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Steppe species in the Late Pleistocene and Holocene small mammal community of the Urals

N.G. Smirnov*, E.P. Izvarin, E.A. Kuzmina, Y.E. Kropacheva

Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Russian Federation

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ABSTRACT

Finds of steppe mammal fossils in Pleistocene-dated deposits in regions situated hundreds/thousands kilometers apart from their modern distributions are considered as markers of certain events in climate and landscape dynamics in North Eurasia during the late Pleistocene. Fossil data were used to examine peculiarities of area shifting in several species of the steppe mammal communities in response to the climate and landscape dynamics of the late Pleistocene and Holocene intervals. The main attention was paid to the data from the Ural region. The main idea of this study was to reveal regularities of distribution concerning some species of small mammals representing steppe biota found in Late Pleistocene and Holocene sediments in the Urals. The research concentrated mainly on the northern border position limiting these species' ranges during different time intervals.

1. Introduction

Late Pleistocene distribution patterns of small mammal steppe species were shown to differ significantly from today (Markova et al., 2008). Northern and western limits of the areas occupied by the narrow-skulled vole (*Microtus gregalis* Pallas, 1779), steppe lemming (*Lagurus lagurus* Pallas, 1773), and steppe pika (*Ochotona pusilla* Pallas, 1769) during the late-Pleistocene are over a thousand kilometers away from their modern positions. Two moments seem to be of special interest in this regard. First of all, invasions of the steppe animals indicate events in the climate and landscape history. On the other hand, invasion of one or another species into some new environments undoubtedly indicates the species adaptive abilities and changes of ecological niches.

The Ural region is of special interest concerning these problems. On both eastern and western slopes of the Ural Mountains, throughout all latitudes from the Arctic seas to the Kazakhstan semi-deserts (over 2000 km in total), numerous karst cavities were found and examined including abundant fossils of Quaternary age. Even during the LGM time practically the whole territory (except the highest peaks) was not covered with ice, whereas in other regions of Europe glaciers made barriers preventing northward spreading of terrestrial mammals.

This article is based on the studies and further generalization of results provided by excavations of several dozens of sites with numerical ages. Modern patterns of the steppe species areas in the Urals have been analyzed, in order to compare them with the pictures registered for the Pleistocene and Holocene intervals. This comparison allows to judge the nature of the factors limiting northward expansion of certain animal species and species groups both nowadays and during the Pleistocene. The main object of this study was to reveal regularities of spread of some species of small mammals representing steppe biota found in Late Pleistocene and Holocene sediments in the Urals. The research concentrated mainly on the northern borderline position limiting these species' ranges during different time intervals.

2. Materials and methods

2.1. Material

Solution of the problem under study can be provided at one or another level of accuracy. The latter was shown to depend upon several factors, i.e. the amount of examined bone fossils, number of sites which provided the collections for examination, and the selected way of joining of data into series of spatial and temporal groups.

* Corresponding author.
E-mail address: march272@yandex.ru (N.G. Smirnov).

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The whole pool of available data on small mammal faunas suitable to be analyzed included 93 sites which provided information on about 288,000 rodent and pika molars (Table 1, Fig. 1). The major part of the sites including small mammal remains were bone accumulations in karst cavities collected due to feeding activities of birds. It is known that animals of open habitats usually prevail among the preyed species whereas forest-dwellers are marked in lower numbers (Gromov, 1957; Andrews, 1990). We considered such feeding selectivity to be useful for the study of the steppe species distribution patterns. The data obtained from nine regions were arranged into 5 latitudinal groups; four consist each of two distinct parts attached either to western or eastern slope of the Ural Mountains (Fig. 1).

Urals. The narrow-skulled vole showed super-dominance in middle-latitude areas. The steppe lemming occupied a similar position in the south. In order to determine full taxa lists in such faunas, including both rare and extremely rare species, one should examine the collections numbering no less than 1000 teeth.

Holocene-dated faunas usually do not reveal significant dominance of one species. These faunas (especially of the forest and forest-steppe types) usually demonstrate relatively equal proportions of species. In these cases, full taxa lists including rare and extremely rare species might be possible for collections numbering several hundreds of teeth.

These data make it possible to propose that the distinguished spatial/temporal groups of sites might be estimated related to the relative probability of revealing the most complete fauna taxa lists. Thus, this probability level seems highest in regard to collections numbering dozens of thousands of teeth. Intermediate probability level might be proposed for teeth numbers of a few thousand. We can expect the lowest probability values if a collection is not more than a thousand teeth.

Table 1
Number of sites (highest value) and amount of fossils (lowest value, thousands of teeth); spatial groups are shown on Fig. 1.

Time span		Spatial groups									Total
		I	II	III	IV	V	VI	VII	VIII	IX	
Late Pleistocene	LGM[a]	2 >1.2	1 1.5	1 7.2	–	–	3 0.9	2 4.3	–	1 1.7	10 16.8
	LGT	1 >0.5	3 >1.1	4 71.4	–	4 7.5	1 16.3	4 7.0	1 0.5	1 1.4	19 105.7
Holocene	Early (PB–BO)	1 >0.3	2 >4.0	3 12.0	1 6.5	4 26.8	1 1.4	2 3.4	–	3 8.4	17 62.8
	Middle (AT–SB-1)	–	3 >2.2	3 1.4	–	5 6.1	1 6.6	2 0.4	1 0.8	–	15 17.5
	Late (SB-2–SA)	6 3.4	3 >2.8	3 >3.1	–	9 53.5	2 3.2	5 7.1	–	4 12.1	32 85.2
Total		10 >5.4	12 >11.6	14 >95.1	1 6.5	22 93.9	8 28.4	15 22.2	2 1.3	9 23.6	93 288.0

[a] LGM – Last Glacial Maximum, LGT – Late-Glacial Time, PB – Preboreal, BO – Boreal, AT – Atlantic, SB – Subboreal, SA – Subatlantic.

