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Late Pleistocene and Holocene mammal fauna of the Southern Urals

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ABSTRACT

The present paper analyses changes in the composition and ecological structure of large and small mammal faunas in mountains in comparison with the Transuralian peneplain region during the Late Pleistocene and Holocene. At present, the study area is one of a small number of regions in Northern Eurasia where a series of local faunas have been dated. Small mammal fauna changes occurred mostly due to shifts in species ranges, while large mammal fauna changes occurred as a result of both range shifts and of extinctions. Large and small mammal faunas varied synchronously across the Southern Urals. The transition from the periglacial (mammoth) to the Holocene assemblage is recorded approximately at the Pleistocene/Holocene boundary and seemingly occurred over all of the Southern Urals. Changes in the species composition both of small and of large mammal faunas were directed largely along the same line. From the end of the Pleistocene through the Holocene, both groups of faunas show an increase in the number of inhabitants of partly forested landscapes and forests, and a decrease in the number of open landscape species. This trend was more strongly pronounced in the mountain region in comparison to the peneplain. Changes in species composition of mammal fauna in the Southern Urals, the southern part of Eastern Europe, and the Altay mountains, Southern Siberia and the Baikalian region followed the same basic pattern.

1. Introduction

The Southern Urals includes two large geomorphologic units: the mountain region and the Transuralian peneplain. At present, they belong to different landscape zones: namely, the forest zone (the mountain region) and the steppe (the peneplain) (Chernov, 1984). The boundary between the zones is extremely sharp. Accordingly, the modern theriofaunas in the two regions differ dramatically and belong to different zoogeographic complexes. In this regard, the study of the fauna in the area is of interest because it allows tracing the history of modern fauna formation to the time of contact between the two different zones.

The Southern Urals is a regions for which a sufficient volume and quality of the material has been accumulated for study (Smirnov et al., 1990; Yakovlev, 1997; Kuzmina, 2000; Kuzmina et al., 2001; Smirnov and Kuzmina, 2001; Strukova, 2002; Kuzmina, 2003, 2009; Antipina, 2004; Yakovlev et al., 2006; Petrenko and Asylgaraeva, 2007; Danukalova et al., 2008, 2011; Kosintsev and Gasilin, 2008; Sataev et al., 2009). The studied territory is also one of a small number of regions in Northern Eurasia in which a series of local faunas have been dated, which permits the description of changes in mammal faunas since the end of the Late Pleistocene through the Holocene. At the present time, the history of small mammal faunas in the Late Pleistocene and Holocene has been described for selected areas of the Southern Urals and the Southern Trans-Urals. The history of large mammal fauna, on the other hand, has received less attention in the mountain region of the Southern Urals. The large mammal fauna of the Southern Trans-Urals has not been described in the literature (Kosintsev and Gasilin, 2008). Thus, at present, there are no published studies devoted to the comparison of the processes taking place among the small and large mammal faunas of the Late Cenozoic in the area. In addition, there are no studies including comparative analysis of mammal fauna in the mountains and plains of the Southern Urals.

The purpose of this paper was to reconstruct the history of the mammalian fauna of the Southern Urals. The primary challenge of the work was to compare the changes in the small and large mammal faunas and their respective developmental features in the mountains and plains during the Late Pleistocene and Holocene.

2. The modern situation: some components of the Southern Urals biota

The Southern Urals and the neighbouring orographic province are located between 51° and 56° N and between 56° and 62° E. This area includes two major geomorphologic regions: a mountain region and the Transuralian peneplain. The modern climate of the

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Southern Urals is moderately warm and continental, with warm summers and long, cold winters (Rumyantseva, 1964). In the mountainous areas of the region the climate is cooler and more humid than in the peneplain.

The geographical conditions and vegetation of the Central Province of the Southern Ural Mountains are substantially different from those of the Transuralian peneplain, which consists of the forest-steppe and steppe zones. In mountainous areas, there are a number of altitudinal belts of vegetation in the Southern Urals due to significant meridional length and altitudinal differences. In this area there are mountain-steppe, mountain-forest, mountain-subalpine and mountain-tundra altitudinal belts (Gorchakovskiy, 1975). The mountain-steppe altitudinal belt is evident only in the south-eastern part of the Southern Urals. The mountain territory of the Southern Urals consists of mountain-forest belt. The axial section of mountains of the South Ural is occupied by coniferous taiga forests of spruce and fir. On the western slope there are broadleaf forests consisting of linden and oak, and on the eastern slope there are light coniferous pine and larch forests (Igoshina, 1964). Mountain-subalpine altitudinal belts occur only in the upper slopes of the highest mountains (Smirnov et al., 1990). Light forests containing mostly spruce and fir form this altitudinal belt. On the tops of large ridges (Iremel, Yaman-Tau) there is a mountain-tundra altitudinal belt. The area of the mountain-subalpine and mountain-tundra zones is very small.

In the Southern Urals, mammals are distributed according to biotopical characteristics of the environment. In the mountain area, rodent species adapted to forest habitats dominate (Table 1), and the largest share of land is occupied by voles of the genus *Clethrionomys* (Bolshakov et al., 1986). Some steppe species of rodents occur only in the steppe altitudinal belt within the mountain section of the Southern Urals (Table 1). Some species of lagomorphs, carnivores and ungulates are adapted to forest and forest-steppe habitats in the mountain area. In the peneplain steppe species of rodent dominate, and forest species are absent. In this area, among the representatives of other groups, there are also forest-steppe species.

3. Materials and methods

Fossil materials from localities situated in the mountain and plains of the Southern Urals were used in this study (Fig. 1). All of the fossil materials were dated using radiocarbon (Table 2) or archaeological methods. Their ages ranged from 35,000 to 200 BP. In total, 18 local small mammal fauna of the Late Pleistocene and Holocene (Appendix, Tables A.1), 15 local large mammal fauna of the Late Pleistocene (Tables A.2), and more than 60 local large mammal fauna of Holocene have been studied. Only localities dating to the Holocene with numerous remains of larger mammals are listed in Tables A.3. We also used information about the individual finds of large mammal bones with radiocarbon dating (Table 2). All local small mammal fauna and large mammal fauna of the Late Pleistocene and one fauna (Bayslan-Tash) of the Holocene were recovered from localities in caves. Other large mammal fauna of the Holocene are from archaeological sites. Information about the local small mammal fauna have been published (Smirnov et al., 1990; Yakovlev, 1997; Kuzmina et al., 2001; Smirnov and Kuzmina, 2001; Strukova, 2002; Kuzmina, 2003, 2009; Danukalova et al., 2008, 2011) (Tables A.2 and A.3). The majority of data regarding local large mammal fauna have been published (Smirnov et al., 1990; Antipina, 2004; Yakovlev et al., 2006; Petrenko and Asylgaraeva, 2007; Danukalova et al., 2008, 2011; Sataev et al., 2009) (Tables A.2 and A.3). Information on new local large mammal fauna comes from Sikiyaz-Tamak, Ust'e, Tyubyak, Yukalikulevo, Azanuy, Krasnosel'skaya, Pegova, and Kalinovskaya (Tables A.2 and A.3). The information presented on individual bones of large mammals is also new to the present study. Tables A.1 describes the absolute number of teeth belonging to small mammals in each local fauna. Tables A.2 and A.3 describe the

Table 1
Modern mammal fauna of the Southern Urals and Transuralian peneplain.

