ISSN 1067-4136, Russian Journal of Ecology, 2023, Vol. 54, No. 1, pp. 42–53. © Pleiades Publishing, Ltd., 2023.
Russian Text © The Author(s), 2023, published in Ekologiya, 2023, No. 1, pp. 46–57.

Environmental Preferences of the Bank Vole (*Clethrionomys Glareolus* Schreber, 1780) under Different Biotopical Conditions in the Protected Territory of the Middle Urals

L. E. Lukyanova*

Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia
**e-mail: lukyanova@ipae.uran.ru*

Received November 30, 2021; revised May 20, 2022; accepted May 24, 2022

Abstract—The environmental preferences of the bank vole were studied in the protected area of the Middle Urals in different biotope conditions formed as a result of the consequences of natural catastrophic events. According to the abundance of the population, the "success" of the existence of the species in four biotopes with varying degrees of disturbance by wind and pyrogenic effects was assessed. A statistically highly significant level of differences between the compared biotopes was shown for six microenvironmental variables that assess the food-protective conditions of animal habitats. In general, the biotopic variability turned out to be higher than the chronographic (interannual) variability. Over the long period of the study, the bank vole prevailed in numbers in the undisturbed biotope, which was distinguished among the studied biotopes by high values of microenvironmental indicators that assess mainly the food resources of animal habitats: the coverage of areas by shrubs and herbaceous vegetation. Habitat conditions in the biotope undisturbed by natural catastrophic factors are most consistent with the environmental preferences of the bank vole.

Keywords: *Clethrionomys glareolus* (syn. *Myodes glareolus*), different biotopic conditions, environmental preferences, natural disasters, microhabitat characteristics, protected area

DOI: 10.1134/S1067413622060091

INTRODUCTION

Knowing the features of the choice of environment by different species makes it possible to understand the reasons for the distribution of organisms in a certain space and time, as well as to predict the state of populations under changed conditions caused by various disturbances [1]. The degree of well-being of the existence of a species in the natural environment, its biological success and adaptive plasticity reflect such population indicators as abundance and spatial structure [2, 3]. In this regard, the identification of environmental preferences of species based on the study of their population dynamics in different biotopic conditions is an important environmental problem.

Species preferences manifest at the macro- and microenvironmental levels [1, 4–7]. The microenvironmental structure of biotopes plays a decisive role in the choice of habitat conditions for small mammals, since the vital activity of many species during specific periods of their life cycle takes place in areas that are incommensurable with the territory of the entire population [8]. The choice of environment is influenced by a variety of factors, including the availability of food, the suitability of shelters, the presence of competitors, the risk of predation, parasitism, and diseases [9–19]. The environmental preferences of rodents in habitats disturbed by natural or anthropogenic impacts can change, since species features that are not realized under stable conditions manifest in a destabilized environment [20]. The mosaic nature of the environment, caused by the consequences of natural catastrophic events, is reflected in the nature of the use of habitats by small mammals, which leads to a spatial redistribution of the abundance of species [20–27]. It has been shown that the differentiated use of living space becomes the most important element of the adaptive strategy of mobile organisms with a pronounced mosaicity of the environment in short time intervals [28]. This makes great biological sense, since, on the one hand, it determines the most efficient use of fodder, protective, microclimatic, and other environmental resources, and, on the other hand, it serves as the basis for sustainably maintaining the required level of intraspecific (intrapopulation) contacts between individuals [29].

The bank vole (*Clethrionomys glareolus* Schreber, 1780) is a representative of the forest vole genus (*Clethrionomys*, the name *Myodes* is more often used in modern taxonomy), is a background species of temperate forests. In the taiga zone, it reaches its highest abundance in berry spruce forests and clear cuts adjacent to them. It is common in floodplain forests, and everywhere it avoids forests with a closed stand, inhabiting light secondary forests [30]. Bank voles prefer habitats with rich and varied food resources (high yield of seeds and berries, abundant grass vegetation) and favorable protective conditions that provide the animals with wide opportunities for housing. The population distribution of the species is influenced by such characteristics of the environment as the state of the undergrowth (developed undergrowth, abundance of shrubs), the composition of the forest stand, and the degree of littering of plots (litter, fallen dead trees) [31–37].

We showed [38] that the choice of environment by the bank vole in ecologically contrasting biotope conditions in two protected areas of the Urals has distinctive features: species preferences in the biotopes of the Middle Urals area disturbed by windfall and fire are associated with the stages of post-catastrophic restoration successions, and the choice of environment in stable habitat conditions in undisturbed territory of the Northern Urals is largely determined by the landscape structure of biotopes.

The purpose of this study is to identify the environmental preferences of the bank vole in biotope conditions that differ in the degree of disturbance by natural catastrophic factors. The main tasks to be solved: (1) to study the long-term dynamics of the bank vole abundance in biotopes with varying degrees of natural disturbances; (2) to compare the microenvironmental structure according to seven main characteristics that reflect the food-protective conditions of rodent habitats; (3) to assess the interannual variability of microenvironmental characteristics; and (4) to show the relationship between the abundance of the bank vole and the parameters of the microenvironment in different biotopic conditions.

MATERIALS AND METHODS

The study used bank voles caught in the period of 2013–2021 on the territory of the Visim State Natural Biosphere Reserve (Sverdlovsk oblast, Middle Urals, 57°19′–57°31′ N and 59°20′–59°50′ E). Various biotopes were found in a wide range of habitats of *Clethrionomys glareolus* in the Middle Urals, including post-forest plant formations in clearings and burnt areas, as well as several anthropogenic habitats [39]. The population dynamics of the bank vole and its environmental preferences were studied in different biotopic conditions formed as a result of natural catastrophic events: a windfall in 1995 and a subsequent fire that arose in 1998 from lightning during a "dry thunderstorm" that covered only part of the studied windfall territory. In 2010, a second fire broke out in the reserve, from which the part of the windfall territory not disturbed by the previous pyrogenic impact was primarily affected, as well as the previously burned part, which eventually turned out to be a twice pyrogenically disturbed windfall territory.

