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Specific Features of the Formation of Animal Species Communities in Technogenic and Urbanized Landscapes

V. N. Bol'shakov, O. A. Pyastolova, and V. L. Vershinin

Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences, ul. Vos'mogo Marta 202, Yekaterinburg, 620144 Russia

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Abstract—The formation of the species composition and specific functional, physiological, and phenotypic features of populations in technogenic and urbanized areas was studied by analyzing murine rodents, amphibians, and soil invertebrates. It is shown that, against the background of decreasing total abundance and biomass of animals, their formerly continuous ranges become mosaic, with the locally increasing animal density and heterogeneity and specific population dynamics. Species diversity decreases; however, species alien to the natural ecosystems of the given territory appear. Changes in the strategies of reproduction and food resource use were revealed in the species communities of small mammals and amphibians.

Key words: community ecology, ecosystem stability, murine rodents, amphibians, soil invertebrates, anthropogenic transformation of the environment.

Today, humankind may be regarded as a unique integrating component of the biosphere. Its powerful influence qualitatively transforms the Earth's ecosystems. Individual species and their communities respond to environmental changes by undergoing active adaptation. This natural response of the communities involves the processes that may be regarded as microevolutionary transformations at the population level (Shvarts, 1974). This is why the ecosystems of urbanized and technogenic landscapes are among the most interesting objects for ecologists, as they are a natural testing ground for studying the rapid microevolution of populations, their reaction norms, and the ranges of variation, tolerance, and adaptive capacities. Many trends in population dynamics and microevolutionary transformations become especially distinct under conditions of spatial isolation, low population density, and changes in chemical and other parameters of the environment.

New, rejuvenated biogeocenoses lack internal balance characteristic of ancient communities and are less autonomous. The number of dominant species in such biogeocenoses is sharply reduced, and the stability of a community is maintained owing to the biological plasticity and intraspecific population heterogeneity of the dominant species (Shvarts, 1976). This entails changes in the species composition, abundance, and other population parameters important for the formation of stable and productive biological communities. In such a situation, a decrease in biological diversity is at issue. Since the animals respond differently to various doses of pollutants (Pyastolova *et al.*, 1989), specialists studying the effects of anthropogenic factors on some organisms should take into account their biological features, reaction norm, place and role in the structure of trophic relationships, etc. Regrettably, trends in the dynamics of biodiversity in a gradient of anthropogenic factors have rarely been studied in real situations.

This work deals with the analysis of changes in ecosystem biodiversity in the gradient of technogenic pollution and urbanization.

METHODS

Observations were performed to collect information at different levels of biological organization, namely, the ecosystem, species, population, organism, and cytological levels. As population mechanisms play an important role in maintaining the biogeocenotic balance, emphasis was made on the population approach.

We performed a comprehensive study of specific structural and functional features of anthropogenically transformed biocenoses, having analyzed in detail the species composition of anthropogenic communities of murine rodents, amphibians, and soil invertebrates. Attention was given to the species actively involved in the flows of matter and energy. We often used estimations of biological diversity and the constituent population parameters, with the concept of "biological diversity" encompassing the genetic variability of species, populations, and life forms; the diversity of species complexes and their interactions; and the structural and

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functional variation of ecosystems and processes which they affect or on which they depend.

As observation objects, we used three groups of living organisms: soil invertebrates (mainly of the family Elateridae), amphibians (Siberian salamander *Salamandrella keyserlingii* Dyb., 1870; common newt *Triturus vulgaris* L., 1758; marsh frog *Rana ridibunda* Pall., 1771; and brown frogs *R. arvalis* Nilss., 1842 and *R. temporaria* L., 1758), and small mammals (mainly common vole *Microtus arvalis* Pall., 1779 and bank vole *Clethrionomys glareolus* Schr., 1780).

The study of small mammals in the areas transformed under the impact of mining was carried out in 30 dumps, quarries, and mines of the Sverdlovsk, Perm, and Chelyabinsk oblasts. With respect to the degree of colonization by small mammals, they were conventionally divided into three groups: (1) the areas where the colonies of one or several species could occur, (2) the areas where traces of life activity (burrows, excrement, etc.) were found and single individuals of some species were captured, and (3) the areas where no signs of life activity were found during the study. The areas included in the first group were as follows: waste rock dumps (20–30 years and older), old coal-mine dumps (70–80 years), overgrown peat fields, building-stone quarries and ore mines with a small disturbed area (2–3 ha), and mines abandoned since 1917. In the examined dumps and quarries of the middle Urals, we found 15 species of small mammals of three orders: rodents (Rodentia), 12 species; insectivores (Insectivora), two species; and carnivores (Carnivora), one species (Kulikova and Bol'shakov, 1984).

