



ECOLOGICAL SPECIFICITY OF AMPHIBIAN POPULATIONS

**ADVANCES
IN AMPHIBIAN RESEARCH
IN THE FORMER SOVIET UNION**



**Volume 7
2002**

 **PENSOFT.**

**IUCN (The World Conservation Union)
Species Survival Commission
Declining Amphibian Populations Task Force
Regional Group for the Commonwealth of
Independent States**

**Russian Academy of Sciences
A.N. Severtzov Institute of Ecology
and Evolution**

ECOLOGICAL SPECIFICITY OF AMPHIBIAN POPULATIONS

**ADVANCES IN AMPHIBIAN RESEARCH
IN THE FORMER SOVIET UNION**

Volume 7
2002



**Sofia - Moscow
2002**

IUCN (The World Conservation Union)
Species Survival Commission
Declining Amphibian Populations Task Force
Regional Group for the Commonwealth of
Independent States

Russian Academy of Sciences
A.N. Severtzov Institute of Ecology
and Evolution

ADVANCES IN AMPHIBIAN RESEARCH IN THE FORMER SOVIET UNION

ISSN 1310-8840

Editor:

Sergius L. Kuzmin, Moscow

Associate Editor:

Ronald Altig, Mississippi State University

Editorial Board:

Nikolai N. Iordansky, Moscow

Yurii B. Manteifel, Moscow

Andrew N. Misyura, Dnepropetrovsk

Mikhail M. Pikulik, Minsk

Evgeny M. Pisanetz, Kiev

Emilia I. Vorobyeva, Moscow

All inquiries about subscription should be addressed to:

Pensoft Publishers

Dr. Lyubomir D. Penev, Akad. G. Bonchev Street, Bl.6, Sofia 1113, Bulgaria

Fax: +359-2-8704508

E-mail: pensoft@mbox.infotel.bg

Pensoft Online Bookshop: www.pensoft.net

Copyright

By submitting a manuscript, authors agree to transfer the copyright of all published material to the publisher.

© Pensoft *Publishers*

All rights reserved

ISBN 954-642-178-2 (Volume 7)

Photo on the cover by S. L. Kuzmin: *Rana temporaria*

Ecological Specificity and Microevolution in Amphibian Populations in Urbanized Areas

VLADIMIR L. VERSHININ

Institute of Plant and Animal Ecology, Uralian Branch of Russian Academy of Sciences, 8 Marta, 202, Ekaterinburg 620144 Russia

Accepted 10 November 2002

CONTENTS

Introduction	2
1.0. Amphibian populations in urban environments	6
2.0. Landscape typification and materials and methods	10
3.0. Hydrochemical features of spawning ponds	17
4.0. Habitat specificity of amphibians in urban areas	18
5.0. Genetics and “striata” morphs in <i>R. arvalis</i> and <i>R. ridibunda</i>	33
6.0. Amphibian physiology and urban ecosystems	37
6.1. Sodium balance in amphibians from urban areas	38
6.2. Oxygen consumption and urbanization	40
6.3. Excitable tissues in <i>Rana arvalis</i> and urbanization	42
6.4. Myocardial contraction of brown frogs and urbanization	46
7.0. Phenotypical and morphophysiological features	48
7.1. Morphophysiology of juvenile brown frogs from urban areas	48
7.2. Morphometric characters and their variability	52
7.3. Morphological anomalies in urban areas	58
8.0. Reproductive specificity of amphibians in urban areas	71
8.1. Sex ratio and longevity and urbanization	71
8.2. Fecundity and egg size variability	75
8.3. Brown frogs mortality at various stages and urbanization	91
8.4. Abnormal amphibian clutches in urban areas	99
8.5. Phenological specificity in amphibian reproduction and development ...	101
9.0. Trophic relationships of juveniles in urban areas	106
9.1. Trophic relationships of juveniles at beginning of terrestrial life	106
9.2. Rate of food passage in juvenile <i>Rana arvalis</i>	115
10.0. Methods of bioindication and amphibians	117
11.0. Conclusions	121
Acknowledgments	127
References	127

РЕЗЮМЕ: Экологическая специфика и микроэволюция популяций земноводных урбанизированных территорий. В.Л. Вершинин. Работа посвящена изучению структурно-функциональных особенностей видовых группировок земноводных в условиях урбанизации на примере ряда промышленных городов Урала. Проведено комплексное разностороннее исследование процессов, протекающих в популяциях земноводных при антропогенном изменении среды. Сформулирована концепция трансформации видового комплекса земноводных в условиях промышленного загрязнения в сочетании с прогрессирующей урбанизацией. Показано, что специфика динамики численности приводит к возникновению особенностей генетической, половозрастной структуры, изменению стратегии размножения. Микроэволюционные изменения и их скорость определяются условиями среды обитания, пространственной изоляцией городских популяций, низкой численностью при высокой локальной плотности населения, высоким уровнем загрязненности и трансформированности естественных сообществ. В этих условиях формируются адаптивные изменения поведенческих реакций, возникают физиологические адаптации, касающиеся нервной и мышечной тканей, получают преимущество животные с высоким уровнем обменных процессов, низкой кожной проницаемостью, растет устойчивость эмбрионов и личинок к загрязнению водной среды. Получены данные о зависимости морфогенеза от согласованности популяционных, физиологических и пролиферативных процессов в условиях антропогенно преобразованной среды. Найдено объяснение различий в устойчивости отдельных видов к антропогенным трансформациям. Некоторые из установленных особенностей свидетельствует о наличии микроэволюционных сдвигов в изучаемых популяциях, дают возможность оценить уровень изменений в природных сообществах и могут стать важным звеном в системе экологического мониторинга.

ABSTRACT: This work addresses structural and functional peculiarities of amphibians exposed to the conditions of urbanization in industrial cities of the Urals. I formulated an idea for the transformation of species complex of amphibians in the conditions of industrial pollution combined with progressive urbanization. The specificity of the dynamics of population number leads to the appearance of peculiarities of genetics, age, and sexual structures and to changes in reproductive strategy. Microevolutionary changes and their rates are determined by the conditions of the environment, spatial isolation of urban populations, low numbers at high density of individuals, high levels of pollution, and transformation of natural communities. In these conditions, adaptive changes of behavioral reactions occur, physiological adaptations concerning neural and muscular tissues arise, animals with high levels of metabolic processes and low skin permeability obtain an advantage, and resistance of embryos and larvae to water pollution increases. I obtained data on the dependence of morphogenesis on the coordination of population and physiological and proliferative processes in the conditions of anthropogenically transformed environments. I found an explanation for differences in the resistance of various species to anthropogenic transformations. Some of these regularities are evidence for the presence of microevolutionary shifts in the populations. They allow us to estimate the level of changes in natural communities and may become an important link in the system of ecological monitoring.

INTRODUCTION

Evolution of man and development of a human society have resulted in a situation where the technological opportunities of our civilization exceed the ability of mankind to adequately estimate and predict the consequences of technology. The evolution and

destiny of mankind depend in many respects ways of development of civilization in the future. For a long time the economic activity of man has influenced global character and has reached planetary scales. Even non-specialists know about global changes in the biosphere of our planet as a result of a human activity (e.g., background pollution and climatic changes). Results of this activity are easily comprehensible for water, air and soil. It is comparable in volume to geological processes that can have an effect for the condition of the biota and its evolution.

It is necessary to consider mankind if we are to understand our role as a unique integrating natural component of ecosystems, and our universal presence has made ecosystems of the Earth more open from the point of view of an exchange of substance and energy (Jacobs, 1975). "Young" biogeocenoses, without an internal coordination characteristic of older communities, differ by a smaller degree of isolation; the number of dominant species in such biogeocenoses is sharply reduced, the stability of the community is supported by biological plasticity, and populational interactions are governed by heterogeneity of a dominant species (Shvarts, 1976a). Most populations are changed and polluted by man and soon become an arena of fast evolutionary change (Zakharov and Sergievskii, 1984; Bengtsson and Rundgren, 1988). Some examples of high rates of microevolution are already axiomatic. The representations about the process of microevolution - "the elementary evolutionary phenomenon" (*sensu* Timofeev-Resovsky, 1958), have developed on the basis of synthesis of Darwinian doctrine of natural selection and modern genetics. The concept of microevolution by the various authors is interpreted a little differently. Many authors (Dobzhansky, 1954; Grant, 1980) define microevolution as regular change in frequencies of homologous alleles, chromosome sites or whole chromosomes in a local population; also, microevolution means any increase or reduction in frequencies of genes of any alternative form or a change in chromosome structure (Wright, 1964) that continue in a population from generation to generation. An elementary evolutionary phenomenon was understood by Timofeev-Resovsky et al. (1969) as a long and vectored change in the genotype structure of a population, which in itself is not an evolutionary process. The elementary evolutionary phenomenon is a hereditary change fixed by selection as a new adaptive attribute of a heterozygote, in particular of balanced polymorphisms (Zavadsky, 1973).

V.I. Vernadsky (1978) in the field of the evolutionary theory, which subsequently has received the name microevolution, adhered to principles of selectionism and considered a community of organisms as the elementary carrier of evolution. Evolution is determined by a struggle for existence in conditions of a complex mutual relation between the elements of a biogeocenosis, and the biogeocenosis is an arena of primary evolutionary transformations, while the population, including its structure, is the lowest unit of evolution.

Microevolution is the process of adaptive transformation of populations from the occurrence of hereditary changes of individuals to the development of new adaptations and the appearance of a new species (Severtsov, 1987). It is possible to define the adaptation of populations to varying conditions of environment-through genetic polymor-

phism-hereditary determined variants of a given attribute in two ways, each of which is adapted to any condition of external environment or the account of phenotypical polymorphism; the organism responds to changes of the environment without a change in genotype. The first way is characterized by a narrow norm of reaction, and the second case is characterized by a wide norm of reaction (Severtsov, 1987). The change of environmental conditions causes long and directed changes in genetic structure of a population (i.e., the end leads to the phenomena) which is possible to call a microevolutionary phenomena (Shvarts, 1969). Against the homeostatic transformations of a population genetic structure, the microevolutionary process is essentially irreversible (Shvarts, 1980). Microevolution begins with the occurrence of ecologically irreversible transformations of populations that determine the course of its further development but not leading to reproductive isolation of populations from other species. The last definition most fully and precisely reflects the essence of microevolutionary processes according to Shvarts (1969, 1977, 1980) and we follow it in our work.

Among anthropogenically transformed landscapes, cities and urban areas belong to a special category. In areas of large industrial cities with conditions of significant complex pollution and high heterogeneity of all environmental parameters, the scales of microevolutionary transformations differ from those in natural ecosystems. Observable biocenotic transformations, in the anthropogenically changed environmental conditions, and the examples of fast evolution (in particular, occurrence of toxic-tolerant populations) display the processes representing a natural reaction of communities to environmental changes (Shvarts, 1976a). The new communities must respond to man-made environments, and the ecological situation often is not controllable and does not allow forecasting.

For these reasons, urban ecosystems represent one of the most interesting arenas for population ecologists and microevolutionists. They have a convenient natural range for study of fast microevolution in populations, norms of reaction, ranges of variability, tolerances, and adaptive opportunities, as well as stability. In conditions of spatial isolation and low population numbers, changed environmental chemistry and other parameters provide regularity in populations dynamics, and microevolutionary transformations display a sharp character. The rates of these processes are often higher than in natural communities. There are adaptive and negative components in observable changes. The first promotes population success, survival, and normal reproduction in populations in new conditions. The second reflects consequences of low numbers, inbreeding, growth of genetic risk in conditions of urban environment, pollution, and influences of others stressors of different kinds.

The state and structure of urban ecosystems are directly related to problems of ecology of man and sanitary-epidemiological and psychophysical conditions. Many tendencies in the dynamics of urban populations of vertebrates provide an opportunity and potential danger of occurrence of the same features in urban populations of men. This situation is confirmed by growth of the prevalence of malignant tumors, diseases of

heart, vessels, and the nervous system, and occurrences of new “civilizations diseases.” Problems of urban ecology are the quintessence of modern ecological problems. Biota in and near urban agglomerations is subject to powerful and deep transformation because of the complex transformation of the environment and various kind of pollution. The essential changes occur at all levels of organization: communities, populations, individuals, tissues, and cytogenetics (that can have the rather serious future genetic consequences). Thus, urbanization, as the main feature of a modern civilization that directly represents most parts of the world and a special case of a common “ecological” problem, which in essence is biological (preservation of biodiversity, in particular survival of the man as species) and on the way to its solution, social. It is necessary to solve these problems as soon as possible and more competently. The correct and proper statement of a problem will allow us to generate public opinion and to unite and coordinate efforts of the society for changes of this ecological situation for the better.

The microevolutionary consequences of global activity of man in many respects remain unpredictable and frequently unknown. Unfortunately, in most cases we do not have time to fix the initial condition of the populations at the beginning of an anthropogenic influence, and we lose the opportunity to estimate the size and speed of microevolutionary changes (Yablokov and Yusufov, 1989). The necessity has demanded a complex approach to all aspects of ecological problems facing populations living in large urban areas in immediate proximity with highly developed industry. It means that a part of species populations should exist in an anthropogenic landscape, so we also should change the traditional methods of management.

The ecological situation frequently is not controllable and does not allow forecasting. For maintenance of general balance of the biosphere at a level ensuring optimal development of the human society, it is necessary to introduce ecological examination and ecological monitoring of industry and agriculture. At the moment, there is no uniform complex and not enough objectivity of ecological monitoring. An objective estimation of environmental condition is inconceivable even based of the definition of pollutant concentrations in air, water and soil. The final conclusion about allowable concentration of a number of substances can be made only on the basis of extensive research in nature and in experimental conditions. It is most widely applicable, and the ecological monitoring at the level of populations and ecosystems is convenient.

We studied features of microevolutionary processes in conditions of anthropogenic influences on a complex of local amphibians. The research included different levels: ecosystem, species, population, organism, and cell, and some laboratory experiments and elements of environmental chemistry raised objectivity of the data. The greatest attention was given to the approach at a level of populations and ecosystems. The formation of specific features in populations and species assemblages subjected to the conditions of an anthropogenic landscape can become a key to understanding the general patterns that determine the ways that ecosystems form and function. The microevolutionary processes in ecosystems in areas transformed by human activity display changes in biodiversity

at all structural levels of the biota organization. It proves to be true by complex research in territories changed as a result of human activity.

According to our work, amphibian species profoundly raise the objectivity of the data and enables us to find patterns of ecosystem transformation of anthropogenic changes of an equilibrium condition of the environment, including processes of an exchange of substance and energy, to develop the general conception of formation of structurally functional features of ecosystems in anthropogenic landscapes, reactions of the basic structural elements of a different hierarchical rank in biocenoses taking place under different anthropogenic pressure, to determine microevolutionary mechanisms of maintenance of homeostasis in populations and ecosystems in environmental conditions that are changed by anthropogenic influences. The new results allow an analyze of a spectrum of natural and anthropogenic variability to determine morphological specificity of populations from most transformed habitats, to make representations about tolerance of those or other populations of animals, and optimal structure, minimal number and sizes of habitats under the conditions changed by the man that can be useful at development of necessary and optimal protection strategy of vulnerable and endangered species and populations. All this enables us to reveal not only negative consequences of pollution but also to carry out more effectively the purposeful control of an ecological situation. This approach opens ways to understand mechanisms of ecosystem stability, to predict the direction of microevolutionary changes, and to allocate parameters reflecting presence of adaptive and microevolutionary changes in structure of communities.

1.0. AMPHIBIAN POPULATIONS IN URBAN ENVIRONMENTS

Studies of the literature existing on a case in point, and also the analysis of the original long-term data, allowed us to speak about the presence of a number of general patterns for different kinds of anthropogenic influences including transformations of amphibian species complex in conditions of industrial pollution in combination with progressing urbanization. Some of these patterns concern populational processes in different systematic groups (Glivitch, 1980) and likely concern others terrestrial vertebrates. The influences of man results in changes in biota that can occur indirectly through the changes of the physicogeographical environment and biocenosis (Danilov, 1973). Major factors dangerous for amphibians populations are habitats destruction, harvesting for commercial and other purposes, threat of replacement by introduced species, and recreational pressure (Mittermeier and Carr, 1994), and the first group of threats is the most serious.

Mass mortality of amphibians seldom occurs under the direct action of anthropogenic factors (Garanin, 1971). Nevertheless, in cases of separate populations and small groups, this factor can be very important. Burton (1976) listed consequences of amphibian capturing by children and schools, road mortality, and destruction and pollution of reproduction ponds. Among different variants of direct amphibian destruction, the road

mortality during migrations is an important factor. Mortality on the way to places of reproduction and hibernation in spring and autumn can be estimated in thousands animals per day (Van Gelder, 1973; Shitova, 1981; Kolodenko, 1981). Capture of many amphibians for scientific research also can cause a significant loss (Andrushko, 1973). Scientific collections, taxes in commercial objectives (Thatcher, 1992), amateur capturing, and the removal of many clutches by children have led to reductions of the numbers of *Rana temporaria* in suburbs of London (Beebee, 1973, 1979). Uncontrollable development of the private trade of animals in the former USSR makes illegal trade in amphibians more and more widespread (Kuzmin, 1994). The population size in *Rana ridibunda* in Krasnodar decreased mainly as a result of direct killing of animals by people (Zhukova, 1978). Medical, biological and educational institutions use at least a million specimens annually. The removal of such large number of mature animals that have rather slow rates of population recovery has resulted in sharp reduction in frogs number close to cities and then in the remote areas (Bannikov and Rustamov, 1974). The harvesting of amphibians is especially dangerous in the season of reproduction when animals concentrate in ponds (Honegger, 1978).

Introduction of animals from different systematic groups can represent a threat for native populations of amphibians (Moyle, 1973; Beebee, 1981; Banks and Laverick, 1986; Dolmen, 1987). Some exotic amphibians represent a danger to other species of aquatic organisms including other amphibians (Goin and Goin, 1962; Bury and Luckenbach, 1976). A consequence of introduction can be hybridization of geographically isolated forms and subspecies that leads to distortions of the natural genetics of the populations.

During their formation and growth, urban areas gradually incorporate neighboring natural suburban communities with all their animal populations. As a whole, species of an amphibian community in such a territory as a rule is various enough to maintain successful reproduction in most species (Larionov, 1976; Toporkova, 1977; Vershinin and Toporkova, 1981; Fedoseeva, 1987; Gureev et al., 1990). Quite often amphibians use artificial ponds for reproduction and as habitats (Larionov, 1923; Toporkova, 1977; Kuranova, 1980); in some cases human activity can promote increase of numbers of some amphibian species because of the creation of additional places for reproduction (Garanin and Ushakov, 1970; Ishchenko, 1978, 1989a). Many examples include artificial pond use by amphibians for reproduction and hibernation (e.g., Ruzskii, 1894; Sharleman, 1917; Larionov, 1923; Bogachev, 1938; Dubinin, 1954; Garanin, 1969, 1971; Ushakov and Garanin, 1973). However, the situation at which human activity renders positive influence is characteristic under condition of incidental influences or early stages of anthropogenic transformations of the environment (Bugs, 1984; Munkhbayar, 1987).

The first stages of transformation are characterized by general reductions of distribution ranges and numbers of amphibian species (Vershinin and Toporkova, 1981; Ilyashenko, 1984a) and changes in the species structure, ratio of dominant species (Bugs, 1989), population density (Vershinin and Krinitsyn, 1985), fecundity, growth of clutch asymmetry (Vershinin, 1990a), and accumulation of pollutants (Lyubashevskii et al., 1985).

Thus the proportion of ecologically plastic species most widespread in natural ecosystems (e.g., *Bufo viridis*, *Rana arvalis*, *R. amurensis*) is usually increased (Vershinin and Toporkova, 1981; Bugs, 1989). The main forms of economic activity of people at this stage are pesticide use in forests (Strelkov, 1964), ameliorative measures and ponds creation (Kuranova, 1984; Ilyashenko, 1984a), and formation of pastures and other agricultural sites (Kuranova, 1980; Kuranova and Grigoriev, 1980). The creation of large reservoirs can result in the decrease of moisture of the ground because of the increase in speed of winds that increase evaporation (Garanin and Ushakov, 1970).

At stronger levels of changes and longer influences of the anthropogenic factors, in connection with strengthening of pollution and radical changes in the vegetation components of communities, amphibian decline continues, especially in the typically forest species with narrow norms of reaction (e.g., *Salamandrella keyserlingii*, *Bufo bufo*, *Rana temporaria* and *R. amurensis*; Tagirova, 1978; Vershinin, 1980a; Zhukov, 1984; Ilyashenko, 1984a). Clear cutting and the reduction of habitat humidity caused by the destruction of a continuous cover of vegetation result in disappearance of aquatic amphibians (Garanin and Popov, 1958; Orser and Shure, 1972; Astradamov, 1973; Beshkov, 1978). The regulation of river drainages and routing rivers through pipes causes declines of amphibian (Beebe, 1973; Ilosvay, 1977; Sharygin and Ushakov, 1979). Amphibian mass proportional to total vertebrate biomass varies (Ravkin and Lukianova, 1976). Negative tendencies begin to dominate in populations of amphibians. Disturbances in demographic structure and sex ratio appear (Sinsch et al., 1980; Grefner, 1982; Cummins, 1989). Such levels of anthropogenic pressure is characterized by the increase of frequencies of all types of morphological anomalies (Vershinin, 1982, 1989; Mizgirev et al., 1984; Basarukin, 1985; Flax, 1986), increase the proportions of mutations (Vershinin, 1988) and of abnormal clutches (Vershinin, 1990b), destruction of eggs as a result of changes in environmental chemistry (Freda and Dunson, 1985; Pierce, 1985; Gunter and Plotner, 1986; Hazelwood, 1970), and occurrence of individual adaptations as a response to the action of new factors (Vershinin and Tereshin, 1991). The changes in landscapes connected with significant growth of cities have strong influences on number, species structure and amphibian distribution (Bannikov, 1955; Beskrovnyi and Burmenskaya, 1970; Beebe, 1973; Prest et al., 1974; Lebedinsky, 1981). The massive asphalt coverings is one of the most pernicious factors for amphibians in cities. In the central part of cities, ponds are regularly cleared, and the shore is covered with a granite or concrete (Bannikov and Isakov, 1967) that results in complete disappearance of amphibians. Recent data corresponds with the hypothesis that global reduction in amphibian numbers is appreciably connected with thinning of the ozone layer in the atmosphere and strengthening of the ultra-violet radiation which leads to the increasing mortality of eggs, especially in shadow-water species (Hileman, 1993; Blaustein, 1994; Kleiner, 1994; Blaustein and Wake, 1995; Scheller, 1995).

It seems impossible that only one factor determines amphibian disappearances. Rather, there is a complex of factors connected to habitat infringement (Halliday, 1993).

Species of amphibians living in conditions of considerably transformed environment are characterized by the occurrence of adaptive changes on populations level (Vershinin, 1990), a part of which is determined by the specificity of conditions of growth and development as well as population dynamics of larvae and juveniles (Vershinin, 1983a; Gatiyatullina, 1989; Kuranova, 1989; Vershinin and Trubetskaya, 1992; Gatiyatullina and Shchupak, 1992). The specificity of phenotypic and genetic structure of populations (Vershinin, 1987a, 1990c) is formed. In many regions, there are populations of introduced species, whose existence is possible only in an environment changed by man (Toporkova, 1978; Belimov and Sedalischev, 1980; Zhukov, 1989; Yakovlev, 1990). High local numbers of introduced species can represent a certain danger for a native batrachofauna (Vershinin, 1990a; Yakovlev, 1990). Near urban areas, besides the disappearance of one species and replacement of a part of species by others (with prevalence of one or few species), the spatial structure of populations varies; compact isolates with high local density are formed. Greater life duration (compared with small mammals), high skin permeability and peculiarities of development make amphibians very good bioconcentrators of pollutants (Byrne et al., 1975; Hall and Kolbe, 1980; Lubashevskii et al., 1985). This feature also causes change in metabolic processes in mature animals, decrease of fecundity, and breaking of the process of normal formation of sexual products and egg fertilization (Hazelwood, 1970; Misyura, 1985). Pollution, as a strong stressor factor, promotes a sharp increase in mutation frequency, deviations in development, abnormal regeneration, and neoplasia. Duration of embryonic development in urban populations is reduced because of thermal pollution of the environment, and the duration of larval development is stretched under the influence of changed environmental chemistry (Grefner and Slepyan, 1989; Kuranova, 1989). Rather high mortality at early stages of development results in formation of genetic specificity of new generations. In conditions of urban ponds, animals survive to larger sizes (with modified surface-volumetric ratios), and these individuals have a high level of exchange processes.

Behavioral and physiological specificity is formed in relation to the whole complex of conditions of a large industrial city. High values of the index of heart and greater relative mass of the liver are observed in froglets in populations in an urban area. The presence of adaptive changes in individuals leads to change in energy expenditure and, in turn, to the changes in growth (Tarasenko and Tarasenko, 1989; Vershinin and Tereshin, 1991; Vershinin, 1992). These changes are observed in trophic relationships of *R. arvalis* froglets; the proportion of phytophages in a food spectrum increases from stages 53-54 (stages of Dabagyan and Sleptsova, 1975), and this change may indicate the shortening of trophic chains and the increase of rate of exchange of substance and energy in urban ecosystems (Vershinin, 1991). High levels of metabolic processes, higher survival of larger individuals, and high levels of pollution promote occurrence of different size and age structure in urban populations of *R. temporaria* (Vershinin and Volegova, 1993). Sexual maturity is attained at years 2-3 (vs. 3-4 in natural populations), and the general life duration does not exceed 4 years (vs. 6-7 years). Specific features of cytological,

physiological and phenotypic levels occur. They include both adaptive and negative components that are present at all stages of life cycle and lead to the potential opportunity of increased reproduction and tolerance of populations. On the other hand, the modified system has the special configuration of flows of substance and energy determined by complex interrelations, dynamics of population number, and level of metabolic processes.

The study of the basic regularities of population dynamics in amphibians in anthropogenic landscapes also has practical importance because it allows us to conduct the search for convenient test objects and parameters. We can carry out an estimation of quality of environment and reveal the latent negative tendencies in externally safe ecosystems and populations (Vershinin, 1982a, 1990e; Pyastolova and Trubetskaya, 1988, 1989). These data display the existence in anthropogenic ecosystems of a complex of features promoting maintenance of a variety at different structural levels of organization and consequently ecosystem stability. The evolution of a biosphere in conditions of anthropogenic influence results in the occurrence new ecosystems with high stability that influence the biosphere as a whole.

2.0. LANDSCAPE TYPIFICATION AND MATERIALS AND METHODS

The present work is based on materials collected in the course of the study of natural amphibian populations in urban areas. A few words are needed about the reasons of a choice of the objects of this research. The amphibians are first terrestrial vertebrates, dependent on water and having features transient to higher vertebrates. In connection with an amphibious life, this group of animals links trophic chains of freshwater and terrestrial ecosystems by being in different phases of life cycle consumers of the 1st, 2nd and sometimes 3rd levels (Garanin, 1977, 1981).

Frogs have been considered especially convenient object of study (e.g., Shvarts, 1974a). Amphibian populations are the most simply organized of terrestrial vertebrates. Their numbers are significant enough in different habitats that one can get necessary numbers. During the whole life, amphibians remain in rather small areas compared with, for example, birds. The long duration of amphibian life, in comparison with small mammals, allows us to observe result of longer influences of the various factors on these organisms. Because of these biological features, as well as their role in their ecosystems, they are the most convenient objects among terrestrial vertebrates for the estimation of anthropogenic changes of the environment. High tolerance gives them an opportunity to exist in areas where others vertebrates are absent. Thus, among vertebrates they seem to have the highest sensitivity to pollution because all stages of development live in the same environment. Investigations on urbanized and technogenically transformed territories and the experimental research showed that embryonic and larval stages of amphibians can be used for indication of the condition of natural environment (Vershinin, 1982; Bugaeva, 1983).

Their high sensitivity to changes of microelement content in water (Shvarts, 1954), as well as development, mortality, cytological parameters, metabolism, morphology of animals, and accumulation of these substances, are well-known (Cooke, 1973; Hemmer and Kadel, 1980; Misyura, 1981; Tarasenko, 1981). This enables us to determine a level of pollution in different areas. The bioconcentration of pollutants by amphibians allows us to detect pollution before it becomes significant. It is known that tadpoles of anuran amphibians can accumulate pesticides in concentration 60 times exceeding their contents in the water (Hall and Kolbe, 1980). Tissues and bodies of adult animals selectively concentrate various chemical elements (Sharygin, 1980a) and substances (Zhukova and Kubantsev, 1980). Another important factor is that this group can be used successfully not only in the field of scientific researches but in laboratory experimentation (Bannikov and Rustamov, 1974; Garanin, 1975). On the basis of research of experimental larval "populations" of amphibians, general conclusions about mechanisms of population regulation mechanisms of growth and development can be made (Shvarts, 1974a).

This work was conducted in several cities of the Urals. The main part of the materials were collected from the area near Ekaterinburg City and its suburbs from 1977-1995; in 1980-1981 samples were taken from the urban areas of Chelyabinsk and Serov cities. Based on published data (Milkov, 1973, 1978; Gninenko, 1975) and our own materials, I developed a typification scheme of urban landscapes. Depending on the level of anthropogenic influence, four zones were delimited, and amphibian habitats were ranked by these zones. These zones differ in the degree of construction (e.g., height, density and other features of houses, and the presence of household and industrial pollution). The zone belonging to a particular habitat was determined, mainly, not by its topographical situation, but the degree of total anthropogenic transformation of the given part of territory.

Zone I: areas of a city (mainly central) with multistory buildings, massive asphalt coverings, reservoirs with strong industrial pollution, and small rivers and streams drained via pipes.

Zone II: areas of multistory buildings with mastered territories, waste grounds, sites with open soils, and small ponds with high levels of pollution.

Zone III: areas of low buildings, mainly areas engaged in houses of individual sector with gardens and kitchen-gardens, waste grounds, and parks; quite often habitats of this zone adjoin forest parks.

Zone IV: Forest parks are mainly under the influence of recreational pressure. Control sites with natural amphibian populations (*S. keyserlingii*, *Triturus vulgaris*, *B. bufo* and *R. arvalis*) were located 23 km from Ekaterinburg City. The acceptability of the present typification for such studies was confirmed by the data of the hydrochemical analyses of the main ponds from these habitats.

The species inhabiting the area near Ekaterinburg were as follows: Caudata: Hynobiidae: Siberian Newt (*Salamandrella keyserlingii*), Salamandridae: Smooth Newt (*Triturus vulgaris*); Anura: Ranidae: Marsh Frog (*Rana ridibunda*), and two Brown

Frogs, *Rana arvalis* and *Rana temporaria*. The allocation of amphibian habitats in the urban area allowed us to conduct a detailed study of the batrachofauna on a regular basis. The sizes of studied sites were determined so that whole populations occupying a given habitat would be covered. In a habitat we understand the spatially limited site populated with a group of amphibians of one or several species that is separated from other similar groupings by areas lacking amphibians.

During the breeding period, the number of clutches in each research pond was visually counted, and the fecundity of *S. keyserlingii*, *R. arvalis* and *R. temporaria* was estimated. The number of eggs in one egg sac of *S. keyserlingii* was determined by direct count, and in brown frogs the eggs number in clutch was counted by the sparing technique (Cooke, 1975a). Volume of clutches was determined with a measuring glass and then the volume of 100 eggs was determined, and on the basis of these figures the eggs numbers in clutches of brown frogs *R. arvalis* and *R. temporaria* was calculated.

I found abnormal clutches of *S. keyserlingii*, *R. arvalis* and *R. temporaria* near urban areas from 1978-1996. Among clutches of urban amphibians, there are the following types of anomalies: 1 and 2 (eggs or clutches without embryos) = the entire or part of the clutch does not contain embryos, there is only internal membrane; 3 (joined clutches) = eggs in a clutch are located like strings and have no individual jelly envelope; the eggs are very close to each other, sometimes adjoin, the development does not occur; 4 (twin eggs) = 2-5 embryos in one egg; 5 (reduced eggs) = eggs shrunken, abnormally small and do not develop; and 6 (coagulated clutches) = clutches do not swell in water and do not develop, eggs pale colored. Abnormal clutches were not founded during 1977-1996 in natural populations outside the city. In total, 6676 egg sacs of *S. keyserlingii*, 11,200 clutches of *R. temporaria*, and 12,978 clutches of *R. arvalis* were examined.

The duration of the breeding period was determined by the occurrences of the first and last clutches, termination of embryonic development by the appearance of first larvae, and termination of larval development by the appearance of the first metamorphs. The developmental stages of anuran larvae were determined by Dabagyan and Sleptsova (1975, in Detlaf and Vasetskii, 1991) and for *T. vulgaris* by Liosner (1975, in Detlaf and Vasetskii, 1991). Larval populations densities were stated as the number of individuals per liter of water.

Data on survival rate in larvae and froglets of brown frogs, obtained in experimental conditions as well as the results of only field researches on influence of a level of anthropogenic influence on number dynamics of larvae and froglets, do not provide a total picture of the process. In this connection, I used both field and experimental methods of mortality estimation during the ontogeny of brown frogs from populations with different levels of anthropogenic pressure. The dynamics of larval and froglet numbers of brown frogs in populations from the urban area of Ekaterinburg was studied from 1980-1990. The numbers of froglets were censused at stages 53-54 in all years, and censuses of the number of larvae was done at stages 41 and 49 in 1980-1981 and 1984 and at stage 49 in

1986. For estimation of larval population numbers, the tadpoles of *R. arvalis* and *R. temporaria* were stained with Neutral Red (see Cooke, 1978; Severtsov and Surova, 1979). The concentration of the stain was 100 mg/ liter prepared in the field. The number was determined by the Petersen-Lincoln index (Petersen, 1986). The total number of eggs deposited in a pond was determined using the estimation of mean number of eggs per clutch and total number of clutches (Vershinin, 1983b). Standard measurements (Terentjev and Chernov, 1949; Terentjev, 1950; Bannikov et al., 1977) were made with vernier calipers (0.1 mm), and I also noted sex, presence of morphological anomalies, and diseases. In July-August 1984 near Ekaterinburg and its suburbs, and also near Talitsa Town (Sverdlovskaya Province, Trans-Urals), I carried out censuses of amphibian numbers in 10 x 10-m plots. The vegetation was cut off and manual searches for amphibians were made. The censuses of the numbers of adults and young-of-the-year were done by individually marking by toe-clipping (Martof, 1953) and with a cohort mark. In newts, this mark was clearly visible for 2-3 months (regeneration after marking lasts more than 6 months; Griffiths, 1984) and in anurans it lasted for their whole life. After marking, animals were released in the same place from where they were caught. Recapture of marked animals allowed me to determine population size. The number was determined under the same formula as for tadpoles.

For calculation of indices of liver and heart in young-of-the-year *S. keyserlingii*, *R. ridibunda*, *R. arvalis* and *R. temporaria*, I determined the masses of the body, liver and heart by the method of morphophysiological indicators (Shvarts et al., 1968). In 1977, I determined morphophysiological parameters of adult animals (*R. arvalis* and *S. keyserlingii*). In other years I studied only morphophysiological parameters in the young-of-the-year. Body and liver mass was weighed with a torsion balances (0.2 mg). The definition of relative mass of liver and heart was done for estimation of morphophysiological specificity of separate groups of animals. Sample size was 15-20 specimens. After dissection, the animals were fixed in 70% ethanol. The comparison on indices of liver was conducted on years between young-of-the-year from different populations and between early and late metamorphosed animals from one population. Data on frequencies of morphological abnormalities allow us to understand conventionality of a border between norm and pathology (Tyler, 1989) and to know about the natural spectrum of modifications and their frequencies. The data given below represent the result of generalization of long-term studies on the territory of urban areas (Ekaterinburg) from 1977-1993 on all amphibian species living there. I used the classification types of anomalies by Dubois (1979) and Tyler (1989) as the basis.

1. **Limb anomalies:** polydactyly (extra fingers), ectrodactyly/oligodactyly (short or lack of fingers), syndactyly (joined fingers), clinodactyly (branched finger), non-flexible limbs, hemimely (lack of distant limb part), brachymely (shortened leg), taumely (strong changes in limb plan), polymely (extra leg), and ectromely (lack of some leg's parts).

2. **Eye anomalies:** anophthalmy (lack of eye), reduction of some eye components and/or eyelids, and depigmentation of the iris.

3. **Axial skeleton deformities:** skull deformations, mandibular hypoplasia, and vertebral column deformations.

4. **Skin anomalies:** pointed back pattern (fragmentation of pigmentation), albinism, pigment spots, and skin neoplasia.

5. **Edema:** edema of the bottom of the mouth cavity, and edema of the abdominal cavity.

6. **Internal anatomy anomalies.**

The study of features of growth and development of amphibians in conditions of variable environmental hydrochemistry in 1980 and 1981 was done with water from the main reproduction ponds. The analysis was carried out after the end of metamorphosis (end of July-August). I determined general contents of Cl^- , SO_4^{2-} , CO_3^{2-} , NO_2^- , NO_3^- , NH_4^+ , K^+ , Na^+ , Mg^{2+} , and Ca^{2+} . In 1981, at the moment of larvae output from eggs and in the premetamorphic period, I determined the biological consumption of oxygen (BCO_2), permanganate oxygenation, contents of petroleum, and extractive substances in the majority of the ponds. In 1987-1989, I determined the concentrations of lead, iron, and detergents. Water temperature was measured at every visit (thermometer, 0.5°C).

The material for measurements of egg diameter of *R. arvalis* was collected from near Ekaterinburg and its suburbs in 1990-1995. I separated 20 eggs from fresh clutches and fixed them in 10% formalin. Egg diameter was measured with an ocular micrometer (0.1 mm). Stages of development were determined by Dabagyan and Sleptsova (1975 in Detlaf and Vasetskii, 1991). We believe that the diameter of egg adequately reflects its size because there is a positive correlation between mean diameter of egg and mean dry mass of the egg (Crump and Kaplan, 1979). In 1990 the egg sizes were determined at the beginning of egg division to late blastula from samples from 294 clutches. In 1991, the comparison of the egg sizes was carried out on 10-18 stages of development on samples from 240 clutches.

The material for cytological studies was collected within the city limits from 1995-1997. In 1997, we also estimated mitotic activity in postmetamorphic frogs grown in the laboratory from eggs collected from the same populations. The eye cornea was used for cytogenetic analysis (Vershinin and Kamkina, 2001). The corneal epithelium is convenient because it contains no blood vessels, and metabolites are distributed over the cells uniformly via the basement membrane. This tissue fulfills a protective function, and it is in direct contact with environmental pollutants. The protoplasmic growth in such tissues may be measured by counting dividing cells per unit of area in a population or a sample of animals (Ebert, 1968). Carnoy's liquid was the fixation (Kalyuste, 1968; Lillie, 1969). Total preparations were made by methods of Epifanova (1965) and stained with hemotoxylin (Roskin and Levinson, 1957). To estimate the cell density, we counted cells within a microscopic field delimited by a rectangular diaphragm ($3025 \mu\text{m}^2$) and calculated the mean size of an epithelial cell (in μm). The mitotic activity was determined in the same preparations. The number of mitoses was counted in 50 microscopic fields ($3025 \mu\text{m}^2$ each) at a magnification of 1350x. The preparations were examined with a

Biolam D.13 microscope with a 90x immersion objective and a 10x ocular along two perpendicular diameters. The mitotic index (MI) was expressed as the number of mitoses per thousand cells.

The collection of the samples of *R. arvalis* and *R. temporaria* in 1977-1994 were analyzed by skeletochronology (Kleinenberg and Smirina, 1969; Castanet, 1975). For this purpose, I cut a toe from the right hind limb in every animal under study. The sample size analyzed by the skeletochronology was 127 adult *R. arvalis* and 96 *R. temporaria*.

In 1984-1988 in Ekaterinburg and its suburbs, in parallel with the number dynamics of brown frogs (*R. arvalis* and *R. temporaria*) young-of-the-year, I analyzed the contents of the gastrointestinal tract in stages 53-54 of Dabagyan and Sleptsova (1975). Censuses of soil invertebrates were done simultaneously. I took 6 soil samples with an area 0.045 m² and a depth of 0.05 m. The soil was placed in glass funnels under electrical lamps, and invertebrates fell into glasses with 70% ethanol because of the thermal and light gradient. A total of 89 tests, or 534 samples were extracted. Overlap of the food spectrum was determined by the modified Morisita index (Hurlbert, 1978). A total of 1267 froglet stomachs of *R. arvalis* and 471 of *R. temporaria* were analyzed.

For the most objective estimation of the biocenotic role of amphibians and its features in the urban ecosystems, I conducted an experimental study of the speed food passed through the gastrointestinal tract of *R. arvalis* froglets in 1985-1986. In August 1985, preliminary experiments were carried out with improvement of the technique with usage of specially made color plastic markers (0.3 x 0.3 mm). All experiments were carried out at 21°C in terraria. Experiment 1 included the introduction of markers each hour for 12 h in constant presence of live invertebrates collected from nature. After 12 h, the finishing mark was added, and 5 animals were fixed in ethanol every hour in the next 12 h. The duration of intervals in experiment 2 was reduced to 4 intervals for 6 h and the last experiment it was reduced to 2 for 3 h. In 1986, all intervals in experiment 3 were equal to 3 h, and some of the froglets was fixed once in the 3-h period. In experiment 4, with an interval of 3 h the marks of 5 different colors were used, and after 12 h from the beginning of the experiment the froglets were fixed every 3 h for 12 h. The intestine was measured, and the length of stomach and the distance passed by each mark were recorded. Froglets that did not eat during the experiment were excluded from analyses because in an empty gastrointestinal tract the markers either moved quickly or remained for a long time in the stomach. The results of experiments 1 and 2 and 2 and 3 were combined. Whenever possible, the sparing method of research were used so that damage to urban amphibian populations was minimized (Vershinin, 1983b, 1985a; Cecil and Just, 1979).

I made joint physiological investigations with the persons at the Ekaterinburg Medical Scientific Center. To determine the functional condition of the nervous and muscle frog tissue, we destroyed the central nervous system, made preparations of the both hind legs and maintained them for 30 min in Ringer's solution of the following composition (mm/liter): Na 113.4; K 3.25; Ca 2.70; Cl 119.7; HCO₃ 2.38; glucose 5.5; pH 7.4. After

that we determined the rheobase of the excitative thresholds of a nerve and muscle at various gradients of a single stimulus, taking into account the effects of reduction of the muscle. The functional state of the neuromuscular system was determined with an ESL-2 electronic stimulator, an accommodometer, and silver chloride electrodes with a screened chamber. Oxygen consumption was determined with an AKTs-2 digital oxygen analyzer. The modified circuit of the accommodometer allowed us to adjust the gradient of irritating stimulus by consecutive introduction of condensers of 0.001, 0.002, 0.003, 0.004, 0.01, 0.02, 0.03, and 0.05 microfarads. A constant of time of the growth of the current force, $T \cdot (m \cdot sec)$, was determined by the formula $T = R \cdot C$ where C is the capacitance of the condenser in farads and R is the resistance of the accommodometer in ohms. For nervous and muscular tissues, we applied a resistance of 500 ohms. A constant of tissue accommodation, λ (m/sec) was calculated by the formula $\lambda \cdot V_{gr} / V - V_0$ where V_0 is the threshold of the tissue for an instantly increasing current and V is the threshold of the tissue for a current increasing with the speed T .

