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Mammoth steppe: a high-productivity phenomenon

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ABSTRACT

At the last deglaciation Earth's largest biome, mammoth-steppe, vanished. Without knowledge of the productivity of this ecosystem, the evolution of man and the glacial–interglacial dynamics of carbon storage in Earth's main carbon reservoirs cannot be fully understood. Analyzes of fossils ^{14}C dates and reconstruction of mammoth steppe climatic envelope indicated that changing climate wasn't a reason for extinction of this ecosystem. We calculate, based on animal skeleton density in frozen soils of northern Siberia, that mammoth-steppe animal biomass and plant productivity, even in these coldest and driest of the planet's grasslands were close to those of an African savanna. Numerous herbivores maintained ecosystem productivity. By reducing soil moisture and permafrost temperature, accumulating carbon in soils, and increasing the regional albedo, mammoth-steppe amplified glacial–interglacial climate variations. The re-establishment of grassland ecosystems would slow permafrost thawing and reduce the current warming rate. Proposed methods can be used to estimate animal density in other ecosystems.

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1. Introduction

During the Last Glacial Maximum (LGM), mammoth steppe (MS) was Earth's most extensive biome. It spanned from Spain to Canada and from arctic islands to China (Adams et al., 1990; Guthrie, 1990; Sher, 1997; Alvarez-Lao and García, 2011). Modern man evolved in this biome (Guthrie, 1990). During interglacial warming, forests expanded northward, and northern Siberia, Alaska, and the Yukon were an MS refugium. Trees and shrubs would have also penetrated to these places, but they were not the dominate vegetation cover (Sher, 1997). However, at the beginning of the Holocene, mossy forests and tundra displaced MS even there. Many lakes and wetlands have appeared. It has been assumed that, during the Holocene, in contrast to other previous interglacials cold dry steppe-like climate switched to a warmer wetter climate that, in turn, caused the disappearance of grasslands and their megafauna (Guthrie, 1990; Vereshchagin and Tikhonov, 1990; Velichko and Zelikson, 2001; Schirrmeister et al., 2002; Sher et al., 2005). However, ^{14}C dating has indicated that mammoths persisted on islands until the mid-Holocene (Guthrie, 2004; Vartanyan, 2007). Bison in Alaska and the Yukon, and horses and musk ox in northern Siberia lived throughout the Holocene (Stephenson et al., 2001; Sher et al., 2005). ^{14}C data and pollen records indicate that climate warming during the deglaciation in Alaska was accompanied by an increase in the productivity of grasslands, and in the density of herbivores (Guthrie, 2006). Data (Guthrie, 2006) indicate that only after the appearance of man, ∼12,370 ^{14}C years ago, did the number of animals decrease, and only afterward did the area of grassland begin to decline. This can be considered as a proof for Overkill Hypothesis (Martin, 1967).

In contrast to Climatic Hypothesis we propose an Ecosystem Hypothesis (Zimov and Chupryninm, 1991; Zimov et al., 1995; Zimov, 2005), which assumes that the mammoth ecosystem was relatively insensitive to climatic variation and that numerous animals maintained highly productive grasslands over a wide range of climates. Under such a strong disturbance regime, mosses and shrubs were trampled, and highly productive actively transpiring graminoids and herbs dominated (Zimov and Chupryninm, 1991; Zimov et al., 1995; Zimov, 2005). During the Pleistocene–Holocene Transition (PHT) the rise in precipitation was accompanied by increased temperature, so climatic aridity did not change substantially. The Ecosystem Hypothesis proposes: "In some places, such as sandy and stony ground, trees and shrubs would have appeared. This might have caused changes in the relative proportion of horses and moose. But overall, if climate was the only controlling factor, the total grassland productivity and the number of herbivores should have increased in the Holocene" (Zimov, 2005, p. 798). During the deglaciation, warming created more favorable

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conditions for human survival in the north (Guthrie, 2006). As a consequence of strong hunting pressures, the density of animals became insufficient for grassland maintenance (Zimov et al., 1995). The resulting decline in abundance of animals would have reduced forage consumption, causing an accumulation of surface leaf litter, insulating the soil, and reducing summer soil temperatures. This would have initiated a cascade of other ecosystem changes, including a decline in productivity and transpiration, wetter soils, and lower nutrient availability. These, in turn, would have altered the competitive balance among species, promoting the growth of mosses and shrubs and reducing the abundance of grasses. The net effect would be a decline in forage quantity and quality, leading to continued decline in animal numbers (Zimov and Chupryninm, 1991; Zimov et al., 1995; Zimov, 2005). An important implication of the Ecosystem Hypothesis is that the grassland ecosystem could be regenerated in the north if one could increase the density and diversity of animals.

MS has no present-day analog. Many assume that MS was very unproductive and that the carbon content of the biome soils was very low (Cwynar and Ritchie, 1980; Adams et al., 1990; Friedlingstein et al., 1998). However, MS soils have been preserved in the permafrost of Siberia and Alaska (locally called “yedoma”). MS soils are the largest reservoir of organic carbon in the past and at present. If this permafrost thaws in the future, this reservoir will be a strong source of greenhouse gases (Walter et al., 2006; Zimov et al., 2006; Schuur and Abbott, 2011), and modern ecosystems covering the yedoma will be disrupted by erosion due to ice-wedge thawing. Ice wedges constitute half of the yedoma volume. After thawing the surface will subside by ~10–30 m, and grasslands will appear on the fertile yedoma remnants. Therefore, the possibility exists for reintroducing herbivores and for a revival of ecosystems similar to MS (Zimov et al., 1995) that could slow permafrost degradation and mitigate global warming (Zimov et al., 2012). However, to assess future possibilities, MS trophic structure and physiology must first be known.

2. Chronological support for the ecosystem hypothesis

Recent publication of many new ^{14}C dates of animal fossils from Alaska and Yukon provide an opportunity to clarify the relative chronologies of animal extinction, vegetation dynamics, and human colonization (Guthrie, 2006). In this section we compare these data with chronologies assumed by the Ecosystem and Climatic Hypotheses. We presented the data in a form of probability distribution (each ^{14}C data is presented as a bell-curve with a 400 yr base). The total ^{14}C data density curve is sum of area of all the bell-curves (Fig. 1).

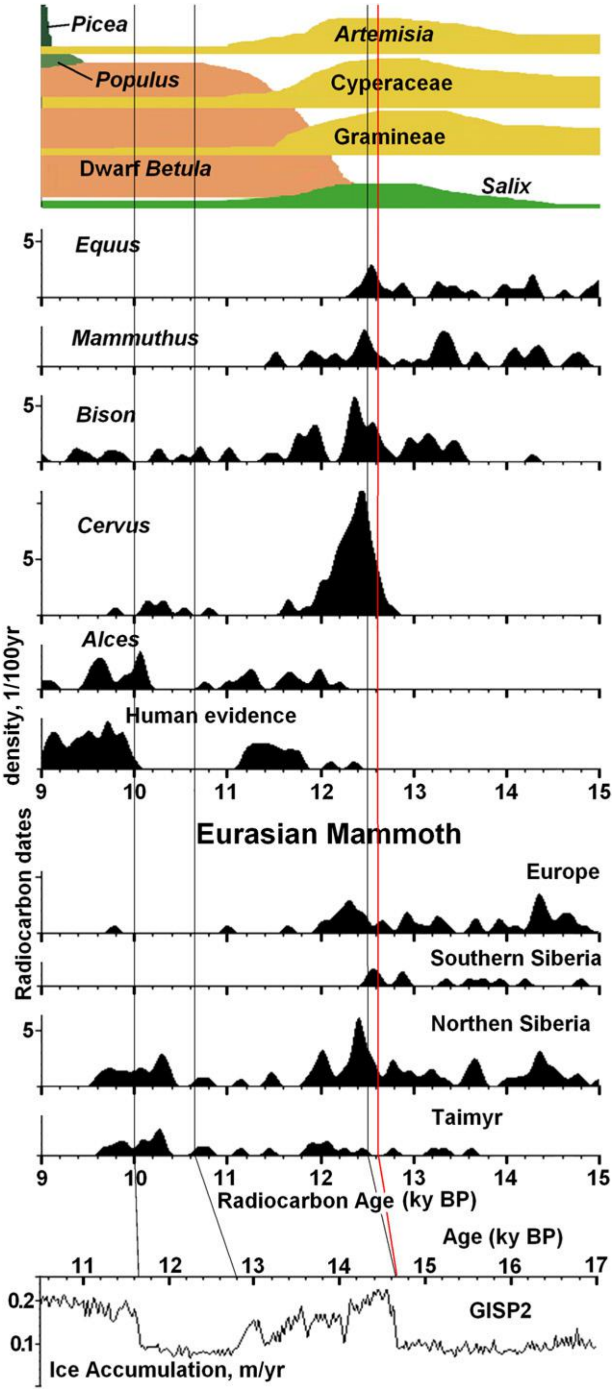

Fig. 1. Upper part: generalized pollen record, density of ^{14}C dates of animals and human evidence for Alaska and Yukon (from Guthrie, 2006). Lower part: density of ^{14}C dates of mammoths for Europe, southern Siberia and China (Vasil'chuk et al., 1997; Kuzmin et al., 2001), the entire Siberian Arctic (Vasil'chuk et al., 1997; Kuzmin et al., 2001; Sher et al., 2005), and the Taimyr Peninsula (Sher et al., 2005); snow accumulation for Greenland (Severinghaus and Brook, 1999). Vertical black lines represent Younger Dryas boundaries based on IntCal04 (Reimer et al., 2004); the red line is a corrected (elk peak correction) Bowling radiocarbon boundary. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Greenland ice cores show abrupt temperature and precipitation fluctuations at the PHT. At 14,650 calendar yr BP (approximately 12,500 ^{14}C yr BP, Reimer et al., 2004) the average Greenland temperature rose sharply (up to Holocene levels), and precipitation doubled (the Bolling Warming Event, BWE). During the Younger Dryas (11,600–12,800 calendar years ago) climatic parameters returned to their initial state, and at the end of the Younger Dryas temperatures again rose sharply (Severinghaus and Brook, 1999). Similar climatic dynamics were recorded at both high and low latitudes of the northern hemisphere (Severinghaus and Brook, 1999). Close dynamic should also be recorded for Alaska.

If the Climatic Hypothesis explained vegetation and animal dynamics, steppe-like vegetation would have been replaced by tundra vegetation during the BWE, and the steppe would have been reestablished during the Younger Dryas, when the climate returned to glacial conditions. But in fact, Guthrie (2006) data indicates opposite. Glacial climate was not favorable for animals in Alaska and the Yukon. During the LGM nine animal species went extinct there (Guthrie, 2006). When the climate warmed from 15,000 to 12,400 radiocarbon years BP there was a substantial rise in abundance of grasses and sedges, and animal densities increased (Fig. 1). Pollen influx of *Artemisia*, a drought-adapted species, rose even more than the influx of other species (Fig. 1). This suggests that aridity did not decrease at the PHT.

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The BWE did not affect plant species composition but affected animals (Fig. 1). Data on Fig. 1 indicates that strong warming and increases of snow depth during the BWE was not accompanied by the extinction of any species. On the contrary animal populations grew. During glaciations the elk (*Cervus*) population was very small (only two ^{14}C dates, Guthrie, 2006). This population increased sharply by ~12,600 ^{14}C yr BP. The Elk peak is statistically the most reliable (50 dates). Its right slope is very steep. The ^{14}C dating represented by this slope has a standard deviation of ±90–240 years (Guthrie, 2006). We did additional smoothing (±200 yr) in building the figures of ^{14}C date density. Thus in reality this slope is almost vertical – there was a sharp population rise. Reintroduction of musk-oxen to Wrangel Island is a contemporary example of such a rise. Their population grew 100 times in 35 years (Vartanyan, 2007).

