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Spatiotemporal Population Structure of the Bank Vole in a Gradient of Technogenic Environmental Pollution

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Abstract—Between 1998 and 2005, specific features of spatiotemporal distribution of small mammals in transformed habitats were studied using the example of the bank vole living in a gradient of chemical environmental pollution (the Middle Urals). Technogenic degradation of spruce–fir forests proved to entail significant changes in the spatial structure and abundance of vole populations. Differences in colonization of disturbed and intact territories by bank voles at different stages of population dynamics were revealed.

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According to modern views, insularization of habitats suitable for most species is a general biological phenomenon accompanying increasing anthropogenic impact on biogeocenoses. A formerly continuous or occasionally disconnected species range is separated into fragments surrounded by an environment that is inappropriate for this species. The size of isolated fragments is important for the population: one large area with relatively high animal abundance is preferable for its long-term survival over a similar area subdivided into several small plots, as animal abundance in them is usually lower and the risk of extinction is higher.

Fragmentation of the environment entails modification of qualitative characteristics of the territory. The levels of survival and fecundity sufficient for the life of the population in optimum habitats may be insufficient for it in qualitatively inferior plots. In some cases, changes in microenvironmental parameters may have a triggering effect. Under pessimal conditions, animals may acquire adaptive ecological features allowing them to colonize anthropogenic biotopes. In particular, this concerns changes in the spectrum of food objects, migration activity, and behavioral responses (Shilova, 1999).

Recently, much attention has been devoted to analysis of relationships between the structure of habitats and the spatial distribution and demographic characteristics of individual species populations. However, relevant publications usually concern either contrasting habitats of natural origin or experimentally created habitats (Mazurkiewicz, 1986; Rajska-Jurgiel, 1992; Buyal'ska et al., 1995; Luk'yanova and Luk'yanov, 2004). Only a few studies deal with the spatiotemporal distribution of small mammals in anthropogenically transformed habitats (Luk'yanova and Luk'yanov, 1992, 1998; Mukhacheva, 2005a; Paradis and Croset, 1995).

In the Middle Urals, long-term technogenic impact on ecosystems has resulted in active degradation of forest phytocenoses followed by fragmentation of habitats. Therefore, the abundance and spatial distribution of typical forest species in technogenically transformed and undisturbed areas may differ significantly. The purpose of this study was to analyze the spatiotemporal distribution and population dynamics of the bank vole (*Clethrionomys glareolus* Schr., 1780) in the gradient of technogenic environmental pollution.

MATERIAL AND METHODS

The data on the spatial structure of bank vole populations in the gradient of technogenically modified habitats were collected in the vicinities of the Middle Ural Copper-Smelting Plant (MUCP) in the snow-free periods of 1998 to 2005. The MUCP has been in operation since 1940, and the impact zone around it is well-defined. Test plots were located west of the source of emissions, at different distances from it: in the impact zone (1 and 2 km) and in the buffer zone (4 and 6 km). Two control plots, where the technogenic load was assumed to be minimum (at the regional background level), were 20 and 30 km from the MUCP. The study area was described in more detail previously (Vorobeichik et al., 1994; Mukhacheva and Luk'yanov, 1997). To characterize ban vole habitats, the microenvironment of each key plot was mapped by recording ten quantitative parameters in 75 squares (5 × 5 m, with a trap in the center). These parameters reflected the state of vegetation and the area under fallen tree trunks,

Table 1. Parameters characterizing habitats and spatial distribution ($M \pm m$) of bank voles in the technogenic pollution gradient (the Middle Urals, 1998–2005)

Parameter	Zone		
	background	buffer	impact
Distance from pollution source, km	30	5	1
Habitats			
Number of squares described	75	75	75
Area under			
living trees, m^2	1.01 ± 0.09	0.55 ± 0.06	0.26 ± 0.05
basal branches of conifers, %	0.0	5.2 ± 0.8	23.1 ± 1.8
shrubs, %	25.0 ± 2.6	25.6 ± 2.5	15.5 ± 1.9
herbs and dwarf shrubs, %	50.5 ± 2.6	17.2 ± 1.9	11.1 ± 0.9
moss, %	24.5 ± 1.4	14.4 ± 1.1	16.6 ± 1.8
needle and leaf litter, %	0.5 ± 0.1	37.6 ± 2.9	33.7 ± 2.9
dead branches, m^2	0.16 ± 0.03	0.22 ± 0.04	0.21 ± 0.03
fallen tree trunks, m^2	1.27 ± 0.13	0.82 ± 0.17	0.76 ± 0.10
Total area of broken ground, m^2	0.25 ± 0.11	0.11 ± 0.09	0.03 ± 0.01
Humidity of the plot, grade	0.55	0.08	0.04
Spatial distribution of voles			
Number of trap-days	5650	3480	3620
Number of trapped voles	278	94	58
Total abundance, ind./100 trap-days	4.92 ± 0.01	2.70 ± 0.03	1.36 ± 0.02
Specific abundance, ind./100 trap-days	35.46 ± 0.03	32.64 ± 0.14	29.26 ± 0.23
Populated area, %	15.08 ± 0.99	8.21 ± 0.93	4.78 ± 0.63
Aggregation, rel. units	2.35 ± 0.07	3.98 ± 0.11	6.11 ± 0.13