Species	Mountain part of Southern Urals, altitudinal belt				Plain part of Southern Urals
	Mountain-tundra	Mountain-subalpine (subgoltsy)	Mountain-forest	Mountain-steppe	
Ochotona pusilla	−	−	−	+	+
Lepus imidus	Occasionally	+	+	+	+
Lepus eropaeus	−	−	−	+	+
Pteromys volans	−	−	+	−	−
Sciurus vulgaris	−	+	+	−	−
Tamias sibiricus	−	−	+	−	−
Marmota bobak	−	−	−	+	−
Marmota baibacina	−	−	−	−	+
Castor fiber	−	+	+	+	−
Spermophilus major	−	−	−	+	+
Spermophilus pygmaeus	−	−	−	−	+
Eliomys quercinus	−	−	+	−	−
Sicista subtilis	−	−	−	+	+
Sicista betulina	+	+	+	+	−
Allactaga jaculus	−	−	−	−	+
Apodemus uralensis	−	−	+	+	−
Apodemus flavicollis	−	−	+	+	−
Apodemus agrarius	−	−	+	+	−
Micromys minutus	−	−	+	−	−
Rattus norvegicus	−	−	+	+	+
Ellobius talpinus	−	−	−	+	+
Allocricetulus eversmanni	−	−	−	−	+
Cricetulus migratorius	−	−	−	−	+
Cricetus cricetus	−	−	+	+	−
Clethrionomys rufocanus	+	+	+	−	−
Clethrionomys rutilus	+	+	+	−	−
Clethrionomys glareolus	+	+	+	+	−
Lagurus lagurus	−	−	−	−	+
Myopus schisticolor	+	+	+	−	−
Arvicola terrestris	−	+	+	+	+
Microtus gregalis	−	−	−	−	+
M. oeconomus	+	+	+	+	−
M. agrestis	+	+	+	+	−
M. arvalis	+	+	+	+	+
Canis lupus.	+	+	+	+	+
Vulpes vulpes.	−	−	+	+	+
Vulpes corsac	−	−	−	−	+
Ursus arctos.	−	−	+	−	−
Martes martes	−	−	+	+	−
M. erminea	+	+	+	+	+
M. nivalis	+	+	+	+	+
M. lutreola	−	−	+	+	+

Table 1 (*continued*)

Species	Mountain part of Southern Urals, altitudinal belt				Plain part of Southern Urals
	Mountain-tundra	Mountain-subalpine (subgoltsy)	Mountain-forest	Mountain-steppe	
M. eversmanni	–	–	+	+	+
Meles leucurus	–	–	+	+	+
Lutra lutra	–	–	+	–	–
Lynx lynx	–	–	+	–	–
Sus scrofa	–	–	+	+	+
Capreolus pygargus	–	–	+	+	+
Alces alces	–	–	+	+	Occasionally

absolute number of bone and teeth belonging to large mammals in each local fauna.

The radiocarbon dates and archaeological artefacts allow for the combination of these local faunas into groups according to chronological periods (Tables 3 and 4).

a) The end of the Nevyansk Interstadial (Bryansk Interstadial, Middle Weichselian, MW; MIS 3) – 35,000–24,000 BP;
b) The Maximum of the Polar-Uralian (Polyarnouralsky) stadial (Ostashkov Stadial, Late Weichselian, Last Glacial Maximum, LGM, MIS 2) – 24,000–17,000 BP;
c) The Late Glacial (Late Weichselian, Last Glacial Transition, LGT, MIS 2) – 17,000–12,400 BP;
d) The Interstadial warming Bölling – Alleröd (Late Weichselian, Bölling – Alleröd Interstadial Complex, BAIC, MIS 2) – 12,400–10,900 BP;
e) The Early Holocene (Preboreal – Boreal; PB–BO; MIS 1) – 10,200–8000 BP;
f) The Middle Holocene (Atlantic – Subboreal; AT–SB; MIS 1) – 8000–2500 BP;
g) The Late Holocene (Subatlantic; SA; MIS 1) – 2500–200 BP.

There are few data on the Younger Dryas fauna, so it was excluded from consideration. Likewise, no data are available on the small mammal fauna of the Southern Ural plains dated to the late Nevyansk Interstadial (MW), nor on small mammals in mountains at the interstadial warming Bölling – Alleröd (BAIC).

Faunas of small and large mammals are analysed separately because of the different taphonomy of their localities. Of the small mammals, representatives of the orders Rodentia and Lagomorpha are considered. The orders Insectivora and Chiroptera are excluded

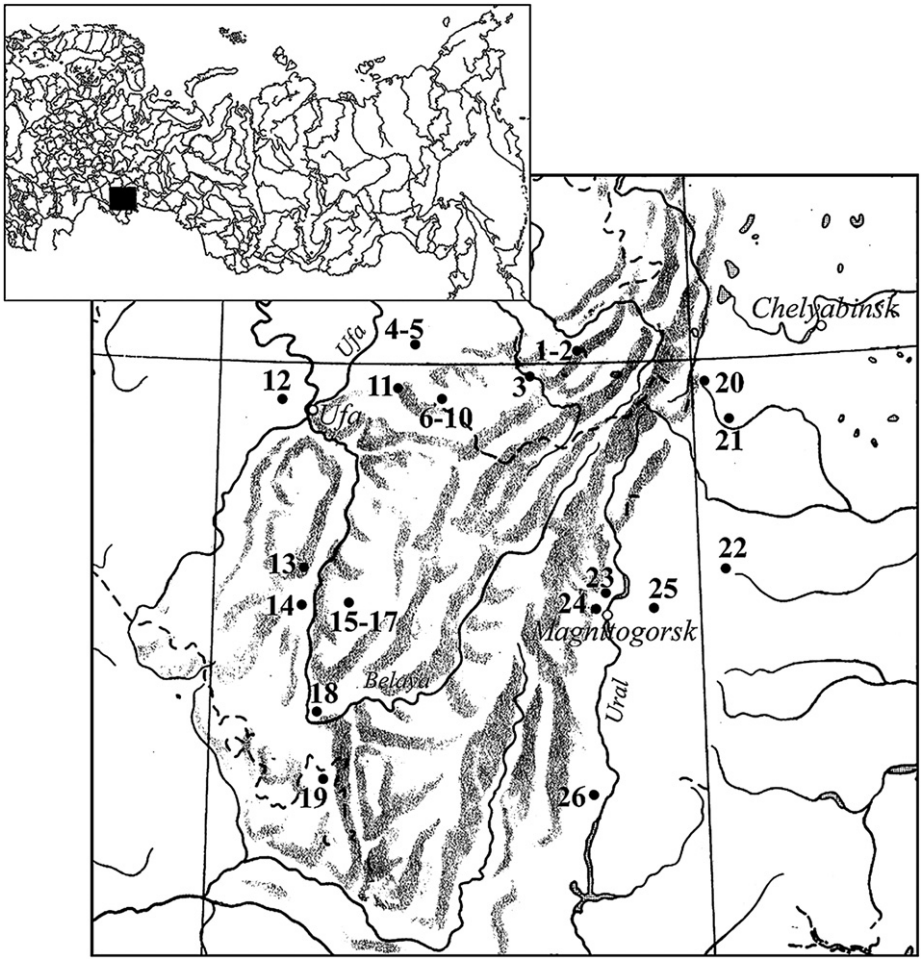

Fig. 1. Distribution of fossil mammal localities in the Southern Urals. 1 – Sikiyaz-Tamak cave; 2 – Nikol'skaya cave; 3 – Ust'-Katavskaya cave; 4 – Kalininskaya; 5 – Pegova; 6 – Serpievskaya cave; 7 – Prizhim II cave; 8 – Idrisovo; 9 – Kapova cave; 10 – Ignatevskaya cave; 11 – Yukalikulevo; 12 – Ufa-II; 13 – Azanuy; 14 – Muradymovskoe; 15 – Maksyutovskiy grotto; 16 – Bayslan-Tash; 17 – Balatukay; 18 – Tuybyak; 19 – Gorny; 20 – Ustinovo; 21 – Krasnosel'skoe; 22 – Ust'e; 23 – Smelovskaya cave; 24 – Syrtinskaya cave; 25 – Arkaim; 26 – Alekseevskaya cave.

