

Can we Infer Humidity Gradients across the Ural Mountains during the Late Quaternary using Arvicoline Rodents as an Environmental Proxy?

E. A. Markova^{a, *}, T. V. Strukova^{a, **}, and A. V. Borodin^{a, ***}

^a Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia

*e-mail: emrk@yandex.ru

**e-mail: strukova@ipae.uran.ru

***e-mail: bor@ipae.uran.ru

Received May 24, 2022; revised July 1, 2022; accepted July 15, 2022

Abstract—The study aims to answer the question on the possibility of using the data on arvicoline rodent occurrence for revealing large-scale gradients of humidity in the central part of Northern Eurasia. We classify all arvicoline species known in the study area since the Late Pleistocene into 5 groups based on the vegetation type and moisture balance of breeding and survival habitats of their extant representatives and assign habitat moisture preference rates from 1 to 5 to the species associated with xero-, mesoxero-, meso- mesohygro- and hygrophytic vegetation. The obtained ordinal variable called relative humidity of arvicoline habitats (RH_A) is estimated for paleontological and neontological datasets subdivided into geographical segments. In the Southern, Middle and Northern segments of the Ural Mountains, the relative humidity of arvicoline habitats increased northwards and increased over time from the Late Pleistocene to the Late Holocene. During the Late Pleistocene–Holocene, the species of xeric habitats were less frequent on the western slope of the Ural Mountains than on the eastern slope. However, the differences between the slopes are not detected in the neontological dataset. The data on arvicoline habitat humidity reveal the increased gradual mesophytization of the communities in all geographical segments of the study area from the Late Pleistocene to the Late Holocene. Arvicolines associated with mesophytic vegetation predominate on the western slope of the Southern, Middle, and Northern Urals and on the eastern slope of the Middle Urals since the Early Holocene. On the eastern slope of the Southern Urals, the arvicolines of mesic habitats predominate since the Late Holocene. The results suggest that arvicoline rodents may be successfully used for reconstruction of spatiotemporal environmental gradients using the data on relative humidity of their habitats. Suggested approach may contribute to multi-proxy paleoenvironmental reconstructions for the Late Quaternary and appears to be important for paleoarchives comprising no reliable paleobotanic data (e.g., numerous karst caves of the Ural Mountains).

Keywords: paleoecology, micromammals, habitat moisture, Late Pleistocene, Holocene

DOI: 10.1134/S1067413622060108

Continental-scale humidity gradients in the central part of Northern Eurasia are determined by latitudinal insolation changes with the southward increase of evaporation, the moisture paths resulting from atmospheric circulation, and the relief [1]. The Ural Mountains subdivide European and Asian parts of the continent and stretch submeridionally for more than 2000 km serving as a barrier against the Atlantic warm and humid air masses. The barrier role of the Ural Mountains intensifies climatic contrast between the adjacent territories of the East European and West Siberian plains. On the western slopes of the Urals, the precipitation during the year is 1000–1500 mm in the Polar and Sub-Polar Urals, 650–750 mm in the Northern and Middle Urals, and about 360 mm in the Southern Urals. On the eastern slopes, the summary

precipitation is about 100–200 mm less. The differences in humidity are reflected in the amount of water in streams and rivers, distribution of soil types, vegetation, and fauna [1–3].

Geological and geomorphological evidence suggest that modern topography of the Ural Mountains was formed in the Neogene–Quaternary [4, 5]. Numerous paleoarchives of the Quaternary have been studied in the Urals and in its western and eastern foothills (e.g., summarizing publications: [6–9]). Paleontological resources are primarily found in caves with abundant vertebrate remains but scarce paleobotanical records, in lakes, bogs and peatlands yielding detailed palynological and plant macrofossil sequences but lacking vertebrate remains, and in fluvial archives yielding both plant and animal fossils with the high

rates of reworking. Paleoenvironmental reconstructions based on the fossils preserved in different types of localities represent a complex task because taphonomic factors vary both among and within localities reducing the likelihood that a given assemblage in one locality would simultaneously comprise both faunal and floral components of one real ecosystem to which they belonged. From a paleoecological perspective, a possible way to solve the problem of discontinuities and heterogeneity of the materials passed through different taphonomic filters is to improve our understanding of ecological requirements and functional roles of biological species and higher taxa that we use as biotic proxies of particular environmental characteristics. The better we know the ecology of each taxonomic group identified in the fossil record, the more exact and reliable the multi-proxy environmental reconstructions because the inferences based on different types of fossils might control each other to prevent single-proxy biases.

Among vertebrates preserved in the Uralian localities, micromammals are the most abundant. The collected data banks and publications on micromammals have been used for outlining the latitudinal spread of natural zones in the central part of Northern Eurasia during the Late Quaternary [10–12] and for inferring large-scale spatial trends in faunal diversity [7, 9, 13]. Micromammal assemblages are dominated by arvicoline rodents (Arvicolinae, Cricetidae, Rodentia). The Late Neogene and Quaternary radiation of the subfamily Arvicolinae throughout the Northern Hemisphere has resulted in a rich variety of herbivorous species. Being the first order consumers in natural ecosystems, they use specific vegetation types for food and shelter. Thus, the logical chain “herbivore–vegetation–climate” might be potentially used for inferring the environmental properties of their habitats.

In Quaternary paleoecology, arvicoline rodents have long been considered as markers for climatic reconstructions in different regions of Eurasia and North America [9, 14–24]. However, there is still no unified view of using this group of mammal for paleoecological reconstructions. There are two main viewpoints in the debate over interpretation of the ecological preferences of particular species: those who directly link ecological preferences with abiotic factors and those who aim at reconstructing ecosystem parameters of different hierarchical levels (e.g., microhabitats, communities, ecosystems or even biomes). In a previous study [23], we have suggested that arvicolines might serve as indicators of vegetation type in their breeding and survival habitats thus being useful as indirect proxies for assessment of environmental moisture. Here, we further develop this approach and suggest an index of relative humidity of arvicoline habitats based on the distribution patterns of sympatric arvicoline species along local environmental gradients in contemporary ecosystems.

Water availability in natural ecosystems is not only a function of climate, topography and other abiotic factors [1] but is also regulated by autogenic processes during ecological successions. In forests, water storage results, for example, from the accumulation of organic material on the forest floor in later successional stages [25]. In grasslands, tussocks might favor water accumulation by reducing transpiration during dry periods [26]. Thus, the composition of herbivorous species, such as arvicolines, is determined in natural ecosystems by a combination of biotic and abiotic factors. Biotic interactions at the level of particular ecosystems might potentially obscure the effects of large-scale climatic gradients on the composition of arvicoline species at the local scale.

This study aims to answer the question on the possibility of using the data on arvicoline rodent occurrence in quaternary assemblages dated back to the Late Pleistocene and Holocene for revealing large-scale gradients of humidity in the central part of Northern Eurasia. The hypothesis is that the arvicolines with different moisture preferences are equally abundant on different slopes of the Ural Mountains and the average values of relative humidity index of arvicoline habitats remain the same in the datasets collected along the latitudinal gradient and on the western and eastern slopes of the Urals.

MATERIAL AND METHODS

Regional Setting

Study area encompasses the Southern, Middle and Northern geographical segments of the Ural Mountains, and the Trans-Urals. The North-South borders of the segments are defined based on the key physical features [1] and their approximate geographical coordinates are taken here as the divides between the geographical subsets as follows. The Northern Urals stretch between the latitudinal flow of the Shugor River and the source of the Us'va River (63°59'–58°59' N). The Middle Urals are between the source of the Us'va River and the latitudinal flow of the Ufaley River (58°52'–55°55' N). The Southern Urals are between the latitudinal flows of the rivers Ufaley and Ural (51°–55°55' N). The East-West divides between the geographical subsets are confined to the border between the western and eastern macroslopes of the Ural Mountain Range. Based on geographic coordinates and position on either western or eastern macroslopes of the Ural Mountains, all observations included in paleontological and neontological datasets are subdivided into six geographical subsets. Those are the western and eastern slopes of the Northern Urals (NUW, NUE), the western and eastern slopes of the Middle Urals (MUW, MUE), and the western and eastern slopes of the Southern Urals (SUW, SUE). The scheme of the subsets is shown on Fig. 1.

