

## The impact of mammoths on their biome: clash of two paradigms

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Mammoths, woolly rhinoceroses, musk oxen, primitive bisons, and horses of northern races were stenobiotic cryoxerophiles living only under extreme cryoarid conditions according to the 'steppe-tundra crash paradigm'. These animals are considered to be strict grazers on arid steppe-tundra grasses; hence, the possibility that mammoths maintain their pastures the way modern elephants do is rejected. Climatists claim that mammoths and their faunal satellites were killed by the Holocene warming a result of their inability to feed themselves in any of modern landscapes and to withstand the weather-caused losses. Their survival throughout interglacials is considered as resulting from climatic instability: short warm episodes are said to have alternated with very cold ones. It is believed that a permanent Arctic Ocean ice-shield persisted along the Siberian coast even in summer; its cooling and aridifying influence maintained steppe-tundras and similar ecosystems throughout Northern Eurasia. On the contrary, the stable Holocene warming resulted in the disappearance of this ice-shield, in the destruction of the ecosystem of the mammoths, and in megafaunal extinctions. This conception is based mainly on the properties of Eemian Greenland ice layers. However, these layers do not indicate the real Eemian climate. Non-altered Antarctic ice cores and Atlantic deep sea cores show that the Eemian optimum climate was as stable as the Holocene one. The idea of the persistence of the Arctic ice-shield throughout interglacials also contradicts with this evidence. The real reason why woolly mammoth and rhino persisted throughout interglacials (as well as throughout glacial) is in their tolerance to a vast range of climates and their ability to maintain highly productive pasture ecosystems. Contrary to the opinion of climatists, these pachyderms were polyphages that ate various herbaceous and woody plants. They held back forest and tundra vegetation by various direct and indirect influences. Whatever the climate was, pachyderms prevented the appearance of closed forests and they ensured the predominance of grasses and herbs over mosses and shrublets, as well as high mosaicism of the vegetation. The pachyderms trampled on snow and broke the frozen snow crusts, thus facilitating the smaller ungulates to overwinter. Similarly, *Paleoloxodon* and *Dicerorhinus* created vast meadows throughout the temperate forest zone. Giant deer, bisons, horses, etcetera, used these meadows. The ecosystem impact of the climate-resistant pachyderms caused remarkable stability of pasture ecosystems throughout the Pleistocene. In addition, the largest carnivores were important prehistoric stabilising agents, due to their pressure on populations of humans, wolves and herbivores. The Pleistocene crisis in the Palearctic included the same main processes as in other continental realms: (1) liberation of mankind from carnivore control, (2) human-induced removal of pachyderms, (3) drastic environmental changes harmful to megafauna as a result of this removal, (4) secondary extinctions of herbivores as a result of environmental effects of pachyderms, (5) impoverishment of the large predator guild due to the great prey shortage aggravated by the other reasons, (6) other secondary extinctions, (7) installation of a new equilibrium. Due to the long coevolution of Palearctic megafauna with man, the extinction process in Palearctic was long-lasting and less catastrophic when compared to the Nearctic situation.

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## INTRODUCTION

The key point of the Pleistocene extinction debate is (are) the factor(s) that favoured the worldwide thriving of diversified sets of large quadrupeds. If this factor was of a climatic nature, the climatic explanation of mass extinctions without replacement of the terrestrial megafauna would gain credibility. If it was of a biotic nature, the most probable explanation of these extinctions would be the man-caused upset of the Pleistocene ecological equilibrium. Some aspects of this problem as applied to mammoth ecosystems are considered below. The following terms are used:

‘kyBP’ - ‘thousands of years before present’

‘large herbivores’ - herbivores weighing more than 50 kg

‘giants’ or ‘pachyderms’ - those herbivores weighing more than 1000 kg

‘eurybiotic’ (= euryoecious) - species tolerant to a wide range of environmental conditions

‘stenobiotic’ - species tolerant to a narrow range of environmental conditions

‘climatist’ - proponent of climatic models of Pleistocene extinctions

‘biotists’ - proponents of biotic models of Pleistocene extinctions

‘Eem’ and ‘Riss/Würm’ are used as synonyms.

The dominant climatic concept as applied to mammoth ecosystems is the well known ‘steppe-tundra crash paradigm’. It asserts that woolly mammoth and rhinos existed only under steppe-tundra extreme cryoarid conditions and were killed by the outcomes of the Holocene warming. The main non-climatic explanation of the Pleistocene extinctions was the ‘overkill’ paradigm for a long time (Martin 1984). By now it is gradually being replaced by the ‘key herbivores removal’ (Owen-Smith 1987, 1988; Schule 1990; Maslov & Antipina 1994; Zimov *et al.* 1995) and panbiotic (Putshkov 1988, 1989a, 1989b, 1997) models. According to these, only pachyderms were overhunted among the mainland animals. The other species have perished chiefly due to the ecosystem changes caused by cessation of activity of the

giants. As applied to mammoth ecosystems the main cause of the ‘mammoth pastures’ maintenance were the mammoths themselves. In what follows we define the most important divergences of both viewpoints without giving the detailed argumentation. For such argumentation in favour of the ‘steppe-tundra crash paradigm’ see Guthrie (1990a, b) and Sher (1995, 1997a, b); for that in favour of panbiotic explanation see Putshkov (1989a, b; 1997).