The data were also arranged according to certain chronological intervals, from the stage of the last glacial maximum to late Holocene. The following intervals were distinguished: last glacial maximum (LGM), late glacial time (LGT), early Holocene time (Preboreal and Boreal time), mid-Holocene (Atlantic time and the first stage of Subboreal), late Holocene (different stages of Subboreal time and Subatlantic). Subdivision of the Holocene was according to both Blytt–Sernander system (Khotinsky, 1977; Arslanov et al., 1999) and the official scheme of the International Commission on Stratigraphy (Walker et al., 2012).

These spatial and temporal groups differ significantly in both numbers of sites included and total amounts of examined fossils. According to both parameters, the most abundant data were obtained from the southern part of the Middle Urals western slope (Table 1). Distinct chronological intervals were represented by significantly different numbers of fossils. Faunas of LGM period have not been found. Abundant collections corresponded to the early Holocene (26,795 teeth from 4 localities) and especially the late Holocene interval (53,465 teeth from 9 localities). Minimal amount of fossils represent the South Urals eastern slope, where a single site had been found (Ustinovo shelter) containing small mammal remains dated to terminal mid-Holocene and LGT. However, the collection was not large enough in order to characterize fauna contents and structures of both time spans.

It is known that the probability to reveal fossils of numerous, usual, rare and extremely rare species depends upon the total amount of bones under study and upon species' former proportions. It was shown that LGM and LGT faunas demonstrated significant disproportions in numbers of different species fossil remains (Smirnov and Markova, 1996). Frequency levels of super-dominating species bones in those make up to 70–90%. The hoofed lemming was the dominant species in northern regions of the

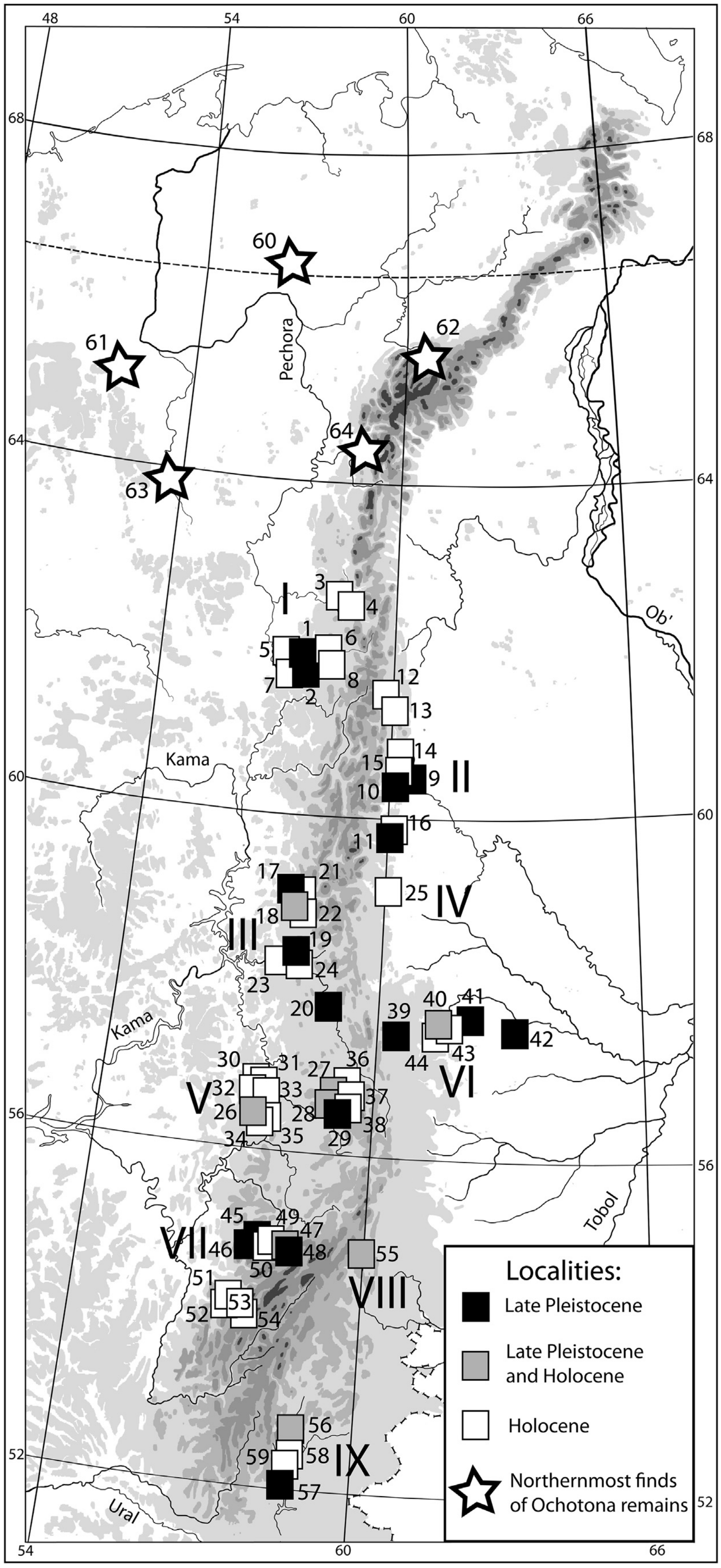
2.2. Criteria of site selection

Sites including small mammal remains were selected for the analysis according to the following criteria:

The described fauna taxa list must include at least one zonal steppe species of small mammals specific to the steppe biota complex. The list of these species is presented in the modern distribution of small mammal steppe species in the Urals. The narrow-skulled vole is considered as a polyzonal species. Thus, the presence of this species remains in the site taxa list, with no other steppe species registered, provided no reason to include the site into the analyzed pool.

