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Impact of Climate Change On Population Dynamics of Forest Voles (*Myodes*) in Northern Pre-Urals: The Role of Landscape Effects

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Abstract—In recent years in northern Pre-Urals, the population dynamics of forest voles has undergone significant changes. In the foothill area, the abundance of the red-backed vole has decreased and that of the bank vole has increased significantly. As a result, the latter becomes the dominant species. In nearby lowland areas, the population of the bank vole has remained stable while the red-backed vole has increased. The main cause of these changes is the transformation of the environment under the influence of global climate change. This affects mainly foothill conifer forests and, to a lesser extent, lowland forests. As a consequence, responses of various vole species to these changes in different landscape areas are not identical.

Keywords: red-backed vole, bank vole, population dynamics, climate, landscape impact
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Global warming is a peculiarity of modern climate change. On the territory of Russia from 1907 to 2006, mean annual temperature increased by 1.1–1.29°C (Anisimov et al., 2007; *Otsenochnyi doklad*..., 2008; Gruza and Ran'kova, 2012; IPCC, 2013). Its most notable increase was observed in the period from 1976 to 2009, when the rate of warming for the European North rose to 5.2°C per 100 years (Anisimov et al., 2011). The beginning of the new century was the warmest in the history of instrumental observations (*IPCC Fourth Assessment Report*, 2007; *Vtoroi otsenochnyi doklad*..., 2014). Trends in precipitation were weak. They were most visible only on the territory of the European part of Russia (*Otsenochnyi Doklad*..., 2008).

Consequences of global warming are significant changes in the distribution and population number of various animal species (Parmesan, 2006), including small mammals (Francl et al., 2010; Rowe et al., 2015). Reactions of different species are not identical: abundances of some species have declined, while others have increased (Bernstein et al., 2004; Istomin, 2009; Moritz et al., 2008; Myers et al., 2009). In some regions there were disturbances in the periodicity of population cycles in some vole species (Ims and Fuglei, 2005; Elmhagen et al., 2011; Zakharov et al., 2011; Sheftel, 2014). Different responses of species to climate change caused structural transformations of animal populations (Lavergne et al., 2010; Rowe et al., 2010; Maiorano et al., 2011).

The main consequences of global warming that affect long-term changes of the abundance of small mammals are the transformation of habitat, alteration of food availability and survival of animals (Newman and Macdonald, 2013). Broad transformation of habitats leads to changes in species structure of animals (Istomin, 2009; Lukyanova, 2015). Similar changes have occurred in recent years in the populations of forest voles in the foothill region of the Pechora-Ilych Nature Reserve (Bobretsov et al., 2015), where in recent years the red-backed vole ceded its dominant position to the bank vole. However, there was no change in dominants in the neighboring plain district. This paper analyzes different structural rearrangements in populations of forest voles in different landscapes of the nature reserve.

MATERIALS AND METHODS

We used materials of annual censuses of small mammals in lowland and foothill areas of the Pechora-Ilych Nature Reserve from 1989 to 2015. Censuses were conducted using ditches and covered different habitats. This method reflects not only the number of animals, but also their mobility (Shchipanov et al., 2003). At the same time, indices of abun-