Table 2
Radiocarbon dates for Quaternary mammal remains from localities of the Southern Urals.

Locality	Date[a]	±; (>) Infinite date	Laboratory No[b]	Lat. °N	Long. °E	Species	Date object
Ablayzamovskoe luga	3460	70	SOAN – 3850	53,14	59,11	*Ovis aries*	Bone
Alekseevskaya (layer 1, horizon 1)	1470	90	GIN – 11,330	52,59	58,44	Mammal indet.	Bone
Alekseevskaya (layer 1, horizon 2)	2550	100	GIN – 11,331	52,59	58,44	Mammal indet.	Bone
Alekseevskaya (layer 2, horizon 4)	8100	240	GIN – 11,333	52,59	58,44	Mammal indet.	Bone
Alekseevskaya (layer 2, horizon 5)	8450	200	GIN – 11,334	52,59	58,44	Mammal indet.	Bone
Alenushka cave	2718	171	IPAE – 53	54,54	57,47	*Capreolus pigargus*	Bone
Arkaim	3940	180	GIN – 6173	52,38	59,34	–	Charcoal
Asha-1	29,040	385	COAH – 7043	55,00	57,12	*Ursus spelaeus*	Bone
Balatukay (horizon 10–13)	13,450	120	Ki – 14,960	52,54	56,52	Mammal indet.	Bone
Barsuch'ya nora cave	26,320	1790	GIN - 14,244	53,02	56,26	*Ursus rossicus*	Bone
Bayslan-Tash cave	2095	25	OxA – 222,168	52,54	56,52	*Cervus elaphus*	Bone
Bayslan-Tash cave	8216	344	IEMEZ – 1369	52,54	56,52	*Lepus timidus*	
Bayslan-Tash cave (layer 2)	1600	50	GIN – 10,852	52,54	56,52	Mammal indet.	Bone
Bayslan-Tash cave (layer 3)	7140	170	GIN –10,854	52,54	56,52	Mammal indet.	Bone
Bayslan-Tash cave (layer 4)	13,560	250	GIN – 10,854a	52,54	56,52	Mammal indet.	Bone
Cave Pobeda	27,500	350	COAH – 5145	54,10	56,51	*U. spelaeus*	Bone
Dal'nee bagarakskoe	25,800	260	OxA – 22,254	56,13	61,29	*Alces alces*	Bone
Elaninskaya 1	12,135	60	OxA – 22,171	55,12	58,37	*Cervus elaphus*	Bone
Gornova	24,550	120	GIN – 13,528	54,54	55,53	*Bison priscus*	Bone
Gorny	3740	90	AA – 10,259	54,34	54,46	–	Charcoal
Ignatevskaya cave (pit 2, layer 2a)	14,038	490	IEMEZ – 366	54,53	57,46	Mammal indet.	Bone
Ignatevskaya cave (pit 5, layer 3)	>27,620	–	IPAE – 59	54,53	57,46	Mammal indet.	Bone
Kapova cave	13,930	300	GIN – 4853	53,01	57,02	–	Charcoal
Krasnosel'skaya	1825	26	OxA – 22,104	54,35	61,06	*Cervus elaphus*	Bone
Krivoe ozero	3522	36	OxA – 12,536	54,01	60,41	*Bos taurus*	Bone
Kul'metovskiy grotto	10,260	55	OxA – 10,676	55,09	58,42	*Megaloceros giganteus*	Bone
Maksyutovsky grotto (layer 2)	15,650	150	SOAN – 7755	53,01	56,57	*B. priscus*	Bone
Maliy grot u omuta	2270	60	LU – 5126	54,55	57,45	*Capreolus pigargus*	Bone
Nikol'skaya cave	13,120	140	Ki – 14,961	55,19	59,19	*Equus* sp.	Bone
Nikol'skaya cave	14,450	75	OxA – 10,920	55,19	59,19	*Coelodonta antiquitatis*	Bone
Nikol'skaya cave	16,130	310	SOAN – 4804	55,19	59,19	*Mammuthus primigenius*	Bone
Nikol'skaya cave	18,100	215	SOAN – 5310	55,19	59,19	*C. antiquitatis*	Bone
Nikol'skaya cave	21,080	205	SOAN – 5144	55,19	59,19	*Cervus elaphus*	Bone
Novo-Bayramgulovo	4335	110	COAH – 7273	54,12	59,04	*Bos primigenius*	Bone
Novo-Bayramgulovo	4415	125	COAH – 7274	54,12	59,04	*Equus ferus*	Bone
Prizhim II (horizon 2)	16,650	400	IPAE – 32	55,59	57,46	Mammal indet.	Bone
Prizhim II (horizon 2)	17,070	1017	IEMEZ – 700	55,59	57,46	Mammal indet.	Bone
Prizhim II (horizon 6)	21,085	630	IPAE – 37	55,59	57,46	Mammal indet.	Bone
Serpievskaya II (layer 3)	25,200	1800	IPAE – 46	54,05	57,53	Mammal indet.	Bone
Sikiyaz-Tamak 7 (layer 8)	10,775	75	OxA – 10,704	55,19	59,19	*M. giganteus*	Bone
Sikiyaz-Tamak 7 (layer 9)	15,370	80	OxA – 11,069	55,19	59,19	*C. antiquitatis*	Bone
Sikiyaz-Tamak 9 (layer 9)	12,135	60	OxA – 22,171	55,19	59,19	*Cervus elaphus*	Bone
Smelovskaya II cave	25,000	600	GIN – 8403	52,49	58,49	*M. primigenius*	Bone
Smelovskaya II cave	31,400	1700	GIN – 8401	52,49	58,49	*Equus* sp.	Bone
Smelovskaya II cave	41,000	1800	GIN – 8402	52,49	58,49	*M. primigenius*	Bone
Syrtinskaya (horizon 13)	13,990	340	SOAN – 5134	52,50	58,45	Mammal indet.	Bone
Syrtinskaya (horizon 18)	17,160	190	SOAN – 5132	52,50	58,45	Mammal indet.	Bone
Syrtinskaya (horizon 24)	22,050	200	SOAN – 5133	52,50	58,45	Mammal indet.	Bone
Troitskaya 1	16,300	300	IPAE – 165	54,05	61,23	*M. primigenius*	Bone
Tyubyak	3454	32	OxA – 14,201	55,24	54,06	*Sus scrofa*	Bone
Uluir-10	1761	28	OxA – 22,169	55,08	58,38	*Cervus elaphus*	Bone
Uluir-10	10,020	40	OxA – 19,685	55,08	58,38	*M. giganteus*	Bone
Ust'e	3488	32	OxA – 12,562	53,19	60,38	*B. taurus*	Bone
Ust'-Katavskaya cave	35,650	450	OxA – 10,890	54,56	58,08	*Crocuta crocuta*	Bone
Ustinovo (layer 1)	4383	168	IPAE – 47	55,48	59,57	Mammal indet.	Bone
Ustinovo (layer 3)	12,400	300	IPAE – 49	55,48	59,57	Mammal indet.	Bone
Zapovednaya cave	28,700	1050	LU – 3715	54,33	57,16	*U. spelaeus*	Bone
Zhemchuzhnaya cave	17,960	320	COAH – 4805	54,54	57,47	*M. primigenius*	Bone

[a] Dates are not calibrated.
[b] Laboratory codes for dates: AA – University of Arizona, Tucson, USA; GIN – Geological Institute, Russian Academy of Sciences (RAS); IEMEG – Institute of Animal Evolution Morphology and Ecology, RAS; IPAE – Institute of Plant and animal Ecology, Ural division of RAS; Ki – Kyiv Radiocarbon laboratory, National Academy of Sciences of Ukraine; LU – St. Petersburg University, RAS; OxA – Oxford Accelerated, University of Oxford, UK; SOAN – Institute of Geology and Geophysics, Siberian Branch, RAS.

from consideration, as no remains of those orders have been determined to the species level.