## WOOLLY MAMMOTHS AND RHINOS: EURY- OR STENOBIOTIC FORMS?

Climatists consider these animals as stenobiotic cryoxerophiles living only under steppe-tundra extreme cryoarid conditions. It is stated that the giants could not resist the outcome of the Holocene warming, being unable to feed themselves in the established forests, swamps and tundras as well as to withstand the losses caused by deep or/and ice-crusted snow, by the soaking of their wool, etc. Even modern steppes and forest-steppes are an inappropriate environment: the summer temperatures are too high and the vegetation too monotonous for efficient feeding (Vereshchagin 1979, 1988; Sher 1971, 1995; Velichko 1973; Guthrie 1990a, b; Lister & Bahn 1994).

However, a comprehensive analysis of the available data (Putshkov 1989a, 1991, 1997) shows that both giants were highly polyphagous and eurybiotic creatures. Both were well adapted for locomotion over swampy, snowy, ice-covered and other surfaces as well as for the destruction of the frozen snow crusts during the feeding and locomotion. Size and strength were potent advantages during all seasons. Both pachyderms inhabited a wide range of climates (from warm-temperate and mesic to extremely cold and dry) and landscapes (from completely treeless to quite well forested; with and without permafrost; with and without considerable swamps). The giants were invariably accompanied by horses, bisons and lions whereas species indicating now exclusively tundra and northern

taiga (reindeer, arctic fox, lemmings) or dry steppe (saiga, etc.) conditions are present in some but absent in other mammoth sites. There are also many sites where both pachyderms are accompanied mainly by animals of temperate forests and forest-steppes.

### **REGIONAL PARADOX OR WORLD-WIDE GIANTS PASTURES?**

It is impossible to put the variety of mammoth environments to the Procrustean bed of the 'crioxerotic treeless steppe-tundra' sensu Velichko (1973) or Sher (1971). Refusing to admit this fact openly, climatists did recognize it silently by proposing an excessively broad understanding of 'steppe-tundra'. Now they include into 'steppe-tundra' (Sher 1995, 1997a) or 'mammoth steppe' (Guthrie 1990a, 1990b) even the mesic parklands of scattered northern taiga trees (birch, larch, willow, etc.) with rich herbaceous cover of meadow plants. However, even such interpretation could not be applied to certain well-forested and forest-steppe mammoth ecosystems that indicated warm-temperate and/or mesic climate conditions (see Putshkov 1989a, 1997 for a review).

On the other hand, all mammoth ecosystems indeed possessed qualities very important for the large herbivores (Yurtsev 1976; Sher 1982; Vereshchagin & Baryshnikov 1983; Musil 1985; Verkhovskaya 1988; Guthrie 1990a, b): (1) highly mosaic vegetation cover, (2) the prevalence or, at least, abundance of plants and plant associations precious for large grazers feeding, (3) in case of tree presence, closed forests never appeared: open woodlands, parklands or cryophytic savannas with rich herbaceous cover grew instead, (4) the rich megafaunal set of mammoth ecosystems strikingly resembled such sets of African savannas in spite of certain differences. These features are inconsistent with low productivity and certain other modern taiga and tundra vegetation particularities. Hence the catchword 'steppe-tundra paradox' has appeared (Vereshchagin 1988). However, this paradox is only a particular

case of the more general phenomenon that has already been noted by Darwin and called the 'paradox of prehistoric pastures' (Putshkov 1989a, 1992a). The cited features were inherent not only to mammoth ecosystems, but to other dominant Pleistocene mainland ecosystems too (Schule 1992, May 1993). The main prehistoric plant communities were often similar not to modern zonal formations, but to the places of their contact (ecotones) or to non-climax communities of diverse stages of the plant succession. Due to this there were an increased local biotic diversity, including the unusually (in comparison with most Holocene ecosystems) high large mammals density and diversity. Even more, the ecosystems that were more favourable for large mammals than the Holocene ones had been globally distributed during most of Cenozoic era.

It has been shown that quasi-global pre-Holocene distribution of fertile pasture ecosystems could not be explained by mere climatic reasons; it was a natural and inevitable consequence of the feeding of giant herbivores and of other activity as shown by ecosystem impacts of modern pachyderms (see Putshkov 1989a, 1992a, 1997 for a review).

### **CRYOARID CLIMATE KEY REASON FOR MAMMOTHS' WELLBEING?**

The dominant taiga and tundra vegetation (mosses, lichens, shrublets, spruce) is unfavourable for the large grazers feeding. Plants grow slowly, their nutritive value is low; spruce and many other plants are even toxic (Guthrie 1990a, 1990b). Such vegetation is not merely a climatic product: dominant plants maintain their communities themselves. So, moss and/or fallen conifer needles carpets resist to evaporation thus cooling and excessively moistening the soils. Hence, mosses and shrublets obtain advantages over the meadow grasses even in the scattered larch stands of NE Siberia (Sher 1997a: 25), though lime-rich fallen larch needles improve the soil quality for meadow plants (Shennikov 1964). In the spruce forests the

meadow vegetation could not grow, not only because it needs drier and richer soils but also due to overshadowing and increased soil acidity (Guthrie 1990a, 1990b; Rabotnov 1996). Stands of other full-grown boreal and temperate trees also oppress herbs and grasses to a various extent. Due to all this, spruce forest and -to a lesser extent- other northern plant communities 'exclude' many cold-adapted herbivores from ecosystems. The density and ranges of cervids, bison, bighorn sheep largely depend on the resources of the restricted azonal habitats such as riverside or alpine meadows, willow thickets, glades, post-fire sites, steppe-like vegetation of the southern slopes, etc. For 'strict grazers' such as horses, musk-oxen, woolly mammoths and rhinos there is no place at all (Guthrie 1990a, 1990b). Thus, climatists argue that only climate driven aridization could convert taiga and tundra biomes to fertile mammoth steppes (Sher 1995, 1997a). However, such a statement contradicts other, no less important evidence.