We also studied sodium permeability of skin. For determination of the passage speed for Na ions through the skin of *R. arvalis* captured from urban and suburban areas with a different level of pollution, we destroyed the central nervous system under anesthesia and allocated removed the belly skin. The skin was placed in a glass tube and immersed from both sides with Ringer's solution for measurement of the difference of potentials (DP) of submission of the current. We used two pairs of silver chloride electrodes with an agar electrolytic bridge. The current was issued for 10-15 sec every 5 min. To exclude the skin swelling in conditions of short circuit, the experiments were carried out at 24-25°C with constant aeration of the Ringer's solution. The measurements of the current of short circuit (CSC) and DP began 20 min after the assembly of installation. For 10 min, we registered reference values of the parameters that were taken as 100%. Usually DP of a skin changed within the limits of 30-40 mV, and CSC changed within the limits of 20-30 mA/sm².

In 1988-1990, I measured oxygen consumption of mature male *R. arvalis* from zones with different levels of anthropogenic influence. Frogs were collected during spring and summer after the end of reproduction. Immediately after animals were captured, oxygen consumption was determined with an AKTs-2 digital oxygen analyzer. I measured the difference in the contents of the oxygen before and after the addition of a frog for a total of 60 min while accounting for the frog's body mass, temperature of the environment, and the pressure. I calculated absorption of the oxygen in mg/ min/g body mass.

For two years I studied the physiological status of isolated myocardium of *R. arvalis* and *R. temporaria* by biophysical methods (Shklyar et al., 1999; Shklyar and Vershinin, 2000). Myocardial preparations from frogs from two areas distinguished by the degree of anthropogenic influence and pollution there were used. Contractal ability of the myocardium, the ability to develop pressure by contraction, was measured by a number of standard parameters (Isakov, 1981): isometrics of pressure (P_{max}), ratio "length-force"

(Frank-Starling rule), maximum speed of development (dP/dT_{max}), ratio "length-pressure of rest," and useful work (A). For this purpose we used a unique complex "Myoton" which allowed us to record and analyze the basic characteristics of contractility of isolated myocardium (Blyachkman et al., 1989). The comparative analysis of the basic characteristics of myocardium contractibility was carried out at different calcium loads (1-5 mM Ca^{++}). For estimation of the myocardium contractibility in strictly controllable conditions, we recorded the basic parameters of mechanical activity in the myocardium preparations in isometric and physiological modes (Schklyar and Vershinin, in press). Results were analyzed with regression analysis and ANOVA with Statgraf and Systat.

3.0. HYDROCHEMICAL FEATURES OF SPAWNING PONDS

Small ponds of urban territories where amphibian reproduce usually represent closed water bodies. They contain a lot of different pollutants which are washed in from soil and roads, fall from the atmosphere with rain and snow, and quite arrive with industrial and household wastes concentrates. The hydrochemical analyses of breeding ponds were carried out in 1980-1981 and 1987-1989. The tests were done in the spring after the end of spawning and in summer at the time of metamorphosis.

Investigations of the condition of water environment in urban ponds done in 1980-1981 showed that ponds in zones of multistory and low building zones represent the main area of anthropogenic influence. They differ significantly in general mineralization and high contents of sulfates and petrol compared with forest parks and forest (Vershinin, 1985a). The level of pollution in the urban and suburban areas has not changed significantly during the last decades (Table 1). The concentration of petrol in ponds has remained the same as before. It is higher than in forest ponds. In habitats of a zone of multistory buildings the level of detergents is significant, and the lead concentration in most cases exceeds the admissible extremes. The biological consumption of oxygen (BCO_5) in the ponds of all zones of city has increased. The range of variation of concentrations of pollutants varies significantly in the urban area which follows logically from features of the urban landscape and high heterogeneity of particular habitats in the composition of the pollutants (Table 2). Statistical processing of all available data on pollution of water environment revealed sig-

Table 1. Hydrochemical parameters of the ponds (mg/liter) in 1981 and 1989. Notations: II - multistory buildings, III - low buildings, IV - forest park, and C - forest.

1981				1989		
Zones	Sulfates	Petrol	BCO_5	Sulfates	Petrol	BCO_5
II	94	3.3	6	8.76	1.5	8.98
III	6	1.7	4	25	0.75	7.68
IV	36	0.98	4	20	0.41	4.51
C	6.4	0.88	5	9.6	0.59	3.94

Table 2. Ranges of average hydrochemical parameters of ponds (1980-1989).

Zones	Sulfates, mg/l	Petrol, mg/l	BCO ₅ , mg O ₂ /l	pH	Detergents, mg/l	Pb, mg/l	General mineralization, g/l
II	8.76-95	0.45-3.3	3.64-9.25	6.0-8.4	0.18-4.20	0.03-0.19	0.4198-0.8157
III	6.2-30.9	0.5-1.85	3.02-9.9	6.0-8.3	0.12-0.62	0.02-0.08	0.3174-0.5668
IV	2.1-99	0.41-2.7	1.79-7.23	5.2-8.2	0.18-0.64	0.03-0.37	0.0714-0.4867
C	1.7-21.1	0.1-1.5	2.24-5.46	5.8-8.2	0.08-0.4	0.03-0.06	0.1236-0.1584

nificant differences in pH ($F = 2.663$; $p = 0.05$). The value in the urban area is close to 7 and 6.5 beyond the city. General mineralization is significantly ($F = 9.836$; $p = 0.0008$) higher in urban areas; also there are significantly higher concentrations of detergents ($F = 3.672$; $p = 0.018$) and the BCO₅ ($F = 2.99$; $p = 0.036$). This evidences for the increased eutrophication of urban ponds threatens the growth and development of amphibian larvae and presents dangers for adults that hibernate in water.

Presence of rather high concentration of various pollutants in the environment of breeding ponds in the zones of multistory and low buildings promotes the increase of mortality of embryos, larvae, and froglets, and results in the formation of physiological, phenotypic and genetic (through not-selective elimination) specificity of urban populations of amphibians at all phases of their life cycle. It is necessary to remember the synergistic action of pollutants, for example, the joint action of pH and aluminum (Bradford et al., 1991; Jung and Zafoe, 1994). The realization of amphibian reproductive function and ontogeny in ponds with complex pollution, combined with the action of other anthropogenic factors, lead to significant changes in morphogenesis and variability, to the occurrence of various adaptations and, finally, determines population specificity in urban communities in many cases.

4.0. HABITAT SPECIFICITY OF AMPHIBIANS IN URBAN AREAS

Concentration of populations in cities, and also significant growth of industry, results in the appearance of special conditions where the populations and species differ significantly from those in natural areas. The occurrence and genesis of urban ecosystems is connected with the development of modern cities which include various groups of organisms occupying microhabitats in urban areas. Species composition and structure of populations and communities, as a rule, are not random and are reflect objective processes in specific conditions of urbanized areas. Quite often the urbanization process is combined with the growth of industry, and consequently also serious changes in the environmental chemistry that also immediately results in the appropriate reaction of the biota.

The history of industrial development in the Urals covers more than 270 years. The majority of large Uralian cities were established as factories, therefore the problem of

industrial pollution here has arisen simultaneously with settlements. During this time, in parallel with modernization and integration of the industrial enterprises, there was a growth of cities. The significant complex pollution of the water, soil and atmosphere has existed for a long time and over extensive areas (Meleshina, 1975; Menshikov, 1975; Shamanaev and Brayalovskii, 1975). As a result, the Urals contains a unique complex of urban areas with a high concentration of large industrial enterprises that for a long time have produced significant influence on the environment, whose changes, in turn, could result in appearance of new species and populations. Ekaterinburg is an old industrial center in the Urals with a population of more than 1.5 million, with plenty of industrial enterprises of mechanical engineering, power, metallurgy, chemistry and petrochemistry, and a building and food-processing industry which has polluted the urban environment. Total emissions of harmful substances from the industrial enterprises making 175,000 tons/year, the proportion of carbon oxide is 63%, carbohydrates 14%, solid substances and oxides of nitrogen 10%, sulfur dioxide less than 2%, and other specific substances in the tenths of a percent. The emissions of automobiles make about 66% of the total anthropogenic emissions; an average/year of the concentration of nitrogen dioxide and formaldehyde exceeds allowable norms by 1.5-2 times. The pollution of air by several kilograms per year of the toxic benz(a)pyren is especially great. In winter, the average benz(a)pyren contents for one month exceeds the norm by 20-25 times (Bezuglaya et al., 1991). With southwest winds, additional air pollution is created by emissions from the towns of Revda and Polevskoi. Air in the central and western parts of the city is the most polluted. The presence of ponds, parks, and neighborhoods along the Iset River and its tributaries reduces a little the effects of pollution in the summer time. This large area with significant concentration of human population and intensive and various commonwealth activity maintains a high heterogeneity of the urban environment.

Studies of amphibian species complexes and soil invertebrate microfauna revealed a general decrease of animals number in all investigated species with growth of pollution and anthropogenic influences (Bolshakov et al., 2001). Some species not characteristic of natural ecosystems of a given geographical zone, appear there, and the continuous areas split into a mosaic with local increases of density and heterogeneity. Habitat fragmentation can influence all complexes of processes in ecosystems, from individual behavior to population dynamics and ecosystem replacement. There is a strong effect of dependence of habitat fragmentation on the density of population and probability of meeting at small mammals (Robinson et al., 1992).

Distribution of amphibians in the urban territory of Ekaterinburg is a mosaic and non-uniform (Fig. 1a). Small ponds which serve as places of reproduction and habitats usually have a technogenic origin and were colonized by amphibians from natural sources that have since disappeared. The species abundance varies by year, but to 1984-1985 the species in Ekaterinburg (in decreasing order) were *R. arvalis*, *R. temporaria*, *T. vulgaris*, *S. keyserlingii*, and *R. ridibunda*. By 1990, this sequence changed to *R. arvalis*, *R. temporaria*, *R. ridibunda*, *T. vulgaris*, and *S. keyserlingii* (because of degradation of

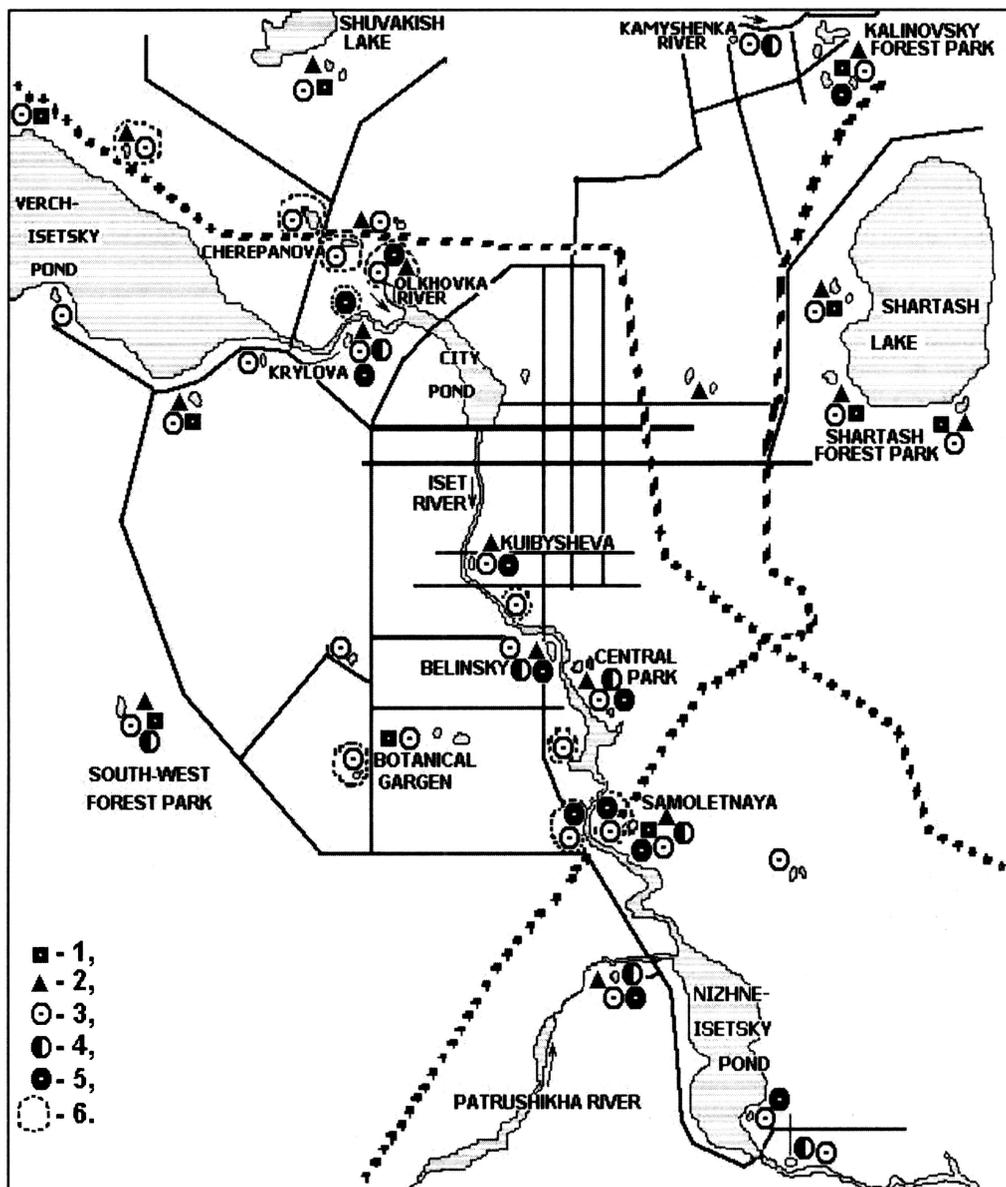


Fig. 1a. Distribution of amphibians in Ekaterinburg City.

1 - *Salamandrella keyserlingii*, 2 - *Triturus vulgaris*, 3 - *Rana arvalis*, 4 - *Rana temporaria*, 5 - *Rana ridibunda*. 6 - extinct populations.

habitats in *T. vulgaris* and the introduction of *R. ridibunda*). *Bufo bufo* is infrequent in the city and seems to be the most vulnerable in urban and suburban areas (Toporkova, 1981; Kneitz, 1995). Among 27 habitats of amphibians in urban and suburbs that existed at

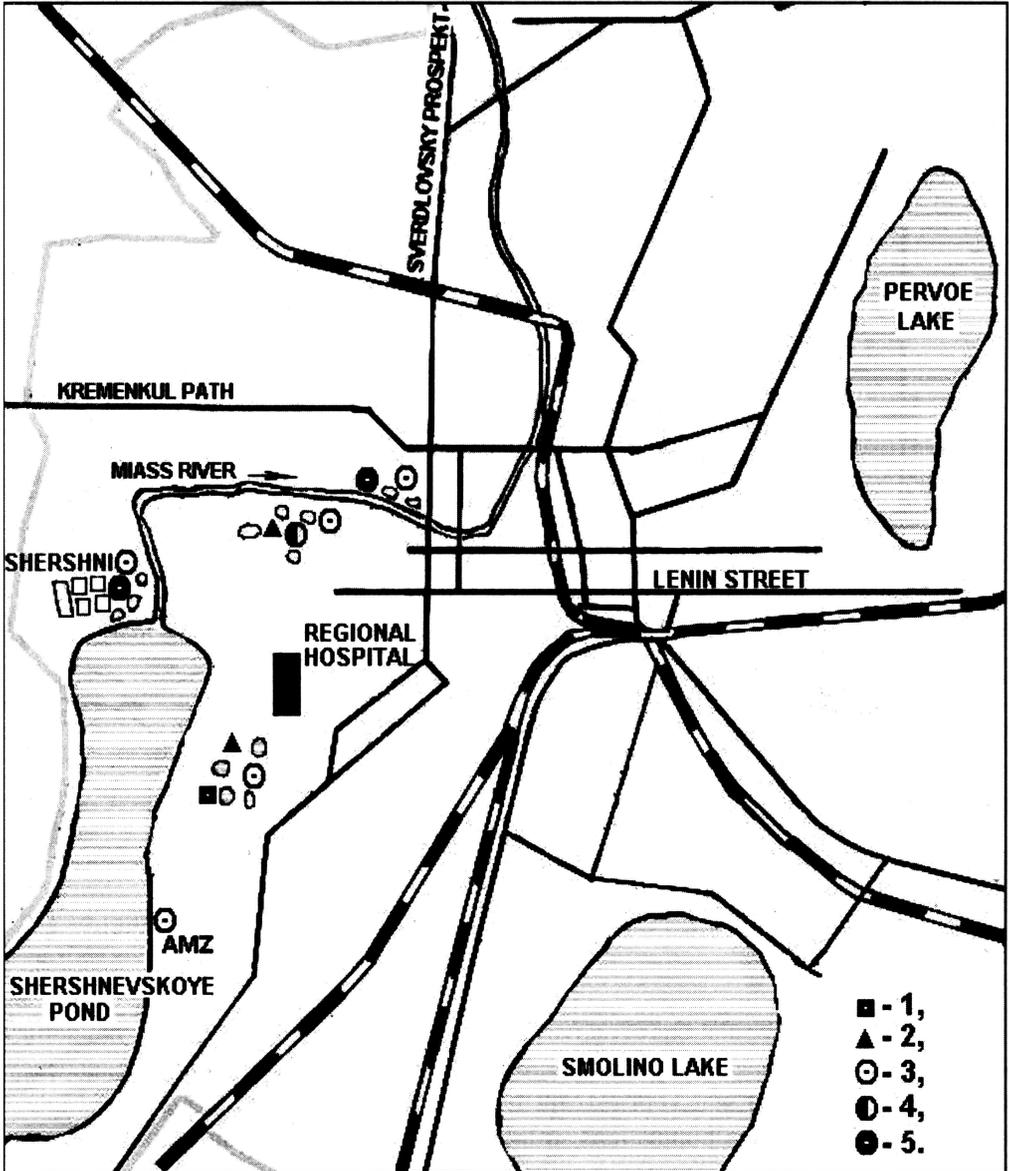


Fig. 1b. Distribution of amphibians in Chelyabinsk City.

1 - *Salamandrella keyserlingii*, 2 - *Triturus vulgaris*, 3 - *Rana arvalis*, 4 - *Rana temporaria*, 5 - *Rana ridibunda*.

the beginning of our research, 11 have been destroyed by human activity (only 4 in 1990), and in two, amphibians have disappeared. This is because construction is still going on without concern for animal population on the areas or any ecological examination.

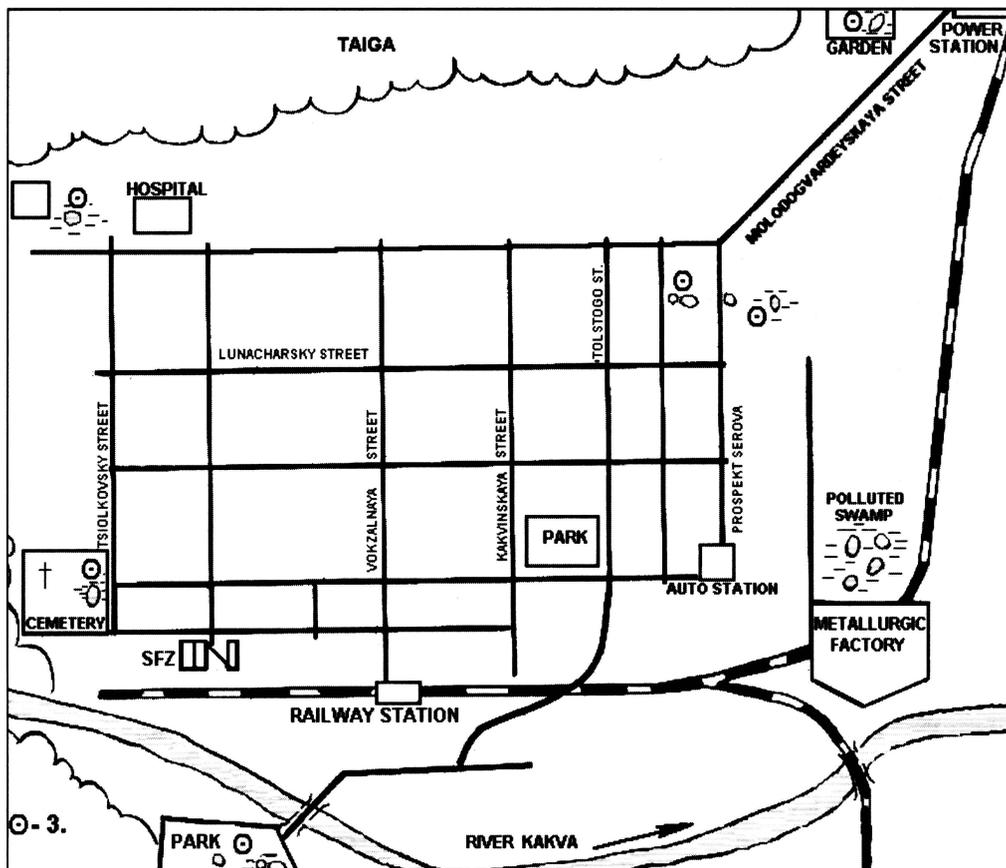


Fig. 1c. Distribution of amphibians in Serov City.
3 - *Rana arvalis*.

The number of populations of native species occupying zones of multistory buildings was reduced for 10 years everywhere (Table 3). In areas of low buildings, the tendency to decrease in number was kept (except for one population *R. temporaria* and introduced *R. ridibunda*). In populations in the forest park zone, changes are not so unequivocal. The number of species, mainly *R. arvalis*, has increased but remained low in Shartash Forest Park in comparison with numbers found in 1977 (250 individuals). *Triturus vulgaris* and *S. keyserlingii* became rarer in degraded and most polluted Shartash Forest Park, whereas in Kalinovskii Forest Park the number of *S. keyserlingii* has increased. In forest populations the essential changes were noted only in the population of *R. arvalis* (numbers have increased more than 4.5 times). Number and ratio of amphibian species depend on the ability of populations to reproduce in a changed environment. *Salamandrella keyserlingii* is able to reproduce successfully only in the forest park

zone because tolerate the microclimatic changes that have developed. *S. keyserlingii* has a huge geographical distribution that extends from Nizhegorodskaya Province to Sakhalin. In natural conditions it is typical of forest habitats and shaded, cold and clear ponds. Determinants for the life of this species are light, temperature and humidity. It prefers shady places (Ishchenko, 1961); after the period in on the sun, it becomes languid, rejects food and soon dies, and at temperature about 27°C it dies even if in the shade (Bannikov et al., 1977). It cannot resist habitat transformation under the pressure of anthropogenic factors. Its distribution is usually limited to forest parks of cities (Vershinin, 1980a) where the number can be rather high (Toporkova, 1977). In a rather small ponds (~60 m²) there sometimes are up to 319 egg sacs (Vershinin and Toporkova, 1981).

The number of egg sacs of *S. keyserlingii* and their density reach the maximum in the forest park zone (Fig. 2). For the last 5 years the maximal density of egg sacs in the forest park was 3.6, and beyond the city there were 1.3/m² of water surface. It is possible to explain high clutch density in forest park ponds by a decrease in suitable places for reproduction. In 3 of 4 ponds the number of egg sacs fluctuated near a certain mean characteristic for each. In the population of *S. keyserlingii* from Shartash Forest Park, since 1978 I observed a natural decrease of clutch number and the numbers of breeding animals; in 1977, 875 sacs were counted, and the minimum for all years of investigation fixed in 1986: 61, or 6.9 % of the number in 1977.

According to data from Ischchenko (1968), in the 1960s the numbers of *S. keyserlingii* population in Shartash Forest Park on an area of about 0.3 km² was 2-2.5 thousand specimens with a maximal density up to 10 animals/1 m². The level of change which have occurred is incommensurable with normal long-term populations fluctuations. During the last 10 years, the forest park area did not change essentially, but consid-

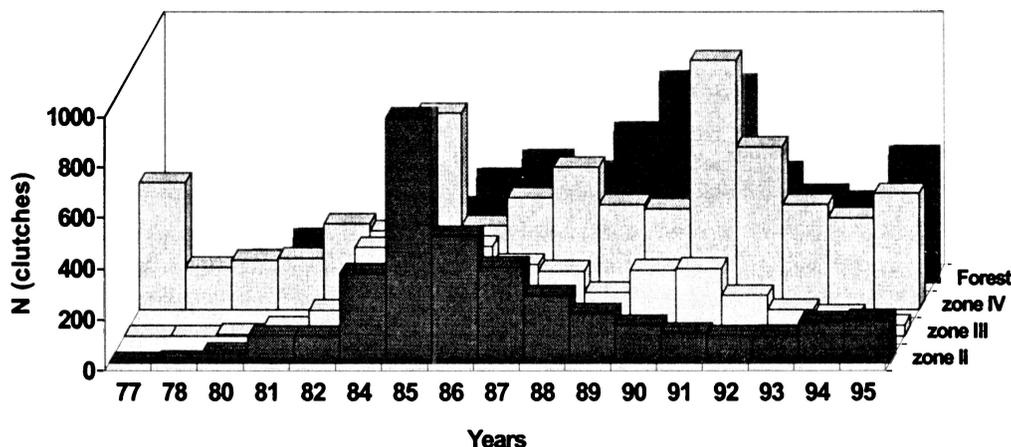


Fig. 2. Dynamics of *Rana arvalis* clutch number.

erable recreation pressure has increased in connection with intensive building in the immediate neighborhood. Pollution level of ponds is highest for a long time compared with other forest parks and forest area (Tables 1 and 2); that proves to be true by the absence of basic distinctions in pollution by oils and petroleum in 1981 (Vershinin, 1985a) and 1987. The soil litter density or its disappearance under intensive recreation in the forest park zone has negative effects. The newts live in the litter during the terrestrial phase of its life, and because it is widespread in forest ecosystems of suburbs, it is highly sensitive to the first stages of environmental transformation.

Triturus vulgaris is less sensitive to the structure of vegetative communities. The distributions of *T. vulgaris* and some other Caudata species depend on the presence of soil litter (Van Gelder et al., 1992) and low vegetation (Orser and Shure, 1972; Frazer, 1978; Beebee, 1979) which creates favorable microclimatic conditions. Not just the species composition of vegetation communities but only height and density of the vegetation cover are important (Garanin and Popov, 1958). The abundance of *T. vulgaris* depends also on pond acidity. This species inhabits ponds with pH from 6.0-9.0 (Beebee, 1981) but generally does not occur at pH < 6.0 (Beebee, 1983), although some animals are found at pH = 5.8 (Arnold, 1983). At pH < 3.9, *T. vulgaris* are absent, and invertebrates are rare (Frazer, 1978). Increases of acidity significantly reduces larval feeding efficiency (Prest, 1992; Griffith, 1993). Optimal ion concentration is about 380 particles/10⁶ with limits from 150-1750 particles/10⁶ (Beebee, 1981).

Triturus vulgaris prefers small ponds with rich aquatic vegetation, which in urban areas is plentiful in reservoirs polluted with metal ions (Cooke and Frazer, 1976). The presence of fish in ponds negatively influences newt numbers and reproduction (Beebee, 1981; Banks and Laverick, 1986; Dolmen, 1987). Captures by collectors and children and cleaning of ponds have negative effect on the newt number in cities (Beebee, 1979). Industry emissions and simply anthropogenic pressure lead to vegetation destruction, soil erosion and, as a consequence, to a decrease of humidity of the surface air and disappearance of prey objects (Simms, 1969; Beshkov, 1978). The use of herbicides, although it does not contribute to the species disappearance, reduces the suitability of spawning ponds (Cooke, 1977). Newt reproduction does not occur in significantly polluted urban ponds (Vershinin, 1983b).

Triturus vulgaris is a well-known, widespread species in urban and suburban territories (e.g., Sharleman, 1917). This species is common in small ponds of urban parks and gardens of Great Britain. It usually is second in abundance after brown frogs (*R. arvalis* and *R. temporaria*) or together with *R. temporaria* (Beebee, 1973; Mathias, 1975; King, 1979; Banks and Laverick, 1986). In London, populations of *T. vulgaris* reproduce successfully in conditions where frogs and toads disappeared long ago (Beebee, 1973). Cryptic behaviors of *T. vulgaris* in the terrestrial period of life favors the use of urban territories (Vershinin, 1996a). In agricultural areas it is the most widespread amphibian species (Beebee, 1981) and rather easily adapts to anthropogenic changes of environment (Cooke, 1977; Cooke and Arnold, 1982; Arnold, 1983).

In our country the data about distribution of *T. vulgaris* in urban areas shows that it occurs mainly in the forest park zone and suburbs (Toporkova, 1973; Pliss and Khudolei, 1979; Lebedinsky, 1981, 1984a; Kuranova, 1989). According to my data, the stability of *T. vulgaris* in response to anthropogenic influences and distribution in urbanized areas of Ekaterinburg is next after *R. ridibunda*, *R. arvalis* and *R. temporaria* (Vershinin, 1980a, 1983b). This species follows brown frogs by the extent of distribution, and recently (1984-1985) even exceeded them. The changes have taken place because of the destruction of some habitats by economic activity. The number of urban populations is usually low, but sometimes they are significant even in habitats that are significantly transformed by man (Table 3); the picture of *T. vulgaris* distributions in the cities of the Urals is similar in many respects with the situation in cities of Great Britain. Apparently, the ubiquitous habits of *T. vulgaris* in urban areas are explained by biological features of this species.

Small body size and a reclusive life mode reduce vulnerability from man, and the ability to reproduce in small ponds allows the species to breed in urban conditions. In comparison with another aboriginal newt species, *S. keyserlingii*, living and breeding only in suburbs and the forest park zone, *T. vulgaris* is considerably less dependent on sunlight exposure and pond temperature, changes in water chemistry and species structure of vegetation communities. In those habitats where the number of *S. keyserlingii* is stable, it is usually more numerous than *T. vulgaris* (Table 3). In more transformed habitats, species ratio changed towards of a prevalence of *T. vulgaris*. An estimation of species structure of amphibians in Niznii Tagil Metallurgical Factory area in 1988 shown that *T. vulgaris* begins to occur from 14 km from main factory areas, while *S. keyserlingii* only occurs from 25-27 km. *Triturus vulgaris* has potential opportunities for inhabiting ponds in urban parks and gardens and can also serve as the indicator of the quality of environmental conditions. It is more eurytopic than *S. keyserlingii*. The position of *T. vulgaris* in urban ecosystems and features of its populations are determined by species specificity, relative tolerance to changes of environmental chemistry, and ecological plasticity that accompanies a number of general regularities characteristic for urban amphibian isolates.

Rana temporaria has lower ecological plasticity than *R. arvalis* (Vershinin, 1987a; Vershinin and Trubetskaya, 1992), and its distribution in urban territories is more limited. It is determined by biological features of the species; hibernation takes place in rivers and springs. In addition, it requires good soil litter, which is a limiting factor of dispersal from pond shores in the zones of active recreation (Sharygin and Ushakov, 1979). Places of reproduction and hibernation are most important than other habitat parameters in *R. temporaria* (Lebedinsky, 1984a; Cummins, 1989). *R. arvalis* is capable of using a wider range of habitats (Rahmel and Eikhorst, 1988), and the decrease in the abundance of *R. temporaria* is remarkable for urban areas (Bannikov and Isakov, 1967; Burton, 1976; Cooke 1972; Cooke, 1985) with human-induced environmental changes (Cooke and Arnold, 1982).

Garanin (1964) explained this fact by the expansion of *R. arvalis* in connection with the reduction of forest areas. Astradamov (1973) believed that the decrease in habitat humidity has resulted in the replacement of hygrophilous *R. temporaria* by less hygrophilous *R. arvalis*. At the same time, when habitats suitable for this species are present, *R. temporaria* can exceed other species in number (Figs. 3 and 4) and density (Table 4; Beebee, 1979; Lebedinsky, 1981). It is capable of colonizing artificial ponds (Banks and Laverick, 1986) and is absent only in places of the highest level of economic activity (Hildmann and Kronshage, 1988). Mean density of *R. temporaria* in Zones II and III in 1984 was 100 and 88.9 adults/ha and 150 and 44.4 froglets, respectively.

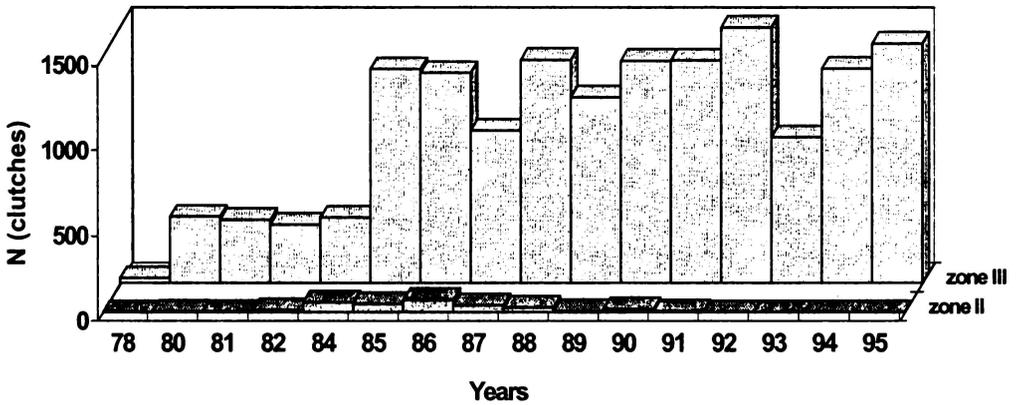


Fig. 3. Dynamics of *Rana temporaria* clutch number

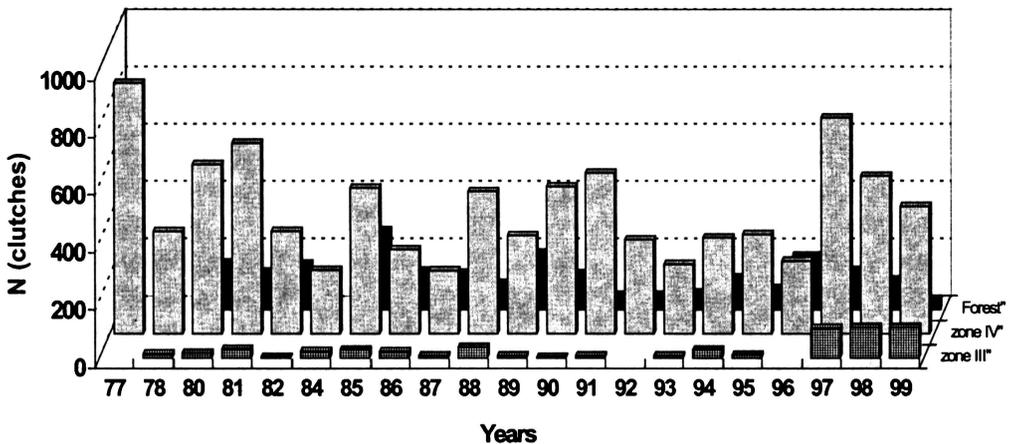


Fig. 4. Dynamics of *Salamandrella keyserlingii* clutch number.

Garanin (1964) explained this fact by the expansion of *R. arvalis* in connection with the reduction of forest areas. Astradamov (1973) believed that the decrease in habitat humidity has resulted in the replacement of hygrophilous *R. temporaria* by less hygrophilous *R. arvalis*. At the same time, when habitats suitable for this species are present, *R. temporaria* can exceed other species in number (Figs. 3 and 4) and density (Table 4; Beebee, 1979; Lebedinsky, 1981). It is capable of colonizing artificial ponds (Banks and Laverick, 1986) and is absent only in places of the highest level of economic activity (Hildmann and Kronshage, 1988). Mean density of *R. temporaria* in Zones II and III in 1984 was 100 and 88.9 adults/ha and 150 and 44.4 froglets, respectively.

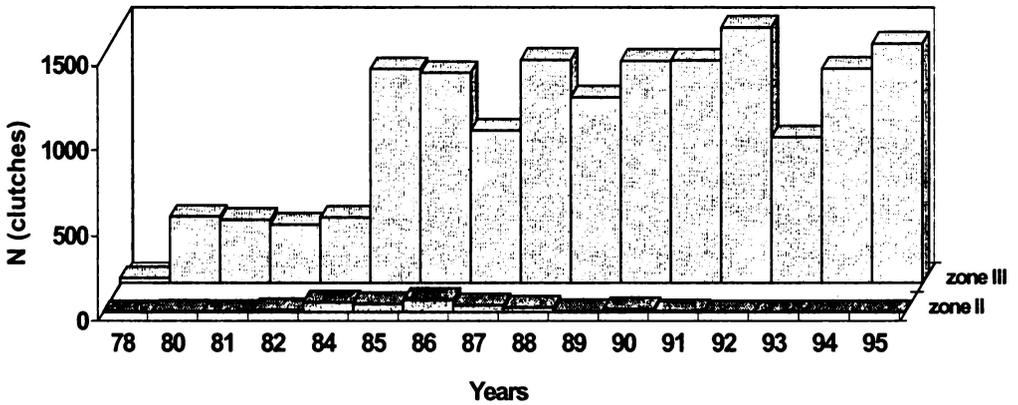


Fig. 3. Dynamics of *Rana temporaria* clutch number

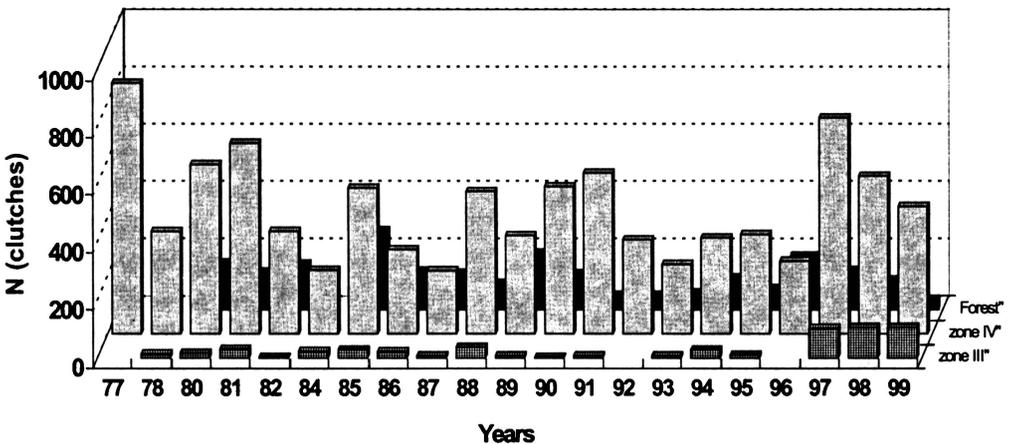


Fig. 4. Dynamics of *Salamandrella keyserlingii* clutch number.

Table 4. Estimations of amphibian abundances (animals/ha).

Adults	Juveniles	Zones	Number of plots
<i>Rana arvalis</i>			
120		5	15
8.89	10.34	4	58
33.33	55.56	3	9
66.67	316.7	2	6
<i>Rana temporaria</i>			
88.89	44.4	3	9
100	150	2	2
<i>Salamandrella keyserlingii</i>			
80	26.6	5	15
5.45	1.81	4	55

For comparison, in natural landscapes, the density of *R. temporaria* varies in different types of habitats from 2.1-116 animals/ha, mean = 28 (Goncharenko, 1988). In identical conditions of development, *R. arvalis* has higher variability of the growth rate and development because of the environmental component (Surova, 1988). When larvae of *R. arvalis* and *R. temporaria* live together, *R. arvalis* are suppressed by *R. temporaria* (Pikulik, 1976), and under these conditions *R. temporaria* metamorphoses earlier (Loman, 1994). *Rana arvalis* young-of-the-year are more sensitive to the influence of density than *R. temporaria* of similar size (Lyapkov, 1988). Some authors assume competition between *R. arvalis* and *R. temporaria* (Lardner, 1995).

According to Sabaneev (1874), *R. temporaria* was "widely distributed in Ekaterinburg Urals." Forty years ago, this species was numerous and encountered often. The decline in number, probably connected first of all to the disappearance of springs and pollution of rivers (where *R. temporaria* hibernates) by industrial wastes (Toporkova, 1973). The results on embryonic and larval survivorship of *R. arvalis* and *R. temporaria* under the exposure to detergents confirm this suggestion (Trubetskaya, 1994): embryonic mortality in *R. temporaria* is twice as high. *Rana arvalis* is the most successfully reproducing species near Ekaterinburg (Figs. 1a and 4) and other cities of the Urals and dominate natural ecosystems (Vershinin, 1980a, 1983b; Toporkova, 1981). Adaptive opportunities of *R. arvalis*, living on the Far North "attain amazing perfection - even at temperature about 0° their digestive enzymes maintain high activity, the amplitude of reductions amplifies, and the speed of contractive development of the myocardium increases" (Shvarts, 1974a).

Censuses carried out in 1984 (Vershinin, 1987a) showed that the highest density of *R. arvalis* is observed in the forest (Talitskii District, Sverdlovskaya Province): 120 animals/ha. Within the limits of urban area, the maximal density of adult *R. arvalis* was

found in the most urbanized habitats (multistory building zone), up to 66.7 animals/ha; in a low building zone the density was lower, 33.3 animals/ha, and in forest park 6.9 (mean local density in habitats is indicated). On average for the whole urban territory, the density of amphibians is low because of small population sizes. The number of *R. arvalis* clutches per 10 m² of water surface for zones with different extent of urbanization has its highest in the forest park (0.89), and lowest in the zone of multistory buildings (0.13). In other words, on the comparable area of breeding ponds and terrestrial areas suitable for amphibian life, the parameter is smaller in zones with a significant urbanization degree. The censuses of froglets on plots have given results similar to the adults (Table 4).

High polymorphisms and wide reaction norms promote success in reproduction and highest prevalence of *R. arvalis* in technogenic landscapes. Because *R. arvalis* hibernates on land, it does not require aerated non-frozen ponds. The wide distribution of this species is connected with a capability to hibernate on land and to resist lower temperatures in comparison with water-hibernating frogs. The resistance to low temperatures is provided with accumulations of glycerol (Schmid, 1982). *Rana arvalis* uses natural and artificial ponds for reproduction (Larionov, 1923; Toporkova, 1977). In technogenic ponds, that appeared some years ago in the forest area, up to 90% of mature females of *R. arvalis* may breed (Ishchenko, 1978a). The reproduction and development can occur in ponds of various sizes, temperatures, and sunlight exposures. The small body sizes (in comparison with *R. temporaria*) make this species less vulnerable to urban habitat conditions. *Rana arvalis* occurs at all places of urban areas where amphibians live.

Rana ridibunda, introduced in Ekaterinburg, even in the conditions of ponds with thermal pollution does not breed every year (Vershinin, 1990). The expansion of the range of *R. ridibunda* by human activity is known (Toporkova, 1977, 1978; Toporkova et al., 1979; Belimov and Sedalishchev, 1980; Ivanova, 1995). The northern border of its natural distribution in the Urals passes considerably to the south of Ekaterinburg (Toporkova, 1973). The distribution of *R. ridibunda* outside its natural range is possible because of industrial activity of men and association with thermal pollution. A source of introduction in such cases is medical and biological stocks or fish breeding complexes (Toporkova, 1978). It is known that this species shows resistance to pollution and anthropogenic transformations (Misyura, 1989). This species was first noted in Ekaterinburg area in 1977 (Vershinin, 1981; Vershinin and Toporkova, 1981). The information on Green Frogs in the Ekaterinburg Urals from 1874 (Sabaneev, 1874) were apparently erroneous (Toporkova, 1973). In 1978, in the central part of Ekaterinburg, we found two populations of *R. ridibunda*; one consisted of 15-20 animals (Belinskogo Street) and another of about 100 mature animals (Krylova Street). In 1986, we found a population on Kuibysheva Street that numbered about 20 animals. Single animals of this species were repeatedly found in a number of ponds (Fig. 1a), but the reproduction was not observed anywhere.

