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Rodents of the North Urals in the Late Pleistocene and Holocene

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A B S T R A C T

Data on fossil micromammals known at present from the North Urals sites allow us to trace the history of rodent communities beginning from the Middle Weichselian up to the present and to reveal some temporal and spatial patterns in their changes. Five fauna types were distinguished among the fossil local faunas known at present. Throughout the Late Pleistocene only tundra–steppe faunas existed in the North Urals, which differed in time and space mainly by relative abundances of three dominant species – *Dicrostonyx gulielmi*, *Microtus gregalis* and *Lemmus sibiricus*, and in some cases by species diversity. Early and Middle Holocene faunas reflect a transition from communities characteristic of tundra–steppe to forest and, in particular, taiga environments. Late Holocene faunas have a typical taiga character. Tendencies of temporal dynamics of faunas correlate with those revealed for other parts of the Urals. Differences between faunas of the different slopes (western and eastern) of the North Urals can be explained by the same factors which determine the different climate conditions there at present.

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1. Introduction

The North Urals is part of the Urals mountain range situated between 59° N and 63° N. The climatic regime of the territory differs east and west of the watershed due to the barrier role of the mountain range which blocks Atlantic moist air masses from moving to the east, so the humidity in the Pre-Urals and mountain part of the territory is higher than on the eastern slopes and in the foothills of the Trans-Urals. The North Urals falls almost completely within the northern taiga subzone and only in the southern part includes a Middle taiga area. Altitudinal vegetation belts are pronounced at the highest mountain peaks (Urals and Pre-Urals, 1968).

In this paper, only rodents and lagomorphs (pikas) are considered, because the identification of insectivore fossil remains constitutes a separate and complicated problem.

2. Rodent faunas of the North Urals

The North Urals rodent fauna at present consists of forest species typical of the taiga zone: *Clethrionomys glareolus*, *Clethrionomys rufocanus*, *Clethrionomys rutilus*, *Micromys minutus*, *Microtus agrestis*, *Myopus schisticolor*, *Pteromys volans*, *Sciurus vulgaris*, *Sicista betulina*, and *Tamias sibiricus*, and intrazonal species preferring riverine habitats: *Arvicola terrestris* and *Microtus oeconomus*. Besides, there are two synanthropic species *Rattus norvegicus* and *Mus musculus*, and one introduced species *Ondatra*

zibethicus. Distribution area borders of several species lay in the region: *Apodemus uralensis*, *Apodemus agrarius*, and *Microtus arvalis* are present in the southern part (up to 60° N), and the southern edges of *Microtus middendorffii* and *Ochotona hyperborea* areas reach the northern part of the North Urals. Dominant species in the rodent communities are voles of the genus *Clethrionomys* (Gromov and Erbajeva, 1995; Berdyugin, 1999; Bolshakov et al., 2000).

The work presented in this paper is based on the analysis of 21 rodent local faunas of different ages from 10 cave excavation sites (Fig. 1) (Smirnov, 1996; Smirnov et al., 1999; Teterina, 2002; Teterina and Ulitko, 2002). All sites known at present are situated in the southern part of the territory (the southernmost at 59° N, the northernmost at 62° N). Faunas were dated by ¹⁴C or dates are based on the archaeological data, and in some cases the morphology of species (mostly *Dicrostonyx* sp.) and correlations with other, dated faunas from nearby territories were used for this purpose. Some of the sites are multilayered and contain material of different ages, allowing us to trace temporal changes in communities. The most informative for the purpose of a reconstruction of the temporal dynamics of rodent communities is Cheremuhovo 1, containing a sequence of layers with bone material of different ages beginning from 28 ka up to the present (Fig. 2).

Existing materials allow us to characterize rodent faunas beginning from the Middle Weichselian (the oldest faunas were beyond the ¹⁴C method and their age was assessed on the basis of *Dicrostonyx* morphology) up to the present.