The effects of industrial pollutants were studied in the regions of the Middle-Ural Iron and Steel Works (Revda) and the Karabash Copper-Smelting Plant, in the secondary herb and grass–herb birch forests that are now dominant in the area formerly occupied by pine forests with fir and spruce. The mesophytic variant of these birch forests, which grow in the lower parts of the slopes on brown mountain–forest soils, was studied. The control area was in the forest range of Mount Iremel', 130 km away from the Karabash plant and beyond the zone affected by its discharge. In addition, the environmental impact of oil and gas production in the Tevlinsko-Ruskenskoe oil and gas condensate field was estimated. In both cases, the objects of analysis were soil invertebrates and small mammals. The populations of amphibians and murine rodents of urbanized landscapes were studied in the region of the Bovanenkovskoe gas condensate field (Yamal) and in technogenic and urban landscapes of the northern, middle, and southern Urals (the cities of Serov, Yekateriburg, and Chelyabinsk, respectively). In all cases, slightly disturbed areas in the suburbs and nature reserves (e.g., the Visim Reserve and Olen'i Ruch'i National Park) were used as control.

In studies on the growth and development of amphibians in urbanized landscapes, a six-component analysis of water in the main spawning water bodies was performed upon the end of metamorphosis (in late July and August). We determined the total mineral contents, ion concentrations (Cl^-, SO_4^{2-}, CO_3^{2-}, NO_2^-, NO_3, NH_4^+, K^+, Na^+, Mg^{2+}, and Ca^{2+}), biological oxygen consumption (BOC_5), permanganate oxidizability, and the content of petroleum products and extractable substances. In addition, the concentrations of lead, iron, and synthetic surfactants were measured.

In experimental studies on the survival of amphibian eggs, embryos, and larvae, we used *R. arvalis* tadpoles that emerged from eggs taken in a natural habitat 23 km away from Yekaterinburg. To study the complex of soil invertebrates, 31 soil samples (0.25×0.25 m) were taken from each test plot. In the area of the Karabash Copper-Smelting Plant, the contents of heavy metals (Pb, Cu, Cd, Mn, Zn, Fe, Co, Ni) in snow samples were measured.

The most important biodiversity indices reflecting the degree of transformation and the quality of the environment can be divided into the cenotic, demographic, morphological, phenogenetic, and cytogenetic groups. Cenotic indices characterize communities in terms of general abundance, species diversity, and species distribution with respect to their biocenotic significance. Demographic indices characterize populations from the structural and functional aspects and concern their spatial structure, sex ratio, age-related functional structure, migration pattern, and parameters of reproduction and mortality. They reflect biological success of a species and the degree of its adaptation to the natural environment (Shilov, 1977). The age of *R. arvalis* frogs was estimated by the method of skeleton chronology (Smirina, 1980).

Morphological and phenogenetic indices are conventionally used in population studies on the effects of environmental factors, including pollution, on individual development. To this end, specialists estimate the frequencies of various morphogenetic disturbances and assess the stability of the individual development by analyzing the fluctuating asymmetry of bilateral structures at the population level. We studied the occurrence of various morphological anomalies in amphibians.

Cytogenetic analysis was performed using the cornea of common voles (*M. arvalis*) and postmetamorphic *R. arvalis* frogs (Gatiyatullina, 1990). In studying tissue growth, we determined cell density, cell number per microscopic field limited by a rectangular diaphragm 3025 μm^2 in area, and the average size of an epithelial cell in square micrometers. Mitotic activity was estimated in the same preparations by examining 100 microscopic fields (15000 cells) in each and determining the proportion of dividing cells.

RESULTS AND DISCUSSION

Response of Small Mammals to Environmental Pollution and Urbanization

Small mammals, being an important component of natural ecosystems and agrocenoses, are widely used as model objects in ecological studies, including those concerning the problems of anthropogenic environmental transformations. Owing to its position in the trophic chains of ecosystems, this large animal group is directly affected by the impact of various adverse environmental factors on large areas and, hence, can be used for the indication of environmental disturbances.

Comparative studies on the faunas of small mammals in urban tree stands and their natural environment are interesting for several reasons. First, it is important to know the main consequences of exposure to the impact of large cities for natural communities and the main factors promoting the acceleration of evolutionary processes in anthropogenic ecosystems (Zakharov and Sergievskii, 1984). The high rates of microevolution under certain conditions have already become textbook examples (Shvarts, 1974). Moreover, the study of small mammals in the urban environment is also of practical interest: changes in the species and demographic composition of communities can provide information about the degree of environmental disturbances. Owing to "synurbization" processes (Andrzejewski *et al.*, 1978), the populations inhabiting urbanized landscapes differ in many parameters from the populations of natural ecosystems. Among mammals involved in synurbization, nonsynanthropic species deserve special attention, as little information is now available on the processes of their adaptation to the urbanized environment or their capacity for population outbreaks under urban conditions, which increase epidemiological hazard in the cities.