First, climatists often consider the so-called steppoids, the azonal cryoarid steppe-like plant associations of North-Eastern Siberia and Alaska, as relics of the notorious steppe-tundras. However, due to soil infertility, warmth and humidity deficiency, mighty winds and insufficient snow cover in winter the steppoid plants are low, scattered and slow growing. Their productivity, at least under Chukotka conditions, is 'insufficient even for a hare feeding' (Kozhevnikov 1977: 445). It is meso- and hygrophilous meadow vegetation that has the high productivity and nutritive value for herbivores in Arctic and Subarctic (Yurtsev 1976; Kozhevnikov 1977, 1986; Verkhovskaya 1988). Such vegetation and not the xerophilous one has dominated in NE Siberia during global warmings. The role of meso- and hygrophilous plants remained essential even during stadial coolings that caused expansion of steppoids. Therefore the opinion that mesic and hygrophilous plants were the staple fodder of mammoths -and their satellites- in the most of the Euro-

Siberian area seems to be well founded. This view corresponds with the direct data on these animals feeding too (see below). Second, mammoths with satellites became extinct even there where deep snow, wet winters and a continuous moss carpet over swampy soils have never appeared due to the constant domination of the dry and markedly continental climate throughout the Quaternary. Such is the case of Transbaikalian and Mongolian steppes and forest-steppes as well as one of the Central Yakutian scattered larch stands with rich mesic meadow cover over dry soil. Horses and cattle feed here in the wild all year round; in winter they dig for food through thin crumbly snow. Even these ecosystems are less favourable for large grazers than mammoth meadows of Kazantsevo (Eem) and Kargin (Mid-Würm warming) optimum times were (Verkhovskaya 1988). It shows once again that climate driven aridisation was not the key factor of such phenomenon: during these warmings the East Siberian climate was warmer and wetter than it is now (Putshkov 1989b, 1997).

Third, the experimental enriching of northern soils with fertilizers, as well as grazing by horses and cattle, lead to the ousting of mosses, sedges and shrublets by meadow grasses and forbs (Guthrie 1990a: 200-205; Zimov *et al.* 1995). This allows us to think that intensive grazing by mammoths and their satellites could drive taiga and tundra communities to a zonal grassland condition even without any general climate-caused increase in aridity (Putshkov 1989a, b; 1993b; 1997; Zimov *et al.* 1995). Climatists neglect or discard such a possibility. How well justified is their position?

#### **NORTHERN GIANTS, ARID GRASSES AND NORTHERN TREES**

Guthrie (1990b: 50, 51) claims that there could be no valid analogy between the 'unusual ecological effect' of mixed grazers/browsers such as African elephants, and that of 'strict grazers' such as woolly mammoths

and rhinos. The woolly giants 'did not rely on browse for the dry winter season', never '...made significant use of woody plants, especially the birch, alder, spruce, larch and pine that were taking over the northern steppes as mammoths became extinct ...'. As their predominant diet were 'arid grasses' the giants '... could not have held back the mesic forests' either by direct or by indirect effects. Eating exclusively grasses they could only accelerate the demise of their grassland habitats, when climate became favourable for woods or moist tundra. Such statements are largely based on clear-cut grazing adaptations of mammoths and their satellites, such as hypsodont teeth with a complicate masticatory surface, the bifid tip of the mammoth trunk allowing to pluck even very low plants, cranial and upper lip morphology of woolly rhino, wide muzzles of horses, musk-oxen and bison. The other proof is the predomination of grasses and sedges in the digestive tract of frozen carcasses of the mentioned animals (Formozov 1990; Guthrie 1990a, 1990b). However, these assertions are rather misleading and biased.

First, observations on the modern ungulates and the isotopic evidence from dental substances of extinct herbivores have demonstrated that no grazing specialisation makes the browsing impossible. Hypsodont teeth do enable ungulates to feed efficiently on grasses but they by no means prevent the use of the less abrasive food - bark, young branches and leaves (Schule 1990, 1992; Haynes 1991; Putshkov 1997). The hypsodont northern grazers such as bison, wild sheep and goats, chamois and ghorals switch in winter to browsing (Formozov 1990; Heptner et al. 1961). Both modern elephants and many tropical herbivores also have a mixed diet or a diet switching seasonally from grazing to browsing (Kingdon 1979, 1982; Penny 1987; Owen-Smith 1988). It should be particularly emphasised that specialised grazers destroy tree seedlings and saplings far more efficiently than brachyodont browsers. For this reason they often impeded the reforestation and

'eternalized' grasslands or early successional stages of the forest restitution in various climatic zones (see Putshkov 1989a, 1997 for review).