For a description and analysis of the faunas, the species were divided into four zonal-biotope groups according to their environmental preferences:

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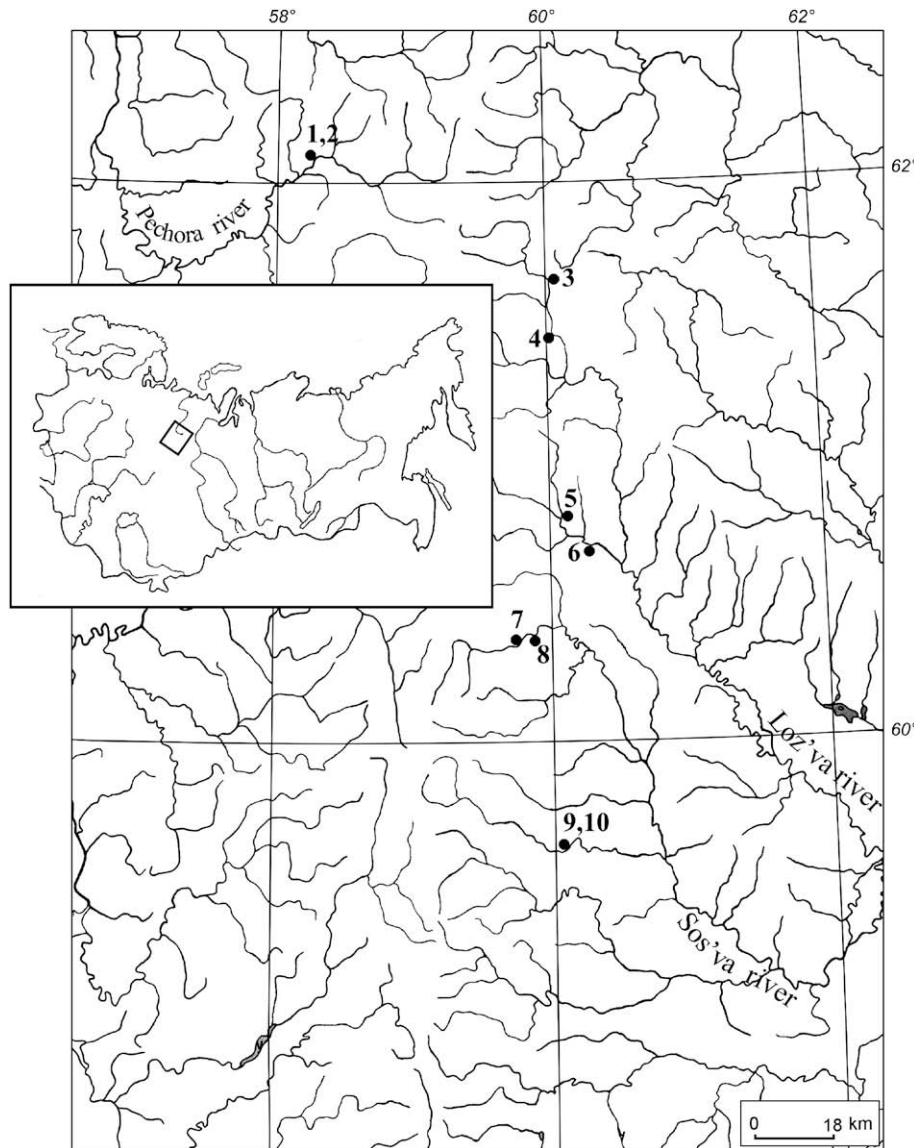


Fig. 1. Location of fossil rodent remains cave sites in the North Urals. Western slope: 1 – Studenaya cave, 2 – Medvezhiya cave; eastern slope: 3 – Ushma 1; 4 – Ushminskaya cave; 5 – Toltiyskaya cave; 6 – Shaitanskaya cave; 7 – Lis'ya cave; 8 – Cheremuhovo 1; 9 – Zhilische Sokola; 10 – Kakva 4.