Four biotopes with varying degrees of disturbance by natural catastrophic factors were selected for the study: a windfall and two fires (biotope I), a windfall and one fire (biotope II), partial (along the periphery of the site) windfall and one fire (biotope III), and a habitat undisturbed by external adverse influences (biotope IV). Prior to natural catastrophic events, biotopes I and II were included in the fir–spruce forests of primordial and conditionally indigenous linden forests, as well as conditionally indigenous small-grass-reed forests (with an admixture of birch and aspen). At present, these biotopes are windfall-cinder forest communities at different stages of restoration successions: biotope I is a post-fire reed–willow–herb community under a sparse tree canopy, biotope II is a post-fire birch–fir–spruce woodland. Biotope III is part of the fir–spruce–birch large-tailed sedge-linden forest and biotope IV is located in the primary tall grass–fern fir–spruce forest community. All studied biotopes have a similar landscape and are located in the near-top part of low mountains: biotopes I–III occupy the gentle slope of Mount Lipovy Sutuk (495 m a.s.l.), and biotope IV is located on the slope of Malyi Sutuk (560 m a.s.l.).

The condition of the bank vole population was assessed by the level of its abundance. The standard trap-line method was used to capture the animals; the abundance index was calculated from the number of individuals caught during the first 5 days calculated on 100 trap-days (ind./100 trap-days). At the end of the summer season, 50 wire traps were simultaneously placed in each biotope in a line 500 m long, the exposure time was 5 days. The check was carried out daily in the morning. Each trap had a constant location throughout the long-term observation period and was provided with a constant number, which is important for accounting for the captures of animals and analysis of their spatial distribution. The total number of bank voles included in the work was 532 individuals.

A quantitative description of the characteristics of the microenvironment was carried out twice during the study period (in 2013 and 2017) in August around each trap located in the center of a square with sides of 3.33 m (area was 10 m^2). The parameters characterizing the forage-protective habitat conditions of the bank vole were evaluated according to [8], with minor changes. The coverage area of microsites measured: (1) moss cover (*MC*), (2) herbaceous cover (*HC*), (3) shrubs (*CS*), (4) trunks of living trees (*TC*), (5) trunks of standing dry trees and stumps (*SC*), (6) trunks of lying trees (*LC*), and (7) undergrowth of tree species (*AU*) with a height of no more than 1 m (Table 1).

The frequency of quantitative descriptions chosen by us is explained by the fact that the vast majority of these characteristics of the microenvironment are subject to insignificant interannual fluctuations, and they reflect its static properties [8]. When selecting microenvironmental variables, the "physical" properties for the bank vole were taken into account. Based on the "functionality" of the selected seven variables of the microenvironment, all of them generally characterize the forage-protective conditions of the habitats of the species under study. It is noted that the microenvironmental variables that assess the herbaceous and shrub cover reflect, to a greater extent, the forage characteristics of the habitats. Along with this, the features associated with the coverage of areas with moss, living trees, and tree undergrowth characterize the forage-protective properties, but with an emphasis on the protective aspect, and in the "pure" form, the protective conditions for the bank vole provide characteristics that evaluate the coverage of areas with stumps and dry trees [8].

The herbaceous tier in the four biotopes studied by us is generally of the same type; it includes *Calamagrostis langsdorffii, Calamagrostis obtusata*, and *Chamaenerion angustifolium*, which dominate in post-fire communities (biotopes I and II). The herbage of biotope III includes *Carex macroura*, *Aegopodium podagraria*, and *Equisetum sylvaticum*. Ferns dominate in the herbage of an undisturbed indigenous tall-herb-fern fir–spruce forest (biotope IV), among which *Dryopteris assimilis* predominates. The shrub undergrowth of the studied biotopes is formed mainly by *Rubus idaeus* and *Rubus matsumuranus*, as well as *Rosa acicularis*, which provides favorable feeding conditions for bank voles. *Rubus idaeus* and *Rosa acicularis* are the dominant shrubs in biotopes I and II disturbed by windblows and fires. The shrub vegetation of the partially disturbed biotope III and the undisturbed biotope IV also includes *Lonicera xylosteum*.

The state of the forest stand in the studied biotopes is different: it is significantly sparse in disturbed communities. Its composition is represented mainly by *Betula pubescens* with an admixture of *Betula pendula*, as well as *Tilia cordata*. The tree canopy of biotope III is less sparse compared to biotopes I and II: along with *Betula* and *Tilia cordata*, the stand includes *Picea obovata* and *Abies sibirica*. The undergrowth of this biotope is mainly represented by *Betula pendula*, *Tilia cordata*, *Picea obovate,* and *Abies sibirica*. The forest stand of the undisturbed biotope IV is not closed: it includes *Picea obovate*, *Abies sibirica,* and *Betula pendula*, as well as *Pinus sibirica*. *Abies sibirica* dominates in the first and second tiers of the tree canopy.

It is known that the bank vole's ability to dig holes is very limited. Voids under the roots of old living trees, root hollows where the animals arrange simple dwellings, along with rotten, mossy stumps, deadwood heaps, and twisted windbreak roots, are the preferred natural shelters for this species [31]. There are practically no living mature trees in the post-fire forest communities (biotopes I and II), the forest stand is represented mainly by young species; it is significantly sparse, so its protective role for the bank vole is significantly reduced. Stumps and trunks of dead trees lying on the ground are the main shelters for rodents in disturbed habitats. The bark of young trees can be used by the bank vole for food; therefore, the forest stand in the disturbed biotopes studied by us to a greater extent characterizes the feeding conditions of the habitats of the species. The area occupied by live, as well as dry trees and stumps, was estimated by the diameter of the trunk, measured at the base at a distance of no more than 0.5 m from the ground. Based on the calculated values, the area of the base of each trunk and stump within the site was calculated, the results were summarized to estimate the total area. The area covered by the microsections with the trunks of fallen dead trees was calculated by multiplying the length and width of each trunk, the obtained values were summed up. A total of 400 quantitative descriptions were carried out.

Table 1. Characteristics used to analyze the microhabitats of the bank vole

Characteristics	Designation
Plot area (m^2), covered with:	
1) moss	*MC*
2) herbaceous vegetation	*HC*
3) shrubs	*CS*
4) living tree trunks	*TC*
5) trunks of standing dry trees and stumps	*SC*
6) lying tree trunks	*LC*
7) undergrowth of tree species, pcs./m^2	*AU*

Multiple regression analysis with standardized partial regression coefficients β, showing how many standard deviations the species abundance differs when environmental variables change by one standard deviation, was used to study the relationship between bank vole abundance and microenvironment characteristics (predictors). The coefficient of determination (R^2) was used to estimate the proportion of explained variance. The reliability of the regression equations was assessed by the F-criterion. We analyzed the distribution of the residuals of the multiple regression model and tested the predictors for "normality." When they deviated from the normal distribution, the logarithm procedure was performed. Pairwise comparisons of bank vole abundance values in the compared biotopes were performed using the nonparametric Mann–Whitney test and the significance of the obtained differences was assessed by the Z-test.