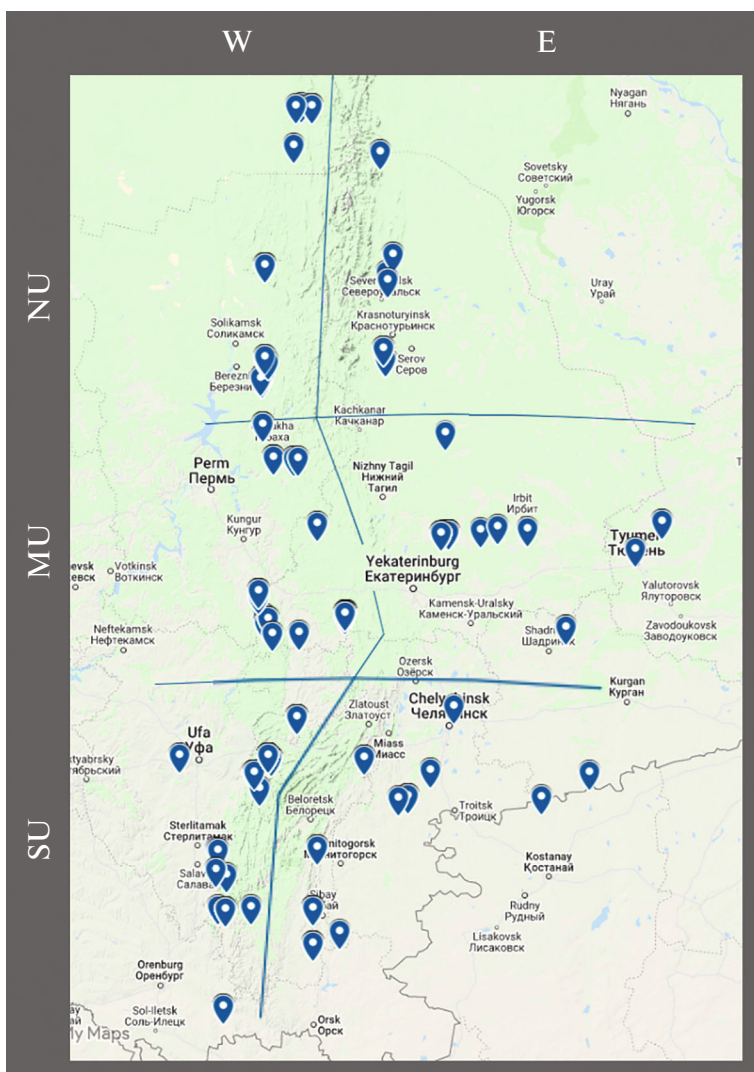


Fig. 1. A scheme of the geographical subsets outlined by the approximate borders of the Southern (SU), Middle (MU) and Northern Urals (NU) and by the approximate divide between the western (W) and eastern (E) macroslopes of the Ural Mountains (solid lines) and situation of localities included in paleontological dataset (see Supplementary 1 for details).

Data Acquisition

The data on micromammal localities considered in this study are taken from previously created databank [27] with the addition of published [8, 28–51] and some unpublished materials. Complete list of paleontological localities is shown in Supplementary 1.

Based on the absolute and relative dating methods, the dataset is divided into the Late Pleistocene (LP), Early (EH), Middle (MH), and Late Holocene (LH) subsets. In some cases, radiocarbon dates are used to show particular time intervals within the Late Pleistocene. Radiocarbon dates are shown in Supplementary 1 as they were presented in cited publications.

For comparative purposes, we created a neontological dataset comprising the lists of arvicoline species occurring in natural reserves, protected areas and long-term monitoring plots in the Southern, Middle

and Northern Urals [52–86]. A complete list of localities included in neontological dataset is shown in Supplementary 2.

Arvicoline Rodents as a Proxy of Environmental Humidity

Our previous review has shown that humidity is one of the factors limiting the distribution of arvicolines in natural ecosystems, and moisture regime of breeding and/or survival habitats may serve as one of several possible criteria for classification of arvicolines as paleoenvironmental proxies [23]. The difference of our classification from other approaches existing in paleoecological literature is summarized as follows. We strongly suggest avoiding classifications of arvicolines based on the occurrence in the existing terrestrial biomes (e. g., tundra species, steppe species, etc.)

Table 1. Classification of extant arvicoline species of the central part of Northern Eurasia by the relationship of their breeding and survival habitats with environmental humidity (modified after [23]) and ecological groups (1–5), defined in this study by the moisture preference rates

Ecological characteristics	Arvicoline species groups									
	1		2		3		4		5	
	<i>Ellobius talpinus</i> <i>Lagurus lagurus</i> <i>Eolagurus luteus</i>	<i>Microtus socialis</i>	<i>Craseomys rufocanus</i> <i>Dicrostonyx torquatus</i>	<i>Lasiopodomys gregalis</i>	<i>Terricola subterraneus</i> <i>Microtus agrestis</i> <i>Clethrionomys rutilus</i>	<i>Microtus arvalis</i> sensu lato <i>Clethrionomys glareolus</i>	<i>Lemmus sibiricus</i> <i>Myopus schisticolor</i>	<i>Alexandromys middendorffi</i> <i>Alexandromys oeconomus</i>	<i>Ondatra zibethicus</i>	<i>Arvicola amphibius</i>
Succession stages preferred by the species	a	b	a	b	a	b	a	b	a	b
Habitat types classified by moisture content	Xeric		Xeric-mesic		Mesic		Mesic-wet		Wet	
Moisture preference rate, k	1		2		3		4		5	

(a) Non-initial stages of ecological successions when the amounts of humidity in terrestrial ecosystems (or amounts of oxygen in semi-aquatic ecosystems) are regulated by autogenic processes; (b) initial stages of successions starting in the environments with particular levels of humidity.

because voles and lemmings are capable of spreading from one biome to another using extrazonal, azonal and intrazonal landscapes [sensu 86]. Instead, ecological requirements of arvicolines should be classified by the properties of their habitats. Among the variety of biotopes in which a species might occur, we focus on those used for breeding and/or seasonal survival. When considering habitat properties, we focus on the herbaceous layer because of direct relatedness of this stratum with arvicoline activity in terrestrial ecosystems. Among abiotic factors, the relationship of arvicoline species with environmental moisture appears the most clear, though indirect. Feeding primarily on plants and living in local environments formed by plants, arvicoline species occupy local gradients of humidity in terrestrial ecosystems following the distribution of habitats with different amounts of water. The amount of water in a habitat determines one of three major types of vegetation (xero-, meso- or hydrophytic) and each of those are used by different arvicoline species with different levels of intensity. Moreover, there are arvicolines tolerating different degrees of wetness (either between xeric and mesic or between mesic and wet habitats). Thus, the types of moisture regime of arvicoline habitats might be designated using traditional ecological classifications of plants [e.g., 87] based on the attitude to moisture.

Here, we further develop the previously suggested approach of using arvicoline rodents to infer habitat humidity and identify five ecological species groups based on the relation to xero-, mesoxero-, meso-,

mesohygro-, and hygrophytic vegetation and xeric, xeric-to-mesic, mesic, mesic-to-wet, and wet conditions respectively (Table 1). First group includes the species capable of surviving and reproducing in xerophytic plant communities even in the absence of mesophytic vegetation. Second group contains the species, whose breeding and/or survival habitats are either confined to areas of mesoxerophytic vegetation or vary from meso – to xerophytic depending on local or seasonal conditions. Third group comprises the species whose breeding nests and survival locations are confined to mesophytic habitat types. Fourth group includes the species whose breeding and/or survival habitats are associated with sufficiently moist environments and vegetation types varying from mesohygrophytic to mesophytic. Fifth group is for semi-aquatic species capable of utilizing hydrophytes and reproducing in wetland biotopes with hygrophytic and hydrophytic vegetation.

This study considers the species known in the central part of Northern Eurasia since the Late Pleistocene until present. The list of species comprises all arvicolines occurring in the Ural Mountains and Western Siberia [23] and also *Terricola subterraneus* and *Microtus socialis* inhabiting adjacent regions. Being related to final succession stages of forest ecosystems [88], *T. subterraneus* might benefit from soil water storage resulted from the accumulation of organic material on the forest floor during succession (for cases of increasing soil water reserves in late stages of forest successions see [25]). For ecological prefer-

ences of *M. socialis*, we refer to the publication on the occurrence of this species during the landscape change from desert to steppe [89].

We assign habitat moisture preference rates from 1 to 5 to each species according to the ecological group, in which the species is a member in Table 1. The lowest rate of moisture preference (rate 1) is for the species of xeric habitats (Table 1). *Ellobius talpinus* tends to get independent of succession stages in arid and semi-arid environments; it might occur in any stage of succession due to its underground mode of life and it depends on the presence of the well-developed soils. *Lagurus* and *Eolagurus* are associated with mature xerophytic grasslands. *M. socialis* exists in early stages of succession that starts in xeric environments.

Moisture preference rate 2 is assigned to the species of moderately dry habitats. Those are *C. rufocanus* that tolerates moderately dry stages of forest successions due to the use of the protective properties of nanorelief, *D. torquatus* as the inhabitant of shrublands and heaths, and *Lasiopodomys gregalis* living in mesoxerophytic grasslands on well-drained soils that are not prone to over-drying.

Inhabitants of primarily mesic habitats are considered as the species with the moisture preference rate 3. They are either associated with the later stages of ecological successions when autogenetic processes regulate water availability by creating mesic microhabitats on the surface of soil (3a) or occur in early stages of succession that starts in mesic environments (3 b). In the group 3a, *T. subterraneus* is associated with dead organic material on the forest floor, *M. agrestis* requires well-developed grass layer or tussocks in open and semi-open patches, *C. rutilus* exists in various types of ground cover in forests that enable sufficient but not exceeding water content in a habitat (moss, microrelief, undecomposed tree litter).