The site should be supplied with reliable geological dating. In this study, radiocarbon dates were considered as satisfactory (non-calibrated values). In rare cases, with no radiocarbon dates available, age estimations were based upon archaeological finds. Late-Holocene age of some sites also could be estimated according to the presence of synanthropic species.

The locality should reveal no signs of mixed differently-aged bones. In some cases, when such mixing could be proposed, bones were examined to compare some special physical and chemical characters (Smirnov et al., 2009) indicating their relative ages. The site was excluded from the analysis if radiocarbon dates appeared contradictory to the bones' positions in the section (as the Grotto Oleniy).


Pechora
Kama
Kama
Ob'
Tobol
Ural
I
II
III
IV
V
VI
VII
VIII
IX
Localities:
Late Pleistocene
Late Pleistocene and Holocene
Holocene
Northernmost finds of Ochotona remains

Several sites with neither registered fossils of steppe species also have been analyzed. That was done because their fauna lists revealed bones of animals representing genus *Ochotona*, which cannot be accurately identified to the species rank. Thus, we cannot be sure that the remains belonged to the steppe species *O. pusilla*. Furthermore, several Holocene-dated sites along the North Urals western slope (3–8 on Fig. 1) expected to reveal presence of steppe species in fossil communities there were examined, but no remains of the latter have been discovered among abundant collections.

2.3. Steppe species selection for analysis

According to the intentions of the study, the main attention was paid to zonal steppe species widely distributed in the Urals, which might be accurately identified by their bone remains. Our list of those included the following species: steppe pika, steppe lemming, yellow steppe lemming (*Eolagurus luteus* Eversmann, 1840), grey hamster (*Cricetulus migratorius* Pallas, 1773), mole vole (*Ellobius talpinus* Pallas, 1770) and jerboa (*Allactaga major* Kerr, 1792). It was impossible to neglect the species most abundant in the Ural faunas of the Late Pleistocene time, the narrow-skulled vole, and it was included into the analysis. This species, characteristic of several natural zones, was widely represented not only within Late-Pleistocene faunas, but in modern animal communities, inhabiting areas of tundra, forest-tundra, forest-steppes and steppes in the Urals. Modern “northern” (tundra) subspecies of the narrow-skulled vole are perfectly distinguished from the “southern” (steppe and forest-steppe) forms not only by the occupied territories but in morphological features. However, a similar distinction is not accessible for the Late-Pleistocene forms. This was the reason why the presence of the species remains was discussed in the study only in relation to the sites where *M. gregalis* bones were found together with fossils of some other zonal steppe species.

The study concentrates on the northernmost finds of steppe species remains, whereas examination of southern limits of these species' distribution is a separate problem demanding special investigation along the contact area between steppe and desert zones. Due to this reason, several species related mainly to the desert animal complex and rare in the Ural collections are only mentioned in the article. These are: dwarf fat-tailed jerboa (*Pygeretmus pumilio* Kerr, 1792), little ground squirrel (*Spermophilus pygmaeus* Pallas, 1778), and Eversmann's hamster (*Allocricetulus eversmanni* Brandt, 1859). Marmots, usually not regarded as small mammals, also remained beyond the discussion.

2.4. Problems of species identification

Several taxa demonstrate the problem of species identification based upon isolated teeth and other skeleton fragments. This is true in concern to remains of two pika species, two birch mouse species, and large souslik forms.

Two representatives of *Sicista* genus (northern birch mouse *S. betulina* Pallas, 1779 and southern birch mouse *S. subtilis* Pallas, 1773) are registered within modern fauna complexes of the Urals. They are but rarely met in Quaternary fauna lists, and no accurate methods exist to distinguish birch mouse fragmented bones between the two species. Thus, we excluded these remains from our study.

Modern fauna complexes of the Urals also often include two pika species. These are *O. pusilla* living in the steppe zone and northern pika (*O. hyperborea* Pallas, 1811) inhabiting upper mountain belts of the Pre-Polar and Polar Urals. The two species are reliably identified by lower jaw patterns but isolated molars cannot be distinguished. In the Urals, the northernmost reliably identified finds of steppe pika remains are known from the Medvezh'ya cave (62° N; Kuzmina, 1971). Most of the southern pika fossils were identified to the steppe pika. Some isolated pika teeth (probably *O. hyperborea*) were found significantly farther north (about 500 km from Medvezh'ya cave): site at the Kozhym-river (Kryazheva and Ponomarev, 2014); site at Schuger-river (Ponomarev and Kryazheva, 2011); site Laya-6 at the Laya-river (Guslicer and Isaichev, 1978); and sites Pizhma-1 and Sed'yu-1 (Ponomarev et al., 2012, 2013); all these finds lacked species identification. Thus, these remains should be regarded as representing genus *Ochotona*, but should not be discussed in relation to steppe species distribution patterns.