Biotopic and chronographic (interannual) variability of species abundance and habitat microenvironment variables were studied using two-way analysis of variance, where a "biotope" was a fixed factor, and a "year" was used as a random factor. In order to reduce the number of microenvironmental variables, factor analysis was used to characterize the compared biotopes. The load values were taken into account for the first two factors, *F1* and *F2*, the total proportion of the variance of which contributed to the overall variability of the microenvironmental structure of habitats was the largest. All methods of multivariate statistical analysis used in the study were carried out in Statistica 6.0 (modules Basic statistics, Multiple regression, Nonparametric statistics and distributions, ANOVA, and Factor analysis).

RESULTS AND DISCUSSION

The analysis of variance of the microenvironmental characteristics of the four compared biotopes, carried out based on the results of quantitative descriptions in 2013 and 2017, revealed statistically significant differences between all variables, with the exception of one that estimates the area of coverage of microsites by fallen trees. In general, the level of biotopic variability of the microenvironment of the bank vole habitats was higher than the chronographic (interannual) one (Table 2). According to the data of researchers who studied the microenvironmental structure of the undisturbed habitats of the island population of the bank vole [8], the variables characterizing the herbaceous, moss, and shrub cover, as well as the coverage of microareas with stumps and deadwood, are characterized by the greatest interannual variability. The variable that estimates the coverage by living trees is the least variable; the intermediate value in this series is occupied by the feature associated with the number of undergrowth [8].

When analyzing the interannual variability of microenvironmental characteristics in disturbed biotopes (I–III) and undisturbed habitat (biotope IV), we found that the variables evaluating the coverage of plots by moss (*MC*) and herbaceous covers (*HC*) were the most variable (Table 3). Shrub cover area (*CS*), a feature that largely reflects the feeding conditions of the bank vole habitat, had no year-to-year differences in biotopes II–IV; it differed statistically significantly over the years in the most disturbed biotope I. Variables assessing the foraging conditions of microhabitats of voles: cover with trunks of live (*TC*), dry trees, and stumps (*SC*), were characterized by the lowest variability in all biotopes. Deadwood area in all habitats, with the exception of biotope III, also turned out to be the least variable feature. The number of undergrowth (*AU*) had stable interannual values only in undisturbed biotope IV (Table 3).

Analysis of variance in the variability of bank vole abundance indicators showed a highly significant level of biotopic and interannual differences (Table 2). In general, the population of the species was higher in the undisturbed biotope over the entire study period, except for 2015 (Fig. 1). Pairwise comparison of abundance indicators using the Mann–Whitney test showed significant differences between the most disturbed and undisturbed habitats (biotopes I and IV, respectively) for the entire study period. The exceptions were 2013 and 2019, which are characterized by a low level of the bank vole population in all compared biotopes (Table 4). The abundance of the species differed statistically significantly between biotopes I, II and II, III only in 2015, and in 2017, in the most (biotope I) and partially (biotope III) disturbed habitats (Table 4). The abundance of the species was characterized by zero values in all compared biotopes in 2018 and 2021, and also in 2015 in biotope III (Fig. 1). In the long-term population dynamics of the population of the bank vole in 2017, it is distinguished by the nature of the distribution of abundance in different biotope conditions: the indicators are arranged in ascending order from the most disturbed (biotope I) to the undisturbed (biotope IV) (Fig. 1). Analyzing the effect of environmental factors on the population of shrews in the same area of the Visim Reserve, we showed [40] that, according to the values of the average temperature and total precipitation, the spring–summer season of 2017 was characterized as relatively favorable. The revealed statistically significant differences in the abundance level of the bank vole in the compared habitats under similar macroenvironmental (weather) conditions of this year can obviously be explained by biotopic differences in the microenvironmental structure.

Factor analysis of the structure of the microenvironment of four biotopes showed that the first two factors (*F1* and *F2*) make the greatest contribution to its variability; in total, it amounted to 42.5–54.0% (Table 5). In biotopes I–III, the proportion of the explained variance for these two distinguished factors belongs to variables that assess the foraging conditions of microhabitats, and to variables characterizing predominantly foraging conditions in biotope IV.

Biotope III was distinguished by the greatest microenvironmental originality, in which the proportion of the explained variance of variables for the first two factors exceeded 50% (54.5 and 51.6% in 2013 and 2017, respectively), which distinguishes this habitat of the bank vole from the other three biotopes. Presumably, the peculiarity of the microenvironmental situation in biotope III, in which the number of variables significant in terms of the contribution turned out to be maximum, can be explained by the higher heterogeneity of the environment of this habitat, partially disturbed by windblow and fire. As noted above, the abundance level of the bank vole population in this biotope in 2017 was characterized by the highest values for the entire observation period, as in biotope IV (Fig. 1). The level of variability in the microenvironmental structure of the most disturbed habitat (biotope I) in 2013 (3 years after the repeated pyrogenic disturbance) turned out to be the lowest (42.6%) (Table 5), which may be caused by a decrease in the heterogeneity of the microenvironment observed in early stages of restorative succession in a doubly pyrogenically disturbed forest community. A significant contribution to the microenvironmental structure of biotope I during

Table 2. Two-way analysis of variance of biotopic and chronographic variability of microenvironmental characteristics of habitats of the bank vole in the territory of the Visim Reserve