The species of moderately wet and humid microhabitats (moisture preference rate 4) are either tolerant to excessive water content in soil due to diminished relationship of nests with the soil layer (Alexandromys) or associated with vegetation of humid microhabitats (Lemmini).

The highest rate of moisture preference (rate 5) is assigned to semi-aquatic species capable of feeding on hydrophytes (ecological relationships with moderately eutrophic water bodies and reedbeds).

Ecological requirements of species are assumed stable within the time interval considered in this study (from the Late Pleistocene to the Holocene and present). In paleontological dataset, chronospecies of *Dicrostonyx* and forms identified as *Dicrostonyx* sp. are assumed to show the same requirements as their living descendant, *D. torquatus*. Morphologically and ecologically similar sibling species *Microtus arvalis* and *M. rossiaemeridionalis* are considered together as *M. arvalis* sensu lato. For the sake of completeness, we include an introduced species *Ondatra zibethicus* in

the classification table because this species might be found in the most recent layers of the micromammal-bearing localities in the study area. However, we do not include *O. zibethicus* in calculations and focus on native species only.

Taxonomic interpretations at the level of species are taken from published species lists. In cases of different scientific names used for the same taxon, we unify taxonomic designations according to the nomenclature suggested by Abramson and Lissovsky [90] with the only exception of generic name *Clethrionomys* Tilesius, 1850 used here instead of *Myodes* Pallas, 1779 (see [91] for details).

Analysis

The moisture preference rates for each species are taken from Table 1 and are treated as the values of an ordinal variable in quantitative analyses. We consider that variable to reflect relative humidity of arvicoline habitats and use its arithmetic mean and mode as two measures of central tendency, both meaningful in our data. To show the mode and range of the moisture preference rates we use bar and line charts reflecting the ecological structure of the assemblages, communities or spatiotemporal datasets.

The arithmetic mean of the moisture preference rates of all arvicolines in any unit of the analysis (assemblage, community, or spatiotemporal dataset) is suggested as the index of relative humidity of arvicoline habitats, RH_A . Although the values of RH_A are meaningless for inferring actual moisture, they are useful for comparing arvicoline assemblages, communities or spatiotemporal datasets to each other in terms of relative humidity.

The index of relative humidity of arvicoline habitats is calculated using the formula:

$$RH_A = \sum N_i^* k_i / \sum N_i,$$

where \sum is the notation of sum, i runs from 1 to 5 and designate ecological groups according to Table 1, N is the number of times each ecological group is recorded in the unit of analysis, and k is the moisture preference rate specified for each ecological group in Table 1.

In our study, the unit of analysis is a large-scale spatiotemporal set of data. Thus, in paleontological dataset, N is the number of strata in which the species included in each ecological group are recorded within the specified limits of geological time and geographical extent regardless of the number of remains in those strata. In neontological dataset, N is the number of sessions and plots used in cited publications to collect census data on micromammals regardless of the number of individuals of each species recorded at a time.

In this study, we undertake analysis on the large-scale longitude-latitude grid (Fig. 1) subdividing both paleontological and neontological datasets into spatial units of the analysis (=geographic subsets NUW,

Table 2. Results of the Kruskal-Wallis tests comparing variation in the values of relative humidity index of arvicoline habitats (RH_A) in neontological and paleontological datasets

Factor	H	DF	N	p
Neontological dataset				
Geographical segment (SU, MU, NU)	16.2	2	49	0.0003
Macroslope (W, E)	3.1	1	49	>0.05
Paleontological dataset				
Geological age (LP, EH, MH, LH)	14.8	3	2272	0.0020
Geographical segment (SU, MU, NU)	26.6	2	2272	0.0000
Macroslope (W, E)	12.6	1	2272	0.0004

NUE, MUW, MUE, SUW, SUE), and paleontological dataset into temporal units (= temporal subsets LP, EH, MH, LH). When considering temporal patterns, the data on recent arvicolines is used for qualitative comparisons but not included in statistical testing because of the different sampling methods.

Three null hypotheses are as follows. 1 – The values of relative humidity index of arvicoline habitats remain the same in the temporal datasets from the Late Pleistocene to the Early, Middle and Late Holocene. 2– The values of relative humidity index of arvicoline habitats remain the same in the datasets collected along the latitudinal gradient in the Urals. 3 – Arvicolines with different moisture preferences are equally abundant on different slopes of the Ural Mountains.

To test the hypotheses of this study, non-parametric Kruskal-Wallis analysis of variance is used because the distributions of moisture preference rates exhibit significant deviations from the normal pattern. The analysis relies on Statistica Software v.10 (StatSoft Inc., 2011).

RESULTS

In neontological dataset collected along the latitudinal gradient on both slopes of the Urals, the differences among NU, MU, SU are significant (Table 2) suggesting that arvicolines with different moisture preferences are not equally abundant in different latitudinal segments. Pairwise tests suggest that SU is different from MU ($H(1, N = 1) = 11.9, p = 0.001$) and NU ($H(1, N = 34) = 8.7, p = 0.003$), however, there is no significant difference between MU and NU. There is also no difference between different slopes of the Urals (Table 2).

Analysis of the paleontological dataset suggests that differences in arvicoline habitat humidity are significant for factors geological age, geographical segment and macroslope (Table 2). The null-hypotheses are rejected and the species with different moisture

preferences rates are not equally abundant in the geographical and temporal subsets of the paleontological dataset.

Paleontological data reveal stepwise increase in the values of arvicoline habitat humidity from SU to MU and NU, and also from W to E. There is also temporal change in the values of RH_A from LP to EH subsets (Fig. 2). The results show that relative humidity of arvicoline habitats increased from the Late Pleistocene to the Late Holocene; relative humidity of arvicoline habitats increased with the increasing latitude and the species of xeric habitats were more frequent on the eastern slope of the Ural Mountains than on the western one.

Collectively, the results suggest that the Urals played a noticeable role in shaping the west-east differences in habitat humidity during the Late Quaternary. However, in present, there is no difference in relative humidity of arvicoline habitats between the eastern and western slopes of the Urals. In modern fauna, arvicolines associated with mesophytic vegetation (mesic habitats) predominate (or co-dominate) in all geographic segments (Fig. 3, gray columns). The frequency of this ecological group increased since the Early Holocene to the Late Holocene in all geographic segments of the study area (Fig. 3, red curves). Mesophytization of the communities was accompanied by the stepwise decline of arvicolines associated with xerophytic vegetation. The latter ecological group of Arvicolinae went extinct in the NUW segment in the Middle Holocene and then the decline proceeded until their recent disappearance in NU and MU (Fig. 3).

Ecological grouping of arvicoline species based on the habitat moisture preferences appears to be useful when considering the spatiotemporal dynamics of the arvicoline faunas and the history of particular ecological groups (Fig. 4). Visualizing temporal changes on line charts with the inclusion of available radiocarbon dates (compiled materials from [29, 34]), we observe a decline of the species related to mesophytic vegetation at about 16–17 ka BP on the western and eastern slopes

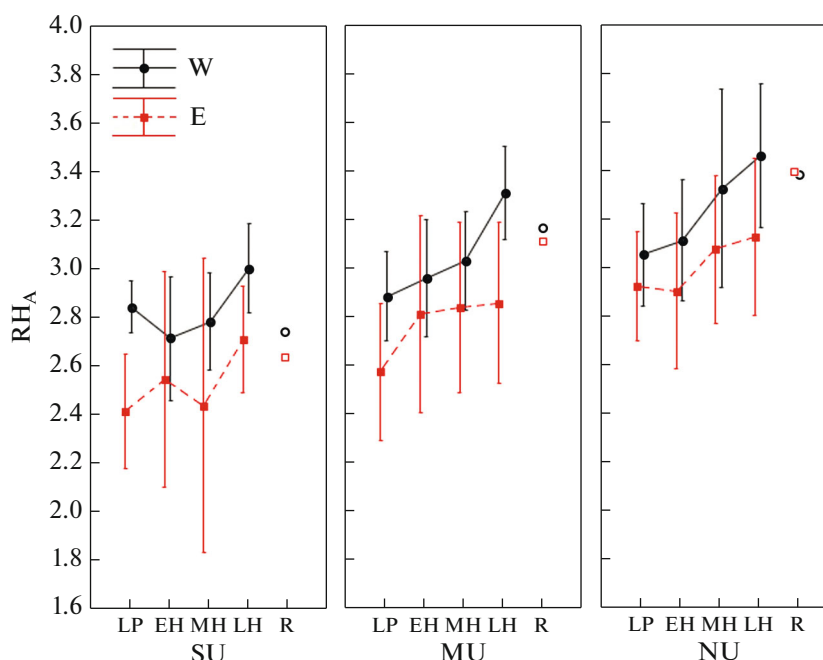


Fig. 2. Mean values and 95% confidence intervals of the values of relative humidity index RH_A estimated for the datasets of arvicoline occurrence in the Late Pleistocene (LP), Early (EH), Middle (MH) and Late (LH) Holocene on the western and eastern slopes of the Southern (SU), Middle (MU) and Northern Urals (NU) (reference values of RH_A calculated for recent arvicolines (R) included in neontological dataset are shown as open markers).

of the Southern Urals. That decline might be associated with dry and cool conditions of the Oldest Dryas.