3.1. Notes on taxonomy

In publications (Smirnov et al., 1990) addressing the mountain section of the Southern Urals, two species of ground squirrels are addressed: *Spermophilus superciliosus* Kaup, 1839 and *Spermophilus major* Pallas, 1778. *S. superciliosus* existed during the Late Pleistocene to the Early Holocene (Gromov and Baranova, 1981) and was an ancestral form of *S. major* (Gromov et al., 1965; Nadachowski, 1982; Gromov and Erbajeva, 1995); the latter appeared later in the Holocene. Some authors attribute remains of ground squirrels from Late Pleistocene localities to *S. major* (Smirnov, 1993; Kuzmina et al., 2001). In this paper, both species are considered as a group *Spermophilus ex.gr. superciliosus- major.*

Table 3
Species composition of small mammals in the Southern Ural during the Late Pleistocene and Holocene.

Вид	Pleistocene				Holocene			
	MW	LGM	LGT	BAIC	BO	AT	SA1-2	SA3
Ochotona pusilla	+/[a]	+/+[a]	+/+[a]	/+[a]	/+[a]	+/[a]	+/+[a]	−/+[a]
Pteromys volans	−/	−/−	−/−	/−	/−	−/	−/−	+/−
Sciurus vulgaris, L.	−/	−/−	−/−	/−	/−	+/	+/−	+/−
Tamias sibiricus	−/	−/−	−/−	/−	/−	−/	−/−	+/−
Spermophilus ex gr. *superciliosus- major*	+/	+/+	+/+	/+	/+	+/	−/+	−/+
Spermophilus pygmaeus	−/	−/−	−/−	/−	/+	−/	−/+	−/+
Eliomys quercinus	−/	−/−	−/−	/−	/−	−/	−/−	+/−
Sicista sp.	−/	−/−	+/−	/−	/+	+/	+/+	+/+
Allactaga jaculus	−/	−/+	+/+	/+	/+	−/	−/+	−/+
Allactaga elater	−/	−/−	−/−	/−	/+	−/	−/+	−/−
Alactagulus sp.	−/	−/−	+/−	/−	/−	−/	−/−	−/−
Pygeretmus sp.	−/	−/+	−/+	/−	/−	−/	−/−	−/−
Apodemus sp.	−/	−/−	−/−	/−	/+	+/	+/+	+/+
Rattus sp.	−/	−/−	−/−	/−	/−	−/	−/−	+/+
Ellobius talpinus	−/	−/−	−/−	/+	/+	+/	+/+	−/+
Allocricetulus eversmanni	+/	−/+	+/−	/−	/+	+/	+/+	−/+
Cricetulus migratorius	+/	+/+	+/+	/+	/+	+/	+/−	−/+
Cricetus cricetus	+/	−/−	−/−	/−	/+	+/	+/+	+/+
Clethrionomys. rufocanus	+/	+/−	+/−	/−	/−	+/	+/−	+/−
Cl. ex gr *rutilus-glareolus*	+/	+/+	+/−	/−	/+	+/	+/+	+/−
Lagurus lagurus	+/	+/+	+/+	/+	/+	+/	+/+	−/+
Eolagurus luteus	+/	+/+	+/+	/+	/+	−/	−/−	−/−
Dicrostonyx sp.	+/	+/+	+/−	/+[b]	/−	−/	−/−	−/−
Lemmus sibiricus	+/	+/−	−/−	/+[b]	/−	−/	−/−	−/−
Arvicola terrestris	+/	+/+	+/+	/+	/+	+/	+/+	+/+
Microtus gregalis	+/	+/+	+/+	/+	/+	+/	+/+	−/+
M. oeconomus	+/	+/?	+/+	/+	/+	+/	+/+	+/+
M. agrestis	+/	−/−	−/−	/−	/+	+/	+/+	+/+
M. arvalis	+/	−/+	+/+	/+[b]	/+	+/	+/+	+/+

[a] Data for the mountains area gives in numerator and data for the Transuralian peneplain gives in denominator.
[b] Found in the northern part of Transuralian peneplain only.

Table 4
Species composition of large mammals fauna in the Southern Urals during the Late Pleistocene and Holocene.

Species	Pleistocene				Holocene		
	MW	LGM	LGT	BAIC	PB–BO	AT-SB	SA
Lepus timidus L.	+/+[a]	+/+[a]	+/+[a]	+/+[a]	+/+[a]	+/+[a]	+/+[a]
Castor fiber L.	+/+	−/−	−/−	+/+	+/+	+/+	+/+
Marmota bobak Můller	+/+	+/+	+/+	+/+	+/+	+/+	−/+
Canis lupus L.	+/+	+/+	+/+	+/+	+/+	+/+	+/+
Alopex lagopus L.	+/+	+/+	+/+	+/+	−/−	−/−	−/−
Vulpes corsac L.	+/+	+/+	+/+	+/+	+/+	−/+	−/+
Vulpes vulpes L.	+/+	+/+	+/+	+/+	+/+	+/+	+/+
Ursus arctos L.	+/+	+/+	+/+	+/+	+/+	+/+	+/+
U. spelaeus Rosenmuller	+/−	−	−	−	−	−	−
U. savini Andrews	+/+	−	−	−	−	−	−
Martes zibellina L.	−/−	−/−	−/−	−/−	−/−	−/−	+/−
Martes martes L.	+/−	−/−	+/−	+/−	+/+	+/+	+/+
Gulo gulo L.	+/+	+/+	+/+	+/+	+/+	+/+	+/+
Mustela erminea L.	+/+	+/+	+/+	+/+	+/+	+/+	+/+
M. nivalis L.	+/+	+/+	+/+	+/+	+/+	+/+	+/+
M. eversmanni Lesson	+/+	+/+	+/+	+/+	+/+	+/+	+/+
M. putorius L.	−/−	−/−	−/−	−/−	−/−	−/−	+/−
Meles meles L.	−/−	−/−	−/−	−/−	+/+	+/+	+/+
Meles leucurus Hodgson	−/−	−/−	−/−	−/−	−/−	−/−	+/+
Lutra lutra L.	+/+	−/−	−/−	−/−	+/+	+/+	+/+
Crocuta c. spelaea Goldfuss	+/+	−	−	−	−	−	−
Panthera spelaea Goldfuss	+/+	+/+	+/+	+/+	−	−	−
Lynx lynx L.	+/−	−/−	−/−	−/−	+/−	+/−	+/−
Mammuthus primigenius Blumenbach	+/+	+/+	+/+	+/+	−	−	−
Equus (*E.*) *ferus* Boddaert	+/+	+/+	+/+	+/+	−	−	−
E. (*E.*) *ferus gmelini* Antonius	−	−	−	−	+/+	−/+	−/+
Equus sp. (small forma)	−/+	−	−	−	−	−	−
Coelodonta antiquitatis Blumenbach	+/+	+/+	+/+	+/+	−	−	−
Sus scrofa L.	−	−	−	−	+/+	+/+	+/+
Camelus ferus Przewalski	−/+	−	−	−	−	−	−
Capreolus pygargus Pallas	−	−	−	−	+/+	+/+	+/+
Cervus elaphus L.	+/+	+/+	+/+	+/+	+/+	+/+	+/+
Megaloceros giganteus Blumenbach	+/+	−	−	+/+	+/+	−	−
Alces alces L.	+/+	+/+	+/+	+/+	+/+	+/+	+/+
Rangifer tarandus L.	+/+	+/+	+/+	+/+	+/−	+/−	+/−
Bison priscus Bojanus	+/+	+/+	+/+	+/+	−	−	−
Bos primigenius Bojanus	−	−	−	−	−/+	−/+	−/−
Saiga tatarica L.	+/+	+/+	+/+	+/+	−/+	−/+	−/+
Ovis ammon L.	+/−	−	−	−	−	−	−