In this article, all fossils referred to large souslik forms and found in Late Pleistocene and Holocene faunas of the Urals are termed “large sousliks” (*Spermophilus* spp.)”. In other publications, fossil remains of large sousliks were referred to different species forms (*Citellus superciliosus* Kaup, 1839 (foss.), *Citellus/Spermophilus major* Pallas, 1778). Some authors (Pavlinov and Lissovsky, 2012) consider both genus names (*Citellus* and *Spermophilus*) as synonyms. The Pleistocene large souslik *S. superciliosus* based on morphologic features was distinguished as an extinct form ancestral to modern large sousliks referred to genus *Spermophilus* (Gromov et al., 1965). However species identification of large souslik remains was reliably based on series of fossils (Gromov et al., 1965), whereas in the Urals only isolated fossils of large sousliks have been registered in Late Pleistocene and Holocene sediments.

Fig. 1. Map showing the main Late Pleistocene and Holocene localities in the Urals which were used for analysis **I. *North Urals, western slope (62° N; 58° E)***:1 – Medvezh'ya Cave, 2 – Studenaya Cave (Smirnov, 1996), 3 – Kibla-1, 4 – Kibla-2 (Sadykova, 2007), 5 – Sobinskaya, 6 – Shezhim, 7 – Pikhtovka, 8 – Iordanskogo (Sadykova and Smirnov, 2005). **II. *North Urals, eastern slope (59°–61° N; 59°–60° E)***: 9 – Shaytanskaya Cave (Smirnov, 1996), 10 – Cave Cheremuhovo-1 (Strukova et al., 2006; Teterina, 2009), 11 – Grotto Kakva-4 (Smirnov et al., 1999), 12 – Ushminskaya Cave, 13 – Grotto Ushma-1, 14 – Toltiyskaya Cave, 15 – Lis'ya Cave (Teterina, 2009), 16 – Grotto Puzan (Sadykova, 2013). **III. *Middle Urals, northern part, western slope (57°–59° N; 57°–58° E)***: 17 – Cave Makhnevskaya-2, 18 – Grotto Rassik (Fadeeva and Smirnov, 2008), 19 – Cave Dyrovatye Ryobra V (Izvarin, 2008), 20 – Grotto Dyrovaty Kamen' at the Tchusovaya-river (Smirnov, 1995), 21 – Bol'shaya Makhnevskaya Cave, 22 – Kamen' Kozy (Fadeeva and Smirnov, 2008), 23 – Grotto Bol'shoy Glukhoy, 24 – Grotto Shaytansky (Smirnov, 1995). **IV. *Middle Urals, northern part, eastern slope (59° N; 60° E)***: 25 – Lobvinskaya Cave (Smirnov, 1995). **V. *Middle Urals, southern part, western slope (56° N; 57°–59° E)***: 26 – Grotto Bobylek, 27 – Grotto Dyrovaty Kamen' at the Serga-river (Smirnov, 1993), 28 – Rock shelter Svetly (Volkov et al., 2007; Izvarin, 2009), 29 – Cave Arakaevo VIII (Smirnov, 1993), Grotto Bazhukovo III (Smirnov, 1993), 30 – Rock shelter Ust'-Log I, 31 – Rock shelter Ust'-Log V, 32 – Rock shelter Krasnosokol'ye-2, 33 – Grotto Nizhneirginsky (unpublished), 34 – Alikaev Kamen' (Izvarin, 2004), 35 – Grotto Sukhorechensky (Smirnov et al., 1992), 36 – Starik Rock shelter, 37 – Smotrovoy Rock shelter (Sadykova, 2011), 38 – Grotto Filin (Sadykova, 2006). **VI. *Middle Urals, southern part, eastern slope (57° N; 60°–62° E)***: 39 – Shaytanoozersky Kamennyi Ostrov-1, 40 – Pershinskaya Cave, 41 – Lebyodkino, 42 – Retchkalovo (Borodin et al., 2000; Strukova, 2000), 43 – Mironovskaya Cave (Rupysheva and Strukova, 2010), 44 – Bosonogaya and Grotto Golenduhino (Rupysheva, 2009). **VII. *South Urals, northern part, western slope (54° N; 57° E)***: 45 – Ignatievskaya Cave, 46 – Cave Prizhim-2, 47 – the First Serpievskaya Cave, 48 – the Second Serpievskaya Cave, 49 – Rock shelter Sim I, 50 – Grotto Sim III (Smirnov et al., 1990), 51 – Grotto Lemeza I, 52 – Cave Lemeza II and Cave Lemeza III, 53 – Cave Lemeza IV (Yakovlev et al., 2005; Danukalova et al., 2008), 54 – Nukatskaja Cave (Yakovlev et al., 2000). **VIII. *South Urals, northern part, eastern slope (54° N; 59° E)***: 55 – Ustinovo Rock shelter (Smirnov et al., 1990). **IX. *South Trans-Urals, eastern slope (53° N; 59° E)***: 56 – Syrtinsky, 57 – Alexeevsky, 58 – Khudolaz, 59 – Cnernishevsky-III and Chernishevsky-V (Kuzmina, 2009) ***Northernmost finds of genus Ochotona remains (asterisks)***: 60 – Laya-6 (Guslicer and Isaichev, 1978), 61 – Pizhma-1 (Ponomarev et al., 2012; Ponomarev et al., 2013), 62 – Kozhim-1 (Kryazheva and Ponomarev, 2014), 63 – Sedyu-1 (Ponomarev et al., 2012; Ponomarev et al., 2013), 64 – Shuger-4 (Ponomarev and Kryazheva, 2011).