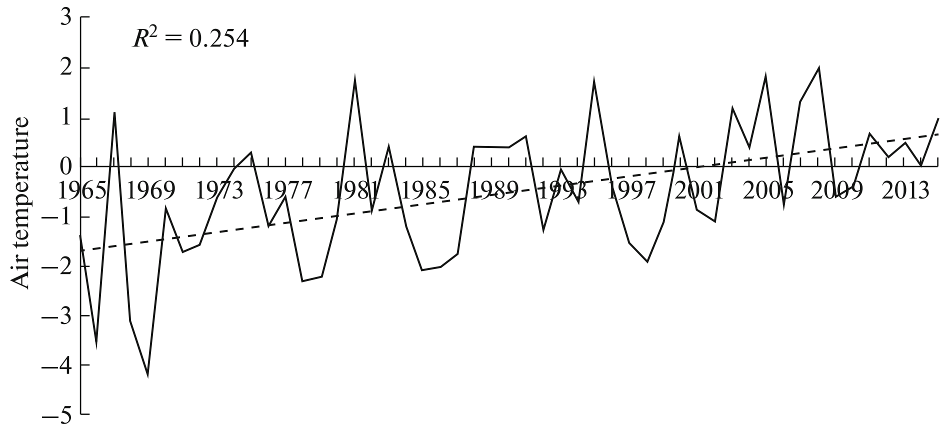

Fig. 1. Dynamics of the mean yearly air temperature (curve) and its trend (dotted line) in Northern Pre-Urals.

dance obtained by the ditch method and by the other most commonly using method of trap lines are significantly correlated with each other. For example, for the red vole from the foothill region, the value of Spearman rank coefficient was +0.88 ($t = 9.25$; $p < 0.001$). Ditches with a length of 50 m with five cones were opened in the second half of the summer for 12–15 nights. The cones were 1/3 filled with water. For the measure of relative abundance, the number of animals caught per 100 cone/nights (individuals per 100 cone/nights) was taken. In the plain district we treated 9370 cone/nights and, in the foothills, 5925 cone/nights. We caught about 4000 forest voles.

The analysis of climate change was carried out according to the data from Yaksha Weather Station. We used mean monthly air temperature and rainfall. To identify the relationship of animal abundance with these climatic factors, we used nonparametric and parametric statistical methods. In the first case, we widely used the Spearman rank correlation coefficient and the second linear multiple regression analysis with stepwise selection of variables (Ferster and Rentz, 1983). Calculations were performed using Statistica 6.0 for Windows. To assess the significance of differences between indicators of environmental parameters, we used the nonparametric Mann–Whitney test.

Changes in soil cover were analyzed based on quantitative descriptions conducted in 2000 and 2014. For this task, in two habitats (high-mossy spruce forest and green-mossy wet fern spruce forest) we laid 100 plots 10 m^2 each in size. Within them, we assessed the main environmental parameters such as soil cover, m^2, with moss and herbaceous vegetation. We also took into account the amount of tree undergrowth.

DESCRIPTION OF NATURAL CONDITIONS IN LANDSCAPE AREAS

Natural conditions in the landscape areas significantly differ from each other. The plain district is located within the eastern edge of the Russian Plain. It is characterized by a homogeneous terrain. Lowland vegetation in the district is quite monotonous. Pine forests of various types are predominant (86%), among whom nearly half (43%) are lichen–pine forests. The second integral element of this landscape is swamps. Alternating pine forests and swamps is a characteristic feature of the plain area. The spruce accounts for only 11% of the forested area. They are local and are confined mainly to river valleys.

The foothill area is located within the Ural Mountain country (the North Urals). It is a rolling elevated plain in which the meridional direction is crossed by several ridges. Most of the territory (76%) is occupied by grass–dark conifer taiga. In the arboreal layer, in addition to spruce, there are also fir, cedar, and birch, as well as, to a lesser extent, aspen and pine. Plantings are mostly over mature. In the depressions between ridges, green-mossy, high-mossy, and sphagnum spruce forests prevail. Slopes of ridges are covered with spruce–fir forests with a large participation of large ferns in the ground-floor layer.

RESULTS

Global trends in climate change are known on the territory of the Pechora-Ilych Nature Reserve. A significant increase in the mean annual air temperature from 1965 to 2015 was observed (Fig. 1). The rate for the period from 1965 to 2002 amounted to –0.9°C and, for the period from 2003 to 2015, it was just +0.6°C. The increase amounted to 1.5°C. Abnormally cold years occurred in the second half of the 1960s, when the mean temperature was three times (1966, 1968–1969) lower than –3.0°C. Since 2003, the annual temperature does not fall below –0.7°C. The number of years with positive annual temperature in the first period was relatively low, 26.3%; in the second period it rose to 77%. The years 2005 and 2008 were notable as the warmest over the entire observation period. Warming was most pro-

