the mammoth herd density. The principal limiting factor was winter, when the herds were confined to river valleys, with water and some, although limited, food supply.

The majority of Paleolithic sites dated to this interval are located in the middle belt of the hyperzone. This reflects the close interrelation between conditions of human survival and distribution of mammoth. Humans settled on slopes of large and small valleys, and on peninsulas at river confluences, near places where mammoth herds concentrated. This facilitated hunting, especially in winter, when the animals were weak and famished. On the other hand, mammoth carcasses preserved in permafrost were presumably used during warm seasons, when they began to thaw.

The existing dispersal in radiocarbon dates over a wide range, even where the remains analyzed have been recovered from the same site, may be attributed to the repeated appearance of humans at long abandoned campsites due to renewed favorable conditions for mammoths within the same part of the valley (such as newly formed icings suitable as watering places). However, another explanation of the ^{14}C dates scattering is also possible, namely that humans could use bone material recovered from older deposits.

Even within the middle belt of the hyperzone, the most favorable for mammoths, they were distributed extremely unevenly. Their remains, in common with the Paleolithic sites, are concentrated in the western half of the subzone, where rainfall was somewhat higher than in the east and ensured fodder supply in greater amounts. The special features of environments and climates of the time that mammoth and early humans coexisted refer only to a definite paleogeographic interval, namely to the maximum cooling during the Late Valdai ice age.

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