

The Narrow-Skulled Vole (*Microtus gregalis* Pall.) in the Dynamics of Zonal Rodent Communities of Northern Eurasia¹

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Abstract—On the basis of abundant fossil and subfossil bone remains, the ecological and faunal role of the narrow-skulled vole in zonal rodent communities of northern Eurasia is analyzed over the period from the Late Pleistocene to the present time. Special attention is given to the correlated dynamics of relative abundance of *Microtus gregalis* and other rodent species in the course of transition from one zonal type to another and to specific features of this correlation in the southern, middle, and northern parts of the species range. It is shown that distinctive dimensional and morphotypic features of the two currently existing subspecies, *Microtus gregalis major* Ogn. and *M. g. gregalis* Pall., are the product of concordant development of the species and environmental conditions in the past 3000–4000 years (transition from the Holocene optimum to the present-day climate and state of the natural environment).

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INTRODUCTION

The narrow-skulled vole *Microtus gregalis* Pall. inhabits vast territories of northern Eurasia that form two belts: one within the Subarctic (from the Northern Dvina River in the west to the Chukchi Peninsula in the east), and the other extending over forest–steppes, steppes, and semideserts from the Cisural region to the Amur River. During the Late Pleistocene, the species range not only covered all these regions but extended beyond them in all directions. Regions of the forest zone, now devoid of *M. gregalis*, were inhabited at that time by communities of the “mammoth complex,” which included this vole species; moreover, *M. gregalis* was often dominant among small mammals. In the west, the range of species area reached the British Isles and central regions of present-day France.

By its zonal bias, *M. gregalis* is a polyzonal species. It is known that animal species differing in the type of adaptation to the same environmental conditions can be distinguished even within the same natural zone. Therefore, it is important to determine the actual position of this species within the animal zonal assemblage and estimate the level of its adaptation achieved at a certain stage of development. In this study, two interrelated processes are considered: the first is the dynamics of a small mammal community depending on climate and

landscape changes, and the second is evolutionary reorganization of the species itself. The study of the latter is especially difficult, because such processes are governed not only by ecological factors but also by a variety of other factors. Data on the phylogeography of *M. gregalis* based on cytochrome B genetic distances (Abramson, 2006) indicate that the history of intraspecies groups is more complicated than had been considered on the basis of fossil evidence and analysis of morphological features in recent forms (Dupal, 2000; Golovachev et al., 2001).

Ecological and evolutionary aspects of *M. gregalis* intraspecies differentiation were analyzed by S.S. Shvarts and his collaborators (Shvarts et al., 1960; Shvarts, 1963). They revealed two distinct adaptive types, “northern” and “southern,” which had not diverged enough to reach the species rank but represented two well-differentiated subspecies. The northern (*M. g. major*) and southern (*M. g. gregalis*) subspecies differ in their responses to changes in environmental conditions, as well as in some biological and morphological features. The northern subspecies is characterized by a large body size, a short tail, distinctive skull proportions, high growth rates, early subnivean reproduction, and higher fecundity. Fossil evidence available in the 1960s was insufficient for discussing the concrete historical pathways of formation of these two adaptive types and subspecies. However, an ecological and evo-

¹ The article was translated by the authors.

Classification of rodent and pika species by zonal groups

Tundra	Taiga	Steppe	Intrazonal waterside	Azonal grassland
<i>Dicrostonyx torquatus</i>	<i>Apodemus uralensis</i>	<i>Ochotona pusilla</i>	<i>Arvicola terrestris</i>	<i>Cricetus cricetus</i>
<i>Lemmus sibiricus</i>	<i>Clethrionomys rufocanus</i>	<i>Spermophilus major</i>	<i>Microtus oeconomus</i>	<i>Microtus arvalis</i>
<i>Microtus middendorffii</i>	<i>Cl. ex gr. rutilus-glareolus</i>	<i>Sp. pygmaeus</i>		
	<i>Microtus agrestis</i>	<i>Marmota bobak</i>		
	<i>Myopus schisticolor</i>	<i>Allactaga major</i>		
	<i>Pteromys volans</i>	<i>Allocricetullus evermanni</i>		
	<i>Sciurus vulgaris</i>	<i>Cricetulus migratorius</i>		
	<i>Tamias sibiricus</i>	<i>Lagurus lagurus</i>		
		<i>Eolagurus luteus*</i>		
		<i>Alactagulus pumilio*</i>		

* *Eolagurus luteus* is also a member of semidesert complexes.

lutionary analysis of adaptations provided a basis for the conclusion that the northern *Microtus* voles are of steppe origin and that *M. gregalis* has lived in the Subarctic for a long time. Shvarts wrote: "Differentiation of the tundra populations of the narrow-skulled vole has not reached the species rank not because of time shortage but because colonization of new environments by this species proceeded along an original pathway of changes in reproductive physiology and perfect use of microclimatic features of habitats, which required no change in the type of physiological and biochemical reactions" (Shvarts, 1963, p. 113).