Thus, the grazing adaptations of mammoths, woolly rhinos, horses, hemionos, bison, yaks, musk-oxen, bighorn sheep, saiga and reindeer could not be considered as signs of their harmlessness to woody vegetation. In line with this are direct data on mammoths and their satellites' food. Contrary to Guthrie's claim, grasses and sedges from frozen Siberian mammoths, horse and bison carcasses are meso- and hygrophilous and not 'arid' ones (Ukrainseva 1985, 1993). Next to these, bracken, mosses and forbs were usual and, at times, important food ingredients. These data correlate well with the fact that it is meso- and hygrophilous meadow vegetation and not a xerophilous one that has and had a high productivity and nutritive value for herbivores in the Arctic and Subarctic (see above). The xerophilous steppe vegetation should be the staple of mammoths and their satellites' diet only in more southern regions (Putshkov 1997).

Woody plants are also invariably present in the frozen mammoths' carcasses: the macrorests of currant, chosonia, willow, larch, tree birch and alder were found (Ukrainseva 1985, 1993). Hence, Guthrie's statement that mammoths did not eat the three latter species is incorrect. The feeding on pine, spruce and poplar is not proven though not excluded (*ibid.*). Though the browsing fraction is low as opposed to the grazing fraction it should be stressed that we do not know the winter food of mammoths, when browsing could play a far more important role: carcasses from permafrost belong to animals, that perished during warm seasons (*ibid.*). Opinion that mammoths always ate the non-graminoid plants only in small quantities for the sake of the metabolism correction (Guthrie 1990a, 1990b) contradicts to the isotopic evidence in the hydroxyapatite from tusks of Great Lakes mammoths that inhabited the spruce-dominated woodlands. These

data show 'a much greater proportion of browse in their diet than had previously been thought' (Haynes 1991: 88). In line with this is the pattern of the variability of Old World woolly mammoths' dentition. The so-called boreal mammoths had teeth adapted to forage with greater amount of forbs and woody plants, the periglacial ones possessed teeth more specialised to coarser grasses. The former (boreal) type always occupied most of Europe; during warming it replaced the periglacial type more or less completely in European Russia, and in Siberia too, as the role of arboreal vegetation in ecosystems increased (Foronova & Zudin 1986). A similar phenomenon has been observed in the woolly rhinos skull structure that changed from 'strictly grazing' to 'grazing/browsing' type in regions and/or epochs with more or less well developed woody vegetation (N.E. Garutt, pers. comm. 1995). It means that strictly grazing white rhino is not so good model of woolly rhino adaptability.

Even if woolly mammoths and rhinos indeed recurred to feeding on large trees relatively rarely, one must remember that pachyderms destroy young and full-grown trees not only by feeding but also as a result of other aspects of their behaviour. Mammoths, much as the modern elephants (Kingdon 1979; Owen-Smith 1988), would destroy many trees during their sexual behaviour, simply out of pleasure, to clear paths, for the sake of communication, etc. (*ibid.*, Putshkov 1989a, 1997). Rhinos, wisents and stags also break young trees simply for the sake of physical exercise (*ibid.*).

It is plausible that spruce has hardly been eaten by extinct large herbivores as it is unwillingly eaten by the living ones (Heptner *et al.* 1961; Walter 1982). But, on the other hand, the mammoth fauna did coexist for hundreds of thousands of years with spruce and pine woods, though not so closed as Holocene forests (Vangengeim 1977; Musil 1985; Stuart 1991). Most likely mammoths prevented the appearance of closed spruce forest without heavy browsing on spruces. In

the course of succession, birch or aspen woods with juvenile spruce or pine in the undergrowth precede the climax stages of mature spruce or cedar pine forest. The rapidly growing birches or aspens protect young conifers from excessive sunlight and belated frosts (Rabotnov 1996). Such protection is necessary for young conifers during many years: spruce and cedar pine needles that resist to winter frosts of - 40°C or more, are damaged by night frosts of - 7°C in warm seasons (Walter 1982). The repeated damage of the broadleaved protective cover by mammoths and their satellites should inevitably lead to the destruction of many spruce and pine seedlings and saplings (Putshkov 1997). However, even dense birch or aspen grove stage often could not be attained due to mammoth' -with satellites- pasture activities. The repeated action of hooves of various sizes and forms destroyed the moss cover and prevented its reappearance. It caused the deep soil thawing and drying in summer. Eating up enormous quantity of plant biomass, animals abundantly fertilized the soil with the dung and urine; dung beetles reinforced the fertilizing effect. Under such conditions grasses and herbs, rapidly growing on fertile soils and resisting herbivores more efficiently by rapid compensatory growth than by deterrent substances (Guthrie 1990a, b), had an advantage. They ousted slowly growing plants, including spruce seedlings that could realise their odds (protection with toxic compounds) only on poor, unfertilised soils. Due to all this steppe-like plant communities established under drier conditions, and the meadow-like communities under wetter climatic conditions.

