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The Ecology of Quaternary Mammals in the Urals

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Abstract—Special aspects of solving certain key problems in the ecology of Quaternary mammals using materials from the Ural region are considered. Possibilities and limitations accounted for by specific features of the region are analyzed. The nature of "mixed" (mammoth, tundra–steppe, hyperborean) faunas and their diversity are considered in the context of questions related to trends in the dynamics of range boundaries and relative abundance of different mammal species during the Late Pleistocene and Holocene.

Keywords: mammals, Pleistocene, Holocene, paleoecology, natural zonality

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By the 1970s, the Ural school of population ecologists founded by Academician S.S. Shvarts had successfully evolved at the Institute of Plant and Animal Ecology (IPAE) of the Ural Scientific Center of USSR Academy of Sciences. At that time, the Laboratory of Ecological Bases of Variation in Organisms (organized by V.N. Bol'shakov) embarked on a new program dealing with problems in evolution that could be resolved on the basis of Quaternary research. Remarkably, the inaugural issue of the journal *Ekologiya* (*Soviet Journal of Ecology*, vol. 1, no. 1) included the article "On the establishment of biogeocenoses in recent landscape zones of Western Siberia" based on analysis of the first extensive collections of Pleistocene rodents from the Urals (Maleeva, 1970).

This research has been scaled up owing to collaboration with geologists from Tyumen and Yekaterinburg and archaeologists from all over the Ural region. Today, the IPAE's archaeozoological collections of large mammals include an assortment of specimens from about 2000 Pleistocene and Holocene sites in a vast area extending from the Volga region to Primorye and from the Yamal Peninsula to the Aral Sea (more than 800000 depository items). All items in the collections of small mammals are impossible to calculate, but there are hundreds of thousands of fossils from hundreds of sites in the Urals and Western Siberia. Thus, the IPAE has built one of Russia's largest collections of materials related to Quaternary zoology, and their analysis can provide a basis for solving a number of problems. Some of them are considered below.

Specific Features of the Ural Region Relevant to Solution of Problems in Quaternary Paleoecology

The Urals extend for 2000 km from the Arctic coastal tundras in the north to steppes and semideserts in the south. Throughout the length of the mountain range itself, the areas lying east and west of it at distances of approximately 50–100 km, with elevations of about 200 m a.s.l., have karst topography with caves and grottos, and excavations in these landforms have yielded abundant paleozoological material. However, not all of this territory has been explored in detail, and different time sections have also been studied unevenly. Paleontological materials from alluvial sites in the Western Siberian Plain have been used to study the history of the faunas and ecosystems of this territory, which neighbors the Urals (Smirnov et al., 1986; Borodin, 2012; Zinoviev, 2006). Frozen bodies of Pleistocene mammals have been found in the Yamal and Gydan peninsulas. They include the well-known baby woolly mammoth named Lyuba. Studies on its anatomy and morphology, macro- and microremains found in the digestive tract, and analysis of stable carbon and nitrogen isotopes in tissues allowed the first reconstructions of the biology and ecology of the mammoth during the first month of life (Fisher et al., 2012; Kosintsev et al., 2012; Rountrey et al., 2012; van Geel et al., 2011). Studies of the Mongochen mammoth from the Gydan Peninsula made it possible to reconstruct, for the first time, the environment and feeding conditions for mammoths in the north of Western Siberia at the Last Glacial Maximum and obtain data on the life-time dynamics of the aforementioned isotopes in these animals (Mazepa et al., 2010; Kosintsev et al., 2012). Some paleozoological collections have come from excavations in campsites, burial grounds, and sanctuaries of different epochs and cultures, from the Paleolithic to the Middle Ages. The available archaeozoological material provided a basis for monographic generalizations on the historical ecology of ancient populations of regions such as the Yamal Peninsula, forest–tundra and taiga zones of Western Siberia, and the southern Transural region.

A Complex of Issues Concerning the Nature of "Mixed" Faunas

One of central problems in Quaternary paleoecology—the problem of understanding the nature of so-called mixed (mammoth, tundra–steppe, disharmonic, hyperborean) communities—has not yet been solved. The reality of simultaneous presence in such faunas of species that today never occur together has not been questioned since the first dating of fossil rodent remains by high-resolution AMS radiocarbon analysis (Stafford et al., 1999). It each particular case, it is necessary to estimate to what extent bone remains from the same layer differ in age. If large amounts of bone remains from several species are concentrated in the same area, it is expedient to obtain data on the relative age of a large number of specimens, in addition to absolute dating. For this purpose, parameters are determined that indicate the degree of fossilization, such as the accumulation of some rare earth elements and the degree of loss of organic matter from the bone tissue (Smirnov et al., 2009).