Studies on the fauna of small mammals in various technogenic areas of the middle Urals showed that dumps are primarily colonized by widespread and ecologically flexible species that are common in many anthropogenic landscapes. These are common and bank voles (*M. arvalis* and *C. glareolus*) and the common shrew (*Sorex araneus*). Common voles were found in 12 different dumps and prevailed in the samples from waste-rock, coal-mine, and building-stone dumps (52.3–89.8%). The high ecological flexibility and synanthropy of this species enable it to enter the anthropogenically disturbed areas and, under conditions of sufficient food and shelter, to settle there. Bank voles were found in nine dumps and prevailed in the samples from peat bogs and coal-mine dumps. Common shrews were found in 11 dumps and, as the previous species, were most abundant in peat bogs (24.6%). However, although the proportion of shrews was fairly high, the samples included mainly juveniles (young of the year), and no adult reproductive individuals were found. The absence of sites with a thick forest litter rich in food, which are typical *S. araneus* habitats, is apparently one of the factors hindering the colonization of dumps by this species. A great number of juvenile males and females in the dumps may be attributed to a high mobility of common shrews: according to Karulin *et al.* (1974), individual animals cover the distances of 1.1–2.5 km per day.

The occurrence of other small mammals in the dumps—field mice (*Apodemus agrarius, A. sylvaticus*), root vole (*Microtus oeconomus*), water shrew (*Neomys fodiens*), and others—is limited by insufficient food supply and small number of shelters and suitable habitats. The house mouse (*Mus musculus*), common hamster (*Cricetus cricetus*), large-toothed red-backed vole (*Clethrionomys rufocanus*), field vole (*M. agrestis*), and weasel (*Mustela nivalis*) were rare, and their occurrence in the middle-Ural dumps was apparently accidental. Comparison of the species composition and quantitative ratios of small mammals in the waste-rock dumps and the adjacent biotopes revealed significant changes in the faunistic complexes, associated with the anthropogenic transformation of animal habitats. Their fauna is restored owing primarily to voles, whereas under the initial conditions (in primary forests), the bulk of the small mammal community is comprised by shrews (Kulikova and Bol'shakov, 1984).

Generalizing the phenomenology of responses of small mammal communities and populations to technogenic pollution (with heavy metals, acid gases, and organic compounds), it was found that the cenotic response of the community is governed by the relation between the nature of cenosis and the spatial localization of pollutants. The basic mechanism of action of technogenic pollutants on communities involves their mediated effects on the ecological capacity and structuring of the environment. As the ecological capacity decreases, the total species abundance decreases as well, whereas species diversity either decreases or increases, depending on changes in the structuring of the environment (Luk'yanova *et al.*, 1994). The increasingly mosaic pattern of the environment is responsible for the increase of species diversity in communities with an initially high level of dominance upon their exposure to weak or moderately strong environmental stress factors; under a considerable technogenic load, however, the species diversity of these communities decreases. The response of small mammals to technogenic pollutants largely depends on the trophoecological specificity of the species: consumers of higher ranks are more sensitive to technogenic pollutants.

Technogenic pollution leads to changes in the indices of general species abundance in the small mammal community, which are inversely related to the technogenic load. Different types of pollution can affect the indices of species diversity, uniformity, number, and the proportions and abundance of species belonging to different ecological groups in the small mammal community (Luk'yanova *et al.*, 1994). The rate and amplitude of population dynamics in small mammals are strongly modified under the effect of technogenic factors, and the response of the population depends on the level of pollution; the nature, location, and spread of pollutants; and on the ecological specificity of the species, position of the population within the species range, and the type of habitat.

Upon heavy environmental pollution by discharges from metallurgical enterprises, population dynamics acquires a disjunctive (discontinuous) pattern characteristic of unstable temporary colonies of small mammals in suboptimal habitats (Luk'yanova *et al.*, 1994). Animal abundance under these conditions is maintained at a low level owing to the regular immigration of animals from the preserved donor habitats. The marginal populations of small animals are more sensitive to the effects of technogenic pollution than populations from the center of the species range. At temperate latitudes, a moderate technogenic load usually leads to an increase in the temporal amplitude of population dynamics characteristic of marginal populations. Upon local environmental pollution (e.g., with petroleum products) in small areas forming a certain territorial mosaic, the type of population dynamics in small mammals usually remains unchanged, whereas its amplitude decreases because the upper limit of the ecological capacity of the environment becomes lower.

The demographic response to the factors of technogenic pollution in the populations of small mammals depends on the nature of pollutants and the intensity, duration, and stability of their effects, on the one hand, and on the biological specificity of species and population systems that actively resist stress effects, on the other. Although the demographic responses of small mammal populations to the factors of technogenic pollution are fairly diverse, even relatively short-term ecological–population studies (several years long) can reveal the basic technogenic effects: a decrease in preimplantation mortality and an increase in actual fecundity, the proportion of juveniles, and the rate of their maturation.

In addition to the aforementioned ecological parameters, cytological indices were used for assessing the state of populations of small mammals. It is known that corneal epithelial cells divide permanently, as the cornea performs a protective function. The dynamics of mitotic activity in the corneal epithelium proved to be a fairly informative index, although its assessment was labor-consuming. In common voles caught 4–5 km away from the emission source, mitotic activity in the corneal epithelium was significantly lower than in control voles: 32.32 ± 6.0 vs. 50.22 ± 6.0 ($p = 0.05$). This parameter is known to depend on the physiological state of animals. Moreover, the proportion of abnormal mitoses in the animals from the polluted zone was significantly higher than in the control animals: 11.8 and 7.4%, respectively.