Abbreviations of characteristics	Source of variability	*df*	Sum of squares	Mean square	*F*-criterion	Significance level, *p*
MC	Biotope	3	288.51	96.17	41.37	<0.01
	Year	1	144.48	144.48	62.16	<0.01
	Biotope × year	3	41.62	13.87	5.97	<0.01
	Intragroup	392	911.17	2.32		
	General	399	1385.78			
HC	Biotope	3	183.06	61.02	13.83	<0.01
	Year	1	64.88	64.88	14.71	<0.01
	Biotope × year	3	225.17	75.06	17.01	<0.01
	Intragroup	392	1729.51	4.41		
	General	399	2202.62			
CS	Biotope	3	77.46	25.82	32.30	<0.01
	Year	1	0.03	0.03	0.04	ns
	Biotope × year	3	1.86	0.62	0.77	ns
	Intragroup	392	313.40	0.80		
	General	399	392.75			
TC	Biotope	3	0.45	0.15	56.11	<0.01
	Year	1	0.004	0.004	1.43	ns
	Biotope × year	3	0.007	0.002	0.93	ns
	Intragroup	392	1.04	0.003		
	General	399	1.50			
SC	Biotope	3	0.12	0.04	17.32	<0.01
	Year	1	0.0009	0.0009	0.43	ns
	Biotope × year	3	0.005	0.002	0.77	ns
	Intragroup	392	0.87	0.002		
	General	399	0.99			
LC	Biotope	3	1.13	0.38	1.04	ns
	Year	1	0.08	0.08	0.23	ns
	Biotope × year	3	3.21	1.07	2.97	<0.05
	Intragroup	392	141.03	0.36		
	General	399	145.45			
AU	Biotope	3	763.09	254.36	8.80	<0.01
	Year	1	1759.80	1759.80	60.84	<0.01
	Biotope × year	3	2002.53	667.51	23.08	<0.01
	Intragroup	392	11339.02	28.93		
	General	399	15864.44			
Abundance	Biotope	3	31.98	10.66	21.91	<0.01
	Year	6	49.32	8.22	16.90	<0.01
	Biotope × year	18	18.76	1.04	2.14	<0.01
	Intragroup	1372	667.54	0.49		
	General	1399	767.60			

Table 3. Interannual dynamics of microenvironmental characteristics of bank vole habitats in biotopes (I–IV) of the Visim Reserve

Abbreviations of characteristics	2013		2017		Significance level, *p*
	$\overline{X} \pm SE$	*S*	$\overline{X} \pm SE$	*S*	
	Biotope I				
MC	0.89 ± 0.19	1.31	0.02 ± 0.01	0.08	***
HC	5.47 ± 0.32	2.27	6.68 ± 0.35	2.45	**
CS	0.21 ± 0.06	0.39	0.43 ± 0.07	0.51	**
TC	0.003 ± 0.001	0.01	0.007 ± 0.001	0.01	ns
SC	0.004 ± 0.002	0.02	0.01 ± 0.005	0.04	ns
LC	0.77 ± 0.09	0.65	0.75 ± 0.09	0.66	ns
AU	0.11 ± 0.03	0.24	1.28 ± 0.13	0.90	***
	Biotope II				
MC	2.52 ± 0.31	2.22	0.02 ± 0.01	0.099	***
HC	6.49 ± 0.24	1.72	5.49 ± 0.25	1.77	***
CS	0.66 ± 0.17	1.23	0.75 ± 0.14	0.99	ns
TC	0.004 ± 0.001	0.009	0.005 ± 0.002	0.01	ns
SC	0.007 ± 0.003	0.018	0.009 ± 0.003	0.02	ns
LC	0.78 ± 0.10	0.73	0.55 ± 0.06	0.45	ns
AU	0.16 ± 0.04	0.29	0.49 ± 0.095	0.67	***
	Biotope III				
MC	1.26 ± 0.24	1.69	0.71 ± 0.13	0.92	**
HC	5.71 ± 0.33	2.35	3.22 ± 0.27	1.92	***
CS	0.24 ± 0.06	0.43	0.13 ± 0.04	0.26	ns
TC	0.08 ± 0.02	0.07	0.06 ± 0.006	0.04	ns
SC	0.02 ± 0.006	0.04	0.03 ± 0.006	0.05	ns
LC	0.69 ± 0.07	0.47	0.94 ± 0.09	0.67	**
AU	0.49 ± 0.05	0.38	0.67 ± 0.07	0.46	**
	Biotope IV				
MC	3.29 ± 0.31	2.17	2.17 ± 0.25	1.79	***
HC	7.15 ± 0.26	1.85	5.16 ± 0.29	2.11	***
CS	1.33 ± 0.17	1.24	1.27 ± 0.19	1.32	ns
TC	0.081 ± 0.01	0.084	0.07 ± 0.01	0.08	ns
SC	0.05 ± 0.01	0.09	0.05 ± 0.008	0.06	ns
LC	0.66 ± 0.07	0.47	0.78 ± 0.09	0.62	ns
AU	0.47 ± 0.08	0.54	0.47 ± 0.07	0.51	ns

$\overline{X}$—average value of the microenvironmental parameter, *SE*—standard error of the mean, *S*—standard deviation; significance levels of statistics (from zero): ns—$p > 0.1$; *—$p < 0.1$; **—$p < 0.05$; ***—$p < 0.01$.

this period was characterized by variables that estimate the area covered by herbaceous vegetation and undergrowth.

In 2017 (at the later stages of post-pyrogenic recovery), a significant contribution to the variability of the structure of the most disturbed biotope was made by a variable that characterizes the area covered by the bases of trunks of living trees (Table 5). Along with this significant contribution, the characteristics that determine the protective conditions of the habitats of the bank vole differed: the area covered by deadwood in biotope II in 2013 and in both years in biotope III. The variability of the microenvironmental structure of the undisturbed biotope IV was significantly determined by the variable associated with the area of the shrub in 2013 and with the number of undergrowth in 2013 and

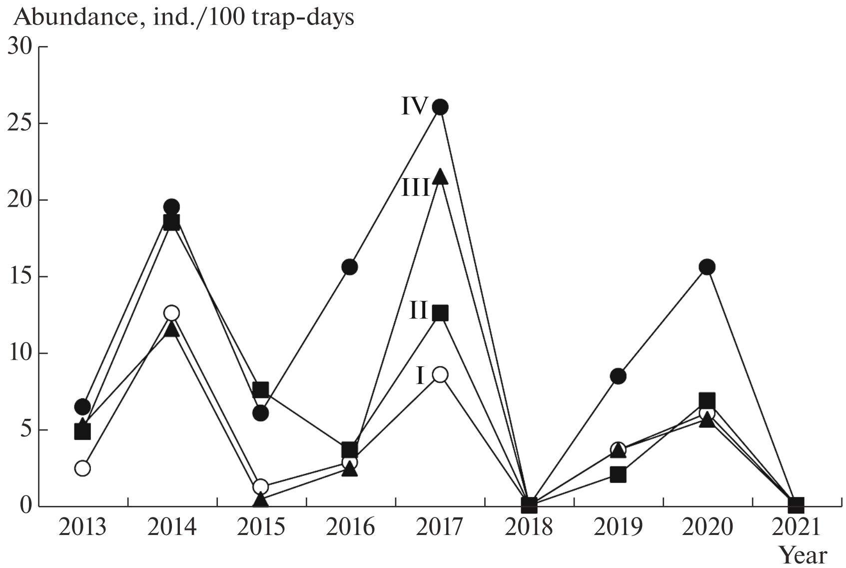

Fig. 1. Long-term change in the abundance of the bank vole in biotopes (I–IV) of the Visim Reserve.