The literature presents a whole spectrum of views on the nature of faunas that inhabited tundra–steppe communities and the environment in which they lived (Markova et al., 2008). The version most popular today is based on the concept of so-called mammoth steppes, i.e., highly productive pasture ecosystems capable of providing sufficient food for herds of large and giant herbivores and also for numerous predators and scavengers associated with them. According to reconstructions, mammoth steppes extended as a wide band from western Europe, throughout northern Eurasia and Beringia, to Alaska and then to the east of North America (Guthrie, 1990). Their climate was characterized by severe winters with little snow and sufficiently warm summers, which provided conditions for the growth of rich herbaceous vegetation that remained standing until the next growing season. The presence of large herbivores in these cold steppes was the key factor in the maintenance of the nitrogen cycle and adequate soil aeration. The effect of their extinction was sufficient for switching plant successions in the mammoth steppes from meadow–steppe to moss tundra type, with climatic shifts in the corresponding period being insignificant (Zimov and Chuprynin, 1991).

The Ural region offers ample opportunities for analyzing latitudinal and temporal gradients in the composition of mixed faunas and the structure of Late Pleistocene mammal communities in order to understand their specific features as compared to present-day zonal communities. For such an analysis, we used data on the species composition and numbers of large mammal remains from 49 sites in the Southern Urals and southern Transural region (between 51° and 56° N), the Middle Urals and Transural region (between 56° and 59° N) and the Northern Urals (between 59° and 64° N) (Ulitko, 2003; Bachura and Kosintsev, 2007; Kosintsev, 2007; Kosintsev and Bachura, 2013). We selected sites containing sufficiently large numbers of remains (no less than 300 specimens) dated by the radiocarbon method (more than 200 dates) and accepted the following boundaries of chronological groups: the first half of the Late Pleistocene: marine isotope stages (MIS) 4 and 3, 74–24 kyr BP; the last glacial maximum (LGM): the first half of MIS 2, 24–17 kyr BP; and the last glacial termination (LGT), the second half of MIS 2, 17–10.3 kyr BP.

The geographic distribution of fossil remains from 33 large mammal species was analyzed. All fossils of the Pleistocene ass were found south of 54° N; fossils of camel and argali, south of 55° N; of the corsac fox, cave hyena, otter, and giant deer, south of 58° N; of the beaver, small cave bear, badger, and lynx, south of 60° N; of the marmot and red deer, south of 61° N; and of the muskox, north of 56° N. The remaining 19 species were distributed throughout the Ural region.

The camel and ass are species characteristic of deserts and desert steppes, whereas the argali is a mountain steppe species, but the estimated northern boundaries of their ranges almost coincided at 54°–55° N. This fact suggests that the northern boundary of the desert–steppe faunistic assemblage (the southern variant of the hyperborean assemblage in the mammoth fauna) shifted to the above latitude in some periods of the Late Pleistocene. Another major zoogeographic landmark is at 58°–60° N: the northern distribution boundaries of the beaver, corsac fox, small cave bear, badger, otter, hyena, lynx, and giant deer passed at these latitudes. The above species markedly differ in ecological characteristics: the lynx is closely connected with woody vegetation; the badger and giant deer, with temperate natural complexes; the corsac fox and small cave bear, with steppe and desert–steppe complexes; and the hyena belongs to a "typical" mammoth complex. In the aggregate, these species mark the northern distribution boundary of both the "typical" variant of hyperborean assemblage and the "interstadial" variants of the mammoth fauna (characteristic of relatively warm periods). The northernmost finds of marmot and red deer also mark the northern boundary of the typical hyperborean assemblage. Thus, analysis of the geographic distribution of fossils from individual species has made it possible to determine the limits of expansion for zonal variants of the hyperborean assemblage of mammoth fauna.

Zonality in the Late Pleistocene manifested itself not only in the species composition of animal communities but also in their structure. The latter aspect was analyzed by assessing changes in the ratio between the fossil remains of individual species in size–trophic groups such as mountain hare–bobak marmot and Arctic fox–red fox–corsac fox and in the group of ungulates: the horse, Pleistocene ass, woolly rhinoceros, red deer, giant deer, moose, reindeer, steppe bison, saiga, muskox, and argali.