- tundra (collared lemming, Siberian lemming, Middendorff's vole),
- steppe (narrow-skulled vole, steppe lemming, yellow steppe lemming, gray hamster, ground squirrel, steppe pika),
- forest (common red-backed vole, gray large-toothed red-backed vole, northern red-backed vole, field vole, wood lemming, northern birch mouse, harvest mouse, wood mouse, squirrel, Siberian chipmunk, flying squirrel),
- intrazonal riverine (root vole, water vole).

Cluster analysis performed on data on relative abundances of different species remains in local faunas allowed us to distinguish five types of fauna and within two of these also subtypes. They principally differ by dominant species and their relative abundances, and consequently replaced each other in time and space. Most of the fauna types are represented by different chronological and local variations.

2.1. Late Pleistocene

All faunas include remains of three species: *Dicrostonyx gulielmi*, *Lemmus sibiricus* and *Microtus gregalis*, and the share of their

summarized relative abundances constitutes not less than 70% of the total number of remains. Differences between faunas are determined by the different proportions in the abundances of these species remains. Low species diversity and a high degree of non-correspondence are the characteristics for faunas of this period (Table 1).

2.2. Middle Weichselian

2.2.1. Fauna type 1

Dicrostonyx sp. dominates. **Subtype 1a** *M. gregalis* is subdominant. The subtype is represented by the local fauna from pit section 2 of Zhilische Sokola on the eastern slope. The other known faunas of this subtype are dated to a later period, the Last Glacial Maximum and the deglaciation. Compared to these, the fauna of Zhilische Sokola differs: no sharply pronounced *D. gulielmi* dominance; significant species diversity due to the number of forest and steppe species; a comparatively high share of steppe species remains. Species preferring xerophytic habitats (*D. gulielmi*, *M. gregalis* and steppe species) constitute the bulk of the remains; the

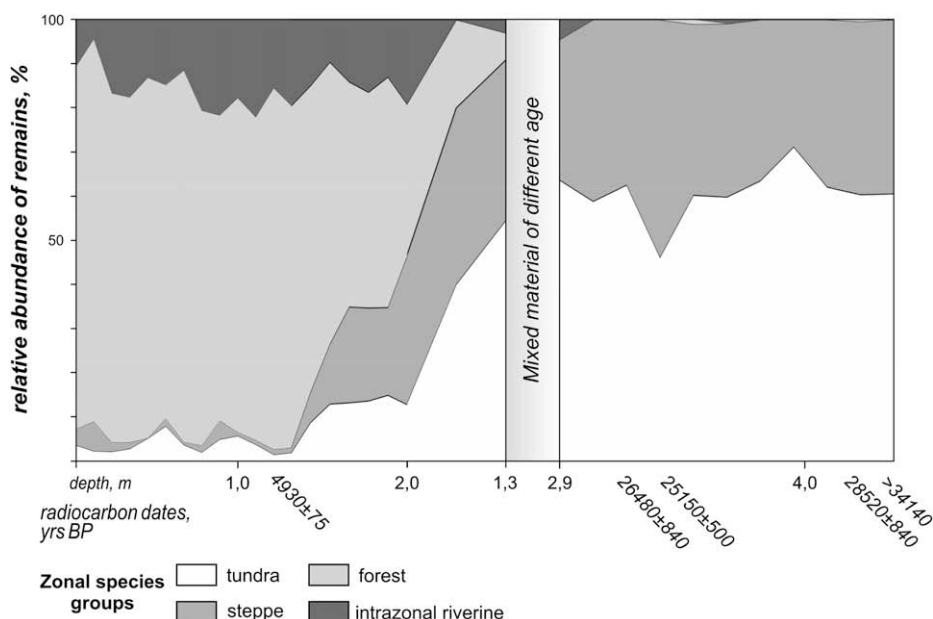


Fig. 2. Changes in the relative abundances of remains in the zonal species groups in the sequence of Cheremuhovo 1.

proportions of remains of tundra and steppe species are very similar.