We propose the following scheme of biological indices reflecting changes in the biodiversity of small mammals under the effects of anthropogenic factors at the levels of communities, populations, and individuals:

1. Cenotic indices:

1.1. Species composition of small mammal communities in ecosystems.

1.2. General abundance of small mammals.

1.3. Analysis of species distribution according to ecological valence.

2. Demographic indices:

2.1. Abundance.

2.2. Spatial structure of the population.

2.3. Sex ratio.

2.4. Functional and age structure of the population: (a) age structure, (b) number of generations, and (c) functional structure.

2.5. Migration structure and mobility of the population.

2.6. Indices of population reproduction: (a) fecundity of animals of different age groups, (b) potential fecundity of animals, (c) general reproduction rate, (d) duration of different stages of spermatogenesis, (e) relaxation index, (f) spermogram, (g) functional state of incretory cells, and (h) number of yellow bodies in the ovary.

2.7. Mortality indices: (a) specific mortality of animals of different demographic groups and (b) pre- and postimplantation mortality.

2.8. Parameters of population turnover: (a) the age of reproductive maturity, (b) life span, and (c) specific rate of population renewal.

3. Morphological and phenogenetic indices:

3.1. Morphogenetic aberrations and malformations in populations: (a) teratological disturbances of external characters, (b) morphophysiological deviations, (c) structural aberrations of the skeleton.

3.2. Epigenetic variation in mammalian populations: (a) frequency dynamics of morphogenetic aberrations in time and (b) the level of differentiation of colonies.

3.3. Bilateral skeletal structures: (a) the variance of fluctuating asymmetry in quantitative skeletal characters, (b) the frequency of morphogenetic aberrations per individual, and (c) factorial and stochastic components of fluctuating asymmetry.

3.4. Morphophysiological indicators of the state of populations for monitoring polluted territories: (a) experimental selection of adequate morphophysiological characters (indicators) and (b) multivariate morphophysiological analysis of populations and intrapopulation groups.

4. Cytogenetic indices:

4.1. Genotoxic effects of anthropogenic pollution of agrocenoses (assessment with the use of indicator spe-

Table 1. Contents of heavy metals in the snow in the vicinity of the Karabash Copper-Smelting Plant (10^{-9} g/g)

Direction and distance from the pollution source, km	Mn	Zn	Cu	Fe	Cd	Co	Pb	Ni
SE–3.5	35.9	214.0	251.0	2378.0	1.53	0.74	443.0	8.42
SE–6.5	54.1	394.0	1116.0	758.0	8.45	1.79	314.0	7.90
SE–7.5	54.1	432.0	857.0	716.0	2.77	0.69	379.0	10.47
SE–10	30.2	419.0	361.0	692.0	1.30	0.94	262.0	9.43
NW–3	48.4	591.0	1467.0	3067.0	3.72	2.34	510.0	18.86
NW–5	35.7	395.0	398.0	1221.0	5.53	0.90	197.0	9.19
NW–5.5	23.5	551.8	200.8	245.0	4.65	1.05	51.9	0.59
NW–10	13.2	167.0	75.0	672.0	0.82	0.24	125.0	4.41
Iremel'–130	9.4	33.0	26.0	204.0	1.62	0.19	25.0	1.90
Detection limit	0.3	0.4	0.3	2.5	0.003	0.03	0.2	1.0

cies): (a) the frequency of chromosome breaks and (b) the frequency of aneuploid cells.

Studies on the effects of urbanization on small mammals revealed several trends in the formation of species composition and demographic parameters of rodent and shrew communities in each park forest studied in Yekaterinburg. The thinning of tree stands and herbaceous cover leads to a decrease in the number of shelters for small mammals and in animal abundance. The level of anxiety and the presence of shelters, rather than industrial pollution or automobile exhausts and noise, are the main factors affecting the abundance of small mammals (Chernousova, 1995).

The field mouse *Apodemus agrarius* is an uncommon species in the natural rodent communities of forests, and its appearance in the latter may be regarded as an indicator of their transformation. In some areas, *A. agrarius* reaches a high abundance and becomes a background species, which is evidence that transformation of the natural forest community exceeded a certain threshold.

The most significant effects of the burrowing activity of rodents on soil processes in the middle Yamal tundra, both in undisturbed areas and in the zone of strong anthropogenic impact (Bovanenkovskoe gas condensate field), is the formation of hummock-and-hole nanoreliefs on the soil surface, which promotes soil aeration and moistening to a greater depth. The results of studies in anthropogenically disturbed areas (oil and gas fields in northern Yamal) allow us to propose the comparative quantitative assessment of burrowing activity for indicating the early stages of anthropogenic degradation of tundra biogeocenoses.