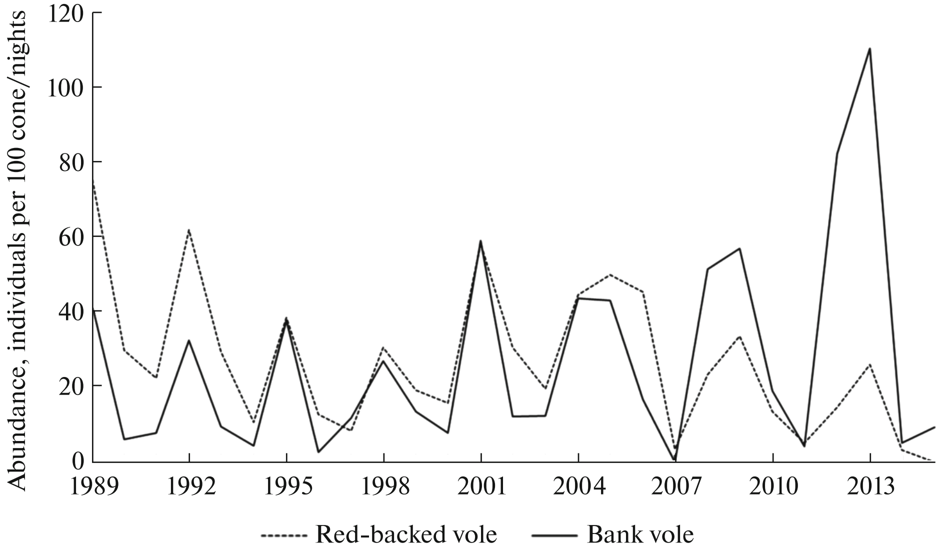

Fig. 2. Multiyear changes in forest vole numbers in the foothill region of Pechora-Ilych Nature Reserve.

nounced in winter and spring months. At the same time, differences in annual rainfall between these two periods were low and insignificant.

The territory of Pechora-Ilych Nature Reserve is inhabited by three species of forest voles, northern red-backed (*Myodes rutilus*), bank (*M. glareolus*) and grey-sided (*M. rufocanus*) voles. The first two species are widely distributed in all landscape areas, while the grey-sided vole is found mainly in the mountains and in small numbers in the foothill parts of the reserve. In general, for the plains and foothill areas, the proportion of the red-backed vole in total catches of forest voles was 58.3%, that of the bank vole was 38.5%, and the grey-sided vole was 3.1%. The populations of the first two species are cyclic: spectral analysis revealed significant periodic components equal to 3–4 years (Bobretsov, 2015).

The number of the red and bank voles over the observation period underwent significant changes. Especially notable structural transformations occurred in the foothill areas of the reserve (Fig. 2). In the population dynamics of forest voles, three periods are clearly distinguished. In the first period, 1989–1994 the red-backed vole prevailed in all years. Its proportion was 69.2%, whereas the proportion of the bank vole was 30.8%. In the second period, 1995–2007, there was a decrease in abundance of the first species and an increase in number of the second one. The proportion of species in catches has leveled off, respectively, to 56.7 and 43.3%. Significant changes in the population structure of animals occurred in the last two cycles in 2008–2015. The number of red-backed voles decreased and that of the bank vole increased dramatically. Differences in the indices of abundance for these two species in 2013 (the peak of abundance) were exceeded more than four times: for the red-backed vole 26.1 individuals and the bank vole 110.3 individuals per 100 cone/nights. The proportion of the first species decreased to 27.1% and the percentage of the second increased to 72.9%.

Changes in numbers of forest voles and their proportions have taken place in all habitats of the foothill region (Table 1). In this respect, data for high-moss upland spruce forests are most important. They are the most optimal habitats for the red-backed vole. In the beginning of observations, this species almost completely dominated there, 80% in catches of forest voles, whereas the bank vole was a rare species recorded only at the phase of peaks in the number. In the last period, in 2008–2015, the abundance of the red-backed vole in this habitat decreased almost three times and the bank vole increased four times. The proportion of species, respectively, accounted for 27.3 and 72.7%.