Approximately 12,400 years ago an abrupt change occurred: horses vanished, bison disappeared for over 300 years, and mammoth and elk populations began to decrease sharply (Fig. 1). It is clear that this abrupt faunal change was not triggered by vegetation change, because vegetation was stable during this period (Fig. 1). The only thing corresponding with these massive extinctions was the first evidence of humans (12,370 ^{14}C years before present) (Fig. 1). It therefore appears plausible that a relatively small number of hunters triggered the collapse of several herbivore populations (Martin, 1967).

After the first appearance of humans, some of the species recovered their populations (which is in agreement with modeling results, Alroy, 2001), but human population continued to increase and this led to herbivores' extinction. It was only well after that that pastures degraded and dwarf *betula* appeared (Fig. 1). The appearance of moose (*Alces*) at 12,200 radiocarbon years BP closely corresponds with a decrease in *Salix* and rise in dwarf *Betula*, which is not the usual forage for the moose. One possible explanation for this shift is that, as long as there were abundant bison, elk, and mammoth, which actively ate willow sprouts, willow shrubs would not have grown above the snow cover. Moose (tallest hoofed animal) may have appeared in large numbers only when populations of other animals had decreased, creating a new feeding niche–tall willow shrubs.

The increase in ^{14}C dates of mammoths at the BWE can also be observed in Europe and the Siberian north (Vasil'chuk et al., 1997; Sher et al., 2005) (Fig. 1). During the Holocene the mammoth population on Wrangel Island increased substantially. There were five-fold more Holocene dates there (3730–7710 years BP range) than Pleistocene dates (Vartanyan, 2007). This occurred despite the fact that, in contrast to Alaska where loess accumulated throughout the Holocene (Muhs, 2003), in Siberia sedimentation stopped (Schirrmeister et al., 2002; Sher et al., 2005), and most of the bones remained on the surface, where they would have been destroyed by weathering.

3. The mammoth steppe climatic envelope

The essence of the Climatic Hypothesis is as follows: Mammoths, other extinct animals, and their pastures (i.e., the mammoth steppe) required a certain range of climatic parameters that defined their climatic envelope. In the Holocene, climate changed radically, and territories with climate suitable for the mammoth steppe disappeared throughout the planet. To further assess the Climatic Hypothesis, we define the mammoth steppe climatic envelope, i.e., the optimal and peripheral climatic space of the mammoth steppe.

Here we discuss two climatic characteristics – heat and moisture, as aridity level is determined by these two factors. We characterize moisture by annual precipitation (P) and heat by annual radiation balance (R), which correlates closely with mean summer temperature. We consider a two-dimensional climate space with these two parameters (coordinates). Aridity can be assessed using Budyko's radiation aridity index (Budyko, 1984), which is the ratio of R (in this case energy received by the landscape) to the energy needed to evaporate an amount of water equal to P. If this index is less than 1, the climate is humid; if greater than 1, the climate is arid: with values between 1 and 2 equivalent to steppe, 2–3 semi-desert and >3 desert environments (Budyko, 1984).

Such a two-dimensional climate space is illustrated in Fig. 2, which shows the most important boundaries for desert, arid and humid climates (Budyko, 1984). Beside those we show the approximate position of three additional boundaries: the snow line where R equals the energy needed to melt an amount of ice (snow) equivalent to annual precipitation; the northern (altitudinal) forest border; and the boundary of polar desert. Vertical movement in this climate space is equivalent to latitudinal movement in real (geographical) space. Movement to the right of this climate space is equivalent to movement from the ocean to the continental interior. Movement to the upper left quadrant is equivalent to moving upward in elevation: colder with more precipitation.

On the basis of this envelope, we make 5 arguments: (1) Similar to geographical space, in climatic space the mammoth ecosystem should have an optimum zone and a peripheral zone where conditions for survival are sub-optimal; (2) The mammoth steppe existed in different climates on a huge territory for a long period of time. Mammoths lived simultaneously in Spain, England, Mongolia, China and arctic islands (Vasil'chuk et al., 1997; Kuzmin et al., 2001; Sher et al., 2005; Alvarez-Lao and García, 2011). It is obvious that climate differed between these regions, therefore, it can be assumed that the mammoth steppe climatic area was spacious; (3) If mammoths became extinct in the Holocene everywhere because of climate then there is currently no place on the planet where the climate would still be suitable for the mammoths. It then follows

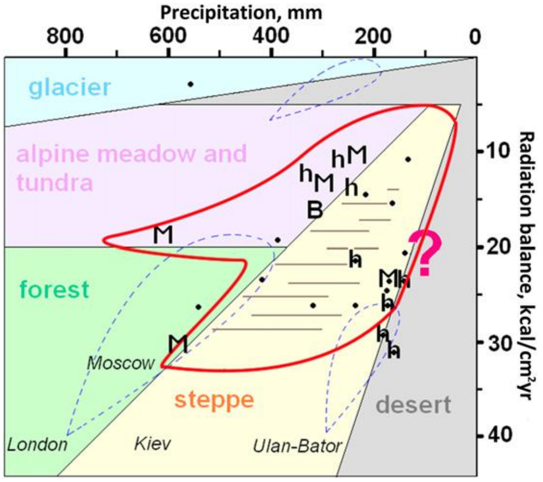

Fig. 2. Climatic space with the most important landscape boundaries shown. The axis R could also represent average summer temperatures (20 kcal/cm^2/yr approximately corresponds to 10 °C). Black dots are the meteorological stations of northeast Siberia (see Fig. 3). **h** represents Holocene and modern horse grasslands in Siberia; **M** and **B** are Holocene grasslands of mammoths and Siberian bison. Brown cross-hatching lines represent Holocene natural bison habitat of interior Alaska and northwestern Canada. Question mark ('?') is the presumed locations of the mammoth steppe climatic envelope that are consistent with the Climatic Hypothesis. The red solid line is our estimate of the boundary of the continuous climatic envelope of mammoth steppe. Dashed blue lines enclose areas where climatic trajectories lie, during the Last Glacial cycle, in 3 geographical locations: London, Ulan-Bator and top of the 1700 m mountains near the Oymyakon region. Today's snow line of the Oymyakon Mountains is situated on 2300 m. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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from the Climatic Hypothesis that mammoths were living under a unique combination of R and P, which are not met anywhere today; (4) It seems that the mammoth steppe optimum must be situated in the colder part of the steppe sector (Fig. 2), and their range should move smoothly into temperate climate steppe; (5) The range of climatic optimum for mammoth steppe was approximately 150–300 mm of precipitation and 8–10 °C summer temperatures, which corresponds to climatic reconstructions for Eastern Europe, where mammoth ecosystem received annually 250–300 mm of precipitation (Velichko and Zelikson, 2001).

Many believed that in today climate of the north-east Siberia is humid, but we showed that in fact it is arid (Zimov and Chupryninm, 1991; Zimov et al., 1995). Fig. 3 shows the meteorological stations of north-eastern Siberia, where radiation balance observations are conducted (all circumpolar, including islands and continental); these are also shown on Fig. 2 with black points. We see that even though this region has abundant lakes and wetlands its climate is arid. The most arid part is in the Pole of Cold in Oymyakon (Budyko's index = 3.28; the most right and lowest black dot on Fig. 2), and most humid is in mountains near the glacier, not far from Oymyakon (Budyko's index = 0.1; the most upper and left dot). We can use another known climatic index, in which potential evaporation is calculated by summer temperatures, but we get the same results – the climate is arid (Sokolov and Konyushkov, 1998). Around 400–500 mm of precipitation evaporates from lake surfaces or high productive grasslands in these territories; this is twice precipitation this region receives (Zimov and Chupryninm, 1991; Zimov et al., 1995). Lakes persist only because of drainage from slowly transpiring forests and tundra. In Central Yakutia vast steppe territories grazed by semi-wild Yakutian horses do not have any river drainage (Pavlov, 1984). Nevertheless, proponents of the Climatic Hypothesis suggest that the climate of northeast Siberia and Alaska is too wet for the mammoth steppe (Guthrie, 1990; Vereshchagin and Tikhonov, 1990; Velichko and Zelikson, 2001; Sher et al., 2005). If correct, the climatic envelope of the mammoth steppe would be restricted to a small area between the upland cold deserts of Tibet and the polar deserts of the Canadian Arctic (indicated with a red question mark in Fig. 2). The Climatic Hypothesis assumes that this small envelope occupied a huge territory of Eurasia and Northern America during both the LGM and the BWE. This climate space was characterized by only ∼100 mm of precipitation, raising questions of how the glaciers of Europe could have developed and persisted.

The last mammoth refuge on the continent was the north of Taimyr Peninsula, where they persisted until the Holocene (Sher et al., 2005). If the Climatic Hypothesis holds, in the Holocene the climate of Taymir (77° North) became too warm for the mammoth, and the entire climatic envelope of the mammoths should be situated in even more severe conditions (polar desert?). However mammoths lived in the south of the Iberian Peninsula (Alvarez-Lao and García, 2011), which would suggest that summer there (37°N) was colder than in Taimyr today (i.e., 25–30 °C colder than today). This is not possible. Evidently, the Climatic Hypothesis as currently stated (i.e., "colder and dryer") is unrealizable. The mammoth steppe could exist at 100 mm precipitation and with northern Taimyr summer temperatures, but it's unlikely that this represented optimal conditions.

It is possible to amend the Climatic Hypothesis by assuming that R and P changed very quickly, and that every region had its own subspecies of mammoth that were adapted to local conditions. Hence mammoths wouldn't have had time to adapt to fluctuations or migrate to more suitable regions. However this would not explain why in Europe, Northern Siberia and America mammoths sustained climatic jumps of BWE yet vanished under relatively

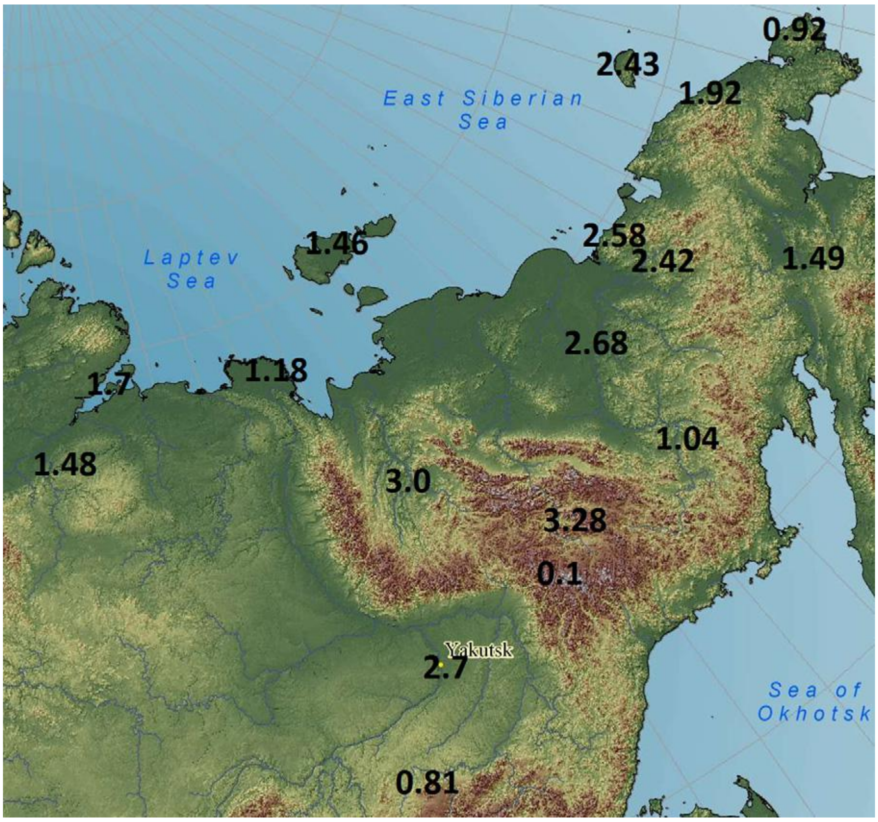

Fig. 3. Budyko's radiation aridity index in different locations north-eastern Siberia.