Long-term stationary studies on trends in the formation of population structure and population dynamics of northern red-backed and large-toothed red-backed voles in the middle Urals revealed the key role of trophic conditions in the population dynamics of red-backed voles (Dobrinskii *et al.*, 1994). The anthropogenic transformation of the environment leads to changes in the demographic parameters of small mammal populations: the rate of sexual maturation increases, the sex ratio changes in favor of females, the ratio of functional age groups shifts toward rapidly growing and rapidly maturing individuals, and the mobility of populations increases. The stability of populations of small mammals in technogenic areas is accounted for by an individual adaptive response, namely, intensification of life activities and the ensuing increase in the rate of physiological processes and energy expenditures at the individual level. In the context of the evolutionary-ecological approach (Shvarts, 1980), this mechanism represents the first stage in adaptive changes (the most primitive and energy-consuming); however, it provides for the existence and integrity of population systems of small mammals on technogenic territories.

Soil Invertebrates under Conditions of Technogenic Pollution

Soil animals at all stages of their life cycles are convenient model objects for assessing the state of the environment. Their relative abundance, role in soil formation, and high sensitivity to various factors determine the significance of this group in the analysis of community transformation under conditions of technogenic pollution. Measurements of heavy metal contents in the snow near the Karabash plant (Sadykov, 1994) indicated that the area around the emission source was an obvious geochemical anomaly with respect to most of these pollutants. In particular, concentrations of Pb, Cu, and Cd in the vicinity of the plant exceeded the background level by factors of 20, 45, and 5, respectively (Table 1).

Table 2 shows data on changes in basic indices of the soil invertebrate fauna along the southern transect, which correlate well with the level of disturbance of the herb–dwarf shrub and moss–lichen layers. Thus, the

Table 2. Changes in some parameters of the soil mesofauna in the pollution gradient

Parameter	Distance from the source of emissions, km				
	2	10	20	30	67
Abundance, ind./m^2	6	16	172	316	552
Biomass, mg/m^2	116.6	450.4	754.3	1919.5	5742.8
Group diversity	2	6	10	12	14

Table 3. Distribution of wireworms in dwarf shrub–green moss spruce forests in the pollution gradient

Parameter	Distance from the source of emissions, km				
	70	30	20	10	2
Abundance, ind./m^2	72	61	56	2	2
Biomass, mg/m^2	2042	649	523.5	48	36
Species abundance, %:					
Paranomis costalis	97.1	93.4	100	–	–
Athous haemorrhoidalis	2.9	3.3	–	100	100
Sericus brunneus	–	3.3	–	–	–

aboveground phytomass and the number of plant species near the source of pollution (2 km) were approximately five and four times smaller than in the control area, (67 km), and the biomass and group diversity of the soil mesofauna in these areas differed by factors of 50 and 7, respectively.

Particular attention was given to snapping beetles of the family Elateridae. Their larvae (wireworms) are an important component of the soil invertebrate complex, and their abundance and biomass in the study area are relatively high (almost one-third of the total biomass of the soil mesofauna). As the distance from the plant decreased, the abundance and biomass of wireworms decreased as well (Table 3). A sharp change in these indices in the interval of 10 and 20 km from the pollution source indicates that the concentrations of pollutants and other environmental parameters of wireworm habitats in this zone approach the threshold of maximum allowable values. We observed a regular change in the ratio of wireworm species, which indicated that *Athous haemorrhoidalis* was more tolerant to technogenic impact than *Paranomis costalis*.

The result of our studies showed that, as the level of soil pollution by discharge from the integrated iron and steel works increases, the species composition of soil invertebrates becomes depleted; their distribution becomes nonuniform; and their abundance, biomass, and species diversity decrease to the extent that some species disappear from the soil mesofauna.

Species Complex of Amphibians

Amphibians are convenient object for studying the effects of various factors on animal organism because they are relatively abundant, long-lived, and usually remain within relatively small home areas. A high flexibility of amphibians allows them to survive in anthropogenically transformed environments in which other animals are often lacking. Among vertebrates, they appear to be most sensitive to pollution, as all developmental stages proceed after birth. Observations performed in urbanized and technogenic areas and experimental studies indicate that amphibian embryos and larvae can be used for indicating the state of the environment.

The skin of amphibians is especially permeable, which explains their high sensitivity to changes in the concentrations and composition of trace elements and other substances in the aquatic environment. This is manifested in the direct effects of these substances on the growth, development, mortality, cytological indices, metabolism, and morphology of animals. Moreover, amphibians accumulate pollutants, which makes it possible to detect pollution before it becomes significant. It is known that tadpoles can accumulate pesticides to concentrations that exceed those in water by a factor of 60 (Hall and Kolbe, 1980). Tissues and organs of adult animals selectively accumulate different chemical elements and compounds.

The brown frog *R. arvalis* is the most abundant and widespread amphibian species in natural and anthropogenic landscapes of the Urals. We used it in several field and laboratory studies aimed at revealing specific features of individual development at early stages under the effects of different pollutants.

The effects of chemical compounds commonly occurring in the complex of anthropogenic pollutants (phenol, copper sulfate, sodium sulfate, calcium chloride, and oil) were studied under laboratory conditions. The response to these factors proved to be unspecific and involved an increase in embryonic mortality, a decrease in body weight and an increase in its variation, retardation of development, an increase in the average size of hepatocytes and their nuclei (the nucleoplasmic ratio increased), and the appearance of giant hepatocytes. The increased metabolic rate in postmetamorphic animals and high energy expenditures in the period of metamorphic climax were observed. Experimental animals, compared to the control group, were characterized by the increased frequencies of mutations, developmental pathologies, and cases of abnormal regeneration. The experiment revealed the direct dependence of the parameters studied on the concentrations of test substances.