Subtype 1b *L. sibiricus* is subdominant. The fauna is described from pit section 1 of Zhilische Sokola. No similar faunas are known in the Urals. The *Dicrostonyx* dominance is poorly expressed; the total proportion of tundra species remains is the highest and that of the steppe species, accordingly, the lowest among all local faunas known from the eastern slope. Species preferring wet habitats (*L. sibiricus*, *M. middendorffii*, *M. oeconomus*, and *A. terrestris*) constitute considerable numbers of remains. The relative abundance of Middendorff's vole is much higher here than in any other local fauna of the North Urals. The presence of remains of such typical steppe species as steppe lemming gives the fauna a pronounced disharmonious appearance.

2.2.2. Fauna type 2

L. sibiricus dominates. Such faunas were found only in the lower layers of the Studenaya cave on the western slope of the North Urals. The degree of *L. sibiricus* dominance changes with depth (from 76 in the lower to 46 in the upper part), *D. gulielmi* is the second in abundance, followed by *M. gregalis*.

Compared to other Late Pleistocene faunas, all faunas of the Middle Weichselian are characterized by a considerable proportion of remains of species preferring wet areas of the modern tundra, first of all *L. sibiricus* and on the eastern slope also *M. middendorffii*. *M. oeconomus* and *A. terrestris* are always present in these faunas, while in faunas of the succeeding Last Glacial Maximum and deglaciation periods they are absent or extremely rare (*M. oeconomus*). The share of the total number of remains of the three dominant species (70–79%) in the faunas of the eastern slope is the lowest over the whole Late Pleistocene period in the North Urals. As only four local faunas of this time are known and they have no accurate dates, it is impossible to describe the patterns of temporal dynamics of the faunas throughout this period.

2.3. Bryansk interstadial (Denekamp), Last Glacial Maximum and deglaciation

Three local faunas of this time are known from the eastern slope and two from the western. Beginning from the Bryansk interstadial

and nearly up to the beginning of the Late Glacial interstadial, all known faunas are of **type 1** and **subtype 1a**, in which *D. gulielmi* dominates and *M. gregalis* is subdominant. All faunas have a very similar appearance. The dominance of *D. gulielmi* is pronounced (in the different faunas of the eastern slope 40–50%, of the western 74–87%). The share of *L. sibiricus* remains is not more than 15%. The species diversity is low. Other species present in the faunas beside the dominants are *Clethrionomys* voles, *M. oeconomus*, *M. middendorffii*, *Ochotona pusilla* and on the eastern slope also *Lagurus lagurus*; the total share of these species remains is extremely low (not more than 10%). On the western slope, the relative abundance of *D. gulielmi* remains is much higher and the species diversity is lower than on the eastern slope; to some extent this can be explained by the more northern location of the sites.

Two faunas (layer 9 in the Shaitanskaya cave and the lower part of layer 8 in Cheremuhovo 1) are younger than the others and very similar in species composition and structure. They are distinguished by a lower total share of tundra species remains (55–56%, while in the other faunas this is 60% and more) and a higher total share of forest and intrazonal species remains (9% in Cheremuhovo 1 and 4% in Shaitanskaya, while in the other faunas this is not more than 2%).

2.4. Late Glacial interstadial

For this period one ¹⁴C dated local fauna is known from the western slope and two from the eastern, dated by the position in the sequence in relation to ¹⁴C dates and archaeological data. One other fauna, from Kakva 4, is very close to this period (¹⁴C date – 12 800 ± 300 ka BP) and analogous to the faunas of this period by species composition and structure. All faunas are of **type 3**, in which *M. gregalis* dominates (the relative abundance of remains is 32–42%). On the western slope, *L. sibiricus* is the first subdominant (26–30%) and *D. gulielmi* is the third in relative abundance – **subtype 3a**.