3. Modern distribution of small mammal steppe species in the Urals

These animals are strictly attached to open-land (non-forested) habitats. Modern fauna of the Urals and adjacent territories numbers 10 zonal steppe species of small hares and rodents (Marvin, 1969). They are: *Ochotona pusilla*, *Spermophilus major*, *Spermophilus pygmaeus*, *Allactaga major*, *Sicista subtilis*, *Allocricetulus eversmanni*, *Cricetulus migratorius*, *Ellobius talpinus*, *Lagurus lagurus*, and *Microtus g. gregalis*.

These species areas are not limited by the steppe zone only. Along northern area edges, many of them intrude through steppe-like or meadow biotopes into the forest-steppe regions, sometimes to the very border-line with the forest zone. In the south, at the contact with semi-deserts, some occupy habitats practically reaching the desert zone. However it does not mean that in the Ural region these animals occupy all suitable habitats within forest-steppe and steppe biotopes. Their areas reveal peculiar configurations, not only due to non-uniform human-made transformation of steppe landscapes, but also influenced by different biotic and abiotic factors. One of the latter is non-uniform humidification of the western and eastern slopes of the Ural mountains which probably always existed, resulting from west to eastward atmosphere precipitation transport from the Atlantic. Probably this factor might be one among those causing significantly northern points of some steppe species distribution along the Urals eastern slope as compared to the western one.

Though not high, the Ural ridge disrupts the latitudinal continuum of the forest-steppe and steppe zones. The forest zone, 200–300 km wide, forms a north–south strip about 700 km long.

An important feature of the Ural region is that three large insular forest-steppe areas surrounded with forested lands are situated on the western slope, stretching from north to south for 250 km. These are the Kunghursky, Krasnoufimsky, and Mesyagutovsky forest-steppe islands. Today, not a single steppe animal species is registered there. During the Holocene, territories of Krasnoufimsky and Mesyagutovsky forest-steppe islands were part of the narrow-skulled vole range. Plots near the Mesyagutovsky forest-steppe south borders in late-Holocene time were inhabited by mole-voles and probably by steppe pikas.

According to our data, the modern northern limit of the steppe species complex distribution is marked by the northernmost points of fossils identified to *Microtus g. gregalis* and to *Spermophilus major*, 58° N (north of Irbit), on the eastern slope. On the western slope, the northernmost plots inhabited by these animals are of interest, because the species ranges are reduced significantly due to human-made landscape changes.

Thus small mammals steppe species collected in the Urals can distinctly follow the pattern of the animal areas northward shifting along the eastern slope and by the Trans-Urals. The northernmost points of the species finds during the last half-century form the following series: *Microtus g. gregalis* – 58° N (Smirnov et al., 2015), *Spermophilus major* – 58° N (Lemesh and Pogodina, 2010), *Allactaga major* – 56°30′ N, *Ellobius talpinus* – 56° N, *Sicista subtilis* – 55°10′N, *Allocricetulus eversmanni* – 55° N, *Lagurus lagurus and Ochotona pusilla* – 54°20′ N, *Spermophilus pygmaeus* – 52° N, and *Cricetulus migratorius* – 51° N (Marvin, 1969; Rudi, 2000). This distribution developed due to latitudinal gradients of precipitation, soil, and vegetation characteristics. Their most significant borders follow those marking distinct natural zones. Thus, the border separating the forest zone and the forest-steppe follows 57–58° N, and the line between the forest-steppe and steppe zones follows the Uy-river, at 54° N. Within the steppe zone, subzones of northern and southern steppes are distinguished, the separating line in the Trans-Urals at about 52° N (The Urals and the Pre-Urals, 1968).

To be more accurate when comparing ancient and contemporary data to the species distribution patterns, one should consider not the present-day information during the last tens of years, but also the data on so-called reconstructed areas which allow taking into account the area changes caused by human activities during the last hundreds of years. Beside this human-effected dynamics, during the latest tens/hundreds of years the areas also changed due to climate changes. Furthermore, in some rodent species the reasons for significant area shifting have not been determined. An example of the latter situation is the fact of eastward retreat (farther than the Urals south edges) of the area western limit of the narrow-skulled vole during recent decades (Rudi, 2000). Even more remarkable, there was an abrupt reduction of huge part of yellow steppe lemming area registered in Kazakhstan during historical time (Gromov and Polyakov, 1977). Both cases probably might be regarded as processes inherited from the former Pleistocene–Holocene area dynamics of these species.

It appears even more difficult to describe the “modern” or reconstructed area state if the same species demonstrates differently-directed area shifts over several dozens of years. Many animal species revealed changes of this type during the last century. For example, processes of this kind were described for the deserted Caspian steppes and the dry steppe of the Syrtovaya plain in the Trans-Volga region (Oparin et al., 2010). Some part resulted from human-made environmental transformation, whereas others probably developed due to natural climatic changes. In similar cases, we regarded reconstructed areas as an averaged state throughout the period of changes under study.