[a] Mountains/Transuralian peneplain.

The list of species has been changed in comparison to previously published lists, as some new data have been recently obtained. Paleo-DNA studies, in particular, proved that the Don hare (*Lepus tanaiticus*), previously considered to be a typical Late Pleistocene species of Eastern Europe and Siberia, was in fact an ecomorph of *Lepus timidus* (Prost et al., 2010). Similarly, it was suggested that two horse species, *Equus* (*Equus*) *latipes* and *E.* (*E.*) *uralensis*, inhabited the Southern Urals in the Late Pleistocene (Smirnov et al., 1990). Analysis has shown, however, that those taxa are actually subspecies of a single species (Kosintsev and Plasteeva, 2009), so they are considered here to belong to the species *Equus ferus*. It was also believed that only one badger species, *Meles meles*, inhabited the Southern Urals during the Holocene (Kosintsev, 2007). A careful revision of the *Meles* genus remains showed that two badger species, *M. meles* and *Meles leucurus*, occurred there at that time (Gasilin and Kosintsev, 2010).

The small cave bear *Ursus savini* lived in the Urals during the Late Pleistocene (Kosintsev, 2007). Its remains from Middle Uralian localities are dated by radiocarbon to approximately 36–32 ka BP (Pacher and Stuart, 2009). Bone remains of this species are dated to 26,320 BP from localities in the Southern Urals. *U. savini* bones were also found near the Late Mousterian in the Ural River (Shirokov et al., 2011). Thus, *U. savini* inhabited the Southern Urals almost to the end of the Nevyansk interstadial (the Middle Weichselian). *Microtus arvalis* is considered to be a common vole (sensu lato).

Among the large mammals of the Nevyansk (Middle Weichselian) age, there have been found remains of a small horse subsequently referred to as *Equus* sp. (small forma). It may be safely suggested that the horse belongs to the *Equus* (*Sussemiones*) group, which lived in southern Siberia until the end of the Middle Weichselian (Orlando et al., 2009).

4. Dynamics of species composition of small mammal fauna

The following conclusions can be drawn from an analysis of published data with respect to local small mammal fauna of the Southern Urals in the Late Pleistocene and Holocene (Smirnov et al., 1990; Yakovlev, 1997; Kuzmina, 2000, 2003, 2009; Kuzmina et al., 2001; Strukova, 2002; Antipina, 2004; Yakovlev et al., 2006; Petrenko and Asylgaraeva, 2007; Danukalova et al., 2008, 2011; Kosintsev and Gasilin, 2008; Sataev et al., 2009). During the Late Pleistocene in the mountain region, the species composition does not show any noticeable changes from the Nevyansk Interstadial to the interstadial warming Bölling – Alleröd (Table 3). It changed abruptly between 14 ka BP and the Early Holocene (Table A.1). At that time, *Dicrostonyx* sp. disappears from the fauna, and new species, including *Apodemus* sp., *Ellobius talpinus* and *Microtus agrestis*, appear (Table 3).

In the Transuralian peneplain region during the Late Pleistocene, the species composition of small mammal fauna changed slightly between the Nevyansk Interstadial and the interstadial warming Bölling – Alleröd (Table 3). A drastic change in the fauna occurred between the Bölling – Alleröd and the Atlantic period of the Early Holocene (Table 3). In a broad sense, this interval corresponds to the transition from the Pleistocene to Holocene. It was within this interval that four species disappeared from the faunal assemblage, including *Pygeretmus* sp., *Cricetulus migratorius*, *Lemmus sibiricus* and *Dicrostonyx* sp., while at least seven species appeared: *Spermophilus pygmaeus*, *Sicista* sp., *Allactaga elater*, *Apodemus* sp., *Allocricetulus eversmanni*, *Cricetus cricetus*, *Clethrionomys* ex gr. *rutilus-glareolus* (Table 3).

Until the Bölling – Alleröd, there was a single small mammal assemblage, the periglacial (or "mammoth") assemblage, that was widespread over the entire area of the Southern Urals. Between the end of the LGT and the Early Holocene, the small mammal fauna was transformed into the Holocene faunal assemblage. Changes in the fauna composition were similarly directed and occurred simultaneously in the mountains and on the peneplain.

The second important change in small mammal fauna occurred during the Late Holocene and 200 BP simultaneously in the mountain and peneplain regions (Table 3). This change corresponds to the transition from the middle to the final stages of the Late Holocene (Subatlantic 2/Subatlantic 3), which coincides with a change to the modern state of fauna. Four new species found in the mountain region date to that time period: *Pteromys volans, Sciurus vulgaris, Tamias sibiricus, Eliomys quercinus,* and *Rattus* sp. Three other species *(A. eversmanni*, *C. migratorius*, and *Lagurus lagurus*) disappear (Table 3). In the Transuralian peneplain fauna, two species (*C. migratorius*, *Rattus* sp.) appeared and one species (*A. elater*) disappeared (Table 3).

Changes in species composition of small mammal faunas at the Pleistocene/Holocene transition occurred synchronously in the mountain region and in the region of the Transuralian peneplain, after BAIC. The transition to the modern fauna took place simultaneously over the entire area of the Southern Urals, at the Atlantic 2/Atlantic 3 boundary.

5. Dynamics of species composition of large mammal fauna

An analysis published and new data on species composition performed for large mammal faunas (Table 4) permitted a distinction among several chronological and geographical faunal assemblages that existed in the Southern Urals during the second half of Late Pleistocene and Holocene.

5.1. Chronological assemblages

The difference is most evident between assemblages dated to the Late Pleistocene (the mammoth assemblage) and assemblages dated to the Holocene (the Holocene mammal assemblage). The Bölling – Alleröd and the Preboreal – Boreal faunas are distinguished by 12 species. The species *Alopex lagopus*, *Panthera spelaea*, *Mammuthus primigenius*, *Coelodonta antiquitatis*, and *Bison priscus* are absent from the Holocene faunas. The species *M. meles*, *Lutra lutra*, *Lynx lynx*, *Sus scrofa*, *Capreolus pygargus*, and *Bos primigenius* are absent from the faunas of the Late Pleistocene (Table 3). Additionally, the assemblages included different horse species: *Equus* (*E.*) *ferus* and *E.* (*E.*) *gmelini.*

The mammoth theriocomplex (mammal assemblage) of the 2nd half of the Late Pleistocene was represented by two variants: the Nevyansk (Middle Weichselian) and the Polar Uralian (Late Weichselian). The first and earlier subcomplex included *Ursus spelaeus*, *U. savini*, *Crocuta c. spelaea*, *L. lutra*, *L. lynx*, *Equus* sp. (small form), *Camelus ferus*, and *Ovis ammon*. Those species are not found in the second (Polar Uralian) subcomplex (Table 3). No variation with time has been recorded in the species composition of the Polar Uralian variant (Table 3).