On the eastern slope, the first subdominant is *D. gulielmi* (24–36%) and *L. sibiricus* is in third place – **subtype 3b**. The total share of the other species remains is 17–20%, in Kakva 4–10%; on the western slope these are *M. oeconomus*, *M. agrestis*, and *A. terrestris*, voles of the genus *Clethrionomys*, *M. schisticolor* and *O. pusilla*, and on the eastern slope also *L. lagurus* and *Cricetulus migratorius*.

Table 1
Percentages of remains (calculated on the basis of minimum number of individuals) in tundra-steppe rodent faunas from the cave sites in the North Urals. Numbers denoting sites correspond to those on the map (Fig. 1)

Site, layer	Middle Weichselian				Late Glacial Maximum – deglaciation (24–12.4 ka BP)					Lateglacial interstadial – Younger Dryas (12.4–10.2 ka BP)			
	1, layers 3–4	9, pit section 1	9, pit section 2	8, layers 11–12	1, layer 2	2, brown loam B	8, layer 10	8, lower part	6, layer 9	10	2, brown loam A	8, layer 8, upper part	6, layer 8
¹⁴ C date, ka BP				>34140, 28520 ± 840		16130 ± 150, 17980 ± 200	26480 ± 840, 25150 ± 500		14485 ± 65	12800 ± 300			
<i>Dicrostonyx gutilelmi</i>	12–29	33–34	31–43	47–53	87	74–81	35–52	40	36	17–20	30	25	
<i>Lemmus sibiricus</i>	46–78	24–30	9–20	8–12	2	8–10	7–12	16	11	26–30	10	15	
<i>Microtus middendorffii</i>	<1	11–18	3–9	1–2	<0.5	<0.5	2						
<i>Microtus gregalis</i>	6–22	13–19	17–32	32–35	10	9–14	33–47	37	42	33–37	40	42	
<i>Lagurus lagurus</i>		2–4	6–15				<1	3	3			3	
<i>Cricetulus migratorius</i>			<0.5										
<i>Ochotona pusilla</i>		1	1	5	+	+	6	+					
<i>Spermophilus</i> sp.			<0.5										
<i>Clethrionomys</i> ex. gr.	<1	<1	1	<0.5	<0.5	<0.5	<0.5	3	2	2	6	6	
<i>Rutilus glareolus</i>										1			
<i>Clethrionomys rufocanus</i>		<1	<0.5			<0.5		3	0.5		12	<1	
<i>Microtus agrestis</i>	<1		<1					1–2	1	1–7	2	2	
<i>Myopus schisticolor</i>					2			+	<0.5	4	+	<1	
<i>Sciurus vulgaris</i>									0.5				
<i>Microtus oeconomus</i>	2–4	1–6	1–5					3	2	6	3	6	
<i>Arvicola terrestris</i>		<2	<0.5						0.5	1			
Total number of molars	>400	1819	12667	2736	>1100	>1200	1526	136	802	>500	170		

The species diversity of faunas is higher than that of the preceding period, mostly due to the presence of more riverine and forest species, but the general appearance of the faunas stays the same, as the bulk of the remains belongs to the three dominant open habitat species.

2.5. Preboreal – Boreal

There are no reliable data on faunas of this period. Supposedly it can be characterized by materials from layer 7 of the Shaitanskaya cave and the upper layers of the Medvezhiya cave. There are no ¹⁴C dates in both cases; the material is dated on the basis of the location in the sequence in relation to ¹⁴C dates and archaeological artefacts. Probably, the lower horizons of layer 7 in Cheremuhovo 1 also belong to this period. In the Shaitanskaya cave the most abundant are remains of the three species which dominated the Late Pleistocene faunas, their total share is 72%; an insignificant number of remains constitute those of two typical steppe species (1.7% total), and the rest (24%) is made up by forest and riverine species. To give an accurate characteristic of the fauna structure of the Medvezhiya cave is difficult because of the limited quantity of bone material there. A considerable number of remains belong to the same three species (total share 41–46%). At the same time the proportion of remains of voles of the genus *Clethrionomys* is also high (34–29% total), and the remains of the other species constitute not less than 5%. The presence of *S. vulgaris* remains should also be noted.