Analysis of this ratio in the mountain hare–bobak marmot and Arctic fox–red fox–corsac fox groups in all periods of the Late Pleistocene showed that the proportions of marmot fossils in the first group and of red fox and corsac fox fossils in the second group decreased consistently in the south–north direction, especially upon transition between the Southern and Middle Urals. In the Southern Urals, the ratio of red fox + corsac fox to Arctic fox fossils was close to 1 : 1, and the proportion of marmot fossils was greater than or similar to that of hare fossils. In the Middle Urals, fossils of mountain hare and red fox were dominant (72–92 and 83–95%, respectively). Collections from the Northern Urals contained no fossils of the corsac fox, and all fossils of the bobak marmot dated from no later than the first half of the Late Pleistocene.

In the ungulate fauna, the proportion of reindeer fossils in all periods proved to increase in the south–north direction, while the proportions of all other species decreased. As in the previous case, the most significant changes in the structure of the fauna were revealed between the Southern and Middle Urals. Thus, the proportion of reindeer fossils increased across this boundary from 11 to 57% in the first half of the Late Pleistocene and from 27 to 56% during the LGT, while that of steppe bison fossils decreased from 12 to 8% and from 22 to 4%, respectively. The proportions of most other species also changed significantly between these regions.

Geographic changes in the composition and structure of the fauna indicate that the boundary passing at 55°–57° N was of special significance in its dynamics. North of this boundary, the fossils of marmot, beaver, corsac fox, cave hyena, red deer, giant deer, and moose occur sporadically or with a very low frequency; those of argali and camel have not been found; and the fossils of muskox do not occur south of it. Therefore, it may be concluded that the above latitudes mark the zonal boundary for the fauna of large and medium-sized mammals.

The temporal dynamics of the composition and structure of small mammal fauna were analyzed using the material from a relatively compact region on the western slope of the Middle Urals (56°–58° E): 80 km from north to south and 100 km from east to west. This material consisted of 74548 teeth of small mammals from multilayer deposits in 14 karst cave sites. Data on 38 radiocarbon-dated layers and horizons were included in analysis. It is for this region that the seasonal course of temperatures during the LGM–Late Glacial transition was reconstructed by analyzing stable oxygen isotopes in the tooth enamel of a fossil bison (Velivetskaya et al., 2011). Atmospheric air temperatures were estimated to vary from –25°C in winter to 10°C in summer. The reconstructed paleotemperatures correspond to the present-day climate of the southern Yamal Peninsula but are 9°C lower in winter and 7°C lower in summer than temperatures currently recorded in the Middle Urals. This contributes to knowledge about regional climatic characteristics based on paleotheriological data, which provide strong evidence not only for low temperatures but also for moisture deficit. This follows from the composition of the fauna and from the structure of the mammal community from the layer with bison fossils.

The composition of small mammal fauna in the Middle Urals has changed significantly since the Late Pleistocene to present times. A total of 20 species have been recorded in the region, and only 3–4 species have inhabited the region throughout this period. Changes of dominants took place five times (Fig. 1). Prior to the LGM, the root vole was dominant, with a significant proportion of narrow-headed voles, and the abundance of Siberian lemmings relative to Arctic lemmings was fairly high. The narrow-headed vole became absolutely dominant at the LGM (with the Arctic lemming being a codominant) but decreased in abundance by the Early Holocene, when forest voles (*Clethrionomys* spp.) and the field vole gained dominance and retained it throughout the Holocene (alternately with the water vole). Gray voles *Microtus* spp.) became dominant only in historical times, which is usually attributed to the development of agriculture. The Pleistocene–Holocene transition in the regional fauna was not accompanied by mass extinction of any group of species. It appears that only the Siberian lemming and jerboa, rare species in the local fauna, retreated from the region at that time (the former to the north and the latter to the south). The Arctic lemming and a group of steppe species lived there until the Middle Holocene, and the narrow-headed vole, almost up to historical times.

The dynamics of small mammal fauna in the Northern Urals were similar (Smirnov, 1996; Teterina, 2009), except that the Siberian lemming that dominated prior to the LGM was replaced by the Arctic lemming at the LGM, and the latter, in turn, was replaced by the narrow-headed vole in the Late Glacial. Beginning from the Early Holocene, species of the taiga assemblage gained dominance, while steppe species gradually disappeared from the regional fauna, but the sequence and chronology of this process need more detailed analysis. Steppe and yellow lemmings, gray dwarf hamster, and steppe pika remained there for some time during the Holocene, but only as rare species against the background of prevailing taiga and meadow forms. The species list of small mammal fauna of the Northern Urals during the Late Valdayan to the Late Holocene includes a total of 18 species, but only two or three of them (forest and meadow species) remained in the region throughout this period, while others periodically moved to the north (upon warming) or to the south (upon cooling).