DISCUSSION

Arvicoline rodents have long been used for inferring moisture regimes of terrestrial ecosystems based on the frequency of indicator species associated with wet (e.g., intrazonal) or dry (e.g., steppe) environments [14, 16, 21, 92] or using multi-species bioclimatic modelling [93, 94]. Attempts have been also made to develop morphological criteria, which distinguish the species growing in either dry or humid environments [24, 95]. Our study further develops the first traditional approach because we use the frequency of arvicolines with different moisture preferences. However, the principal novelty is that we avoid focusing on indicator taxa but include all arvicoline species occurring in the fauna of the central part of Northern Eurasia and assign habitat moisture preference rates from 1 to 5 to each species (according to the association with xero- mesoxero-, meso, mesohygro- and hygrohyte vegetation). By doing so, we can treat the moisture preference rate as an ordinal variable in quantitative analyses. We call this variable relative humidity of arvicoline habitats, or RH_A . In contrast to bioclimatic modelling, we do not make attempts to infer precipitation in mm because RH_A is not a proxy of climate itself but rather a biotic characteristic of the environment.

In paleoecology, various proxy methods exist to reconstruct environmental humidity and each method has its strengths and limitations (e.g., [96–100]). The obvious limitation of our approach (and any approach based on rodents) is that the relationship between herbivorous mammals and climate humidity is mediated by vegetation. The effects of atmospheric moisture and precipitation might not be distinguished from the effects of biotic self-regulation during ecological successions. In Table 1, we provide information on the beneficial stages of the succession for each arvicoline species that could be used for further development of the approach. The understanding of successional stages favorable for the species might potentially be useful when analyzing the patterns of habitat partitioning between the species with equal moisture preference rates. In each ecological group defined in our study, the species associated with the later successional stages (subgroups a in Table 1) might be also considered as relatively more demanding on the stability of habitat moisture (or water availability in case of muskrats) than those included in subgroups b.

In all geographical subsets of the paleontological dataset, the arvicoline habitat humidity increased from the Late Pleistocene to the Late Holocene. This trend principally coincide with the inferences from paleobotanical data for Northern Eurasia [99, 100]. In our study, climatic fluctuations during the Holocene might not be revealed because of the large-scale generalization of the paleontological dataset. However, a

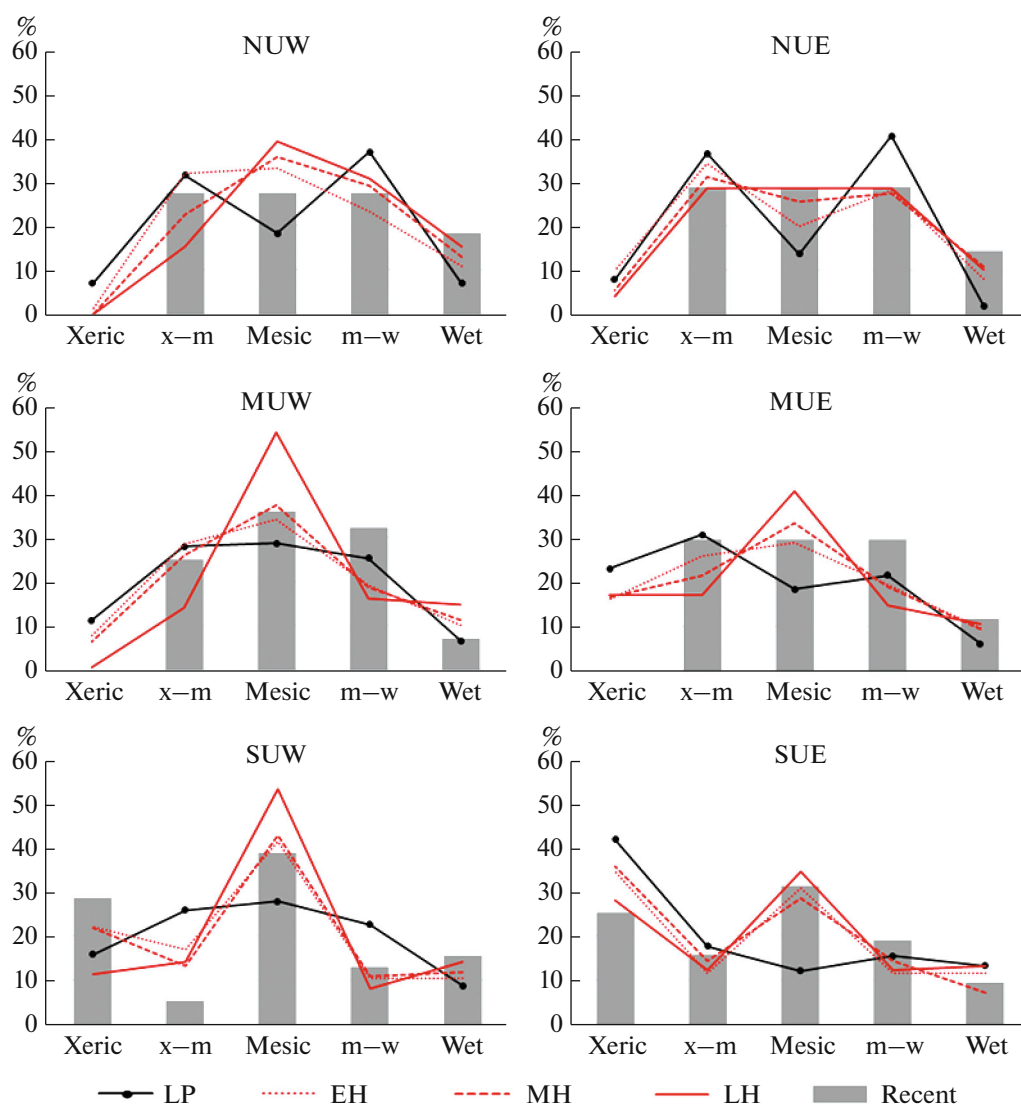


Fig. 3. Percentages of the occurrence of arvicoline groups of wet, wet-to-mesic, mesic, mesic-to-xeric and xeric habitats on the western (W) and eastern (E) slopes of the Southern (SU), Middle (MU) and Northern Urals (NU) during the Late Pleistocene – Holocene (curves) and in present (columns).

climatically-driven event might be hypothesized at 16–17 ka BP by the ecological turnover in the arvicoline assemblages of the Southern Urals (based on compiled data from [29, 34]). During that time, the species associated with mesic habitats experienced a decline in both SUW and SUE segments of the Urals. The species associated with mesoxerophyte vegetation were predominating on the western slope and the species of xeric habitats prevailed on the eastern slope of the Southern Urals. These changes in the arvicoline fauna might be associated with dry and cool conditions of the Older Dryas. Interestingly, this period appears to be more severe for the arvicoline assemblages in the Southern Urals than the Last Glacial Maximum when the frequency of the species of mesic habitats was higher than at 16–17 ka BP. Further stud-

ies are necessary to obtain a more nuanced record of the arvicoline fauna transformation because the knowledge of the composition of particular ecological groups may reveal the critical periods in the history of regional biota, which, in turn, might be correlated with the Quaternary climate transitions on a larger scale.

The relationship between arvicoline occurrence and habitat humidity considered in this study might potentially shed new light on the problem of extinction of the species associated with xerophyte and mesoxerophyte vegetation observed in the central part of Northern Eurasia during the Holocene and in historical time [22, 37, 92]. The increased role of the species associated with mesic habitats (e. g., *M. arvalis sensu lato*) and disappearance of the species of xeric and mesic-to-xeric habitats (for example, the extinction of