There are no data on the Holocene rodent fauna history from the western slope with the exception of the two layers of the Medvezhiya cave described above. So in the characterization of the later period only faunas of the eastern slope were considered (Table 2).

2.6. Atlantic

2.6.1. Fauna type 4

Faunas of transitional appearance were found in layer 7 of Cheremuhovo 1 (dated by archaeological data), Lis'ya cave (¹⁴C dated), Toltiyskaya cave, and layer 3 of Ushminskaya cave (dated on the basis of the location in a sequence in relation to archaeological data). The faunas reflect the change of the composition of the community from tundra-steppe to modern taiga. Each biotopic group of species in these faunas is represented by significant numbers of remains and each of such groups includes species with a relative abundance of not less than 10%; in comparison with preceding and succeeding periods faunas have a higher 'equitability index' (not less than 0.87). Remains of forest and riverine species constitute half or more of the total number of remains. The forest species diversity is the highest of the North Urals for the whole period considered. At the same time all the species characteristics of the Late Pleistocene continue in the fauna composition. The existence of such a fauna type, in which species with different biotopic preferences constitute a significant part of the remains, is a result of the mountain environment in which differently oriented slopes provide conditions suitable for different vegetation types, and thus the mosaic of biotopes forms in which animals sharply different in their ecological demands can exist.

2.7. Subboreal – present

All faunas of this period belong to the **type 5** – taiga faunas. They reflect the composition and structure of rodent communities close to those of the modern taiga. The bulk of the remains belongs to forest and riverine species, while the total share of tundra and steppe species remains constitutes not more than 5%. Unlike the modern fauna, they include several species not inhabiting the North Urals at present: *Dicrostonyx* cf. *torquatus*, *M. gregalis*, *L. sibiricus*, *M. middendorffii* and *O. pusilla*. The last two species were

Table 2

Percentages of remains (calculated on the basis of minimum number of individuals) in transitional and taiga rodent faunas from the cave sites in the North Urals. Numbers denoting sites correspond to those on the map (Fig. 1)

Site, layer ¹⁴ C date, ka BP	Preboreal – Boreal			Atlantic		Subboreal – present			
	2, upper layers	6, layer 7	8, layer 7	7	5	4, layer 3	8, layers 2,3,6 (lower part)	4, layers 1–2	3, upper layers
				5037 ± 173 (upper part), 7213 ± 60 (lower part)					
<i>Dicrostonyx</i> ex. gr. <i>gulielmi-torquatus</i>	8–9	24	9–15	<0.5	10	20	1–5	7	1
<i>Lemmus sibiricus</i>	17–20	16	+	9			<1		
<i>Microtus middendorffii</i>			<1				<0.5		
<i>Microtus gregalis</i>	13–21	32	7–32	21	8	6	1–4		
<i>Lagurus lagurus</i>		1	<1		<1				
<i>Cricetulus migratorius</i>		<0.5	<0.5						
<i>Ochotona pusilla</i>	+		<1	<1			<0.5		
<i>Spermophilus</i> sp.				<0.5					
<i>Clethrionomys</i> ex. gr. <i>rutilus glareolus</i>	17	8	13–21	20	6	22	16–29	37	7
<i>Clethrionomys rufocanus</i>	12–17	4	12–26	17	14	24	19–25	22	9
<i>Microtus agrestis</i>	8–10		8–16	5	13	11	18–27	6	9
<i>Myopus schisticolor</i>	5	2	4–8	3	8	13	5–12	24	4
<i>Sciurus vulgaris</i>	<1		<1	2	9	2	<0.5		10
<i>Tamias sibiricus</i>				<0.5					<1
<i>Pteromys volans</i>									<1
<i>Sicista betulina</i>			<1	<1			1		<0.5
<i>Apodemus uralensis</i>			<0.5						
<i>Micromys minutus</i>			<1						
<i>Microtus oeconomus</i>	7–13	12	10–18	13	14		11–21	4	21
<i>Arvicola terrestris</i>	8		<1	7	19	2	<1		37
Total number of molars	>250		4042	1778	435		9550		1721