On the plain area of the reserve we observed a completely different situation. From 2004, we noted a significant growth in red-backed vole numbers against the background of relatively stable dynamics of the bank vole. The mean value of abundance of the red-backed vole over the period from 2004 to 2015 increased two times (19.8 individuals per 100 cone/nights) when compared with the earlier period (10.0 individuals). The last three cycles displayed a high level of number at the phase of peaks, from 34.3 to 52.2 individuals per 100 cone/nights. The red vole prevailed in the plain district during the period of observations. In the years between 1989 and 2003, its proportion in the population of voles constituted 69.8%, and in subsequent years it increased to 76.3%.

DISCUSSION

Changes in the number of small mammals, caused by the transformation of climate, were noted by both

Table 1. Population number, individuals per 100 cone/nights, and the proportion, %, of forest vole species in different periods of observations in a foothill area of the Pechora-Ilych Nature Reserve

Species	Period, years					
	1989–1994		1995–2007		2008–2015	
	abundance	%	abundance	%	abundance	%
High mossy watershed spruce forest						
Red-backed vole	46.4 ± 13.2	80.0	26.4 ± 5.1	64.8	16.4 ± 6.2	27.3
Bank vole	11.6 ± 5.2	20.0	14.8 ± 3.9	35.2	43.8 ± 16.3	72.7
Grassy floodplain spruce forest						
Red-backed vole	30.6 ± 7.7	57.5	19.0 ± 2.9	41.6	18.2 ± 5.0	29.4
Bank vole	22.6 ± 8.4	42.5	26.5 ± 5.9	58.4	43.7 ± 13.3	70.6

domestic and foreign researchers. Even for closely related species, different trends are revealed. The reasons are often different climatic factors. A gradual decrease in the number of red-backed vole and the increase in the abundance of bank vole were recorded in Udmurtia and in the north of Arkhangelsk oblast (Okulova et al., 1998, 2004), as well as the reduction in the abundance of the red-backed vole occurring in Karelia (Yakimova, 2008). It is believed that transformation of the number of forest voles in the north of Europe is caused by changes in temperature regime (Okulova and Kataev, 2006). An increased abundance in the bank vole was observed in Central Russia (Puzachenko and Vlasov, 2000; Bernshtein et al., 2004; Okulova et al., 2005; Istomin, 2009). A key factor in this process in the Central Black Earth Nature Reserve was increased rainfall in spring and early summer (Puzachenko and Vlasov, 2000). In North America in recent decades, a marked increase in the abundance of white-footed mouse, *P. leucopus* (Myers et al., 2009), accompanied in some areas with a reduction in the number of the meadow vole *Microtus pennsylvanicus* (Deitloff et al., 2010) and the reindeer hamster *P. maniculatus* (Myers et al., 2005), was noted. The increase in the abundance of white-footed mouse in the Great Lakes region of North America was caused by the reduction of snow cover during warm and short winters and coincided with a significant increase of the minimum temperature of April (Martin, 2010; Roy-Dufresne et al., 2013). In the central part of North America, the number of reindeer hamster upon a reduction of annual precipitation of more than 11% began to decrease (Reed et al., 2007).

In Pechora-Ilych Nature Reserve a marked relationship between the abundance of forest voles and the number of climatic parameters was noted. Six factors influence population dynamics of the bank vole and only three influence the red-backed vole (Table 2). This is considerably less when compared with other areas of the European north, where the abundance of