For the first time reproduction of *R. ridibunda* in urban territory was recorded in 1980 in isolated ponds on the bank of the Iset River (Krylova Street). In the largest

populations of *R. ridibunda* (Krylova Street) from 1981-1987 tadpoles did not survive to metamorphosis despite an abundance of clutches in the spring; larvae probably were eaten by *R. ridibunda*. In 1988, there was a decrease of *R. ridibunda* number because of adverse changes of the habitat (sharp decrease of water level and strong plant overgrowth), and for the first time in seven years metamorphosis of *R. arvalis* and *R. temporaria* was recorded. *Rana ridibunda* is the most tolerant to anthropogenic influence, and in the certain conditions it can negatively influence the level of reproduction of native amphibian species by feeding on their larvae and froglets (Lyapkov, 1989; Vershinin, 1990d; Yakovlev, 1990). In Switzerland, *R. ridibunda* displaced two species of other green frogs, *R. lessonae* and *R. esculenta*, and other amphibians. On the Iberian Peninsula, *R. ridibunda*, *R. lessonae* and *R. esculenta* hybridize with *R. perezi* to create the danger of disappearance of the latter species (Arano et al., 1995). Introductions of *R. catesbeiana* from the USA also results in reduction of natural numbers of amphibians (Moyle, 1973).

The presence of thermal pollution in cities creates a potential opportunity for occurrence of local populations *R. ridibunda* outside its natural range. In 1981, *R. ridibunda* was found in Chelyabinsk (Vershinin, 1983b). After years of investigation, *R. ridibunda* was found in Ekaterinburg ponds situated in the immediate proximity of the Iset River. Because of this introduction (possibly, repeated) it is commonly encountered at five sites and in three of them it does not reproduce every year (Shvarts, 1980). Froglets were found in 1980-1981, 1986, 1988-1991, 1994, and 1997-2000. In 1998 the reproduction of *R. ridibunda* in low building zones and in forest parks was recorded for the first time. Occurrence of this introduced species under environmental changes in urban area is one of the sides of anthropogenic transformation. Perhaps *R. ridibunda* is a typical synanthropic species in the Urals. The maximal survival of the species (after metamorphosis) at different levels of anthropogenic influence are given in Table 5.

The urbanization process causes significant transformation of spatial structure of amphibian populations. Except for spatial isolation in urban habitats, the sharp reduction of the area of their terrestrial part is typical. Quite often it is limited by a belt of vegetation on the shore that is only 3-4 m wide. Populations in Zone II occupy sites small in area, but density of animals is higher than in the Zone III and the forest park (Vershinin and Krinitsyn, 1985). High local density is the reason of spatial limitation of the terrestrial

Table 5. The upper survival limit during metamorphosis of amphibians in urban areas (% of total number of deposited eggs).

Zones	<i>Salamandrella. keyserlingii</i>	<i>Rana ridibunda</i>	<i>Rana arvalis</i>	<i>Rana temporaria</i>
Multistory buildings	Not reproduced	57.7	5.0	2.5
Low buildings	Not reproduced	No data	2.3	2.0
Forest park	18.1	No data	3.39	No data
Forest population	0.5 (Far East: Tagirova, 1979)	Not reproduced	0.69	No data

part in amphibian urban habitats. There is a constant exchange by individuals within natural populations of amphibians (i.e., between micropopulations). In such cases a significant mortality or the destruction of one micropopulation does not mean the demise of the population as a whole (Shvarts, 1980) because the number of micropopulations is high. The situation in urban territories is different. The majority of populations (not subdivided into micropopulations) are spatially separated and have no contact with each other. Thus the number of such groups and their number on most urbanized sites of the territory are small (Table 3) in comparison with the number of natural populations, at which hundreds to several thousand of individuals are supposed (Yablokov, 1987). Therefore, the fall in reproduction of each particular group has more serious consequence, and there may be the complete disappearance of the population because immigration is absent. It is known that fragmentation of a forest interferes habitat recolonization (Richards et al., 1994). The disappearance of micropopulations of *R. lessonae* in Sweden are supposed to have resulted from a critical level of isolation in combination with stochastic environmental changes of the system (Gulve, 1994).

As I already noted, a part of information on urban populations of amphibians was collected in Serov and Chelyabinsk (see Section 2). Serov has a population of more than 100,000 people. There is a large metallurgical factory, and the Kakva River flows through the town. There is a lot of swampy sites, small ponds and springs. The central part of the town with multistory (3-5 floors) buildings is insignificant. Most of the area is occupied by low buildings (1-2 floors) with gardens and kitchen-gardens. The forest park zone is absent, and just beyond the town taiga begins. Near Serov and its suburbs only *Rana arvalis* occurs. It is widespread in marshy sites in the urban area (Fig. 1b). Reproduction and development in roadside ditches and ponds and directly in the yards between houses in low building zones was noted. I have not found *R. arvalis* in the central part of the town which is built up by multistory stone houses and covered with asphalt. There is no habitats suitable for amphibian life and reproduction. On the area of the metallurgical factory and in the extensive zone subject to action of its emissions and industrial drains, no amphibians were found. I found 6 habitats of *R. arvalis* in the urban area and suburbs (Fig. 1b). Other amphibian species on the urban territory and in suburbs were not found. *Salamandrella keyserlingii* was not found closer than 50 km from Serov (N.G. Erokchin, pers. comm.).

Chelyabinsk consists of more than one million people. The city occupies a large area, there is a set of industrial enterprises, and the River Miass flows through the city. According to our estimation, the general urbanization of Chelyabinsk is a little higher than in Ekaterinburg, and it is caused by features of the building process. The whole central part of Chelyabinsk is engaged in new multistory buildings, and even in squares of this part of the city small ponds, necessary for amphibian reproduction and development, are absent. This has resulted in complete amphibian disappearance from the two former zones. The amphibians were recorded mainly in the forest park belt of the city (Zone IV) and, insignificantly, in a zone of low buildings and along the Miass River (Fig.

1c). In a low building zone, *R. arvalis* and *R. ridibunda* occur (in 1981 on the bank of the Miass River *R. ridibunda* was found). It means that in Zone III of Chelyabinsk only tailless amphibians live (mainly *R. arvalis* and probably *R. ridibunda*). Caudate amphibians and *R. temporaria* remain only in the forest park zone. In the forest park zone *S. keyserlingii* and its clutches occur, and *R. arvalis*, *T. vulgaris* and *R. temporaria* are widespread (Fig. 1c). In the Chelyabinsk area I found one habitat of *S. keyserlingii*, two of *T. vulgaris*, five of *R. arvalis*, and two of *R. temporaria*.

Ecological surveys in 1988 near Nizhni Tagil City (with a large metallurgical factory and accompanying manufacturing) provided similar patterns (Fig. 1d). Amphibian species in a radius up to 14 km from the metallurgical factory is represented only by anurans (*R. arvalis* and *R. ridibunda*) most tolerant to pollution. Among caudates, more sensitive to pollution, *T. vulgaris* occurs outside the 14 km zone. *S. keyserlingii* is recorded only at 27-30 km from the city.

The following common features of amphibian distributions may be listed for the area of the cities under investigation: central part of city with multistory buildings and asphalt areas almost lack amphibians (single records) because of the absence of places suitable for reproduction and living. The increase of urbanization can result in disappearance of amphibian from Zone II (Chelyabinsk). Amphibian populations are found on the borders of areas of multistory buildings (Zone II). This zone is poorly occupied by tailed amphibians. Mainly anurans present there: *R. ridibunda* and *R. arvalis*, in smaller numbers, *R. temporaria*, with a prevalence of *R. arvalis*. The most varied community is in the zone of low buildings (Zone III). Synantropic species come into this zone as they are able to reproduce only in environment changed by the man (*R. ridibunda*). Forest species (*S. keyserlingii*) remain, but are unable to reproduce successfully in habitats significantly transformed by men. Therefore, in one habitat of the Zone III up to 5 amphibian species can be encountered. Species composition in the forest park zone (Zone IV) differs a little from those outside the urban territory (*S. keyserlingii*, *T. vulgaris*, *R. arvalis* and *R. temporaria*). Only one typically forest species, *B. bufo* encountered beyond a city, is absent from the forest park zone. The absence of that species in anthropogenic landscapes is known also in other parts of its range (e.g., Pushchino, Zubakin et al., 1981; Nizhny Novgorod, Lebedinsky, 1981; London, Beebee, 1981).

Thus, the study of amphibian distribution on urban territory and number of populations revealed that some species (*B. bufo* and *S. keyserlingii*) are most vulnerable and also more primitive and ancient in their origin within respective amphibian orders. *Triturus vulgaris* reproduces in cities successfully but is absent from habitats with the maximal anthropogenic influence. In these conditions, advantage may have rather "young," more ecologically plastic and eurytopic species which often prevail in natural ecosystems and which are widespread and successfully reproduce in urban areas. The indirect confirmation of these conclusions represent the results on variability of the basic morphological parameters (Vershinin, 1987a), sex ratio and number of others population parameters discussed below.

5.0. GENETICS AND “STRIATA” MORPHS IN *R. ARVALIS* AND *R. RIDIBUNDA*

Intrapopulation polymorphism, caused by genetic heterogeneity of natural populations, determines adaptive opportunities and can form the basis for the subsequent microevolutionary transformations, being “a mobilization reserve of internal variability” (Gershenzon, 1941). Environmental changes in some cases can be of positive importance of a combination and separate mutations, which were indifferent or harmful earlier. Any appreciable distinction in useful attributes should be examined as an indication of the efficiency of natural selection. Shvarts (1980) mentioned that, depending on conditions of environment, including such as amphibian species composition in a pond, phenotypically different froglets are formed. With abrupt environmental changes, the rare genotypes can gain an advantage. Criteria of a population reaction on pressure of the new factor can increase the frequencies of rare phenotypes (Pavlov, 1982). Therefore, analysis of phenotypical features represents, by our opinion, one of the methods of control for changes in populational structure of amphibians in urbanized areas. For urban populations of *R. arvalis* and *R. ridibunda* I have found a steady deviation of a ratio in frequency of the “striata” morph in comparison with natural populations (Vershinin, 1987b, Vershinin, 1990d).

The maintenance of a dynamic polymorphism in amphibian populations is probably determined by differential survivorship of various genetic variants at different stages of ontogeny and in different environmental conditions (Pikulik, 1978). The ratio of various morphs in populations reflects specificity of genetic structure. In our case, it is the frequency of individuals with a pale middorsal stripe (striata) in populations of *R. arvalis* and *R. ridibunda*. It is known that in many species of amphibians, including *R. arvalis*, in populations subjected to anthropogenic influence, the frequency of “striata” increases (Vershinin, 1980b, 1987b, 1990c, d; Toporkova, 1985; 1978; Gogoleva, 1989; Kolyakin, 1993). Schreiber (1912) gives the name and detailed description of this morph. In populations of *R. arvalis*, individuals with the medial stripe on the back are always present. According to hybridization experiments (Schupak, 1977), the presence of the middorsal stripe is determined by the action of one diallele autosomic gene “striata” at complete dominance (the allele dominates, which determines the presence of a stripe). Similar data were received at experimental hybridization of individuals of the Japanese *Rana limnocharis* (Morivaki, 1952) and North American *Rana sylvatica* (Browder et al., 1966). Thus, “striata” is a good phenetic marker, with the help of which we can study phenotypic features of changes in genetic structure of a population.

As already noted, color polymorphism have been known in many amphibian species, and it has a genetic nature that determines physiological distinctions between individuals of various morphs. Neutral polymorphism in populations of amphibians is a rather rare phenomenon (Gray, 1984). Individuals of “striata” have larger body (in comparison with “maculata” morphs) and liver mass that indicative of an increased ability for energy accu-

mulation. The sensitivity of an animal of this morph to hibernation asphyxia phenomenon (deficiency of oxygen) is significantly higher (Shvarts and Ishchenko, 1968). Animals of this morph have a higher metabolic rate; the consumption of CO₂ per unit of time per 1 g body mass is 1.5-2 higher times that of "maculata" individuals (Dobrinisky and Malafeev, 1974). "Striata" also has higher initial levels of oxygenation-reduction processes (Runkova, 1975). that can determine the adaptive value of the "striata" in conditions of pollution and urbanization. Individuals of this morph possess a number of physiological features giving them advantage in a population inhabiting conditions of anthropogenic influences that lead to increase of its frequency in these conditions (Gogoleva, 1989; Petrova, 1995).

It appears that individuals of this morph accumulate Sr-90 at a much greater degree than "maculata" individuals (Usachev et al., 1993). This is especially clear in froglets and 1 year-old animals, which the authors also connected with features of exchange processes. According to our data (Pyastolova and Vershinin, 1999), individuals of "striata" prevail in areas with high levels of radionuclide pollution (46.7%, $p < 0.01$, $N = 60$: froglets; 58.3%, $p < 0.05$, $N = 12$: adults) against 22.2% ($N = 54$) and 18 % ($N = 11$) respectively in "clean" areas.

According to Ishchenko (1978b), higher initial levels of oxygenation-reduction processes in "striata" in comparison with "maculata" are caused by high migration ability and tolerance to dry conditions. At the same time, in natural populations of *R. arvalis* of this morph differ by early sexual maturity and relatively shorter life duration (Ledentsov, 1990; Ishchenko, 1994). Our research of skin sodium permeability (see Section 6) on froglets of *R. arvalis* (Vershinin and Tereshin, 1989, 1996) shows the presence of significant differences between the morphs; "striata" individuals have a permeability 2X lower (at different modes of testing the significance of differences, $p = 0.004- 0.0005$). It is obvious that because of hereditary determined physiological specificities of the animals, the morph "striata" receives selective advantages in the populations occupying anthropogenically transformed areas.

Sharygin (1980a, b), based on the study of microelement content in animals and geochemical background, believes that there is a connection of geochemical habitat conditions and frequency of the striped and spotted forms in *R. arvalis* populations on the Ural. The high concentration of microelements in environment, by the opinion of this author, promotes survival of the "striata" morph, and on the contrary, negatively effects the survival of others morphs. Comparisons of chemical composition has revealed that the contents of some metals in the organism of the striped morph is several times lower (explained by low skin permeability) than in the maculate morph, except for iron (it is 2X higher). The presence of a large amount of hemoglobin in "striata" may be connected with the increased content of iron. The increased contents of hemoglobin in the blood of "striata" can explain its best adaptability to mountain conditions (Bakushev, 1989). As the habitat breath in amphibians is adjusted by the contents of oxygen in the blood (instead of carbon dioxide as in amniotes), the adaptations to breath in adverse gas environment in amphibians are solved by the increase of the amount of blood and hemoglobin (Chugunov, 1974). In popu-

lations from natural ecosystems with a low degree of anthropogenic influence, the frequency of "striata" specimens is usually lower. High proportions of the "striata" morph in populations in the polluted areas is evidence for the directed changes of genetic structure to prevalence of individuals with a high level of metabolism.

Frequencies of "striata" morph in populations of *R. arvalis* in Ekaterinburg increases with strengthening of anthropogenic influence (Vershinin, 1980, 1982, 1982a, 1983). The process is connected with changes in frequencies and variety of phenotypes, which were also found in populations of *R. temporaria* and *R. arvalis* in the Nizhny Novgorod area (Lebedinsky, 1984a, 1995). Frequencies of the "striata" morph are higher among froglets of *R. arvalis* from habitats with the maximum anthropogenic pressure (Zone II) with the highest mortality of larvae and froglets (Vershinin, 1983a). Dynamics of larvae and froglet number in the conditions of significant anthropogenic influence is rather specific (Fig. 13). High mortality at early stages of development is compensated by its significant decrease at late stages (Vershinin, 1985), that is, less viable individuals are eliminated early.

Taking into account the influence of non-selective elimination on genetic structure of a population (Shvarts, 1969, 1980), and also the features of the "striata" morph, it is possible to make a conclusion that higher frequencies of this phenotype in an urban area is caused by a number of advantages in these conditions. In some isolated populations of *R. arvalis* from urbanized habitats, the percent of striped animals among froglets is 72.7%, and among adult animals it may be more than 50%. As a whole for populations of *R. arvalis* of Zone II, the percent of "striata" individuals in some years does not exceed 51.5% in froglets and 50% in adults; total percentage of this morph for all years of investigation is even lower (Table 6). Presence of a certain part of non-striped animals in

Table 6. Frequency of the "striata" morph in *Rana arvalis* populations (1977-1995).

Zones	Froglets		Adults	
	%	N	%	N
II	44.73	2611	42.05	88
III	37.55	514	42.86	42
IV	29.26	3835	34.65	127
C	19.51	2466	22.02	109

Significance of differences by "chi square" criterion				
Adults				
Zones	II	III	IV	C
II	X			p<0.01
III	p<0.01	X		p<0.05
IV	p<0.01		X	p<0.05
C	p<0.001	p<0.001	p<0.001	X

Froglets				
----------	--	--	--	--

these populations, despite of advantages of the “striata” morph, may be connected with high viability of heterozygotes that phenotypically look like “striata.”

It was mentioned above, that larvae of this morph are sensitive to asphyxia at hibernation. It allows them to assume the presence of a similar situation with higher mortality. Such conditions arise at excessively high density of larval shoals. By our data, high density of larval shoals occur in amphibian habitats with the maximum anthropogenic pressure (Zone II). These situations are rarer than in habitats less influenced by humans. High density of larval groups are considered when there are 10-15 larvae/liter (Pyastolova and Ivanova, 1978), whereas in urban area we deal with densities from 0.3-0.003 tadpoles/liter. The exclusive case, when the metamorphosis of the “striata” froglets does not occur, was recorded at a density of 9.3 tadpoles/liter. At a insignificant increase of density, animals of this phenotype survive better (Ishchenko and Shchupak, 1979). There is no difference in selective mortality of larvae with dominant allele of the “striata” locus and other animals in natural conditions. Differences in frequency of individuals having a stripe between animals developing in different micropopulations in nature has a consequence non-uniform distribution of genotypes in mature frogs on territory occupied by a population (Shchupak and Ishchenko, 1981). Species of one generation can have homologous genes and show identical variability (Vavilov, 1967). Therefore, it can be assumed that many features of the phenotype “striata” can be peculiar in species of these generations. The inheritance of the middorsal stripe in *R. ridibunda* is also caused by monogenetic dominant alleles (Berger and Smielowski, 1982) that provide the basis to expect that this species has a similar physiological specificity.

Frequency of the striped morph in adult *R. ridibunda* in urban areas of Ekaterinburg was 99.2% (N = 120) and in froglets it was 36.2% (N = 914; $p < 0.001$). In populations of *R. ridibunda* established by introduction in Verkhniy Tagil City, frequencies of this morph in froglets was 19% and 60% in adults (Toporkova, 1978). In populations of *R. ridibunda* from the vicinity of Poti Town, Georgia in 1985, the frequency of the “striata” among froglets was 24.6% (N = 57) and 32.9% (N = 243) of adults (not significant; Vershinin, 1990c).

There are difference among froglets in populations of *R. ridibunda* in the “striata” morph. In populations located below the dams of a city pond, some animals have a very narrow medial stripe (0.3-0.5 against 1.0-2.0 mm), and the frequency of this variant is 16.78% (N = 143). It makes 58.5% of the number of all striped animals in these isolates. This fact is evidence for the essential genetic distinctions between *R. ridibunda* populations that live above and below the dam. In our opinion, it may be explained in terms of different sources of introduction and founders. Obviously, the animals of the “striata” morph have selective advantages in populations of amphibians of technogenic zone of the Urals region.

It is known that small froglets have less chance to survive than large ones as a result of difference in energy storage (Shvarts, 1980; Crump, 1981). According to our data, froglets of *R. arvalis* from the most polluted habitats (where the “striata” frequency is

maximum) are significantly ($p = 0.001$) larger in comparison with froglets from other zones (see Table 12). Apparently, the large sizes of froglets is caused by a selective survival of large, energetically efficient individuals in conditions of industrial pollution. Ivanova (1982) found similar data; *R. arvalis* larvae from the polluted pond 30 km from Ekaterinburg were 1.6 times larger than the same age individuals from a clean pond. The increase of body size is characteristic for populations of other species of urban amphibians that is associated, probably, to a more favorable surface-volume ratio in large animals. This is displayed in males and froglets of *R. arvalis*, adult *S. keyserlingii* and *R. temporaria*, and also in the adult and young-of-the-year of *T. vulgaris* and *R. ridibunda*. Larvae with high growth rate attain bigger sizes earlier and become less sensitive to pollution and have a reduced vulnerability from predators (Werner, 1986). The large body sizes in amphibians in the conditions of anthropogenic influence were found also by many other authors (Ushakov et al., 1982; Bugaeva, 1983; Gogoleva, 1985; Misyura, 1989).

Ushakov et al. (1982), in Nizhny Novgorod City, found that the body length in age-1 *R. temporaria* is significantly larger in the zone with the maximal degree of urbanization. On the same material, Lebedinsky (1984a) showed the change of phenotypes frequencies, including the increasing frequency of spotted animals with the degree of urbanization. The change of phenotype frequencies, including increase of the proportion of the "striata" individuals (Zhukova et al., 1986) with increase of urbanization is characteristic both for the representatives of genus *Rana* and for other families of Anura (Peskova, 1995). High mortality at early larval developmental stages in the conditions of pollution, isolation and low population number results in survival of larger viable individuals or animals with a number of hereditary determined physiological features that provide selective advantage in new environmental conditions.

In populations of *R. arvalis* and *R. ridibunda* inhabiting anthropogenic transformed and polluted areas, selective advantages are present in individuals of the "striata" morph with hereditary determined features of physiology which are rather rare in natural populations. This increase the chances of survival, but in natural conditions it is harder to estimate the advantages of these attributes. It is possible to conclude that individuals with the stripe are preadapted to biogeochemical environmental anomalies. Thus, intrapopulation polymorphism determines population success of survival and reproduction in new environmental conditions and probably further evolutionary destiny.

6.0. AMPHIBIAN PHYSIOLOGY AND URBAN ECOSYSTEMS

There is a certain generality in principles of organization and functioning of various biota levels, and these principles can be applied to the evolution of biological systems of different structural levels. These are some patterns working at the ecosystems level that can, apparently, be used as objects of physiological research (Levchenko, 1990). The

same patterns work both on micro- and macrolevels. Because of such similarity, there is a parallelism of evolutionary patterns for different objects. Individual adaptation has huge advantages in the case of fast changes in environment. These are first steps of further transformation of a species by slower process of evolution. The adaptive updating is established at a change of environment in the first generation at all individuals. "The population determines the destiny, conducting a physiological condition of the individuals, composing it" (Shvarts, 1973). Thus, the study of animal physiological specificity of populations which live in extreme environmental conditions of habitats transformed by men allows (in comparison with zoological methods) for short-term return of new items of information on processes of adaptation and microevolution.

6.1. Sodium balance in amphibians from urban areas

Because of the high sensitivity of aquatic organisms to long-term influences of low concentrations of pollutants, the condition of aquatic biogeocenosis serves as the best criterion of chemical changes in this environment (Shvarts, 1954; Buyanovskaya, 1973). Various hydrobionts have been used to estimate changes in the condition of the hydrosphere. The greatest number of studies was made on fishes and invertebrates. It is much less than those done on amphibians, although these animals, whose development occurs in water environment, react to the slightest changes of its composition. Many authors specify individual (and population) reactions of amphibians on pollution and urbanization (Rose and Harshbarger, 1977; Ilosvay, 1977; Feldmann, 1978; Pliss and Khudoley, 1979). Many of these reactions are adverse and have characters of known infringement. Shvarts (1954) noted high sensitivity of morphophysiological characteristics of amphibians to presence of microelements in the water environment. In many respects it was caused by such characteristics of amphibian features, like high skin permeability, which makes them in a maximum degree vulnerable in relation to environmental pollution. It is known that in conditions of significant pollution, the albumin and lipid metabolism in amphibians increases (Misyura, 1982), and this response, apparently, can reduce their permeability for pollutants (Misyura, 1989). As already noted, ponds from zones of multi- and low buildings most subject to anthropogenic influence differ significantly in general mineralization and high content of sulfates and petroleum in comparison with those in the forest park zone and forest (Vershinin, 1985a).

The research of sodium permeability of the skin of *R. arvalis* (metamorphosed juveniles in 1993, grown ones before hibernation in 1989) revealed a number of significant differences (Table 7). Permeability of the skin of animals from the zone of multi-story and low buildings was more than 2X lower than in animals from populations of the forest park and forest. The permeability of skin is naturally reduced in inverse proportion to a gradient of pollution. The reliability of the given relationship observed in 1989 on froglets of *R. arvalis* and *R. temporaria* was very high ($F = 8.432$; $p < 0.0001$). Interspecies distinctions were less sharp ($p = 0.002$), and as a whole sodium permeability

Table 7. Sodium permeability of skin (mV; mean \pm S.E.) in juvenile and grown froglets (1993).

Zones	Grown froglets (1989)			Juveniles (1993)		
	Experiments	N	Experiment with KJ	N		N
II	19.0 \pm 5.8	15	19.9 \pm 6.9	6	4.95 \pm 2.05	24
III	30.8 \pm 5.8	15	28.6 \pm 4.9	12	6.88 \pm 2.89	12
IV	42.7 \pm 7.5	9	38.6 \pm 5.7	9	12.47 \pm 2.05	24
K	47.1 \pm 4.6	24	30.9 \pm 6.9	6	17.90 \pm 2.89	12

in *R. temporaria* skin appeared less than in *R. arvalis*. The difference in skin permeability of juvenile Moor Frogs also was significantly different ($F = 5.393$; $p = 0.002$). The influence of the solution KJ on the skin and difference in potentials (DP) in froglets from Zone II remain practically unchanged, whereas in animals from other zones these values decreased, and, hence, significant differences between zones disappeared. After the skin flap was washed with Ringer's solution, the difference did not appear again; the DP in juveniles from the Zone II remained at the same level, and in those from other zones it did not increase to the initial value.

First we put forward a hypothesis on the decrease of intensity of sodium exchange through amphibian skin that is connected with adaptive character explained by changes in structure and albumin-lipid composition of skin and the protective reaction to pollution. It shows a certain degree of biocenotic transformation and also reflects a level of changes in environmental chemistry of habitats. Later, the analysis of experimental data showed that morphs of *R. arvalis* significantly differ in the skin permeability; in striped frogs, this parameter was significantly lower (under different testing conditions, significance of differences varied considerably, with $p = 0.004-0.0005$). Zonal differences in skin permeability resulted solely from an increased proportion of "striata" individuals in populations from the Zones II and III. Therefore, we apparently are dealing with preadaptation. To have an opportunity to penetrate successfully into a new niche or adaptive zone, species should be preadapted to it. We call an organism preadapted if it is able to pass into new habitats; a structure is termed preadaptive if it can allow the undertaking of a new function without disturbance of the initial function (Mayr, 1974). Porter (1972) considered the presence of certain preadaptations as a necessary condition for successful fast evolution of amphibians populations in conditions of strong pollution. There are confirming data from the investigation of Collembola populations tolerant to pollution (Straalen and Wensen, 1986). Preadaptations are an important condition allowing animals to make the first step towards colonization of a new environment (Shvarts, 1980). Greater proportion of the "striata" in *R. arvalis* in urban populations is a marker of changes in their genetic structure under the new environmental conditions. Characteristics of skin permeability explain how the "striata" morph gained selective advantage in populations inhabiting anthropogenically transformed territories. In our opinion, this is one of the best examples of adaptogenesis strategy to new environmental conditions, when some fea-

tures of population polymorphism enable a species to exist successfully in new ecosystems. These results allow a new look at the whole complex of the "striata" features.

6.2. Oxygen consumption and urbanization

Our results showed that oxygen consumption by mature males of *R. arvalis* significantly varied among populations and differed from that of controls. Compared to control values, oxygen consumption by frogs from different zones was higher in Zone IV by 17.3%, in Zone III by a factor of 2, and in Zone II by 72.4% (statistically significant) (Vershinn and Tereshin, 1992). Experiments on 14 animals captured in 1993 and 1994 at the 500-1000 Ci zone of the East Urals radioactive trace (EURT) showed that the level of oxygen consumption by adult *R. arvalis* depends both on body mass and on the location of habitat, but the former variable is more significant ($F = 8.832$, $p < 0.0001$) than the latter (zonal) one ($F = 4.987$, $p = 0.006$). As the degree of urbanization increases (Table 8), oxygen consumption initially increases as well (from the control to Zone III) but then decreases in populations from Zone II, which may be evidence for adaptive modifications of a higher level than energy-consuming physiological ones (Shvarts, 1969, 1980). In the sample from the EURT, a considerable decrease in this parameter was noted, which we attributed to specific features of populations living under conditions of radioactive contamination; the exposure to radionuclide contamination may lead to a sharp inhibition of metabolic processes like hypooxygeny (Testov, 1993). Large energy-consuming individuals and those with a hereditary high level of metabolism (Dobrinsky and Malafeev, 1974; Vershinin, 1995) prevail in amphibian populations living within city borders (i.e., in the area with the maximum level of anthropogenic impact). Comparison of changes in the level of oxygen consumption and the liver index in young-of-the-year and adult frogs depends on the degree of urbanization which demonstrates that the zonal dynamics of these parameters are similar. This is evidence that the same changes that occur in populations from urbanized territories (Table 8, Fig. 5). Thus, frogs from the population exposed to anthropogenic impact proved to have a higher level of metabolism. This fact indicates that the level of oxygen consumption by amphibians, combined with other biophysical

Table 8. Oxygen consumption and liver index in juvenile and adult *Rana arvalis*.

Zones	O ₂ consumption, ml	Average liver index, ‰				
		N	Juvenile	N	Adults	N
EURT	0.000676±0.000019	14	53.05±2.0	30	34.6±5.6	11
II	0.001551±0.000023	10	51.4±0.54	651	104.3±7.5	5
III	0.001589±0.000032	5	53.5±0.79	306	54.8±5.8	8
IV	0.002299±0.000028	7	53.07±0.38	1350	56.7±5.5	9
C	0.000941±0.000022	11	48.9±0.53	666	43.1±1.5	117

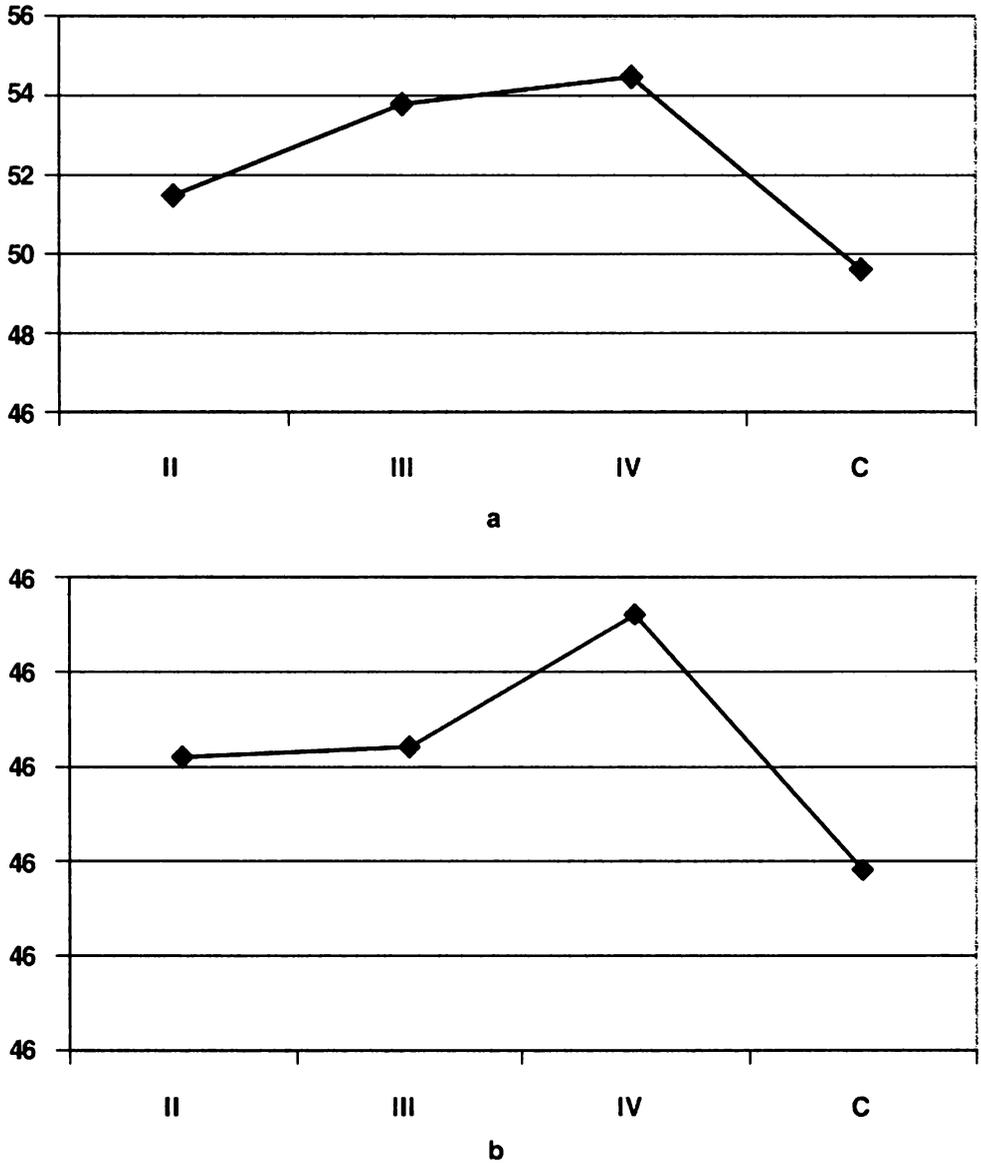


Fig. 5. Mean liver index (a) in *Rana arvalis* juveniles (‰) and the consumption of oxygen (b) (in mg/g · 10⁻³) depending on degree of urbanization (years 1980 - 1995).

(Tereshin and Vershinin, 1989) and electrophysiological tests (Vershinin and Tereshin, 1993) may be used in the general complex methods of bioindication, in particular, for estimating the degree of adaptive shifts in populations inhabiting anthropogenic landscapes.

6.3. Excitable tissues in *Rana arvalis* and urbanization

In the course of environmental transformation animals specifically respond to changes in ambient conditions. At the same time, individuals with more elaborate morphophysiological reactions are selected, and the population acquires heritable morphophysiological traits. This pathway is not advantageous thermodynamically. The next stage is the selection of individuals capable of maintaining an energy balance without developing pronounced morphophysiological adaptations (Shvarts, 1980). The level of adaptation determines the profoundness of transformations in the population. This draws attention to the analysis of variation in the functional state of excitable tissues of the organism (i.e., nerve and muscle tissues) that determine the mobility of individuals, the rate of their reactions to external factors, and eventually the state of organism as a whole and probably the stability of a species under new conditions. One of the integral parameters characterizing the functional state of excitable tissues, along with excitability, is the capacity for accommodation (Khodorov, 1969). This parameter reflects the level of functional ability of the tissue and directly depends on the accommodation capacity of individual nerve and muscle fibers (Bretag and Stampfl, 1975).

Because of the accommodation ability, the organism has an opportunity to react to new irritations, to be adjusted on new levels of ability, and to live and adapt to new conditions of existence. Accommodation of tissue properties indicate that as an irritant appears the threshold progressively grows. The accommodation speed is designated as $1/\lambda$, and λ is a constant. Accommodation parameter serves as a factor of functional stability of tissue. The decrease of this stability is connected to deviation of absolute meanings from the optimum. Increase in λ show a decrease in functional stability to adjustment of a tissue on a mode-repeated reaction on external influence and the reduction to breaking of the function (Khodorov, 1969, 1975). Accommodometry proved to be informative in the comparative study on estimating physiological activity of sapropel components (Tereshin et al., 1981; this method detected changes in concentrations of microelements in the environment).

The part of the investigations addressed specific features of excitability and accommodation capacity in *R. arvalis* exposed to different levels of pollution and urbanization and the relationships of these parameters with some characteristics of frog populations. Experiments were performed on 18 mature males during the field season of 1987-1988. The animals were taken from populations in different zones of an urban landscape depending on character of buildings, level of pollution, and the degree of use by humans according to our typification (Vershinin, 1980a; 1982a). Capture of animals was made in spring and summer seasons.

Table 9 shows the results of determining excitability of the nerve and muscle tissues of frogs from these zones. According to the results of a two-way ANOVA, the excitability of the nerve tissue had a significant zonal specificity ($p = 0.05$, $F = 2.632$) which disappeared after 30-min washing of the tissue in the Ringer's solution. A significant decrease in this parameter (i.e., higher excitability threshold) compared to that in the control was observed as the level of anthropogenic impact and pollution increased.

Table 9. Excitability of nerve and muscle tissues of frogs. Notations: V_0 and V_1 = excitability before and after washing.

Zones	Nerve				Muscle			
	$V_0 \pm m'$	N	$V_1 \pm m$	N	$V_0 \pm m$	N	$V_1 \pm m$	N
II	0.579±0.059	11	0.454±0.78	9	2.67±0.83	12	3.87±1.68	12
III	0.433±0.069	8	0.352±0.88	7	2.42±1.01	8	3.12±2.06	8
IV	0.457±0.054	13	0.546±0.78	9	1.72±0.80	13	1.41±1.76	11
C	0.383±0.038	27	1.191±0.46	26	2.26±0.53	30	4.06±1.08	29

Muscle tissue excitability had certain specific features but, as significance of differences was low, we can only note a certain tendency. Lower excitability (higher excitability threshold) was revealed in animals from Zones II and III where they are exposed to the greatest anthropogenic impact. The decrease in excitability may be regarded as a sign of adaptation of physiological systems to new environmental conditions. It should be noted that after washing the preparations for 30 min in fresh Ringer's solution, the values of excitability of the muscle tissue decreased (excitability thresholds became higher) in frogs from all zones (except Zone IV) and were not significantly different among themselves. This fact suggests that changes in muscle excitability in this case are not irreversible. Thus, changes of muscle excitability in frogs from areas with different levels of urbanization differ from corresponding changes in the nerve tissue. The greater the anthropogenic transformation of the environment, the lower the excitability of nerve tissue (the excitability threshold for rectangular electric pulses progressively increases). The values of absolute excitability of the amphibian nerve tissue may serve as a criterion for estimating the level of anthropogenic impact on the population and the ecosystem.

The results of determining the accommodation capacity of nerve and muscle tissues in frogs from populations living within city limits are shown in Table 10. The accommodation constant of the nerve tissue had significant zonal differences ($p < 0.05$, $F = 3.018$). Its values in frogs from the Zones III and IV were lower than in frogs from the Zone II and the control. After 30-min washing in fresh Ringer's solution, nerve tissue preparations retained this zonal specificity ($p < 0.05$, $F = 2.894$). Accommodation constants were noticeably reduced in Zones III and IV compared to those in the Zone II and the

Table 10. Accommodation capacity of nerve and muscle tissues of frogs. Notations: L_1 and L_2 - accommodation constant before and after washing.

Zones	Nerve				Muscle			
	$L_1 \pm S.E. (T=0.25)$	N	$L_2 \pm S.E. (T=2.5)$	N	$L_1 \pm S.E. (T=0.25)$	N	$L_2 \pm S.E. (T=0.25)$	N
II	5.00±0.64	10	34.71±4.75	9	0.529±0.36	12	4.99±0.91	12
III	3.93±0.69	8	14.90±5.41	7	0.555±0.44	8	5.64±1.11	8
IV	3.49±0.58	12	20.41±4.75	9	0.726±0.34	13	6.74±0.88	13
C	5.39±0.38	27	22.25±2.79	26	0.814±0.22	30	5.00±0.59	28

control. The highest accommodation capacity of the nerve tissue (the lowest accommodation constants) was revealed in animals from the Zones III and IV. The same is true for dynamics of the accommodation constant. It may be assumed that frogs suffering from relatively lower (Zone IV) and moderate (Zone III) anthropogenic impact are characterized by a comparatively greater adaptability of the nervous system.

The pattern of changes in the constant of muscle tissue accommodation depending on the level of urbanization differs from that of nerve tissue accommodation (Table 10). The lowest constant (the highest accommodation capacity) for muscle tissue was found in frogs from Zone II. Accommodation capacity decreased (accommodation constant increased) at lower levels of anthropogenic impact. After 30-min washing of muscle tissue in fresh Ringer's solution, this capacity became slightly lower in frogs of the control group than in frogs from other zones, although the difference was insignificant. These results demonstrate that frogs from populations exposed to the strongest impact (Zones II and III) are characterized by relatively higher adaptability than frogs from the control group and Zone IV.

The accommodation capacity of excitable tissues in frogs from urban territories was also studied in a stronger gradient of the test stimulus ($T = 2.5$ ms). The accommodation constants for nerve and muscle tissues of frogs from all the investigated zones did not differ significantly from those in the control group. The same was observed after 30-min washing in fresh Ringer's solution. Thus, frogs from the Zones II and III proved to have lower nerve excitability (a higher excitation threshold) than control animals: 0.579-0.433 vs. 0.457-0.383 ms. Changes of excitative threshold and index of heart are similar (Table 9; Fig. 6). Most probably, observable differences in nerve tissue excitation and excitation threshold show that except populations in which we found earlier adaptive physiological adaptation took place, because after washing up nerve tissues in Ringer's solution the difference disappeared. I did not find significant distinctions between right and left feet in any parameter.

The constant of nerve tissues accommodation and its dynamics in animals from Zones III and IV were significantly lower than in the Zone II and in the control (3.49 and 3.92 vs. 5.0 and 5.38 ms, respectively, $p = 0.038$; $F = 3.018$). This is evidence for higher accommodation capacity of these frogs (i.e., the existence of adaptive physiological changes in the absence of significant population differences in zones where the anthropogenic pressure does not reach the maximum value). Frogs from the forest population apparently had a lower accommodation capacity than those living beyond the zone of significant anthropogenic influence, and animals from Zone II demonstrated some profound qualitative differences (Vershinin, 1987a) which makes physiological adaptations less important. Physiological compensations as a way of adaptation to different conditions of environment are very elaborate but are thermodynamically inefficient (Shvarts, 1974a). Apparently, excitability of the nerve can reflect the levels of disturbance and pollution under conditions of urbanization, while its accommodation capacity reflects the degree of adaptive changes in populations at anthropogenically transformed environment.