uprooted trees (including holes in the ground), windfall, debris (branches, needles, and leaves), and basal branches of living conifers (Buyalska et al., 1995).

The model object, *Cl. glareolus*, dominates in the small mammal communities of the study area. A census of these animals was taken by the method of irreversible removal with crush trap lines (50–100 traps each) for 5 days. Each trap in a line had an individual number for locating capture points. The field work amounted to more than 13600 trap-days (8100 on disturbed plots and 5500 in the control area), and 433 bank voles (157 and 256, respectively) were trapped. To characterize the spatial population structure, indices of total and specific abundance, populated area, and aggregation (Luk'yanova and Luk'yanov, 1992) were calculated. The data on relative abundance were recalculated into indices of density according to Bernshtein et al. (1995). Statistical data processing was performed using the EXCEL 6.0 and STATISTICA 5.0 program packages.

RESULTS AND DISCUSSION

Characteristics of Bank Vole Habitats in Technogenic Pollution Gradient

The bank vole is a background species in forests of the temperate zone. These animals prefer open forest areas, forest margins, and clearings with abundant undergrowth, dense forest herbage, and berry-bearing dwarf semishrubs. Conditions in forest areas strewn with coarse woody debris, rotten stumps, and fallen trees are also favorable for them. In general, bank voles choose habitats depending on food supply, microclimate, availability of natural shelters, and competitive relationships. The results of some studies (*Evropeiskaya…*, 1981) show that, under normal conditions (in the absence of extreme factors), food supply is the main factor. However, Mazurkiewicz and Chetnicki (1992) consider that an uneven distribution of bank voles in forest habitats is accounted for by differences in the protective properties of the plant cover (the presence of undergrowth, fallen trees, tall ferns, etc.).

Table 1 shows basic microenvironmental characteristics of key plots (one plot per zone). The initial forest type in all zones is the same: spruce–fir forest with linden. In the control area (20–30 km from the MUCP), plant association is of the nemoral–sorrel type (Vorobeichik et al., 1994). The proportion of healthy trees is approximately 50%, and the area occupied by them is four times greater than in the impact zone. The herb–dwarf shrub layer (48 species) and the moss layer cover approximately 50 and 25% of the area. In most squares, dense ferns and piles of fallen tree trunks and branches are common.

In areas located closer to the source of emissions, the life state of tree stand deteriorates, its destruction proceeds more actively, renewal is retarded, and the horizontal structure of vegetation undergoes fragmentation. The type of plant association in the buffer zone remains the same, but the lower vegetation layer has changed significantly: its species richness is 20% lower and the area occupied by herbaceous plants is 2.5–3 times smaller than in the control area.

In the impact zone, the phytocenosis undergoes more profound transformations. The life state of tree stand further deteriorates, the average diameter and height of trees decrease, and the proportion of dead trees increases. The herbaceous layer covers no more than 10% of the area and consists mainly of grasses and horsetail. Approximately one-third of the area is covered with a deep litter layer and is almost devoid of vegetation. Basal branches of conifers (fir and spruce) are well developed and may be regarded as additional protective elements.

Degradation of phytocenoses is most severe in the immediate vicinity of the pollution source. The area adjoining the MUCP (up to 0.5 km west) is a technogenic desert almost devoid of higher vegetation and upper soil horizons. This extremely homogeneous environment is unsuitable for bank voles.

The contents of heavy metals in the components of biocenosis (soil, litter, and food for voles) significantly decreases in areas located farther from the pollution source. The contents of copper in soils of the buffer and background zones are five to ten times lower than in the impact zone (Kaigorodova and Vorobeichik, 1996), and those in the diet of voles are 6.5–14.5 times lower, respectively (Mukhacheva, 2005b).