4. Distribution of small mammal steppe species in the Ural region during the late Pleistocene and Holocene intervals

4.1. Narrow-skulled vole (Microtus gregalis)

In the late-Pleistocene time, the narrow-skulled vole was the most wide-spread and most abundant species of small mammals throughout North Eurasia, showing lower numbers only during cold intervals, as compared to the hoofed lemmings (genus *Dicrostonyx*) in the north and steppe lemming in the south territories. In the Urals it was marked during all late Pleistocene intervals and in all sites where fossils were found. Beyond the limits of the modern area, its latest fossils were found in the sites of insular forest-steppes situated on the western slope of the Middle and South Urals (the voles lived there until the XIX century (Smirnov et al., 1992)). In the Mid-Urals northern part and in the North Urals, the species latest finds are dated to the Middle Holocene (Atlantic time). Relative numbers of the narrow-skulled vole were extremely high in the sites of LGM and LGT intervals situated on the North Urals eastern slope (35% and more), those of late-glacial time (LGT) in the Mid-Urals north, western slope (up to 45%), and in the south regions all over the Middle Urals dated from LGM to early Holocene time inclusively (30–44%).

The species showed the highest values of relative abundance in the LGT sites situated on the South Urals western slope (up to 80%) with average relative numbers about 60%. In the Early Holocene (both Preboreal and Boreal) and the Middle Holocene, the values decreased to 40%, later falling to 1%. In the very south of the region at study, the South Trans-Urals, the narrow-skulled vole showed significantly lower relative numbers as compared to both *Lagurus lagurus* and *Eolagurus luteus*, but it was dominant by the early Holocene, and retained this position (30–40%) throughout the whole interval.

Westward from the Urals, the species inhabited all ice-free territories of northern and middle Europe, including the British Isles and a significant part of France (Gromov and Polyakov, 1977;

Markova et al., 2008). Eastward from the Urals, throughout southern Siberia (to the Yenissey-river at least), during LGT the species dominated or was a co-dominant (Andrenko, 1998). Further to the east, this position was occupied by other species.

4.2. Steppe lemming (Lagurus lagurus)

This species is one of the most typical one among those inhabiting modern zonal steppes. Thus, it can be considered as an indicator of steppe communities. Of the whole territory studied in the Urals, the species inhabited constantly only the south Trans-Urals. From the LGM time until the Holocene, it was super-dominant (up to 80% of the total amount of fossils) or dominated with ~50% of bones. In the Holocene faunas, the species frequency numbers were less than 20% (Kuzmina, 2009). During the LGT in the sites of South Urals, the species fossils' proportions reached 50% on the eastern slope, whereas on the western slope the figure did not exceed 15%. During the Holocene, the species remained at low numbers as a relic form in the South Urals, in the communities of the insular forest-steppes.

In south regions of the Mid-Urals, these animals were also significantly more abundant on the eastern slope compared to the western one; for LGT, the corresponding values are 29% vs. 18%. A series of sites excavated on the eastern slope and aged to LGM gave steppe lemming proportions from 23 to 48%. The latest find of the species remains at this latitude showed mid-Holocene age.

Steppe lemming remains were also registered in northern regions of the Mid-Urals, but the species percentages in communities did not exceed 10% even during the LGT, and the latest finds were extracted from the Early-Holocene (Preboreal) layers. The northernmost steppe lemming fossils dated to LGT were collected in the Shaytanskaya cave on the North Urals eastern slope (61° N). The species bones in the region were also found in some more sites but with ages not older than 12,800 BP (Smirnov, 1996). This makes us to conclude that in the Urals, northern borderline of steppe lemming area during late-Pleistocene time lay 750 km distant from its modern position.

In Western Europe, several sites are known which included *Lagurus lagurus* fossils in late-Pleistocene layers. One of those, Regourdou in southwest France (Chaline, 1972), is the most distant one from the species' modern area borders. Further eastwards, in middle Europe, the species finds are known from late-Pleistocene sediments in Germany (Burgtonna), Czech Republic (Kulna Cave), Hungary (Tata), and Poland (Mamontova Cave, etc.) (Nadachowski, 1982; Nadachowski et al., 2009). In carefully examined cave sediments of the Czestochowa Upland in Poland, only a few steppe lemming fossils were found.

In Eastern Europe, the species stripe-like area spread from Belorussia, the fossils been found in LGM layers (Motuzko, 1992) and in late-glacial site Gozha-2 (Ivanov, 2008), to the Bulgarian site Bracho Kiro (Kowalski and Nadachowski, 1982) and Moldova (Lozan, 1970). In southern regions, finds were included in LGM sediments. Northern specimens were found in layers dated to time intervals just before and after the late-Pleistocene cold maximum.

Eastward from the Urals, in southern Siberia, steppe lemming was quite numerous. The late-glacial fauna from Elenevo cave at the Yenissey middle reaches numbered up to 20% of the species bones (Andrenko, 1998). Further eastwards, in Pre-Baikalia, during LGM and LGT the species showed full dominance and even super-domination (Khenzykhenova, 2008; Erbaeva et al., 2011).

4.3. Yellow steppe lemming (Eolagurus luteus)

This species occupies a special place among other steppe animals. It was regularly marked (as an ordinary species, with frequency numbers about 10%) in communities of the South Trans-Urals during LGM. Later on, in LGT complexes it was registered as a co-dominating species with up to 30% of fossils (Kuzmina, 2009). During the Holocene, the species proportions in the communities decreased gradually. The latest find occurred in the second half of the Late-Holocene (Subatlantic). Northward, in the South Urals, a few bones were collected from LGT layers on both eastern and western slopes. The latter also gave some species fossils of Early Holocene age. The species also inhabited regions in the Middle Urals, regularly found up to 57° N in LGT, and later at 56° N. The species was identified from the Shaytanskaya cave collection (60°30′ N) but its age cannot be estimated accurately, only as "late-Pleistocene". Thus in the Urals, the southward reduction of the species area from the late Pleistocene to late Holocene time is estimated to 900 km.