Thus, mammoths prevented the closed forests appearance even in the regions climatically fit for the dark-needled taiga. The fertile meadows maintenance in the present larch taiga zone was by far an easier task for them. The Pleistocene predomination here of birch over larch (Sher 1995, 1997a) was the consequence of intense pasture activity too. Birch is excluded now from vast monodominant larch taiga regions due to the thick con-

tinuous moss carpet presence causing the high position of upper limit of permafrost and water logging of the thawed soil layer. The moss carpet elimination and other large grazers effects (see above) caused the lowering of the permafrost upper limit as well as soil warming, drying and fertilizing effects profitable to grasses, forbs and birches. The latter preceded larches in the succession. Rapid growth gave to birch an additional advantage: birches coped easier than larches with the harm caused by mammoths' cold season browsing.

### **MAMMOTHS AND TUNDRA ZONE VEGETATION**

A catchword 'tundra is taiga lacking trees' (Chernov 1980: 7) means that presence of a thick moss carpet is equally characteristic for both biomes. This carpet's effects in tundra are as baneful for meadow grasses and herbs as they are in taiga. It is noteworthy that in tundras small meadow patches appear not only due to local abiotic conditions, but also when soil receives fertilisers such as garbage and excrements. These patches occur on the monotonous moss-covered flats in places with high lemming density, around Arctic foxes burrows, on tops of hillocks serving as dining places for birds of prey and near the human settlements. Dense, highly productive and rapidly growing grasses and forbs develop there, oppressing mosses and lichens up to the moment when soil loses its fertility (*ibid.*).

In the Pleistocene such meadows inevitably became the dominant vegetation in all areas, climatically fit for present-day typical and shrub tundras, since everywhere soils got enough fertilisers in the form of urine, excrements and large animals carcasses (Putshkov 1989a, 1989b, 1997; Zimov *et al.* 1995). The reappearance of a moss carpet was hindered because grass and forbs cover did not prevent the deep soil thawing during the warm season and has dried up the soil considerably by the high evaporation rates. If a moss carpet nonetheless reappeared, it were soon torn to

pieces by hooves or eaten up in spite of its low digestibility (food masses from some frozen mammoths are rich in mosses; Ukraintseva 1993). Thus, repeated pasture exploitation 'eternalised' the competitive advantages of meadow grasses and forbs over mosses and shrublets. The Pleistocene Arctic and Subarctic meadows were at the same time sustained by the large herbivores herds and nourished them (Putshkov 1989a, 1989b, 1997; Zimov *et al.* 1995). Due to impacts of the herds on soils and vegetation, the invertebrate communities differed from those of modern taiga and tundra. Among insects, the role of species connected with steppe and meadow vegetation remained considerable, even during the warm mesic phases (Kiselev 1980; Sher 1995). Among soil oribatid mites, there were even species now extinct (Krivolutsky & Druk 1982). The impact of large herbivores has favoured the northward expansion of cold resistant trees that obtained possibilities for germination, sprouting and subsequent growth over moss carpet-deprived, well dried, deeply thawed and fertilized soils. Consequently, birch and other trees penetrated during Kazantsevo (Eem), Kargin (Mid-Würm) and Early Holocene warmings far more northwards than now.

### **ZOGENIC VEGETATION MOSAICISM AND STEPPIDS PRODUCTIVITY**

Mammoths were the principal forces that created and perpetuated the zoogenic meadows. Thanks to them horses, bisons, musk oxen, other ungulates had high population densities and could freely migrate through woodland and brushy spaces by meadow or cryophitic 'savanna' corridors (Putshkov 1989b, 1993b, 1997). These herbivores in their turn considerably reinforced and modified the ecosystem impact of pachyderms, increasing the mosaicism of plant communities as do now various herbivores in elephants dominated ecosystems (*ibid.*, Kingdon 1979, 1982). Not only overgrazing, but also undergrazing leads to degradation of meadows in forest and tundra zone regions

(Shennikov 1964, Zimov *et al.* 1995). Seeds of many meadow and steppe plants are distributed by large animals (*ibid.*, Janzen 1984). Ungulates are the best agents for the spreading of seeds of herbs and grasses of disturbed places. Plants, covered with excrements, mostly die, giving place to young plants, rapidly growing from the seeds that have been deposited with the dung and then buried by dung-beetles. Moving over considerable distances, large herbivores 'sowed' the plants far from the places where the seeds were eaten. Thus they locally restore plants disappearing for various reasons. Different herbivores were efficient as feeders on different woody and herbaceous plants, and more or less efficient propagators of their seeds. These phenomena have largely contributed to the maintenance of the locally diverse vegetation, mosaicism and productivity (*ibid.*, Putshkov 1989a).

The opinion that cryoxerotic vegetation was the principal food source for North-East Siberian mammoth does not correspond with the evidence. However, it is probable that the opposite view (that completely negates the alimentary significance of the cryoxerotic vegetation for the North-East Siberian Pleistocene ungulates) is biased too: the Pleistocene Arctic and Subarctic steppoids might be more fertile than Holocene ones due to the activity of mammoths and their satellites (see Putshkov 1997 for the details).

#### **MAMMOTH IMPACT ON SNOW COVER**

Mammoths (etc.) increased not only the mosaicism of the vegetation but the mosaicism of the snow cover as well (Putshkov 1989a, 1997). Partly the latter was a consequence of the former: snow was deeper and 'crumblier' in forests, while snow was more condensed and shallower in open areas. Macromosaic animals caused subsequent variations of this snow cover. Mammoths tusks, rhino horns, and hooves of various ungulates hooves raked and shoveled the snow over large areas during the feeding of

the herds. A patchwork of feeding places connected by wider and narrower paths trampled by animals appeared. This patchwork was renewed after snowfalls and took a new pattern when the foraging places changed.