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stable climate significantly later (see Fig. 1). A better explanation is that the mammoth steppe did not disappear due to climate.

4. Climatic envelope of mammals of the mammoth steppe ecosystem

In this section we revisit the numerous radiocarbon dates for bones of animals which used to live in the mammoth steppe ecosystem. Many of these bones date from the Holocene and therefore experienced a climate similar to the modern climate. By looking on climatic maps at the modern climate (R and P) of these locations, we can directly estimate the climate experienced by Holocene populations of these species. These points in climate space are shown in Fig. 2.

The lack of horses in Alaska during the Holocene has been lead to suggestions that the modern Alaskan climate is not suitable for them (Guthrie, 2006). However, in Siberia, where the climate is similar, horses persisted well into the Holocene (up to 2200 ^{14}C years BP) in the arid far north (Lena delta and New Siberian Islands) and in humid climates (the Taimyr) (Sher et al., 2005). Modern semi-wild Yakutian horses extend up to the tundra region and also on the “pole of cold” in the Oymyakon region (Fig. 2).

With bison, the situation is the reverse, with only one Holocene bison date in northern Siberia (9300 ^{14}C years BP) (Sher et al., 2005), but extensive bison distributions in interior Alaska and the Yukon throughout entire Holocene. They occurred along the arctic coast as far north as Victoria Island and as far south as southern Alaska near Anchorage (Stephenson et al., 2001). The climatic envelope of the American bison is shown in Fig. 2 with a dotted line.

Reindeer now live on the far north and in Mongolia. In historical times their southern boundary passed through Germany along the steppes of Eastern Europe (Syroechkovskii, 1986). Therefore the climatic envelope of reindeer occupies almost the entire climate space of Fig. 2. In many regions of Siberia and America musk-oxen have lived until historical time (Sher et al., 2005), and as a result of recent reintroductions they currently live in Norway, Siberia, and Alaska.

We have no Holocene dates for the wooly rhinoceros, but their bones tend to occur in regions that are more arid than those of mammoths. For example, the northwestern portion of Eurasia to the north of 62°N including Taimyr is a humid part of the mammoth steppe. Many mammoth remains were found there but no rhino (Garrut and Boeskorov, 2001). On the other hand, wooly rhinos were common in the most arid regions of mammoth steppe, south of Central Siberia and Mongolia (Garrut and Boeskorov, 2001), where mammoths are rare (Kuzmin et al., 2001).

Mammoths existed in the arid zone in the Holocene (Wrangel Island, with the most recent date of 3730 ^{14}C years BP) (Vartanyan, 2007), in the humid zone on the north of Western Siberia (Gydan peninsula, 9730 ^{14}C years BP), in the northern Taimyr (9670 ^{14}C years BP) (Sher et al., 2005), in the very humid St. Paul Island in the Bering Sea (5700 ^{14}C years BP) (Guthrie, 2004; Veltre et al., 2008), and on the coast of Gulf of Finland (9780 ^{14}C years BP) (Vasil'chuk et al., 1997). While the early Holocene climate may not have been the same as today; it is indisputable that on Wrangel Island and on St. Paulo Island mammoth lived in late Holocene climate.

On the climatic space (Fig. 2) these sites are situated very far from each other. Wrangel Island is dry polar desert, and St. Paulo is a very humid climate with no permafrost. And the fact that mammoth lived on these two islands genetically isolated for the long time suggest that the mammoth's climatic envelope was very wide.

The ^{14}C data indicated that even during the LGM mammoths lived on the archipelago of New Siberia (79–80°N). They also lived there in the beginning of Holocene (Sher et al., 2005). On Wrangel Island mammoths lived both in the LGM and in historical time (Vartanyan, 2007). In the present climate, July temperatures on the islands are approximately 0 °C. Today's vegetation would not feed a mammoth population. The essence of the paradox is that in the current climate, the same place can be a desert (in the absence of animals) or grassland (if animals are present). Modern vegetation of Wrangel Island can't be considered an analog of mid-Holocene vegetation. In the middle of the twentieth century Wrangel Island was inhabited only by lemmings. At that time it was estimated that the island was capable of sustaining up to 1000–1500 reindeers (Vartanyan, 2007). This is approximately 100 tons of zoomass, which is equivalent only to tens of mammoths. In 1948 and 1952, 150 domestic reindeers were introduced. By 1975 their population reached 5000. In the same year 20 musk oxen were introduced (half of them have survived), and the shooting of reindeer began. Finally in 1980 only 113 reindeer were left. After that hunting decreased, and the reindeer population reached 5000–7000 (Vartanyan, 2007). Also there are now more than 1000 musk oxen on the island (Vartanyan, 2007). In summary, during the last 50 years ungulate biomass has exceeded intended densities by almost by an order of magnitude. We suggest this happened because the biomass of forage has increased as herbivores maintain their grasslands. This is only the beginning of ecosystem succession. In modern arctic tundra in places with high animals density, productivity increases by an order of magnitude, and the ratio of uneatable vegetation sharply decreases (Chernov, 1985; Zimov and Chupryninm, 1991; Zimov et al., 1995) (Fig. 4). The potential pasture productivity on Wrangel Island is shown in Fig. 5. Several mammoths could live on 1 km^2 of such pasture. Biological productivity in the north is limited less by photosynthesis than by nutrients (Chapin et al., 1995). Nutrient cycling is limited by slow decomposition and nutrient release from soil organic matter. Only in the warm stomachs of animals can this process be substantially accelerated.

In summary, the animals of the mammoth steppe occupied a broad climatic envelope. Similarly the distribution of modern tundra does not depend on aridity but occurs in sites ranging from 50 to 1000 mm of annual precipitation. Based on the above information, we tried to reconstruct the boundary for a continuous climatic envelope for the mammoth steppe (Fig. 2). In geographical areas that now lie inside the envelope, the mammoth steppe ecosystem would not vanish because of R and P changes. The next important question is whether animal population densities in the mammoth steppe were high enough to prevent expansion of moss, shrubs, and trees.

5. Density of the mammoth skeletons in the Duvanniy Yar region

Animal density for MS can be estimated from the number of bones found in permafrost. However, only a hundredth or even a thousandth of the bones are preserved in permafrost; from most of the skeletons, only one bone or nothing is preserved (Guthrie, 1990; Sher et al., 2005). Our studies confirm this conclusion.

We reconstructed animal densities by several methods for different places. We have done this most precisely based on data collected at Duvanniy Yar (DY) in the Kolyma River lowland (68°38′N, 159°07′E) (Fig. 6), the largest yedoma exposure (Vasil'chuk et al., 2001; Zimov et al., 2006) (Figs. 7–9). The main exposure at Duvanniy Yar is 10 km long and 35–50 m in height. We roughly surveyed this exposure twice annually (for a total of more than 50 visits).

The bone concentration in DY yedoma (as for most other yedoma and loess) is small, only one bone (or bone fragment) for each ~500 m^3 (Fig. 10). Therefore it is complicated to find bone on

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Fig. 4. (a) Tundra vegetation close to the mouth of Kolyma river, (b) same site, meadow developed 2 years after reindeer breeders camped during summer.

cliffs (exposures) and in order to see it a person would need to walk along the exposure slope for hundreds of meters.

Average annual commercial collections of mammoth tusks from DY are about 250 kg/yr, and range from 70 to 450 kg/yr, Due to the length of the exposure (10 km) and the rate of erosion (2.5 m/yr), the density of tusks is equal to 10 tons/km^2. Relatively intact tusks represent ~40% of commercial tusk collections. The average weight of a tusk in this region is 25 kg (39 kg for males and 11 kg for females) (Vereshchagin and Tikhonov, 1990). From that follows that frequency is 4 tons of intact tusks per km^2 (160 intact tusks/km^2). If we use an average thickness for the yedoma of 50 m, the frequency is 1 tusk/312,500 m^3. The length of one tusk is ~1.5 m. Tusks can lie in the permafrost parallel to the exposure front. So, the average soil thickness, from which a tusk would stick out and be visible is ~1 m. Therefore, on the slope of an exposure one tusk should be found in an area of 312,500 m^2. If a man examined a 20 m tall (width) cliff (slope), then finding one tusk would require that he walk ~16 km along the cliff. Duvanniy Yar cliffs and steep slopes usually represent only 20% of the exposure; the rest are screes that are mostly overgrown by tall grass. Therefore, finding tusks *in situ* in permafrost at Duvanniy Yar requires that the area be investigated several times (within an interval greater than a week) throughout the entire exposure. The unique feature of the Duvanniy Yar is that it provides opportunity to observe all bones from the melted yedoma. Observation of all bones is possible only on the exposed shores, where all sediments and bones slide or crumble. Sediments are washed from the area by waves and streams, but bones are left on the beach. If the water level decreases rapidly after a strong storm, and if the mud slides are not too extensive and do not cover the washed-out bones, all the bones are well exposed on the surface of the beach.

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Fig. 5. Wrangel Island is the last mammoth refugium. The picture shows a grassland near the Ushakovskaya weather station, where the average July temperature is 1 °C. The unique site is characterized by high animal nitrogen inputs. It is middle of September, but photosynthesis continues.

Bones are initially deposited at the location of an animal's death. Predators can disperse some of the bones, but not tusks and molars of mammoths. On the large beaches at DY, mammoth bones occur in groups several tens of meters from one another and belong to one animal (one skeleton), making it possible to directly calculate the density of mammoth skeletons. Accumulations of mammoth bones rarely (randomly) coincide with the accumulation of other species or of another mammoth, indicating that bone accumulations do not result from physical processes. Such processes would cause bones to gather from different skeletons into one accumulation. On average, each accumulation is 8–10 bones. Fragments of tusks and (or) molars present in the most of the accumulations.

Unique conditions for skeletons counts occurred in 1998 on the western part of the exposure, when mudflows subsided and waves washed away silt, creating a clear bank approximately 10 m in

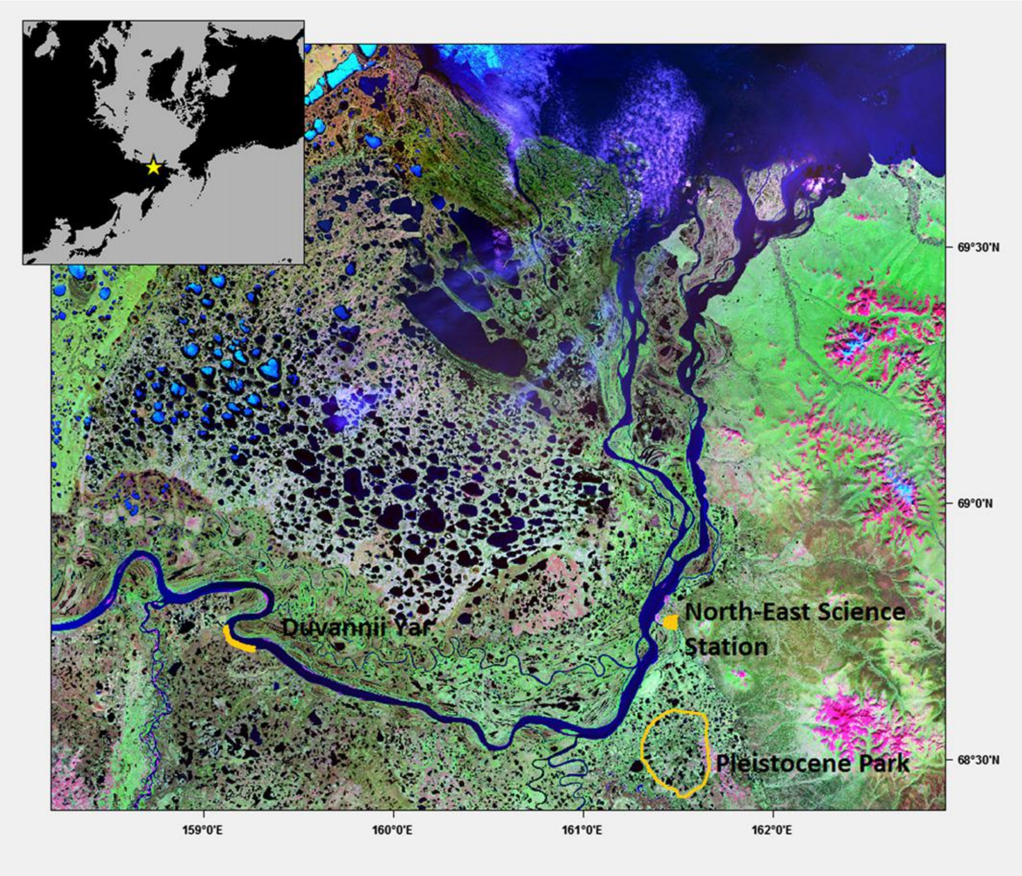

Fig. 6. Map of Duvanniy Yar and Pleistocene Park locations.