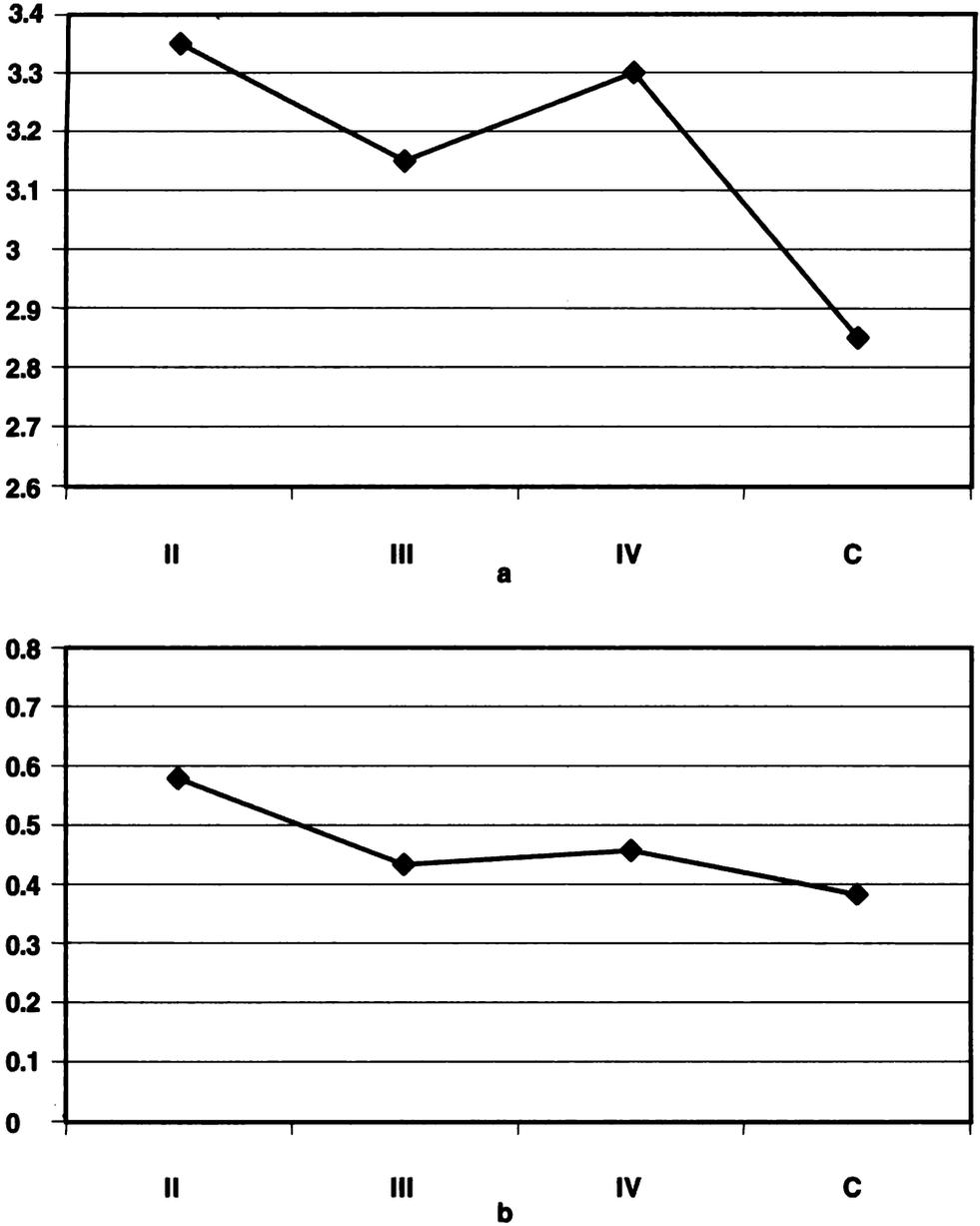


Fig. 6. Mean heart index in *Rana arvalis* juveniles (a: in %) and the excitability threshold of the nerve tissue (b: in V) in dependence from urbanization degrees (years 1980-1995).

6.4. Myocardial contraction of brown frogs and urbanization

Ecophysiological research undertaken together with the Department of Biophysics of the Ural State University in 1998-1999 involved studies of the physiological status of isolated amphibian myocardia (*R. temporaria* and *R. arvalis*) with biophysical methods. The heart muscle was chosen as an object of research because its myocardium has high sensitivity to various factors and is directly or intermediately influenced by molecular processes supportive of contraction. Thus, the task of this research was the estimation of the effects that anthropogenic factors (urbanization and accompanying it pollution) has on amphibian myocardium contractive function. The analysis of isometric contraction parameters has shown that the effort actively developed by isolated myocardium preparations for amphibians of the control group was significantly higher than amphibians from urban territory.

P_{\max} in urban animals averaged 83.3 ± 6.3 mg/mm² and the controls were 126.3 ± 15.3 mg/mm² ($p < 0.05$). The speed of isometric effort development in amphibians from urban populations was lower than in animal from forest population: 2.7 ± 0.4 and 5.2 ± 1.1 , respectively ($p < 0.05$). The data for the analysis of connection "length-force" were done in a mode and physiological sequence of variable loadings that simulated characteristic myocardium loads on an intact heart. At each fixed relative loading of a frog muscle from urbanized areas, the muscle shortened to a lesser degree. In other words, the muscles of this group are capable of moving the same mass a shorter distance. The ratio between changes of length and developed effort was used in the performance made by muscle (A). The coefficients of linear regression relationship of A on size of relative loading were: urban area - $b = 183.4$ ($R = 0.6$) and forest population - $b = 569.3$ ($R = 0.58$). The data showed that the useful work performed by muscles, in the first case is lower than in second. The estimation of the rest effort showed that the urban amphibian myocardium preparations had increased rigidity compared with the myocardium of forest animals. Coefficient of regression for the relation "change of length-change of effort of rest" for frogs from urbanized territory was $b = 8.27$ ($R = 0.83$) and for the control $b = 4.76$ ($R = 0.58$). The increase of calcium loading served as a test for myocardium sensitivity, a key ion for initiation and realization of contraction. Under increased Na^{++} in a perfusion with 1-5 mM, an unequal gain of isometric effort in two groups was found. In amphibians from urban populations it was $80.1 \pm 16.5\%$ (at 2mM Ca^{++}), $136 \pm 33.8\%$ (3 mM), $267 \pm 77.4\%$ (4 mM), and $323 \pm 94.4\%$ (5 mM) ($p < 0.05$). For animals from the control population the values were 181.9 ± 16.5 , 334 ± 37.5 , 633.0 ± 93.4 , and $912.9 \pm 98\%$, respectively. The data indicate a significant decrease of myocardium sensitivity in amphibians from urbanized territories to Ca^{++} .

The comparison of the basic parameters of contractive activity showed that the function of the myocardium in urban amphibians is significantly reduced. The results show that urbanization and accompanying environmental pollution are among the main causes in changes of the organism physiological parameters. Under the influence of anthropogenic pressure not only species composition, number, and variability but also

norms of individual reactions changed significantly (Shvarts, 1973; Andrzejewski et al., 1978). Medical and biological investigations showed that processes taking place in urban biota also having influences on human populations. Thus, the comparative research of the isolated myocardium of amphibians from populations from two qualitatively different territories showed that myocardium contractive function undergoes serious changes as a result of the influence of anthropogenic factors, and these changes lead to reorganization of mechanisms of electromechanical interface and myocardium contractive act kinetics. As a result, there is a decrease in the myocardium contractive function in amphibians from populations exposed to anthropogenic pressure. As a result, adaptive organism reaction arises that looks like heart hypertrophy and compensation of the contractive myocardium activity. As already noted above, in a number of works the increase of amphibians heart index was found in conditions of strong industrial pollution (Vershinin, 1985, 1997; Misyura, 1989). However, these mechanisms were not discovered. The result of our investigation suggest that the heart index increase correlates with the process of compensation hypertrophy developed as in response to a decrease of contractive myocardium properties. This phenomenon can be considered as a physiological reaction of an amphibian population in anthropogenic landscapes to the effect of industrial pollution and urbanization. These tendencies, in our opinion, allows us a better understanding of the biological influences of population processes under the conditions of urbanization and can provide the basis for new methods of bioindication of environmental condition and ecological monitoring.

The individual adaptation (accommodation) always appeared on the base of historically formed hereditary structure (i.e., it always resulted because of a certain inherited norm of reaction). All these "direct" adaptations are known in the main part of higher animals. They are expression of a wide ability for adaptive reactions and appeared as a result of a long history that was accompanied by complication and expansion by their inherited "norms of reactions." For this reason, an investigation of animal physiological reactions under fast environmental changes and connected with norm of reaction is most informative. Combinations of different methods is one of the ways of discovery of the most adequate and versatile information about processes that take place at different structural levels of biota organization. It enables us to reveal general regularities of investigated processes and to estimate depth and direction of observable changes.

Biophysical research give us the possibility to find a number of physiological adaptations in populations in an area but also provides a more constructive and versatile estimate of our earlier results on the same populations that we got with the use of traditional zoological methods. Presence or absence of physiological specificity can serve as an indirect indication of adaptive changes under the effect of urbanization and pollution. Urban habitat conditions result in formation of structurally functional specificity of amphibian populations expressed in behavioral, physiological, biochemical and morphological features of these isolates and the rate of metabolic processes. Being formed under

the influence of urbanization and pollution, amphibian populations have high stability and adaptive opportunities of nervous and muscle systems. Structure and mechanism of skin permeability in these animals have appeared under exposure to serious changes in environmental chemistry. The rate of metabolic processes is high (as compared with natural populations) and that allows them resistance to environmental influences in anthropogenic habitats. Some of the discovered features reflect processes of microevolution and allow an estimate of pollution and extend of observed transformation of communities. Because of the complex approach and use of methods from adjacent scientific fields, we have found an explanation for a number of the phenomena uncovered by traditional zoological techniques. Our experience seems to be a good example of fruitful scientific cooperation.

7.0. PHENOTYPICAL AND MORPHOPHYSIOLOGICAL FEATURES

7.1. Morphophysiology of juvenile brown frogs from urban areas

Environmental ecology features, where the processes of growth and development of animals proceed, form population specificity displayed in a number of parameters of relative mass of some organs (Shvarts et al., 1968). These parameters allow us to approximate information about a physiological condition of an individual at that moment. Biogeochemical anomalies can result in essential changes of internal organ indices (Shvarts, 1954) to one or another limit depending on a microelement composition of the environment. Relative mass of a liver is a convenient indicator of the influence of environmental chemistry (Petrov and Sharygin, 1981; Pyastolova and Trubetskaya, 1989). Analysis of morphological and cytological parameters of juvenile *R. arvalis* liver reflects changes in populations. In conditions of strong industrial pollution, the indices of liver, heart and kidneys in juvenile lake frogs increase (Misuyra, 1989; Zhukova et al., 1990). Change of the liver index can be induced by starvation, although for amphibians there is a well known but insignificant loss of liver mass with starvation. Changes in environmental conditions lead to increases of the level of metabolism which increases the heart functions and the index values (Shvarts et al., 1968).

Areas of urban growth represent areas with significant biogeochemical specificity and industrial pollution (Sharygin, 1980; Petrov and Sharygin, 1981). The frequency of people visiting such places results to a change of animal behavior (Sharygin and Ushakov, 1979; Lebedinsky, 1984a, b). Increased anxiety quite often is connected with additional locomotory activity, obviously, promoting to the heart index increase (Vershinin, 1985a). During 1977-1995 I collected data on a number of population parameters of brown frogs living on an area of urbanization including morphophysiological indices of froglets (Table 11). The preliminary results allowed me to ascertain only high values of relative heart mass in juvenile *R. arvalis* in populations from the entire city. The increase of liver indices in some strongly polluted sites was noted only in adults (Vershinin, 1983b).

Table 11. Morphophysiological (liver and heart) indices of juveniles frogs.

<i>Rana arvalis</i>				
Zones	N	Hep‰	N	Cor‰
II	708	50.34±0.52	708	3.38±0.04
III	306	53.53±0.79	306	3.16±0.06
IV	1376	52.78±0.37	1376	3.03±0.028
C	722	49.1±0.51	722	2.88±0.039
<i>Rana temporaria</i>				
II	132	45.88±1.32	132	3.09±0.12
III	700	45.41±0.57	700	3.36±0.05
<i>Rana ridibunda</i>				
II	183	53.5±1.08	183	2.62±0.06
C	57	27.7±1.93	57	3.19±0.11

The analysis of the indices in juveniles in *R. arvalis* from urban areas and beyond the city showed significant differences ($p = 0.05$). They are higher than in individuals from forest population (Fig. 5). The same we found for adult Moor Frogs. The differences in liver index of juveniles from urban and forest populations of *R. arvalis* correlated with significantly larger body sizes of froglets from those in populations under strong anthropogenic pressure (Vershinin, 1987a). Larger animals have higher relative liver mass (Shvarts et al., 1968). On the other hand, it can be induced by significant changes of environmental chemistry in urban area (Tables 1 and 2; Vershinin, 1985a, 1987b, 1990a). Frequency of the “striata” morph that is known for its physiological specificity is significantly higher in *R. arvalis* populations on urban territory (see Sections 5 and 6). Animals of this morph usually have high values of liver index (Shvarts and Ishchenko, 1968).

Dynamics of liver indices differences in metamorphosed animals (stage 53 of Dabagyan and Sleptsova, 1975) and ones in stage 54 for a long term period is shown on Fig.7. The presence of positive correlation ($R = 0.57$; $t_z = 1.6$) is noted in dynamics of differences in froglet indices in populations of from zones of multistory and low buildings. Dynamics of difference in froglets indices in populations of the forest park zone and the forest also differ and are positively correlated ($R = 0.62$; $t_z = 2.25$).

Comparisons of heart and liver index dynamics in 1980-1995 in juvenile *R. temporaria* from populations in the zones of multistory and low buildings have not revealed significant differences. At the same time, the dynamics of differences in froglet indices of metamorphosed animals and ones at stage 54 showed a positive correlation ($R = 0.56$; $t_z = 0.63$; Fig.7). Comparisons in morphophysiology of adult animal from populations in the multistory building zone and the forest population showed that the heart and liver indices in animals from the populations of the Zone II are significantly ($p < 0.0001$) lower than in the control. Relatively low liver index of animals from the zone of multistory buildings

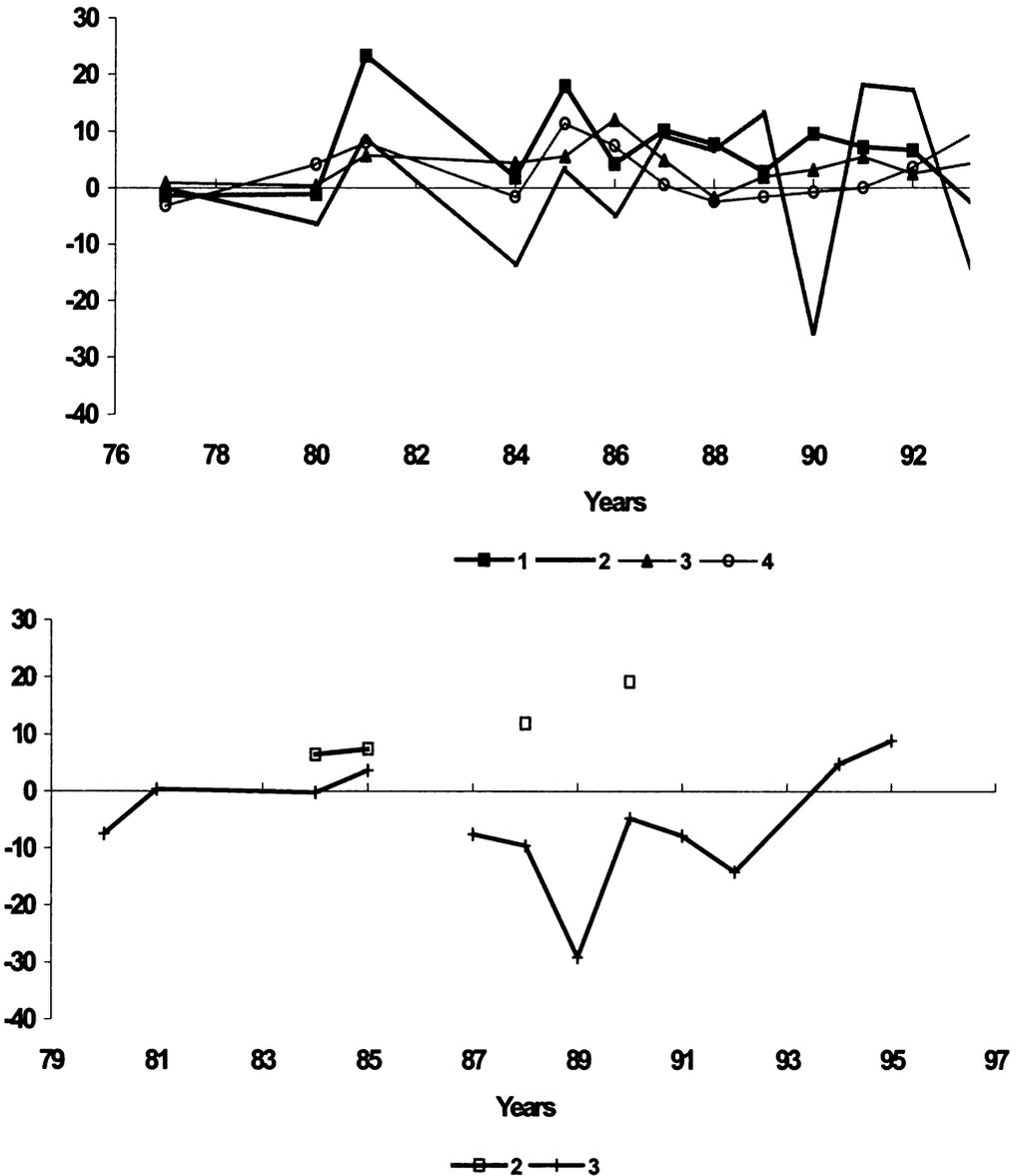


Fig. 7. a. Dynamics of the liver index difference value (%) in *Rana arvalis* juveniles (years 1980 - 1995). 1 - zone II, 2 - zone III, 3 - zone IV, 4 - forest. b. Dynamics of the liver index difference value (%) in *Rana temporaria* juveniles (years 1980 - 1995). 2 - zone II, 3 - zone III.

can be explained in terms of significant energy loss of the species at adaptation (Tarasenko and Tarasenko, 1989) in comparison with more ecologically plastic *R. arvalis*.

The initial hypothesis explaining high heart indices values in juvenile *R. arvalis* from populations of urban area is that the increase reflects anxiety. That is confirmed by investigations of the accommodation constant of muscle tissue in the adults (Vershinin and Tereshin, 1989). Animals from urban populations have low muscle excitation (high excitation threshold), and that is also explained by an increase of the anxiety. Pesticide pollution causes hyperactivity of tadpoles (Cooke, 1971), and variability of spontaneous locomotory larval activity is increased in lead-polluted water (Taylor et al., 1990). According to our data (Vershinin, 1990a), lead pollution of breeding ponds can reach 0.03 mg/liter. There is no significant difference in dynamics of the heart index values in juvenile *R. temporaria* from populations of multistory and low building zones because all samples were taken from urban areas.

Comparative investigations (on the materials from 1998-1999) of isolated myocardium preparations from *R. temporaria* and *R. arvalis* from populations in two territories distinguished on the degree of anthropogenic influence and pollution show that the myocardium contractive function undergoes essential changes as a result of influence of the anthropogenic factors. This leads to reorganization of electromechanical interface mechanisms and contractive act kinetics (Shklyar et al., 1999). There is a decrease in myocardial contractive function of individuals from populations exposed to anthropogenic pressure. As a consequence, adaptive reactions of organism arises as was shown in amphibian heart hypertrophy and directed on compensation of the myocardium contraction activity. The result of our research (Shklyar and Vershinin, 2000) gives a possibility to indicate anthropogenic transformation and pollution that could result in the reorganization of mechanisms of electromechanical interface and myocardium contractility kinetics. As a result of this process, the myocardial hypertrophy arises as a compensation.

Although the relative heart mass is a more sensitive parameter changed in all urban areas, the physiological features of animal populations on urban area influences the dynamics of liver index differences at metamorphosis (stage 53) and stage 54 froglets of *R. arvalis* and *R. temporaria*. The limits of this parameter are much wider in populations from multistory and low building zones (in comparison with animals from forest and forest park populations), that, by our opinion, reflects a high instability and heterogeneity of urban area conditions. Presence of a positive correlation between dynamics of this parameters in *R. temporaria* in populations from multistory and low building zones shows a similarity with this process in the two species under investigation despite of higher general sensitivity of *R. temporaria* (Vershinin, 1987a) to negative environmental changes in a low building zone in comparison with *R. arvalis*. Physiological and biophysical researches of adult *R. arvalis* from populations from urban and forest territories made at the same time have shown similarity of zonal dynamics in consumption of oxygen and liver indices and froglet heart indices and muscle excitation threshold. It indicates the reality of certain natural changes in urban populations of amphibians and an opportunity of the application of morphophysiological indices to population research of changes that take place in animal organisms

under the effect of anthropogenic factors. The analysis of long-term dynamics of these parameters not only showed the presence of some interrelated morphophysiological features in populations located in urban areas but also allowed conclusions about the specificity of the parameter dynamics. They are connected, on our sight, with differences in the degree of metabolic processes with adaptive changes leading to additional energy expenditures (Shvarts, 1980) and in some occasions with intoxication reactions with serious changes of environmental chemistry of urban territories.

7.2. Morphometric characters and their variability

Environmental influences on the main morphological features of amphibian development is very important. Embryogenesis proceeds in the eggs with permeable albumin (jelly) envelopes, and the whole period of larval development occurs in the external environment of breeding ponds. Initial conditions of the early developmental stages determine the features of all subsequent phases of life cycle and the phenotype of the individual.

As shown for *T. vulgaris* from different habitats of the forest park zone of Ekaterinburg, it is not isolation but the particular habitat conditions that play the major role in population divergence by morphological parameters (Ishchenko, 1966). Multifactorial ANOVA application to morphological indices of *S. keyserlingii*, *T. vulgaris* and *R. arvalis* (in 1977-1981) revealed differences among populations of these species from zones with different urbanization levels, but marked phenotypic features were not connected with anthropogenic transformation of the environment and reflect specificity of local developmental conditions (sizes of a pond, light exposure, temperature, density, quantity of food resources). In *S. keyserlingii* the highest level of these differences was found for the population from Shartash Forest Park based on the indices $L-L.c/L.c$ and $L/L.cd$ ($p < 0.0001$) (L = body length, $L.c$ = head length, $L.cd$ = tail length). In *T. vulgaris* the differences of the index $L-L.c/L.c$ ($p = 0.001$) in the population from the zone of low buildings and sexual differences in the index $L/L.cd$ ($p = 0.0001$) were revealed. In populations of *R. arvalis* from territories with different levels of urban transformation there were significant differences in the index $D.p/C.int$ ($p = 0.019$) ($D.p$ = first toe length, $C.int$ = height of the inner metatarsal tubercle) between Zones II and III, H and IV, IV and forest population (Table 12).

The most informative morphological parameter was the length of the body (L : Table 13). In populations of *R. temporaria* and *T. vulgaris* there was a significant increase of the body length in mature animals with increasing urbanization ($p < 0.0001$; $p = 0.0057$, respectively), and in *S. keyserlingii* there was only a tendency to increase body length. In *R. temporaria* the male size in the Zone II increased more significantly than the female size. In this regard, it should be noted that in populations of this species there is natural selection on larger male sizes (Giacoma et al., 1994). In *R. arvalis*, with the increase of environmental anthropogenic transformation, the female body length de-

Table 12. Morphological features, $M \pm S.E.$, of juvenile amphibians in urban sites.

<i>Rana arvalis</i>							
1980			1981				
Zones	N	L/T	CV	N	L/T	CV	
II	73	2.58±0.044	14.6	103	2.56±0.034	13.47	
III	20	2.41±0.04	7.48	43	2.51±0.024	6.3	
IV	363	2.65±0.014	10	206	2.61±0.012	10.9	
C	90	2.69±0.027	9.66	190	2.64±0.019	9.9	
1980			1981				
Zones	N	L/L.c	CV	N	L/L.c	CV	
II	73	2.82±0.033	10.11	103	2.6±0.018	6.99	
III	20	2.64±0.047	7.9	43	2.66±0.03	7.7	
IV	363	2.65±0.013	9.0	206	2.64±0.015	8.0	
C	90	2.65±0.022	7.9	190	2.65±0.014	7.4	
1980			1981				
Zones	N	Sp.c.r/D.r.o	CV	N	Sp.c.r/D.r.o	CV	
II	73	1.3±0.029	19.1	103	1.22±0.02	17.1	
III	20	1.34±0.038	12.7	43	1.3±0.033	16.6	
IV	363	1.42±0.012	16.5	206	1.33±0.01	11.3	
C	90	1.36±0.018	12.8	190	1.32±0.014	14.3	
1980			1981				
Zones	N	D.p/C.int	CV	N	D.p/C.int	CV	
II	73	2.21±0.08	32.7	103	2.2±0.054	24.8	
III	20	2.09±0.14	30.8	43	2.04±0.13	40.3	
IV	363	2.42±0.04	31.9	206	2.24±0.04	24.4	
C	90	2.26±0.05	20.8	190	2.23±0.41	25.5	
<i>Rana arvalis</i>			<i>Triturus vulgaris</i>				
Zones	N	L	CV	N	L	CV	
II	874	16.5±0.09	16.7	43	21.04±0.45	14.0	
III	355	14.6±0.09	11.5	16	19.53±0.88	18.1	
IV	1767	14.5±0.04	12.6	57	19.47±0.26	10.2	
C	892	14.7±0.07	14.0	7	17.84±1.43	21.2	
<i>Salamandrella keyserlingii</i>			<i>Rana temporaria</i>				
Zones	N	L	CV	Zones	N	L	CV
IV	186	25.31±1.15	61.7	II	132	15.28±0.19	13.9
K	7	23.64±0.91	10.2	III	812	12.74±0.08	17.6
<i>Rana ridibunda</i>							
Zones	N	L±m	CV				
II	315	27.69±0.63	40.6				
C	57	21.13±0.31	11.1				

Note: See text for morphological abbreviations.

creased ($p = 0.008$), but there is no significant differences in the body size in males. Depending on environmental conditions, phenotypically different juveniles are formed (Shvarts, 1972a). It was confirmed experimentally that the differences in larval life conditions result in significant changes of limbs proportions in froglets (Pikulik, 1977; Mitskevich, 1978).

Comparison of amphibian juveniles from different zones by the basic body proportions in some cases revealed the presence of significant differences (Table 12). For example, juveniles of *S. keyserlingii* from Kalinovskii Forest Park differ in the relative head length, $L-L.c/L.c$ from the animals from Shartash Forest Park ($p = 0.0015$; $F = 10.32$) and in the index $L/L.cd$ ($p < 0.0001$; $F = 20.06$). Within the Shartash population juveniles that metamorphosed from different ponds there were differences in indices $L-L.c/L.c$ ($p = 0.0002$; $F = 5.025$) and $P.a/P.p$ ($p = 0.0014$; $F = 4.052$) ($P.a$ = forelimb length, $P.p$ = hind limb length). There were significant differences in the index L/T ($p = 0.0006$; $F = 11.947$) between froglets of *R. temporaria* between the Zones II and III. *Rana ridibunda* juveniles, developing in conditions of different density and with different durations of development, differed in the relative head length. In *R. arvalis* juveniles, significant differences in some parameters are also known. Steady differences existed in the relative froglet shin length in Zones II and III from those in the forest park and the forest population ($p < 0.0001$; $F = 10.42$). Froglets from Zone II differed from those in the forest park and the forest in the indices $L/L.c$ ($p = 0.005$; $F = 4.27$) and $Sp.c.r/D.r.o$ ($p < 0.0001$; $F = 13.64$) ($Sp.c.r$ = snout width, $D.r.o$ = rostro-ocular distance). Most significant ($p = 0.01$) differences in proportions of the body were noted in *R. arvalis* juveniles from the Polzunova Street habitat (Zone II) where development was finished in drying conditions at a density of 9.3 larvae/liter (Vershinin, 1985a). There are differences in the indices L/T , F/T , and $D.p/C.int$ (T = thigh length, F = shin length) from froglets from other habitats. Juvenile from Zones II and III differed in average body length, some proportions, and phenotypical features from the young-of-the-year from Zone IV and the forest population, and these differences were caused by specific conditions of larval density, temperature, and water chemistry. All the morphometric indices stay within limits characteristic for each amphibian species (Bannikov et al., 1977). As a whole, the sharp changes in the juvenile body proportions are noted rarely and connected with significant deviations in developmental conditions. Adult animal morphological indices are stable.

The body sizes of a juveniles from populations under different degree of anthropogenic influence also differ significantly in three species: *T. vulgaris*, *R. arvalis* and *R. temporaria* (Table 13). In all cases I observed the increase of the body size with the increase of urbanization ($p = 0.037$, < 0.0001 and < 0.0001 respectively). The values of variation coefficient of the main morphological parameters in both juvenile and adult *R. arvalis* and *R. temporaria* in Zones III and IV are low (as compared with the forest population) and increased in populations from Zone II and quite often exceeded parameters of the forest population.

Table 13. Morphological features, $M \pm S.E.$, of adult amphibians from urban sites. Morphological abbreviations are given in the text.

<i>Salamandrella keyserlingii</i>						
L						
Zones	N	Females	CV	N	Males	CV
III	2	57.75±5.25	6.7	4	61.63±3.7	6.2
IV	169	56.77±0.57	15.4	198	58.02±0.53	11.4
C	22	55.26±1.58	9.7	19	57.56±1.70	6.6
L-L.c/L.c						
Zones	N	Females	CV	N	Males	CV
III	1	4.0		4	4.1±0.15	7.2
IV	96	2.59±0.14	51.5	95	2.6±0.14	52.3
C	21	3.88±0.11	13.4	19	3.95±0.14	14.9
L/L.cd						
Zones	N	Females	CV	N	Males	CV
III	1	0.90±0.82		4	4.1±0.03	6.1
IV	96	1.96±0.09	47.1	95	2.64±0.09	47.8
C	21	1.11±0.04	16.8	19	3.95±0.09	33.8
P.a/P.p						
Zones	N	Females	CV	N	Males	CV
III	1	0.90±0.14		4	0.97±0.04	8.6
IV	96	0.98±0.02	15.3	95	1.01±0.02	14.8
C	21	0.98±0.03	11.9	19	0.95±0.02	7.3
<i>Triturus vulgaris</i>						
L						
Zones	N	Females	CV	N	Males	CV
II	99	39.77±0.31	7.2	57	37.24±0.41	7.1
III	39	38.47±0.5	8.3	28	37.08±0.59	8.9
IV	42	37.16±0.48	10.2	20	36.82±0.7	9.1
C	14	36.79±0.83	8.4	5	36.38±1.39	10.8
L-L.c/L.c						
Zones	N	Females	CV	N	Males	CV
II	99	3.38±0.04	13.2	55	3.04±0.06	13.4
III	23	2.77±0.09	14.8	28	2.94±0.11	19.7
IV	42	3.38±0.09	18.4	20	3.14±0.21	29.2
C	15	3.61±0.09	10.5	5	3.05±0.33	24.3
L/L.cd						
Zones	N	Females	CV	N	Males	CV
II	99	1.07±0.02	20.9	55	0.87±0.02	17.2
III	23	1.07±0.11	48.6	28	0.88±0.02	11.4
IV	42	0.99±0.02	10.6	20	0.91±0.02	8.6
C	15	0.99±0.03	10.3	5	0.80±0.07	18.2

Table 13. Continued.

P.a/P.p						
Zones	N	Females	CV	N	Males	CV
II	99	1.03±0.01	9.0	55	0.99±0.01	8.4
III	23	1.00±0.01	6.8	28	1.03±0.02	9.1
IV	42	1.01±0.01	9.1	20	0.99±0.02	10.2
C	15	1.02±0.02	6.8	5	1.02±0.03	7.6
<i>Rana arvalis</i>						
L						
Zones	N	Females	CV	N	Males	CV
II	34	45.19±1.15	21.6	38	54.67±1.09	14.8
III	18	47.11±1.59	13.2	23	52.71±1.40	12.1
IV	46	49.49±0.99	14.7	72	52.79±0.79	8.7
C	31	51.72±1.21	14.2	72	53.43±0.79	10.4
L/T						
Zones	N	Females	CV	N	Males	CV
II	23	2.19±0.05	12.5	26	2.19±0.03	7.5
III	17	2.12±0.04	7.0	15	2.16±0.04	6.9
IV	36	2.09±0.03	4.9	17	2.25±0.03	7.5
C	14	2.17±0.04	4.5	7	2.20±0.03	5.4
L/L.c						
Zones	N	Females	CV	N	Males	CV
II	23	3.21±0.07	11.8	26	3.02±0.08	12.2
III	17	3.17±0.09	10.9	15	3.22±0.03	3.7
IV	36	3.06±0.04	4.6	17	3.29±0.05	10.8
C	14	3.27±0.07	5.6	7	3.32±0.06	6.3
Sp.c.r/D.ro						
Zones	N	Females	CV	N	Males	CV
II	23	1.09±0.04	22.2	26	1.00±0.06	12.5
III	17	1.03±0.03	10.3	15	1.01±0.03	11.1
IV	36	1.06±0.04	16.9	17	0.95±0.02	10.9
C	14	0.98±0.1	25.2	7	1.06±0.03	11.7
D.p/C.int						
Zones	N	Females	CV	N	Males	CV
II	23	1.75±0.18	41.2	26	2.17±0.06	12.7
III	17	1.69±0.09	20.9	15	1.74±0.08	19.9
IV	36	1.61±0.12	28.1	17	1.76±0.05	18.1
C	14	1.98±0.21	28.0	7	1.97±0.13	23.9
<i>Rana temporaria</i>						
L						
Zones	N	Females	CV	N	Males	CV
II	3	64.53±5.1	14.9	22	70.67±1.89	14.9
III	30	57.98±1.62	21.8	60	65.47±1.14	11.7
IV	27	70.09±1.70	10.3	17	67.84±2.15	9.2
C	45	53.85±1.32	16.6	41	52.55±1.38	14.8

Table 13. Continued.

<i>Rana ridibunda</i>						
L						
Zones	N	Females	CV	N	Males	CV
II	26	69.38±3.95	33.8	16	75.21±5.04	17.3
C	110	63.71±0.77	13.5	133	59.29±0.70	12.9

The range of modification variability depends on the lability of structures (more precisely, from developmental processes) of an organism and from variation of the environment. If the organism's development occurs under a complex of various conditions, its structures should be adaptive and the reactions should reach wider ranges of changes. If the general variability decreases, a population ne the result of increases in its stabilizing form, and the increase of variability and dilation of variation is only the result of a decrease in selection. The study of variability of the larval body sizes in *R. arvalis* in experimental imitations of pollution (Bugaeva, 1983) revealed that the influence of phenol, sodium and cooper sulphates solutions increase the variability of the body size by 2X. Genetically related clutches were used in the experiment. So the variability of growth may be explained by a relaxation of a genotypic spectrum of phenotypical realizations at environmental deviations. In Caudata, more sensitive to habitat changes (*S. keyserlingii*, *T. vulgaris*), the variability decrease is noted in populations subjected to the maximum anthropogenic pressure where normal reproduction is impossible. Examples of the decrease of variability of morphological parameters in tailless amphibians with increasing anthropogenic influence are well known (Petrova, 1995). The data on variability of the basic morphological parameters of amphibians are stable for a number of years and reflect, on the one hand, the appearance of adaptive changes in brown frog populations in multistory building zones and, on the other hand, the significant heterogeneity and occurrence of new components in most urbanized parts of the city habitats. Phenotypical features are formed in local environmental conditions on the base of existing reaction norms and reflect habitat specificity and are mostly not connected with anthropogenic transformations. Based on our results, it is possible to conclude that one of the main features of urban landscapes is the high habitat environmental heterogeneity in a small area. That has effects during growth and development of amphibians in the appearance of a number of features. The occurrence in some cases of significant differences in proportions of the body in different populations shows habitat or microhabitat specificity of environmental components.

Among all years of investigation, the picture of variability dynamics of the main morphological parameters depends on urbanization degree is repeated and reflects the presence of adaptive changes in populations in Zone II (in ecologically plastic species). This indirectly confirms the data obtained using the nerve-muscle accommodometry in *R. arvalis* for the presence of physiological adaptation in animals from Zones III and IV

and the absence in those from the forest population and Zone II. Dynamics of variability of morphological parameters illustrates ecological rigidity of species not tolerant to anthropogenic transformation of habitats.

7.3. Morphological anomalies in urban areas

The features of biology of the amphibians, whose development proceeds in aquatic environment outside the parental organism, cause significant dependence of these animals on peculiarities of the environment. Individuals with various morphological deviations almost always occur in amphibian populations (Hebard and Brunson, 1963; Borkin and Pikulik, 1986; Talvi, 1994). The causes of these deviation are different: mutation process (Wittouck, 1980; Neff et al., 1987), partial neoteny (Breuil, 1981), parasites (Ruth, 1987), habitat isolation (Reynolds and Stephens, 1984), injures of development (Obukhova, 1984), and abnormal regeneration (Baranovskii and Kudokotsev, 1988). The same defect can be induced by various mutations (Uehlinger and Beauchemin, 1968), viruses (Fisher, 1976), and temperature influences (Voitkevich, 1961; Van Vallen, 1971) and also may result from natural hybridization (Gollmann et al., 1984; Roberts and Verrell, 1984; Ogielska, 1991).

Alongside the natural causes, there are examples when responses are induced by such indirect consequences of human activity as environmental pollution by waste of various kinds (Hazelwood, 1970; Rose and Harshbarger, 1977; Mizgireuv et al., 1984; Harshbarger and Rose, 1989), pesticides (Cooke, 1973a; Brooks, 1981; Osborn et al., 1981; Alvarez, 1995), changes in pH (Gosner, 1957; Flax, 1986; Andren and Nilsson, 1988), radioactivity (Okawa, 1994), genetic isolation resulted from natural habitat fragmentation (Simberloff, 1983) and changes of genetic structure of populations related to their declines (Flindt, 1985; Cunningham et al., 1994). The long of life of amphibians and their trophic niche and the specificity of the life cycle make them sensitive to chronic influences of toxicants (Gendron et al., 1994). Among the causes inducing anomalies in amphibians is ultra-violet radiation caused by thinning of the atmospheric ozone layer (e.g., Grant and Licht, 1994). The mutation forms are specific for every organism, and the frequency of any single mutation is different. Frequency of mutations is influenced by different factors. However, the specificity is obviously determined by the organism itself with its historical hereditary basis. Some organisms are tolerant and have few mutations while others mutate intensively. The forms with more significant individual variability appear to be very plastic during evolutionary process and react to environmental changes much faster. Usually the anomalies may be divided in two large groups: hereditary and acquired anomalies. The anomalies arising as a result of developmental injures and atypical regeneration in many cases are determined by inhibition or activation of the thyroid function by pollutants, and these may lead to suppression of proliferate and morphogenetic processes in larval development and limb regeneration (Syuzumova, 1985) and influence the level of metabolic processes (Tokar et al., 1991).

The majority of data concerns abnormalities in relation to their environment (Pliss and Kchudoley, 1979; Cooke, 1981; Pyastolova et al., 1981; Vershinin, 1982a; Dumpert, 1986; Baranovskii and Kudokotsev, 1988; Meyer-Rochov and Asashima, 1988). Experimental research on amphibian confirm the influence of many chemical agents on the increase in frequency of morphological abnormalities (Bugaeva, 1982; McCue, 1989; Rengel and Pisano, 1989; Taban et al., 1982). In discussions of the frequencies of morphological anomalies, it is necessary to understand a border between the norm and pathology (Tyler, 1989). The classification of selected types of morphological anomalies was provided above in Section 2.

The data below is a result of generalization of long-term investigations on the areas of urban development (Ekaterinburg) from 1977-1993 on all amphibians in this area. The results indicate a species age-specificity of distribution in abnormality types and their frequencies in amphibian populations subjected to different levels of anthropogenic influence (Table 14). In adult *S. keyserlingii* in the forest park city zone, over a half of all anomalies concern limbs, and the rest concern pigmentation, the axial skeleton, eyes, and hernia. In juveniles, except for limb anomalies, only edema was found; in forest populations the ratio of anomalies types is almost the same. Significant differences are not found, although the number of anomalies types in adult animals in the forest population is more than two times lower compared with the forest park zone.

Table 14. Occurrence of different types of anomalies in amphibians from urban sites. Notations: II - multi-story buildings; III - low buildings; IV - forest park; C - forest population; AD - adult; and JUV - juvenile.

<i>Salamandrella keyserlingii</i>								
ZONES -->	II		III		IV		C	
AGE CLASSES -->	AD	JUV	AD	JUV	AD	JUV	AD	JUV
polydactyly					1	1		
ectrodactyly					8	5	1	
syndactyly					4			
clinodactyly								1
brachymely					1	1		
taumely					1			
polymely					2			
eye defects					2			
axial skeleton deformities			1		4		2	
pigmentation defects					4			
edema						1		
defects of internal organs							1	
Total anomalies			1		28	8	5	0
N			6		382	300	55	8
Total percentages			6.7		7.3	2.7	9.1	0

Table 14. Continued.

<i>Triturus vulgaris</i>								
polydactyly	2							
ectrodactyly	3							
clinodactyly	3		1					
brachymely	1							
taumely						1		
skin neoplasm	3							
edema		1						
defects of internal organs		1	3				1	
Total anomalies	13	2	4	0	1	0	1	0
N	156	67	70	17	64	57	18	7
Total percentages	8.2	3.0	5.7	0	1.6	0	5.6	0
<i>Rana arvalis</i>								
ectrodactyly	6	7				2		1
syndactyly	1							
clinodactyly	1						1	
non-flexible limb		1						
hemimely		1	1	2	1	1		2
ectromely	3	6				1		
eye defects		1			1			1
iris depigmentation	1	55		14	1	67	1	10
axial skeleton deformities	1	2			2	1		1
mandibular hypoplasia		2		1		5		5
pointed back pattern	8	46	2	5		4		1
pigmentation defects	3	9	2	2	2	3		1
edema		1		2	1			
Total anomalies	24	142	5	27	8	90	1	23
N	170	3422	53	1004	183	5309	57	2939
Total percentages	14.1	4.2	9.4	2.7	4.4	1.7	1.8	0.78
<i>Rana temporaria</i>								
ectrodactyly			1	3				
clinodactyly				1				
hemimely				1				
taumely				1				
ectromely				1				
eye defects		1	1	1				
iris depigmentation			1	3				
pointed back pattern			1					
pigmentation defects		3	5	2				
edema		2		1				
Total anomalies	0	6	9	12	0			
N	41	235	151	2239	203			
Total percentages	0	2.6	6.0	0.54	0			

Table 14. Continued.

<i>Rana ridibunda</i>		
ectrodactyly		2
non-flexible limb		8
pigmentation defects	1	28
edema		4
defects of internal organs		2
Total anomalies	1	44
N	123	953
Total percentages	0.8	4.6

In populations of *T. vulgaris* from the zone of multistory buildings, 75% of all anomalies concern defects of the limbs and more than 25% involve skin neoplasms. In populations from other zones (low buildings and forest), the anatomical pathologies are ovarian hernia and lung defects. Juvenile anomalies are fixed only in the zone of multistory buildings: premetamorphic edema and hernia. Significant differences were not found, but only one of five types of anomalies was noted in adult individuals in the forest population.