The Holocene mammal assemblage varied insignificantly with time. Three chronological stages may be recognised. The first stage is the early Holocene (Preboreal – Boreal), with relict species of the mammoth assemblage, such as *Megaloceros giganteus*, still persisting in the fauna. The second stage is the middle Holocene (Atlantic – Subboreal), during which *B. primigenius* is present while *Mustela putorius* and *M. leucurus* are absent. The third stage is the Late Holocene (Subatlantic) fauna, which is distinct for the absence of *B. primigenius* and the presence of *M. putorius* and *M. leucurus*.

5.2. Geographical variants of mammal assemblages

There are only insignificant differences between the species compositions of the mammoth assemblages the mountain region and the Transuralian peneplain (Table 2). During the Nevyansk period (Middle Weichselian), the mountains were not inhabited by *Equus* sp. (small forma), or by *C. ferus*. *U. spelaeus*, *Martes martes*, *L. lynx*, and *O. ammon* were absent from the peneplain region. *U. spelaeus* remains are known only from localities on the western slope of the Southern Urals (Table 4). The faunas of the two regions dated to the Polar Uralian period (Late Weichselian) are distinguished by one species (*M. martes*) only, such that their species compositions are nearly the same (Table 3). It is easily observed that geographic diversity in the composition of the mammoth assemblage decreased at the end of the Late Pleistocene in the Southern Urals. This decrease in diversity could be due to extinctions and changes in the ranges of some species.

The Holocene assemblages of the mountain region were also different in species composition from those of the Transuralian peneplain. In the early Holocene, the mountain mammal fauna included *Vulpes corsac* and *Equus* (*E.*) *gmelini*, while *Marmota bobak* was present in that fauna in the Early and Middle Holocene (Table 3). Thus, typical species of open landscapes were present in the mountain faunas as late as the middle Holocene. *L. lynx* and *Rangifer tarandus* persisted in the mountain region through the Holocene, while *M. putorius* appeared in the Late Holocene (Table 2). The Transuralian peneplain region was inhabited by *V. corsac*, *E.* (*E.*) *gmelini* and *Saiga tatarica* during the entire Holocene. *B. primigenius* lived there in the Early and the Middle Holocene (Table 3).

As follows from the analysis of changes in the large mammal fauna with time, the mammoth assemblage restructuring began as early as the end of the Pleistocene, at the transition from the Nevyansk (Middle Weichselian) period to the LGM. At that time, *U. spelaeus* and *U. savini* became extinct, and *Crocuta c. spelaea*, *Equus* sp. (small forma) and *O. ammon* permanently changed their ranges. The restructuring was completed at the Pleistocene/Holocene transition, as a result of the extinction of *P. spelaea*, *M. primigenius*, *C. antiquitatis*, and *B. priscus*, permanent changes in the range of *A. lagopus*, and the appearance of some new species in the fauna (*M. meles*, *L. lutra*, *L. lynx*, *S. scrofa*, *C. pygargus*, *B. primigenius*). It seems probable the *Equus* (*E.*) *ferus* also transformed into *E.* (*E.*) *gmelini* at that time.

In the Early Holocene, *Canis familiaris* appeared in the Southern Urals. In the Middle Holocene (SB2) *Bos taurus*, *Capra hircus*, *Ovis aries, Sus scrofa domestica* and *Equus caballus* also appeared in this territory (Table A.3). It thus appears that this period corresponded with the domestication of some animal species.

6. Dynamics of the ecological structure of mammal fauna

A comparison of the species compositions of the periglacial and Holocene small mammal assemblages in the Transuralian peneplain has yielded the following conclusions. The Holocene fauna lost the cold-tolerant species *L. sibiricus* and *Dicrostonyx* sp., as well as the desert inhabitant *Pygeretmus* sp. In their place, some species associated with arboreal and mesophytic plants appeared (*Apodemus* sp., *Sicista* sp., *C. cricetus*, and *Clethrionomys* ex gr. *rutilus-glareolus*) (Table 2). A similar comparison between small mammal assemblages of different ages performed for the mountain region revealed the disappearance of a cold-tolerant species (*Dicrostonyx* sp.) and the appearance of *Apodemus* sp. and *M. agrestis*, which are associated with arboreal and mesophytic plants (Table 2). Thus, mountain and peneplain faunas were both subjected to similar changes in composition when the periglacial assemblage was replaced by the Holocene assemblage. Both regions lost cold-tolerant species, while species associated with arboreal and mesophytic vegetation increased in number.

The modern small mammal assemblage in the mountains developed by way of the disappearance of open landscape dwellers (*A. eversmanni*, *C. migratorius*, and *L. lagurus*) and the appearance of forest (*Pteromys volans, Sciurus vulgaris, Tamias sibiricus,* and *Eliomys quercinus*) and synanthropic species (*Rattus* sp.). At present, in the mountain region, there are two steppe species (*Ochotona pusilla, E. talpinus*), which are located only in mountain-steppe altitudinal belts (Table 1).

The Transuralian peneplain's modern fauna is distinct for the disappearance of a species typical for semideserts and dry steppes (*A. elater*) and the appearance of steppe (*C. migratorius*) and synanthropic (*Rattus* sp.) species. The modern small mammal assemblage developed along similar lines in the mountain and peneplain regions: in both cases, species associated with xerophytic vegetation decreased in number, while those associated with mesophytic and arboreal vegetation increased. The process was particularly striking in the mountain region, where all of the open landscape dwellers vanished, and typical forest animals appeared instead. The arrival of synanthropic species is a feature the two regions have in common.

A comparison between chronologically different faunas of large mammals (Table 3) has shown that noticeable alteration in their species composition began as early as the Late Pleistocene. At the transition from the Nevyansk (Middle Weichselian) to the Polar Uralian (Late Weichselian) periods, some species became extinct (*U. spelaeus*, *U. savini*, and possibly *Equus* sp. [small forma]), while the ranges of others were permanently changed (*Crocuta c. spelaea*, *C. ferus*, and *O. ammon*). The process continued through the Pleistocene–Holocene transition, when additional species went extinct (*P. spelaea*, *M. primigenius*, *C. antiquitatis*, and *B. priscus*), and some others changed their ranges permanently (*A. lagopus*, *M. meles*, *L. lutra*, *L. lynx*, *S. scrofa*, *C. pygargus*, and *B. primigenius*). Alterations in fauna composition continued in the Holocene. For example, one relict from the Pleistocene, *Megaloceros giganteus,* disappeared by the beginning of the middle Holocene. Another species, *M. putorius*, appeared in Late Holocene. Therefore, the mammoth assemblage was not momentarily replaced by the Holocene mammal assemblage. The replacement proceeded in three stages, namely: the end of the Karginsky (Middle Weichselian) interglacial and the beginning of the Polar Uralian (LGM, Late Weichselian) periods; the Bölling–Alleröd–Preboreal; and the Boreal – Atlantic.