Paleontological methods used in this study allowed us to trace the dynamics of only a few species characteristics of narrow-skulled voles (dimensions, morphotypic peculiarities of the first lower molars, and relative abundance in communities). However, these characteristics, examined along the latitudinal transect (from the Arctic coast to the extreme south of the Urals) and grouped according to the periods of climate and landscape transformations following the last glacial epoch, provide a deeper insight into the role of the narrow-skulled vole in the past and present rodent communities.

MATERIAL AND METHODS

Fossil remains used in this study were collected during excavations of loose deposits in karst cavities, having been accumulated there due to the feeding activity of predatory birds and mammals. Methods for reconstructing the past composition and structure of small mammal communities were described previously (Smirnov, 2004).

Data on the faunas were grouped with regard to the latitudes of sampling sites and the affinity of specimens to a certain zonal complex. These complexes were delimited using general approaches accepted in Russian biogeography (Chernov, 1984). In the Holocene, three zonal groups (the tundra, taiga, and steppe spe-

cies), one intrazonal group (waterside animals), and one azonal group (meadow dwellers) were distinguished. *Microtus gregalis* could be attributed to two zonal complexes, those of the tundra and steppes. In addition to zonal affiliation, it is also important to discuss the position of this species in the classification of rodents by biotopic preferences. Many authors in Europe regard *M. gregalis* as a species inhabiting the steppes. In Russia, specialists dealing with animal communities of arid regions classify this vole as a mesophilous animal and, among Subarctic rodents, as an inhabitant of elevated, dry tundra plots. This reflects the actual diversity of habitats used by *M. gregalis*.

In the Pleistocene, the small mammal fauna consisted of the same species as in the Holocene (except for the *Dicrostonyx* lemmings represented by different species in these epochs). However, the composition of zonal faunal complexes was markedly different, especially in the latitudinal belt corresponding to the present-day forest zone. The zone that was there in the Late Pleistocene has no recent analogues: its faunal complex included mammals that became extinct during the Late Pleistocene–Holocene transition (the mammoth, woolly rhinoceros, cave bear, cave hyena, etc.), as well as a series of species currently inhabiting either steppe or tundra regions. This complex has been designated by a variety of terms (tundra–steppe, no-analog, mixed, etc.), but the term "hyperboreal" appears to be more adequate (Smirnov, 2001): it emphasizes the specificity of this biota (instead of representing it as a "hybrid" of those inhabiting different recent zones), severity of environment conditions, and location in the area presently covered by boreal forests. Three latitudinal variants of this faunal complex (northern, typical, and southern) are distinguished. In the corresponding small mammal communities, *M. gregalis* played an important role, together with *Dicrostonyx* lemmings in the northern variant and by *Lagurus* voles in the southern variant.

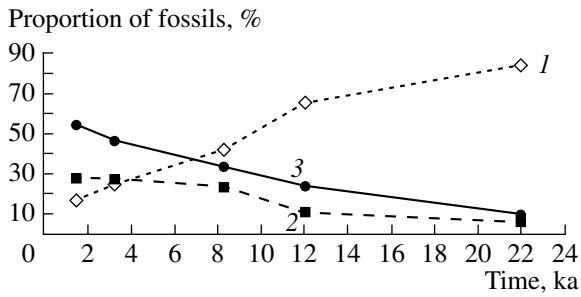


Fig. 1. Dynamics of (1) xerophilous and (2) mesophilous species and of (3) *Microtus gregalis* in the Late Pleistocene and Holocene small mammal communities of the Southern Transural region.

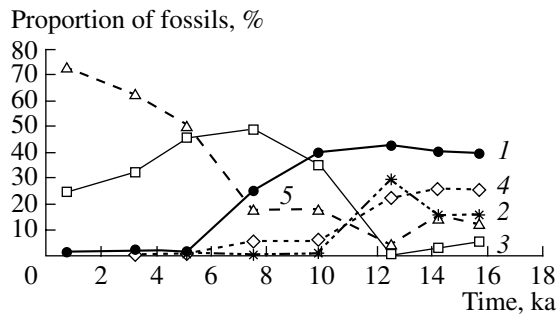


Fig. 2. Dynamics of relative abundance of (1) *Microtus gregalis* and groups of (2) tundra, (3) forest, (4) steppe, and (5) meadow and waterside rodent species in animal communities of the Middle Urals in the Late Pleistocene and Holocene.