Thus, the test plots form a series of technogenically transformed habitats with the degree of degradation increasing as the source of emissions is approached. The number of microsites suitable for small mammals decreases in the zones of technogenic pollution, and this is accompanied by deterioration of their "consumer qualities" for bank voles. This is reflected both in the pattern of animal distribution over the area and in their abundance.

Spatial Distribution of Bank Voles

Table 1 shows the main parameters characterizing the spatial distribution of bank voles and their abundance in the technogenic pollution gradient. *The index of total abundance (I)* refers to the relative abundance of animals throughout the study area, including both the sites suitable for them and unpopulated sites. The average indices recorded in the buffer and background habitats of bank voles are 2.0–3.6 times higher than in the impact sites ($f = 15.36$; $P = 0.001$).

The index of specific abundance (A) characterizes the relative abundance of animals only in the populated part of the study area. Its values in disturbed sites decrease insignificantly: the difference from the control is less than 20% ($f = 5.96$; $P = 0.024$). The holding capacity of the fragments of spruce–fir forest remaining in the impact zone is not much lower than that of intact forest areas. Under favorable conditions, the local population density of voles in these fragments may approach that in the background area. The results of our previous studies show that habitats near the source of emissions (1 km) may be considered transitional: they are populated mainly by migrating animals, and no permanent colonies are formed there (Mukhacheva and Luk'yanov, 1997). Only single cases of offspring rearing in such habitats were recorded over the 15-year observation period.

The spatial distribution of animals was analyzed using the *index of populated area* (*F*) and the *index of aggregation* (*Ag*). The former index characterizes the holding capacity of the habitat for a certain species and shows the proportion of area populated by its representatives (%) relative to the total habitat area. Average *F* values show that bank voles populate approximately 5% of the area in the impact zone, whereas the proportions of populated area in the buffer and background zones are 1.7–3.2 times greater ($f = 15.56$; $P = 0.001$). According to other authors (Luk'yanova and Luk'yanov, 1998), the proportion of populated area near copper-smelting plants is only 3%, compared to approximately 60% in undisturbed areas.

In natural habitats, the proportion of the area populated by the bank vole increases with an increase in its population density. For example, in spruce forests with an admixture of birch and aspen (Kemerovo oblast), bank voles populate 10–20% of the accessible area at a density 5 ind./ha, 30–40% at 7–15 ind./ha, and 60–70% at 25–30 ind./ha (*Evropeiskaya…*, 1981). Calculations concerning the region of MUCP show that the proportion of populated area in the test and control is significantly lower than the aforementioned values, although it depends on vole population density ($R = 0.85$). Thus, less than 10% of the territory is occupied at a population density of up to 6 ind./ha and 20–40% is occupied at a density of 10–40 ind./ha. At the highest population density over the observation period, 60–80 ind./ha, only 20% of the area in the plots remained vacant (Fig. 1).

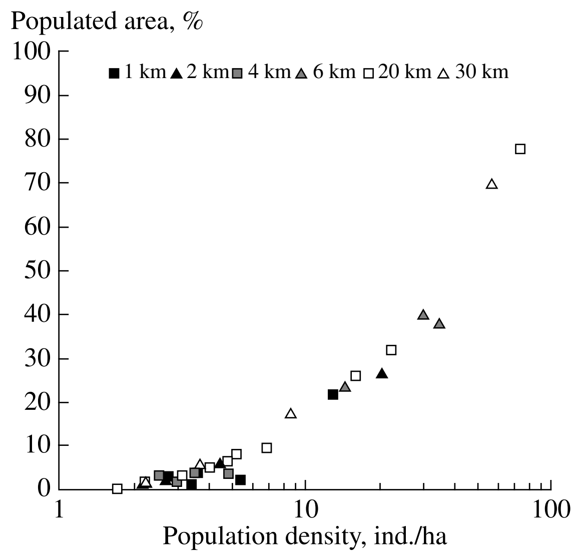

Fig. 1. Changes in the index of populated area as a function of bank vole population density in the gradient of technogenically transformed habitats.

This may be explained by an increase in the size of animal home ranges in disturbed areas. It is known that the home ranges of bank voles are larger in habitats with unfavorable conditions and at a low population density than under optimum conditions, with their size varying from 0.04 to 1 ha or, in exceptional cases, up to 2.2 ha (*Evropeiskaya…*, 1981).