The survey of amphibian communities inhabiting urbanized landscapes showed that their distribution is nonuniform and has a mosaic pattern. More than 50% of small water bodies in which amphibians live and spawn are of technogenic origin. The statistical processing of all available data on water pollution revealed significant differences in water pH, which proved to be close to 7 within the city limits and to 6.5 in the suburbs ($F = 2.663$; $p = 0.05$). Water bodies located within the city limits are also characterized by significantly higher mineralization ($F = 9.836$; $p = 0.0008$), concentrations of surfactants ($F = 3.672$; $p = 0.018$), and the contents of rapidly oxidizable organic matter (BOC_5) ($F = 2.99$; $p = 0.036$). This is evidence for their high eutrophication, which can endanger larval growth and development and be hazardous to the adult representatives of species wintering in the water (Vershinin, 1997).

With respect to prevalence in habitats on the territory of Yekaterinburg, amphibian species can be arranged in the following descending series: *Rana arvalis*, *R. temporaria*, *R. ridibunda*, *Triturus vulgaris*, and *Salamandrella keyserlingii*. These species strongly differ in their capacity for reproduction in urban areas. *Salamandrella keyserlingii* can normally reproduce only in the park–forest zone of the city because it is intolerant of plant community transformation and related microclimatic changes. *Triturus vulgaris* is less demanding of the composition of plant communities; its main requirement is the presence of the herbaceous layer, which aids in maintaining humidity in the surface air layer (Garanin and Popov, 1958), and its reproduction in urban water bodies becomes impossible only upon their heavy pollution. The populations of *R. temporaria* can live in urban landscapes fairly successfully if there are nonfreezing and well-aerated water bodies necessary for their wintering. Ecologically, this species is less flexible and less tolerant than *R. arvalis* (Vershinin, 1997), which may be attributed to the prevalence of hereditary factors over environmental in control of its ontogeny (Surova, 1988).

In *R. ridibunda* (an introduced species in Yekaterinburg), even under conditions of heat pollution of water bodies, reproduction is not necessarily observed every year nor in all habitats. In the period of our studies, postmetamorphic juveniles appeared in 1980, 1981, 1986, 1988–1991, 1994, and 1997. Within its natural range, this species is known to be extremely resistant to pollution and anthropogenic transformation of the environment.

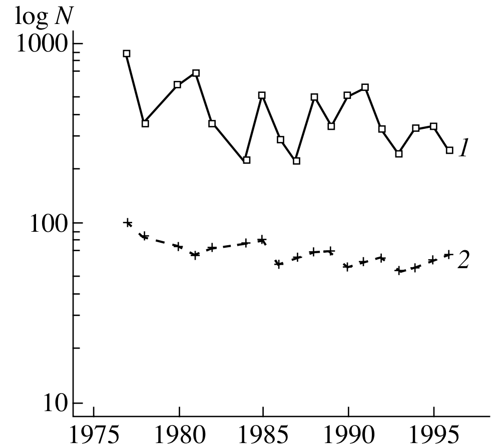

Fig. 1. Dynamics of (*1*) the number of clutches and (*2*) fecundity of *Salamandrella keyserlingii* Dyb. in the park-forest zone.

It is known that exposure to pollutants can lead to disturbances of oogenesis in amphibians. In the zone of industrial pollution, changes in protein and lipid metabolism that resulted in deviations from the normal course of gametogenesis were observed. Insufficient feeding causes a significant increase in the number of atretic oocytes and a decrease in the weight of ovaries (Saidapur and Prasadmuthv, 1988). Spawners with such pathologies produce clutches containing eggs without embryos, and animal fecundity in urban populations decreases with the increase of anthropogenic pressure. Thus, the average number of eggs per clutch in the *S. keyserlingii* population from the park–forest zone of Yekaterinburg decreased significantly during the 19-year observation period (Fig. 1). It was found that the decrease of fecundity under the increasing recreational load positively correlates with the decrease in the number of spawners ($r = 0.78$; $t_z = 3.48$) but does not correlate with their size; simultaneously, the range of variation broadens and the proportion of asymmetrical clutches increases (Vershinin, 1997). In *R. arvalis* from the zone of multistory buildings, a decrease in the average number of eggs per clutch was observed (Fig. 2). A probable explanation is that female frogs in this zone were smaller than those from other populations, although their average age was the same (Table 4). The observed process is similar to changes in fish reproduction upon anthropogenic impact: the rate of reproduction increases in young fish and decreases in old fish because of greater energy expenditures; if environmental conditions continue to deteriorate, mass egg resorp-

Table 4. Body size and average age of female *R. arvalis* frogs

Zone	*N*	*L* ± *m*, mm	*CV*, %	Age, years	*N*
Multistory buildings	34	45.19 ± 1.15	21.6	3.0 ± 0.45	5
Low buildings	18	47.11 ± 1.59	13.2	3.5 ± 0.71	8
Park forest	46	49.49 ± 0.99	14.7	3.1 ± 0.63	7
Suburban population	31	51.72 ± 1.21	14.2	3.3 ± 0.33	11

tion is observed (Koshelev, 1988). Similar processes leading to decreased fecundity were also observed in the populations of passerine birds exposed to technogenic pollution.