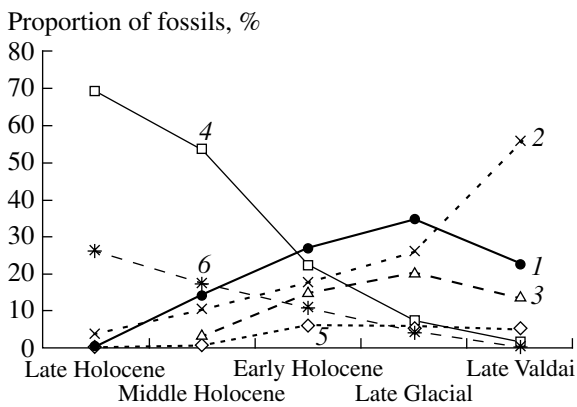


Fig. 3. Dynamics of relative abundance of (1) *Microtus gregalis*, (2) *Dicrostonyx*, (3) *Lemmus*, and groups of (4) forest, (5) steppe, meadow, and (6) waterside species in Late Pleistocene and Holocene rodent communities of the Northern Urals.

It is impossible to reconstruct characteristics of *M. gregalis* as a dominant of these communities without understanding the specificity of environmental conditions in the hyperboreal zone. It is usually considered that its climate was relatively cold and arid; however, animal communities were characterized by high species diversity and productivity. To understand this paradox and other characteristics of the hyperboreal zone, it is important to reveal the composition of the biota and the proportions of species within communities, as well as to estimate what kinds of associations were formed by their constituent species. Unfortunately reconstruction of such associations in Quaternary paleoecology is as yet impossible; however, the responses of animal species to the dynamics of the environment can be estimated from changes in their abundance. An analysis of correlations between these responses makes it possible to identify groups of species with similar requirements for environment conditions. This method is not perfect, as the fact that the directions and rates of changes in abundance coincide does not necessarily confirm that they are accounted for by common factors; however, such an approach makes sense. Multivariate factor analysis was used to examine subfossil small mammal assemblages from different sites of the forest and forest-steppe zones and a series of Pleistocene assemblages of the hyperboreal type (Smirnov, 1992). Pairwise correlations were also calculated for different zonal complexes to compare the indices of relative species abundance in their historical variation. Congruence of the curves of relative abundance was qualitatively analyzed over the period from the Late Pleistocene to the Holocene and to the present time.

The results obtained by different methods lead to the same conclusion: a high degree of congruence in the dynamics of species abundance over a long period of time is evidence that these species belong to a certain group unified by the same requirements concerning biologically significant parameters of the environment.

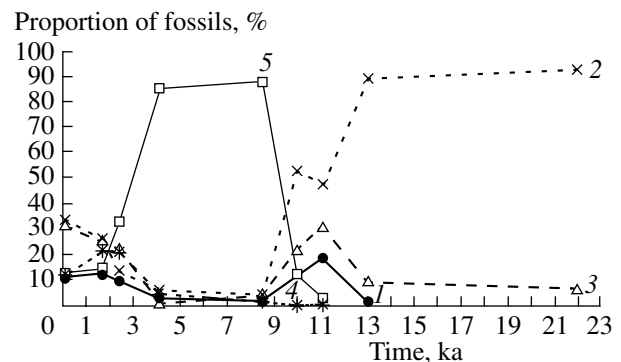


Fig. 4. Dynamics of relative abundance of (1) *Microtus gregalis*, (2) *Dicrostonyx*, (3) *Lemmus*, (4) *Microtus middendorffi*, and (5) groups of forest and waterside species in Late Pleistocene and Holocene rodent communities of the Ural Subarctic.

However, this congruence should not be interpreted as an absolute proof that the corresponding species are of the same zonal group. An illustrative example is the pair of lemmings, *Dicrostonyx* and *Lemmus*. Both species are certainly tundra dwellers and members of the hyperboreal complex, but the *Dicrostonyx* lemmings reached the peak of abundance during the cold and arid periods of the Pleistocene, whereas the *Lemmus* lemmings were most abundant during cold and moist periods. In virtually all assemblages examined, the patterns of *M. gregalis* population dynamics were congruent to those of the collared lemming (*Dicrostonyx*), whereas positive correlations with *Lemmus* were very rare.

In this study, the dynamics of *M. gregalis* abundance and its relationship with those of other small mammal species were analyzed qualitatively, on the basis of curves shown in Figs. 1–4.