The index of animal *aggregation* was calculated as the ratio of the indices of specific abundance and populated area ($Ag = A/F$). The degree of aggregation proved to depend inversely on the relative abundance ($R = -0.41$). The values of this index were minimum in the background area and increased along with the degree of habitat fragmentation (by a factor of 1.7–2.6 in the buffer and background plots) (Table 1). It is known that animals usually aggregate into groups when their total abundance in the population is low, and their density in the area occupied by such a group is three to four times higher than in surrounding areas (Okulova and Khelevina, 1989). Moreover, young voles often prefer to keep together, regardless of population density. The majority of the population in disturbed areas, especially in the impact zone, consists of migrating animals, with dispersing juveniles prevailing among them (Mukhacheva and Luk'yanov, 1997). The same applies to the parameters of spatial distribution of voles near the emission source.

Now, having generally characterized the abundance and spatial distribution of bank voles, let us consider variation of these parameters in time (during the snow-free period and at different phases of the population cycle).

Table 2. Indices of bank vole abundance and spatial distribution ($M \pm m$) in the gradient of technogenically transformed habitats at different phases of population dynamics (the Middle Urals, 2004–2005)

Parameter	Phase of population cycle		Amplitude (max/min)
	depression	peak	
Background zone			
Total abundance, ind./100 trap-days	1.69 ± 0.02	22.25 ± 0.01	18.5
Specific abundance, ind./100 trap-days	26.39 ± 1.28	41.98 ± 0.07	1.6
Populated area, %	8.00 ± 2.96	53.00 ± 3.53	9.5
Aggregation, rel. units	3.30 ± 0.37	0.79 ± 0.07	6.2
Buffer zone			
Total abundance, ind./100 trap-days	0.70 ± 0.03	12.65 ± 0.02	18.1
Specific abundance, ind./100 trap-days	28.57 ± 5.05	34.26 ± 0.22	1.2
Populated area, %	3.11 ± 3.01	33.75 ± 3.74	10.1
Aggregation, rel. units	9.18 ± 0.98	1.02 ± 0.11	9.0
Impact zone			
Total abundance, ind./100 trap-days	0.49 ± 0.04	4.52 ± 0.02	9.2
Specific abundance, ind./100 trap-days	25.00 ± 8.94	32.76 ± 0.56	1.3
Populated area, %	2.22 ± 0.98	13.81 ± 3.24	6.2
Aggregation, rel. units	11.25 ± 0.57	2.37 ± 0.24	4.7

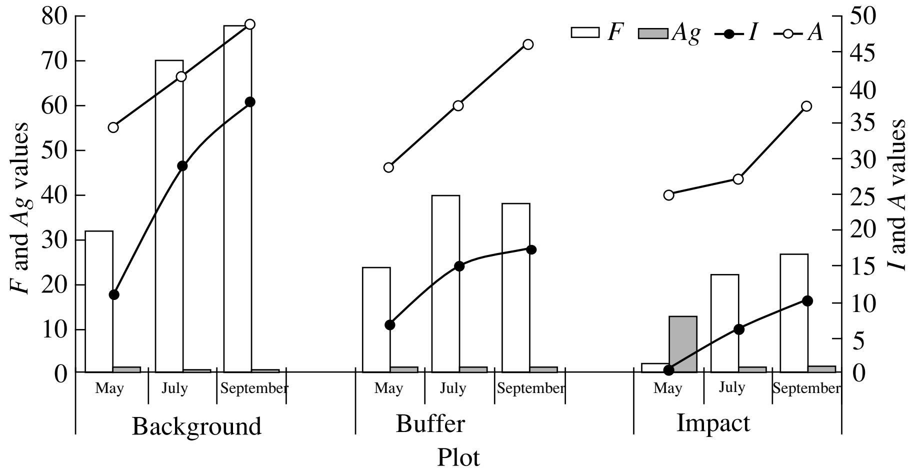

Fig. 2. Seasonal dynamics of the indices of total abundance (*I*), specific abundance (*A*), populated area (*F*), and aggregation (*Ag*) of the bank vole population in the gradient of technogenically transformed habitats.

Features of Spatial Structure at Different Phases of the Population Cycle

The bank vole population of the study area is characterized by a consistent three-year cycle with the phases of depression, growth, and population peak. For comparative analysis, parameters recorded at the peak phase in 2004 and at the depression phase in 2005 were chosen. The pattern of change in these parameters is generally the same throughout the technogenic pollution gradient (Table 2): the total abundance and population density are low at the depression phase and significantly increase at the peak phase, the degree of animal aggregation drastically decreases, whereas the index of specific abundance changes only slightly.