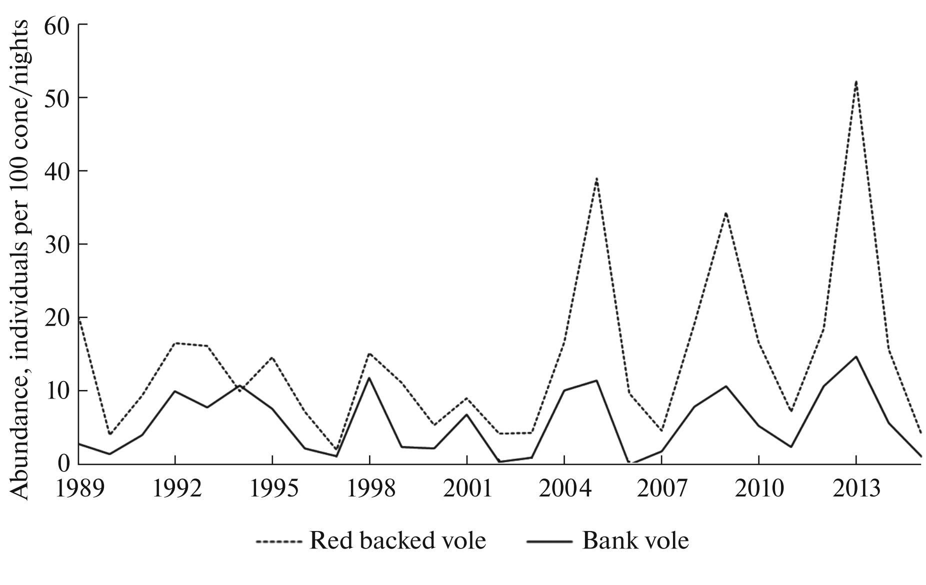

Fig. 3. Multiyear changes in the numbers of forest voles in plain region of Pechora-Ilych Nature Reserve.

Table 2. Estimation of the influence of climatic factors on number dynamics of forest voles in Pehora–Ilych Nature Reserve: results of multiple regression analysis

Factor	Bank vole			Red vole		
	β	*t*	*p*	β	*t*	*p*
Air temperature:						
in February of the current year	–	–	–	–0.432	2.32	0.031
in March of the current year	–0.578	3.89	0.0008	–	–	–
in April of the current year	–	–	–	–0.470	2.44	0.024
in October of the current year	+0.667	4.25	0.0003	–	–	–
Precipitation:						
in March of the current year	–	–	–	+0.41	2.20	0.040
in June of the current year	–0.430	3.10	0.008	–	–	–
in August of the current year	+0.357	3.04	0.009	–	–	–
in September of the current year	+0.395	2.91	0.012	–	–	–
in October of the current year	–0.320	2.25	0.041	–	–	–

β is standardized regression coefficient, *t* is Student criterion, and *p* is level of significance.

forest voles is under the control of a larger number of climatic parameters of the current year and the previous season (Okulova et al., 2004; Ivanter, 2005).

For the bank vole, the temperatures in March (the colder it is, the more there are) and in October of the former year (the warmer this month is, the more animals there are in the following year) are significant. Precipitation in June of the current year (years with moderate humidity were favorable) and in August, September, and October of the former year was important. Rainy weather in August and September most likely has no direct influence on the abundance of the bank vole, but it is indirect through the yield of different seasonal food. Precipitation in June also has the same effect. This was indicated by Teplov (1960), who analyzed population dynamics of forest voles in the taiga of the Upper Pechora. Dry weather in October combined with higher air temperatures have a positive effect on the survival of animals than rainy and cool weather. Of all these factors, the most significant changes in 2008–2013 (years of domination of the bank vole)—when compared with the previous period—occurred in the air temperature in March and October of the previous season. March was 2.3°C colder and October of the previous year was 2.5°C warmer. The influence of summer temperatures on the abundance of the bank vole found in other regions (Imholt et al., 2015) was absent in this case.

For the red-backed vole, of great importance is the air temperature in February and April and the amount of rainfall in March: at that time they fall in the form of snow. It is very difficult to interpret the first dependence from a biological point of view, although a similar relationship was noted for the red-backed vole at the north of Arkhangelsk oblast (Okulova et al., 2004). In 2008–2013, this month was much colder (2.8°C) than in previous years. Warm weather in April has a negative impact on the autumn number of red-backed voles, but at the same time it has no effect on the abundance of bank vole. The highest mortality rate of the voles in the Pechora taiga occurs in early spring during the period of their sexual maturation. Positive temperatures in April destroy the snow cover ahead of time, causing instability of environmental conditions in the surface layer: as a result of frequent returns of cold, a significant proportion of animals die (Bobretsov, 2009).