Farther north, in the Ural Subarctic region (67° N), rodent communities at the LGM consisted of only two species, Arctic and Siberian lemmings, with the

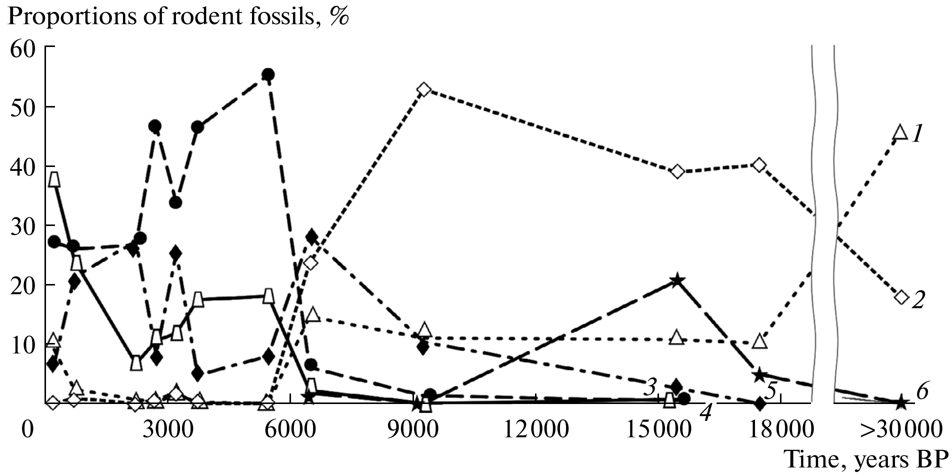

Fig. 1. Temporal dynamics of the proportions (%) of fossil remains of highly abundant rodent species in taphocenoses of the Middle Urals: (*1*) *M. oeconomus*, (*2*) *M. gregalis*, (*3*) *M. arvalis*, (*4*) *A. terrestris*, (*5*) *Clethrionomys* sp., (*6*) *Dicrostonyx* sp.

The curves are plotted on the basis of data from the following sites: Filin (recent); Smotrovoi (layer 1, 2, horizon 1, 2—recent; layer 2, 3, hor. 4–6—40 ± 90 IEMEZh-1406, 440 ± 70 IEMEZh-1405, 455 ± 30 IEMEZh-1404; layer 3, hor. 7—700 ± 90 IEMEZh-1403); Starik (hor. 1, 3—recent; Sadykova, 2006); Bazhukovo III (layer 1—recent); Sukhorechenskii (hor. 1—recent, hor. 2—248 ± 158 IERIZh-107, hor. 3—612 ± 135 IERIZh-108, hor. 4—791 ± 136 IERIZh-109, hor. 5—921 ± 204 IERIZh-110, hor. 7—2047 ± 132 IERIZh-112, hor. 8—2050 ± 115 IERIZh-113, hor. 9—3210 ± 121 IERIZh-114, hor. 10—3120 ± 163 IERIZh-115, hor. 11—2863 ± 143 IERIZh-116, hor. 12—3208 ± 171 IERIZh-117); Krasnosokol'e 2 (recent); Ust'-Log 5 (surface, hor. 1, 2—recent; hor. 7—1824 ± 100 SPb-921, hor. 15—3980 ± 100 SPb-922, 3958 ± 100 SPb-916); Nizhneirginskii (hor. 2—795 ± 30 SPb-971; hor. 3—2579 ± 70 SPb-913, 2650 ± 70 SPb-915; hor. 5—2945 ± 80 SPb-809; hor. 6—3350 ± 100 SPb-806, 3120 ± 80 SPb-808; hor. 7—3770 ± 100 SPb-914); Ust'-Log 1 (surface, hor. 1—2664 ± 100 SPb-920; hor. 12—5730 ± 70 SPb-807); Svetlyi (layer 4, hor. 8—6300 ± 120 SPb-812; layer 5, hor. 13–19—16400 ± 165 IEMEZh-1414); Dyrovatyi Kamen' on the Serga River (layer 2, hor. 8—6462 ± 46 IEMEZh-1365; layer 3, hor. 11— 9327 ± 158 IEMEZh-1072; layer 4, middle part, hor. 24—14810 ± 130); Bobylek (layer 2a, upper part—14300 ± 200 GIN-14742; layer 2a, lower part—17565 ± 200 SPb 640; layer 4—over 33000); Arakaevo 8 (hor. 12— 15739 ± 590 IEMEZh-230).