In Europe, the westernmost finds of the species fossils are known from late-Pleistocene sites in Moldova (Lozan, 1970). Dated to late Holocene time (earlier than 19th c.), it was marked in Kazakhstan steppes and semi-deserts. Later (end of the XIXth–XX cc.) the species area was reduced significantly, with its present-day western limit marked in the Zaisansky depression. Consequently, during the late Pleistocene–late Holocene interval, the species area was reduced eastward by about 1500 km. During the last century, the species northern limit retreated southward and eastward 1000 km. Thus, the northernmost find of *Eolagurus luteus* bones (in Pleistocene sediments in the Urals) is 2000 km distant from its modern habitats in the Zaisan depression.

4.4. Steppe pika (haymaker) (Ochotona pusilla)

Late Pleistocene pika area in the Urals spread to at least 62° N (Medvezh'ya cave) (Vereshchaghin and Kuzmina, 1962). Southward from this latitude, the species showed wide distribution in the Urals during LGM and LGT. Pika was an ordinary species (1–5% of fossils) in northern regions of the Mid-Urals western slope. Its latest finds there were dated to mid-Holocene time (Atlantic), whereas in south Mid-Urals the latest specimens corresponded to the Late Holocene (Subatlantic).

In Europe the westernmost pika finds are known from France and British Isles. Probably the northernmost specimen of the pika fossils in West Europe is that from late-glacial sediments in Denmark (Degerbol, 1964; Aris-Sorensen, 1995). In East-Europe, the species is known by bones from LGM and late-glacial layers of Poland and Belorussia (Motuzko, 1992). Nearer to mid- and late-Holocene time, the area's west border was shown to shift about 3000 km east. This process continued in the historical period (Gromov and Erbajeva, 1995).

4.5. Gray hamster (Cricetulus migratorius)

The gray hamster in the Urals was registered up 60° N (Shaytanskaya Cave on the eastern slope of the North Urals) and 59° N (Lobvinskaya cave on the eastern slope, Rassik grotto on the western slope, both in Mid-Urals north part). Further southward, the species was marked (though not numerous) in collections of all sites examined on both slopes of the Middle and South Urals and Trans-Urals. The highest relative numbers of the animal remains were registered in the cave Dyrovaty Kamen' at Tchusovaya-river (up to 8% in LGT layers) and up to 5% in some LGT sites on the South Urals western slope. In the northern Mid-Ural regions, the species occurred until the Early Holocene (Preboreal), in Mid-Ural south part until the Middle Holocene (Atlantic), and in the South Urals until the first part of the late-Holocene (Subboreal).

The pattern of the species Pleistocene distribution in Europe seems uncertain, as in many cases the species fossils are described under different names. However, gray hamster's area differed from that of steppe lemming. In Czestochowa Upland region in Poland the gray hamster was registered more often than steppe lemming remains and within a wider time interval. It was found in several cave sequences dated to two chronological stages of fauna history younger than 11,000 BP (Nadachowski et al., 2009).

4.6. Large sousliks (Spermophilus spp.)

In our studies the northernmost souslik fossils were registered at 59° N, in several caves situated on the Mid-Ural western slope and in Lobvinskaya cave on the eastern slope, from LGT to the beginning of Early Holocene (Preboreal), and in the south Mid-Urals until the Middle Holocene (beyond modern area limits). Modern area of the species covers regions slightly eastwards and at the same latitude. In the South Urals, large souslik bones were marked from LGM until late-Holocene.

4.7. Jerboa (Allactaga major)

In the Urals, beyond the modern limit, the jerboa was registered within a single layer in Bobilyok grotto in south Mid-Urals (western slope), with no accurate age estimation (marked as sediments of late Pleistocene age, older than LGT). In the South Urals, sediments dated to LGT in some caves also contained few jerboa fossils. In the Trans-Ural regions forming part of the species modern area, it was noted regularly. As an extremely rare species, the animal was registered in late-Pleistocene sites of Middle and Eastern Europe. Among fossils extracted from the sequence of Komarowa Cave near Krakow in Poland, few specimens were identified as jerboa. They were dated to a limited time span, ca. 30–39,000 BP (Nadachowski et al., 2009). Reduction of the species area western part might be estimated at about 500 km.

4.8. Mole vole (Ellobius talpinus)

Most fossils identified to the species were collected within its modern area limits in the Urals and in other regions, sometimes a few dozens of kilometers northward or westward. No bones were found in the sites of Mid-Urals western slope. On the eastern slope, the mole-vole fossils were extracted from early- and mid-Holocene layers in Pershinskaya cave (57°29′ N, 61°25 E), about 100 km northward from the species modern limit. Beyond modern area limits, mole-vole remains were found in some Holocene sites in the South Urals, but lack accurate dating.