2017 (Table 5). The area of shrub vegetation in biotope IV had higher values compared to disturbed biotopes I–III, and tree undergrowth in biotope I was characterized by the highest numbers (Fig. 2), which is typical for forest communities with a sparse forest stand. It is known that undergrowth characterizes the metabolism of the ecosystem, it is an indicator of the well-being of the forest, its normal state, and viability. The presence of undergrowth of tree species under the canopy is the main factor in the continuous existence of the forest, since the viability of the plant community is determined by its ability to restore the number of populations, replacing dead specimens with new ones. The undergrowth is most abundant in those parts of the forest where the tree tier is sparse [41].

An analysis of the relationship between the abundance of the bank vole and the characteristics of the microenvironment showed that individuals of the species in the disturbed biotope II are least associated with the microenvironment structure. A statistically significant relationship was found only in 2019 with a variable assessing the area covered by the bases of living tree trunks (*TC*) (Tables 6, 7). In the most disturbed biotope I, rodents in 2013 also preferred areas covered with living trees (*TC*) and deadwood (*LC*), and in 2019 abundance of the species was significantly associated with herbaceous (*HC*) and moss (*MC*)

Table 4. Results of pairwise comparisons according to the Mann–Whitney test of the bank vole abundance in biotopes (I–IV) of the Visim Reserve

Biotope	Year						
	2013	2014	2015	2016	2017	2019	2020
	Z (p)						
I, II	–0.73 (ns)	–1.48 (ns)	–1.73*	–0.34 (ns)	–0.50 (ns)	0.66 (ns)	–0.63 (ns)
I, III	–0.41 (ns)	–0.39 (ns)	0.34 (ns)	0.17 (ns)	–2.19**	–0.14 (ns)	–0.28 (ns)
I, IV	–0.62 (ns)	–2.12**	–1.58*	–3.24***	–3.16***	–0.08 (ns)	–2.63***
II, III	0.28 (ns)	1.13 (ns)	2.07**	0.51 (ns)	–1.59 (ns)	–0.82 (ns)	0.37 (ns)
II, IV	0.06 (ns)	–0.65 (ns)	0.09 (ns)	–2.97***	–2.46**	–1.70*	–2.12**
III, IV	–0.20 (ns)	–1.83*	–1.91*	–3.38***	–0.87 (ns)	–0.96 (ns)	–2.47**

Significance levels of the Z-test (from zero): ns—$p > 0.1$; *—$p < 0.1$; **—$p < 0.05$; ***—$p < 0.01$.

Table 5. Factor loadings of microenvironmental variables of the bank vole habitats in biotopes (I–IV) of the Visim Reserve

Abbreviations of characteristics	Year	Biotope							
		I		II		III		IV	
		F1	*F2*	*F1*	*F2*	*F1*	*F2*	*F1*	*F2*
MC	2013	–0.043	–0.560	**0.811**	0.0001	**0.860**	0.054	–0.205	0.666
	2017	–0.379	–0.243	0.239	–0.675	**0.866**	0.084	0.590	0.157
HC	2013	**–0.711**	0.198	0.077	**–0.891**	–0.191	**–0.803**	–0.655	–0.078
	2017	**0.879**	–0.149	**0.757**	–0.173	–0.377	**–0.765**	0.077	0.699
CS	2013	0.199	–0.546	0.207	0.536	0.533	–0.493	**–0.795**	–0.078
	2017	–0.125	0.664	0.044	–0.644	0.350	–0.493	0.175	0.647
TC	2013	0.479	0.382	–0.393	0.288	–0.383	0.225	0.456	–0.436
	2017	**–0.801**	–0.196	**–0.775**	0.0785	–0.395	0.251	–0.650	0.005
SC	2013	–0.040	**–0.714**	0.106	0.479	0.467	0.454	–0.032	0.545
	2017	0.078	0.574	0.173	0.462	0.415	0.219	0.286	–0.412
LC	2013	–0.423	0.399	**0.877**	0.029	**0.797**	0.064	0.110	0.616
	2017	0.343	0.467	0.185	0.471	**0.865**	–0.060	0.678	–0.114
AU	2013	**0.736**	0.122	–0.569	0.255	–0.109	**0.749**	**0.750**	–0.381
	2017	0.009	0.632	–0.683	–0.198	–0.322	0.683	**–0.710**	–0.469
σ	2013	1.50	1.48	1.97	1.46	2.07	1.71	1.89	1.47
	2017	1.70	1.51	1.76	1.38	2.19	1.42	1.85	1.33
Δσ, %	2013	21.41	21.18	28.07	20.87	29.60	24.45	26.95	20.96
	2017	24.23	21.53	25.20	19.71	31.36	20.24	26.49	19.07

σ—dispersion, Δσ—proportion of explained variance. Variables in bold type are statistically significant at $p < 0.05$.