Considering the ecological requirements of the extinct and newly appearing species, the following conclusions may be drawn. The species that went extinct are largely dwellers of open landscapes (*A. lagopus*, *U. spelaeus*, *U. savini*, *Crocuta c. spelaea*, *Equus* sp. (small forma), *C. ferus*, *B. priscus*, *O. ammon*) and periglacial (*P. spelaea*, *M. primigenius*, *C. antiquitatis*, and *M. giganteus*). Most of the latter may also be grouped with open landscape inhabitants. Some species that live in the steppe and forest-steppe arrived in the region (*M. putorius*, *M. meles*, *L. lutra*, *L. lynx*, *S. scrofa*, *C. pygargus*, and *B. primigenius*).

Large mammal fauna showed pronounced geographical differentiation during the Nevyansk (Middle Weichselian) period. Later, during the Polar Uralian (Late Weichselian) period, the difference lessened, but in the Holocene the difference was gradually increased and reached its peak in the Late Holocene (Table 3). Faunal assemblages in the mountain and peneplain regions evolved to their present state during the Late Holocene.

The transition from the periglacial (mammoth) assemblage to the Holocene assemblage proceeded in several stages. The transition itself occurred simultaneously over the regions of Europe, the Urals and Northern Asia. In every region, the species *U. spelaeus*, *Crocuta c. spelaea* and most likely *U. savini* and *Equus* sp. (small forma) were first to become extinct; somewhat later, *P. spelaea*, *C. antiquitatis*, *B. priscus* and *M. primigenius* disappeared from the continental part of their range. Finally, *M. giganteus* and *M. primigenius* went extinct on islands (Stuart et al., 2002, 2004; Rohland et al., 2005; Stuart and Lister, 2007, 2011; Orlova et al., 2008; Kosintsev and Vasil'ev, 2009; Kuzmin, 2009; Pacher and Stuart, 2009; Markova et al., 2010).

In general, changes in species composition of mammal fauna in the Southern Urals, the southern part of Eastern Europe (Markova et al., 2008), the Altay mountains (Dupal, 1998), Southern Siberia (Ovodov et al., 1992), and the Baikalian region (Ermolova, 1978; Khenzykhenova et al., 2001) followed the same basic pattern. The mammal faunas of those regions exhibit regular decreases in the number of open landscape dwellers, while species of semi-open and forested landscapes and those associated with mesophytic vegetation became more abundant.

7. Conclusions

Alterations of small mammal and large mammal faunas recorded in the Southern Urals at the end of the Late Pleistocene and during the Holocene resulted from several processes. Small mammal fauna changes occurred mostly due to shifts of the species' ranges, while large mammal faunas varied as a result of both range shifts and extinctions. Large and small mammal faunas varied synchronously over all of the Southern Urals. The transition from the periglacial (mammoth) assemblage to the Holocene assemblage is recorded approximately at the Pleistocene/Holocene boundary and seemingly occurred over all of the Southern Urals. Changes in the species composition of both small and large mammal faunas were directed largely along the same lines. From the end of the Pleistocene through the Holocene, both groups of faunas show an increase in the number of inhabitants of partly forested landscapes and forests and a decrease in the number of open landscape species. The process of species replacement was more active in the mountain region in comparison with the peneplain. As a result, the mountain mammal fauna had practically no species of open landscapes remaining by the end of the Late Holocene. The general trend in mammal fauna evolution reflects the process of arboreal vegetation increasing in abundance from the Late Pleistocene to the present day in the landscapes of the Southern Urals (Lapteva, 2006).

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Appendix A

Table A.1
Remains number of small mammal species from localities in the Southern Ural.

Species	Local faunas, date (yr BP)																	
	Mountain part of Southern Urals										Plain part of Southern Urals							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Ochotona pusilla	87	26	12	5	63	820	235	–	–	–	1	4	3	3	9	6	26	6
Pteromys volans	–	–	–	–	–	–	–	2	1	–	–	–	–	–	–	–	–	–
Sciurus vulgaris	–	–	–	–	–	–	1	2	–	–	–	–	–	–	–	–	–	–
Tamias sibiricus	–	–	–	–	–	–	–	2	10	–	–	–	–	–	–	–	–	–
Spermophilus. superciliosus- major	45	20	–	10	43	1	–	–	–	2	1	1	1	2	1	1	1	1
Spermophilus pygmaeus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	–
Eliomys quercinus	–	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–	–	–
Sicista sp.	–	–	1	–	–	8	4	2	8	–	–	–	–	–	5	4	14	10
Allactaga jaculus	–	–	–	2	1	–	1	–	–	40	1	2	–	2	5	10	4	2
Allactaga elater	–	–	–	–	1	–	–	–	–	–	–	–	–	–	3	3	4	–
Alactagulus sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pygeretmus sp.	–	–	–	–	–	–	–	–	–	–	1	1	1	–	–	–	–	–
Apodemus sp.	–	–	–	–	–	52	73	3	55	2	–	–	–	–	3	4	3	6
Rattus sp.	–	–	–	–	–	–	–	2	8	50	–	–	–	–	–	–	–	–
Ellobius talpinus	–	–	–	–	–	83	68	–	–		–	2	–	12	38	99	73	72
Allocricetulus eversmanni	4	–	–	8	9	20	12	–	–	20	2	2	–	–	5	7	6	4
Cricetulus migratorius	74	25	6	3	31	17	7	–	–	–	–	2	7	9	–	–	–	–
Cricetulus sp.	–	–	–	–	–	–	–	–	–	10	–	–	–	–	8	3	–	1
Cricetus cricetus	1	–	–	–	–	46	31	10	68	–	–	–	–	–	13	55	54	47
Cl. rufocanus	3	–	3	–	16	8	30	1	5	–	–	–	–	–	–	–	–	–
Cl. ex gr rutilus-glareolus	17	7	2	4	16	342	1145	110	119	–	1	–	–	–	2	6	6	1-
Lagurus lagurus	365	67	27	50	105	788	252	–	–	10	114	71	42	225	76	127	104	95
Eolagurus luteus	1	–	1	3	5	–	2	–	–	–	14	59	29	16	18	26	2	–
Dicrostonyx sp.	158	26	19	–	50	–	–	–	–	–	1	–	–	6	–	–	–	–
Lemmus sibiricus	13	2	–	–	1	–	–	–	–	–	–	–	–	5	–	–	–	–
Arvicola terrestris	28	–	1	–	27	56	49	12	58	295	1	2	1	4	20	42	71	71
M. gregalis	383	69	41	40	277	245	113	–	–		7	31	21	26	99	315	174	349
M. oeconomus	100	24	7	13	60	52	27	9	2		–	29	7	4	11	38	11	25
M. agrestis	7	–	–	–	5	57	85	14	27	38	–	–	–	1	1	–	7	12
M. arvalis	–	–	–	3	–	93	193	13	77	35	1	–	–	–	31	39	78	108
Total bone	1286	266	120	142	710	2688	2328	182	445	500	145	207	112	315	350	787	639	819

1 – Serpievskaya cave (25,200 yr BP); 2 – Prizhim II (21,800 yr BP); 3 – Prizhim II (16,650 yr BP); 4 – Maksyutovsky grotto (15,650 yr BP); 5 – Ignatevskaya cave (14,038 yr BP); 6 – Baislan-Tash cave (7140 yr BP); 7 – Baislan-Tash cave (1600 yr BP); 8 – Lemeza (200 yr BP); 9 – Sim (200 yr BP); 10 – Gusikha (200 yr BP); 11 – Syrtinskaya cave (22,050 yr BP); 12 – Syrtinskaya cave (17,160 yr BP); 13 – Syrtinskaya cave (13,990 yr BP); 14 – Ustinovo (12,400 yr BP); 15 – Alekseevskaya cave (8450 yr BP); 16 – Alekseevskaya cave (8100 yr BP); 17 – Alekseevskaya cave (2550 yr BP); 18 – Alekseevskaya cave (1470 yr BP).