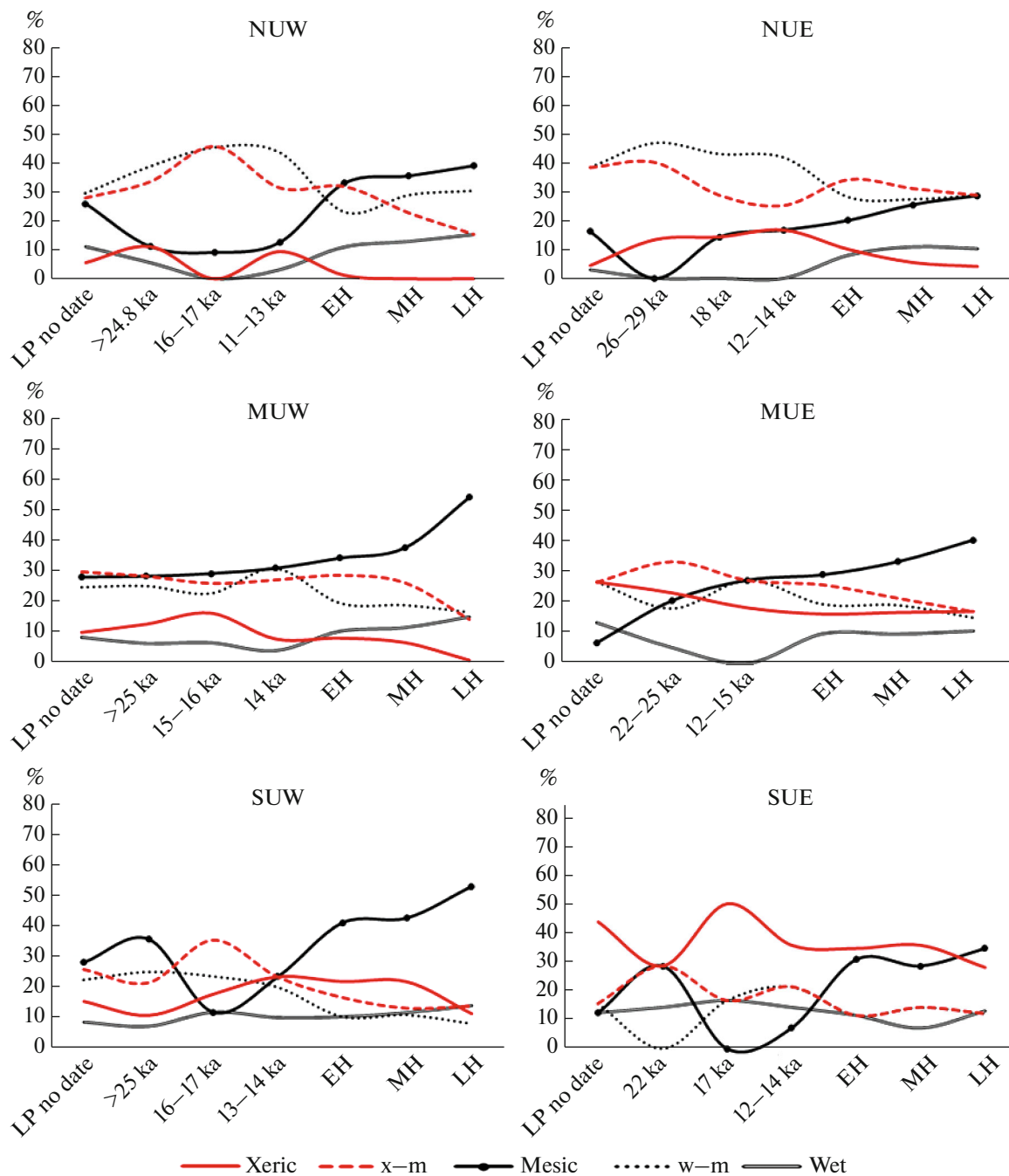


Fig. 4. Temporal changes in the composition of ecological groups of arvicolines reflecting habitat wetness on the western (W) and eastern (E) slopes of the Southern (SU), Middle (MU) and Northern Urals (NU). See Supplementary 1 for localities included is spatiotemporal subsets and radiocarbon dates used to specify the intervals within the Late Pleistocene (where available).

L. gregalis on the eastern slope of the Middle Urals) have been interpreted as the consequences of the natural development of the forest zone and agricultural activity in steppe ecosystems [101]. Generalization of the data on arvicoline occurrence over the large-scale spatial grid makes it visible that the process of disappearance of the species with moisture preference rates 1 and 2 preceded the onset of agriculture in the Urals

and started in the Early Holocene. Most probably, the primary cause of that disappearance was the degradation of the Late Pleistocene biomes with a gradual decline of xeric and mesoxeric habitats. Autogenic processes in the newly developed ecosystems might have had a coherent negative effect together with human impact on the exclusion of the species of xeric and mesoxeric habitats first from the more humid

western slope and then from the NU segment of the eastern slope. For the species associated with mesic habitats, the effects of autogenic regulation in Holocene ecosystems was positive (as could be seen from the common trend to mesophytization in all segments of the Urals considered in our study).

The predominance of the species of mesic habitats on the western slope of the Southern, Middle and Northern Urals, and on the Eastern slope of the Middle Urals was first achieved in the Early Holocene. On the eastern slope of the Southern Urals, the predominance of the inhabitants of mesic biotopes was established relatively recently (since the Late Holocene). Thus, the arvicoline-based data on habitat humidity suggest that the ecosystems of the Southern, Middle, and Northern Urals have experienced gradual mesophytization since the beginning of the Holocene and this process was faster in the SUW, MUW, NUW, and MUE segments of the study area than in SUE and NUE.

In the Late Pleistocene and Holocene, the latitudinal gradient of the northward increase in arvicoline habitat humidity was clearly pronounced and the differences between the slopes were statistically significant. The average values of arvicoline habitat humidity were higher on the western slopes of the Southern, Middle and Northern Urals. This result indirectly confirms the role of the Ural Mountains in shaping the west-east humidity gradient during the Late Pleistocene – Holocene. In neontological dataset, only the latitudinal gradient might be revealed using the RH_A variable, which is significantly lower in the Southern Urals than in the Middle and Northern Urals. The absence of W–E difference in neontological dataset (by contrast with paleontological data) could be explained as either artifact resulting from sampling difference between the datasets or a natural trend towards the formation of continuous longitudinal biomes. All paleontological localities along the mountain range of the Urals are confined to caves of either western or eastern slopes and the divide between the slopes appears to coincide with the pattern of sampling. The data on extant arvicolines represent contemporary biomes rather than formal subdivision of the macroslopes and some trapping plots are situated very close to the W–E divide so that their attribution to the slope is rather formal. However, the disappearance of the difference between the slopes in the values of RH_A might also be natural and reflect the formation of continuous biomes in NU and MU segments, because it follows the trend of stepwise changes in the composition of ecological groups of arvicolines from the LP to LH.

CONCLUSIONS

Ecological grouping of arvicoline species by moisture preference rates provides insights into the proportion of particular habitat types in the ecosystems. Geographical segments of the Urals exhibited contrasting distribution patterns of the species with different mois-

ture preferences during the Late Pleistocene. During that time, arvicolines associated with xerophyte vegetation prevailed in SUE; inhabitants of mesic habitats prevailed in SUW, MUW; the species of wet/mesic and mesic/xeric habitats prevailed in NUW, NUE, MUE. Those differences among W–E geographical segments levelled off during the Holocene.

Calculation of the index of relative humidity of arvicoline habitats, RH_A as the average value of moisture preference rates of all arvicoline species in spatiotemporal units of the analysis appears to be useful for reconstructing the gradients of humidity in terrestrial ecosystems. In the Ural Mountains, the relative humidity of arvicoline habitats increased over time from the Late Pleistocene to the Late Holocene, and with the increasing latitude. During the Late Pleistocene – Holocene, the species of xeric habitats were more frequent on the eastern slope of the Ural Mountains than on the western slope. However, the differences between slopes are not detected in the neontological dataset.

The data on arvicoline habitat humidity reveal the increased mesophytization of the communities in all geographical segments of the study area from the Late Pleistocene to the Late Holocene. The predominance of arvicolines associated with mesophytic vegetation was established in the Early Holocene on the western slope of the Urals (all segments) and on the eastern slope of the Middle Urals. On the eastern slope of the Southern Urals, the arvicolines of mesic habitats predominate since the Late Holocene.

The results suggest that arvicoline rodents may serve as indicators of habitat humidity. The data on their occurrence can be used to reveal both the structure of habitats with different moisture content in terrestrial ecosystems and the gradients of humidity over large spatial scales. When interpreting those gradients, both abiotic and biotic factors must be taken into account because the relationship between arvicolines and humidity is mediated by vegetation.

From a paleoecological perspective, the approach based on arvicolines may contribute to multi-proxy paleoenvironmental reconstructions and appears to be especially important for paleoarchives comprising no reliable paleobotanic data (e.g., numerous karst caves of the Ural Mountains). The understanding of relationship between arvicolines and their habitat humidity might also shed light on the problem of extinction of the species associated with xerophyte vegetation observed in some segments of the study area in historical time.

ACKNOWLEDGMENTS

We wish to thank Dr. A.V. Lagunov, Dr. O.V. Soroka and all colleagues working on the unpublished chronicles of nature available online and used in this study to obtain comparative data on recent micromammal fauna, including State Nature Reserves Yuzhno-Ural'sky, Orenburgsky, Shaitan-Tau, Shul'gan-Tash, Vishersky, Malaya Sos'va, and National Park Zyuratkul'.

FUNDING

The study is supported by Russian Scientific Fund, project no. 22-14-00332.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1134/S1067413622060108>.