The effects of chemicals lead to changes in the protein composition of egg envelopes, and this prevents subsequent swelling of the jelly coat and interferes with normal development of the embryo (Hazelwood, 1970). In the city of Yekaterinburg, the proportion of abnormal clutches in *R. arvalis* populations varies in different years between 0.23 and 44.6%; in *R. temporaria*, between 0.7 and 12.5%; and in *S. keyserlingii*, between 0.4 and 3.9% (Vershinin, 1997). The long-term sustainable existence of species such as *R. arvalis* and *R. ridibunda* under urban conditions implies the occurrence of adaptive changes at different levels. Thus, adult *R. arvalis* from the zone of multistory buildings proved to have a higher muscle excitation threshold (Vershinin and Tereshin, 1999). We regard this fact as evidence for their physiological adaptation to the factor of increased anxiety. Long-term studies on the dynamics of difference in liver indices in juvenile brown frogs revealed correlative similarity between the dynamics of this index in populations inhabiting the zones of multistory and low buildings and, in *R. arvalis*, higher values of the index in populations from the zone of multistory buildings. The latter appears to be a response to a high level of environmental pollution. In

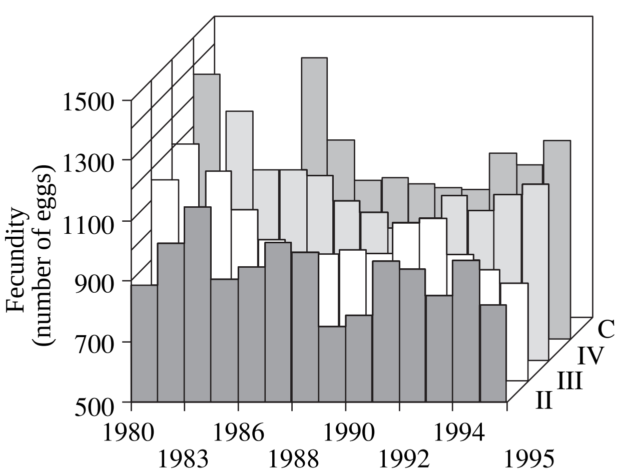

Fig. 2. Average fecundity of *R. arvalis* frogs in the zones of (II) multistory buildings, (III) low buildings, and (IV) park forest and (C) in the control suburban population.

T. vulgaris populations from the zone of multistory building, adult animals proved to remain in water for a longer period of time (Vershinin, 1997).

An increase in the frequencies of rare phenotypes can serve as a criterion of population response to the impact of a new factor. In the urban populations of brown frogs (*R. arvalis* and *R. ridibunda*), the frequency ratio of the striata morph proved to differ consistently from that in control populations (Vershinin, 1997).

Frogs of this morph, which have a median light stripe on the back, are always found in *R. arvalis* populations. This character is controlled (Shchupak, 1977) by one diallelic autosomal gene (*striata*) with complete dominance of one allele determining the presence of the stripe. Thus, striata is a good phenetic marker for analyzing changes in the genetic structure of populations by phenotypic manifestations. The frogs of this morph apparently have selective advantages in populations of the zone of multistory buildings.

Some specific features of metabolism and permeability of the skin for sodium in *R. arvalis* (Vershinin and Tereshin, 1999) may account for the adaptive value of striata under conditions of pollution and urbanization. In certain urban populations of *R. ridibunda*, some postmetamorphic frogs of the striata morph have a significantly thinner stripe (0.3–0.5 mm vs. 1.0–2.0 mm). Their frequency is 4.5%, and this fact, in our opinion, provides evidence for the existence of at least two different sources of *R. ridibunda* introduction in Yekaterinburg. Changes in the ratio of morphs under the increasing impact of urbanization and the emergence of new phenotypes that never occur in natural populations are also characteristic of other species of the genus *Rana* (Zhukova *et al.*, 1986).

One more feature of urban amphibian populations is the increase of body size, which is apparently related to the fact that the surface–volume ratio in larger individuals (smaller area per unit of weight) is more favorable in the polluted environment. This trend was observed in male and juvenile *R. arvalis*, adult *S. keyserlingii* and *R. temporaria*, and in adult and juvenile *T. vulgaris* and *R. ridibunda*. Growing to a certain optimal size, amphibian larvae become less sensitive to pollution and less vulnerable to predators; therefore, a high growth rate is an advantage (Werner, 1986). A large body size in amphibians living under conditions of anthropogenic impact was also noted by other researchers (Ushakov *et al.*, 1982).

A negative aspect of population response to anthropogenic factors (primarily to changes in environmental chemistry) is an increase in the frequency of morphological abnormalities, which emerge due to genetic changes, developmental disturbances, abnormal regeneration, neoplastic transformation, etc. The frequency pattern of these abnormalities varies depending on systematic group (Urodela and Anura) and animal age (juveniles and adults of both groups). In the Urodela, they occur more frequently in adults than in juveniles and include mostly the cases of abnormal regeneration, pathological development, and neoplasms.