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Fig. 7. Part of Duvanniy Yar, where the ice-wedge thaw is active. In June the river water level is high and the beach absent.

Fig. 8. The most of time, the Duvanniy Yar shore is covered with mud. In the autumn of 2007 only this small section was clear.

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Fig. 9. August 2011, the central part of the Duvanniy Yar. In this image we show bones from all four accumulations with mammoth jaws.

width by 2.8 km in length (Stone, 2001). Along this bank, we found 29 mammoth bone accumulations (3–14 m across) each of which had 3 to 16 bones. Nineteen of the accumulations had fragments of tusks and/or molars. If each bone accumulation represents the remains of one mammoth, the area has a skeleton frequency of 1030 skeletons/km^2 (29 skeletons/(0.01 km × 2.8 km)).

Favorable conditions occurred again in 2009. Over the extent of the whole exposure a narrow (4–6 m), well-washed erosion terrace appeared. On this terrace, in the central part of DY over a distance of 1.96 km, we counted 160 mammoth bones and fragments. Four bones were single. Five accumulations contained two bones. In 26 accumulations we found 3–8, 12, and 17 bones. In 18 of the accumulations we found fragments of tusks and/or molars. The average size (diameter) of the accumulations of mammoth bones on the beach of DY was ~10 m, which is twice the width of the well-washed terrace (4–6 m) on which we counted mammoth skeletons in 2009. Even if the center of accumulation rested inside the width of the terrace, only part of the bones from the accumulation would be on the terrace. The terrace must also contain bones from accumulations whose center rests beneath the terrace to a distance of up to 5 m. We found a few single bones and small accumulations, and most of them must represent accumulations with centers situated beyond the investigated terrace.

To calculate skeleton frequency, we either needed to exclude single bones and small accumulations, as was done for data collected in 1998, or increase the terrace width from 5 to 15 m in order to fit the centers of all of the detected skeletons into the terrace. Using the latter method we determined a skeleton frequency of 1170/km^2 (35 skeletons/(1.96 km × 0.015 km)). In addition, in the same year in the western part of the terrace along a 1.74-km transect we collected 156 mammoth bones – 4 single bones, 6 double bone accumulations, and 26 accumulations that contained 3–7, 10, and 19 bones. In 13 of the accumulations, we found fragments of molars and/or tusks. For this terrace, mammoth skeleton frequency was ~1380/km^2 (36 skeletons/(1.74 × 0.015 km).

The third time favorable conditions were in August of 2011, in the central part of the DY. The width of the washed shore was on average 8 m. There on a transect of 1570 m we found 169 mammoth bones and bones fragments. 5 bones were singular, 4 accumulations with 2 bones, and 32 accumulations with 3–10 bones or their fragments. In 29 accumulations were fragments of molars or tusks. Accepting that each accumulation or singular bone is a single skeleton (41 units) and increasing width of the shore by 10 m (8 + 10 m) yields a skeleton frequency of 1450 per km^2. On Fig. 9 we show 4 accumulations with mammoth jaws. In 2009 on this transect we found only 1 jaw. Note that on this photo bones of other animals also appeared.

Our estimate of skeleton densities based on 2009 and 2011 collections is higher than our estimate based on 1998 collection. One of the reasons for that is that in 1998 small bones and fragments we did not try to detect, focusing only on the big bones. Some skeletons (especially of young mammoths) we likely missed. In more recent years we tried to detect all bones. From the available 4 estimates (1030, 1170, 1380 and 1450/km^2) we accept the most conservative – 1000 skeletons/km^2. This is an average frequency of skeletons of adult animals. As with elephants, most dead mammoths would have been young mammoths which would often have been smaller than bison. Their bones were soft and most frequently nothing would have been preserved in the permafrost even from an entire skeleton. There are two more methods for the mammoth skeleton density estimation.

The density of commercial tusks from DY is 200 pair per km^2. Most of the tusks preserve only as small fragments. If we assume that only 20% of tusks (by weight of all tusks) are preserved in

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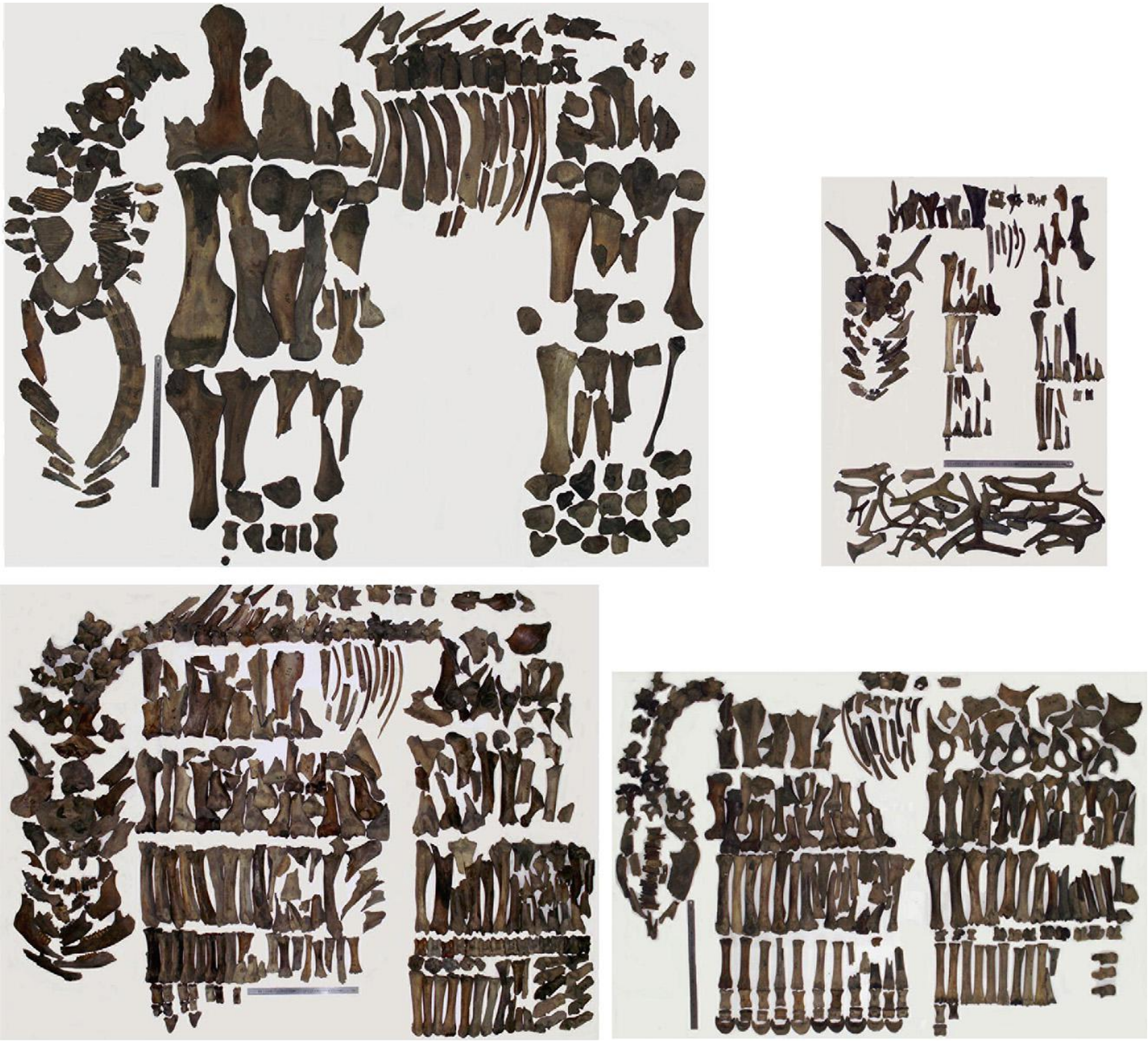

Fig. 10. Bones of mammoths (upper left), reindeer (upper right), bison (lower left) and horses (lower right) collected on the shore of Kolyma river on the western part of Duvanniy Yar exposure on the area of ~1 ha. Totally there were found ~1000 bones and bone fragments. From that follows that bone density on the site is 1 bone per 10 m^2, or (taking into account, that exposure height is 50 m) 1 bone per 500 m^3. Bones are positioned to be consistent with their place in the skeleton.

permafrost, then we obtain 1000 skeletons/km^2, the same density that we calculated from mammoth skeleton density.

On average, only ten bones were preserved from a mammoth skeleton. This was also tested by observations of skeletons thawing out of the permafrost *in situ* and exposing mammoth bone accumulations in permafrost using a motorized pump. Knowing the average number of bones in an accumulation and knowing the total number of bones in yedoma, one can estimate skeleton frequency. This was an additional method that we used.

6. Skeleton density of ungulates and predators

Bone accumulations of smaller animals are rarely found. Therefore for the skeleton density estimation we used the histogram method, the method of probability of bone preservation, and method of paired bones.

In 2009, we collected 204 bison bones, 180 horse bones, and 78 reindeer bones on 0.087 km^2 of the well washed terrace in the west part of DY beach. The number of single bones of bison was 80, horses 101, and reindeer 69. Histogram for the bones in accumulations for these animals and mammoth showed on Fig.11. The examined terrace width is half the width of the average diameter of an accumulation; therefore the number of bones in each accumulation, as recorded by this study, is smaller than the real number of bones that probably persisted in this accumulation. Some single bones and small accumulations from our collection probably belonged to larger accumulations whose centers lie beyond the width of the terrace and hit the terrace only at its edges. If we were to count the number of bones in accumulations in this wider concept of a terrace it would result in an increase in the number of large accumulations on the histogram and a decrease in the number of small accumulations and single bones – the histogram “bell” would move to the right. On the histogram for mammoths, the maximum would most likely shift to a value of 10 and occurrences of one or two bones would almost disappear. The number of single bones in histograms for ungulates would also decline.