The most complete data were received for *R. arvalis*, which is widely distributed both in natural and an anthropogenic landscapes of the Urals. In populations in multistory building zone, over 30% of the froglets have alterations to the spotting pattern of the back (fragmentation of coloration) and others pigment deviations of the skin. There is a high frequency of iris depigmentation which can be regarded as partial albinism (Dubois, 1979) and represents a recessive mutation (Rostand and Darer, 1970). In homozygotes, this leads to complete absence of xanthophores and iridophores (Richards et al., 1969) and, apparently, in some species can influence survivorship of individuals (Browder, 1975). About 6% concerns limb anomalies. Others involve defects of the eye, axial skeleton, edema, and mandibular hypoplasia. In the forest population about a half of all deviations involve iris depigmentation, almost 25% have mandibular hypoplasia and a few limb anomalies. Among adult animal from populations from multistory building zones, almost half of the defects concerns limb anomalies and the same percent have spotted back skin (spotted pattern and other disturbances of skin pigmentation) as well as iris depigmentation and curvature of the axial skeleton. A part of the anomalies were found in froglets and not among adult because of the decrease of viability of individual carriers or higher lethality (Droin, 1988). These are edemas, non-flexible legs, mandibular hypoplasia, and some eye defects. Only iris depigmentation was found in the forest population. Adult individuals from populations in Zone II significantly differed from those in the forest and the forest park zones ($p < 0.01$ $\chi^2 = 6.66$; $p < 0.01$; $\chi^2 = 10.15$, respectively).

Rana arvalis froglets from populations in all zones differed significantly from each other ($\chi^2 4.5-70.9$; $p = 0.05-0.001$), but the differences between populations from Zones II and III were not as serious as between the populations from urban territories and

forest. In adult *R. temporaria*, anomalies were found only in populations from zones of low buildings and their main part (about 65%) were connected with abnormal skin pigmentation, iris depigmentation, and eye and limb defects. Among froglets, the percent of abnormal individuals was higher in populations of multistory building zones and mainly represented by skin pigmentation defects, edema, and iris depigmentation. In low building zones, a half of the deviations were connected with limbs, and iris depigmentation, defects of skin pigmentations, and edema also occurred. In adult *R. ridibunda*, only anomalies of skin pigmentation were found. They prevailed in froglets (more than 50%), about a quarter presented in animals with limb anomalies, all the rest co-occur with edema and deviations of internal organs.

The presence of a high percentage of limb anomalies in adult *S. keyserlingii* in many cases is determined by their abnormal regeneration after damages during mating. In Sakhalin populations, this may occur in 13-31% of individuals (Basarukin and Borkin, 1984). In Caudata, the high natural variability of limb skeleton structure occurs quite often (Dinmore and Hanken, 1986; Zaffaroni and Zavanella, 1989). In comparison with froglets, percentages of abnormal animals was much higher because there is a summation of inherited anomalies and developmental deviations with cases of abnormal regeneration that quite often is under conditions of changes in environmental chemistry (Zavanella et al., 1984). Total frequencies of anomalies in adult animals varied from 5.9-16.6%. I also found direct dependence of the frequency of anomalies with the level of environmental pollution (Vershinin, 1990e).

The deviation spectrum in *T. vulgaris*, except for higher frequencies of limb anomalies as compared with *S. keyserlingii*, included skin neoplasms which reflects the level of environmental pollution by cancerogenic substances (Breedis, 1952; Dumont et al., 1979). Skin lesions were used as a special "newt's test" (Pliss and Khudoley, 1979). The general level of morphological anomalies frequency in populations of the central part of Ekaterinburg surpass that of London populations of *T. vulgaris* (Roberts and Verrell, 1984): 8.22% vs. 4.56%. By my opinion, that shows higher pollution level of urban environment in the Urals. The abnormality frequencies in mature newts also increased with increasing environmental changes and urbanization. Anomalies in juvenile newts were noted only in populations of the multistory building zone and their frequency was lower (2.99%) than in adults, probably because the origin of the most deviations in this species is caused by abnormal regeneration and neoplasmas.

Comparisons of anomaly spectra in adults and froglets of *R. arvalis* show that among adult there are no s mandibular hypoplasia and non-flexible legs which are lethal for the animal. When analyzing the types of limb anomaly frequencies, we noted that there is a tendency for distal elements reduction that usually accompanies an intensification of microevolutionary processes in populations (Hanken, 1985). Skin pigment deviations may be connected to the specificity of the genetic structure of urban populations and to the disturbances of melanophore aggregation dynamics under the influence of pollution. Contaminations can cause dissipation and fragmen-

tation of normal coloration (Voronova et al., 1983) and also increase the skin melanosomes (Linnenbach et al., 1987). Percent of individuals with iris depigmentation in froglets from urban areas in 1985 reached 6.13% in one population. It is considered that, in most cases, this defect is caused by a recessive mutation and therefore can indicate the intensity of mutations. For comparison, the frequency of this anomaly in *R. esculenta* in central France varied from 0.2-7% (Dubois, 1979). Detailed studies of the frequency of iris depigmentation dynamics (Fig. 8) from 1980-1998 (Vershinin, in press) showed evidence for the presence of inbreeding depression in urban populations and for high mutagenesis in the urban environment. During all years of investigations of froglets from populations living on urban territory, I have found 147 individuals with unilateral defects (1.4%) and 30 individuals (0.27%) with bilateral (N = 10953), right-sided 0.6% (22), and left-sided 0.5% (19). In forest population in all years of study, I have found 8 froglets with unilateral display of this character (0.24%, N = 3306), among them 6 that were left-sided (0.18%), 2 that were right-sided (0.06%), and 5 that were (0.15%) bilateral. Animals with unilateral iris depigmentation are rare. The coloration of the skin in all abnormal individuals did not differ from normal ones.

If we estimate the ratio of this given defect to the general number of anomalies in populations of different zones in urban territory (Vershinin, 1995) and in forest population, we see that this value changes from 38.7% to 74.4%, and in most cases there are significant differences (only between the forest park zone and Zone II; $\chi^2 = 8.42$; $p < 0.01$). As a whole, frequencies of the anomalies among juveniles in urban territory is 52.5%, and in the forest population it is 43.5% that makes almost a half of recorded

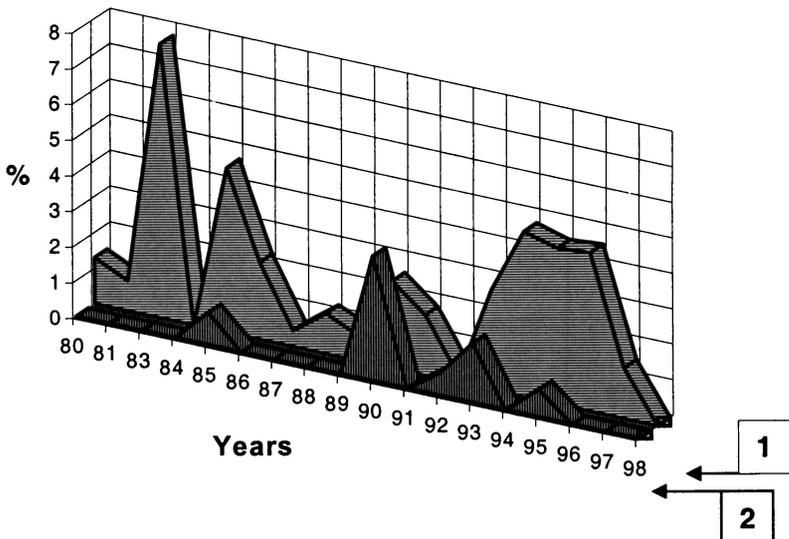


Fig.8. Frequency of anomalies in urban and forest populations. 1 - urban populations (summarized), 2 - forest.

morphological deviations. For the whole period of study in populations on the urban territory, I recorded three adults (0.36%; N = 826) individuals with this defect. In 1987 (right-sided, immature animal), in 1991 (bilateral immature male, 0.12%, N = 826; 1976-1998), and in 1992 (left-sided, mature male). Among all adult animals from the forest population for all years of investigation, I noted only one immature individual (1989) with a left-sided defect (0.15%, N = 648; 1976-1998). The frequency of anomalies among froglets from urban areas and the forest population differed significantly ($\chi^2 = 28.99$; $p \ll 0.001$). Comparison of adult animals from the urban territory and from the forest population did not show significant differences ($\chi^2 = 0.585$).

Frequency of anomalies in adult *R. arvalis* in the forest population is 0.15%, which is close to the values for adult *R. esculenta*, 0.07% (Dubois, 1979). The comparisons of the frequencies of iris depigmentation in froglets of *R. esculenta* (data from Dubois, 1979) and *R. arvalis* (my data) showed that animals from the urban populations (Ekaterinburg) differ significantly ($\chi^2 = 58.28$; $p \ll 0.001$), but this is not the case of the animals from the forest population ($\chi^2 = 3.59$). According to our data (Fig. 9), frequencies of anomalies in froglets and adult animals in urban areas differed by 4.4 times ($\chi^2 = 8.04$; $p < 0.01$) and in the forest population by 2.6 times ($\chi^2 = 0.876$; difference not significant). The total frequency of defects in all juveniles was higher than in all adult by 4.9 times ($\chi^2 = 12.39$; $p < 0.001$). It is possible that iris depigmentation can somehow influence the possibility of juveniles to survive to adult. Probably, despite the lack of obvious reasons for decrease in animals viability caused by this anomaly, there is a connection with survivorship which was already noted by others (Rostand, 1953; Dubois, 1979) for the green frogs complex.

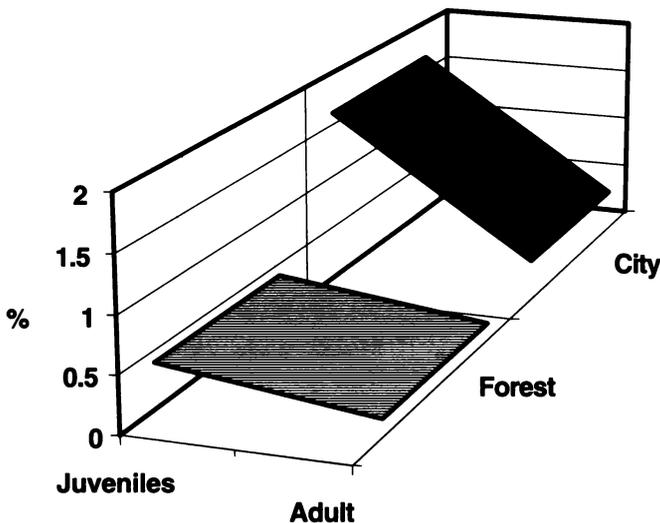


Fig. 9. Summarization of abnormality frequencies in juveniles and adults.

As already mentioned, there are unilateral and bilateral variants of defects (e.g., eyes). If we believe that the anomaly is caused by a developmental deviation, it is logical to assume independent formation of this feature on each side. The probability of unilateral display is equal for an individual from division of quantity depigmented eyes on the double general number of animals. Hence, the probability of a symmetrical variant (independent formation of the feature on each side) will be equal to the square of the probability of frequency of this anomaly, and the theoretical number of symmetrical variants in a sample will be equal to a multiplication of total individuals number on the calculated probability of the symmetric variant. Having calculated (on juveniles) a prospective "symmetries" number, I have compared it to the real data. I found that the actual probability of a symmetrical variant on two order above (above prospective) is 0.00246 vs. 0.0000625 ($\chi^2 = 32.45$; $p < 0.001$). The results are evidence against the hypothesis of independent formation of a given anomaly from each of the sides in individuals with two depigmented eyes. I believe that it is an argument for a hereditary nature of depigmentation in this case. Probably, eye depigmentation has a genetic nature, as well as all anomalies having similar phenotypic appearance. Most likely, it is the whole complex of recessive features, which in homozygotes can promote, on the one hand, high frequency of abnormal individuals appearance. With low survivorship caused by inbreeding depression in the conditions of urban isolates, there arises a result of natural habitats fragmentation and low number of a population reproductive part (Simberloff, 1983). Among the prospective causes of the fluctuations of this character, we selected the influence of the temperature in the initial period of development because the years when this defect was not found were characterized by the absence of spring frosts (i.e., in the period of reproduction and embryonic development). It is possible that the appearance of this anomaly is promoted by low temperatures in spring. It is known that the thermal factor can influence the frequency of amphibian anomalies (Voitkevich, 1938; Voitkevich, 1961; Van Valen, 1974; Obuchova, 1984). In brown frogs close to *R. arvalis*, *R. temporaria*, in all years of study that anomaly was noted in urban areas only once in froglets (0.00039%, $N = 2534$) and once in adults (0.2%; $N = 491$). It was never observed in the forest population. Thus the low frequency of this defect in *R. temporaria* can be connected with rather greater, than in *R. arvalis*, role of hereditary components in ontogenetic processes, lower ecological plasticity (Surova, 1988), and with its higher tolerance to low temperatures (Hertwig, 1898; Terentjev, 1950). The dynamic of this defect frequency in different years in *R. arvalis* is similar (Fig. 10). In 1984 and 1998, I did not record this anomaly in urban populations. In 1985, 1990, 1994, and 1996, I noted the highest frequency of this defect, 4.4-4.66%, in the urban populations and one case in the forest population 0.9% ($N = 108$). Probably, the conditions responsible for the external appearance of this anomaly, unlike the others deviations, are similar in all territory of urban areas and in suburban forest. At the same time, the frequency of this feature in *R. arvalis* populations from urban areas, as a whole, were more than twice those in the control forest populations.

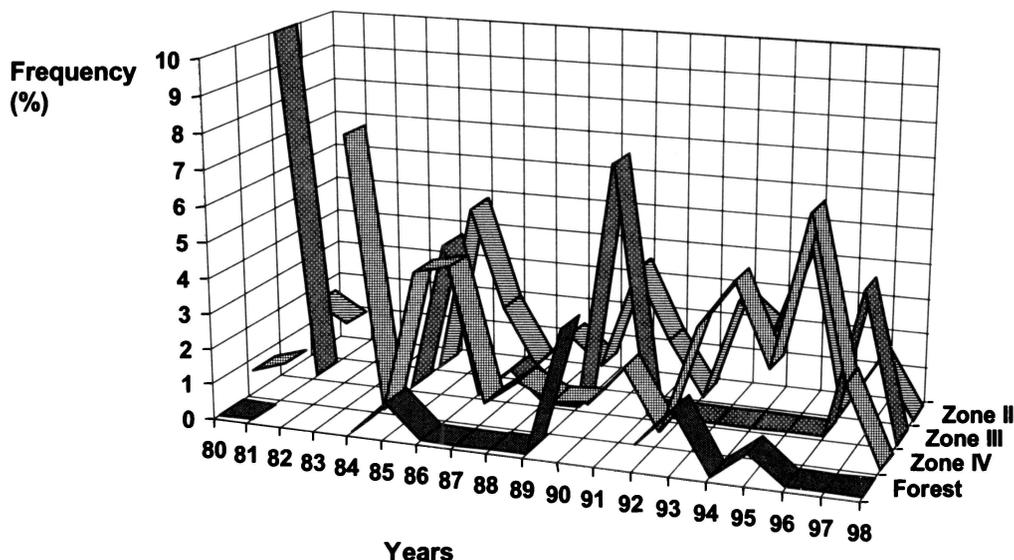


Fig. 10. Dynamics of frequency of anomalies in froglets by zones.

Anomaly frequency in another brown frog species, *R. temporaria*, is lower both among froglets and adults which may be correlated with rather low ecological plasticity of this species and a prevalence of hereditary components. In adult *R. temporaria*, anomalies were found only in the low building zone, and the ratio of deviation types was similar to that in *R. arvalis*; in froglets from multistory building zones pigment deviations prevail compared with froglets from the low building zone where limb defects are more widespread and pigment deviations are second. A narrow spectrum of anomalies and their low frequency are probably caused by high abnormal individuals mortality in an ecologically rigid species in urban areas.

In *R. ridibunda*, as well as in brown frogs, the reduction of distal elements prevails among limb defects, and (for understandable reasons) only among froglets did non-flexible legs occur. Total abnormality frequency is relatively low in adults, 0.81%, and in froglets, 4.62%. By the data for natural populations of green frogs in France, anomalies frequency among the adults is 5.1 and 3.0% among froglets (Dubois, 1979); near Karaganda (Kazakhstan) in *R. ridibunda* frequency of limb pathologies varied from 2.4-8.8% (Aitbaeva et al., 1991). According to our data for the area near Poti, Georgia, the frequency of morphological anomalies in adult *R. ridibunda* was 4.8% (N = 60) and in juveniles 8.1% (N = 74). *Rana ridibunda* is one of most plastic species adapted to transformed and polluted environments and can exist even in industrial discharge areas (Misyura et al., 1990).

If we want to speak about an origin of any type of anomalies, it is difficult to receive the unequivocal answer. With some probability it is possible to tell that there is a signifi-

cant part connected with unusual skin and eye pigmentation that have genetic a basis and also represent somatic mutations. Defects of the axial skeleton and the limbs, having bilateral symmetry, apparently are also more often hereditary as well as some cases of internal organs deviations and lethal postmetamorphic edema. The majority of dominant mutations in populations reduce viability of their carriers (Gershenzon, 1985). At the same time, changes of micronucleus frequencies and accumulation of b-chromosomes in populations of *R. temporaria* and *R. arvalis* living for 40 years in areas of catastrophically pollution is an example of a genetic adaptation to pollution (Eliseeva et al., 1989). The degree of overlap of the spectra of anomalies calculated with the Morisita Index (Hurlbert, 1978) provided interesting results. Comparison of overlapping degrees in juvenile *R. arvalis* anomalies from different zones showed that the greatest distinctions are observed in animals from the Zones II and IV with the forest population (74.45 and 74.03%, respectively). Individuals from Zone III differed from the forest population (little less than 87.31%) and were similar to those from the Zones II and IV (91.27 and 90.69%). Sharper differences are displayed in the adult Moor Frogs; the spectrum of anomalies in Zone II is close to that in the Zone III (64.1%) and is far from that for the Zone IV and the forest population (0.07 and 6.9%). In Zone III it is not overlapped at all with the forest population and overlapped on 40.98% with the animals from the forest park zone which are two times less similar to that from the forest population (21.05%) than from those from Zone III. The stability of population is supported by maintenance of a certain heterogeneity level that is reflected in variability of some population parameters.

The variability of the juvenile morphological anomalies spectrum in *R. arvalis* from populations living in landscapes with different levels of anthropogenic transformation showed a low level of changes (Zone IV). The spectrum is significantly wider (9 types against 8 in the forest population) and an average level (Zone III) is sharply narrowed to 6 types. In populations subject to the highest influence of urbanization (Zone II) it is again increased to 11 types which exceeds the natural level. This definitely indicates qualitative difference of populations from the Zone II and action of internal mechanisms of maintenance of population heterogeneity. Similar dependence is known for adult *R. arvalis* from the forest population to populations from the Zone II. Age changes in the *R. arvalis* anomalies spectrum also have zonal specificity. In the forest population the degree of the spectrum overlaps in adults and juveniles at 69.36%. Seven types of anomalies disappear in adults; in the forest park zone the spectra are overlapped only 28.19%, and 5 anomaly types disappear in the adults. In the low building zone, the similarity of spectra of anomalies is 34.19%, and in the adult condition 3 types of anomalies disappear. In populations of the zone of multistory buildings, juveniles and adult spectra overlap at 63.19%, and in the adults 5 types of anomalies disappear. In comparisons to *R. temporaria* from Zones II and III, juvenile anomalies spectrum overlap on 42.88% and there is a decrease of types anomaly number from 9 to 3 (from Zone III to Zone II) and complete absence of anomalies in the adult individuals in Zone II vs. 5 types in the Zone

III. The froglet and adult anomaly spectra in Zone III overlap by 57% and adults have 5 fewer types of anomalies. The differences of anomaly frequencies in the sympatric *R. arvalis* and *R. temporaria*, in our opinion, reflected the presence of adaptive changes and ecological plasticity of the former species relative rigidity and small adaptive opportunities of the second.

In adult *T. vulgaris* from Zone II only weak (14.1%) overlap with those from Zone III was found. Animals from Zone III are similar (92%) to forest population. It is connected only with conditions of extremely polluted habitats of multistory buildings. The spectrum of anomalies in populations is wide enough and consists of 5 various types in the low building zone of two, and in the populations from forest and forest park of one. Adult and juvenile spectra in the Zone II did not overlap. Probably, these anomalies occurring in juveniles are lethal or promote the decrease of viability. In adult *S. keyserlingii*, the spectrum of anomalies in Zone III overlapped insignificantly with that in the forest park zone (24.93%) and with the forest (62.5%). Thus, the similarity of spectra in animals from the forest park zone and forest is lower (53.57%). In this case, the most varied spectrum of anomalies in populations of Zone IV includes 9 types, in the forest population 4 types, in the Zone III 1 type. Also there were smaller sizes of animals sampled from populations of the low building zone. Juvenile and adult animals in the forest park zone overlapped at 65.78%, and thus in adults only one type of anomaly disappeared and other 6 types remained. In *R. ridibunda*, the spectrum of anomalies in juveniles and adults are overlapped by 87.7%. Among froglets, 5 types of anomalies were found, and adults had only one.

These deviations as a result of unusual changes of environment show the new factors that appear in the urban areas. The increase of anomaly frequency indicates increased anthropogenic transformation, but the change in frequency itself in this case is not the most important. The spectrum of these deviations has a genetic basis and is included in a species reaction norm (some species it is narrower, others wider) that reflects its ecological plasticity. In comparisons with *R. arvalis*, the spectrum of anomalies in populations of *R. ridibunda* under different urbanization levels shown the presence of some changes in reaction norms in populations from Zones II and III as compared with natural ones. The analysis of the full data on frequency of morphological deviations revealed a relationship of the percentage and severity of many anomalies on the sex of individual and also an absence of differences in intensity of mutation process between sexes. At the same time, there is a dependence of the increase of frequency of hereditary determined deviations in populations of amphibians from urban areas by 5-8 times (Vershinin, in press). Thus, the analysis of various types of morphological anomaly frequencies and their spectrum in amphibian populations from territories of urban areas allows us not only to determine environmental transformation levels, mutagens, cancerogens, and others pollutants but also to recognize ecological plasticity of the investigated species and the processes of microevolutionary processes in urban isolates.

The development of amphibians, including metamorphosis, is the regular sequence of events. Partly this sequence is defined by increases of thyroid gland activity and sensitivity of various organism systems to selected hormones. The morphogenesis and regeneration processes in organism are focused on hypophysio-thyroidal axis (Fischman, 1996; Menon et al., 1996). The study of proliferate activity and some morphophysiological parameters (Vershinin and Kamkina, 2001) allowed us to find a number of features showing a high degree of equilibrium of the morphogenetic processes and, probably, promoting the decrease of the frequency of morphological anomalies and probability their appearance in stable environmental conditions. For three years (1995-1997), we studied mitotic activity and sizes of corneal epithelium cells in *R. arvalis* froglets from populations under different level of anthropogenic influence near Ekaterinburg in the initial period of terrestrial life.

We performed regression analysis of mitotic index (MI) with mass and liver index. According to the data from field materials collected in 1995, there is a significant ($p = 0.012$) low correlation ($R = 0.258$) between the liver index and the froglet MI from populations of Zone II. In 1996, $R = 0.317$ ($p = 0.0127$), in 1997, $R = 0.295$ ($p = 0.046$), and by the laboratory data, this correlation was found for the froglets from Zone III ($R = 0.73$; $p = 0.011$) and the forest population ($R = 0.67$; $p = 0.0022$). In experimental conditions (1997) significant correlations of MI were found only with the liver mass in the froglets from forest population ($R = 0.68$; $p = 0.00186$) and in individuals from Zone II ($R = 0.369$; $p = 0.05$).

When summarizing field data for all years and zones, the correlation between MI and liver index in animals from the multistory building zone was weak but significant ($= 0.31$; $p = 0.0014$), whereas there is no correlation between MI and liver mass ($R = 0.191$; $p = 0.0057$). By the field and experimental data of 1997 for individuals from populations of Zone II, mitotic index differed from samples from other zones ($p = 0.05$; $p = 0.0087$). Among zones, the dynamics of the mitotic index values are similar except for field samples from the multistory building zone where this parameter is higher than in the low building zone and forest population. This, most likely, is connected with the selective elimination of individuals with low levels of metabolism processes and, respectively, decreased MI in natural conditions (Pyastolova and Vershinin, 1999). During the period of investigation of the froglets from Zone II this parameter displayed a weak but significant linear correlation between mitotic index and liver index (p fluctuates between 0.0012-0.046). Comparisons of the average cell area of corneal epithelium did not reveal zonal differences in *R. arvalis* metamorphosed in 1995. It can be connected with the end of metamorphosis in the conditions of strong reduction of pond sizes and high density of larval populations as a result of a summer drought.

The sizes of corneal epithelium cells from different urban zones in 1996 were significantly ($F = 3.64$, $p = 0.015$) different (Table 15). In *R. arvalis* populations, subject to the highest anthropogenic influence, the smallest cells were found. In 1997, the cell sizes in froglets from populations of Zone II also were small ($F = 3.55$; $p = 0.016$) and that distinguished them from experimental individuals where the cells were larger than in other zones

(Table 15). Probably, it is connected to intensive animal growth in populations of the multi-story building zone; there froglets, as a rule, reached the biggest body sizes (Vershinin, 1983). Froglets from urban populations have larger body sizes and the smallest cells compared with froglets from the forest. The cell sizes in *R. arvalis* froglets in zones with a different level of urbanization did not differ significantly, but (in comparison with the forest population) in populations of the Zone II they are smaller. Earlier Gatiyatullina (1978) in laboratory investigations did not find any relationship between the body and epithelium cells sizes. In conditions of an urban, frequencies of various morphological anomalies increases (Vershinin, 1982, 1989; Vershinin 1995), and maximum values are attained in populations of the multistory building zone. The frequencies of froglet morphological anomalies in laboratory conditions and in samples from urban territories populations are given in Table 16. As was already mentioned above, anomalies arising as a result of deviations in development and regeneration quite often are induced by the effects of pollutants on thyroid gland activity. This gland is responsible for cell division processes and morphogenesis. Probably, the dependence between mitotic index and liver index of froglets from populations of multi-story buildings is the result of the survival of individuals with a high degree of equilibrium for all the parameters mentioned above. This physiological feature enables populations to exist and reproduce in the conditions of high anthropogenic pressure.

Similar data were obtained in survivorship studies in *R. arvalis* eggs. In laboratory experiments it was possible to show a high tolerance of *R. arvalis* embryos from popula-

Table 15. Proliferative activity in corneal epithelium of froglets (1995-1997).

1995	Zones	N	L, mm	MA	MI, ‰	S, mkm ²
	II	43	17.5±0.27	21.7±0.96	7.61±0.5	74.29±0.79
	III	No data				
	IV	22	15.9±0.36	27.5±2.68	9.96±0.7	73.95±1.87
	C	28	15.0±0.23	22.3±1.54	7.82±0.6	74.3±1.34
1996	II	11	16.6±0.18	35.7±2.3	10.1±0.68	59.3±0.66
	III	No data				
	IV	30	16.4±0.16	24.9±1.36	7.27±0.41	61.6±0.35
	C	21	14.3±0.15	21.2±1.49	6.55±0.43	65.6±0.46
1997	II	46	15.8±0.28	22.2±2.3	6.8±0.71	65.0±1.29
(nature)	III	23	14.1±0.42	16.5±1.54	5.47±0.52	69.9±1.0
	IV	63	15.0±0.22	24.9±1.54	7.99±0.51	67.5±0.73
	C	18	15.3±0.45	15.4±1.9	4.97±0.57	69.5±1.25
1997	II	28	13.6±0.24	8.1±0.82	3.06±0.31	79.3±0.58
(experiment)	III	11	13.5±0.32	12.36±2.1	4.58±0.8	78.0±0.78
	IV	13	12.8±0.59	12.4±1.56	4.52±0.54	77.0±0.83
	C	18	13.8±0.37	11.2±1.8	4.15±0.68	78.4±1.7

Note: L - snout-vent length; MA - mitoses number in 50 view fields, MI - mitoses number per one thousand cells. ±SE are given.

Table 16. Anomaly frequencies (%) in *Rana arvalis* froglets (1995-1997).

Zones	Field data						Experiment			
	1995	N	1996	N	1997	N	Summarized	N	1997	N
II	23.4	158	18.2	11	4.44	90	16.6	259	0	60
III	No data				6.52	92	6.52	92	23.3	30
IV	3.03	33	7.5	40	7.14	252	6.7	325	6.67	30
C	1.59	126	0	32	0	56	0.94	214	0	30

tions of Zone II as revealed by clutches placed in clean water. The resulted were significant ($p < 0.001$; $\chi^2 = 152.19$) with an increase of embryonic survivorship (96.7-93.6%) that exceeded the values (78.8-32.4%) for the clutches from forest population (Vershinin and Trubetskaya, 1992). That, in our opinion, indicates the presence of adaptive changes in populations of urban areas. The specificity of morphogenesis and the degree of its coordination with the processes on cytological and tissues levels are specific features of populations inhabiting habitats with the greatest level of anthropogenic transformation and can promote the survival of new generation in the conditions of pollution and urbanization.

8.0. REPRODUCTIVE SPECIFICITY OF AMPHIBIANS IN URBAN AREAS

8.1. Sex ratio and longevity and urbanization

The specificity of reproduction is modified by composition, number and condition of mature individuals. Optimal sex ratio and age structures of populations are primary mechanisms of animals adaptation to local environmental conditions that influence specificity and success of reproduction. Sex ratio in natural populations of amphibians is close to 1:1, and deviations can be a result of difference in males and females activity, selectivity of capture, etc. (Duellman and Trueb, 1986). Summary data on the sex ratios in *R. arvalis* and *R. ridibunda* froglets, the ratio of males and females number is close to one with insignificant males prevalence in Zone II (52.1 and 54.9%, respectively). In *R. temporaria* froglets, the proportion of males in the Zone II is 43.9% (Figs. 11-13). In populations of *R. arvalis* from the zone of multistory buildings, the sex ratio is close to one also in adults, whereas in other zones there are significant ($p = 0.05-0.001$) changes in favor of males.

Censuses of adults, especially in spring time, always give more males because the females leave the breeding sites after spawning. In this way we can explain the male prevalence in samples in the forest population and the forest park zone in *R. arvalis* (69.2 and 61%, respectively). Samples were made from populations in all zones in the same time by identical methods, so it is possible to believe that the males proportion in populations of Zone II is really less, 52.8% ($p < 0.05$) than in the forest. This fact has the explanation: high mortality of males does not reduce reproductive potential of a population because when a male fertilizes many clutches, the number of fertilized eggs is re-

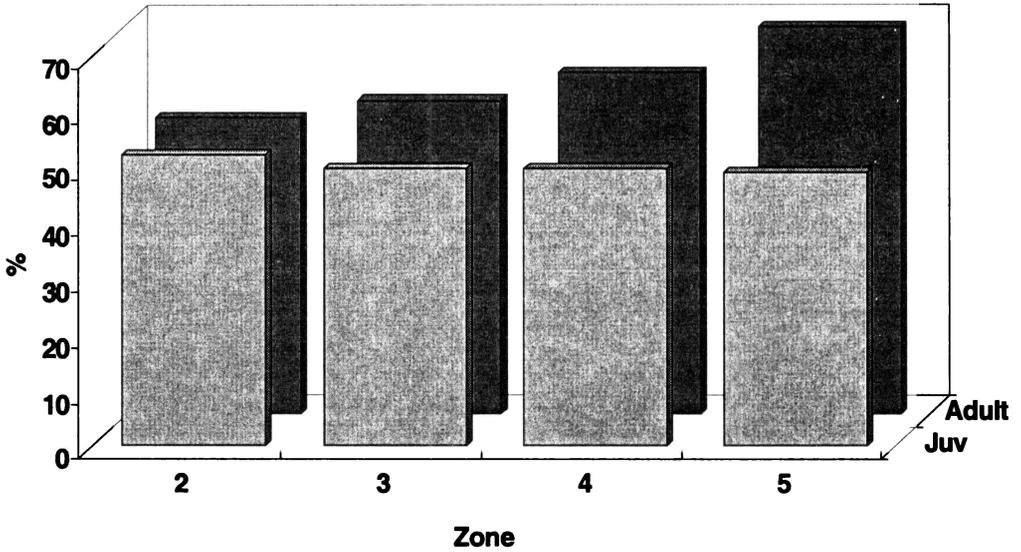


Fig. 11. The percentage (%) of males in *Rana arvalis* populations. 2 - Zone II, 3 - Zone III, 4 - Zone IV, and 5 - forest.

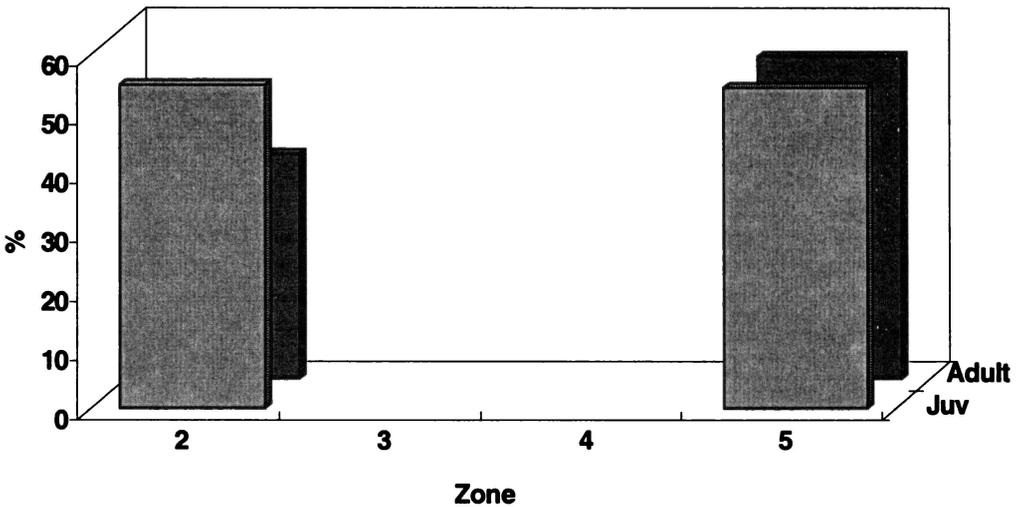


Fig. 12. The percentage (%) of males in *Rana ridibunda* populations. 2 - Zone II, 3 - Zone III, 4 - Zone IV, and 5 - forest.

duced. Significant differences in the age of males and females from zones with different levels of urbanization were not found. Average female age was: Zone II 3.0 ± 0.45 years ($N = 5$), Zone III 3.5 ± 0.71 years ($N = 8$); Zone IV 3.14 ± 0.63 ($N = 7$); and the forest

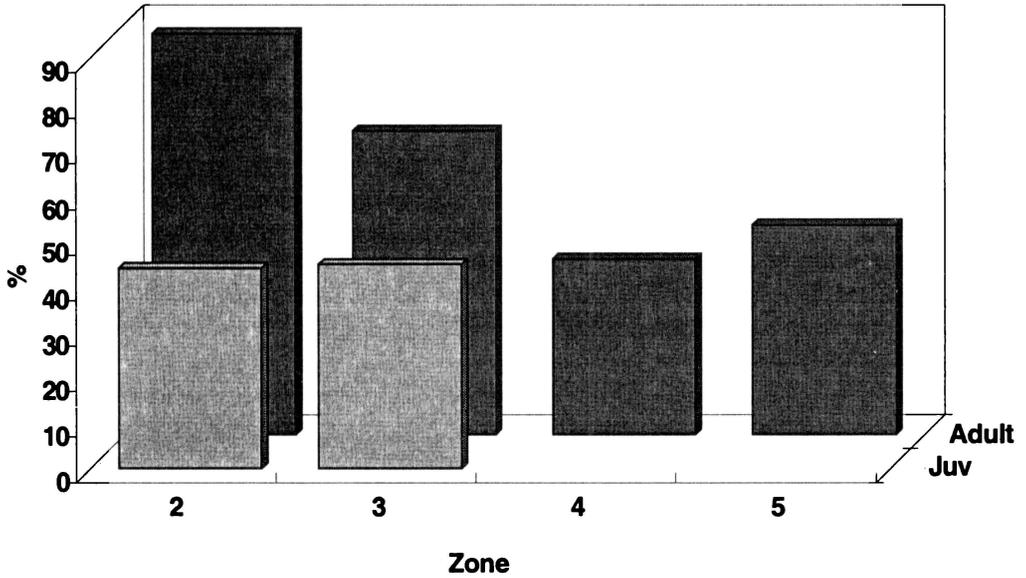


Fig. 13. The percentage (%) of males in *Rana temporaria* populations. 2 - Zone II, 3 - Zone III, 4 - Zone IV, and 5 - forest.

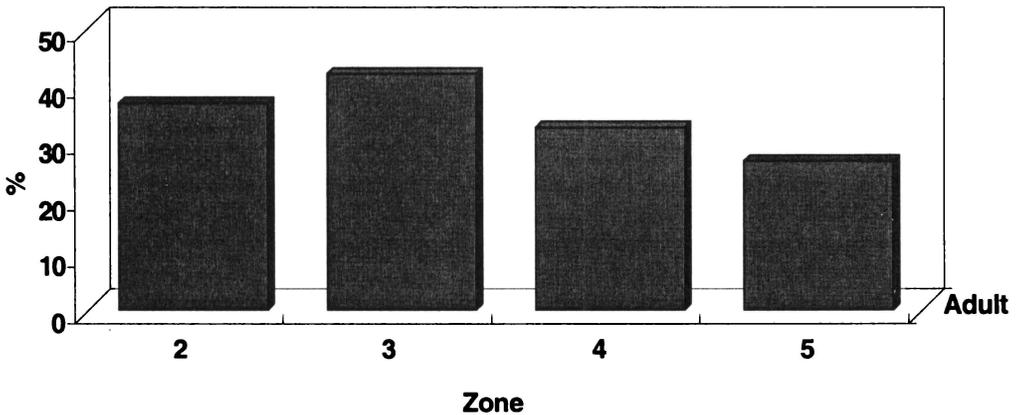


Fig. 14. The percentage (%) of males in *Triturus vulgaris* populations. 2 - Zone II, 3 - Zone III, 4 - Zone IV, and 5 - forest.

population 3.27 ± 0.33 ($N = 11$). Mean male ages were: 3.0 ± 0.21 ($N = 20$), 3.11 ± 0.31 ($N = 9$), 3.24 ± 0.25 ($N = 17$), and 3.1 ± 0.2 ($N = 30$), respectively.

In the populations of *T. vulgaris*, the sex ratio in all zones is shifted toward females, and the largest shift occurs in the forest population (Zone II, 36.5%, forest population 26.3% (Fig. 14; significant differences between the populations from zones with differ-

ent levels of urbanization were not found). A similar proportion was found in populations of *T. vulgaris* in London (Griffiths, 1984). Bell (1977) mentions lower survivorship of *T. vulgaris* males than females. This can be caused by higher males mortality and other reasons. On the other hand, we mentioned extreme cases when the number of males in a local population was 16 times less than the females number, and those can be connected with increased breeding males attractiveness for commercial collectors.

In the species more sensitive to habitat changes, *S. keyserlingii* and *R. temporaria* (Figs. 13 and 15), and in populations from the most transformed habitats, the proportion is displaced toward males: 66.67 and 88% ($p < 0.001$), respectively as in comparison with the forest population: 46.3 and 46.2%. This can be caused by high susceptibility of females in these species to environmental changes and indicates their low potential possibilities of successful reproduction on urban areas. The proportion of females in populations of *R. temporaria* from Zones II and III, as compared with juveniles, is significantly ($p < 0.001$) reduced. In urban populations of *R. temporaria* in Great Britain, sharp decrease of females was also found (Cummins, 1989).

The maximum age of *R. temporaria* in Zone II was 4 years (2.8 ± 0.18 ; $N = 11$) for males and 3 years for females (3.0 ± 0 ; $N = 2$), in Zone III 7 (3.96 ± 0.22 ; $N = 28$) and 5 (4.08 ± 0.29 ; $N = 12$) years, respectively. In forest park zone there were no differences in maximum ages of males and females: 6 years (4.0 ± 0.26 ; $N = 17$) and 4.19 (4.19 ± 0.19 ; $N = 27$, respectively; Vershinin and Volegova, 1993). Maximal life duration in *R. temporaria* in natural populations of the Middle Urals is 8 years (Ishchenko, 1993). ANOVA analyses showed significant differences in the ages of *R. temporaria* depending on the level of urbanization ($p = 0.02$; $F = 4.056$). In natural populations of *S. keyserlingii*, living in extreme conditions above the Arctic circle, the average male age during reproduction was 4.62 years and that of females was 3.96 years (Ishchenko and Berman, 1995).

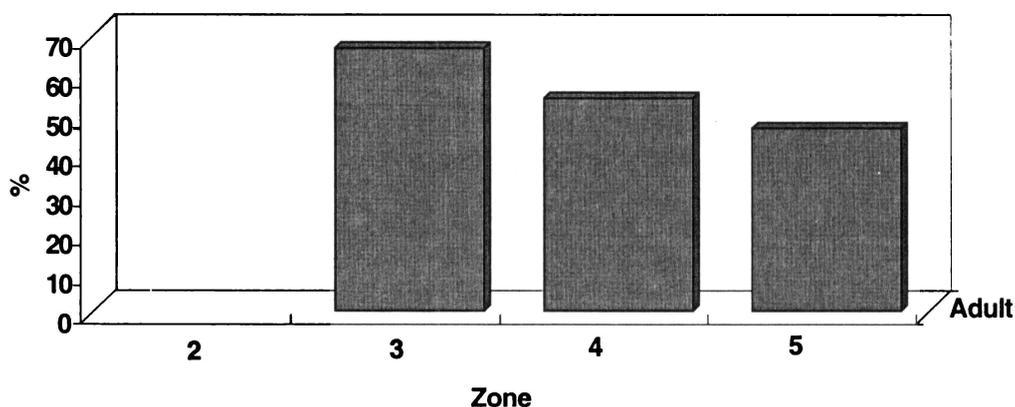


Fig. 15. The percentage (%) of males in various *Salamandrella keyserlingii* populations. 2 - Zone II, 3 - Zone III, 4 - Zone IV, and 5 - forest.

There are published data that show that female *R. ridibunda* hibernating in polluted ponds have reduced and disturbed ovaries (Kosareva and Vasyukov, 1976), and changes in environmental chemistry of breeding ponds can result in the reduction of the female reproductive system (Hazelwood, 1970). Ovaries and eggs contain the highest (in comparison with other internal organs) concentration of iron, magnesium, copper and zinc (Misyura, 1989), and there are sexual differences in bioaccumulation of radionuclides (Usachev et al., 1993).

Death can occur during reproduction periods because of the mobilization of toxins accumulated earlier in fat bodies (Honegger, 1978). Pesticides and other pollution of ponds by industrial wastes influence the female reproductive system in *R. ridibunda* and promote females high sensitivity to pollution and higher mortality (Kubantsev and Zhukova, 1994). According to our data, the females proportion of adults of *R. ridibunda* population was reduced significantly ($p < 0.05$) as compared with froglets: from 54.9-38.09%. Examples of displacement of sex ratios caused by selective toxic elimination of females under the effect of technogenic factors are well known for other vertebrates groups (Lukyanova, 1990). In the region of Nizhny Novgorod, where there are many suitable places for hibernation (clean and non-frozen springs), *R. temporaria* is widespread in urbanized areas, and older age classes are absent (Ushakov et al., 1982). The sexual structure is skewed toward the prevalence of females. Similar changes in sex ratio were mentioned for populations of the European Fire-Bellied Toad (*Bombina bombina*) in a pesticide polluted pond (Peskova, 1995) and in the Common Toad (*Bufo bufo*) in connection with drainages leading to the destruction of breeding places (Sinsch et al., 1980). Under extreme conditions males mortality is higher than that in females (if the susceptibility of both sexes is equal). Therefore, in species successfully reproducing on urban territories, the numeric prevalence of females in populations living in extreme conditions is sufficient to explain the terms of the increase of reproductive potential of a population. The shortening of female life duration in *R. temporaria* populations from Zone II can be connected to the growth of reproductive effort in the conditions of urbanization. Sex ratio and life duration influence the reproductive traits and reproductive effort of a population of the given species in local environmental conditions and consequently this population survival.