Feeding and moving mammoths, rhinos, large herds of bison and horses broke the frozen snow crust over large areas. Other herbivores easily grazed over the fields where the snow-crust was smashed by the mammoths. They also browsed upon branches and trees broken by the pachyderms. Animals used mammoth-made paths and roads much in the same manner as nowadays Far Eastern deer, boars and tigers use the roads trodden by timber-carrying lorries (*ibid.*). Thus, they spared forces evading snow crust and deep snow. Thanks to the spared forces a cave lion caught prey in winter as easy as in summer while ungulates efficiently raked the snow in places untouched by mammoths, when the touched areas became unusable as a result of overgrazing or to secondary condensation of snow by winds, sun or animals. In summary: many other large mammals had better chances to overwinter thanks to the mammoths (*ibid.*).

#### **MAMMOTHS AND THE PLEISTOCENE PASTURE ECOSYSTEMS STABILITY**

So, woolly mammoths (or for the earlier times their ancestors) 'eternalised' the highly productive and mosaic pasture ecosystems. The high tolerance mammoths have to environmental changes assured the stability of such ecosystems in spite of frequent climatic oscillations. Coolings and warmings, aridifications and humidifications caused shifts in the composition of plant species. Yet, the eurybiotic giants, together with other large herbivores, always provided advantages for the rapidly growing grasses and forbs over other plants, thus maintaining highly productive pastures (Putshkov 1989a, 1992a, 1997). While the pre-Holocene major climatic warmings favoured closed forests, moss/shrub tundras existed approximately in the same regions as today. The giants prevented such biomes from installing. They maintained

open woodlands or parklands with rich meadow or steppe-like herbaceous vegetation instead of closed forests, and meadows or meadow dominated parklands instead of tundras. During the coolings zoogenic and climatic agents of deforestation often acted in concert, creating steppe-tundras sensu Sher (1982). However, these treeless formations have never covered Northern Eurasia completely, because there were regions wet enough for closed forests to persist in certain parts of Europe and Eastern Asia. Here mammoths and/or straight-tusked elephants constantly maintained open woodlands with meadow patches (Putshkov 1989a). Predators modified effects of herbivores on vegetation and their interactions between each other. The largest carnivores pressure on human and wolf populations was not a less important element of the 'prehistoric equilibrium' than their control over herbivore populations (Putshkov 1988; 1989a,b; 1992a; 1993a,b; 1997). The combined action of various megafaunal species explains the notorious mosaicism and the stability of 'mammoth ecosystems' and other Pleistocene ecosystems much more convincingly (*ibid.*) than an appeal (Guthrie 1990a,b) to climatic causes.

#### **CO-OCCURRENCE OF MAMMOTH, SAIGA AND REINDEER**

Climatists pay particular attention to the co-occurrence of saiga and reindeer in numerous 'mammoth sites'. For them it means that: (1) Pleistocene climate has no modern analogue, for the mentioned ungulates nowhere occur together now; (2) like saiga, woolly mammoth and woolly rhino were did not tolerate woodland, boggy ground, deep snow and frozen snow crust conditions (Formozov 1990; Sher 1971; Velichko 1973; Guthrie 1990b). Such a position neglects many other 'mammoth' and 'woolly rhino sites' where saiga, reindeer or both are absent (Putshkov 1989a, 1991, 1997). Biotists see the answer in the eurybiocity of the pachyderms and in the variability of 'mammoth landscapes' that were created by climate and pachyderm

impacts superposition. In regions with climatically driven thick snow cover and humid soils, mammoth's activities created satisfactory conditions only for herbivores of considerable mild soil and snow cover tolerance. Hence, the interglacial range of saiga and, to a lesser extent, that of musk-ox, dwindled (as compared to glacial range) to a greater extent than did the ranges of mammoths, woolly rhinos, horses and bisons. But in regions of climatically driven thin snow cover, so widespread even now in Eastern Siberia, snow-scraping and frozen snow crust smashing activities of mammoths created satisfactory conditions even for saigas and hemionies (Putshkov 1997).

#### **THE HOLOCENE: A NORMAL OR AN ABNORMAL INTERGLACIAL?**

Climatists claim that the Holocene climate is sharply different from the interglacial climates, though they disagree on the kind of the difference. Ideas that the Holocene climate is less equable, more severe, or more mild than the interglacial climates, as well as the opinion that the Weichselian/Holocene transition occurred faster than did previous climatic shifts have failed to be tested by the evidence (see Putshkov 1989b, 1997 for a review). Instead, an interglacial 'flickering' climate idea has been proposed (Sher 1995, 1997a, 1997b; Lister & Sher 1995). It states that during interglacials short warm episodes alternated with very cold ones. Due to this the continuous Arctic Ocean ice-shield persisted even in summers. Its cooling and drying influence has maintained steppe-tundras in North-East Siberia and similar pasture ecosystems westwards and southwards. Holocene warming, unlike the previous ones, was stable. As a result, it caused the disappearance of the mentioned ice-shield along the Siberian coast and, as a consequence, that of 'mammoth ecosystems'.