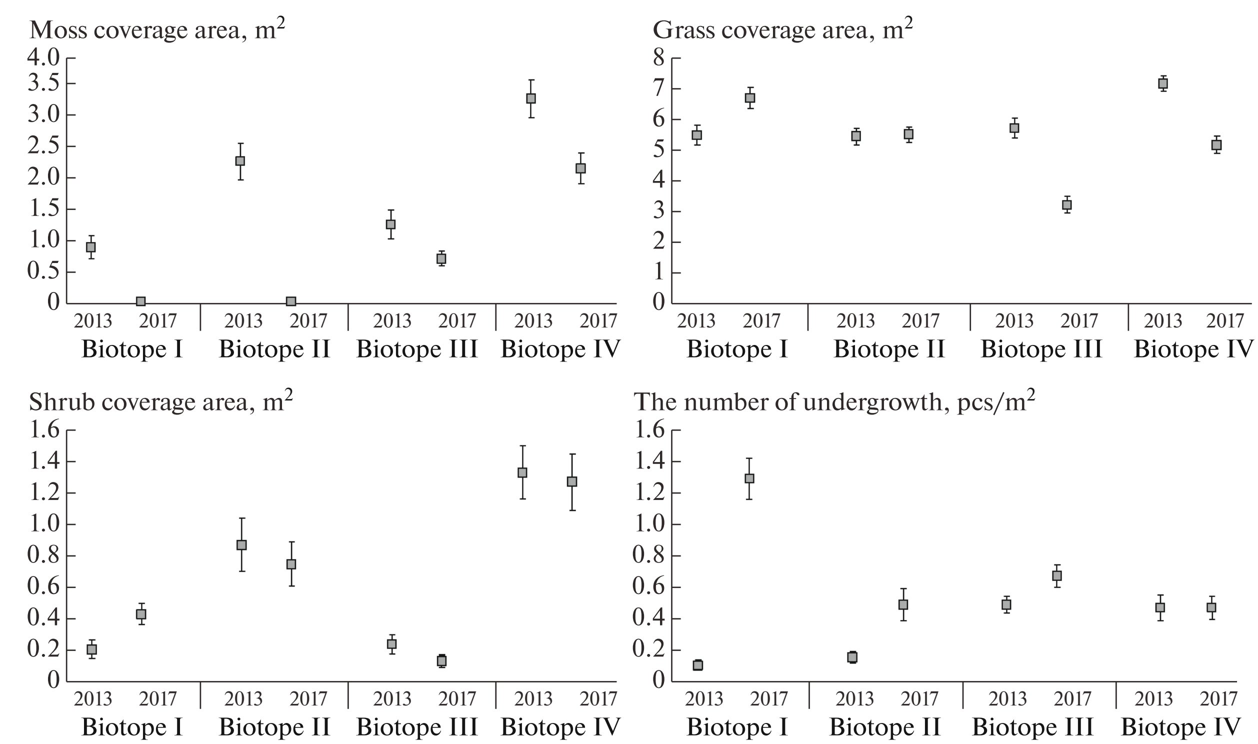

Fig. 2. Dynamics of microenvironmental characteristics of biotopes (I–IV) of the Visim Reserve.

Table 6. Significance levels of differences from zero of standardized regression coefficients (β_{MC}–β_{AU}) of bank vole abundance on microenvironmental variables (*MC*–*AU*) in biotopes (I–IV) of the Visim Reserve

Biotope	Regression coefficient						
	β_{MC}	β_{HC}	β_{CS}	β_{TC}	β_{SC}	β_{LC}	β_{AU}
2013							
I	ns	ns	ns	**	ns	***	ns
II	ns	ns	ns	ns	ns	ns	ns
III	ns	ns	**	ns	***	ns	ns
IV	ns	ns	***	ns	ns	ns	ns
2014							
I	ns	ns	ns	ns	ns	ns	ns
II	ns	ns	ns	ns	ns	ns	ns
III	ns	ns	ns	ns	ns	ns	ns
IV	ns	ns	ns	ns	ns	ns	ns
2015							
I	ns	ns	ns	ns	ns	ns	ns
II	ns	ns	ns	ns	ns	ns	ns
III	ns	ns	ns	ns	ns	ns	ns
IV	**	ns	**	ns	ns	ns	ns
2016							
I	**	ns	ns	ns	ns	ns	ns
II	ns	ns	ns	ns	ns	ns	ns
III	ns	ns	ns	ns	ns	ns	ns
IV	ns	ns	ns	ns	ns	ns	ns
2017							
I	***	ns	ns	ns	ns	ns	**
II	ns	ns	ns	ns	ns	ns	ns
III	ns	ns	ns	ns	ns	ns	ns
IV	ns	ns	**	ns	ns	ns	ns
2019							
I	**	***	ns	ns	ns	ns	ns
II	ns	ns	ns	***	ns	ns	ns
III	ns	ns	ns	ns	ns	ns	ns
IV	ns	ns	ns	ns	ns	ns	ns
2020							
I	ns	ns	ns	ns	ns	ns	ns
II	ns	ns	ns	ns	ns	ns	ns
III	ns	ns	***	ns	ns	ns	ns
IV	ns	ns	ns	ns	ns	ns	ns

Significance levels of statistics (from zero): ns—$p > 0.1$; *—$p < 0.1$; **—$p < 0.05$; ***—$p < 0.01$.

cover of microsites. In 2016 and 2017 voles were "tied" to areas covered with moss, and in 2013 in biotope III they preferred improved environmental conditions provided by standing dry trees and stumps (*SC*) and microhabitats with more favorable feeding conditions with the presence of shrub vegetation (*CS*). In 2020, the abundance of bank voles in this biotope was also associated with shrubs. Thus, the bank vole preferred areas with improved foraging conditions in biotopes with varying degrees of disturbance.

The abundance of the species in the undisturbed habitat turned out to be closely related to the microenvironmental variables that assess predominantly foraging conditions. In 2013, 2015, and 2017, voles preferred microareas with shrub vegetation (Tables 6, 7). Using the example of an island population of the bank vole, it was shown [8] that the choice of microenvironment characteristics by this species differs at different phases of its population dynamics. We also found a close connection of the species with the microenvironment at different phases of population dynamics, but only in the undisturbed environment of biotope IV. It turned out that the bank vole in this habitat prefers areas with a predominance of shrubs both at the phase of low population abundance in 2013 and 2015 and at the peak of population abundance in 2017 (Tables 6, 7). As noted above, this microenvironmental characteristic is characterized by low interannual variability in biotopes II–IV (Table 3). However, a relationship between the bank vole abundance and this microenvironmental parameter at different levels of its population was found only in the undisturbed habitat (Table 7). Moss coverage of plots is an environmental characteristic that is not preferred by the bank vole, but, probably, it determines favorable conditions for the species in combination with other microenvironmental indicators. This characteristic was distinguished by high values in the undisturbed biotope, along with the microenvironment variable, which estimates the area covered by shrubs (Fig. 2).