Climatic factors most likely modify the number of animals and do not play a large role in regulating populations of the voles in the Northern Urals. The values of β-regression coefficients were relatively small. In addition, the abundance of both forest vole species was changing synchronously everywhere. The value of rank Spearman correlation coefficient between indicators of the number of red-backed and bank voles in the plain district was +0.80 ($t = 6.70$, $p < 0.001$), and in the foothills is +0.60 ($t = 3.87$; $p = 0.001$). Nevertheless, they can make a certain contribution to the general trend of changes in the number. This is because climatic conditions in different landscape areas are different: in the foothills, they become more severe due to the proximity of the mountains. The average annual temperature on the plains is –0.6°C and, in the foothills, 1.4°C. Spring processes start in the first area earlier, and the fall phenomena occur later. The average date of onset of spring (the establishment of mean daily air temperature above 0°) falls there on April 13. On the open places the snow melts around May 4, and in spruces it remains until May 19. The onset of spring in the foothill region averages April 18. For the district in general, a somewhat extended timing of the spring period is typical. The snow there in open fields melts off later, on May 13. In dark conifer forests it lies until June 4. Cold weather

Table 3. Changes of environmental parameters in two spruce forests in the foothill region of Pechora-Ilych Nature Reserve: data by descriptions of 100 quadrangles 100 m^2 each

Parameter	Mean value and error		P
	year 2000	year 2014	
High mossy watershed spruce forest			
Moss coverage, m^2	8.06 ± 0.20	6.59 ± 0.21	<0.001
Grass coverage, m^2	3.02 ± 0.16	4.31 ± 0.17	<0.001
Number of undergrowth, individuals	2.61 ± 0.24	9.12 ± 0.61	<0.001
Green mossy and fern spruce forest			
Moss coverage, m^2	6.51 ± 0.22	3.57 ± 0.21	<0.001
Grass coverage, m^2	4.89 ± 0.17	4.35 ± 0.20	<0.05
Number of undergrowth, individuals	3.11 ± 0.24	4.61 ± 0.40	<0.05

frequently returns in this part of the reserve. These landscape differences may, to some extent, differentiate the degree of influence of any climatic factor on the population number of animals.

One of the causes of changes in the number of forest voles in the Pechora-Ilych Nature Reserve has been the transformation of habitats as a result of global climate change. It is a powerful factor shaping different trends in the abundance of small mammals (Morris and Dupuch, 2012; Prost et al., 2013; Baltensperger and Huettmann, 2015). The transformation of habitat may occur due to various causes, among which in old forests of the Northern Urals is the formation of "windows" in the forest canopy, and an increase in their mosaics and windfalls have significant influence. Strong winds significantly influence their dynamics (Gromtsev, 2007). Their frequency in the last two decades in the European north has increased (Vasil'ev, 2009). Their scale is evidenced by the fact that, in the north of Perm krai and adjacent regions of the Komi Republic (which includes the biological station), from 2001 to 2012, 16 sites of massive windfalls with a total area of more than 11500 ha were identified. The length of the largest one was 85 km with a maximum width of 19 km (Shikhov, 2013). Of course, such large-scale windfalls can lead to big changes at the landscape level (Ulanova and Cherednichenko, 2012). However, the area of windfalls occupies a relatively small square, about 5%, but the number of gaps in the forest canopy there increased sharply. The accelerating process of the window dynamics of forests in this area is due also to the fact that in recent years there has been an intensive drying of trees that have fallen during strong winds in the first place.

The increase in the area of the windowed forest mosaic in a few years leads to significant changes in the structure of habitats (Shorohova, 2014). In the green–mossy spruce forests on clearings and windfalls, herbaceous vegetation and deciduous undergrowth appear. In 14 years of observations in the foothills of the Pechora-Ilych Nature Reserve, the most notable changes occurred in high mossy spruce forests (Table 3). The area coverage by mosses decreased there and the area occupied by herbaceous vegetation increased; the number of the undergrowth increased significantly.