Table A.2
Remains number of large mammal species from localities in the Southern Ural in the Late Pleistocene.

Species	Local faunas														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Lepus timidus	67	97	5	38	28	226	95	74	17	186	+	15	492	125	21
Castor fiber	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–
Marmota bobak	83	68	52	3	627	61	130	27	17	17	+	3	75	178	7
Canis lupus.	55	61	18	–	2	3	11	5	–	2	–	11	–	4	–
Alopex lagopus.	28	30	5	1	18	10	18	9	–	7	+	1	4	5	3
Vulpes vulpes.	35	11	6	–	39	–	1	10	–	6	–	1	2	–	–
Vulpes corsac	–	–	–	–	9	–	4	1	–	–	–	–	1	–	–
Ursus arctos.	3	–	9	–	2	–	1	–	–	–	–	–	3	–	–
Ursus spelaeus	54	343	–	–	–	–	–	–	–	–	–	–	–	–	–
Martes martes	1	2	–	–	–	–	–	1	–	–	–	3	–	–	–
Gulo gulo	2	–	–	–	1	–	1	–	–	–	–	–	–	–	–
M. erminea	–	2	–	1	–		3	1	–	1	–	–	24	–	2
M. nivalis	–	–	–	–	1	1	1	1	–	6	–	–	4	–	–
M. eversmanni	–	–	–	–	1	–	–	1	–	2	–	–	1	–	–
Lutra lutra	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Crocuta c. spelaea	28	4	48	–	–	–	–	–	–	–	–	–	–	–	–
Panthera spelaea	5	4	–	–	–	–	2	4	–	–	–	–	–	–	–
Lynx lynx	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Mammuthus primigenius	10	–	2	–	3	–	3	–	–	–	+	1	–	–	–
Equus (E.) ferus	159	27	488	1	53	1	266	3	4	6	+	58	24	4	4
Equus hydruntinus	–	–	16	–	–	–	–	–	–	–	–	–	–	–	–
Coelodonta antiquitatis	112	18	122	–	12	–	144	4	2	–	+	9	2	5	–
Cervus elaphus	92	16	2	–	8	–	28	2	–	–	–	–	1	–	1
Megaloceros giganteus	2	–	2	–	–	–	–	–	–	–	–	–	–	–	–

Table A.2 (*continued*)

Species	Local faunas														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Alces alces	1	–	–	–	–	–	7	–	–	–	–	–	–	–	–
Rangifer tarandus	90	17	2	–	2	8	171	2	12	–	–	34	22	19	12
Bison priscus	58	4	85	–	4	–	294	15	4	1	–	20	4	4	4
Saiga tatarica	1	5	21	1	30	–	8	1	1	1	–	–	1	8	2
Ovis ammon	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total	780	711	890	45	840	310	1188	161	57	235	–	156	660	352	56

1 – Ust'-Katavskaya cave (35,650 BP); 2 – Ignat'evskaya cave (35,000 BP); 3 – Smelovskaya II cave (31,400 BP); 4 – Prizhim II (21,080 BP); 5 – Syrtinskaya cave (17,160 BP); 6 – Prizhim II (16,650 BP); 7 – Nikol'skaya cave (16,130 BP); 8 – Maksyutovskiy grotto (15,650 BP); 9 – Sikiyaz-Tamak (15,370 BP); 10 – Ignat'evskaya cave (14,038 BP); 11 – Kapova cave (13,930 BP); 12 – Serpievskaya 1 (13,870 BP); 13 – Balatukay (13,450 BP); 14 – Ustinovo (12,400 BP); 15 – Sikiyaz-Tamak (10,775 BP).

Table A.3
Remains number of large mammal species from localities in the Southern Ural in the Holocene.

Species	Local faunas														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Lepus timidus	45	–	1	1	17	–	3	1	–	1	–	263	12	25	4
Castor fiber	1	–	–	14	31	6	50	108	2	–	6	38	–	20	30
Marmota bobak	12	–	–	18	24	2	5	–	–	–	–	131	–	–	22
Canis lupus	1	2	4	32	3	3	–	2	–	–	–	11	–	3	1
Vulpes vulpes	3	–	–	8	143	2	11	3	–	–	–	26	–	1	9
Vulpes corsac	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–
Ursus arctos	–	–	1	8	25	1	10	14	4	–	1	5	–	268	24
Martes zibellina	–	–	–	–	–	–	–	–	–	–	–	–	–	7	–
Martes martes	2	–	–	–	–	–	–	4	–	–		10	1	69	2
Martes sp.	1	–	–	–	–	–	1	2	–	–	–	14	7	198	–
Gulo gulo		–	–	–	–	1	–	–	–	–	–	2	–	1	–
M. erminea	67	–	–	–	–	–	–	–	–	–	1	86	–	–	–
M. nivalis	38	–	–	–	–	–	–	–	–	–	–	7	–	–	–
M. lutreola	–	–	–	–	–	–	–	–	–	–	1	1	–	9	–
M. eversmanni	1	–	–	–	1	–	–	1	–	–	–	18	–	–	–
Meles meles	–	–	–	5	5	1	5	–	–	–	–	2	–	9	–
Lutra lutra	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Lynx lynx	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–
Equus ferus gmelini	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Sus scrofa	–	1	7	–	2	–	3	2	–	1	–	–	–	–	–
Capreolus pygargus	1	41	2	10	12	3	11	515	16	46	20	549	2	55	1
Cervus elaphus	–	–	–	8	–	–	–	–	12	–	1	–	–	17	4
Alces alces	–	17	5	33	3	16	36	188	12	6	55	14	209	55	31
Rangifer tarandus	–	–	–	–	–	–	–	2	–	–	–	1	1	35	–
Bos primigenius	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–
Saiga tatarica	–	–	–	45	–	1	–	–	–	–	1	–	–	–	7
Canis familiaris	–	–	12	27	48	8	42	9	–	–	1	–	–	–	67
Equus caballus		–	4902	1061	3793	121	1844	2205	105	1	19	41		16	26,065
Sus scrofa domestica	–	–	57	105	567	8	752	364	–	–	–	–	–	–	4211
Bos taurus	–	–	6525	4153	182,420	732	5310	1881	38	–	2	8	–	–	20,177
Ovis aries et Capra hircus	–	–	3029	1668	33,167	341	1889	363	1	–	29	43	1	2	24,667
Total	173	62	25	392	190	14,913	143	282	317,863	55	13	1199	231	775	75,322

1 – Bayslan-Tash (7140 BP); 2 – Idrisovo (Subboreal 1); 3 – Muradymovskoe (Subboreal 2); 4 – Arkaim (3940 BP); 5 – Gorny (3740 BP); 6 – Ust'e (3488 BP); 7 – Tyubyak (3450 BP); 8 – Yukalikulevo (Subboreal 3); 9 – Azanuy (Subboreal 3): 10 – Idrisovo (Subatlantic 1); 11 – Krasnosel'skaya (1825 BP); 12 – Bayslan-Tash (1600 BP); 13 – Pegova (Subatlantic 2); 14 – Kalinovskaya (Subatlantic 2); 15 – Ufa-II (Subatlantic 2).

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