found only in the lower part of layer 6 in Cheremuhovo 1 dated to 4930 ± 75 ka BP. It is impossible to state for certain if all these species remains are an admixture of an earlier age or not, but the constant presence of *Dicrostonyx* cf. *torquatus* and *M. gregalis* in all Late Holocene faunas is a testimony that these two species disappeared from the North Urals relatively recently. Taiga faunas are represented in two variants. In the first, the greatest part of the remains belongs to forest species, they constitute not less than 55% (upper layers of Cheremuhovo 1 and layers 1–2 of Ushminskaya cave). In the second case, the remains of riverine species constitute more than half of the total number of remains: the upper layers of Ushma 1 shelter, where the most abundant species are *A. terrestris* (37%), and *M. oeconomus* (21%).

3. Discussion and conclusions

The species lists and structures of fossil local faunas in the North Urals change according to their latitudinal characteristics and location on the western or eastern slopes. In faunas of the western slope, among the remains of open habitat species, the proportion of those preferring wet conditions (primarily *L. sibiricus* and *M. middendorffii*) compared to those preferring dry conditions (*D. gulielmi*, steppe species) is higher than the same index in faunas from the eastern slope, with the exception of the Last Glacial Maximum when the values were similar for both slopes. In more northern faunas (Ushma 1 and the Studenaya, Medvezhiya and Ushminskaya caves), the total relative abundance of tundra species remains always exceeds that of steppe species. In the other, more southern faunas, the same ratio is recorded for the Late Pleistocene period, but in the Late Glacial interstadial it changes to more steppe than tundra and does not alter throughout the Early and Middle Holocene.

The main patterns of rodent fauna changes through time can be summarized as follows. Tundra–steppe faunas exist in the North Urals throughout the Late Pleistocene, but their appearance changes in different periods and places. During the Middle Weichselian, the species diversity of the faunas is pretty high and the number of species preferring humid habitats is significant. Later, during the Bryansk interstadial, the Late Glacial Maximum and almost the whole period of deglaciation, faunas are

characterized by low species diversity, very low equitability indexes (0.33–0.76) and uniform composition and structure over the whole territory: *D. gulielmi* dominates strongly, the share of *M. gregalis* remains is large, and the remains of *L. sibiricus* are also numerous in the faunas; the remains of other species are very scarce. At the end of the deglaciation and throughout the Late Glacial interstadial the character of the faunas continues to be tundra–steppe but the role of forest and intrazonal species becomes more significant. The dominant species change, *M. gregalis* becomes the principal dominant species everywhere and subdominants are *L. sibiricus* on the western and *D. gulielmi* on the eastern slopes. In the Holocene, the relative abundances of forest and intrazonal species gradually increase, while those of the three principal species of tundra–steppe faunas in the region (*D. gulielmi*, *M. gregalis*, *L. sibiricus*) decrease. Faunas were of transitional character from tundra–steppe to taiga beginning at least from 7000 ka BP and up to 5000 ka BP. Consequently, the species diversity during this time was higher than at present. About 5000 years ago communities of typical taiga appearance already existed in the North Urals, but such faunas included more species than the present ones. At the same time faunas of transitional character could persist in other areas (the taiga fauna from Cheremuhovo 1 and the transitional fauna from Lis'ya have very close ¹⁴C dates).

Temporal patterns of fauna composition and structure dynamics correlate with those revealed for the other regions of the Urals (corrected for latitudinal differences) (Smirnov, 1994). The spatial differences in fauna composition and structure first and foremost are manifested in the ratios of remains of open habitat species (tundra and steppe). The differences of structure and composition of faunas from different slopes in the Late Pleistocene can be explained by the same factors that determine the differences in climate and landscape conditions of the western and eastern slopes at present, which is primarily a difference in the precipitation regime.

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