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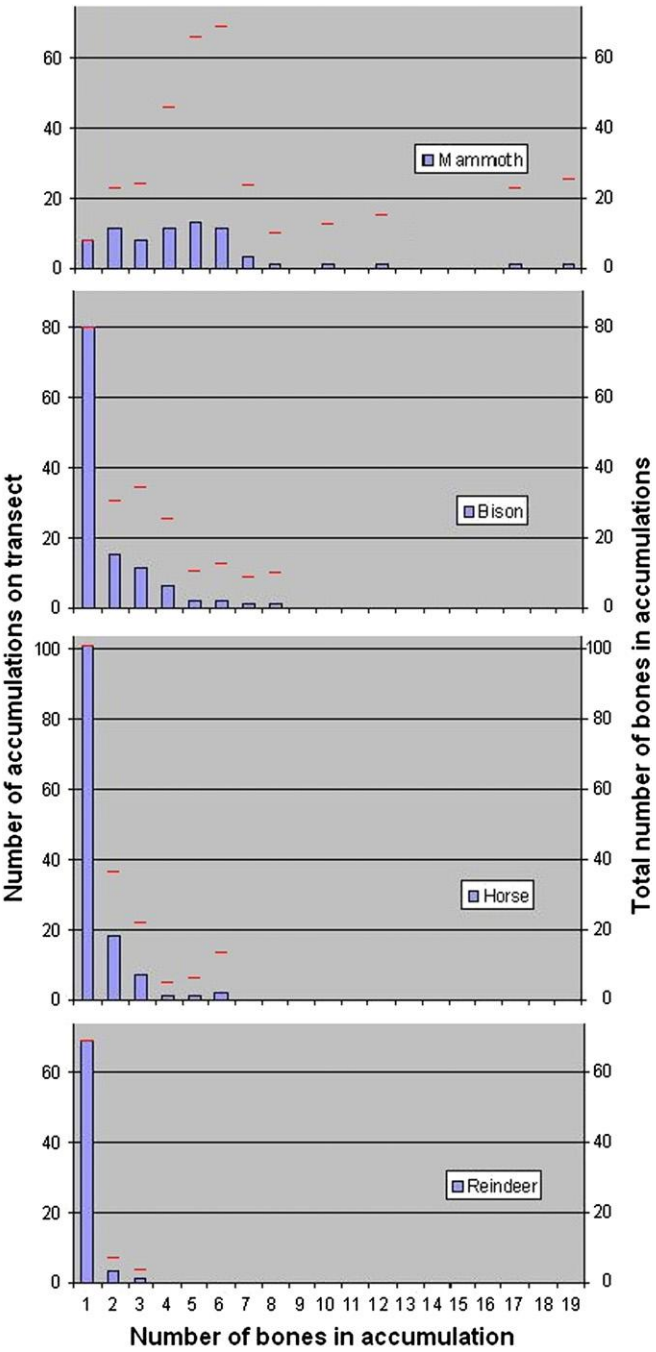

Fig. 11. Histogram for the number of bones in accumulations (red) and for the number of accumulations (blue) in the western part of the beach at Duvanniy Yar. For the mammoth histogram we also used data from accumulations from the central part of Duvanniy Yar. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

However, since the number of single bones for these species substantially exceeded the number of multi-bone occurrences, only a minor part of all of the single bones could have represented the edges of larger accumulations. So, their distribution maximum (maximum on the histogram) would still remain near one.

If bones occurred within a homogeneous region with a stable climate, then the distribution of numbers of bones in an accumulation would be close to the Poisson distribution – "Poisson bell". However, there are likely to have been periods when due to climate that was unfavorable for preservation, on average for example only 0.3 bones per skeleton persisted, and periods with more favorable conditions during which 2 bones persisted per skeleton. Alternatively, there may have been swampy areas where several bones were preserved from each skeleton. The actual histogram of the distribution will in this case be determined by summing the various bell curves, so the recorded distribution would likely have been broader, with less pronounced maxima as a result of these sources of variability. Nevertheless, the maxima in our histograms are very sharp, which indicates, with a high degree of reliability, that a high portion of all skeletons do not preserve even a single bone, and on average not more than one bone persists from each skeleton.

Predators could spread ungulates skeletons apart, which would increase the number of single bones. However, single bones in the yedoma are so abundant that, even when accounting for predators, it is unlikely that more than one bone persisted from a bison skeleton. The horse humerus bone type has more signs of predator teeth than other bone types (Figs. 10 and 12). Among horse and bison bones, for this specific example only, we can reliably say those humeri were transported away from the skeleton by predators. The horse humerus was the only bone that was not present in accumulations, and that was found only as a single bone. Other bone types can be found in accumulations and as singles in equal proportions.

At low temperatures, corpses without skin freeze (becoming covered by a frozen layer) faster than the body is eaten. Therefore, approximately 50% of all body meat in the mammoth steppe was eaten in the frozen state, and mammoth bodies were eaten almost entirely frozen. In the north it is difficult and useless for predators to bury bones in the ground since for nine months of the year the ground is frozen and bones cannot be buried nor dug out of the frozen ground. These factors decrease the ratio of single bones in permafrost.

A clear maximum for single bones on the frequency distribution allowed us to determine that, on average, from each skeleton of a hoofed animal, only one bone or less persisted. From a random number of bones in an accumulation (Poisson distribution), if single bones were twice as abundant as double bones in an accumulation, then, on the average, from one skeleton one bone should persist; if single bones are 5 times more abundant than double, then ~0.4 bones should persist on average. The histogram of the bison bone distribution (Fig. 11) shows that the single bone numbers exceed the number of double bones approximately two-fold. Therefore, on average, only one bone persisted from each bison, and the skeleton density is 22,000/km^2 (204 bones/(1.74 km × 0.005 km)). The ratio of single horse bones is higher than this ratio for bison, so horse skeletons should be more abundant. Reindeer skeletons which performed mostly by single bones, in turn, should be several times more abundant.

In order to obtain a more precise estimate of hoofed animal density, we used full bone collections gathered in 2009 and partly in 2007 over the area of ~0.01 km^2. The collection is shown in Fig. 10. Not shown are 23 woolly rhinoceros bones (that were found in 6 accumulations), 4 musk ox bones, 3 elk bones, 2 moose bones, 1 hare bone, 4 wolf bones, 2 cave lion bones, and 61 unidentified mammoth bone fragments. Many small bone types in the collection are absent or only represented by one or two bones. For example, in the entire collection there is only one patella, and numerous bones of mammoth digits are represented by only one phalanx. No caudal vertebra from ungulates occurred in the collection. The ribs are the abundant bones in the skeleton, but they are not well represented in the collection. On the other hand, it is the massive bones which dominate in the collection.

To compare the skeleton density of different species, we used the relative probability of bones to persist (be found) depending on bone weight. To calculate the relative preservation of bones of

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Fig. 12. All humerus bones of horses were gnawed from the upper end, as in the picture, by predators.

various species (the probability of obtaining the bones in the collection), we calculated the number of bones or their large fragments (over 10% of bone weight) of one type (group) in a collection, and divided it by the number of bones of this type in the entire skeleton for the species. If the collection contained two parts of one bone, we accounted for only one of them.

For the construction of graphs (Fig. 13), we only counted those bones types for which at least three bones existed in the collection. Anatomically similar bones for one species were combined into general groups: all tarsals and carpals of mammoths, except for the calcanea, which are presented separately; the cervical, thoracic, and lumbar vertebrae; and the ribs. The large bones from extremities were combined as follows: we combined all metapodia; we combined radius with tibia; we combined humerus with femur; and we combined scapula with pelvis. The pelvis consists of several fused bones. After an animal's death, these bones quickly disarticulated into relatively symmetrical and sturdy halves. We assumed that the pelvis consists of two bones. Finally, most of the points on the graph (Fig. 13) were based on several tens of bones from the collection.

The probability that bones persist, depends not only on their weight, but also on a bone's shape. Long bones, such as ribs, are heavier than many other bones, but they are thinner and are therefore not well preserved. Therefore, to exclude the influence of

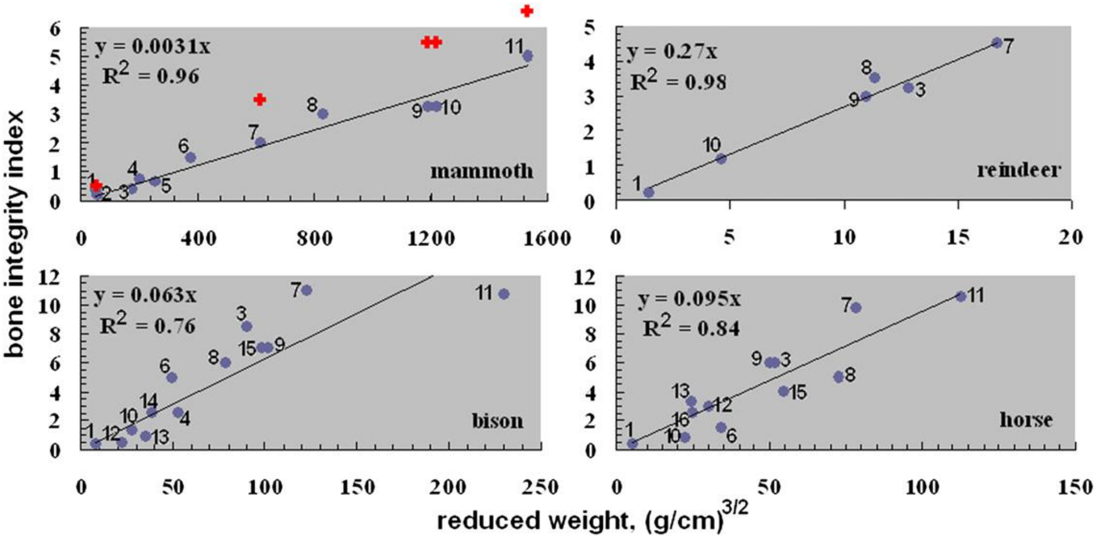

Fig. 13. Dependency of bone integrity on reduced weight. Bone integrity index is the ratio of the number of bones of a specific type in a collection (Fig. 10) to the number of such bones in an entire skeleton of a species. 1 – rib; 2 – caudal vertebra; 3 – metapodial; 4 – carpal and tarsal; 5 – vertebra; 6 – calcanea; 7 – radius and tibia; 8 – mandible; 9 – scapula and pelvis; 10 – molar; 11 – humerus and femur; 12 – phalanx 1; 13 – phalanx 2; 14 – ulna; 15 – talus; 16 – phalanx 3 (hoof). Red "+" – data from the ^{14}C collection (Sher et al., 2005). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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shape (by representing long bones as spherical) and to increase the correlation between bone size and probability to persist, we did not use the weight of the bone but instead used its 'reduced weight'. If we divide bone weight by the bone density we obtain the volume of the bone. By dividing this calculated volume by the bone's length, we determined the average area of the cross-section. The square root from this area is the average thickness of the bone. The cube of the thickness provides a reduced volume, and multiplying this by the bone density allowed us to determine the reduced weight. The unit weight for all of the bones is similar, so to ease the calculations for the reduced weight we used a simpler parameter – (weight of bone (g)/length of the bone (cm))$^{2/3}$. We calculated the reduced weight based on five bones from each group (subgroup). For this we took the largest bone, the smallest bone, and three of the most typical bones for the collection. If a group consisted of two subgroups (for example, humerus and femur), ten bones were utilized, five from each subgroup. If the number of bones in the group was less than five, we weighed all of the bones. If most of the bones were bone fragments for which we could not reconstruct an average bone thickness, we utilized analogous bones from other collections; this mostly applied to large mammoth bones that were largely disintegrated in our collection. For us it was more important to determine the dependence of smaller mammoth bones – calcanea and smaller, since only bones of this size had similar reduced weights as bones of ungulates. Mammoth bones of this size were mostly of good integrity, and it was not difficult to calculate their reduced weight, although we mention that the dependence we obtained from this method for large mammoth bones was similar to the range determined for small mammoth bones. Obtained dependence between reduced weight and probability to persist didn't fit only the most edible bones: the vertebrae of ungulates and the thin-walled humerus and the femur of reindeer. We did not consider mammoth tusks and antlers of the reindeer.