RESULTS AND DISCUSSION

Fossil remains of rodents and pikas were collected from the sequences of six sites compactly located in the southern Transural region, in Chelyabinsk and southern Orenburg oblasts, and at the eastern border of the Bashkir Republic (52° N). More than 26000 molars were identified. Taking into account that a group of steppe species (including *M. gregalis*) was dominant during the Late Pleistocene and Holocene (Smirnov and Kuz'mina, 2005; Kuz'mina, 2006), the zonal type of communities was classified as the steppe type. In the Late Pleistocene associations, the second place (by abundance) belonged to the group of semidesert species (approximately 20% of fossils). In the Early Holocene, during the Boreal time, the group of meadow dwellers occupied this place (with approximately 13% of bone remains) and retained it throughout the Holocene. The abundance of semidesert animals decreased during the Holocene, whereas that of forest and waterside rodents increased.

With respect to requirements for moisture supply (the most important factor in steppe regions), small mammals of the southern Transural region were divided into two categories. The first comprised *xerophilous* species, including steppe inhabitants (without *M. gregalis*) and semidesert animals; the second category comprised *mesophilous* species, including those inhabiting meadow, forest, and waterside biotopes. In Fig. 1, the curve showing the dynamics of abundance of *M. gregalis* fossils is compared with similar curves for *xerophilous* and *mesophilous* species. It can be seen that *xerophilous* elements significantly prevailed during the Late Pleistocene, but their proportion began to decrease gradually after the onset of the Holocene.

The dynamics of abundance of *M. gregalis* fossils showed congruence with those of *mesophilous* rodents. This fact suggests that *M. gregalis* in the southern Transural region behaved as *mesophilous* rodents during the Late Pleistocene and Holocene. This conclusion

agrees with characteristics of this species described for other steppe regions, such as Transbaikalia (Erbaeva, 1970; Khenzykhenova and Alexeeva, 1999).

Available data on the composition and structure of small mammal communities that inhabited low-mountain regions of the Southern Urals (beginning from 55° N) in certain periods of the Late Pleistocene and Holocene (*Istoricheskaiya ekologiya...*, 1990) are insufficient for tracing the dynamics of *M. gregalis* abundance in the region with the same degree of detail as was done for the southern Transural region and some other areas; however, the main trends can be indicated with confidence. At least from the first part of the Late Pleistocene and through the late glacial time, the narrow-skulled vole dominated the rodent communities of the hyperboreal complex in its southern variant. The relative abundance of this species exceeded 30%, reaching 70% during the late Valdai cold maximum. At that time, there lived the narrow-skulled vole identified as an individual subspecies, *M. g. kriogenicus*, first described by Rekovets (1985) from the late-Valdai sediments near the Dnieper River. These voles were fairly large, similar in dimensions to recent *M. g. major*. However, their dental patterns differ significantly from those of all recent forms. In the Holocene, narrow-skulled voles of the Southern Urals were noticeably smaller and their morphological features were closely similar to those of the recent nominative "southern" subspecies, *M. g. gregalis*.

Recent communities of the Middle Urals belong to the southern-taiga type. In the Late Pleistocene, these areas were occupied by animal associations classified as a typical variant of the hyperboreal complex (Smirnov, 1993, 2001). Below, the dynamics of small mammal communities will be discussed on the basis of evidence from a series of sites compactly located in the south of the Middle Urals western slope (57° N). The relevant material amounts to approximately 39000 molars.

The narrow-skulled vole inhabited this region almost throughout the period considered in this study, except for the last several centuries. Today, the western slope of the Middle Urals (where the fossils were collected) is largely covered by the Krasnoufimsk forest-steppe island, a large azonal structure where only small steppe area strips remain amid arable lands and small forest stands and not a single vertebrate species characteristic of steppe associations can be found. However, the subfossil collections provide information on the time and sequence of the disappearance of steppe animal species from this region. The taxonomic list of steppe associations in the Middle Urals was most extensive during the late Valdai and late glacial times. Thereafter, this list became shorter due to elimination of some steppe species and the relative abundance of narrow-skulled voles also decreased (Fig. 2). In parallel, the proportions of meadow and waterside rodents continuously increased beginning from the late glacial

until the present time. After the late Valdai, forest species also increased in numbers and became the most abundant group in the Atlantic time. Subsequently, the group of meadow and waterside species gained dominance, which is indicative of the more mesophilous character of these communities. In the same period, tundra species finally disappeared from the Middle Urals. Species of this group, together with the narrow-skulled vole and steppe animals, formed the bulk of the rodent fauna in the Late Pleistocene and, beginning from the Late Pleistocene–Holocene transition, remained in the region as rare faunal elements. Thus, the dynamics of the rodent fauna in the Middle Urals may be interpreted as degradation of zonal hyperboreal associations during the late glacial time. The fauna of the forest zonal type already existed in the first half of the Holocene, but tundra and steppe animals and the narrow-skulled vole were preserved in it as azonal elements until the end of the Atlantic time.