REFERENCES

- Krivtsov, V.A. and Vodorezov, A.V., *Fizicheskaya geografiya i landshafty Rossii* (Physical Geography and Landscapes of Russia), Ryazan: Ryazan'. Gos. Univ., 2016.
- Gorchakovskiy, P.L., *Ural i Predural'ye. Rastitelnost* (The Urals and Fore-Urals. Vegetation), Moscow: Nauka, 1968.
- Bolshakov, V.N., Balakhonov, V.S., Benenson I.E., et al., *Melkie mlekopitaiushchie Ural'skikh gor (ekologiya mlekopitaiushchikh Urala)* (Small Mammals of the Ural Mountains (Ecology of Mammals of the Urals)), Sverdlovsk: Akad. Nauk SSSR, 1986.
- Puchkov, V.N., Intraplate events in the geological history of mobile belts, at the example of the Urals, *Intraplate Phenomena in the Earth's Crust*, Moscow: Nauka, 1988, pp. 167–175.
- Puchkov, V. and Danukalova, G., The Late Pliocene and Pleistocene history of the South Urals region, *Quaternary International*, 2009, vol. 201, pp. 4–12.
- Smirnov, N.G., Review of the development of Quaternary zoology in the Urals, in *Chetvertichnaya paleozoologiya na Urale* (Quaternary Palaeozoology in the Urals), Ekaterinburg, 2003, pp. 24–54.
- Smirnov, N.G., Kosintsev, P.A., Kuzmina, E.A., Izvarin, E.P., and Kropacheva, Yu.E., The ecology of Quaternary mammals in the Urals, *Russ. J. Ecol.*, 2014, vol. 45, no. 6, pp. 449–455.
- Stefanovsky, V.V., *Pliotsen i kvarter Vostochnogo sklona Urala i Zauralia* (Pliocene and Quaternary of the Eastern Slope of the Urals and Trans-Urals), Ekaterinburg: Inst. Geol. Geokhim. Ural. Otd. Ross. Akad. Nauk, 2006.
- Borodin, A.V., Arvicolines (Arvicolinae, Rodentia) of the Urals and Western Siberia (Eopleistocene – modern time), *Extended Abstract of Doctoral Dissertation (Biol.)*, Ekaterinburg: IPAE Ural. Branch Russ. Acad. Sci., 2012.
- Borodin, A.V., Quaternary small mammal faunas from the West Siberian Plain, *Acta Zool. Cracov.*, 1996, vol. 39, no. 1, pp. 75–81.
- Smirnov, N.G., Markova, A.K., Kitaev, L.M., et al., Zoogeography of the Holocene mammals in Northern Eurasia, *Bull. Acad. Sci. USSR, Geogr. Ser.*, 2001, no. 2, pp. 41–49.
- Smirnov, N.G., Zonal distribution of mammals in the Urals over the Late Pleistocene time, in *Mammoth and Its Environment: 200 Years of Investigations*, Moscow: GEOS, 2001, pp. 209–219 [in Russian].
- Kosintsev, P.A. and Bachura, O.P., Late Pleistocene and Holocene mammal fauna of the Southern Urals, *Quaternary International*, 2013, vol. 284, pp. 161–170.
- Jánossy, D. and Kordos, L., Pleistocene-holocene mollusc and vertebrate fauna of two caves in Hungary, *Ann. Hist.-Nat. Mus. Natl. Hung., Mineral. Geol. Palaeontol.*, 1976, vol. 68, pp. 5–29.
- Galkina, L.I., The history of faunal assemblages of rodents in the south of Western Siberia, in *Problemy zoogeografii i istorii fauny* (Problems of Zoogeography and History of Fauna), Belyshev, B.F., et al., Eds., Novosibirsk: Nauka, 1980, pp. 221–245.
- Gromov, I.M. and Polyakov, I.Ya., *Mlekopitayushchie* (Mammals), Leningrad: Nauka, 1977.
- Semken H.A., Jr., Holocene climatic reconstructions derived from the three micromammal bearing cultural horizons of the Cherokee Sewer Site, Northwestern Iowa, in *The Cherokee Excavations: Holocene Ecology and Human Adaptations in Northwestern Iowa*, New York: Acad. Press, 1980, pp. 67–99.
- Maleeva, A.G., The method of paleoecological analysis of the theriofauna of Late Cenozoic, in *Istoriya i evolyutsiya sovremennoi fauny gryzunov (neogen-sovremennost')* (History and Evolution of the Modern Fauna of Rodents (Neogene–Present Time)), Moscow: Nauka, 1983, pp. 146–179.
- Maleeva, A.G., *Problemy ekologicheskoi interpretatsii paleoteriologicheskikh materialov* (Problems of Ecological Interpretation of Paleotheriological Materials), Sverdlovsk: Ural. Gos. Univ., 1989.
- Smirnov, N.G., Paleoecological methods in the reconstruction of the Pleistocene paleogeographic environments, in *Khronostratigrafiya paleolita Severnoi, Tsentral'noi i Vostochnoi Azii i Ameriki* (Paleolithic Chronostratigraphy of Northern, Central, Eastern Asia and America), Novosibirsk, 1990, pp. 275–280.
- Kolfschoten, T., On the application of fossil mammals to the reconstruction of the palaeoenvironment of northwestern Europe, *Acta Zoologica Cracoviensia*, 1995, vol. 38, no. 1, pp. 73–84.
- Dupal, T.A., Possible reasons of the extinction of *Eolagurus luteus* on most of the Pleistocene distribution area, *Byull. Mosk. O-va. Ispyt. Prir.*, 2005, vol. 110, no. 4, pp. 63–68.
- Markova, E.A., Strukova, T.V., and Borodin, A.V., Arvicolines (Arvicolinae, Rodentia) as paleoenvironmental proxies: classification of species inhabiting the central part of Northern Eurasia based on environmental preferences of their modern representatives, *Biol. Bull.*, 2018, vol. 45, no. 7, pp. 772–782.

24. Luzi, E. and Lopez-Garcia, J.M., Relative size variations in two vole species: A climatic proxy for the identification of humid-arid pulses during Late Pleistocene in Southwestern Europe?, *Quat. Sci. Rev.*, 2019, vol. 223, p. 105920.
25. Leuschner, C., Forest succession and water resources: soil hydrology and ecosystem water turnover in early, mid and late stages of a 300-yr-long chronosequence on sandy soil, in *Forest Development*, Dohrenbusch, A. and Bartsch, N., Eds., Berlin: Springer-Verlag, 2002, pp. 1–68.
https://doi.org/10.1007/978-3-642-55663-0_1
26. Davie, T. and Fabey, B.D., Tussock grasslands and high water yield: A review of the evidence, *J. Hydrol.*, 2006, vol. 45, no. 2, pp. 83–94.
27. Borodin, A., Markova, E., Zinovyev, E., et al., Quaternary rodent and insect faunas of the Urals and Western Siberia: connection between Europe and Asia, *Quat. Int.*, 2013, vol. 284, pp. 132–150.
28. Kuzmina, E.A., Smirnov, N.G., Ulitko, A.I., New data on Late Pleistocene–Holocene small mammal communities from the Ural–Sakmara interfluvium, Southern Urals, *Quat. Int.*, 2016, vol. 420, pp. 56–64.
29. Kuzmina, E.A., The dynamics of small mammal communities from Southern Trans-Urals in Last Pleistocene and Holocene periods, *Extended Abstract Cand. Sci. (Biol.) Dissertation*, Ekaterinburg: IPAE Ural Branch Russ. Acad. Sci., 2006.
30. Danukalova, G., Kosintsev, P., Yakovlev, A., et al., Quaternary deposits and biostratigraphy in caves and grottoes located in the Southern Urals (Russia), *Quat. Int.*, 2020, vol. 546, pp. 84–124.
31. Yakovlev, A.G., Small mammals of the Pleistocene and Holocene of the Bashkir Pre-Urals and the Western slope of the Southern Urals, *Extended Abstract Cand. Sci. (Biol.) Dissertation*, Ekaterinburg: IPAE Ural Branch Russ. Acad. Sci., 1996.
32. Yakovlev, A.G., Danukalova, G.A., Alimbekova, L.I., et al., Biostratigraphical characteristic of the Upper Neopleistocene – Holocene deposits of the natural monument “Atysh waterfall” surroundings (Southern Urals), in *Faunas of Urals and Siberia during Pleistocene and Holocene*, Kosintsev, P.A., Ed., Chelyabinsk: Riphei, 2005, pp. 260–304 [in Russian].
33. Stefanovsky, V.V., Borodin, A.V., and Strukova, T.V., Correlation of the Upper Neopleistocene alluvial and lacustrine sections of Southern Trans-Urals region on the biostratigraphic data, *Stratigr. Geol. Correl.*, 2003, vol. 11, no. 4, pp. 87–100.
34. Smirnov, N.G., Bol’shakov, V.N., Kosintsev, P.A., et al., *Historical Ecology of Animals in the Southern Urals*, Sverdlovsk: Ural Branch USSR Acad. Sci., 1990.
35. Danukalova, G., Kurmanov, R., Yakovlev, A., et al., Palaeoenvironment of the Middle and Upper Neopleistocene at the Gornovo upper Palaeolithic site (Southern Ural foreland, Russia), *Quat. Int.*, 2016, vol. 420, pp. 24–46.
36. Fadeeva, T.V., Kosintsev, P.A., and Gimranov, D.O., Mammals of the mountain part of the Southern Urals during Last Interglacial, *Zool. Zh.*, 2019, vol. 98, no. 11, pp. 1304–1322.
37. Smirnov, N.G., *Small Mammals of the Middle Urals in Late Pleistocene/Holocene*, Yekaterinburg: Nauka, 1993 [in Russian].
38. Izvarin, E.P., Formation of the fauna of small herbivorous mammals of the western slope of the Middle Urals in the Late Pleistocene and Holocene, *Ph.D. Dissertation*, Ekaterinburg: Inst. Plant Animal Ecol., Ural Branch Russ. Acad. Sci., 2017, pp. 1–20.
39. Rupysheva, T.A., New locality of the late quaternary fauna in the Middle Urals, in *Proceedings of the Conference of Young Scientists “Ecology in a Changeable World”*, Ekaterinburg: Akademkniga, 2006, pp. 203–204 [in Russian].
40. Strukova, T.V., Typology of Late Pleistocene and Holocene small mammal faunas of the Middle Trans-Urals, in *Proceedings of the Conference of Young Scientists “Biosphere and Mankind”*, Ekaterinburg: Ekaterinburg Publ., 2000, pp. 251–260 [in Russian].
41. Smirnov, N.G., Data to studying of historical dynamics of the rodents diversity in the taiga regions of the Middle Urals, in *Materials on the History of the Modern Biota of the Middle Urals*, Yekaterinburg, 1995, pp. 24–57 [in Russian].
42. Fadeeva, T.V. and Smirnov, N.G., *Small Mammals in the Perm Pre-Urals during the Late Pleistocene and Holocene Periods*, Yekaterinburg: Goshchitskiy Publ., 2008 [in Russian].
43. Bachura, O. and Kosintsev, P., Late Pleistocene and Holocene small- and largemammal faunas from the Northern Urals, *Quat. Int.*, 2007 vol. 160, pp. 121–128.
44. Smirnov, N.G., Kuzmina, E.A., and Kourova, T.P., New data on rodents of the Northern Urals in the Late Glacial, in *Biota of the Ural Subarctic in the Late Pleistocene and Holocene*, Yekaterinburg, 1999, pp. 68–86 [in Russian].
45. Kochev, V.A., *Pleistocene Rodents from the North-East of Europe and their Stratigraphic Significance*, St. Petersburg: Nauka, 1993 [in Russian].
46. Strukova, T.V., Bachura, O.P., Borodin, A.V., and Stefanovsky, V.V., Mammal fauna first found in alluvial-speleogenic formations of the late Neopleistocene and Holocene, southern Urals, locality Cheremukhovo-1, *Stratigr. Geol. Correl.*, 2006, vol. 14, no. 1, pp. 98–109.
47. Bachura, O.P. and Strukova, T.V., Mammal remains from Cheremukhovo-1 locality (Excavation 4), in *Fauna in the Urals during the Pleistocene and Holocene*, Kosintsev, P.A., Ed., Yekaterinburg: Ripheus, 2002, pp. 37–55 [in Russian].
48. Smirnov, N.G., Small mammal diversity in the Northern Urals over the Late Pleistocene and Holocene, in *Materials and Investigations of the History of*