In the Anura, terrestrial habitats have a small area, are isolated from one another, and animal density in them is low. These factors significantly increase the probability of inbreeding and the resulting genetic defects, some of which are expressed phenotypically.

The degree of land development by man is reflected in the degree of transformation of populations inhabiting the corresponding areas. On this basis, we conditionally regarded the level of ecosystem transformation in the park–forest zone of the city as initial (Vershinin, 1997); in the zone of low buildings, as medium; and in the zone of multistory buildings, significant. At the initial stages of ecosystem transformation, changes occur in the species composition of amphibians, the abundance of background species, and population density; animal fecundity decreases, and clutch asymmetry increases.

At the medium level, as pollution increases and the vegetative component of communities changes radically, *S. keyserlingii* disappears from them and adverse trends begin to prevail in the populations of other amphibians. Ecosystems transformed and polluted to this level are easy to identify by the increased frequencies of all morphological anomalies and mutations, the emergence of abnormal clutches in *R. temporaria*, and adaptive changes at the individual level.

In significantly transformed ecosystems, amphibians are characterized by some adaptations of the population rank. In particular, this concerns specific population dynamics in *R. temporaria* larvae and juveniles, considerable changes in the genetic structure of populations, negative and adaptive phenotypic features, and the appearance of the populations of introduced species capable of existing only in the anthropogenically transformed environment. Changes are also observed in the trophic relations of juvenile brown frogs (*R. arvalis* and *R. temporaria*). Thus, the efficiency of their feeding on invertebrates is higher in urban isolates (on average, by a factor of 2.1). The proportion of phytophagans in the diet of individuals that complete metamorphosis (in the initial period of life on land) noticeably increases as they develop from stage 53 to stage 54 by Dabagyan and Sleptsova (1975). This is evidence for the shortening of trophic chains and the increased rates of matter and energy exchange in urban ecosystems (Vershinin, 1997). In the zone of multistory buildings, juvenile *R. arvalis* are characterized by high feeding efficiency, large body size, low mortality during metamorphosis, and hence high density within the limited territory they inhabit, so that their food supply is relatively low. Under such conditions, amphibians feed on most abundant species (in the city, these are phytophagans), and the contents of their stomachs closely resembles the natural spectrum of invertebrates, in contrast to the situation in natural groups (Vershinin, 1997).

Thus, long-term studies on the distribution of amphibians in the city and some specific features of their urban populations indicated that the evolutionarily young species (*R. arvalis* and *R. ridibunda*) have an advantage over other species under these conditions: they are widespread within the city limits, dominate in many communities, and reproduce as successfully as in natural ecosystems. At the cytological, physiological, and epigenetic levels of organization, the urban populations and species complexes of amphibians have both adaptive and negative features that determine their potential for intensive reproduction and high tolerance, on the one hand, and their low buffer capacity, on the other. A specific structural and functional organization of this system is determined by complex relationships between the dynamics and structure of populations and the extent of their adaptive changes.

CONCLUSION

Studies on the communities of small mammals, amphibians, and soil invertebrates showed that an increase in the level of pollution and anthropogenic transformation of the environment entails a general decrease in the abundance and biomass of animals and characteristic changes in population dynamics. Species ratio changes, species diversity decreases, and the species alien to natural ecosystems of a given geographic zone appear; continuous ranges separate into fragments that form a mosaic with locally increasing animal density and heterogeneity. In amphibians and small mammals, changes in the reproductive strategy and demographic indices of populations are observed; changes in the structure of trophic relations and the strategy of food resource use in the communities of small mammals and amphibians provide evidence for the intensification of metabolic processes.

Owing to specific demographic processes, the populations of anthropogenic landscapes acquire distinctive genetic features that manifest themselves in morphological parameters of animals and their physiological and functional properties. The example of juvenile brown frogs shows that limited and insufficiently diverse food supply leads to a decrease in individual efficiency and an increase in population efficiency.

Thus, anthropogenic biogeocenoses acquire a complex of specific features providing for the maintenance of diversity at different structural levels and, hence, for stability of ecosystems. The evolution of communities under conditions of anthropogenic pressure leads to the formation of new biogeocenoses, which are stable and efficiently function at the higher hierarchical levels of structural organization.

These phenomena fully confirm the concepts of Vernadsky (1965) concerning the evolution of the biosphere under conditions existing today: we observe the interruption of established biocenotic connections, structural simplification of trophic chains, transformation of soils and microclimate, emergence of new biogenic flows, and global change in biogeochemical cycles; however, the factors of organic evolution continue to function.

The aforementioned system has a specific configuration of matter and energy flows, which is determined by complex structural and functional interrelations, different population dynamics, and the level of metabolic processes.

Some features revealed in this work indicate that certain microevolutionary shifts have occurred in populations studied, provide the possibility of assessing the degree of transformation of natural communities, and may become an important link in the system of ecological monitoring and bioindication.

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