Recent rodent communities of the Northern Urals belong to the taiga type, with species of forest biotopes dominating in it. Small mammal communities described from the Late Pleistocene sites are of the same zonal type as those in the Southern and Middle Urals. This is the same hyperboreal type but in its different (northern) subzonal variant. This variant had two distinctive features: (1) the dominant position of *Dicrostonyx* lemmings (instead of the narrow-skulled vole) and (2) significantly poorer taxonomic composition and lower abundance of steppe species.

The collection used to characterize rodent communities of the Northern Urals consisted of about 27000 molars (Smirnov, 1996; Teterina, 2003). Degradation of the hyperboreal complex in this region had the same pattern as in the Middle and Southern Urals. The only difference was that tundra elements were maintained in northern forest communities for a longer period of time. The late glacial-to-Holocene curve of *M. gregalis* relative abundance is almost parallel to those of the collared lemming and other tundra species and of the steppe species group (Fig. 3).

Data on the history of Late Pleistocene and Holocene rodent communities was also obtained from a series of sites situated in regions adjoining the Polar Urals, west and east of the Ural Ridge (Smirnov et al., 1999; Golovachev, 2000). Taken together (Fig. 4), these data are indicative of two periods of low *M. gregalis* abundance. The first was in the late Valdai time, when low temperatures and low annual precipitation limited the variety of taxa in periglacial tundra rodent communities, in which the collared lemming was absolutely dominant. There is also information on rodent faunas in the preceding period (Smirnov et al., 1986), when these communities were characterized by an approximately equal ratio of the narrow-skulled vole, collared lemming, and brown lemmings. The relative abundance of *M. gregalis* increased in the late glacial time and then decreased again upon transition to the forest and forest–

tundra associations of the Holocene optimum. In the Late Holocene, the relative abundance of this species became high again due to a general increase in the proportion of tundra elements and elimination of forest elements in the Subarctic.

Morphological characters of *M. gregalis* molars were analyzed using numerous samples collected in a series of Late Pleistocene and Holocene sites excavated in the Polar Urals and adjacent plains (Golovachev et al., 2001). The results showed that the dental pattern characteristic of the northern subspecies *M. g. major* appeared only at the end of the Holocene. Earlier, when narrow-skulled voles inhabited the Late Pleistocene periglacial tundra and Early Holocene forest–tundra regions, they were significantly smaller than voles of the recent northern subspecies, and “gregaloid” morphotypes prevailed among M1 morphotypes. Therefore, the recent northern subspecies of *M. gregalis* was formed in the Late Holocene, no more than 3000–4000 years ago, when the Holocene optimum with its relatively moderate conditions came to an end and animal associations developed into recent Subarctic communities of the forest–tundra type.

CONCLUSIONS

A review of available data on the relative abundance of *M. gregalis* in different zonal rodent complexes dated to the Late Pleistocene and Holocene made it possible to determine time intervals and regions characterized by the most favorable conditions for this species, compared to other small mammals.

The Holocene extinction of *M. gregalis* in the areas corresponding to the present-day forest zone in Europe and a large part of northern Asia may be regarded as the final phase of degradation of the hyperboreal complex, which included this species as a major zonal element. The specialized form *M. g. kriogenikus* became extinct without leaving descendants.

The congruence of the relative abundance dynamics of *M. gregalis* and other rodent species in the course of transition from one zonal type to another has certain specific features in the southern, middle, and northern parts of the species range. In steppe communities, the dynamics of *M. gregalis* relative abundance coincided with those of the forest and meadow species. In northern regions, when hyperboreal associations transformed into recent forest communities, this species decreased in numbers along with the steppe species group. In regions corresponding to the present-day Subarctic, *M. gregalis* succeeded in passing through two bottlenecks, the first during the late Valdai cold maximum and the second in the period of forest vegetation expansion during the Holocene optimum. Dimensional and morphotypic characteristics of the two recent subspecies, *M. g. major* and *M. g. gregalis*, are the product of species development and transformation of the environment during the past 3000–4000

years, i.e., during the transition from the Holocene optimum to the present-day natural-climatic conditions.

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