CONCLUSIONS

The results of the study allow us to state that among the factors that affect the "success of existence" of the bank vole in different biotope conditions, primarily such as the population level of the species and the microenvironmental structure of its habitats, the latter plays an important role. An analysis of the level of abundance values, an important informative characteristic that reflects the degree of "ecological well-being" of a species in the natural environment, showed that the most favorable conditions for the successful existence of the bank vole in the studied protected area of the Middle Urals are formed in a biotope undisturbed by external adverse impacts, where the species prevails in abundance.

The abundance of the bank vole under the conditions of biotopic heterogeneity caused by the consequences of natural catastrophic events is determined by different microenvironmental parameters. In disturbed habitats, individuals of the species are more attached to areas with improved protective conditions, and a "response" of the bank vole abundance to

Table 7. Results of multiple regression analysis of the relationship between bank vole abundance (dependent variable) and microhabitat characteristics (predictors) of biotopes I–IV

Year	Abundance, ind./100 trap-days	Regression equation	R^2	F	p
Biotope I					
2013	2.4	$Y = -0.047 + 8.090X_{TC} + 0.177X_{LC}$	0.463	6.43	<0.01
2016	2.8	$Y = 0.114 + 1.42X_{MC}$	0.290	4.40	<0.05
2017	8.5	$Y = 0.793 - 0.101X_{HC} + 0.172X_{LC}$	0.494	7.58	<0.01
2019	3.2	$Y = 0.656 + 1.928X_{MC} - 0.069X_{HC}$	0.514	5.49	<0.05
Biotope II					
2019	2.0	$Y = 0.596 + 38.93X_{TC}$	0.369	7.59	<0.01
Biotope III					
2013	5.2	$Y = 0.042 + 6.632X_{SC} + 0.448X_{CS}$	0.485	7.25	<0.01
2020	5.6	$Y = 0.137 + 1.08X_{CS}$	0.522	17.97	<0.01
Biotope IV					
2013	6.4	$Y = -0.021 + 0.256X_{CS}$	0.399	9.09	<0.01
2015	6.0	$Y = 0.369 + 0.137X_{SC} - 0.076X_{MC}$	0.382	4.02	<0.05
2017	26.0	$Y = 0.670 + 0.290X_{CS}$	0.353	6.83	<0.05

The table includes models showing a statistically significant relationship between bank vole abundance and microenvironmental variables.

microenvironmental variables characterizing the feeding conditions of habitats is observed in an undisturbed biotope environment. The level of values of indicators that assess the food resources of the species in different biotopes: the coverage of areas with herbaceous and shrubby vegetation, is generally higher in undisturbed habitats, which undoubtedly affects the choice of habitats by the bank vole.

Thus, it can be concluded on the basis of the results that the environmental conditions of an undisturbed biotope are the most preferable for the bank vole in the territory of the Visim Reserve. This conclusion is explained by the high level of abundance and its close relationship with microenvironmental parameters that assess predominantly the feeding conditions of the species habitats at different population levels.

The identified features of the choice of environment by the bank vole, which prefers the conditions of an undisturbed biotope with a preserved forest stand, to the conditions of lighter habitats in pyrogenically disturbed sparse forest communities, do not fully agree with the published data [30]. Our results only confirm the assumption about the possible manifestation of previously unknown environmental responses in unstable environmental conditions, including food and behavioral responses, of background species to changes in habitat conditions [20].

FUNDING

The study was carried out within the state task of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences no. 122021000091-2.

ACKNOWLEDGMENTS

The author expresses his sincere gratitude to the senior researchers of the Visim State Natural Biosphere Reserve, R.Z. Sibgatullin and N.V. Belyaeva, for constant support in the work and assistance in relevés, as well as I.F. Vurdova and V.D. Arapova for assistance in field research.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

COMPLIANCE WITH ETHICAL STANDARDS

This article does not contain any studies involving humans and animals as research subjects.

REFERENCES

1. Hodara, K. and Busch, M., Patterns of macro and microhabitat use of two rodent species in relation to agricultural practices, *Ecol. Res.*, 2010, vol. 25, no. 1, pp. 113–121.
2. Naumov, N.P., Population structure and population dynamics of terrestrial vertebrates, *Zool. J.*, 1967, vol. 46, no. 10, pp. 1470–1486.