A small number of small bones is associated not only with faster rates of weathering, but also with the fact that these bones were more likely to be eaten or broken by predators. Predators were abundant in the mammoth steppe. Many bones from the collection had signs of predator tooth marks (Figs. 10 and 12). Predators took out marrow from many humerus and femur bones of bison and horses, but large fragments of these bones persisted and were present in the collection. The opposite occurred for the thin-walled humerus and femur bones of reindeer. These bones are easily gnawed into small pieces by predators and do not make it into the collection. Mammoth vertebrae are relatively small bones, and their reduced weight is two times less than the reduced weight of a calcaneum. At the same time they hold a heavy load; therefore, they are relatively strong. In the thin-legged skeleton of a reindeer, the vertebrae are the thickest bones, and the main reservoirs of red marrow, and are, therefore, friable (spongy). Predators easily crack these bones, and gnawing them is not substantially more difficult than eating frozen meat. Therefore, these numerous bones (and the back vertebrae of horses as well) are eaten almost entirely. The back and neck vertebrae of a horse are approximately the same size and weight. For processes of physical weathering, these vertebrae are identical. If weathering was the only agent of destruction, then the number of back vertebrae in the collection must have been 24:7 times higher than the number of neck vertebrae. However, in the collection, the actual number is equal to 4:12. Back vertebrae have a smaller probability of being preserved due to predators. In Pleistocene Park (Zimov, 2005) wolves and wolverines gnawed the backbones of horses frozen in the ice and their stomach contents in less than a month.

In the past mammoth tusks were mostly collected on the beaches, but during the last few years, a rise in tusk market prices increased the collecting intensity on Duvanniy Yar and most of the tusks were collected when they just appear on the exposure slopes (not on the beach) so for our collection we only found small tusk fragments from 11 mammoths. We have 46 kg of mammoth humerus bones, in our collection. The reduced weight of tusks is twice as high, so they should be twice as abundant as humerus bones in the collection, ~100 kg. By accounting for the fact that the collection was gathered on a territory of ~1 ha, the value is equivalent to 10 tons/km^2. The estimate corresponds to the tusk frequency calculated from commercial collection data.

Reindeer antlers are the most numerous of bones in the collection. However, it is difficult to estimate the number of reindeer skeletons using these bones – reindeer shed antlers every year, and one needs to accurately know the average life-time of this species. A bone with an average size of $1 \times 0.5 \times 0.3$ m is impossible to cover with loess. Bones of this size were stepped on by animals several times per year, so they were frequently turned. If the bones lie on the surface and do not get covered by dust, they will weather and disintegrate into smaller pieces. Only afterward can small fragments be transported to the soil. All of the antler pieces in the collection are weathered. The bones have little chance of being preserved. Males shed antlers at the beginning of the winter, and females at the end. From the availability of antlers in a pasture, one can reconstruct the migration of reindeer. If a territory is utilized by reindeer only as a summer pasture, then there should be no antlers. Summer antlers are soft and are eaten in their entirety by predators. The fact that our collection contains the bones of males and females, and the fact that some of the antlers are attached to the skull could indicate that reindeer used the Duvanniy Yar territory during most of the year.

Linear dependence was recorded for all species and holds true for a range of bone weights from grams to kilograms (Fig. 13).

The number of bones in the collection is also proportional to the number of dead animals. Assuming that all four graphs reflect the same functional dependence on bone weight, we determined a relative density of skeletons for four species (using the ratio between equation coefficients, Fig. 13). We determined (rounding) that bison skeletons were 20 times more abundant than mammoth skeletons, horse 30 times and reindeer 80 times. Since we know the density of mammoth skeletons (1000 per km^2), we can calculate densities of other species. These estimates are close to those obtained by using the average number of bones in the accumulations.

The obtained dependence (Fig. 13) can be interpreted as follows: the number of persistent bones is approximately proportional to the skeleton weight. A wolf skeleton is approximately two times lighter than a reindeer skeleton. The number of reindeer bones in the collection (excluding antlers) numbered 87, and wolf bones numbered 4, indicating that the number of dead wolves were approximately 11 times less than the number of reindeer (87/4/2). Cave lions were twice as large as reindeer. Only two lion bones were contained in the collection so their skeletons were 87 times less abundant than the reindeer ((87/2) × 2).

For rough estimate of animal density we used additionally method of dual bones (tusks). Large fossil collections allow the implementation of statistical methods to estimate the probability of preserving bones. Many bones in the skeletons are paired (left and right leg bones, tusks, etc.). The probability of preservation of both left and right bones is the same (p). The probability that both paired bones were preserved is equal to the probability one bone was preserved squared (p^2).

Since we know the proportion of the paired bones in the collection (p^2), we can calculate the probability of preservation of these bones (p). This transformation requires large enough sample size, so that we had to combine all bones of our collection, preservation probability of which is comparable. We combined the following large bones of legs of bison and horses: metapodial,

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radius and tibia; humerus and femur; scapula and pelvis; thus making 8 bones of horses and 8 bones of bison. The total number of bones was 245. Among these in the accumulations of bison and horses bones only four pairs of paired bones were found (8 bones), thus making 3.3% of the entire collection. Which means that ratio between probability of a pair to preserve to probability of a single bone to preserve (p^2/p), is 0.033 indicating that p is equal to 0.033. Therefore, in order to estimate the number of dead animals in a specific territory we need to divide the number of bones found in a specific territory (245) by the probability that the bones are preserved (0.033), and by the number of bones of the full skeleton we used in the calculations ($8 + 8 = 16$). At the end of all we get is the density of skeletons of bison and horses 470 per ha or 47,000 per km^2. The value is close to what we have gotten in our previous estimation (20,000 + 30,000).

This method can be used to assess the probabilities of preservation of bones based on the number of paired halves of the bones. The probability of preserving two similar-size parts of the bone is equal. In the collection, among ungulate animal bones, many halves of bones or fragments existed, but all of them belonged to different bones, indicating a very low probability of small bone preservation. Only for mammoth did we have different fragments of one bone.

7. Animal density in the mammoth steppe

Duvanniy Yar loess accumulated from 42,000 to 13,000 years BP (there are 40 ^{14}C dates from this exposure, Vasil'chuk et al., 2001). In collections gathered from northern Siberia, ~10% of all of the mammoth bones were older than 45,000 years (Sher et al., 2005). Therefore, we took a more conservative estimate that all bones accumulated for ~40,000 years. Average age (calculated by rings of tusks) for a dead mammoth was 40 years (maximum age ~80 years) (Vereshchagin and Tikhonov, 1990). We are making a conservative evaluation of the density of dead mammoths 1000/km^2. From this we determined that the average mammoth density was about 1/km^2 (1000 skeletons/km^2 × 40 yrs/40,000 yr).

There were very few bones of young ungulate animals (Fig. 10); they are relatively soft and therefore are eaten by predators. By accounting for high predator pressure, and the maximum age of modern animals, we assumed that the average longevity of mature horses, bison, and lions was ten years, seven years for reindeer, and five years for wolves.

Assuming that the density of the bison skeletons was 20,000 per km^2, horses 30,000 per km^2, reindeer 80,000 per km^2, wolves 7300 km^2 (11 times less than reindeer), lions 920 km^2 (87 times less then reindeer), and assuming that the average weight of adult bison was 600 kg, horse 400 kg (as recent Yakutian horse), reindeer 100 kg, lion 200 kg, wolf 50 kg, thus making the average animal density per square kilometer of five bison (total weight of 3 tons), 7.5 horses (3 tons), 15 reindeer (1.5 tons), 0.25 lions (0.05 tons), and one wolf (0.05 tons). By adding the weight of the mammoths (2.5 tons, Vereshchagin and Tikhonov, 1990) and the rest of the more uncommon herbivores (0.5 tons), we calculated a total herbivore biomass of 10.5 tons, enough to feed two wolves. All of these estimates were averaged over a period of 40,000 yr. Mammoth density dynamics in the end of Pleistocene and the Holocene are illustrated on Fig. 1 (Kuzmin et al., 2001; Sher et al., 2005; Vartanyan, 2007; Nikolskiy et al., 2009) (Fig. 14). In the LGM, the number of mammoths was the lowest; it increased as climate became warmer.

Are these density figures representative for the entire Siberian North?

During the time of yedoma accumulation, the territory of DY, which was far away from mountains and hills, was a homogeneous plane, and animal density in the area was likely determined by forage availability. We explored approximately 200 river, lake, and coastal yedoma exposures in the Siberian north. Our visual assessment indicated that bone and tusk concentrations, in most regions, are similar to DY – several bones per kilometer of transect along the exposure slope and several tusks per 100 km. Low bone densities are typical for sandy yedoma, which is likely related to low pasture productivity during the Pleistocene, for example, Aleshkinskaya Zaimka and Plakhinskii Yar on the Kolyma River, and Sypnoi Yar on the Indigirka River. Above-average bone concentrations were recorded for some exposures close to mountains. In these areas, animals probably died more frequently in the depression along creeks. We are aware of two such exposures in the watershed of the Filipovka River and one more in the Krasivoe exposure on the Malii Anui River. The exposure is tens times smaller than Duvanniy Yar, we rarely visit it. However, we found the same number of *in situ* tusks as at Duvanniy Yar.

Some may assume that bone abundance in Duvanniy Yar is related to a connection to the big river (animals die more often at the watering place), but in the north the most difficult season for herbivores is winter and spring (highest death rates) and rivers are frozen at that time (for more than 8 months). Additionally, the river bed of the Kolyma was situated to the north of Duvanniy Yar during the Pleistocene. Up and down along the Kolyma River, there were several exposures, and bone concentrations on the slopes and beaches were similar to those found at Duvanniy Yar.

Commercial collection data indicates that the tusk content of the yedoma of different regions is roughly the same (Boeskorov et al., 2008). The number of collected tusks mostly depends on the number of exposures in each region. Some assume that the frequency of tusks in the New Siberian Islands (the main tusk provider) is higher than on the continent. However, this

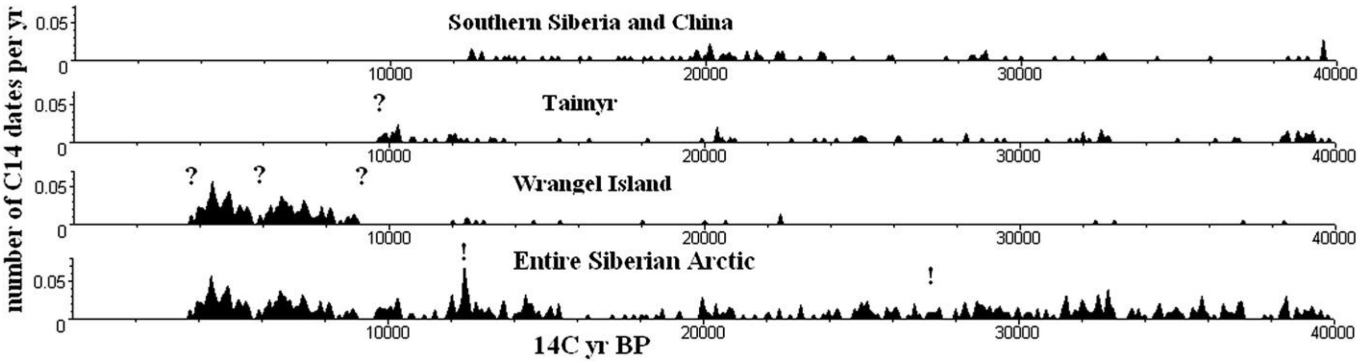

Fig. 14. Density of C14 dates of Siberian mammoths. "?","!" – timing of human arrival.

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assumption is not true. In the north, the ice content in the yedoma is higher (up to 90%). Therefore, there are higher rates of erosion and, as a consequence, rates of tusk appearance on the slope (beach) are higher. Such exposures have insufficient amounts of mud to cover (hide) large tusks.

The uniqueness of DY lies not in the density of bones but in the fact that sometimes all bones are visible. For minor rivers and lakes, large exposures and beaches produced by active erosion are absent.