- the Modern Fauna of the Urals*, Yekaterinburg: Yekaterinburg Publ., 1996, pp. 39–83.
49. Teterina, A., Rodents of the North Urals in the Late Pleistocene and Holocene, *Quat. Int.*, 2009, vol. 201, pp. 31–36.
 50. Teterina, A.A. and Ulitko, A.I., New Localities of the Late Pleistocene and Holocene mammal faunas in Karst Caves of the Northern Urals, in *Fauna of the Urals in the Pleistocene and Holocene*, 2002, pp. 155–182.
 51. Smirnov, N.G. and Sadykova, N.O., Sources of errors in faunistic reconstructions in quaternary paleozoology, in *Quaternary Paleozoology in the Urals. Ural State University*, Ushakova, K.I., Ed., Yekaterinburg, 2003, pp. 98–115 [in Russian].
 52. Markova, E.A., Trofimova, S.S., Zykov, S.V., Sibiriyakov, P.A., and Yalkovskaya, L.E., Species composition and diet of muroid rodents in mesophytic intrazonal habitats in Aytuar Steppe Site of the Orenburg state Nature Reserve (the Southern Urals), in *Orenburg Reserve: Importance for Conservation of Steppe Ecosystems of Russia and Prospects for Development: Proceedings of Orenburg State Nature Reserve*, Orenburg: Gazprompechat, Orenburggazpromservis, 2014, vol. 1, pp. 103–108.
 53. Soroka, O.V. and Debelo, P.V., Rodents and lagomorphs of the Orenburg State Nature Reserve, *Proceedings of FSBI Orenburg Region Reserves “Orenburg Reserves in the Environmental Framework of Russia”*, Saratov: Amirit, 2019, pp. 194–210.
 54. Elina, E.E. and Baltaeva, M.U., Dynamics of species composition of rodents in the Orenburg Reserve, in *Proceedings of Orenburg State Nature Reserve “Orenburg Reserve: Importance for Conservation of Steppe Ecosystems of Russia and Prospects for Development”*, Orenburg: Gazprompechat, Orenburggazpromservis, 2014, vol. 1, pp. 47–51.
 55. Bystrov, I.V., Klassen, D.V., and Pytel, D.B., Communities of small mammals in Orenburg State Reserve, in *Proceedings of Orenburg State Nature Reserve “Orenburg Reserve: Importance for Conservation of Steppe Ecosystems of Russia and Prospects for Development”*, Orenburg: Gazprompechat, Orenburggazpromservis, 2014, vol. 1, pp. 24–27.
 56. Chronicles of nature 2016–17. https://orenzap.ru/partners-and-friends/%D0%9B%D0%B5%D1%82%D0%BE%D0%BF%D0%B8%D1%81%D1%8C%20%D0%BF%D1%80%D0%B8%D1%80%D0%BE%D0%B4%D1%8B_%D0%BA%D0%BD%D0%B8%D0%B3%D0%B0%201_2016-2017_%D0%97%D0%B0%D0%BF%D0%BE%D0%B2%D0%B5%D0%B4%D0%BD%D0%B8%D0%BA%20%D0%A8%D0%B0%D0%B9%D1%82%D0%B0%D0%BD_%D0%A2%D0%B0%D1%83.pdf. Cited May 15, 2022.
 57. Chronicles of nature 2018–19. https://orenzap.ru/%D0%9B%D0%B5%D1%82%D0%BE%D0%BF%D0%B8%D1%81%D1%8C%20%D0%BF%D1%80%D0%B8%D1%80%D0%BE%D0%B4%D1%8B_%D0%BA%D0%BD%D0%B8%D0%B3%D0%B0%202_2018-2019_%D0%B7%D0%B0%D0%BF%D0%BE%D0%B2%D0%B5%D0%B4%D0%BD%D0%B8%D0%BA%20%D0%A8%D0%B0%D0%B9%D1%82%D0%B0%D0%BD_%D0%A2%D0%B0%D1%83.pdf. Cited May 15, 2022.
 58. Korovin, V.A. and Maksimov, S.A., To the mammal fauna of the southern districts of the Chelyabinsk region, *Fauna Urala Sibiri*, 2019, no. 2, pp. 195–203.
 59. Chibilev, E.A., Changes in the fauna of rodents of the museum-reserve “Arkaim”, caused by the reserve regime, in *Natural and Cultural Landscapes: Problems of Ecology and Sustainable Development*, Pskov, 2002, pp. 48–50.
 60. Bolshakov, V.N., Zagainova, O.S., Markova, E. A., and Markov, N.I., Mammals in diet of asian Badger (*Meles leucurus*) of Urals and Western Siberia, *Vestn. Orenb. Gos. Univ.*, 2013, vol. 159, no. 10, pp. 40–45.
 61. Shulgan-Tash State Nature Reserve: recorded species and intraspecies forms. <http://oopt.aari.ru/oopt/%D0%A8%D1%83%D0%BB%D1%8C%D0%B3%D0%B0%D0%BD-%D0%A2%D0%B0%D1%88/bio#bio-64>. Cited May 15, 2022.
 62. Chashchin, S.P., Theriological studies in Troitsk reserve, in *Investigation of Biocenoses in the Forest-Steppe of the Trans-Urals (on the Example of Troitsk Forest-Steppe Reserve)*, Mamaev, S.A., Ed., Sverdlovsk: UNC AN SSSR, 1984, pp. 73–77.
 63. Southern Urals State Nature Reserve. Flora and fauna. <http://www.south-ural-reserve.ru/home/about-the-area/flora-and-fauna>. Cited May 15, 2022.
 64. Lagunov, A.V., Zakharov, V.D., Kulikov, P.V., and Sokolov, S.F., *Natsionalniy Park “Zyuratkul” Chronicles of Nature (Intermediate Report 2002)*, Satka: National Park “Zyuratkul”, 2003. https://studylib.ru/doc/972354/-zyuratkul_. Cited May 15, 2022.
 65. Olenov, G.V. and Kolcheva, N.E., Chronographic variability in the composition and abundance of muroid rodents in the Ilmensky Reserve, *Vestn. Orenb. Gos. Univ.*
 66. Zyus’ko, A.Ya. and Duelli, P.T., Trends in changes of muroid rodent communities Micromammalia in the windfall areas, *Forests of the Urals and their Management*, Ekaterinburg: Ural State For. Eng. Univ., 1998, vol. 20, p. 361–367.
 67. Ecological Monitoring of the State of Natural Complexes in the Territory of Sverdlovsk Oblast, Ekaterinburg: Ural Univ., 2018.
 68. Izvarin, E.P., Zykov, S.V., and Fominykh, M.A., To the fauna of shrews and mouse-like rodents of the Nizhneirginskaya oak forest (Middle Urals), *Fauna Urals Siberia*, 2018, no. 1, pp. 197–202.
 69. Lobanova, N.A., Biotopic distribution of small mammals in Pripyshminskie Bory, in *Ecological Studies in Forest and Meadow Biogeocenoses of the Flat Trans-Urals*, Sverdlovsk: Urals Sci. Center USSR Acad. Sci., 1978, pp. 29–32 [in Russian].