8.2. Fecundity and egg size variability

Fecundity is one of the main characteristics of a population that determines its ability to reproduction over a long period. For amphibians, whose posterity depends largely on abiotic factors, the egg number in a clutch is important and compensates for significant mortality of embryos and larvae at early developmental stages. Thus, the reproduction in amphibian populations depends, on one hand, on abiotic factors, and on the other represents a function of the biotic potential (i.e., size-age structure of a population, state of the reproductive part of population, timing of maturation, energy reserves like fat

bodies, liver glycogen levels, duration of the generative phase of the life cycle, and the number and sizes of egg in clutch).

Hence, reproductive strategy of population represents a balance between these parameters. Wilbur (1977a) defined reproductive strategy as a set of reproductive traits which have arisen on the basis of selection, with the advantages of generations promoting the greatest contribution in the number of progeny. Each strategy assumes a compromise between the distribution of a resource between the current generation and the subsequent one. The benefit of reproduction at the current moment is determined by the power of the cost of adult individual growth by the future fecundity and survivorship of the adult animal. The price can include risk of the individual death during the reproduction or decrease of the adult longevity caused by redistribution of a resource from expenses for supporting the metabolism (energy for existence) and growth on the current reproduction needs. A significant factor determining reproductive strategy is the predictability of environmental conditions at each stages of the life cycle, especially at early stages (Crump, 1984a). Mainly it is a balance between fecundity and average sizes of progeny (Brockelman, 1975; Smith, 1983) that reflects energy expenditure on reproduction and adaptiveness of progeny and parents. The general expenditures on the reproduction also can vary (Wilbur, 1977a).

In the conditions of anthropogenic landscapes, there is a disappearance of the oldest age groups from amphibian populations because of strong pollution and significant intensification of metabolic processes. An advantage in such conditions should influence animals with early maturation, single reproduction, and high fecundity with small sizes of eggs which corresponds to the classical r-strategy (MacArthur and Wilson, 1967; Pianka, 1970). Based on these facts, the egg number in clutches increases under anthropogenic change of environmental conditions in many anuran species (Avramova, 1978). Fecundity in amphibians, as in many other vertebrate groups (Hickey, 1960), depends on body size (Henderson, 1961; Oplinger, 1966) and age. Fecundity correlates positively with the female size in many amphibian species (Banks and Beebee, 1986; McCoid and Fritts, 1989). The content of fat in the organism, glycogen in the liver, and general calorific value influence egg number in amphibian clutches (Avramova et al., 1977). Fat content in the organism of mature frogs from the genus *Rana* is one of the factors of population dynamics (Viegas et al., 1993).

The amounts of lipids and general calories of females increase with age in the Common Spadefoot Toad (*Pelobates fuscus*), and that directly determines the increase of the number of eggs (Bobylev, 1980). Amphibians of similar ages usually are larger in urban than in natural populations (Ushakov et al., 1982; Vershinin, 1983b; Gogoleva, 1985). However, despite higher growth rates of amphibians in polluted ponds, it was found that the decrease in absolute and relative fecundity (Bobylev, 1985) is connected to changes in fractional lipid composition of the animals (Misyura, 1989). With low gonadal fat and liver glycogen and small calorie content, there is a delay of female maturation for one year (Avramova et al., 1977). Moderate or low feeding rates cause a signifi-

cant increase in the atretic oocyte number and reduction of the ovaries mass in *R. cyanophlyctis* (Saidapur and Prasadmurthy, 1988). The decrease of fecundity in urbanized conditions probably reflects the reduction of nutrient storage in mature females. The partial adaptation of amphibians to pollution occurs at the expense of the organism energy resources (Tarasenko and Tarasenko, 1989). Experimental research have shown that the influence of chemical substances results in reductions of the amounts of yolk and granulocytes in the follicle of the Clawed Frogs (*Xenopus laevis*; Pramoda and Saidapur, 1986). The egg mass reduces under a strong anthropogenic influence in fishes (Koshelev, 1988). Anyhow, the change in amphibian fecundity can characterize the severity of destructive processes in a community (Bobylev, 1989; Vershinin, 1995a, b).

Our studies of the dynamics of fecundity in *S. keyserlingii* at early stages of anthropogenic transformation of forest ecosystems have shown that this parameter decreases under the influence of increasing recreational pressure and is positive correlated with the decline in the number of reproducing animals. It does not depend on the female size which is also accompanied by the widening of the limits of variability and increases of the frequency of asymmetrical clutches (Vershinin, 1990a). As in many other amphibian species, the fecundity of *S. keyserlingii* in natural populations is determined by size and age of mature females. It correlates positively with the female size ($R = +0.61$; $t_z = 3.79$; Bikbaeva, 1987). Fecundity of *S. keyserlingii* in various parts of its range varies considerably; near Yakutsk the average egg number in a clutch is 112 (Larionov, 1976), on Sakhalin 80 (Basarukin, Borkin, 1984), and in the area of Perm 143 ± 6.8 (Bolotnikov et al., 1977). According to Shagaeva et al. (1981), mean number of eggs in an egg sac of *S. keyserlingii* from Talitsa Town (Sverdlovskaya Province) is 85 ± 14 . According to our data, the fecundity of this species in populations of the forest park zone of Chelyabinsk City is 68.8 ± 2.3 eggs/sac. The long-term investigations of eggs number per egg sac in populations from the suburbs of Ekaterinburg have shown that this value is different and fluctuates by years near a certain mean value characteristic for each local population. In the population of *S. keyserlingii* living in Shartash Forest Park, the decrease of mean eggs number in the egg sac varied from 102 in 1977 to 63.3 in 1981, and then the egg number fluctuated near another mean value (Table 17). According to the data for 1959-

Table 17. Fecundity (mean±S.E., range, and sample size) in amphibians from urban populations. *Rana arvalis*.

Year	Multistory buildings	Low buildings	Forest park	Forest
1978	No data	No data	1098±79.8 1620-440 N = 20	1200.0±200 1400-1000 N = 20
1980	888.5±55.7 944-833 N = 2	1165.5±167 1333-1000 N = 2	1211.0±148.3 1774-800 N = 5	1372±91.1 2286-571 N = 28
1981	1022.6±83.4 2222-167 N = 41	1001±125.6 2000-500 N = 12	989.3±47.2 2500-333 N = 83	1049±44 1700-200 N = 58

Table 17. Continued. *Rana arvalis*.

Year	Multistory buildings	Low buildings	Forest park	Forest
1982	994±53.6 2000-100 N = 52	1099±59.6 2000-600 N = 51	1213±40.6 1800-300 N = 73	1167±73 1333-1000 N = 5
1984	1146.6±68.4 2000-400 N = 52	1192.6±70.9 1900-600 N = 19	1319±78.8 1867-100 N = 23	No data
1985	907.3±23 1750-286 N = 119	1064.5±27.4 1556-429 N = 54	1128±28.6 3000-450 N = 144	545±11.5 558-532 N = 2
1986	947.0±22.5 1750-140 N = 122	965.6±67.4 1600-500 N = 16	1130.9±41.6 1556-667 N = 33	1427.6±62.7 2100-1000 N = 31
1987	1027.8±30.7 1500-667 N = 62	924.5±99.7 1500-450 N = 12	1109.1±29.2 2333-750 N = 72	1157.0±98.1 3000-600 N = 18
1988	996.3±25.8 1667-100 N = 80	917.8±47.6 1500-500 N = 20	1024.6±71.8 1444-200 N = 19	1022.0±26.6 1300-800 N = 18
1989	749.6±47.8 1600-300 N = 40	933.4±53.4 1200-400 N = 14	989.2±19.3 1200-700 N = 39	1031.9±43.8 1545-800 N = 20
1990	786.5±31.6 1333-600 N = 55	922.1±70.6 2000-500 N = 19	933.5±34.8 1400-444 N = 33	1010.4±21.8 1300-800 N = 51
1991	967.0±23.6 1300-500 N = 53	1019.8±28.8 1200-800 N = 18	916.4±44.2 1500-400 N = 39	999.1±28.4 1154-920 N = 10
1992	940.7±40.4 240-1400 N = 32	1034.9±57.2 700-1300 N = 16	1042.3±32.4 666.7-2000 N = 50	995.4±36.6 380-1363 N = 39
1993	849.5±55.5 250-1800 N = 17	919.4±51.2 583.3-2400 N = 20	993.2±33.4 428.6-1400 N = 47	1115.5±39.2 400-1800 N = 34
1994	969.1±37.6 100-1500 N = 37	868.1±72.4 684.2-1066.7 N = 10	1046.1±27.7 700-1444.4 N = 68	1077.8±38.1 400-1727.3 N = 36
1995	822.5±32.6 109.1-1272.7 N = 49	824.5±61.1 611.1-1200 N = 14	1081.9±28.8 800-1700 N = 63	1153.5±30.6 875-1500 N = 56
1978-95	940.7±10.7 100-2222 N = 816	1006.8±17.7 450-2000 N = 297	1079.8±10.8 100-3000 N = 801	1113.6±15.1 200-3000 N = 408

Table 17. Continued. *R. temporaria*.

Year	Multistory buildings	Low buildings
1981	1566.7±285.1 1900-1000 N = 3	1570.8±170.3 4000-256 N = 32
1982	1507.0±89 2000-750 N = 14	1400.0±120.6 2000-600 N = 11
1984	1378.6±82.2 1750-1150 N = 7	1168.0±46.8 1500-1067 N = 4
1985	1372.3±90.9 2000-1267 N = 7	1228.5±66.6 3000-650 N = 40
1986	1207.0±35.5 1800-857 N = 32	1479.9±82.8 2500-150 N = 39
1987	1653.4±126.5 2500-1320 N = 10	1335.9±107.1 2150-700 N = 17
1988	2000.0±0 2000-2000 N = 2	1225.4±77.7 1667-400 N = 27
1989	1020.0±136.3 1500-650 N = 5	1126.7±66.4 1600-900 N = 12
1990	914.0±114.8 1600-490 N = 10	1012.1±39.4 1250-500 N = 19
1991	1485.6±140.5 1714-1000 N = 5	1219.6±69.9 1500-600 N = 16
1992	Population disappeared	1000.8±120 600-1333.3 N = 10
1993	Population disappeared	1311.2±105.3 1600-900 N = 13
1994	Population disappeared	1196.6±114.4 800-1500 N = 11
1995	Population disappeared	1253.9±109.6 833.3-2800 N = 12
1981-95	1326.2±49.9 490-2500 N = 90	1277.5±30.5 140-4000 N = 241

Table 17. Continued. *Salamandrella keyserlingii*.

Year	Low buildings	Forest park	
1977	No data	102.0±6.7 55-121 N = 11	No data
1978	91.0±6.9 55-113 N = 10	83.9±4.2 32-149 N = 28	61.8±12.6 60-62 N = 2
1980	92.9±6.5 74-120 N = 11	75.3±3.0 20-120 N = 55	67.6±3.6 34-98 N = 25
1981	67.1±4.2 22-125 N = 27	66.3±1.9 0-138 N = 133	67.1±4.2 24-87 N = 27
1982	114.0±15.3 111-117 N = 2	71.4±3.2 18-119 N = 49	76.7±3.8 46-107 N = 22
1984	55.7±4.7 15-87 N = 21	76.4±2.3 6-170 N = 96	No data
1985	89.2±4.1 31-137 N = 28	80.1±2.2 0-145 N = 100	65.7±3.1 32-133 N = 32
1986	90.5±10.8 62-117 N = 4	57.9±2.7 4-94 N = 68	71.8±4.2 25-119 N = 18
1987	77.0±8.8 55-96 N = 6	62.7±2.7 12-116 N = 69	60.8±3.1 36-81 N = 34
1988	81.6±4.8 53-121 N = 20	69.5±1.7 4-154 N = 167	62.2±3.4 32-100 N = 28
1989	79.8±7.7 55-94 N = 8	68.7±2.5 14-113 N = 77	57.5±3.9 25-101 N = 20
1990	83.0±10.8 77-89 N = 4	57.4±2.1 11-113 N = 107	59.2±2.9 25-108 N = 38
1991	76.4±7.7 25-111 N = 8	60.7±2.3 15-110 N = 93	54.2±3.3 28-95 N = 30
1992	No data	63.3±2.9 27-103 N = 61	59.0±4.6 43-87 N = 15
1993	68.3±7.7 45-90 N = 8	52.9±3.4 26-101 N = 43	63.4±5.6 42-78 N = 10

Table 17. Continued. *Salamandrella keyserlingii*.

Year	Low buildings	Forest park	
1994	75.1±4.4	56.9±2.6	43.9±2.7
	38-105	19-100	0-72
	N = 24	N = 72	N = 42
1995	73.7±6.9	65.2±1.9	63.7±3.4
	38-123	20-116	28-86
	N = 10	N = 133	N = 28
1977-95	77.3±1.7	66.6±0.64	60.6±1.2
	15-137	0-170	0-133
	N = 191	N = 1253	N = 378

1965 for the same population (Ishchenko, 1968), the mean eggs number per clutch was 208 (maximum 250). According to my data, in 1977 it was 198.2 (228) and in the year with the minimum fecundity (1986) it was 112.1 (187). The change in the mean length of female body by years is not significant and not correlated with the change of the mean egg number per sac ($R = +0.22$; $t_z = 0.38$). I have no data on the change in the mean length of female body in other populations. For this reason, summarized data for the years 1980-1981 are given for the last three habitats. The decrease in fecundity of *S. keyserlingii* in the Shartash population, apparently, has an irreversible character. It is positively ($R = +0.78$; $t_z = 3.48$) correlated with the decrease in the number of breeding animals. This process, probably, is similar to the changes occurring in fish reproduction under anthropogenic influence. The first reproduction becomes earlier, and delays in late reproduction occur in connection with the increase of energetic expenditure. Under a stable deterioration of environmental conditions eggs mass resorption occurs (Koshelev, 1988). The similar process of the fecundity decrease was noted in populations of passerine birds in the conditions of technogenic pollution (Belskii, 1996).

The limits of the egg number variability per egg sac in the forest park populations are wider than in the forest population (0-198 and 28-119, respectively for all years). Differences in amplitude of variability probably reflect negative changes in the mature part of the population along with the decrease of fecundity and increase of the frequency of sacs with unusually small egg numbers, 4-6 (Verzhinin, 1982a) or even empty sacs (Table 17). Their diameter in the swelled state is 3-5 mm. Frequency of sacs with < 20 eggs changes from 0.37-3.2% in 1985 and 1986 respectively. In the forest population the minimum eggs number is 28. The proportion of such egg sacs is insignificant, but this tendency has been maintained for a significant interval of time and is most common in the disturbed Shartash population with increasing levels of anthropogenic influence. Apparently, this can cause increasing energy expenditure in deteriorating environmental conditions as in *S. keyserlingii* living in the urban pine forest park of Chelyabinsk; eggs/sac changed within 4-54 in 1980 and 1988 with an average 68.9 ± 2.3 ($N = 70$).

For all years of study for each of population, the degree of clutch asymmetry was calculated by the division of smaller egg numbers in one egg sac on the larger one of the same clutch (Basarukin and Borkin, 1984). Shartash populations showed a tendency toward the increase of asymmetric clutch proportion (difference > 30%) to 16.2 against 10.2-11.7% in other populations of Ekaterinburg suburbs. The differences between sacs can reach 89-100% when one sac does not contain eggs or contains an abnormally low number. The maximal difference of absolute numbers is 93 eggs. In *S. keyserlingii* from Sakhalin (Basarukin and Borkin, 1984), the difference between sacs reached 45% (1-34 eggs). In the Talitsa population (Sverdlovsk area) the maximum difference was 39 eggs (Shagaeva et al., 1981). The increase of asymmetry is an alarming signal of changes in the condition of a population and its further increase can lead to significant irreversible changes (Zakharov, 1987). Thus, the relationship of the decrease in fecundity of *S. keyserlingii* with the process of population decline, increased frequency of clutch asymmetries, and anomalies in combination with the decrease of female proportions in the populations (see Section 8.1) indicates destabilization of reproductive processes and prevalence of negative tendencies in the species populations in conditions of the increasing recreation pressure on the forest park zone.

Investigation of clutches in brown frog populations in urban areas showed that the fecundity is similar to data from natural populations from different regions: *R. temporaria*: 670-1400 (Bannikov et al., 1969), 1155-4005 (Terentjev, 1950), and 1067-1608 (Cooke, 1975a); for *R. arvalis* 930-1461 (Ishchenko, 1978b). Comparisons of long-term data on *R. arvalis* populations within urban areas indicate a lower mean fecundity in populations of the multistory building zone that was caused by an increase of the proportion of clutches with small eggs number, and in the last years, there has been a tendency to decrease the mean egg number in clutches from the multistory building, low building, and forest park zones (Table 17). Analysis of regression between the fecundity and the level of habitat transformation has showed a weak correlation, $R = 0.34$; $p = 0.03$. One of the main reasons of low fecundity in *R. arvalis* in urban areas may be caused by small female body size (though significant correlations were not found) and high metabolic processes (Vershinin and Tereshin, 1992).

In populations from the multistory building zone, the mean female length was 45.19 ± 5.5 mm ($N = 34$), in zones of low buildings 47.11 ± 2.3 ($N = 18$), and in the forest park zone 49.49 ± 1.39 ($N = 46$) compared with 51.72 ± 1.34 ($N = 31$) in the forest population. The data are similar to those for a natural population of *R. arvalis* from near Sverdlovsk (Ishchenko, 1978b); the average female fecundity of the lowest size class of frogs was 930-939 eggs, average size was 1140-1161, and largest individuals were 1461 ± 46 - 1161 ± 8.3 . The fecundity of *R. arvalis* in populations from near Chelyabinsk and Serov with the highest level of anthropogenic influence was also lower. In the low buildings zone of Chelyabinsk average eggs/clutch was 737.9 ± 71.3 ($N = 7$), in the forest park 1065.4 ± 487.3 ($N = 34$), and in suburban population 1271.4 ± 287.6 ($N = 7$). In Serov, in a population from a low building zone it was 797.6 ± 117.6 ($N = 5$) and in forest park 977.1 ± 59.8 ($N = 16$).

There are no differences in the average eggs number in *R. temporaria* clutches from populations of multistory and low building zones (Table 17). Maximum fecundity was observed in the multistory building zone 63.2 ± 4.1 ($N = 4$) against 57.9 ± 2.3 ($N = 30$). The animal age in breeding places varied within the limits of 2-3 years in females and 2-4 years in males (Vershinin and Volegova, 1993). In populations from the low building zone, the limits of mature females age were 3-5 and in males 3-7 years; mean body length was respectively 64.8 ± 0.95 and 57.98 ± 2.3 ; in the forest park there were the same parameters in females: 3-6 years and 70.1 ± 1.4 mm, in males 2-6 years and 67.8 ± 1.5 mm. Hence, in this case it is possible to consider the decrease of relative fecundity because the big female body sizes does not lead to increases of the egg number. The latter value is only maintained at the same level which, because of the large clutch sizes, enables some embryos to survive in the conditions of pollution (Trubetskaya, 1994). The reduction of relative fecundity can be connected with differences in the age of mature females (see Section 8.1). *Rana arvalis* fecundity reduced under urbanization increases in parallel with egg diameter decreases (Vershinin and Gatiyatullina, 1994), and that most likely related with the small sizes of females. However, because of the adaptive changes which arise in urban populations natural embryonic mortality there is almost 2X lower ($p < 0.001$; $\chi^2 = 136.3$) than with *R. temporaria* at equal eggs values (Vershinin and Trubetskaya, 1992; Trubetskaya, 1994). The data displayed the prevalence of the large-sized animals in *R. temporaria* populations from the polluted and disturbed areas. These animals have more intensive metabolism that leads to early maturity and shortening of life duration. The absence of significant differences in fecundity in this case may be related to higher energy expenditures as an adaptation to pollution (Tarasenko and Tarasenko, 1989) and also to the loss of the oldest age groups from urban populations (Zhukova, 1978; Ushakov et al., 1982). Thus, the fecundity change in *R. arvalis* populations from urban areas, living in changed environmental conditions, may be determined by the differences in the mean body size of females combined with physiological specificity. The decrease of egg number in clutches is one of the negative tendencies in amphibian populations under significant anthropogenic influence. The deviation of this parameter from norm enables us to estimate the strength of the negative changes in urban communities. Clutch volume and egg sizes vary in essentially all amphibian species. There are hypotheses about adaptive variability of the egg diameter in amphibians. It is considered that the presence of interpopulation differences in variability of egg sizes in salamanders reflects adaptations to habitat environmental changes (Takahashi and Iwasawa, 1988), but that is not true for all species (Beachy, 1989). In some toads (*B. bufo* and *B. calamita*), intrapopulation variability in clutch and egg sizes is based on variability of animal body size, but the correlation between these parameters varies in different populations (Banks and Beebee, 1986). In *R. temporaria*, the variability of the egg size does not depend only on individual age. Thus, the individual size at metamorphose increases and larval period is reduced with increase of egg size (Cummins, 1989).

Individuals that developed from large eggs surely have an advantage because they have better competitive ability as larvae (Morin, Johnson, 1988; Crump, 1989a; Williamson and Bull, 1989a). In addition, large eggs occur in clutches with different mean egg size. Eggs from large clutches of *Ranidella signifera* grow and develop more intensively than egg from "small" clutches (Williamson and Bull, 1989b). As was shown with tadpoles of *R. temporaria*, metamorphic mortality is higher in larvae hatched from small eggs, and those froglets more often have morphological anomalies (Surova and Cherdantsev, 1987). In connection with the above mentioned differences, there is a problem of optimum ratio of the eggs sizes and number. Only in ideal conditions do eggs of all sizes survive with equal success. Hence, females, producing many small eggs confer their viability (Crump, 1984b). Females that produce only large eggs have low fecundity (Crump, 1989a). Therefore, the optimum tactics can be the presence of clutches with broad range of egg sizes that gives equal chances of egg survival for embryos of all sizes in varying environmental conditions. In a discussion of egg size variability within a population, Kaplan and Cooper (1984) noted that the optimum balance between the size and number produced by a female (Smith, 1983) may be hardly substantiated because it is more preferable if a population will be guaranteed independence from fecundity and egg size variability. The scope of variability of egg sizes can be under genetic control but also can develop under the actions of environmental factors. Besides the variability of egg sizes produced by one female in a particular period of reproduction, increases of variation in egg sizes can be achieved in population at the expense of variability when the same female reproductions with eggs of other sizes at other breedings. The amplitude of such variation may be genetically determined (Kaplan and Cooper, 1984). This means that it is difficult to predict the exact egg sizes produced for one female in a particular period of reproduction. As a result of such plasticity, the sizes of eggs produced by one female in any period of reproduction can be closer to the optimum relative to in certain environmental conditions, and in other conditions it may be from the optimum. This type of variation of egg sizes can be combined with the numerous ways of increasing variation of progeny, including intraclutch variation. This class of developmental mechanisms was called "adaptive coin-flipping" by Kaplan and Cooper (1984).

As the size of an egg is determined by vitellogenesis, the final sizes of the egg can be determined by conditions of the female feeding and the degree of her activity (Jorgensen, 1982). It is indisputable that this model, elaborated from research on toads, is quite acceptable to many amphibian species, especially from temperate regions with expressed seasonality in the reproductive period. In cases of growth delay caused by adverse environmental factors (e.g., lower temperature and lack of food), redistribution of energy for growth and reproduction can occur and, hence, a change in number and egg sizes. Another factor can be energy expenditure of the females in polluted habitats. The influence of chemical substances causes reduction of yolk and granulocyte number in follicles of *R. tigrina* (Pramoda and Saidapur, 1986). Kaplan and Cooper (1984) demonstrated that females of the Far Eastern Fire-Bellied Toad (*Bombina orientalis*) de-

posit largest eggs at moderate temperatures and unlimited food resources. Kaplan (1980a; 1980b) demonstrated in *Ambystoma* that larger eggs result in larger larvae.

In "ideal" conditions of the experiment, large larvae of *Hyla crucifer* hatched from large eggs (Crump, 1984a), but these individuals did not receive further advantage in the rate of development or in size before metamorphosis. There was also no increase in their survivorship. The differences existing at early stages of development can disappear in the process of growth and development (Godina and Sytina, 1985; e.g., the diameter of egg changes at the start of gastrulation; Surova and Cherdantsev, 1987). In the embryonic period in natural ponds, eggs are subjected to influences of various factors like temperature, chemical composition of water, clutch number, and position in the pond. After hatching, in the period of larval development when larvae interact with predators and competitors and the probability of pond drying increases, large tadpoles receive a relative advantage (Shchupak and Gatiyatullina, 1987). Research of adaptiveness of the intrapopulation variability in egg size are scarce. Kaplan (1985) found that larvae of *Taricha torosa* hatched from larger eggs pass through metamorphosis faster and at larger body sizes with unlimited resources, but at limited resources they metamorphose at a rather large but the duration of larval period increases. These situations indicate that in nature, when resources are limited, large eggs will not necessarily give an advantage for the larvae developing from them, and in some cases a large number of small eggs can be more preferable. Studies on brown frogs (*R. temporaria* and *R. arvalis*) showed that larvae that hatch from small eggs are capable of changing the initial rates of growth and development at a greater degree (because of more active feeding and/or increases of metabolic level). This actions allows them to metamorphose at the same time as individuals of large size (Surova and Cherdantsev, 1987). Thus, the positive aspects of an increase of the proportion of small eggs in populations of urban area is the increase of the population adaptive opportunities in quickly varying environmental conditions.

On the other hand, the increase of the proportion of clutches with small egg in urban populations, along with the reduction of egg number in clutch, can be dangerous for normal reproduction in these populations, as in pollution conditions *R. temporaria* embryos survive only in the center part of a clutch (Linnenbach and Gebhardt, 1987), and large embryos and larvae are less vulnerable. Our data indicate high mortality of early developmental stages in urban populations of *R. arvalis* (Vershinin, 1985a) and better survival of large froglets (Vershinin, 1985b). In *R. arvalis* populations, living in conditions of increased acidity, intrapopulation variability of the egg sizes is significantly lower, and the embryo and larval sizes are significantly higher in comparison with a population from relatively clean habitat (Andren et al., 1989). In *Ranidella signifera* the egg size does not determine subsequent tadpoles adaptiveness. At transition to the independent feeding, the larvae hatched not from largest eggs reach the largest sizes. Probably there is no direct connection between selection on large eggs and large larvae (Williamson and Bull, 1989b).

A number of authors (Ivanova, 1982; Vershinin, 1982b; Gogoleva, 1985) have found that in conditions of anthropogenically polluted ponds the primary survival of large larvae is observed, and that is likely related to advantageous surface-volume ratios in large individuals. Smith (1987) showed for *Pseudacris triseriata* that individuals that metamorphosed in a short time at large body size become mature on the first year of life after metamorphosis. Semlitsch et al. (1988) demonstrated in *Ambystoma talpoideum* that individuals metamorphosing faster and at larger sizes have larger sizes when they reproduction. This fact is especially important for females because fecundity correlates with body size. *R. sylvatica* that mature earlier spend more energy for growth than for reproduction, and that results in the production of smaller eggs (Berven, 1988). *R. arvalis*, in connection with instability of the environment, metamorphose sooner at a larger body size and create the basis for accelerated maturation but also decreases life duration (Ishchenko and Ledentsov, 1985, 1987; Ledentsov, 1990).

All these data are evidence for the suggestion that despite the ambiguity of adaptive value of the egg diameter, changes of this parameter can reflect certain intrapopulation processes in different amphibian species. In 1990, I determined sizes of *R. arvalis* eggs from urban and suburban populations at the beginning of egg division and late blastula (Table 18). In 1991, the comparison of egg sizes was made at the stages 10-18 (Table 19).

Table 18. Mean egg diameter (mm; stages, diameters, and sample size) in *R. arvalis*, 1990.

Forest area and site					
1.Rezhevskoi Path 2(RR-2)	9	8			
	1.83±0.030 N = 7	1.90±0.044 N = 8			
2.Rezhevskoi Path 3(RR-3)	2	4	5	6	9
	1.72±0.057 N = 6	1.80±0.09 N = 2	1.77±0.023 N = 2	1.74±0.021 N = 8	1.79±0.023 N = 6
3.Rejhevskoi Path 4(RR-4)	4	5	6		
	1.72±0.080 N = 3	1.73±0.027 N = 13	1.77±0.075 N = 3		
Forest parks and site					
4.Kalinovskii 1 (Kfp -1)	2	10			
	1.60±0.034 N = 5	1.85±0.036 N = 4			
5. Kalinovskii 2 (Kfp -2)	2	3	4	9	
	1.59±0.037 N = 6	1.63±0.017 N = 3	1.60±0.036 N = 5	1.74±0.021 N = 3	
6.Shartash 1 (Sh-1)	2	7	10		
	1.70±0.045 N = 10	1.78±0.026 N = 5	1.82±0.026 N = 5		
7. Shartash 2 (Sh-2)	1	2			
	1.66±0.017 N = 10	1.66±0.017 N = 10			

Table 18. Continued.

Low buildings and site					
8.Samoletnaya 5 (S-5)	2	7			
	1.65±0.042 N = 3	1.58±0.044 N = 2			
9. Samoletnaya 4 (S-4)	1	2	3	4	
	1.58±0.079 N = 4	1.62±0.028 N = 9	1.64±0.023 N = 8	1.68±0.013 N = 5	
10.Patrushikha 1 (P-1)	4	5	6	7	10
	1.98±0.035 N = 7	1.98±0.032 N = 6	1.97±0.039 N = 4	1.81±0.021 N = 2	1.64±0.035 N = 2
Multistory buildings and site					
11.Olkhovka River (O)	3	9	10		
	1.73±0.018 N = 2	1.84±0.046 N = 6	1.83±0.034 N = 10		
12.Central Park (CP)	2	6			
	1.51±0.018 N = 2	1.55±0.018 N = 2			
13.Krylova 3 (K-3)	7				
	1.62±0.027 N = 10				
14.Belinskogo (B)	3	10			
	1.52±0.053 N = 2	1.69±0.034 N = 10			
15.Kuibysheva (KB)	2	6	7		
	1.58±0.026 N = 8	1.58±0.059 N = 4	1.67±0.043 N = 5		

 Table 19. Mean±S.E. of egg diameter (mm) in *R. arvalis* clutches from different sites, 1991.

Habitats and site	Forest			
	Stages, diameters, N			
1.Rezhevskoi Path 2(RR-2)	16	17		
	1.88±0.067 N = 3	1.83±0.084 N = 4		
2.Rezhevskoi Path 3(RR-3)	16	17		
	2.04±0.039 N = 6	2.00±0.039 N = 7		
3.Rezhevskoi Path 4(RR-4)	11	12	16	
	1.91±0.023 N = 7	1.89±0.067 N = 4	2.00±0.147 N = 3	
Forest Park				
4.Kalinovskii 1 (Kfp-1)	10	11	12	13
	1.80±0.44 N = 9	1.84±0.020 N = 8	1.87±0.038 N = 9	1.96±0.054 N = 5

Table 19. Continued.

Forest Park				
5.Kalinovskii 2 (Kfp-2)	13	16	17	18
	1.89±0.034	1.91±0.025	2.00±0.019	1.99±0.030
	N = 3	N = 4	N = 11	N = 7
6.Shartash 1 (Sh-1)	16	17		
	1.94±0.020	2.00±0.021		
	N = 7	N = 5		
7. Shartash 2 (Sh-2)	16	17		
	2.02±0.013	2.02±0.058		
	N = 3	N = 6		
Low buildings				
8. Samoletnaya 4 (S-4)	17	16	18	
	1.98±0.035	1.98±0.032	1.97±0.039	
	N = 7	N = 6	N = 4	
Low buildings				
9. Central Park (CP)	16	17		
	1.64±0.013	1.60±0.014		
	N = 3	N = 4		
10. Belinskogo (B)	17			
	1.95±0.043			
	N = 5			
11. Olkhovka River (O)	6	10	11	
	19.3±0.035	19.4±0.088	19.8±0.106	
	N = 2	N = 2	N = 2	
12. Kuibysheva (KB)	5	10		
	1.87±0.034	1.88±0.029		
	N = 3	N = 11		

The data given in Table 18 shows insignificant differences in the average egg sizes in populations from the forest park and forest zones. Significant differences in egg sizes were found only at stage 9 between two ponds (RR-1 and Kfp-2: $t = 2.31$). Much higher variability of egg mean diameters was found between clutches from one pond, especially at the first four development stages (up to eight blastomeres). Interclutch variation of egg sizes in a pond was higher at initial stages of division than on later and reaches 0.44 mm (1.84-1.40 mm) at stage 2 (1 division) and 0.33 mm (2.11-1.78 mm) at stage 10 (late blastula). Differences in egg sizes within clutches are expressed to a higher degree than within clutches. The sizes in separate clutches vary from 0.4-0.7 mm. As a rule, the mean egg diameters at consecutive developmental stages in one pond increase, but within a pond variability in different clutches are insignificant except for the increase of the maximum egg sizes. These features in the *R. arvalis* egg variability in large cities are similar with those in natural population (Talitsa, data for the year 1983; Shchupak and Gatiyatullina, 1987).

Egg sizes in ponds from urban areas are much smaller (Table 18). The differences are significant when comparing egg diameters at separate stages from ponds RR-3 and KB ($t = 2.26$), CP, P-1; RR-4 and K-3 ($t = 2.89$), and RR-2 and B ($t = 3.75$). The frequency of clutches with small eggs is notably higher in populations from the most polluted and urbanized habitats. The mean egg sizes are significantly smaller in the majority of populations from multistory and low building zones. Variability in the mean egg sizes between spawns inside urban ponds is lower in comparison with those from suburban sites and indicates the presence of selection in this populations. For example, at the first division, difference of average egg size diameters between clutches varied from 1.46-1.70 mm (pond S-4). Maximum variation in the egg sizes at stage 2 (1 division) reached 5.18% (pond S-4) while at the same time inside forest ponds it usually exceeded 8% (Vershinin and Gatiyatullina, 1994). The limits of fluctuations in egg size diameter within clutches in urban populations was similar to that observed in the forest (i.e., rather high variability in the mean egg sizes within clutches was observed). The significant variability of *R. arvalis* egg sizes determines the plasticity of a population in its relation with the environment and provides reproductive success in stable conditions. Within the limits of urban isolates suitable for frog reproduction, variability of the egg mean sizes between ponds is lower, and the mean egg diameters are smaller than in the forest.

If we assume that the relationship between the egg size and female age demonstrated for *Hyla crucifer* (Crump, 1989a) and *R. temporaria* (Cummins, 1989) apply to *R. arvalis*, as one of the reasons the mean egg size decreased in *R. arvalis* clutches in 1990 in populations from urban territory, we must consider the small female sizes. Another possible factor can be energy expenditure on growth in mature females in polluted habitats. As I mentioned above, in natural ponds during embryogenesis, the egg is influenced by various abiotic factors (e.g., temperature, chemical water composition, clutch position, and density in a pond). In *R. arvalis* when larvae interact with predators and competitors and the probability of the pond drying increases, large tadpoles have a relative advantage. Differential mortality is possible in urban ponds during embryogenesis at vulnerable developmental stages (gastrulation). In our case, differences in egg sizes at later embryogenesis between urban and forest ponds were equal. For example, in pond KB (Kuibysheva Street) this difference disappears by stage 6. The differences existing at early developmental stages can be leveled in the process of growth and development (Godina and Sytina, 1985). Probably, this was caused by the fact that in most cases it was not possible to reveal essential differences on the diameter of egg between populations in 1991 (Table 19), and the most complete material was collected for stages 16-18. At these stages the smallest egg sizes were recorded in a pond in Central Park. In other ponds the mean egg diameters were comparable. In 1990-1991, I did not find significant correlations between egg diameter and fecundity.

Multifactorial ANOVA of the data on the *R. arvalis* egg sizes in 1990-1995 showed that the diameter of eggs depends significantly on two parameters: urbanization degree and stage. As the diameter of an egg in the process of development increases, it is

necessary to expect a relationship of the diameter in combination with these two factors. The significance of this differences is very high for all years (1990-991, 1993-995; $p < 0.0001$ with F within limits of 15.278-334.146. In spite of the fact that in samples from urban populations later stages were present, the mean diameter of egg without the account of stage remained significantly smaller (Table 20). A similar picture was observed in passerine bird populations living in polluted areas; the proportion of small eggs increased from 3.6% in the control to 48.7% in the impact zone (Belskii, 1996).

The increase of small eggs in clutches of urban moor frog populations, along with increasing eggs number in clutches probably represents a threat to normal reproduction of these populations because of vulnerability of small clutches, embryos and larvae to pollutants. Our data indicate high mortality on early developmental stages in urban populations of *R. arvalis* (Vershinin, 1985a) and to a primary survival of large froglets (Vershinin, 1985b). As shown on tadpoles of *R. temporaria*, metamorphic mortality in larvae hatched from small eggs and frequency at new metamorphosed juveniles is high (Surova and Cherdantsev, 1987). On the other hand, brown frog larvae hatched from small eggs are

Table 20. Mean±S.E. of egg diameters in *Rana arvalis* populations relative to the degree of habitat urbanization (1990 - 1995).

Zone	N	Diameter	Stages
1990			
II	1460	1.71±0.004	2, 3, 6, 7, 9, 10
III	1401	1.68±0.004	1, 2, 4, 5, 6, 7, 10
IV	1693	1.67±0.003	1, 2, 3, 4, 5, 6, 7, 10
K	1420	1.79±0.004	2, 4, 5, 6, 8, 9
1991			
II	918	1.86±0.005	5, 6, 10, 11, 16, 17
III	720	1.95±0.006	16, 17, 18
IV	1718	1.93±0.004	10, 11, 12, 13, 16, 17, 18
C	920	1.96±0.005	11, 12, 16, 17
1993			
II	620	1.75±0.006	5, 6, 7, 8, 9, 10, 11, 12, 18, 19
III	440	1.79±0.007	1, 3, 4, 6, 7, 11, 12, 16, 17
IV	1252	1.80±0.004	2, 4, 5, 7, 8, 10, 11, 12, 13, 16, 17
C	1160	1.79±0.004	2, 3, 4, 5, 6, 8
1994			
II	700	1.72±0.006	2, 5, 6, 7, 9, 12, 16, 19
III	480	1.80±0.007	9, 10, 12
IV	1880	1.83±0.004	2, 3, 6, 7, 8, 9
C	540	1.89±0.007	2, 3, 4, 5, 6, 7, 17
1995			
II	1520	1.67±0.004	2, 3, 4, 5, 6, 9, 11, 12, 13
III	500	1.78±0.007	2, 3, 6, 10, 11, 12
IV	1360	1.84±0.004	2, 3, 4, 5, 6, 7, 8
C	1260	1.85±0.005	2, 3, 5, 6, 7, 8

capable of changing the initial growth and developmental rates to a greater degree (e.g., more active feeding and/or increase of metabolic level) that results in equality (i.e., allows them to become similar to those from larger eggs at metamorphosis; Surova and Cherdantsev, 1987). Hence, the increase of a small eggs ratio in populations of urban area promotes the increase of adaptive opportunities in quickly varying conditions of urbanized landscapes. We have found (Vershinin, 1985b), that in the period of metamorphosis mortality in populations of the multistory building zone is much shorter (see Section 8.3). Thus, successful reproduction with a decrease of mean eggs number and reduction of egg diameter as well as the presence of a number of adaptive features in embryos larvae and froglets may indicate that the reproductive strategy in urban populations *R. arvalis* is different from the typical r-strategy in natural populations.

In *R. temporaria* populations from polluted and disturbed areas with individuals with high growth rates, early maturity and short life duration prevail among mature animals. Significant differences in absolute fecundity in *R. temporaria* from populations from zones of multistory and low building zones were not found, but it is possible that there is a decrease of relative fecundity. The survival of embryonic stages is mainly determined by the large sizes of clutches that corresponds with classical variant of the r-strategy. Thus, in populations of sympatric species of brown frog occupying the same urbanized landscapes have different reproductive strategies. Small eggs, early maturation, single spawning, and high fecundity in a stable environment are favored (Ishchenko, 1989b). At the same time, in the syntopic species of *Triturus-Rana-Bufo*, the tendency towards r-strategy is increased from left to right, and the stochastic probability of disappearance of their populations increases in the same accord (Kuzmin, 1995). Our data confirm this conclusion; the degree of habitat specialization of a species can have the greater importance for its survival than reproductive specificity. Changes in reproductive strategy and its variability lead to the existence of spatially limited small isolates with low mean fecundity and small egg sizes.

8.3. Brown frogs mortality at various stages and urbanization

The successful reproduction of amphibians is in many respects a successful end of metamorphosis in fluctuating conditions of environment (Kaplan and Cooper, 1984; Berven, 1988; Crump, 1989b). Growth rate and differentiation determines success of the aquatic phase of development and metamorphosis in the conditions of temporary ponds (Wilbur and Collins, 1973; Wassersug, 1975; Wilbur, 1980). The Wilbur-Collins (1973) model suggests that successful metamorphosis is possible at a certain minimal body size (an opportunity of survival in small individuals), and the maximal sizes are limited by the impossibility of growing well beyond all limits and the effects of allometric restrictions. Travis (1984) considered that the differentiation rate is set at early stages of larval development. Mortality and growth rates have high variability and in many respects depend on environmental temperature (Smith-Gill and Berven, 1979). As was shown repeatedly,

large larvae have an advantage, especially under resources restriction and in the conditions of increased density (Brockelman, 1975; Licht, 1967; Wilbur, 1977a, b; Alford and Harris, 1988), and the change of feeding mode during a certain period of development does not influence the rate of differentiation. There is also a model explaining the time of metamorphosis by the influence of ecological factors on endocrinological interactions (Wassersug, 1994). A variety of growth rates and development in *R. arvalis* can depend both from environmental and hereditary factors (Ishchenko and Shchupak, 1979), and the rate of development can influence survivorship; in *R. temporaria* larval mortality is directly proportional to developmental rate (Aebli, 1966). As shown for *Pseudacris triseriata*, the individuals metamorphosed at larger body sizes and become mature in a shorter period during the first year of life (Smith, 1987). Large *Ambystoma talpoideum* metamorphosed earlier and had the largest sizes at reproduction (Semlitsch et al., 1988). Earlier maturity in *R. sylvatica* is impossible without achievement of a certain body size (Berven, 1988). Because amphibian development occurs in an external environment of temporary ponds, hereditary nature of growth and development rates is small in most species. The rates of development in brown frogs mainly depends on water temperature (Surova, 1988). Phenotypical variability of early features of development is influenced by environmental parameters, mainly temperature. The important role is played also by parental influences (Kaplan, 1994). Hatching can occur at earlier stages and at different body sizes in the Yellow-Bellied Toad (*Bombina variegata*) at different temperatures (Pawlowska-Indyk, 1980). The success of metamorphosis in the Natterjack Toad (*Bufo calamita*) can also depend on time of spawning (Fejedo, 1993).