The distribution of fossils from different species on DY was very similar to the distribution of bones obtained from ~3000 bones gathered in the entire region of northern Siberia (Sher et al., 2005). So the species distribution on DY is typical of the Siberian north.

To additionally assess dependence of the mammoth bone preservation on reduced weight we explored the entire list of bones collected for ^{14}C dating (^{14}C collection) in the entire Siberian north (Sher et al., 2005). The majority of these dates were obtained with a method requiring bone samples with weight over 1 kg (scintillation method). Therefore this collection contained a few average size bones and no small bones (Note that the reduced weight of ribs is small but their overall weight is high.) For large mammoth bones the dependence of bone integrity on reduced weight was very similar (linear) to that obtained for Duvanniy Yar (Fig. 13). This similarity suggests that the probability of bone preservation is similar across yedoma lowlands. This relationship excludes only those bones that are most “popular” among fossil collectors – tusks and mammoth mandibles.

A rough estimate of animal density can be obtained for other northern regions. Another famous exposure of yedoma is at Mamontovy Khayata on the Bykovskii peninsula, east of the Lena River delta. During the joint Russian–German expedition to this site about 900 fossil mammal bones were found, nearly 160 of them within the main Mamontovy Khayata cliff. 12 of them were found *in situ* in the permafrost (Sher et al., 2005). The length of this exposure is 600 m with a maximum height of 40 m. Accounting for bad exposure (Sher et al., 2005), the total area of eroded yedoma surface ~12,000 m^2. If we assume that all this territory was surveyed five times, then 12 bones were found on the area of 60,000 m^2 or 1 bone per 5000 m^2 – similar to Duvanniy Yar. Duration of sediment accumulation there was also ~40,000 yr (Sher et al., 2005).

The New Siberian Islands are the main provider of tusks. For more than 200 years, every year, 10–12 tons of mammoth tusks were collected for commercial purposes on the islands (Boeskorov et al., 2008). Of this number, 6–7 tons of tusks were gathered from the eroded coast of Bolshoi Lyakhovskii Island (73–74°N). The overall length of the eroded shores of the island was ~150 km, and the average rate of coastal retreat was ~5 m/yr (Boeskorov et al., 2008). Therefore, the tusk content of the yedoma along this long transect was approximately 8 tons/km^2, slightly less then for DY. In these large commercial collections from Bolshoi Lyakhovskii Island paired tusks represent 5–7% of the total collection. As we noted before the probability of preserving a single tusk is also equal to 5–7%. Using this probability, the initial frequency of tusks was ~115–160 tons/km^2. Using an average tusk weight of 25 kg we determined a very high mammoth skeleton frequency of 2300–3200 mammoth skeletons/km^2. The error is due to the fact that not all paired tusks are identified as paired. Paired tusks very rarely lay one above the other, and are most often situated several meters from each another (the average diameter of the place where the remains of a skeleton lie is ~10 m). Therefore, at rates of yedoma erosion of ~5 m/yr, only a minor proportion (roughly one third) of all of the paired tusks were found in the same year, and often a second tusk was found the second or third year after the first. Such tusks were identified and sold as single tusks. So, the actual proportion of paired tusks in the yedoma of New Siberian Islands should be tripled, providing us with a probability for tusks preserved similar to that of Duvanniy Yar. The tusks accumulated (as at DY) for less than 40,000 years (for these islands, 52 ^{14}C mammoth dates are known with just 6 of them older than 43,000 ^{14}C yr BP, Sher et al., 2005). As a consequence, mammoth density on the island was comparable with DY. The ratio between the bones of different species was also close to those that we determined in DY (Sher et al., 2005). Only the ratio of musk ox bones was larger (Sher et al., 2005).

St. Paul Island in the Bering Sea is 1300 km closer to the equator than DY. That island was isolated due to marine transgression at the beginning of the Holocene. Mammoths lived isolated on this small island (100 km^2) for ~5 thousand years (Guthrie, 2004). The population of large animals could only be stable if their number was at least several hundred (Yablokov, 1987). From this fact, we concluded that mammoth density on the island in Holocene exceeded 2 mammoths/km^2 and that inbreeding could be a cause of their extinction.

8. Mammoth steppe of the Wrangel Island

The area of the island is slightly larger than Lyakhovskii Island, but 2/3 of its area is occupied by mountains. Loess sediments and exposures, particularly for the Holocene, are relatively sparse, and there are no active thermokarst lakes (Vartanyan, 2007). Nevertheless S. Vartanyan (2007) found there (mostly in river beds) approximately 200 fossil remains of mammoths. Among those he randomly chose 126 remains – 59 molars, 45 tusks and 20 bones for radiocarbon dating. Such a high ratio of tusks and molars and absence of bone accumulations indicates a very low probability of bone preservation on this island. Remember that on Duvanniy Yar most reindeer bones are singular, and from 10 reindeer skeletons only 1 bone was preserved in the permafrost. Probability of mammoth bones preservation on Wrangel Island is less than probability reindeer bone preservation on DY. All this indicates relatively high mammoth densities in the valleys of this island. Wrangel Island is situated 250 km south of Lyakhovskii Island. On the loamy soils of lowlands, pasture productivity (and correspondingly animal biomass) was probably not lower than on Lyakhovskii Island.

In addition to mammoth fossils on this island S. Vartanyan found 30 remains of other animals, 13 of which were used for radiocarbon dating (bones of horses, rhinoceros, bison and musk ox). One bison fossil was dated as early Holocene (9450 BP); all other are Pleistocene dates. Reindeer bones were not found (they don't preserve), but in deglaciation sediments reindeer excrements were found (Vartanyan, 2007).

The conclusion based on the ratio of number of bones of different species was that the late Pleistocene faunal assemblage on Wrangel Island was similar to that in other regions of northern Siberia and that, in the Holocene, probably only mammoths inhabited the island (Vartanyan, 2007). Thus in the beginning of the Holocene MS experienced a large stress, after which only mammoths persisted.

Holocene mammoth fossil remains on Wrangel Island (108 ^{14}C dates) are substantially more abundant than Pleistocene remains. The intensity of sedimentation in the Holocene was much lower than during the Pleistocene (Vartanyan, 2007), indicating that the higher frequency of Holocene mammoth remains is not related to taphonomy (selective preservation). This difference in frequency of dates suggests that Holocene mammoth frequency on Wrangel Island was many times higher than during the Pleistocene (Vartanyan, 2007). The frequency of mammoth dates in Pleistocene is 16 dates/26,000 yr and in the early Holocene 11 dates/1000 yr which is 18 times more than in Pleistocene.

During the Holocene, mammoths on Wrangel Island were approximately 30% shorter than during the Pleistocene, and

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consequently 2 times lighter (Vartanyan, 2007), resulting in 9 (18/2) times higher biomass of Holocene mammoths. Pollen spectrum data from Wrangel Island indicates that the character of vegetation and productivity of pastures in the late Pleistocene and mid Holocene were similar (Vartanyan, 2007). If pasture productivity is assumed to be similar between these two periods, this suggests that during the Pleistocene mammoths ate only 1/9 of the available forage. If productivity during the Pleistocene was half that of the Holocene, then 2/9 of all forage would have been consumed by mammoths. It is probable that mammoths ate so little because the rest was consumed by competitors (ungulate). This estimate indicates that in Pleistocene on Wrangel Island, as at Duvanniy Yar, mammoths controlled only a minor portion of the biological cycling. However, the Holocene mammoths were the only large herbivore species. It seems important, therefore, to discuss the following phenomenon. The mammoths of Wrangel island were on average smaller in Holocene than in the Pleistocene, but alongside the small individuals, the normal-sized mammoths existed (Vartanyan, 2007). Perhaps it was the beginning of a new sympatric speciation event as in the classic example with Darwin finches. On Wrangel Island the ecological niches of ungulates became vacant in the Holocene and collared lemming (suitably called “hoofed lemmings” in Russian) that became larger and some mammoths that became smaller tried to fill the niches of horse and bison.

The example of the Wrangel Island shows that the mammoth steppe ecosystem can be stable even at the low diversity of the herbivores. But can a mammoth steppe exist in the absence of mammoths? In the African savannah, as in the mammoth steppe, elephants consume only a modest part of the plant biomass, but they are the keystone species limiting expansion of trees and large bushes (Western, 1989; Western and Maitumo, 2004). At the southern border of the mammoth steppe where the trees were large, mammoths were perhaps the key species. On the North, however, the ungulates were able to contain the expansion of the forest and tundra even in the absence of mammoths.

Based on the different regions and the different methods above, we obtained similar estimates of animal density. The estimates are approximate. Many parameters (animal weight, shore width, etc.) were rounded, but the accuracy of these estimates is probably similar to the accuracy of estimates of animal densities in modern ecosystems. Our roughest estimate was for predators, but given that almost all of the back vertebrae of the horses were eaten and that all of the humeral bones were broken by predator teeth we believe that the predator population was large enough to eat everything that could have been eaten.

We also can see large number of herbivores in the north today. Northern Siberia is inhabited by semi-wild horses. Their biomass in Yakutia exceeds the biomass of reindeer (Agricultural Atlas of Yakutia, 1989). The modern density of wild and semi-wild reindeer in the forest and tundra of the Kolyma lowland is only 60 kg/km^2 (1 per km^2) (Agricultural Atlas of Yakutia, 1989). In contrast, the current biomass for horses in the Aleko-Kuel region (300 km west of DY) on the most productive low-lying meadow, is 200 times this value (30 horses/km^2), which is close to the above estimate of 10.5 tons. The same density of ungulate animals is maintained on the grasslands of Pleistocene Park (100 km east of DY) (Fig. 15). This experiment shows that on the North at the high density of the ungulates the steppe can expand in the absence of mammoths.

9. Mammoth steppe physiology

Although the accuracy of any single calculation might be questioned, as with any palaeo-reconstruction, the consistency of patterns that we obtained from many independent data sources and approaches suggest that the following inter-related conclusions are robust:

1. Plant, herbivore, and predator productivity in mammoth steppe was close to the theoretical maximum for a northern ecosystem. The ecosystem very efficiently utilized all resources. The density of animals and their community structure was similar to that of an African savanna. To feed animals, plants utilized all available water
2. The vegetation was dominated by palatable high-productivity grasses, herbs and willow shrubs (Guthrie, 1990; Sher et al., 2005). No other vegetation could maintain 10 tons/km^2 of herbivore biomass.
3. The soils were fertile. The content of bio available phosphorus in yedoma is an order higher than in modern soils (Zhigotsky, 1982). If soils of mammoth steppe appear on the surface due to erosion, they are immediately overgrown by high productive grasses and herbs (Fig. 16).
4. Winters were much longer than summers, and winter forage was a limiting resource. Therefore, summer overgrazing was

Fig. 15. Horses, bison and musk-ox inhabit Pleistocene Park. There are also three species of deer. This represents the highest diversity this area has seen in the last 12,000 years.