The basic arguments of the mentioned idea are the Eemian (125-115 kyBP) Greenland ice-core properties (GRIP project results) that were interpreted as reflecting the surprisingly

fast alternation of short-lived (from 20 to 1700 years) warm and cold phases. The latter are said to be almost as cold as the full glacial cooling. However, it has been conclusively shown that these cores do not reflect the true Eemian climate, as they are being altered by folding and other processes caused by ice flow and bedrock influences (Alley & Bender 1998). The non-distorted Eemian and Holsteinian Interglacial layers of Antarctic ice-cores (Vostok project results) do not show any abrupt climatic flickering either.

Other arguments are changes in Eemian pollen spectra recorded in certain European lacustrine and sea shelf sediments. However, it is not clear to what extent these changes correspond to the real intensity of the climatic oscillations, for they might reflect local succession events caused by the interactions of biotic and abiotic factors. It is beyond question that, due to the presence of rhinos and elephants, the particularities of the interglacial vegetation successions could not be the same as those of Holocene successions. So, the increase of herbaceous plants as revealed by the Eemian sediments of two lakes in the Massif Central in France (Thouveny et al. 1994) might be provoked even by a weak decrease in humidity. Superimposing upon the damage caused by large herbivores, it could markedly oppress trees in favour of grasses and herbs. Such interpretation seems plausible considering the concomittant changes in tree composition: an oak/hazel-dominated community has been replaced by spruce/fir-dominated, and subsequently by pine-dominated ones; oak and spruce, however, did not vanish (Thouveny et al. 1994). These changes by no means confirm the idea of an intra-Eemian 'quasi-stadial' cooling: spruce, pine and oak grow now in the Massif Central mountains. Similarly, the birch domination and spruce presence episode recorded in ancient lake sediments near Bispingen, North-Western Germany (Field et al. 1994) does not necessarily represent the 'Central Siberian' rates of climatic severity; both taxa are not exclusively boreal

ones. It may reflect an intervening successional stage of a mixed mesic forest of cool-temperate type that was fixed by large herbivores pasture activity. Furthermore, there are doubts whether the sedimentation period indeed corresponds to Eemian (Riss-Würm) *sensu stricto*: only the duration of this period (9,7 kyr) is established varvometrically but not the age of this vanished lake (*ibid.*).

The doubts seem even more justified when looking at uninterrupted sediment sequences in deep-sea cores from various parts of the North Atlantic. A number of the independent indices show that during the Eemian *sensu stricto* (125-115 kyBP: sea sediments stage 5e) there were no sharp changes of the mean paleotemperatures of deep-sea and surface water, as well as those of iceberg production rates. The same is true for the Holocene. The Eemian border between polar and boreal waters was constantly placed between Greenland and Iceland, in the very region, where it is placed now (McManus *et al.* 1994; Adkins et al. 1997). On the other hand, within the predominantly warm Early Weichselian time (115-70 kyBP: stages 5d, 5c, 5b and 5a) there was indeed a series of strong cooling when the polar water border approached Ireland, though not to Northern Spain as it did during the Middle and Late Weichselian stadial coolings (*ibid.*).

Sher (1971, 1995, 1997b: 4-6) insists that the Arctic Ocean ice-shield has been destroyed to a lesser degree during interglacials than during the Holocene; notably the direct contact of the mainland and pack-ices remained intact even during summers in the East Siberian Arctic. He interprets the modest interglacial transgression rates in most of the East Siberian Arctic, compared to other Arctic regions, as sufficient proofs of this idea. However, even in East Siberia the traces of these transgressions are found over the present day sea-level. It means that some of the Interglacial transgressions and, therefore, the extent of the Arctic Ocean ice melting were greater than the Holocene ones. Notably, the lowlands of Yamal, Gydan and

Taymyr peninsulas were inundated during the Eemian, whereas their highlands (such as the Rranga mountains) became islands (Gus'kov 1986). Sher's idea also contradicts other important evidence (Putshkov 1991, 1997). Sher (1995: 320) considers the eastwards increase of steppic and/or tundra elements in the Eemian paleofaunas, or the "eastward 'steppisation' of the interglacial environment" as proof of the interglacial steppe-tundra persistence. He reckons all faunas including mammoth, woolly rhino, bison and horse as "mere insignificant variations of the steppe-tundra faunistic complex" (Sher 1997a: 24). Such point of view neglects the vast evidence proving the high eurybiocivity of the mentioned animals (see Putshkov 1989a, 1991, 1997 for a review). The paleofaunas including these species accompanied by steppe and/or forest dwellers could not be considered as steppe-tundra faunas if the predominantly tundra species such as *Lemmus*, *Dicrostonyx*, *Alopex*, *Rangifer* are absent. Apart from the other examples (*ibid.*), we mention the Eemian faunas with *Palaeoloxodon* that inhabited the warm forest-steppe of Eastern Europe (Voronezh, Kuban', Moldavia) (Alekseyeva 1980) and the cool-temperate forest-steppe near Novosibirsk (Vassiliev 1995).