It is known that the red-backed and bank voles prefer different habitats. In the first species, over its large range, there is a close association with forest communities of the taiga type, green–mossy and high mossy forests. The second species prefers nemoral plant communities: conifer and deciduous grass forests. In these habitats the number of species reaches its maximum values.

The formation of windows and transformation of habitats in high mossy spruce forests in recent years has led to the fact that relatively favorable conditions for the bank vole are formed there. Together with the floodplain habitats, which are well represented, the area of habitats favorable for this species significantly expanded there. Increased habitat capacity may be one of the reasons for the rapid growth of the bank vole number. For example, in the middle taiga of Komi Republic, in the middle current of the Vychegda River, according to observations of I.F. Kupriyanova, for a very short time there was a change of dominant species of forest voles: the red-backed vole was replaced with the bank vole (Kupriyanova and Bobretsov, 2006). The trigger for change in the proportion of these close species in this case was a significant increase in the area of growing clearing areas, where the main vegetation spectrum was grasses and deciduous undergrowth. The abundance of the bank vole has increased on clearings and upland forest habitats, whereas the number of red-backed vole has decreased also in mossy spruce forests. A similar situation occurred with these species in the foothill region of the Pechora-Ilych Nature Reserve.

Differences in trends of forest vole numbers in different landscape areas were caused by the peculiarities of the forest-cover transformation there. In the lowland area dominated by pine forests, the windfall dynamics is much less pronounced. Pine is more resistant to wind than spruce (Gromtsev, 2008). In addition, the vegetation there is not changed and remains the same even at the windfalls.

The lowland area can be considered a highly fragmented landscape where green–mossy and grassy spruce forests, most favorable for small mammals, are represented by isolated and small area arrays. In recent years, there has been also a strong fall of trees. However, the number of bank vole in this region has not undergone any significant changes: it remained fairly low throughout the observation period. The fragmentation of the landscape most often negatively affects indices of small mammalian abundance (Andren, 1994; Bennett and Saunders, 2010). In this context, reasons for the increasing red-backed vole population number in the lowland part of the reserve are not quite clear.

CONCLUSIONS

There were significant changes in the population dynamics of forest voles in Northern Pre-Urals over the last 12 years. In the plain part of the territory, the number of red-backed voles have increased. In the last three years, cycle indices of abundance during peaks reached maximum values for the entire observation period. The number of bank vole remained at the same level. In the foothills the situation was opposite. The abundance of bank vole there dramatically increased in the last 6 years and that of the red-backed vole decreased. For the bank vole, a peripheral species in this area, it is an unprecedented phenomenon. Its proportion in populations of forest voles increased to more than 70%. The bank vole became dominant in all habitats, including the upland high mossy spruce forests.

Structural transformations in the population of voles occurred against the background of significant climate change. Climate parameters are among important environmental factors that directly affect the population dynamics of small mammals. This is evident from the presence of significant relations of animal-abundance indicators with temperature and precipitation. However, the number of such relations is small and, in addition, the correlation coefficients are low. One of the more important causes is the change in forest habitats due to the decay of the stands. This is due to the acceleration of spontaneous forest dynamics resulting from the shrinkage of forests and increase in the frequency of occurrence of strong winds. The emergence of a large number of windows led to increased patchiness of forests and to the increase in number of habitats suitable for the bank vole.

However, the transformation of habitats in different landscape areas depending on the dominant types of arboreal vegetation has certain differences. This explains different trends in the number of forest voles more pronounced in the foothill dark-conifer taiga, whereas in the pine forests of the plain part the changes were very weak.

At the same time, it is impossible to explain in full different trends in abundance of different forest vole species by these factors in recent years. Apparently, this is due to the fact that it is rather difficult to determine the exact nature of the reaction of individual animal species to climate change, because species react not only on individual factors, but on a combination of different interacting causes and environmental conditions (Staudinger et al., 2013). There is growing evidence that the impact of climate change on the number of different species has synergistic effects (Brook et al., 2008).

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