3. Shwartz, S.S., Population structure of the species, *Zool. J.*, 1967, vol. 46, no. 10, pp. 1456–1469.
4. Torre, I. and Arrizabalaga, A., Habitat preferences of the bank vole *Myodes glareolus* in a Mediterranean mountain range, *Acta Theriol.*, 2008, vol. 53, pp. 241–250.
5. Andreeva, T.A. and Okulova, N.M., Ecological preferences of forest voles, *Ekologiya*, 2009, no. 2, pp. 149–154.
6. Mohammadi, S., Microhabitat selection by small mammals, *Adv. Biol. Res.*, 2010, vol. 4, no. 5, pp. 283–287.
7. Villanueva-Hernández, A.I., Delgado-Zamora, D.A., Heynes-Silerio, S.A., et al., Habitat selection by rodents at the transition between the Sierra Madre Occidental and the Mexican Plateau, México, *J. Mammal.*, 2017, vol. 98, no. 1, pp. 293–301.
8. Buyalska, G., Lukyanov, O.A., and Meszkowska, D., Determinants of the local spatial pattern of animal density in an insular population of the bank vole, *Ekologiya*, 1995, no. 1, pp. 35–45.
9. Rosenzweig, M.L., A theory of habitat selection, Ecology, 1981, vol. 62, no. 2, pp. 327–335.
10. Morris, D.W., Test of density-dependent habitat selection in a patchy environment, *Ecol. Monogr.*, 1987, vol. 57, no. 4, pp. 269–281.
11. Falkenberg, J.C. and Clarke, J.A., Microhabitat use of deer mice: effects of interspecific interaction risks, *J. Mammal.*, 1998, vol. 79, no. 2, pp. 558–568.
12. Drickamer, L.C., Microhabitat preferences of two species of deer mice Peromyscus in a northeastern United States deciduous hard wood forest, *Acta Theriol.*, 1990, vol. 35, pp. 241–252.
13. Johannesen, E. and Mauritzen, M., Habitat selection of grey-sided voles and bank voles in two subalpine populations in southern Norway, *Ann. Zool. Fenn.*, 1999, vol. 36, pp. 215–222.
14. Johannesen, E., Brudevoll, J., Jenstadt, M., et al., Behavioural dominance of grey-sided voles over bank voles in dyadic encounters, *Ann. Zool. Fenn.*, 2002, vol. 39, pp. 43–47.
15. Trebatická, L., Sundell, J., Tkadlec, E., et al., Behavior and resource use of two competing vole species under shared predation risk, *Oecologia*, 2008, vol. 157, pp. 707–715.
16. Morris, G.J., Hostetler, A., Oli, M.K., et al., Effects of predation, fire, and supplemental feeding on populations of two species of Peromyscus mice, *J. Mammal.*, 2011, vol. 92, pp. 934–944.
17. Letnic, M., Tischler, M., and Gordon, C., Desert small mammal responses to wildfire and predation in the aftermath of a La Niná driven resource pulse, *Austral. Ecol.*, 2013, vol. 38, pp. 841–849.
18. Novillo, A., Cuevas, M.F., Ojeda, A.A., et al., Habitat selection and coexistence in small mammals of the southern *Andean foothills* (Argentina), *Mamm. Res.*, 2017, vol. 62, pp. 219–227.
19. Magnusson, M., Samelius, G., Hörnfeldt, B., et al., Diet shift in bank voles induced by competition from grey-sided voles?, *Integr. Zool.*, 2019, vol. 14, pp. 376–382.
20. Shilova, S.A., Neronov, V.V., Kasatkin, M.V., et al., Fires at the Current stage of evolution of semi-desert in Southern Russia: the influence on vegetation and rodent populations, *Usp. Sovrem. Biol.*, 2007, vol. 127, no. 4, pp. 372–386.
21. Kuleshova, L.V., Ecological and zoogeographical aspects of influence of fire on the forest birds and mammals, *Zool. Zh.*, 1981, vol. 60, no. 10, pp. 1542–1552.
22. Dueser, R.D. and Porter, J.H., Habitat use by insular small mammals relative effects of competition and habitat structure, *Ecology*, 1986, vol. 67, no. 1, pp. 195–201.
23. Hengriques, R.P.B., Bizerril, M.X.A., and Palma, A.R.T., Changes in small mammal populations after fire in a patch of unburned cerrado in Central Brazil, *Mammalia*, 2000, vol. 64, no. 2, pp. 173–185.
24. Istomin, A.V., Influence of windblows on the dynamics of communities of small mammals in natural forests of the southern taiga, *Vestn. Mosk. Gos. Univ., Lesn. Vestn.*, 2009. № 1. C. 196–201.
25. Lee, E.J., Rhim, S.G., Son, S.H., et al., Differences in small-mammal and stand structures between unburned and burned pine stands subjected to two different postfire silvicultural management practices, *Ann. Zool. Fenn.*, 2012, vol. 49, no. 3, pp. 129–138.
26. Zwolak, R., Pearson, D.E., Ortega, Y.K., et al., Mechanisms driving postfire abundance of a generalist mammal, *Can. J. Zool.*, 2012, vol. 90, pp. 51–60.
27. Fordyce, A., Hradsky, B.A., Ritchie, E.G., et al., Fire affects microhabitat selection, movement patterns, and body condition of an Australian rodent (*Rattus fuscipes*), *J. Mammal.*, 2016, vol. 97, no. 1, pp. 102–111.
28. Sadykov, O.F., Bolshakov, V.N., and Bazhenov, A.V., Spatial structure of forest vole populations, *Ekologiya*, 1984, no. 4, pp. 58–64.
29. Shilov, I.A., *Ekologo-fiziologicheskie osnovy populyatsionnykh otnoshenii u zhivotnykh* (Ecophysiological Bases of Population Relationships in Animals), Moscow: Mosk. Gos. Univ., 1977.
30. Gromov, I.M. and Erbaeva, M.A., *Mlekopitayushchie fauny Rossii i sopredelnykh territorii. Zaytseobraznye i gryzuny* (Mammals of Russia and Adjacent Territories. Lagomorphs and Rodents), St. Petersburg: Zool. Inst. Ross. Akad. Nauk, 1995.
31. Evropeiskaya ryzhaya polevka (Bank vole), Aristov, A.A., et al., Moscow: Nauka, 1981.
32. Ivanter, E.V., *Ocherki populyatsionnoi ekologii melkikh mlekopitayushchikh na severnoy periferii areala* (Essays on the Population Ecology of Small Mammals on the Northern Periphery of the Range), Moscow: KMK, 2018.
33. Geuse, P., Spatial microhabitat of bank voles and wood mice in a forest in central Belgium, *Acta Zool. Fenn.*, 1985, vol. 173, pp. 61–64.
34. Mazurkiewicz, M., The influence of undergrowth distribution on utilization of space by bank vole populations, *Acta Theriol.*, 1986, vol. 31, pp. 55–69.
35. Mazurkiewicz, M., Population dynamics and demography of the bank vole in different tree stands, *Acta Theriol.*, 1991, vol. 36, pp. 207–227.

36. Mazurkiewicz, M., Factors influencing the distribution of the bank vole in forest habitats, *Acta Theriol.*, 1994, vol. 39, pp. 113–126.

37. Miklos, P. and Ziak, D., Microhabitat selection by three small mammal species in oak-elm forest, *Folia Zool.*, 2002, vol. 51, no. 4, pp. 275–288.

38. Lukyanova, L.E. and Bobretsov, A.V., Microhabitat selection by the bank vole (*Clethrionomys glareolus* Schreber, 1780) under destabilized and stable habitat conditions, *Vestn. Tomsk. Gos. Univ., Biol.*, 2014, vol. 28, no. 4, pp. 88–107.

39. Bolshakov, V.N., Berdyugin, K.I., Vasilyeva, I.A., and Kuznetsova, I.A., *Mlekopitayushchie Sverdlovskoi oblasti: spravochnik-opredelitel'* (Mammals of Sverdlovsk Oblast: An Index and Reference Book), Yekaterinburg: Yekaterinburg, 2000.

40. Lukyanova, L.E., Ukhova, N.L., Ukhova, O.V., and Gorodilova, Yu.V., Common shrew (*Sorex araneus*, Eulipotyphla) population and the food supply of its habitats in ecologically contrasting, *Ekologiya*, 2021, no. 4, pp. 298–311.

41. Chertovskoy, V.G., *Taezhnoe lesovodstvo* (Taiga Forestry), Moscow: Lesn. Prom-st., 1974.

Translated by M. Shulskaya