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Fig. 16. Part of the Duvanniy Yar exposure. The soils (yedoma) are fertile, so even though it's a cold northern-faced slope, highly productive grasses appear in locations of permafrost erosion. In this part of the exposure, grasses prevent erosion through root reinforcement of the soil. In conditions of cold and dry climate with herbivores absent, thermally insulating litter accumulates on the surface, fertility declines, and in several years grass productivity also declines. If herbivores appear on the site they maintain meadow productivity and also decrease permafrost thawing.

not possible. In the summer animals could eat only half of all available forage. During winter herbivores ate all the rest (Fig. 17), however, without damage to the grass community, since in winter all living parts are preserved in the soil. Therefore, all of the insulated snow cover was trampled, and the soils cooled significantly during winter. A change in snow depth of ~10 cm changes the temperature of the permafrost by 1 °C (Yershov, 1998). Soils were fully trampled throughout the year, preventing the establishment of a moss layer and the expansion of slowly growing shrubs and trees into grasslands (Zimov et al., 1995). We did simple calculation: if area of footprints of all animals that occupy 1 km^2 (their total weight is more than 10 tons) is equal to 2 m^2 and if walking they did one step per second and if they walking one fifth of time then area of their footprints for one year will be 6 km^2. That means that the mammoth steppe has been trampled 6 times per year. Only

Fig. 17. The territory of 'Pleistocene Park' in spring after snowmelt. Ten years prior, the area was a continuous community of 2–3 m tall willow shrubs. Due to erosion and long-term active grazing, the plot developed into a meadow with fertile soils and nutritious grasses. Herbivores therefore graze in this area several times per winter, trample down snow, and eat all the vegetation that grows during the summer. The winter temperature of the soil surface at this site is 15–20 °C colder than for grasslands without grazing. We presume that during herbivore population peaks in spring all of the MS pastures appeared similar.

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grasses and herbs could survive in the condition. The albedo of mammoth steppe was significantly higher than the albedo of forest and shrub lands, especially during the snow season (Foley et al., 1994). Litter did not accumulate in the ecosystem. Therefore, at the beginning of the summer, until new grass had grown bare soil surface (Fig. 8) was intensively heated by the sun.

5. Moderate summer grazing stimulated the regrowth of grasses. As a result, grasses had no time to finish their life cycle and were covered with snow still having a high nutritional value. Due to summer grazing, graminoids shifted from sexual to vegetative reproduction, so grasses are not evident in the pollen record (Guthrie, 1990; Sher et al., 2005). Plant species assemblage is usually determined from pollen records that are collected from loess strata. These records often consist of species that are not common in grasslands (Guthrie, 1990). If on some territory several meters of loess accumulated, it would indicate that another territory with sparse vegetation cover and strong winds would erode the same amount of dust, and that all of the spores and pollen (and everything aerodynamically lighter than sand including insect remains) from deflated areas would appear in pollen-poor grasslands and, in the end, in loess strata. These inferences can be applied to all mammoth steppes that formed on loess-dominated soils. In areas with poor stony or sandy soils, the productivity of palatable plants would be smaller and grazing and trampling would be weaker. Therefore, slow-growing unproductive plants were able to survive and persisted in the regional flora. Mammoth steppe biomes consist of different ecosystems: unproductive deflation areas, productive grasslands on loess or loamy soils, and tundra and forests (savanna) on poor soils. These patterns explain the complicated composition of the pollen spectra.
6. Due to high productivity and corresponding plant transpiration, water was often a limiting resource; grass roots competing for water penetrated the entire depth of the active layer. This is additionally suggested by the fact that in yedoma numerous thin grass roots are preserved (Sher et al., 2005). Near the permafrost table soils were thawed just for few weeks per year, and temperatures never rose substantially above zero, therefore organic decomposition was low, and labile carbon accumulated (Zimov et al., 2009). Therefore, the mammoth steppe was an ecosystem with a high rate of decomposition for aboveground biomass (in animals' stomachs), and a very low rate of decomposition in deeper soils.
7. The similarity of herbivore density and the assemblage of species on the northern and southern parts of the lowlands suggest that regular massive migrations of herbivores with regional differences in mortality were unlikely.
8. Mammoth steppe would only be stable under conditions of very high animal densities, as they had a strong impact on the environment. An expansion of the high-albedo psychrophilic steppe biome, whose dry soils and permafrost accumulate carbon (Zimov et al., 2006, 2009) and do not produce methane (Sher, 1997; Rivkina et al., 2006), would promote climate cooling and permafrost expansion, whereas a degradation of the ecosystem and permafrost in response to recent warming would amplify climate warming (Zimov and Zimov, in review).
9. The north Siberian mammoth steppe was the coldest and driest part of the biome. In other grassland ecosystems, where there was 2–4 times more precipitation, the grasses and herbs productivity and the animal densities were correspondingly higher. An analysis of paleovegetation maps indicates that during the LGM forested areas were ten times smaller than in the Holocene, and that an area of grass-herbs dominated ecosystems, reached 70 × 10^6 km^2 (Adams and Faure, 1998). If similar animals to the mammoth steppe consumed all forage, assuming average herbivore density of 20 tons/km^2 (twice more than in the north of Siberia), we obtain global animal biomass value (1.4 billion tons) close to that obtained via methane emission by herbivores (Zimov and Zimov, in review). During the LGM, wetlands were rare. For that period no ^{14}C basal peat initiation dates are know; in abundance they appeared only in Holocene (Yu et al., 2010). Furthermore, during LGM methane concentration in the atmosphere was almost half of Holocene values (Spahni et al., 2005), and herbivores were the main source of methane due to a total herbivore biomass exceeding total modern biomass of humans and domestic animals combined (Zimov and Zimov, in review). In the Holocene the density of wild herbivores declined by an order.

10. The mammoth steppe and humans

Animals in the mammoth steppe were very numerous, and if humans exterminated a substantial portion, then the north should preserve the evidence of that. However, calculating the probability of finding such evidence suggests otherwise. Assuming that on average over each square kilometer humans killed one to two mammoths and 10 bison. However on the same territory 1000 mammoth and 20,000 bison skeletons that died over the course of the late Pleistocene through natural causes are also preserved. In a collection such as presented in Fig. 10, finding bones from animals killed by humans is unlikely.

The Yedoma plains do not have lithic resources. Therefore, it is likely that for hunting bone tools were mostly used (Pitulko, 1993). Assuming that killing and dressing ten animals required ~100 bone tools. Bone tools are "small bones" – similar in size to bison ribs; so the probability that they persisted in permafrost is low – one out of hundreds (Fig. 13) – leading to the persistence, on average, of no more than several bone artefacts per square kilometer. Even specialists can overlook these artefacts among mudflows and south ends of other bones. To find one such artifact it would be necessary to gather tens or even hundreds of collections such as ours. Also it should be mentioned that in contrast to Alaska, in northern Siberia, in the BWE accumulation of loess stopped (Sher et al., 2005) and any evidence of human activity remaining on the surface would have decayed.

Predators in the mammoth steppe used all of the herbivores (including soft bones) and therefore they could exist in high densities; however only few of their bones are preserved in permafrost. In all of the collections gathered from the Siberian north, there were only several tens of bones from wolves and lions. Human bones are similar in size to those of wolves and lions, but periods of active animal extinctions were 100 times shorter than the time of yedoma accumulation. Therefore even at rational resource consumption rates by humans the probability of finding a mammoth hunter bone is hundreds of times smaller than the probability of finding wolves' or lion's bones, and human bones should be absent in these collections.

Since 1947 on the north of Siberia scientists have discovered three mammoth graveyards and three archaeological sites (Nikolskiy et al., 2009). What is the density of such sites in the permafrost on Siberian north? Annually, 20–30 tons of tusks are collected on the yedoma plains (Boeskorov et al., 2008). The density of tusks in the yedoma is 10 ton/km^2, indicating that on average 2–3 km^2 of eroded yedoma is surveyed annually. That means that 120–180 km^2 were eroded and surveyed for the last 60 years. Thus, there are one graveyard and one archaeological site on 40–60 km^2 area. Appear that such sites are not unique; they are located in permafrost on the distance of ~7 km from each other. We guess

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that most likely mammoth herds died falling down from ice cliffs. Later, ice cliffs backed away (several meters per year), and slipped from the cliffs sediments covered the mammoth bones. In the Berelyokh mammoth graveyard are the remains of over 160 mammoths, on Achchaghyi-Allaikha graveyard over 28 mammoths (Nikolskiy et al., 2009). Thus, each graveyard contains in the average tens of mammoth skeletons. That is tens of mammoths per tens of square kilometers. That is number of mammoth skeletons on their cemeteries corresponds their number in population.

We can't provide definitive proof that humans drove the mammoths extinct. However we can show that humans could do it, both physically and mentally. We showed that the density of artefacts in the north does not contradiction that.

Initially *Homo sapiens* appeared in the southern part of the mammoth steppe and for many thousands of years was part of that ecosystem. Animals were so abundant on the MS that a man would not need to look for animals. In the range of site (2 km radius) man, even on the north, could detect hundreds of big herbivores. In the ecosystem humans could survived even without hunting. There was enough marrow left after another predators. But it was difficult to survive in the ecosystem.

Large herbivores were dangerous. In the ecosystem predators saw humans all time. Humans were the slowest species with the most defenseless young. Biologically, humans are least adapted to cold and long winters. Therefore, the survival of humans and possibilities for expansion into the vast woodless plains of the north were not limited by animal density, but by severe climate conditions, the absence of natural shelters, and their level of technology. Every new dwelling type, weapons, clothes, and fire-making techniques all contributed to increased human efficiency and survival, and therefore the expansion of the human climatic envelope. Humans learned how to build shelters, where they could retreat and store food and animal grease for fire, and thus they became the main predator in all ecosystems. At the end of PHT humans had already learned how to hunt all species and how to survive in any environment. The most striking example of this is an early Holocene archeological site on the small island of Johovo, 500 km north of the Arctic coast (76°N, 153°E). Armed with bone tools, these people lived in those extreme conditions, mostly hunting polar bears (Pitulko, 1993), which are three times larger than the cave lion, and ten times larger than the hunters themselves. If humans could regularly (i.e., with little risk) hunt the biggest and most dangerous predators, in the most severe environments, it means they could hunt mammoths everywhere.

Human expansion north in geographical space reflected climatic changes. People were likely absent or rare in the homogeneous northern Siberian plains in the cold epochs before the BWE. During the BWE the climate in northern Siberia and Alaska became similar to the glacial climate of Eastern Europe, and these territories became more suitable for human occupation.

The BWE also sharply changed the landscape. Ice wedges degradation led to numerous badlands. Tens thousands of thermokarst lakes with steep cliffs as on Fig. 7 (Walter et al., 2006) and canyons appeared. These changes would not have affected animals; however they provide huge advantages for hunters. Heterogeneous landscapes provide better opportunities for hunters to closely stalk their prey. The landscape also became better for cliff hunting. Permafrost degradation would have created such cliffs every kilometer, such that chances for successful and safe hunting were substantially increased. In the south for a long time humans were in equilibrium with other animals, but during extensive migration to the north and to America, experienced hunters met numerous animals that were likely unafraid of people and were therefore easier to kill. Human expansion to the northern mammoth steppe occurred under conditions of unlimited resources. In such cases prey are consumed irrationally. Many of killed animals were either not used or consumed only their little part.

The highest density of ^{14}C mammoth dates in the Siberian north is recorded for the BWE (after 12,600 ^{14}C yrs BP) (Fig. 14). But it is interesting to note that all of the dates that were found to the south of 73°N are found either in mammoth cemeteries or in archeological sites (Kuzmin et al., 2001; Sher et al., 2005; Nikolskiy et al., 2009). This data indicates that to the south of 73°N mammoths died because of humans and became extinct during the BWE, while to the north of 73°N (north of western Siberia, Taimyr and northern islands) mammoths persisted (Kuzmin et al., 2001; Sher et al., 2005). Humans have not reached these extremely sever territory. Humans arrived there only after the next sharp climate warming subsequent to the end of the Younger Dryas cold period. After that mammoths on the continent have disappeared.

11. Conclusion

The modern climate of north-eastern Siberia, central Alaska and Yukon Territory are inside the mammoth steppe climatic envelope (Fig. 2), and climate change could not cause extinction of this rich and self organized ecosystem there. Holocene climate warming became fatal for the mammoth ecosystem, because with warming humans penetrated the north. Our estimates are rough, but they indicate that in northern Siberia there were enough people to cause a decline in the herbivore population, thereby decreasing pastures and ecosystem productivity, with the eventual extinction of megafauna.

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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.quascirev.2012.10.005.

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