Embryonic and larval mortality in many respects has a density-dependent character (Severtsov and Surova, 1989). From stages 30-53 larval developmental takes place. In suitable conditions (e.g., favorable temperature, food resources, and shelter from predators) *R. sylvatica* tadpoles have a number of advantages in comparison with embryos (Herreid and Kinney, 1967). Many authors consider that among the adverse factors influencing mortality and regulating individuals number in amphibians populations, predatory pressure appears to be most effective (e.g., Calef, 1973; Licht, 1974). However Severtsov and Surova (1979b) consider that the predators do not significantly influence the character of larval population dynamics. In ponds with predators, the cumulative action and presence of various microhabitats for tadpoles of *R. temporaria* is reduced (Surova and Severtsov, 1988). High mortality depends on animal density and is determined by intrapopulation mechanisms (Severtsov and Surova, 1979a, b; 1988). Tadpoles mortality relates to tadpole size and density (Shvarts and Pyastolova, 1970a, b), and there no food competition between tadpoles (Severtsov and Surova, 1989). At the same time, there is a relationship between food resources and individual size at metamorphosis (Smith and Feetwell, 1974; Hensley, 1993). At initially high densities, the mortality in the initial period is low and then becomes high, and vice versa at initially low numbers. The rates of brown frog tadpoles mortality do not depend on food resources and predators and are determined by intrapopulation interactions between tadpoles that regularly form

aggregations up to 2000/liter with an average density of 0.002-2/liter (Severtsov and Surova, 1988). The physiological consequences of the action of metabolites have been investigated in various amphibian. Influences on the changes in oxidizing metabolism and energy cost of metamorphosis were experimentally shown, as well as active tissues growth and cytomorphological processes, morphophysiological features of haemopoiesis, formation of the skeleton and other physiological, biochemical and morphological changes (Amstislavskaya, 1971; Gatiyatullina, 1978; Kovalchuk, 1978; Pyastolova and Ivanova, 1978; Suzumova, 1978, 1979). As revealed for *R. arvalis* tadpoles, in the conditions of pollution the effect of low water quality is similar to that of increased population density (Baranovskii and Khudokotsev, 1992). Unicellular algae also can influence tadpoles growth (Richards, 1962). The body sizes and length of larval period frequently but not constantly are correlated (Travis, 1984). Rapid growth allows larvae to pass faster through vulnerable developmental stages. The balance of growth rates and development can stabilize the life cycles of amphibians (Werner, 1986).

The environmental transformation as a result of human activity lead to serious changes in all phases of amphibian life cycle. The anthropogenic factors, as a rule, cause decline of populations number because of mortality in juveniles and adults, and fecundity decreases in all amphibian species (Popov, 1967; Lebedeva, 1970; Skokova and Lobanov, 1973; Kubantsev, 1976; Bannikov, 1977; Bondarenko, 1977; Konstantinova, 1981; Vershinin, 1983a). In anthropogenic landscapes changes concern not only number but also population structure. There is an absence of older age groups of *R. temporaria* in urbanized areas (Ushakov et al., 1982), the proportion of mature individuals is reduced, and sexual structure changes to a numeric prevalence of females. The local populations of amphibians are characterized by rather stable average contribution to a new generation number (20-22 froglets per female). The commensurability of eggs biomass brought into a pond and number of froglets was found (Shchupak, 1970a). In disturbed habitats the reproductive potential is 42-66.1 froglets per female as determined by a decrease of younger animals at the expense of mature animals (Bobylev, 1985). The death rate in many respects determines the ability of a population to reproduce and its phenotypic and genetic structure. In turn, the tailless amphibian reproduction efficiency is determined not by the number of producers but factors influencing habitat conditions (Bobylev, 1985). The first 30 stages from the egg to hatching and beginning of first blood circulation are embryonic stages (Dabagyan and Sleptsova, 1975). In this interval, the mortality of *R. arvalis* is 17.8% (Ishchenko, 1982). Embryonic mortality in *R. ridibunda* in waste waters is 42-76% against 26-34% in undisturbed ecosystems (Bobylev, 1985).

There are various opinions concerning adaptive opportunities of different larval stages and their survivorship. According Shchupak (1970b), egg number in *R. arvalis* decreases by 3 times at the expense of mortality connected to the external factors during the period of embryogenesis; significant changes do not occur at hatching, and before the metamorphosis the numbers are reduced by 10. By the end of metamorphosis (stages 53-54) the number is reduced by 20. Severtsov and Surova (1979a) considered that it is impos-

sible to identify more or less adaptive stages of development. Mortality depends on larval density instead of age and not on the stages of ontogeny. All stages appear to be equally adapted to the ecological conditions where an individual lives in a given moment. Nevertheless, the authors do not deny critical ontogenetic stages as such. The critical periods in laboratory conditions and in natural populations leveled because of high mortality. In different *Rana* species the number of surviving juveniles was 4-8% of the number of eggs (Herreid and Kinney, 1966; Brockelman, 1968; Calef, 1973; Licht, 1974; Cooke, 1975a). In experimental conditions 40% of larvae survived (Calef, 1973). This author specifies high mortality at the last metamorphosis stages. After metamorphosis it does not exceed 10% of the number of recently metamorphosed animals. As shown for *R. arvalis*, there can be a mass mortality of recently metamorphosed animals at unfavorable conditions if they were weakened during development (Pyastolova and Trubetskaya, 1988). Experimental research showed that the action of small doses of various substances increases larval survivorship to metamorphosis by 2 times as compared with the control (Bugaeva, 1983). In studies of simulated pollution, *R. arvalis* larvae grew up to metamorphosis as in controls (Bugaeva, 1985). Field research showed the presence of dynamic specificity in *R. arvalis* larvae and froglets in conditions of urban areas: high elimination at early stages compensated by its significant decrease. That is one of the causes of genetic structure specificity in the urban *R. arvalis* population (Vershinin, 1987a, b).

The contribution of each juvenile generation in the mature part of a population is determined by premetamorphic stages, but as a rule it is not limited to the initial number of generations and breeding pond capacity. Similar restriction takes place only in small ponds (Lyapkov, 1994). Highest survival occurs in early metamorphosed large juveniles whose larval development passed in large and well-warmed ponds (Lyapkov, 1988). Froglets that left ponds earlier survived better irrespectively of size (Lyapkov, 1986). Highest froglets mortality (*R. temporaria*) was observed in the first 3 weeks of terrestrial life. At this time, froglets are most vulnerable to predators. One adult green frog in a terrarium eats on the average 20 froglets a day, and a shrew eats an average of 66 froglets. *Neomys fodiens* eats an average of 166 (Lyapkov, 1987). The proportion of brown frog juveniles in the diet of green frogs is 3.0-66.5% (in the beginning of brown frog metamorphosis) and 25.4% at the end of metamorphosis (Lyapkov, 1987). It is supposed that green frogs make a permanent pressure on brown frog tadpoles and juveniles number. Carabid beetle predation on metamorphosed juveniles of Australian frogs (Robertson, 1989) is known. At significant anthropogenic pressure, the level of available losses in the beginning of terrestrial life should be lower, so the reproduction of these populations became possible. The smaller number of predators in such communities also can reduce losses among metamorphosed juveniles.

In large cities with advanced industry, amphibian frequency is relatively low. One of the most dangerous influences is the destruction and pollution of amphibian habitats. Under the influence of the anthropogenic factors, not only species composition in eco-

systems but also populations dynamics change. Lesnikov (1970) considered pollution as a factor of environment influencing reproductive properties of a population and indicated 3 types of direct influence of pollution. The first type is the destruction of a certain part of a population: young, mature females and males. There may be an analogue with the influence of predators. The second type is pollution that influences the condition of an organism (e.g., metabolism, and is similar to actions of parasites). Thus, there is a reduction of attributes determining the condition of individuals. The third type is the disturbance of oogenesis and ontogenetic processes resulting in the termination of reproductive process or the appearance of non-viable progeny. The strongest influence appears with constant pollutants presence in a pond. The action of substances is often shown not at the moment of pollution but later with the manifestation of unfavorable conditions. Mortality rate determines the ability of a population to reproduce. Dynamics of a new generation number characterizes specificity of a population and in many respects determines its structurally functional features (Vershinin, 1987a).

Depending on the pollution level and complex of concomitant factors, mass mortality of metamorphosed animals may occur (Pyastolova and Trubetskaya, 1988) or survival may increase (Bugaeva, 1983). The research carried out on the territory of urban areas showed the presence of some features of larvae and juveniles number dynamics in *R. arvalis* populations living in the conditions of urbanization (Vershinin, 1983a, 1985b, 1987a). Data on larvae and juveniles survivorship in experimental conditions as well as the results of field research on the influence of anthropogenic pressure on features of their dynamics do not allow a total picture of the processes. In this connection, an attempt of a combination of field and experimental methods to study mortality during ontogeny of brown frogs (*R. arvalis* and *R. temporaria*) and populations with different levels of anthropogenic influence was undertaken.

Field research of *R. arvalis* and *R. temporaria* population dynamics showed that larval mortality to stage 41 in urban areas was higher than in the forest population and in the forest park zone (Vershinin, 1983b). This loss was caused mainly by pollution level of urban ponds (Vershinin, 1985a) where pollutants were concentrated. To the end of larval development, just before metamorphosis (stage 49), larval survival in urban areas in the zones of multistory and low building zones was lower than in the forest park and forest (Table 21, Fig. 16). Survival during metamorphosis (stage 53) in urban areas compensated for the high mortality at early stages and exceeded ($p = 0.05$) values for this period in the forest population. The observable differences increase at stage 54 ($p = 0.01$) when postmetamorphic mortality increases overall estimations. The picture of survivorship in *R. temporaria* in many respects is similar with that in *R. arvalis*, but the limits of variability and survival are a little lower than in *R. arvalis*, and that probably is connected with low ecological plasticity of *R. temporaria* (Surova, 1988). The calculation of mean number of metamorphosed froglets per female in *R. arvalis* and *R. temporaria* has not revealed significant differences between populations from zones with different urbanization levels (Zone II, 15.19 ± 5.0 , $N = 32$; III, 6.66 ± 6.87 , $N = 17$; IV, 11.4 ± 3.9 , $N = 52$;

Table 21. Survival (% of total eggs deposited) in amphibian populations relative to urbanization level (1980 - 1995). $M \pm S.E.$, min - max.

<i>Rana arvalis</i>				<i>Rana temporaria</i>			
Stage	Zones	N	Survival	Stage	Zones	N	Survival
41	II	2	9.56 \pm 1.42 2-41	41	II	2	10.15 \pm 3.88 7.7-12.6
41	III	1	11.90 0-11.9	41	III	3	8.90 \pm 3.17 2.1-14.4
41	IV	3	25.10 \pm 1.16 4-41	49	III	1	0.34 0-0.34
41	C	1	48.50 0-48.5	53	II	5	1.20 \pm 0.29 0.53-2.5
49	II	2	0.54 \pm 1.42 0.2-0.88	53	III	12	0.78 \pm 0.19 0.16-2
49	III	2	1.32 \pm 1.42 0.84-1.8	54	II	5	0.32 \pm 0.08 0-0.63
49	IV	3	5.40 \pm 1.16 1.3-10.9	54	III	12	0.17 \pm 0.05 0.005-0.45
49	C	1	0.90 0-0.9				
53	II	14	1.69 \pm 0.53 0.45-4.5				
53	III	11	0.76 \pm 0.60 0.1-2.3				
53	IV	14	1.01 \pm 0.53 0.047-3.39				
53	C	12	0.34 \pm 0.58 0.0028-0.699				
54	II	13	0.55 \pm 0.55 0.23-1.6				
54	III	11	0.29 \pm 0.61 0.01-0.67				
54	IV	12	0.19 \pm 0.58 0.021-0.58				
54	C	10	0.05 \pm 0.64 0.0003-0.106				
<i>R. ridibunda</i>							
	stage 53	stage 54	stage 54				
Parameters	(% of 49)	(% of 49)	(% of 53)				
N	8	4	5				
Survival	33.2 \pm 10.8	27.8 \pm 14.0	47.2 \pm 11.9				
min - max	4.4-79.7	3.5-65.7	8.45-82.5				

Note: N is number of recaptured individuals, see Chapter 2.

forest population, 18.0 \pm 5.9, N = 23). However, the maximum values are much higher: 83.35 froglets in the Zone II versus 267.7 froglets per female in the forest population.

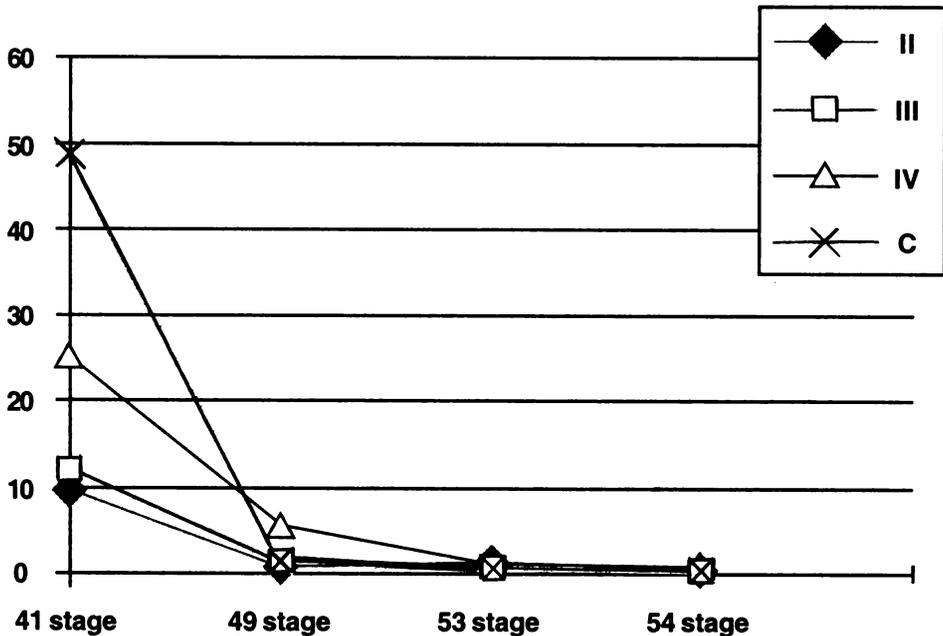


Fig. 16. Survival of larvae and froglets of *Rana arvalis* (% of deposited eggs). II - multistory building zone, III - low building zone, IV - forest park, and C - forest.

Maximal values in *R. temporaria* for Zones II and III are 62.5 and 66 froglets per female, respectively; average values are 18.47 ± 5.7 ($N = 8$) in Zone II and 11.99 ± 3.1 ($N = 27$) in Zone III. In laboratory experiments, it was possible to show a high tolerance of *R. arvalis* embryos from populations of Zone II when the pollution of water effect was removed. That resulted in a significant ($p < 0.001$; $\chi^2 = 152.19$) increase of embryonic survivorship (96.7-93.6%) which exceeds the values for the forest population (78.8-32.4%; Vershinin and Trubetskaya, 1992). In our opinion, this shows the presence of adaptive changes in populations from urban areas. In experiments, mortality of larvae from urban populations was lower than in larvae from the forest. In the latter case, this parameter increases significantly between stages 47-54.

The studies of different concentrations of sodium dodecyl sulfate (surfactant detergent) showed a direct relationship between survival and concentration for three clutches from Zone II. Larval mortality in forest individuals does not follow this pattern. Survivorship in the control was 8% higher than in solutions of high concentration, and on average was 7-15% lower than in solutions of average and low concentration. This result coincides with the data from an experiment on larvae from populations from non-polluted areas (Bugueva, 1983). Thus, the response of two clutch groups from city and forest is ambiguous. Urban larvae are tolerant of detergents and their mortality is directly proportional to concentration. In larvae from natural population such a clear relationship not

present; at low concentration, mortality was lowest (Vershinin and Trubetskaya, 1992; Trubetskaya, 1994). According to the results of field investigations, survival of brown frog juveniles to stage 54 was higher in the zone of multistory buildings and lowest in the forest population.

We can consider that the zone of multistory building has maximum pollution, the most significant mortality occurs at early developmental stages (embryonic period), and that relates with the complex of urban environmental conditions. At later stages high mortality does not occur, even during metamorphic climax (Vershinin, 1985b). This corresponds with the view on general dynamics of larvae in brown frogs (Sevrtsov and Surova, 1988). In populations from other urban zones and the forest sharp decreases in number at early developmental stages do not occur, and the curve of reduction in number is smoother during the developmental period. If we remove the action of natural factors (in the experiment) at embryonic and larval stages in urban animals, we will not observe sharp mortality, while in larvae from the forest it significantly increased to stage 29 and on stages 48-53. The limits of variability of *R. arvalis* survival on the stages under study are notably wider in populations of urban area (in comparison with forest) which indicates survival of most part of the new generation, and the significant heterogeneity of urban environmental conditions is shown in a variety of feedback reactions in the population.

A natural population is subjected to the minimum human influence and stays in the condition of dynamic balance with a relevant biocenosis. Hence, the level of probable mortality in the new generation lies within limits of stable reproduction. The number of biocenotic relationships and trophic levels in natural community is higher than in anthropocenosis so the mortality there can be rather high. Thus, high potential stability of urban clutches realized under favorable conditions seems to be a consequence of adaptive changes promoting maintenance of *R. arvalis* populations in urban areas. Embryonic, larval and froglets features reflect the increase of population adaptive potential in significantly varying conditions of urbanized landscapes. By acceptance of an r-strategy, the adaptive changes are directed to fast growth, early maturation and increases of fecundity that quite often results in shortening of life and low adaptability of individuals as observed in *R. temporaria* populations from Zone II. In conditions of limited resources, the advantage in interspecific competition experienced by individuals is reduced in the processes connected with reproduction (i.e., with lower fecundity). In such conditions the selection is directed towards a decrease in fecundity in the terms of clutch size reduction as observed in *R. arvalis* urban populations. These data show differences in reproductive strategy at interpopulational levels in urban and natural *R. arvalis* populations and interspecific differences in the populations of *R. temporaria* and *R. arvalis* occupying urban territory. The example of various reproductive specificities in two brown frog species in populations from urban territories indicates low efficiency of typical r-strategy in combination with a rather greater role of hereditary components during the development of *R. temporaria* in the conditions of anthropogenic landscapes.

8.4. Abnormal amphibian clutches in urban areas

Because amphibian reproduction and development occur in small and often temporary ponds, the egg is the most vulnerable link in the amphibian life cycle. Quite often many clutches die in fast-drying ponds. Spring frosts may result in freezing and destruction of eggs. A lot of new factors are added on urban territories to the natural factors causing clutch mortality: direct destruction by people for different reasons (Cooke, 1975a; Cooke, 1985). Changes in water chemistry influence indirectly through decrease of resistance to *Saprolegnia* infection (Fryer, 1973; Cooke, 1975a; Leuven et al., 1986). High acidity, synthetic detergents and other kinds of chemical pollution disrupt normal egg fertilization and embryonic development (Ilosvay, 1977; Freda and Dunson, 1985; Pierce, 1985; Gunter, Plotner, 1986). In a number of cases the death of clutches occurs before the end of the reproductive process (Beshkov, 1978). *Rana ridibunda* females, hibernating in places of industrially polluted water discharges, display disintegration and ovarian decay (Kosareva and Vasyukov, 1976a). Pesticide applications cause asynchronous maturation of sexual cells of *R. ridibunda* males and females (Zhukova and Kubantsev, 1980). In amphibians living in the zone of industrial pollution, changes in albumin and lipid exchange occur (Misyura, 1982), and these results in deviation from the normal formation of sexual products (Misyura, 1985). In some cases the action of chemicals lead to changes in albumin structure of eggs envelopes, that subsequently interferes with normal clutch swelling and embryonic development (Hazelwood, 1970).

In this section I describe information on abnormal amphibian clutches in populations living on the territory of urban agglomeration during 1978-1995. Unusual clutches of *S. keyserlingii*, *R. arvalis*, and *R. temporaria* were found. The classification of the types of anomalies in clutches of urban amphibians was described in Section 2.

Frequency of *R. arvalis* abnormal clutches in populations living in urban areas varied by years from 0.219-3.8% (Table 22). The exception is 1978 (44.6%). In populations of *R. temporaria*, unusual clutch frequency varied from 0.076-12.5%, and in *S. keyserlingii* it varied from 0.18-1.6.0% (in 1978, 3.9%). Clutches with eggs without embryos, then "joined" clutches, twin eggs and those with reduced eggs occurred in frequency in *R. arvalis* populations from urban areas. In *R. temporaria* populations the first two cases were most frequent. Clutches without eggs were the least widespread anomaly in urban populations of brown frogs. In *S. keyserlingii*, clutches without eggs and clutches with abnormally low egg number represented the most frequent types, and clutches with partly empty eggs was common.

The first time that abnormal clutches were found was 1978. Their occurrence, apparently, was connected with abrupt changes in environmental chemistry in one of the ponds. The clutches of *S. keyserlingii* and *R. arvalis* did not swell and did not develop from the moment of deposition to days 13 or 24, respectively. Fungal infections were not noted. The low level of water in the ponds, apparently, promoted the increase of pollutant concentrations, which indirectly is evidence for a high percent of skin diseases in *S. keyserlingii* (4.9 %; N = 122) that bred in that pond. Sensitivity of the skin in Caudata

Table 22. Frequency (%) of abnormal (see Section 2) egg clutches in different zones.

Zones	II		III		IV		Forest	
	N	%	N	%	N	%	N	%
<i>Rana arvalis</i>	2009		1624		4664		4681	
Anomaly type								
Clutches without eggs	0	0	0	0	1	0.021	0	0
Egg without embryo	6	0.299	3	0.185	12	0.257	1	0.021
Joined clutches	0	0	0	0	2	0.043	0	0
Twin eggs	1	0.005	0	0	1	0.021	0	0
Reduced eggs	1	0.005	0	0	0	0	0	0
Coagulated clutches	0	0	0	37	0.793	0	0	0
Total	8	0.398	3	0.185	52	1.115	1	0.021
<i>Rana temporaria</i>	281		10919					
Clutches without eggs	0	0	1	0.0009				
Egg without embryo	1	0.3566	0.055					
Joined clutches	1	0.3560	0					
Total	2	0.7117	0.064					
<i>Salamandrella keyserlingii</i>			247		5530		899	
Clutches without eggs			0	0	7	0.127	2	0.222
Egg without embryo			0	0	1	0.018	0	0
coagulated clutches			0	0	7	0.127	0	0
Total			0	0	14	0.271	2	0.222

(*T. vulgaris*, *Ambystoma tigrinum*) in similar situations is a good test for indication of some kinds of pollution (Rose and Harshbarger, 1977; Pliss and Khudoley, 1979).

The unusually low egg numbers in egg sacs of *S. keyserlingii* might be explained by females participating in reproduction being very young. The frequency of similar clutches in the forest population outside the urban area occurred only once. Such sacs were found frequently only in *S. keyserlingii* from Shartash Forest Park (the only exception is Kalinovskii Forest Park). *S. keyserlingii* is a stenotopic species that normally reproduces only in the forest park. Since 1978, in the Shartash population, the decrease in the mean number of eggs per sac reduced from 102 ± 5.8 ($N = 11$) to 56.0 ± 4.8 ($N = 26$) in 1993 was observed in females of similar body sizes (Vershinin, 1982a). Amounts of lipids in organism and general caloric content of females increases with age, and those conditions directly determine the increase of the number of deposited eggs (Bobylev, 1980). Age 1 amphibians usually are larger in urban populations than in natural populations (Ushakov et al., 1982; Gogoleva, 1985; Vershinin, 1987b). However, despite higher rates of growth, the decrease of absolute and relative fecundity occurs in polluted ponds (Bobylev, 1985) and that relates to deviations in lipid metabolism (Misyura, 1982). At a low level of fat content in the gonads, glycogen in the liver, and small general caloric content, there is a delay of female maturation for one year (Avramova et al., 1977). Moderate to weak feeding responses increases atretic oocyte numbers and a reduction

of ovarian mass in *R. tigrina* (Saidapur and Prasamurthy, 1988). The decrease of fecundity in *S. keyserlingii* in urban conditions reflects the reduction in nutrient reserves in females that are connected with energy expenditures for growth in animals from such populations. Clutches with abnormally low egg numbers were first found in 1988.

Since 1982, I have found clutches of *S. keyserlingii*, *R. arvalis* and *R. temporaria* with eggs without embryos in urban areas. The abnormal eggs frequency reached 25-50% of total egg number in a clutch. Some cases of completely empty clutches and one example of egg reduction were found. As known from experiments, the influence of chemical substances results in reduction of the amount of yolk and granulocytes in *R. tigrina* follicles (Pramoda and Saidapur, 1986). Hydrochemical analyses showed significant changes in environmental chemistry of the ponds (Vershinin, 1985a) that leads to functional deviations in female reproductive systems (Hazelwood, 1970). Changes in environmental chemistry promotes an increased probability of the formation of twin eggs in one envelope either by the inclusion of two or more eggs or the splitting of a single egg so that 2-4 embryos occur in one envelope. The case of an unusual egg arrangement in the spawn of *R. temporaria* and *R. arvalis* is also connected with deviations during clutch formation. Egg development in such case was not found, and with abnormal envelopes, they were housed in a common albumin sacs that were frequently joined with each other. The absence of individual envelopes probably is connected with deviations in normal function of initial parts of oviducts that are responsible for the formation of egg albumen envelopes.

The estimation of the importance of distinctions in abnormal *R. arvalis* clutch frequency in the zones with different urbanization level showed that there are no differences between populations of multistory and low building zones, but in all zones of the city the frequency is higher than in the forest population ($p = 0.05-0.001$; at χ^2 5.08-49.6). In *R. temporaria*, the difference between Zones II and III was highly significant: $\chi^2 = 14.3$; $p \ll 0.001$. No significant differences were found in *S. keyserlingii*. In most cases total frequency of abnormal clutches in populations of urban amphibians was insignificant, and it can not have a significant effect on reproductive potential of a population as a whole. On the other hand, the increase of their frequency (compared with the forest population) more than in brown frogs populations and twice that in *S. keyserlingii* shows the presence of negative tendencies. It should be noted that healthy *Bufo calamita* clutches are less sensitive to low pH than clutches with dead eggs (Beebee, 1986). Thus, the increase of abnormal clutch frequency in populations of urban areas reflect the negative influences on reproduction and represents an extreme expression of these processes that can promote early diagnostics.

8.5. Phenological specificity in amphibian reproduction and development

Phenological specificity of species formed on the background of thermal and chemical environmental pollution and the specificity of populations spatial structure is very

important in their reproduction and development. Amphibians are poikilothermic animals so their dependence on thermal conditions of external environment is very high, and other external influences are important. The amount of dissolved oxygen and the temperature of spawning ponds are the most important factors in the aquatic phase. Developmental rate and differentiation are substantially determined by temperature conditions (Doms, 1916; Douglas, 1948). Air temperatures from 5-10°C during larval development of *R. arvalis* inhibit development at moderate latitudes (Pyastolova and Shvarts, 1975). Our data for *R. arvalis* (Vershinin, 1985) revealed that the duration of larval stages and general duration of development are determined mainly by water temperature at the initial stages of development. Mean air temperature in the center of large cities is 1-2°C higher than at the periphery (Odum, 1975). The similar situation is in ponds of Ekaterinburg (Vershinin, 1983b). In Zones II and III, mean monthly temperatures in ponds in May are significantly ($p < 0.0001$) higher (about 3°C) than in Zone IV and the forest, and the limit of the minimum values is exceeded on 0.5-1°C (Table 23). In this connection, the earliest end of development is marked, as a rule, in habitats with the high urbanization. Dependence between the duration of development and water temperature in ponds are usually inversely proportional (Lebedinsky, 1984a). Relatively long spawning period in *S. keyserlingii* in Zones III and IV (Table 24) may be explained, apparently, by microclimatic features of hibernation and reproduction within one habitat, as well as by the age and physiological features of animals.

The high environmental heterogeneity of habitats in urban areas, including thermal biology, results in wide reproduction limits for *R. arvalis* (starts 13 April-May and ends 21 April-27 May) than in the forest (starts 13 April-12 May, ends 26 April-14 May; Table 24). Prolonged reproductive period is also typical for urban populations of *R. arvalis* in Tomsk City (Kuranova, 1989). Mean duration of the reproductive period of *R. arvalis* in the populations from the Middle Urals is 10-12 days (Shchupak, 1973; Pyastolova and Ivanova, 1978). *Rana temporaria* in urban Zones II and III does not have a significant differences in the duration of the main periods of development; the limits are 2X narrower and that probably is connected with relatively narrow range of habitat use in comparison with *R. arvalis* and a lower number of this species in habitats of the multi-story building zone. According to Toporkova (1966), the duration of reproduction in natural populations of *R. temporaria* is about 6 days, embryonic development takes 13-26,

Table 23. Mean±S.E. of monthly temperatures at the initial stages of amphibian development in zones with different urbanization levels (1980 - 1995).

Zones	t°C	Range	N
II	15.57±0.4	4.5-28.5	142
III	14.31±0.5	5.0-27.0	93
IV	11.18±0.38	4.0-28.0	167
C	12.53±0.53	4.0-28.0	84

Table 24. Number of days (mean±S.E.) of basic phenological periods of amphibian development in urban areas (1980 - 1995).

<i>Rana arvalis</i>				
Zones	Reproduction	Embryogenesis	Larva	Total duration
II	5.35±0.6	14.7±0.79	53.1±2.1	67.8±2.2
	13.04-10.05	20.04-26.05	8.06-23.07	
	21.04-16.05			
	N = 55	N = 51	N = 35	N = 35
III	6.06±0.9	14.0±1.1	56.4±2.8	71.2±2.9
	14.04-12.05	24.04-26.05	3.06-28.08	
	24.04-24.05			
	N = 26	N = 23	N = 20	N = 20
IV	6.97±0.54	16.55±0.69	54.7±1.7	71.4±1.7
	14.04-12.05	3.05-30.05	14.05-10.08	
	24.04-24.05			
	N = 73	N = 67	N = 57	N = 57
C	5.18±0.75	16.0±0.92	51.9±2.3	67.5±2.5
	13.04-12.05	2.05-28.05	16.06-20.07	
	26.04-14.05			
	N = 38	N = 38	N = 28	N = 28
<i>Rana temporaria</i>				
II	4.38±0.67	14.9±1.6	43.7±3.2	57.5±3.9
	20.04-6.05	7.05-20.05	20.06-5.07	
	22.04-12.05			
	N = 16	N = 14	N = 6	N = 6
III	5.7±0.45	13.9±1.0	43.3±1.3	57.3±1.6
	13.04-10.05	24.04-19.05	11.06-14.07	
	21.04-19.05			
	N = 36	N = 35	N = 34	N = 34
<i>Salamandrella keyserlingii</i>				
III	14.5±2.9	34.0±5.2	Larvae died	
	16.04-20.05	29.05-19.06		
	22.04-19.06			
	N = 14	N = 4		
IV	12.1±1.6	39.0±2.2	54.6±4.1	89.8±3.7
	14.04-12.05	27.05-15.06	3.07-10.08	
	22.04-18.06			
	N = 46	N = 22	N = 17	N = 17
C	8.7±2.4	39.5±4.2	60.5±8.5	96.0±8.1
	13.04-12.05	28.05-13.06	26.07-22.08	
	26.04-10.05			
	N = 21	N = 6	N = 4	N = 4

larval development 18-36, and general development duration 70-75 days. Thus, on the average, reproduction and embryonic development duration in *R. temporaria* in the urban area are close to the minimum, whereas the larval development exceeds maximum

Table 24. Continued.

<i>Triturus vulgaris</i>		
II		72.7±6.07
	26.04-23.06	20.06-28.08
		N = 7
III		84.0±11.4
	13.05-26.05	3.08-25.08
		N = 2
IV		73.0±6.6
	21.04-17.06	18.07-12.08
		N = 6
C		54.5±11.4
	21.05-21.06	16.07-14.08
		N = 2
<i>Rana ridibunda</i>		
II		74.25±7.3
	10.05-21.06	27.07-4.09

values for natural populations. General duration of development thus appears to be shorter than in forest populations.

The duration of embryonic development in *R. arvalis* with increases of urbanization changes to a smaller degree (Table 24) in comparison with the duration of larval development. That is explained by the greater stability of conditions during embryonic stages. Significant differences in the duration of embryonic development were found only between Zones III and IV (13.7 and 16.55 days, respectively; $p < 0.05$), but the tendency towards the reduction of the duration of embryonic development in urban area is notable. It may be explained by temperature modifications in urban areas caused by thermal pollution of the environment. Thus, the limits of this period are also extended. Regression analysis (reciprocal model) showed a tendency for a weak inverse proportion ($R = 0.30$; $p = 0.027$) between mean duration of embryogenesis and the mean monthly temperatures in the first month of development. The normal duration of embryogenesis is 10 days, and under unfavorable conditions it can be extended to 28-34 days (Shchupak, 1970).

There are no significant differences in the duration of embryogenesis in *S. keyserlingii*, but the tendency to shortening the period with the increase of anthropogenic influence and thermal pollution of environment is clear. The same concerns the duration of larval development and general development. The limits of embryonic development in *S. keyserlingii* are almost identical in all zones (Table 24) because of the greater uniformity of conditions in this period of development. The limits of metamorphosis are a little longer in the forest park zone, and it begins earlier than in forest. According to published evidences (Ishchenko et al., 1995), the duration of embryonic development in *S. keyserlingii* is 13-16 days (Talitsa, Sverdlovskaya Province), or an average of 20-30 days (i.e., 25-29 cell cycles slower than in Northeastern Yakutia; Godina, 1987).

According to Basarukin and Borkin (1984), the duration of embryonic development in *S. keyserlingii* in Sverdlovsk area is 17-37 days (larval hatching 6 May-6 June), and larval development lasts 43-102 days (metamorphosis 19 July-8 August). The most common larval development duration for the latitude of Sverdlovsk is 60-80 days.

At mean monthly temperatures of May from 9.2-14.3°C, total duration of *R. arvalis* larval development is 62-103 days, and when the mean monthly temperatures of May are 14.4-19.8°C, 65-55 days (Vershinin, 1985). Significant differences in the duration of larval development and total duration of development were not found. The maximum dispersion of the timing of metamorphosis was found in populations of the forest park and low buildings zone (Table 24), because well warmed and very shadowed, cold ponds are in these zones. The mean values of the duration of larval development and total duration of development tend to be prolonged in urban areas to 53.1-56.4 days vs. 51.9 days in the forest population. In natural populations of *R. arvalis* the larval development lasts about 48 days (Shchupak, 1970).

The populations of *T. vulgaris* from the zones with different levels of urbanization also differ insignificantly in the total duration of development, but the expansion of breeding and developmental period limits in urban areas and the tendency to extend the total duration of development in urban populations are clear. According to Toporkova (1973), the reproduction of *T. vulgaris* on the Middle Urals begins at the end of April-beginning of May, and metamorphosis finishes by the end of July. The minimum duration of the newt reproduction and development in urban areas and in the forest population (Table 24) are different. The reproduction and the appearance of the recently metamorphosed animals are earlier because of earlier warming of breeding ponds at urban sites. The minimal total duration of development in the city is significantly longer than in the forest. The prolongation of larval development and total time of development in urban ponds may be connected with inhibiting pollutant actions (Bugaeva, 1982; Lebedinsky, 1984a; Danilova, 1992; Baker and Waights, 1994). As shown experimentally, the action of some chemical agents (e.g., urea, copper and cadmium sulfates) retard developmental by 4-11 days (Grefner and Slepyan, 1989), and the differences in the rate became remarkable from stage 49 (Dabagyan and Slepsova, 1975). The variability of developmental and growth rates in newts in natural conditions are also under the control of external factors (Ishchenko, 1984).

Characteristics of populations from the multistory building zone include a prolongation of the aquatic phase in adult animals. Some newts stay in pond until the middle of August, and in natural populations the adults enter land in July (Toporkova, 1973). This phenomenon seems to have an adaptive character and be connected with the small area of terrestrial habitats, limitation of resources, and possibilities of animal dispersal. The transition into a new adaptive zone always begins with behavioral changes. Behavior represents an important evolutionary factor, especially at the presence of new evolutionary tendencies (Mayr, 1974).

One could conclude that features of urban landscapes have a high environmental heterogeneity on a rather small area which results in the occurrence of a number of

features during amphibian growth and development. Significant differences in temperature of ponds lead to increased limits of amphibian reproductive period, embryogenesis and larval development within cities in comparison with forest populations. Low animal number in Zones II and III was associated with short periods of reproduction in each local habitat of these zones. The tendency towards shortening of embryonic development in urban area was observed in *R. arvalis*. The minimum duration of development in this amphibian species was found in multistory and low building zones where the ponds with high temperatures in the initial period of development prevail. There is a tendency to extend the mean duration of larval development and total aquatic development of *R. arvalis*, *R. temporaria* and *T. vulgaris* in urban areas, and that is probably promoted by the inhibiting effect of the pollution of aquatic environment. The features of territorial distribution of urban populations (significant reduction of terrestrial habitats) may be the cause for behavioral specificity in *T. vulgaris*.

9.0. TROPHIC RELATIONSHIPS OF JUVENILES IN URBAN AREAS

9.1. Trophic relationships of juveniles at beginning of terrestrial life

The life and reproduction of organisms are always strictly defined by the environment to which they are adapted. Adaptiveness means the normal ability to live in the given conditions of existence. It is characterized by complex interaction with all factors. Very complex relationships occur together with all normal conditions of existence of the given species. Organisms forming interrelated complex characteristic for certain habitats are called a biocenosis.

Plants play the main role in substance and energy transmission in the vertical direction in a biocenosis and participated in minor circulations of substances. The role of animal population with a mobile life mode in the formation of a biocenosis structure is not so clear. Animals play the main role in horizontal transmitting of substance and energy and participate in the establishment of relations between various small circulations (Voronov, 1968).

The problem of the biocenotic amphibian role has been investigated by many authors and in various aspects. The specificity of amphibian role is determined by the fact that they form a link between terrestrial and freshwater ponds (Garanin, 1976) and play the important role in substance and energy transmitting between ecosystems of different biocycles. At metamorphosis amphibians take 100 times more energy than was in the eggs from the aquatic ecosystems into the terrestrial ecosystems (Seale, 1982). Amphibians occupy specific places in riparian and aquatic ecosystems where they act as consumers of the 1st order and then pass to carnivory (Garanin, 1981). The food spectrum of amphibians indicates their significant role in the control of insects harmful for agriculture and forestry (Shvarts, 1948; Papanyan, 1949). In the process of increasing influence of anthropogenic and pyrogenic factors, the usefulness of many species in-

creases because of the increasing consumption of phytophages (Belova and Kostenko, 1976). The almost complete absence of food specialization, which is determined mainly by sizes of prey object (Loman, 1979), leads to the consumption of insects with cryptic coloration and unpleasant taste and smell that significantly supplements the activity of insectivorous birds (Shvarts, 1948).

Trophic pressure of amphibians on the soil mesofauna depends not only on number but also on physiological condition and size structure of the populations (Ganeev, 1991). The annual withdrawal of invertebrates by amphibians in different terrestrial communities changes within the limits of 2-5% of production, and that is comparable and sometimes exceeds the activities of birds (Gilmanov, 1987). Amphibians require 10 times less food than birds and mammals for formation of similar biomass because of their low metabolic rates (Seale, 1982). The ecological efficiency of poikilothermic vertebrates is estimated as about 10%, which is 2% less than in homeothermic animals (May, 1983). The tadpoles of five various tailless amphibian species use food with almost identical efficiencies of 9.0-13.3% of consumed foods that are transformed to the consumer biomass; such a small dispersion indicates similar intensity of energy balance within the limits of one trophic level (Shvarts, 1975). Amphibian species consume considerable mass of dead organic and unicellular algae that prevents "flowering" (Gaizhauskene and Uselite, 1977). Eating of nitrogen-fixing Cyanophyta algae by tadpoles brings nitrogen into the trophic chain (Seale and Beckvar, 1980).

Tadpoles in communities of stagnant ponds play an important role in regulation of the levels of primary production. This regulation is connected not only with their feeding on algae but also excretion of nutritious substances with feces (Malone, 1994). Larval biomass is so high that their significant role in transfer of substance and energy in biogeocenosis is indisputable (Shvarts, 1973). Throughout larval growth and development the food spectrum reaches a maximum at premetamorphosis stages (Belova, 1964; Kuzmin, 1986). As considered earlier (Li and Lin, 1935; Etkin, 1964, froglets become carnivorous after tail resorption. Actually, metamorphs do not eat during the breakthrough of the forelimbs (Kuzmin, 1987). Feeding stops not in all species, and when it does occurs, the refusal of food embraces only part of metamorphosis (Kuzmin, 1986, 1987). Digestive enzymes necessary for digestion of animal food exist in larval stages (Houdry et al., 1979). The occurrence of animal food in tadpole diets increases at the end of metamorphosis (Belova, 1964, 1965; Motkova, 1977). Growth and development rates in *R. arvalis* tadpoles is higher when consuming a mixed food compared with only animal or only vegetative food (Suzumova et al., 1987).

The transition to feeding on invertebrates starts at the end of tail resorption. In *Rana clamitans* it occurs when the tail is about 7 mm (Jenssen, 1967) and in brown frogs (our data) at 1-13.5 mm. Microarthropods prevail: Collembola, Nematoda, Aphidodeda, soil mites, etc. (Guyetant, 1967; Zhukova, 1979; Wheeler, 1986; Leontjeva, 1987). From the time of tail resorption to the end of metamorphosis, feeding occurs in all froglets, their feeding intensity is higher, and the scope of individual activity and

food spectrum is wider (Vershinin, 1995c). The mean number of food objects per gastrointestinal tract increases with age (Kuzmin, 1984; Lynch, 1985; Vershinin, 1987d), the sizes of maximum accessible food objects increases, and, in some cases, the number of larger prey increases (Ishchenko and Skurykhina, 1981; Whitaker et al., 1983; Wheeler, 1986). This tendency may be reduced because of the large proportion of small objects (Gittins, 1987). Nevertheless, in large animals the tendency of shift to larger prey occurs. Larger prey are more valuable energetically and more visible and apparently are a factor of increase growth as the proportion of this type of food objects increases (Christian, 1982). Different age groups of *R. arvalis* (mature and immature) consume about identical biomass of invertebrates; the change in age group ratio in a population can lead to remarkable change in the biomass consumed (Ishchenko and Skurykhina, 1981).

The functional role of a new generation is determined by its number and proportion in a particular community. Amphibians can exceed the biomass of terrestrial vertebrates (Kopein, 1970; Ravkin and Lukyanova, 1976; Kuranova and Grigoriev, 1980), and the role of this group may be more significant in natural than in urban ecosystems. Also, amphibians quite often are one of few vertebrate animals occupying urbanized territories. The dynamics of biocenotic processes over huge areas is determined by several ubiquitous species under the anthropogenic influence. Simplification and change of biogeocenotic structure and separate diets result in the increase of the role of animal organisms as destructors of organic substance (Shvarts, 1976b). In natural ecosystems amphibians consume 0.03-0.06% of pure primary production, and in anthropogenic complexes, where primary production is low, they consume about 0.1% (Leontjeva, 1990). Individuals in a population use available food resources unequally based on age, size, habitat, and many other aspects. At the similarity of animal developmental conditions for population characteristics, the data on peculiarities in feeding of different micropopulations may be obtained (Kuzmin, 1985). Thus, the higher the hierarchical rank of compared groups, the higher the degree of similarity in their food spectra (Tarkhnishvili and Kuzmin, 1989).