At the depression phase, the total abundance of bank voles is low in all habitats. Near the emission source (1 km), bank voles were not recorded at all in May and June, and only single specimens were trapped between July and September. The proportion of populated area in all plots was insignificant, whereas the degree of aggregation was high (Table 2). Thus, small numbers of voles at this phase concentrated in limited areas (survival stations) that apparently provided more favorable conditions for them. This agrees with published data that, at a low population density in low-quality habitats of natural and anthropogenic origin, bank voles concentrate in separate "islands" where conditions are closer to the optimum (*Evropeiskaya…*, 1981; Luk'yanova and Luk'yanov, 1998; Shilova, 1999).

The phase of population peak is characterized by a sharp increase in the total abundance and density of voles in the plots compared (Table 2). Their total abundance in the buffer and background plots becomes 18 times higher than at the depression phase, while that in the impact zone increases by a factor of 9. The proportion of populated area increases by factors of 9–10 and 6, respectively, but the specific abundance shows only a weak dependence on the phase of the population cycle ($R = 0.67$). The degree of animal aggregation in the year of population peak becomes five to nine times lower.

At the level of local populations, colonization of the area at the phase of population peak has specific features. In the impact zone, animal abundance increases mainly via territorial expansion, with a moderate (up to 30%) increase in the density of voles in local colonies. In the background plots, the growth of abundance is accompanied both by intensive colonization of the area (at the peak phase, the voles occupy more than 50% of the plot) and by an increase in the local animal density by approximately 55%. Conditions for bank voles in buffer areas are apparently intermediate, and this is reflected in the pattern of population formation: compared to the phase of depression, the area occupied by voles increases tenfold, to one-third of the total area, but the local increase in animal abundance is comparable with that in the impact plots and does not exceed 20%.

The extreme values of the parameters of the spatial population structure recorded at the phase of depression in the impact zone and at a peak of abundance in the background zone characterize the entire range of variation in the abundance and spatial distribution of bank voles in the study area. This range is accounted for by natural chronographic variation of the environment, on the one hand, and by its spatial heterogeneity resulting from the impact of technogenic factors, on the other hand. Therefore, it may be used for estimating the contributions of the aforementioned components to the dynamics of the parameters studied (Luk'yanova and Luk'yanov, 1992). The contribution of natural chronographic variation is estimated from the amplitude of variation in population parameters in the control (undisturbed) area. The difference between the entire variation range and this amplitude characterizes the contribution of spatial heterogeneity resulting from technogenic impact. Our calculations show that the action of technogenic factors accounts for about three-fourths of variation in the index of populated area and for more than 60% of variation in the indices of total abundance and aggregation. At the same time, 95% of variation in the index of specific abundance is explained by natural chronographic variation of the environment.

Seasonal Dynamics of Parameters of Spatial Population Structure

A comparative analysis of the seasonal dynamics of spatial structure was based on the data obtained in 2004. The most distinct changes during the snow-free period were recorded in the impact zone. In the buffer and background plots, the abundance and distribution of voles changed gradually (Fig. 2). The total abundance of voles in the plots sites changed mainly between May and July, in the period of mass reproduction, increasing by a factor of 2.2–2.6 in the buffer and background zones and by a factor of 12 in the impact zone. In the summer–autumn period, when reproductive activity decreased, the abundance of voles in slightly disturbed and natural habitats increases by 20–30% and that in the impact site increased by a factor of 1.7. The growth of population density was accompanied by changes in the distribution of bank voles; the index of populated area in all plots changed similarly, whereas the index of aggregation changed in different ways. In the buffer zone, the index of aggregation remained at the same level throughout the season; in the background plots, its values in autumn were two times smaller than in spring. The values recorded in the impact zone differed from each other by an order of magnitude: in May, single individuals gathered in sites with more favorable conditions within the plot; in July, when animal abundance increases due to dispersing juveniles, the distribution of voles became more homogeneous and its parameters approached the values recorded in the buffer zone in spring.

During the snow-free period, voles spread over the area in different ways. In the impact zone, they first occupied all habitable fragments of the surviving spruce–fir forest, and their specific abundance in already populated sites occurred later. In the buffer and background zones, voles gradually occupied all free microstations, with a simultaneous insignificant increase in the index of specific abundance.

Thus, technogenic transformation of habitats entails significant changes in the spatiotemporal structure and abundance of the bank vole population. The absence of permanent vole colonies near the source of emissions is evidence for severe deterioration of the environment in this zone. At greater distances from this source, the quality of habitats improves and becomes sufficient for the sustainable existence of individual voles and the whole population throughout the life cycle. Technogenic factors account for 60% of variation in the indices of relative abundance and aggregation and for 75% of variation in the index of populated area; 95% of variation in the local animal density is explained by natural chronographic variation of the environment.

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