70. Buzmakov, S.A., *Okhrana Prirody I Zapovednoe delo. Priroda I Biota Zakaznika "Preduralye" Nature Protection and Reserve Management. Nature and Biota of the "Preduralye" Reserve*, Perm State Natl. Res. Univ., 2020.
71. Berdyugin, K.I., Davydova, Yu.A., Zykov, S.V., Kshnyasev, I.A., and Fominykh, M.A., Monitoring of the population of mammals in primeval forests of Visim Nature Reserve, in *Chronicle of nature of the Visim State Nature Biosphere Reserve for 2013*, Moscow: Acad. Nat. Sci., 2014, pp. 151–155.
72. Lukyanova, L.E., The species structure of the population of small mammals and the number of sympatric species of rodents and shrews in different biotopic conditions of forest biocenoses of the Visim Reserve, *Chronicle of Nature of the Visim State Nature Biosphere Reserve for 2014*, Ekaterinburg: Maks-Info, 2016, pp. 90–93.
73. Lukyanova, L.E. and Lukyanov, O.A., Small mammal communities in the changeable environment on the territory of Visim Nature Reserve, *Proceedings of the SCIENTIFIC conference "Investigation of the Reference Natural Complexes of the Urals"*, Ekaterinburg, 2001, p. 311–316.
74. *Research Studies in Strict Nature Reserves and National Parks of Russia in 1998–2005*, Otchagov, D.M., Moscow: ARRINP, 2006.
75. Smirnov, N.G., Kropacheva, Yu.E., and Bachurin, G.N., Dynamics of the modern fauna of rodents in pre-forest-steppe forests of the Trans-Urals, *Fauna Urala Sibiri*, 2015, no. 1, pp. 167–175.
76. Kropacheva, Yu.E., Smirnov, N.G., Zykov, S.V., et al., The diet of the Great Gray Owl, *Strix nebulosa*, at different levels of prey abundance during the nesting season, *Russ. J. Ecol.*, 2019, vol. 50, no. 1, pp. 43–49.
77. Smirnov, N.G., Kropacheva, Yu.E., and Zykov, S.V., Prey of small mammal-eating owls (*Strix nebulosa*, *Bubo bubo*) as a source of the selective accumulation of palaeotheriological material, *Zool. Zh.*, 2019, vol. 98, no. 11, pp. 1233–1246.
78. Chernyavskaya, S.I., Mammals of Denezhkin Kamen' reserve, in *Proceedings of the State Reserve "Denezhkin Kamen"*, Sverdlovsk. Kn. Izdat., 1959, no. 1, pp. 87–114.
79. Berdyugin, K.I., Kuznetsova, I.A., and Sysoev, V.A., The current state of the population of rodents of the reserve "Denezhkin Kamen", in *Proceedings of the State Reserve "Denezhkin Kamen"*, Ekaterinburg: Akademknika, 2003, no. 2, pp. 163–179.
80. Vishersky State Nature Reserve. Chronicles of nature 2006–2007, 2008–2009, 2015–2016. <https://www.vishersky.ru/letopis-prirody>. Cited May 15, 2022.
81. Vishersky State Nature Reserve. Chronicles of nature 2010. <https://www.vishersky.ru/letopis-prirody>. Cited May 15, 2022.
82. Bobretsov, A.V., Kupriyanova, I.F., Kalinin, A.A., Lukyanova, L.E., and Shchipanov, N.A., Species diversity of small mammal communities in the gradient of climatic and biotic conditions, *Usp. Sovrem. Biol.*, 2008, vol. 128, no. 4, pp. 409–416.
83. Vasin, A.M., Lykhvar, V.P., Buydalina, F.R., Zaguzov, A.V., and Syzhko, V.V., *Pozvonochnye zhivotnye zapovednika "Malaya Sos'va" (Severnoe Zauralye): Annotirovannyi spisok i kratkiy ocherk* (Vertebrate Animals of the Malaya Sos'va Reserve (Northern Trans-Urals): Annotated List and Brief Essay), Izhevsk: Permyakov S.A., 2015.
84. Ramazanov, F.R., Population of small mammals of the reserve "Malala Sos'va", in *Melkie mlekoopitayischie zapovednykh territoriy* (Small Mammals of Protected Areas), Moscow: Glavokhoty RSFSR, 1984, pp. 24–31.
85. Malaya Sos'va State Nature Reserve: Chronicles of nature 1992. <https://www.m-sosva.ru/syn-search?title=%D0%BB%D0%B5%D1%82%D0%BE%D0%BF%D0%B8%D1%81%D1%8C>. Cited May 15, 2022.
86. Chernov, Yu. I., *Natural Zonality and the Terrestrial Animal World*, Moscow: Nauka, 1975 [in Russian].
87. Shennikov, A.P., *Plant Ecology*, Moscow: Sovetskaya Nauka, 1950 [in Russian].
88. Zagorodnyuk, I.V., Geographic distribution and levels of abundance of *Terricola subterraneus* on the USSR territory, *Zool. Zh.* 1992, vol. 71, no. 2, pp. 86–97.
89. Surkova, E., Popov, S., and Tchabovsky, A., Rodent burrow network dynamics under human-induced landscape transformation from desert to steppe in Kalmykian rangelands, *Integr. Zool.*, 2019, vol. 14, pp. 410–420.
90. Abramson, N.I. and Lisovsky, A.A., Subfamily Arvicolinae, in *The Mammals of Russia: A Taxonomic and Geographic Reference*, Moscow: KMK, 2012, pp. 220–276.
91. Tesakov, A.S., Lebedev, V.S., Bannikova, A.A., and Abramson, N.I., *Clethrionomys* Tilesius, 1850 is the valid generic name for red-backed voles and *Myodes* Pallas, 1811 is a junior synonym of *Lemmus* Link, 1795, *Russ. J. Theriol.*, 2010, vol. 9, no. 2, pp. 83–86.
92. Smirnov, N.G., Izvarin, E.P., Kuzmina, E.A., Kropacheva, Yu. E., Steppe species in the Late Pleistocene and Holocene small mammal community of the Urals, *Quat. Int.*, 2016, vol. 420, pp. 136–144.
93. Hernández Fernández, M. and Peláez-Campomanes, P., The bioclimatic model: a method of palaeoclimatic qualitative inference based on mammal associations, *Glob. Ecol. Biogeogr.*, 2003, vol. 12, no. 6, pp. 507–517.
94. Royer, A., García Yelo, B.A., Laffont, R., and Hernández Fernández, M., New bioclimatic models for the quaternary palaeartic based on insectivore and rodent communities, *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 2020, vol. 560, p. 110040.
95. McGuire, J.L. and Lauer, A., Linking patterns of intraspecific morphology to changing climates, *J. Biogeogr.*, 2020, vol. 47, no. 11, pp. 2417–2425.

96. Khotinski, N.A., *Holocene of the Northern Eurasia*, Moscow: Nauka, 1977 [in Russian].
97. Verschuren, D., Laird, K., and Cumming, B., Rainfall and drought in equatorial east Africa during the past 1,100 years, *Nature*, 2000, vol. 403, pp. 410–414. <https://doi.org/10.1038/35000179>
98. Saurer, M., Borella, S., and Leuenberger, M., $\delta^{18}\text{O}$ of tree rings of beech (*Fagus silvatica*) as a record of $\delta^{18}\text{O}$ of the growing season precipitation, *Tellus B: Chem. Phys. Meteorol.*, 1997, vol. 49, pp. 82–90.
99. Ramirez, L.C., Carrara, R., Silvestro, V.A., and Flores, G.E., First fossil assemblage of darkling beetles (Coleoptera: Tenebrionidae) from Buenos Aires, Argentina: Evidence of dry climate during the Late Pleistocene in the humid Pampas, *Annales Zoologici*, 2016, vol. 66, pp. 643–652.
100. Novenko, E.Yu., Tsyganov, A.N., Babeshko, K.V., et al., Climatic moisture conditions in the North-West of the Mid-Russian Upland during the Holocene, *Geogr., Environ., Sustain.*, 2019, vol. 12, no. 4, pp. 188–202.
101. Smirnov, N.G., Rodents of the Urals and adjacent territories in the Late Pleistocene and Holocene, *Extended Abstract Doctoral (Biol.) Dissertation*, Ekaterinburg: IPAE Ural. Branch Russ. Acad. Sci., 1994.