former being absolutely dominant (Golovachov and Smirnov, 2009). The narrow-headed vole joined them in the Late Glacial, and a series of species characteristic of forest and wetland habitats appeared in the Early Holocene and gained dominance. They retained this status until the Late Holocene, when zonal tundra species (Arctic and Siberian lemmings, Middendorff's vole, and the northern subspecies of the narrow-headed vole) became prevalent in rodent communities of the region. Against this background, trends in climatic changes over the past few decades have accounted for shifts in the structure of rodent communities in favor of *Microtus* and *Clethrionomys* voles.

Thus, the composition of rodent fauna in the Ural Subarctic region (10 species) has been changing significantly over the period since the LGM to present times, with only two or three species permanently inhabiting this region. Replacements of dominant species in rodent communities took place during two periods: at the Pleistocene–Holocene boundary (a sharp change in the community structure) and at the beginning of the Late Holocene.

In the southern Transural region (at about 53° N), characteristic features of rodent fauna and community structure were as follows (Kuzmina, 2009). The composition of the fauna remained almost unchanged over the whole period considered here (excluding historical times), and the replacement of dominant species occurred only once. The steppe lemming strongly dominated at the LGM, with the yellow lemming being a codominant (Fig. 2). A noteworthy fact is that the northern mole vole was absent or extremely scarce in that period but became fairly abundant by the Late Glacial, against the background of decrease in the abundance of lemmings and increase in the abundance of narrow-headed vole and, for a relatively short time, of root vole. The narrow-headed vole then remained dominant throughout the Holocene, with steppe lemming and (notably) yellow lemming also remaining in the communities. The yellow lemming disappeared from the region approximately 2000 years ago but occurred until historical times in areas lying farther south, and the steppe lemming was replaced by the common vole only in the past century. For unknown causes, the range of the yellow lemming underwent further reduction in historical times, and this species in the former USSR territory has survived only in the Zaisan Depression.

The small mammal fauna and community structure on the western slope of the Southern Urals are characterized by higher dynamism than in the southern Transural region (Smirnov et al., 1990). This slope is now covered by mixed and broadleaf forests with the corresponding fauna of rodents. In the Late Valdayan

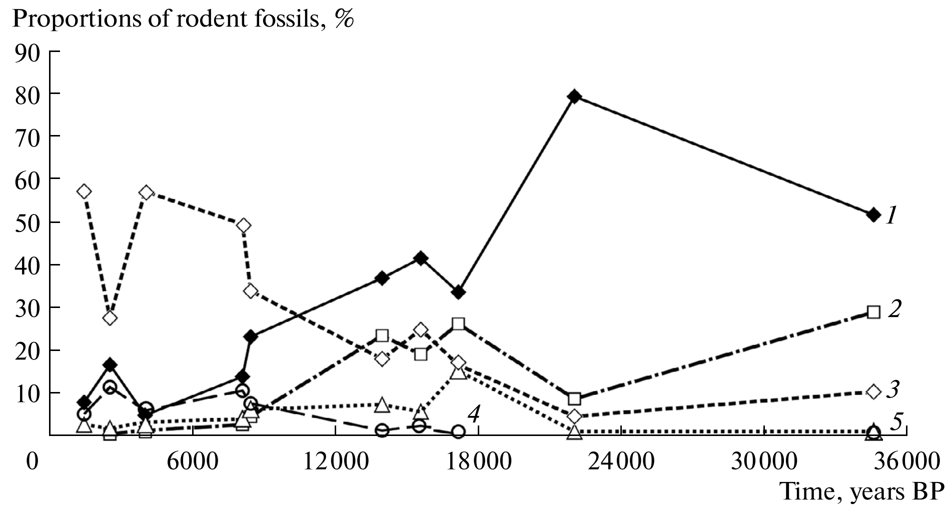

Fig. 2. Temporal dynamics of the proportions (%) of fossil remains of highly abundant rodent species in taphocenoses of the Southern Transural Region (according to Kuzmina (2009), with amendments): (*1*) *Lagurus lagurus*, (*2*) *Eolagurus luteus*, (*3*) *M. gregalis*, (*4*) *Ellobius talpinus*, (*5*) *M. oeconomus*.

and until recent times, the small mammal fauna consisted of 22 species, and approximately half of them permanently inhabited the region. Species closely associated with woody vegetation (squirrel, chipmunk, garden dormouse, yellow-necked mouse) disappeared from it during the Late Glacial or, possibly, LGM; lemmings disappeared in the Early Holocene; and the ranges of steppe species retreated in the Late Holocene.