5. Discussion

Fossil collections obtained from over 60 caves in the Ural region provided information allowing latitudinal estimates of northernmost finds of several steppe species remains extracted from Late-Pleistocene sediments. The most numerous series are dated to the LGT, which is the interval when many different steppe species demonstrated the northernmost expansion compared to their present-day limits. Practically all steppe complex species spread northwards but the process was different in each case. Distances between the known northernmost finds of distinct species bones are no less than 650 km (not including the narrow-skulled vole area and pika fossils found in the Tyman kryazh site). All northernmost specimens from LGT sediments were found between 62° and 56° N. The comparison showed that today, these steppe community species' areas also differ in the position of their northern borderlines. The corresponding distances are significant though not as large compared to the Pleistocene. The span is about 500 km, within 58° and 51° N, east from the Ural ridge.

According to latitudes marking Pleistocene-aged northern fossil finds, the discussed species seem to form four groups. The first one includes the narrow-skulled vole and steppe pika, which demonstrated the most northward expansion (crossing 62° N). Gray hamster and both steppe lemmings are the second group to reach 60–61° N. Souslik did not cross 59° N. Lastly, 56–57° N limited the northern borderlines of jerboa and mole-vole areas. This pattern looks rather similar to that concerning westward expansion of these species to European territories, though differing in details.

The species might be grouped in accord with the distance values (km) dividing the species northern limits today from those during the LGT. Three species, the narrow-skulled vole, yellow steppe lemming and steppe pika, showed values of 900 km and more. The highest value, about 2000 km, is revealed in yellow steppe lemming history, if one takes into consideration the species area retreat to the Zaisan depression during historical time. However, the species would stay within this group even if we regard the state of the XVIII–XIXth cc. as the species' "modern area limits". No reason is yet understood that might cause this extreme area reduction. Probably the process might be inherited from some trends started during the Pleistocene–Holocene transition time.

The narrow-skulled vole enters this group due to the species' peculiar adaptations allowing animals to inhabit open areas of both extreme north and steppe–forest-steppe environments. The species area is thus disrupted, with one part lying in the tundra zone and the other in the forest-steppe zone; they cannot live in forested regions.

Steppe pika spread far to the north in the Urals, followed by significant retreat to the steppe zone, which probably might be regarded as due to the peculiar inhabited biotopes and unique way of food storage. The habitats are dry and possess abundant shelter and projections suitable for storage of hay and bush stems. Thus, soil freezing seems not so important for the species as compared to many other animals.

In the Urals, 750–800 km divides the late-Pleistocene and modern areas' northern limits of the steppe lemming and the gray hamster. Probably, this distance determined the limit of climate-regulated cold-dryness ratio allowing survival of these species. It seems quite reasonable that at latitudes where the northernmost finds of steppe lemming and Eversmann's hamster molars were registered, and surely further northwards, the hoofed lemming dominates small mammal communities, with significant numbers of Siberian lemmings (*Lemmus sibiricus* Kerr, 1792). This fact clearly indicates that temperatures there were lower than those allowing survival of proper steppe animals. Depth of soil seasonal freezing and melting is an important factor limiting habituation of two winter-hibernating species, souslik and large jerboa. These two with mole-vole form a group, members of which showed minimal or no northward shifts during the Pleistocene. Of these three, the mole-vole is most tightly related to soil conditions. Some finds of mole-vole fossils are known north of the species' modern area limits, showing not Pleistocene but mid-Holocene age (interval of the climatic optimum).

The highest proportions of steppe species fossils in late-Pleistocene and Holocene communities northwards from modern steppe regions in the Urals were registered during terminal late-glacial time, when extreme cold and arid conditions of the glacial epoch turned slightly warmer, though still dry. Dated to this interval, a unique northern find had been registered in the site Sed'yu-1 in the Pechora-river basin (south Tyman region, 63°30′ N). *Desmana* remains were found there with fossils of the narrow-skulled vole, pika, Siberian and hoofed lemmings (Smirnov and Ponomarev, 2007).

Long before the late-glacial interval, at the beginning of late Pleistocene time (probably during the Mikulino interglacial), there occurred a northward occupation wave when series of thermophilic species including those of steppe communities moved to inhabit new territories. Probably, the porcupine appeared in the Urals at that period (Fadeeva and Smirnov, 2008). Beside the discussed steppe species, taxa lists of both modern and ancient faunas in the Urals included *Pygeretmus pumilio*, *Sicista subtilis*, *Allocricetulus eversmanni*, but they were quite rare.

6. Conclusions

In distinct species composing the steppe complex in the Urals, the areas' northern limits were shown to differ significantly both today and during the late Pleistocene terminal time. The range of differences was greater during the latter time interval as compared to the modern pattern, by several hundred kilometers. Configurations of the species relative distribution also differed as certain species showed the most northward spread within one but not both time intervals. Differences between the two patterns probably might be due to various limiting agents' ratio during the intervals discussed. For example, modern northward spread of the narrow-skulled vole and souslik is limited by the combination of factors characteristic of the forest zone which did not exist during late-Pleistocene time. The main factor limiting the species north–south distribution pattern in modern forest-steppe and steppe zone is that of climate humidity, whereas during the late-Pleistocene time it was the temperature gradient. A variety of data indicate extremely severe cryoaridity of climate conditions at latitudes over 60° N. *Dicrostonyx* lemmings dominated in small mammal communities.

Fossil data indicate several northward expansions of small mammal steppe species developed in the Urals during the Pleistocene and Holocene. The most significant of those were dated to LGM and especially to LGT intervals, but certain data also indicate the steppe species areas shifted during the last interglacial and mid-Holocene.

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