Another fault of this position is the disregard of the abundant evidence proving that Eemian and some earlier interglacial optimum climates were milder than the present Holocene one (Putshkov 1991, 1997; Kolfshoten 1995). It is noteworthy that interglacial 'steppisation' or, to be more precise, 'prairisation' has touched even England, though its Eemian optimum climate surely was milder than the present one (Stuart 1991). The enormous aurochs and bisons, giant deer, steppe rhinos and hippos grazed here over vast meadows bordering with the rich warm-temperate woods nourishing the straight-tusked elephants and fallow-deer (*ibid.*). The same is true for the interglacial optimum faunas of continental Europe where the mentioned large herbivores and, someti-

mes, horses inhabited the rich open woodlands indicating climatic conditions warmer and wetter than the Holocene ones (May 1993; Kolfshoten 1995). The contradiction is eliminated when the inevitable impact of mammoths and/or straight-tusked elephants is considered: proboscideans with accompanying fauna converted forests to woodland/parkland/grassland mosaics under any climatic conditions. Throughout the forest zone on intensively grazed and sufficiently wet places zoogenic meadows originated, while the drier places overgrew with a steppe-like vegetation. The latter became more important towards the east and south where the climate became drier. But in the deep parts of the forest zone the dense forest patches (though not as closed as now due to presence of pachyderms paths) also were alternated with considerable parkland, open bushland and grassland areas of zoogenic origin. Not only ungulates, but even stenotopic animals living now almost exclusively in steppes (*Lagurus*, *Citellus*, *Cricetus*, *Ochotona*, etc.) or in tundras (*Lemmus*, *Dicrostonyx*, etc.) penetrated deeply into the forest zone and maintained there viable populations. Most likely such is the main reason of coexistence of forest, tundra and/or steppic rodents in the interglacial faunas of Europe and Siberia mentioned by Sher (1995; 1997a). In some cases, however, these mixed faunas do not belong to Eemian optimum stages, but to cooler earlier or later ones as, e.g., the Bielorussian faunas rich in lemmings (Motuzko 1989).

The dissimilarities of interglacial 'mammoth biome' vegetation with that of the modern taiga and tundra, and the persistence of pasture ecosystems in Siberia throughout interglacials are also claimed as proofs of the interglacial steppe-tundra persistence (*ibid.*). However, these phenomena find their explanation in the impact of the pachyderms on the ecosystem. The climatic interpretation would gain credibility only if there were reliable and independent megafaunal indices showing sharp differences between interglacial and Holocene climates. But the situation is just the reverse.

Consequently, the climatic paradigm is still stuck upon the question: why were numerous pre-Holocene glacial/interglacial transitions by no means as destructive for large mammals as the Weichselian/Holocene transition is believed to be?

### **PLEISTOCENE MEGAFUNA EXTINCTIONS IN PALEARCTIC**

There are detailed interpretations of these events from climatic (Vereshchagin & Baryshnikov 1985; Guthrie 1990a, 1990b; Sher 1995, 1997a, 1997b), half-and-half (Stuart 1991) and ecological (Putshkov 1989a, 1989b, 1992b, 1993 a, 1993b, 1994) points of view. According to the latter one the crisis in Palearctic included the same processes as in other realms:

(1) Liberation of mankind from being controlled by carnivores, resulting in the increase of human populations and in certain carnivores extinctions.

(2) Removal of giant herbivores by man took place because pachyderms were vulnerable to human predation due to their low reproductive rates.

(3) Drastic environmental changes caused by this removal. Instead of pachyderms sustaining mosaic woodlands, parklands, meadow and other associations, closed forests, moss/shrublet tundras, and new steppe type originated. Due to the lack of pachyderms, vegetation became everywhere less mosaic, fires more frequent and/or intensive. Animals could no longer use 'mammoth paths' through thickets and snow.

(4) Secondary extinctions of herbivores (giant deer, musk-oxen, primeval bisons, two Central Asian antelopes, European asses, 'forest' races of horses and cave bears), depending on environmental effects of the pachyderms took place chiefly due to the mentioned changes added with the following factors: (a) competition with extant herbivores that were preadapted for the pachydermless environment, (b) human hunting and burning activities and their ecological outcomes,

(c) predation from wolves that multiplied with the decline of lions, leopards and hyenas, (d) local catastrophic events, epizootics, degeneration harmful to depressive populations.

(5) Southward retreat of lions, hyenas, leopards and dholes caused by the impoverishment of large prey aggravated by competition with man (lion, hyena and leopard) or with wolf that was previously suppressed by larger predators (dhole).

(6) Other secondary extinctions among mammalian parasites and soil mites depending on the extinct herbivores activity.

(7) New equilibrium installation. The Holocene 'wild' ecosystems differ from the Pleistocene ones first and foremost by the lack of giant herbivores and their ecological influences.

Due to the long co-evolution with man the three first processes in the Old World were long-lasting and gradual. Therefore, considerably more forms than in America could adapt themselves to environmental changes.

### **CONCLUSION**

The key reason of the maintenance of 'mammoth ecosystems' were the mammoths themselves. Being highly eurybiotic, woolly mammoths and rhinos could not be driven to extinction by the Early Holocene climatic changes even if these changes, contrary to the evidence, were unique events throughout the Quaternary. The ecological impact of mammoths prevented the extinctions of other megafaunal species. The climate-driven environmental changes became harmful for smaller megafauna only when the pachyderms were gone or became too rare for buffering the climatic influences. Human activity is the sole factor that could cause woolly mammoths and rhinos to decline.

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