The closest analogy to mammal communities of the typical mammoth steppe is found in the communities of the Southern Urals, which comprised a number of abundant large ungulate species, predators, a scavenger (the cave hyena), and a minimum number of species associated with cold climate. The effect of cold climate in the southern Transural region was manifested to even lesser extent, while the effect of climate aridity was stronger there. This region differs from others in the conserved species composition of small mammal fauna and relatively weak dynamics of its structure. North of 57° N and to about 63° N, i.e., in the north of the Middle Urals and in the Northern Urals, the mammal faunas retained the steppe component, but it was obviously inferior to the "cold" component. Assemblages of the Middle and Northern Urals markedly differed from those of typical mammoth steppes, since arctic elements prevailed in them. Such impoverished communities could not be highly productive. It was proposed to name them hyperborean communities (Smirnov, 2001). Although mammoths lived near the Arctic Circle and farther north at the LGM, there are no ground to attribute communities that existed in those regions to tundra–steppes. More likely, these were specific arctic ecosystems differing from present-day tundras in having a less humid climate.

Each latitudinal region was characterized by specific temporal dynamics of mammal fauna composition and community structure. Especially sharp and profound transformations in mammal communities occurred in the Polar Urals at the Pleistocene–Holocene boundary. Transformations of hyperborean communities into taiga communities in the Northern Urals and into forest–steppe and forest communities in the Middle Urals were more gradual but also profound and affected many species.

Species extinction is one of basic mechanisms responsible for changes in faunas and ecosystems. Recently, considerable progress in studies on this problem has been made due to implementation of paleo-DNA analysis and large-scale use of radiocarbon dating (for review, see Lorenzen et al., 2011). For example, paleo-DNA analysis has shown that the Don-hare, previously regarded as a "good" paleontological species that became extinct in the Early Holocene, is actually not a true species but an ecomorph of the mountain hare (Prost et al., 2010). Analysis of the series of radiocarbon dates on bone has made it possible to reconstruct the sequence of species extinction in the Ural region. It has been found that the large and small cave bears died out 30000–25000 years ago, and the cave hyena disappeared from the region during the same period. Later, 13000–12000 years ago, the mammoth and woolly rhinoceros died out, and the Eurasian cave lion and muskox disappeared (Bachura and Kosintsev, 2007; Kosintsev and Bachura, 2013). The giant deer, the last representative of the mammoth fauna, became extinct about 7000 years ago (Stuart et al., 2004). These results provide evidence that there was a refugium in the Urals where species of the mammoth fauna could survive for the longest possible period of time.

CONCLUSIONS

Studies on the Late Pleistocene mixed mammal faunas using the material from the Ural region have provided a deeper insight into their nature. Trends in the distribution of mammal fauna composition and community structure in the main periods of the Late Pleistocene have been described along a north–south transect extending for about 2000 km. The results show that latitudinal zonality in the Urals was well manifested in the Late Pleistocene. There were least three zonal assemblages (arctic, hyperborean, and desert–steppe), and three distinct latitudinal variants (northern, typical, and southern) could be distinguished within the hyperborean assemblage. These variants differ from each other in the ratio of indicator species and their proportion in the structure of the fauna. The Late Pleistocene communities of the Southern Urals are the closest analog of typical mammoth steppes.

It has been found that the scale and magnitude of the temporal dynamics of mammal fauna composition and community structure in the Late Pleistocene and Holocene differed considerable between latitudinal segments of the Urals. Factors responsible for selective extinction of certain species and its sequence and chronology require further analysis, but it is already clear that this process had certain region-specific features. It is necessary to realize the importance and prospects of studies on critical "bottleneck" periods and the ways of survive them that have helped existing species to avoid extinction. Progress in the subject matter discussed above largely depends on the solution of the problem concerning the ratio of ecogeographic and ecochronological regularities of variation in morphological characters of mammals.

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