Populations of *R. arvalis* in Zone II occupy habitats small in area, but the density of animals there is higher than in Zone III and the forest park (Vershinin and Krinityn, 1985). The influence of urban populations on invertebrates appears to be more intensive. In natural biogeocenosis the highest mortality of metamorphosing *R. temporaria* and *R. arvalis* occurs in the first 1-3 weeks of terrestrial life (Smirina, 1980; Ishchenko and Ledentsov, 1985). It is reasonable to consider that froglet mortality in the beginning of their terrestrial life depends on density (Severtsov, 1986). Predators may represent one density-dependent mortality factor (Lyapkov, 1987). According to our data, mortality in the first 2 weeks after metamorphosis is significant (Vershinin, 1983a; Vershinin and Trubetskaya, 1992). It is higher in the forest than in urbanized areas, and the mortality of *R. temporaria* on urban area is higher than that in *R. arvalis*. One of the causes of high survivorship from stage 53 to stage 54 in *R. arvalis* in urban popu-

lations apparently is an almost complete absence of natural enemies, except for men (Zhukova, 1978). Sometimes large-sized froglets are less vulnerable for such predators, as a shrew that is capable of eating up to 65.1% of all generation during 1.5 month (Lyapkov, 1987). As already mentioned, body length of *R. arvalis* froglets in Zone II was significantly more than that in the forest population during all years. Large froglet body sizes may influence its feeding behavior. At the completion of tail resorption some of froglets begin to feed. There are significant ($p < 0.05$; $\chi^2 = 5.11$) differences on the proportion of feeding individuals with a tail rudiment between Zone II and the forest. In different populations this proportion varies from 13.2-51.7%. In *R. temporaria* it is significantly ($p < 0.05$; $\chi^2 = 5.58$) higher than in *R. arvalis* in Zone II and smaller in Zone III. Probably the low frequency of froglets feeding up to the end of metamorphosis in Zone II relates to the fact that large froglets have some energy resources whereas small ones do not (Crump, 1981), and these die if they do not begin feeding immediately (Shvarts, 1980). At the beginning of the terrestrial life froglets from Zone II have bigger radii of individual activity, and their food spectrum is less similar to the spectrum of soil invertebrates than in other zones. Larger froglets of *B. calamita* consume a wider taxonomic array of arthropods and may contain an average of 3.5 times more food objects (Golay et al., 1995). The difference relates to the fact that already at the stage 53 the flying forms and others invertebrates appeared and did not include a complex soil micro- and mesofauna (Fig. 17). There is a reduction of the proportion of saprophages and an increase of phytophages in the food spectrum (Fig. 18). Two weeks after metamorphosis, qualitative and quantitative changes in the food spectrum of *R. arvalis* are noted (Fig. 17) most clearly in populations subjected to significant anthropogenic influence (Zone II). Thus, in froglet populations of Zones II and III the phytophage proportion with age increased from 30.8% at stage 53 to 51.2% at stage 54. The proportion of carnivores and saprophages decreases or does not change. Significant differences in the proportions of trophic groups do not occur in the forest park and forest (Fig. 17).

The estimation of food spectra similarity in metamorphosed (stage 53) and grown (stage 54) *R. arvalis* and *R. temporaria* froglets showed their significant overlap and similarity without being related to the level of anthropogenic pressure (Table 27). The changes of stomach contents only in froglets from forest population, as well as the changes of natural invertebrates spectrum, are most significant. On the basis of materials collected in 1977, the comparisons of food spectra in adult and juvenile *R. arvalis* were made. The differences were obvious ($C = 0.62$) in population of Zone II (Polzunova Street) and in the smallest individuals ($C = 0.96$) from the forest population. Thus, the number of invertebrate systematic groups in the food of adult animals from Zones II and III is less than in froglets (7 vs. 13 and 7 vs. 9, respectively). In populations from the forest park zone and forest, this reduction was not found. Comparisons of the degree of overlap in adult diets showed that individuals from multistory and low building zones are most different (Fig. 17a).

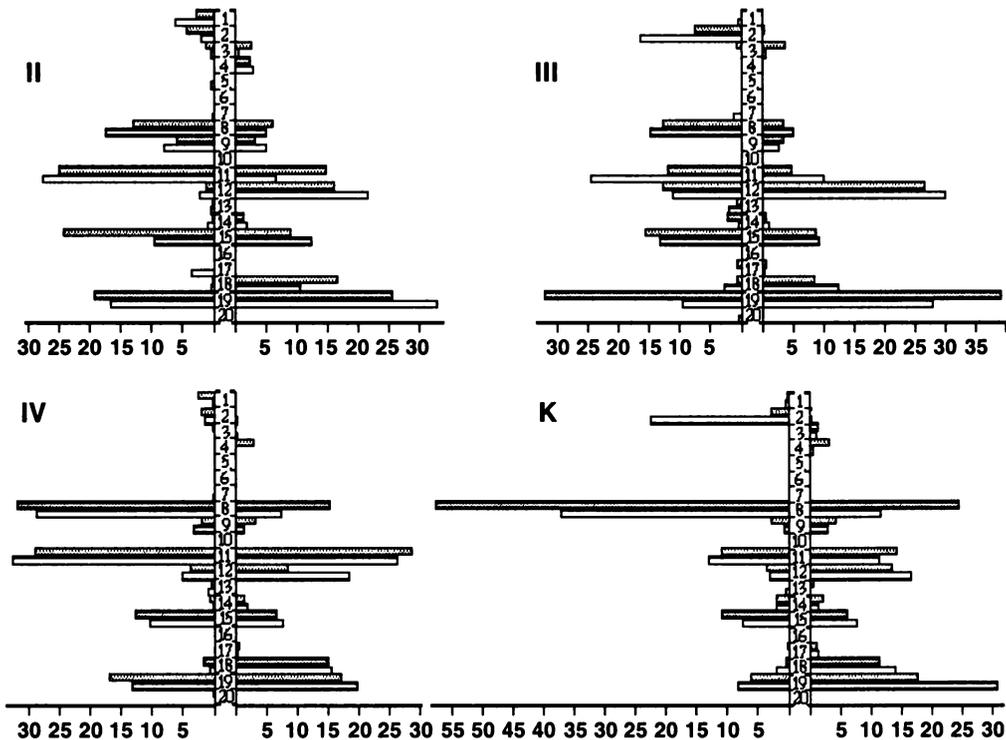


Fig. 17a. The range of invertebrate groups from soil samples and from *Rana arvalis* froglet digestive tracts (% of total number of invertebrates, 1985-1988). II - multistory building zone, III - low building zone, IV - forest park zone, and C - forest. Y-axis: systematic groups, X-axis: percentages; left: soil fauna, right: stomach contents; 1 - Oligochaeta, 2 - Nematoda, 3 - Mollusca, 4 - Crustacea, 5 - Isopoda, 6 - Diplopoda, 7 - Myriapoda, 8 - Acarina, 9 - Aranei, 10 - Pseudoscorpiones, 11 - Collembola, 12 - Homoptera, 13 - Thysanoptera, 14 - Hemiptera, 15 - Coleoptera, 16 - Neuroptera, 17 - Lepidoptera, 18 - Hymenoptera, 19 - Diptera, and 20 - Psocoptera; dark columns: stage 53, light columns: stage 54.

The degree of overlap of the gastrointestinal tract contents with natural invertebrate spectrum in metamorphosed froglets from Zone II is less in comparison with the grown froglets, and this is directly opposite to the results observed in other zones and in the forest. Similar data occur for *R. temporaria* froglets; the degree of overlap in the diets with the natural spectrum increased with age (Fig. 17b). The mean number of food items per stomach to stage 54, in comparison with the stage 53, increased considerably (from 1.9-6.9 up to 3.3-13.05 in *R. arvalis* and from 0.75-1.4 to 4.8-14.8 in *R. temporaria* at the absence of interzonal differences), and in urban area the pressure of froglets on invertebrates, despite the numeric decrease, in most cases remained at significantly higher level ($p < 0.001$; $r^2 = 64.3-1589.7$), than in natural communities (Table 27). Similar data were received for *R. temporaria*, although froglets survivorship in this species in the urban area is lower than in *R. arvalis* (Table 21).

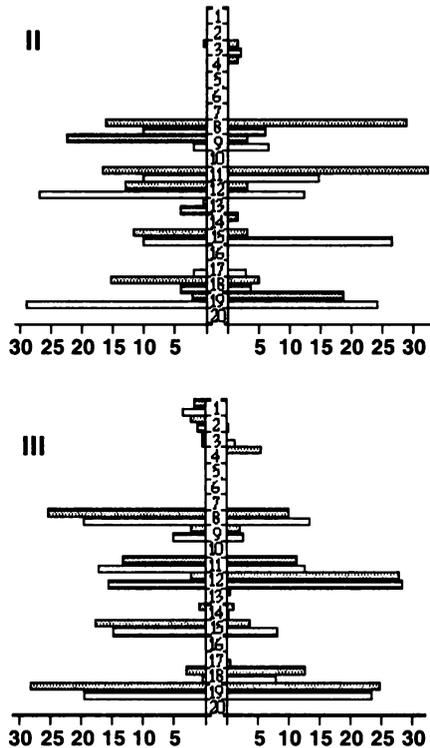


Fig. 17b. Spectrum of invertebrates from soil samples and *Rana temporaria* froglet digestive tract contents (% of total number of invertebrates, 1985-1988). II - multistory building zone and III - low building zone.

Censuses of soil micro- and mesofauna in froglet habitats showed that from the start metamorphosis to stages 54, an increase in general number of objects per unit of area occurred in 62.5 % of the cases (Table 28). In urban habitats such increases were found only in 25% of the cases. In Zone II, the numbers of mites, spiders, collembolans, and thysanopterans increased, while the numbers of hymenopterans and lepidopterans, nematodes, beetles, and flies reduced over two weeks. Homopterans were represented with by phytophages (e.g., Aphidinea, Cicadinea, and Aphrophoridae), and among hymenopterans phytophages were also found (Cynipoidea). In the forest at this time the percentage of nematodes increased and the abundance of mites decreased. In all other zones the were little but significant changes in one or two groups (Fig. 17).

In *R. arvalis*, the similarity of gastrointestinal tract contents with the spectrum of soil microfauna varied from stage 53-54 in populations of Zones III and IV; in the forest it overlap with the invertebrate spectrum in the environment or decreased a little (from 43-94 to 27-81%), and in populations of Zone II it increased (from 45-70 to 38-79%; Table 25). In *R. temporaria*, the similarity with natural spectrum increased in Zones III and II.

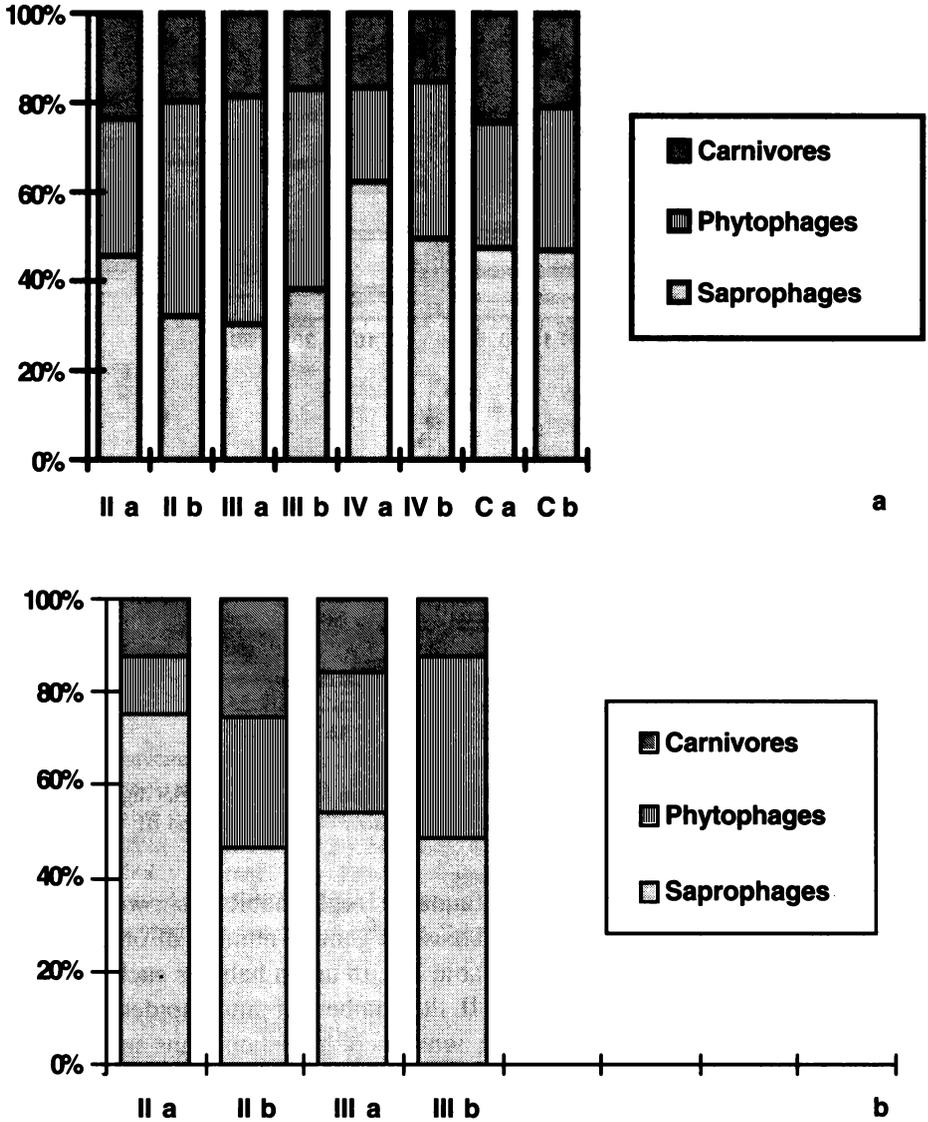


Fig. 18: a. Trophic groups of prey in *Rana arvalis* froglets by stomach content analysis (% , 1985-1988). II - multistory building zone, III - low building zone, IV - forest park zone, C - forest; a - stage 53, b - stage 54. b. Trophic groups of prey in *Rana temporaria* froglets by stomach content analysis (% , 1985-1988). II - multistory building zone, III - low building zone, IV - forest park zone, C - forest, a - stage 53, and b - stage 54.

The index of selectivity characterizes an amphibian population pressure on invertebrate fauna more precisely and in more details. It is determined as the ratio of the fre-

Table 25. Comparison (%) of the food spectrum similarity of brown frogs juveniles at stages 53 and 54 with the natural invertebrate spectrum (1985-1988). Notations: N - number of stomachs; 1 - stage 53 and 54, 2 - stage 53 with the spectrum of invertebrates in nature; 3 - stage 54 with the spectrum of invertebrates in nature; and 4 - overlap of natural spectra of invertebrates.

	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Zone	II				III				IV				C			
<i>Rana arvalis</i>																
Year																
1985	83	70	38	68	83	68	36	67	88	83	75	76	65	45	27	24
		N = 13	N = 14			N = 15	N = 15			N = 16	N = 55			N = 30	N = 19	
1986	76	63	54	75	67	63	63	80	64	32	75	91	43	37	56	
		N = 16	N = 11			N = 9	N = 25			N = 30	N = 19			N = 30	N = 30	
1987	85	45	79	70	91	93	81	81	94	93	77	97	91	67	59	99
		N = 32	N = 32			N = 15	N = 13			N = 61	N = 44			N = 27	N = 30	
1988	93	58	65	82	89	46	63	85	91	94	68	91	39	81	67	88
		N = 39	N = 43			N = 30	N = 22			N = 69	N = 67			N = 30	N = 27	
<i>Rana temporaria</i>																
1985	73	61	71	43	61	21	94	11								
		N = 16	N = 12			N = 28	N = 21									
1986					31	55	61	49								
						N = 23	N = 21									
1987					85	73	80	97								
						N = 30	N = 30									
1988	53	26	74	43	71	49	46	36								
		N = 15	N = 6			N = 28	N = 24									

Table 26. Food spectrum similarity in adult *Rana arvalis* from different zones in 1977.

Zones	II	III	IV	C
II	X	0.76	0.86	0.67
III	0.76	X	0.51	0.57
IV	0.86	0.51	X	0.85
C	0.67	0.57	0.85	X

Table 27. Consumption (% of total number of objects consumed at stage 53) of invertebrates by froglets at stage 54 (1984 - 1988).

Zone	II	III	IV	C	II	III
Year	<i>Rana arvalis</i>				<i>Rana temporaria</i>	
1984	187	5.6	170.9	148.8	29.4	
1985	207.5	243.8	157.3	45.4	34.7	180.3
1986	46.3	72.3	30.6	62.1		160.3
1987	102.5	32.4	35.7	28.9		112.4
1988	34	60.2	28	12.7	82.6	60.1

quency of any group of food objects in the stomachs to the frequency of this group in nature. If the index = 1, the index indicates food avoidance, and if it is > 1, it is possible to

Table 28. Density of invertebrates (individuals/1 m²) at the beginning of stages 53 and 54; N - number of combine samples.

Years	Stages	Zone II	N	Zone III	N	Zone IV	N	Forest	N
1985	53	1567.5	2	1667.5	2	1022.7	4	667.0	1
	54	6670	2	2134.4	2	3779.7	4	11405.7	1
1986	53			3893.8	2	1567.5	2	1827.3	2
	54	2267.8	1	1853.9	2	2040.6	2	1387.0	2
1987	53	2201.1	2	2890.3	3	2081.0	4	2701.4	2
	54	1900.9	2	2423.4	4	1600.9	4	5902.9	2
1988	53	2684.7	5	1984.3	4	1445.2	5	3134.9	2
	54	2067.7	4	1450.7	4	1760.9	5	3068.2	2

speak about the preference of that food group. Graphic interpretation of the data allows a visual estimate of an index of selectivity (Fig. 17). Aranei, Collembola, Homoptera, Lepidoptera, Hymenoptera and Diptera in the forest and Mollusca, Homoptera, Hemiptera, Coleoptera, Lepidoptera, Hymenoptera and Diptera in Zone II are exposed to greater foraging by froglets. The decrease of froglet pressure on invertebrates in natural amphibian populations should be connected with the mortality of a significant part of froglets in each micropopulation because of the greater number of trophic relations and levels (i.e., number of predators is high). In such cases, a significant mortality does not mean failure for an entire population (Shvarts, 1980) because the number of micropopulations is large. The situation in urban area is different. There, a majority of populations (not subdivided into micropopulations) do not have contact with each other, and the number of such groups is small at high local densities. Therefore, a failure in reproduction of each particular group is more serious for it (to its complete disappearance) because of an absence of immigration. According to Lyapkov (1992), there are compensatory mechanisms of unfavorable influence at high densities, and froglets can stop selective foraging on larger forms and transfer to smaller but more numerous ones. The number of invertebrates consumed during the 2 weeks after metamorphosis in habitats of urban areas increased slowly, probably as a consequence of more effective eating of invertebrates in populations (because froglets mortality is low and sizes are large) and also a smaller variety of food objects. This suggests indirectly that large differences in soil invertebrates spectrum in this period (Vershinin, 1995). This opinion is supported by the above mentioned relative narrowing of the adult *R. arvalis* food spectrum (Fig. 17). As known from general approaches to the study of population metabolism, a decrease in resource abundance and diversity ensures energy expenditure at the level of population. The greater number of population functions that are present, individual efficiency of energy use is reduced and population efficiency grows (Mezhzherin, 1988). A city is an open and dependent ecosystem with producers, consumers, and reducers-destroyers. The system-forming elements are the flow of substances, energy and information. The city is also an accumulative system. Positive export causes permanent accumulation of substances in urban areas. There is an accumulation of a huge "cultural"

layer; the initial relief is leveled, rivers are covered with concrete or drained in pipes, and new forms of a relief appear. The chemically active, toxic substances in soil and water accumulate. The import exceeds export to tens and sometimes hundreds of times (Mazing, 1987). In these conditions of biogenic circulation, the descending flows of substance become important. An especially important role is acquired by mineralizing dead, organic substances and organisms decomposers. Juvenile amphibians at the beginning of their terrestrial life are related to this biogeocenotic component that acquires a special importance in urban ecosystems. Thus, specificity of the number dynamics and features of the territorial organization are the causes of the increase of the ecological role of each new brown frogs generation at the beginning of its terrestrial life in urban isolates with a high levels of anthropogenic influence.

9.2. Rate of food passage in juvenile *Rana arvalis*

Investigations of the rate of food passage through the gastrointestinal tract in amphibians are relatively rare (Reeder, 1964; Gossling et al., 1980; Ganeev, 1985). In one case, frogs did not receive food, except for dye, and in others the food objects were represented by forms with rigid chitin exoskeletons (e.g., Coleoptera, Orthoptera, and Hemiptera). This complicates food mass passage through the digestive tract (our data) and the result appears underestimated. All existing works were carried out on adult anurans, and the rate of food passage in froglets, which have two peaks of activity per day (Toporkova, 1973), was not studied. The role of anuran froglets in ecosystems is significant and specific because the period from metamorphosis to hibernation of a new generation is significant in many species which feed on small invertebrates that rare in the food of adult animals (Ishchenko and Skurykhina, 1981; Vershinin, 1984; Leontjeva, 1987).

During 1985 and 1986, several series of experiments on food passage rates of *R. arvalis* froglets were carried out. In August 1985, we conducted the first experiments on the improvement of the technique with the use of colored plastic markers, specially made by us, with the size 0.3 x 0.3 mm. All experiments were done at $t = 21^{\circ}\text{C}$ in terrarium. Experiment 1 provided an introduction of markers every 12 h with constant presence of food (alive small invertebrates caught in nature). The presence of permanent temperature and a wide spectrum of natural food are necessary for obtaining of real and comparable information because it is known that the rate of food movement in the digestive tract depends on temperature and food composition (Schabetsberger, 1991). After 12 h, the finishing marker was added, and 5 animals were fixed over 12 h. The duration of intervals in the experiment 2 was reduced: 4 intervals for 6 h and the last 2 for 3 h. In 1986, the experimental design was changed: all intervals in the experiment 3 were equal to 3 h and some froglets was fixed every 3 h. In experiment 4, with an interval of 3 h, the markers of five different colors were given, and after 12 h from the beginning of the experiment the froglets were fixed every 3 h for 12 h. Intestine and stomach length and the distance traversed by each label were measured. Froglets that did not eat during the experiment were excluded because the markers either moved very

quickly in the empty digestive tract or remained for long time in the stomach. For obtaining of a more complete picture, results of the experiments 1-2 and 2-3 were summarized. The measurements of stomach and intestine length in froglets are given in Table 29. The rate of food mass passage changes within the limits of 1.1-1.9 mm/h, and in the intestine the rate of movement is a little higher than in the stomach. Food mass slowed down the movement just after its exit from the stomach (Fig. 19) and in the back part of the large intestine where not digested remains are accumulated.

In experiments in 1985, I used animals from population of the forest park zone (Shartash Forest Park), and in 1986 frogs from the zone of multistory buildings (Kuibysheva Street) were tested. As a whole, the mean rate of food passage in the digestive tract in froglets from samples in 1985 and 1986 did not differ significantly and was 1.35 ± 0.16

Table 29. Length (mm, mean \pm S.E.) of the stomach and intestine of *Rana arvalis* froglets (1985-1986).

Years	Stomach	Intestine	Total	N
1985	8.1 \pm 0.3	32.6 \pm 1.1	40.6 \pm 1.3	36
1986	10.3 \pm 0.7	29.0 \pm 0.8	38.3 \pm 0.9	32

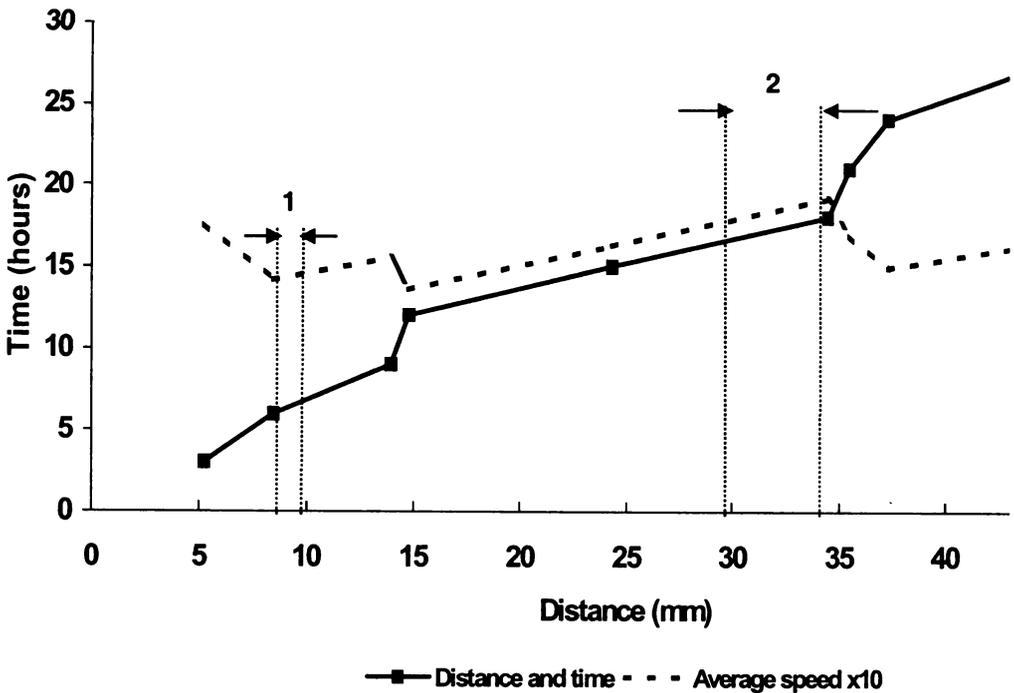


Fig. 19. Food passage through the digestive tract of *Rana arvalis* froglets. 1 - stomach, 2 - large intestine border.

($N = 49$) and 11.63 ± 0.11 mm/h ($N = 103$), respectively. It is possible only to note the tendency to an acceleration of digestion in froglets from Zone II. When summarized for both years, the mean rate was 1.54 ± 0.09 mm/h. The food remains in the stomach 6-7 h and by 15-18 h the food mass reaches the within 30 mm of the large intestine (this border was taken conventionally). After 15-21 h, the digested remains accumulated in the hind region of the large intestine where they may stay during about 12 h before defecation occurs. Thus, the rate of food passage through the intestine was slower than in the experiments of Gossling et al. (1980) and higher than in the experiments of Ganeev (1985). I think that it is determined by differences in food density and probably by age of the froglets. The insignificant increase of digestion rate in froglets from the population from Zone II (with the highest urban transformation) may be related to the increased level of metabolic processes in individuals from populations on urban territories.

10.0. METHODS OF BIOINDICATION AND AMPHIBIANS

The level of industrial development and human activity has reached global scales. At the beginning of the 20th century, Vernadsky (1977) wrote that “. . . for the first time in history of mankind, we are in the conditions of the uniform historical process which has embraced whole the biosphere of the planet.” The biosphere became a global carrier of consequences of this process. Most “pristine” biocenoses are under the influence of anthropogenic pressure because of background pollution, chemically active rains, and climatic fluctuations. In this connection, the understanding of the social importance of “primary” conditions of human existence increases (Yanitskii, 1987). Our aim is to facilitate the formation of productive and stable biogeocenoses with necessary properties in the face of anthropogenic changes of the environment. It means that some species should exist in an anthropogenic landscape and that we should conduct changes in the regulations of natural management. For maintenance of the general balance of the biosphere at a level ensuring optimal development of the human society, it is necessary to introduce ecological examination and ecological monitoring of the urban and agricultural economies. Ecological monitoring at levels of the population and ecosystem is the most widely applicable and convenient. Some ubiquitous species still exist in anthropogenic landscapes, and they perform important roles in maintenance of a natural balance. It also determines the main directions of scientific research (Shvarts, 1973).

Amphibians represent an object convenient for monitoring. Their numbers are large enough, clutches and tadpoles are sensitive to pollutants, and during larval life they are restricted to relatively small areas. Amphibian life duration is 4-7 years in nature which is longer than some small mammals. This makes it possible to study the long-term effects of anthropogenic factors. Correct estimation of environmental conditions is impossible solely based on pollutant concentration measurement in water and soil because it is necessary to know the directions and mechanisms of polluting reactions in ecosystems.

The final conclusion can be made only on the basis of extensive long-term research. Using the typification mentioned above, we can call the level of ecosystem transformation in Zone IV as initial, in the Zone III as average, and in the Zone II as significant.

1. Attributes of an initial level of changes.

a) Changes in species composition. A good parameter of the initial environmental transformation stages is the change of kinds of amphibians present. For example, in the forest park zone a typical forest species, *B. bufo* is almost absent (Vershinin and Toporkova, 1981). When estimating changes in species composition, it is necessary to know the published information about species composition of the pasts in the area under study.

b) Fall in population size and density. Long-term studies reveal the decrease in numbers of clutches of amphibians in the forest park under the increased recreation pressure (Vershinin, 1982a, 1989a). Censuses of animal density show a significant decrease in comparison with forest habitats (Vershinin and Krinitsyn, 1985; Vershinin, 1987a). For sufficient comparisons of clutch density in the same pond, it is possible to count clutches on 10 m² of water surface.

c) Negative changes in populations of forest species. In populations of *S. keyserlingii* from the forest park habitat with increasing anthropogenic pressure and high levels of heavy metal pollution, the decrease of mean numbers of eggs/egg sac (e.g., from 97-102 in 1977-1978 to 56-71.3 in 1986-1988) was found. That change was followed by the general decline in number of breeding animals. Mean lengths of females did not change significantly. The limits of eggs number variability from the forest park zone populations have appeared broader than in the forest population: 0-198 and 28-119 eggs, respectively (totally for all years; Vershinin, 1989b). The differences in the scope of variability reflect, apparently, negative changes in mature females because the minimum egg numbers reached 0-4, and in the forest population it does not decrease below 28. The proportion of such clutches is insignificant (from 0.37-3.2%), but this tendency is maintained for a number of years and is most expressed in the populations under increasing anthropogenic pressure. Under conditions of pollution and environmental transformation, populations in the forest park zone have a number of physiological adaptations at the level of the individual (Vershinin and Tereshin, 1989) that result in additional energy loss (Shvarts, 1980). Partial eggs resorption under the conditions of significant anthropogenic pressure is known also in fish populations (Koshelev, 1988).

The increased level of asymmetry may be a good indicator of changes in populations (Zakharov, 1987). I used this parameter in clutches of *S. keyserlingii* to calculate a ratio of smaller egg number per sac to the higher number in the other (see Basarukin and Borkin, 1984). A tendency to increase this proportion of asymmetrical clutches (with differences between sacs more than 30%) to 16.2% against 10.2-11.7% in other forest park populations was noted in the population from the forest park habitat with the strongest environmental pollution. The differences between sacs can attain 89-100% (when one of sacs does not contain eggs or contains their abnormally low number), and the absolute maximum difference is 93 eggs.

d) Accumulation of pollutants. Knowledge of amphibian longevity influenced by pollutant accumulation allows us to estimate the threat that degree of pollution presents for different trophic levels in an ecosystem (Byrne et al., 1976; Hall and Kolbe, 1980). The study of the fluoride content in forest ecosystems in an area near cryolytic and aluminum factories in the Urals showed that the amphibians concentrate fluoride to a greater extent than other zoological components of ecosystem (up to 580 mkg!SK., here is the mkg again per gram of dry mass; Lyubashevsky et al., 1985). For the estimation of initial stages of an ecosystem transformation, it is convenient to use changes in amphibian species composition, number of common and widespread species, density, decreases of fecundity, increases of clutch asymmetry as well as the accumulation of pollutants.

2. Mean level of changes. At a given level of change in connection with pollution and radical changes of vegetation, *S. keyserlingii* declined; negative tendencies began to occur in the amphibian populations.

a) Morphological anomalies and the increase of frequency of abnormal clutches. All local amphibian species display an increasing general frequency of occurrence of morphological anomalies (Vershinin, 1982a, 1989a). It may involve postmetamorphic edema, abnormal regeneration, developmental anomalies, neoplasms, and genetic anomalies. Many investigations (Rose and Harshbarger, 1977; Pliss and Khudoley, 1979; Cooke, 1981; Dumpert, 1986; Baranovsky and Kudokotsev, 1988; Meyer-Rochow and Asashima, 1988) suggest the use of such deviations in bioindication. Increases of mutation frequency are known. Only the frequency of one mutation, iris depigmentation in *R. arvalis* in urban areas exceeds its percentage in the forest population: 1.39 (N = 5050) vs. 0.03 (N = 2307; Vershinin, 1988). Brown frogs in the urban have clutches with a significant proportion of eggs without embryos or without individual albumen envelopes (Vershinin, 1990b; Vershinin, 1995b). Frequency of these clutches varied from 0.3-12.5%.

b) Occurrence of physiological adaptations at the level of organism. In Zones II and III, in connection with the process of compensatory hypertrophy developing as a response to decreased contractive properties of the myocardium under anthropogenic environmental changes (Shklyar and Vershinin, 2000), I have found an increase of the $Cor\%$ index in the brown frogs juveniles (Vershinin, 1985a). Using biophysical investigations (Tereshin, 1979) of nervous-muscle preparations in adult *R. arvalis* males, I have found that animals from Zones II and III have low nervous excitation (high threshold of excitation) in comparison with those from the forest population: 0.579-0.433 vs. 0.457 and 0.383 ms, respectively. This indicates the presence of adaptive changes at the level of the organism. The accommodation constant of the nerve tissue in animals from Zone III and its dynamics in Zone IV were found to be significantly low (3.49 and 3.92 vs. 5.0 and 5.38 ms). These differences indicates the presence of adaptive physiological changes at the level of organism with the absence of sharply expressed significant differences at the population level in other parameters (Vershinin, 1987a). On our opinion, the nervous excitation may reflect the degree of anxiety and the pollution level under urbanization, and the accommodation ability allows us to estimate the degree of adaptive changes in

populations under anthropogenic environmental transformation (Vershinin and Tereshin, 1989). Thus, the mean levels of transformation and ecosystem pollution are well estimated on the basis of increased frequency of all types of morphological anomalies, increased mutation rates, frequency of abnormal clutches in brown frogs, and the presence of physiological adaptations.

3. Significant level of changes. Amphibians living in the zone of considerably transformed environment are characterized by the occurrence of a number of adaptive features of the level of population.

a) Specificity of population dynamics. The example of brown frogs shows high mortality at early stages of development and a sharp decrease during metamorphosis (Vershinin, 1985b; Vershinin and Trubetskaya, 1992). Dunson and Connel (1982), as well as Cecil and Just (1979), also recommend the use of embryonic and larval mortality rate for an estimation of pollution level.

b) Phenotypic features. Data on *R. arvalis* indicate the increasing froglet body size in populations from the Zone II. That is explicable, on one hand, by the change of a surface-volume ratio for the relative reduction of skin surface area through which toxic substances pass. On the other hand there is a greater energy consumption and better survivorship of large froglets (Shvartz, 1980; Crump, 1981).

c) Specificity of genetic structure. Change of territorial structure and high local density at low population number of mature animals (Vershinin and Krinitsyn, 1985) result in significant changes of genetic structure. The frequency of "striata" and others rare morphs increase (Vershinin, 1980b, 1982a, 1985a, 1987b; Lebedinsky, 1984). The increase of close relatives in these conditions results in external appearance of recessive mutations that usually reduces individual viability (Flindt, 1985; Gershenzon, 1985; Vershinin, 1987c). The examples include lethal postmetamorphic edema, unusual pigmentation, absence of eyelids, and different degrees of foot elements reduction.

d) Occurrence of introduced species. Because of thermal environmental pollution in Zone II, *R. ridibunda* introduction led to successful reproduction and the appearance of populations (Vershinin, 1981). The significant level of ecosystem transformation determines specificity of brown frog larval and juvenile population numbers as estimated by mark and recapture methods. Larval marking was made at stages 44-49 (Dabagyan and Sleptsova, 1975), and froglets were marked en masse by cutting a distal phalanx (Vershinin, 1987a). The significant changes in genetic structure can be recovered because of rare morphs and mutation frequency. Environmental changes lead to the increase of body sizes in *R. arvalis* juveniles and, as a result, in the appearance of populations of introduced species that are capable of existing only in man-changed environment.

Most of the data above was gathered by traditional zoological techniques. I think that it is important to elaborate the basic directions of works that allows correct and quick monitoring and bioindication. The above parameters and methods are consciously given together with their particular results because we assume that depends on the particular purposes of the research and region, the choice of optimal techniques, and the

species most adequately reflecting anthropogenic environmental changes. On one hand, it should be a common and widespread species, and on the other, the species should have sufficient sensitivity to biogeocenotic transformation. It is necessary to use new methods that allow one to carry out effective estimations of the state of ecosystems. For these reasons, I consider it important to conduct full-range population investigations at a modern level including new methods from adjacent scientific fields that allows not to ascertain the phenomenology of the observable facts and estimate the biological sense of the processes. Only complex, full-scale basic research will allow us to produce a high-grade output in applied fields. It is useless to go the way of simplification and to search for a single integrative parameter. Only using this complex approach, will we will discover very important and interesting results as described above.

11.0. CONCLUSIONS

Shvarts (1967) noted “that define more exactly, the general rules managing transformation of different organisms groups, will appear useful at the decision of a number of questions concerning rates of evolution in animals and plants which occupy different levels of phyletic development. The discovery of the rules of evolutionary mechanisms, changing during the historical development of the organic world, will promote to deepen the dialectic developmental conception.” Urbanized landscapes are unique formations which have appeared as a result of the interaction of a developing industrial human society with natural ecosystems. In urban areas, as a result of area splitting and the appearance of isolating barriers, abrupt changes in ecological structure of populations occur, the demographic structure varies, and the numbers of individuals are sharply reduced. These conditions promote fast transformation of genetic structure, mobilization of latent variability for adaptive transformation of population structure, and the change of reaction norms which can render essential influence on evolutionary destiny of such populations. The analysis of microevolutionary processes may be carried mainly in terms of concepts and laws known in the microevolution doctrine (Yablokov and Yusufov, 1989).

The biosphere, from the moment of its appearance, represents a complex of live forms capable of performing geochemical functions (Vernadsky, 1931) that conducts the processes of metabolism in the Earth crust (Vernadsky, 1978), and increasing entropy of the biosphere is one of the most essential characteristics of the life (Bauer, 1937). In the wild, the processes of production prevails above the destruction, the ecological systems become complicated and more productive and stable, and the degree of heterogeneity within the limits of particular biogeocenosis and the degree of biocenotic heterogeneity of the Earth increase continuously. In urbanized environments the situation changes profoundly; ecosystems become simpler and “rejuvenated” (Shvarts, 1976a). Feature of the present stage of the Earth history is that the evolution of the biosphere proceeds as a significant influence of human activity on biogenic migration of atoms (Vernadsky, 1977).

As a response to external environmental changes, separate species and their communities display active adaptations to survive in the environment changed by man, and not only bacteria and insects but also rather slowly reproducing frogs begin to acquire new properties. The evolution occurs in front of our eyes (Shvarts, 1973). The study of patterns above the species level of organization should become one of the main future tasks in the evolutionary theory (Kolchinsky, 1981). Vernadsky (1928) emphasized continuity of the evolution of species and biosphere. "The species evolution transforms in the evolution of biosphere" (Vernadsky, 1977). The ecological structure of a population is an elementary unit of evolution that can render a decisive influence on efficiency of evolutionary processes in biogeocenosis. As the system of the best biological integration provides the stability at the expense of homeostatic mechanisms (i.e., the evolution of a biogeocenosis can use evolution of organisms; Shvarts, 1974a). The harmonic development of a biogeocenosis depends on population mechanisms fixed by evolution and regulating the number of dominant species and optimum interrelations between species belonging to different trophic levels. The analysis of data on urban populations of amphibians allows us to formulate the concept of amphibian species complex transformation in the conditions of industrial pollution in a combination with progressing urbanization. Except for the disappearance of some species and replacement of one species by another (with the maintenance of the dominant), the spatial structure of populations vary. Compact isolates with high density (surpasses only the density in natural forest ecosystems) and small number are formed. The habitats of urban amphibians live on local isolated areas; terrestrial areas and reproductive ponds occupy in a relatively small area. The features of urban populations spatial structure (isolation, small area of occupancy and high density at small population size) promote the formation of polymorphisms and genetic specificity. Various sort of pollutants from neighboring territories are washed into ponds that serve as places for amphibian reproduction. They are accumulated there in concentrations considerably exceeding the allowable limits. Because of relatively longevity and because of some biological features of amphibians, they represent very good bioconcentrators of pollutants (Hall and Kolbe, 1981; Lyubashevskii et al., 1985). This feature also results in a number of physiological (Vershinin and Tereshin, 1996) and biochemical (Misyura, 1982) changes in mature animals that cause the decrease of absolute and relative fecundity (Bobylev, 1985) and/or breaking of the process of normal formation of sexual products and fertilization of eggs (pathological clutch frequency increases to 44.6%). A decrease in fecundity of *R. arvalis* and *S. keyserlingii* populations is known. Relative fecundity of *R. temporaria* is reduced, and the proportion of clutches with small eggs in populations of *R. arvalis* in urban areas is increased (Vershinin and Gatiyatullina, 1995). The mortality of amphibian eggs can occur at the moment of spawning in a polluted pond. Within the limits of the zone of multistory buildings, there are ponds where the deposited eggs do not develop. However, when they are placed just after the deposition in pure water in laboratory, embryos and larvae develop normally (Vershinin and Trubetskaya, 1992). Changes of environmental chemistry can promote

the increase of egg infection by the fungi *Saprolegnia* sp. (Cooke, 1975b; Leuven et al., 1986). One of the negative aspects of populations reaction on anthropogenic factors (mainly on changes in environmental chemistry) is the increase of frequency of morphological anomalies caused by genetic changes, deviations in development, abnormal regeneration, and neoplasms. Frequency of such anomalies is different in Caudata and Anura and in juveniles and adults. In Caudata, anomalies occur more often among adult animals than among juveniles. These are mainly abnormal regeneration and developmental deviations and neoplasm that are explained by the sensitivity of Caudata to chemical pollution and by a high regeneration ability throughout life.

The small sizes of terrestrial isolates and generally low numbers in populations of Anura increase the probability of breeding of close relatives. This leads to the appearance of numerous genetic defects, some of which are visible externally. Various morphological anomalies are noted in almost all amphibian populations, but the frequencies of all types of anomalies depends also on the extent of anthropogenic influence. It should relate to a complex of causes including changes in environmental chemistry, territorial limitation of populations, and small numbers of mature animals. The breeding duration in populations to various degrees is subject to anthropogenic influence. However, there are not significant differences between populations. The duration of embryonic development in urban populations tends to shorten; in the zone of low buildings, it differs significantly ($p < 0.05$) from populations of the forest park zone because of thermal pollution of the urban environment. However, the duration of larval development and general period of development do not differ significantly. Changes in water chemistry in the places of reproduction likely promotes the inhibition of larval development despite a significantly higher temperatures of urban ponds. The strong heterogeneity of urbanized territories leads to a significant disorder in terms of reproduction and development within the margins of cities in comparison with natural populations.

The research of brown frog population dynamics from the egg to the adult showed that the ways of this part of the life cycle in natural and urban populations differ significantly. High mortality at early stages of development is compensated by an abrupt decrease during metamorphosis. Postmetamorphic mortality includes actual mortality and mortality from predators whose numbers are higher in the forest because of the greater number of trophic relations and levels in natural ecosystems. The significant level of losses in a new generation in this case is "programmed" and does not serve as an obstacle to subsequent increases of a population. Urban populations may keep a stable size over a long time, but the level of allowable losses at this stage of life cycle should be lower. As shown experimentally (Vershinin and Trubetskaya, 1992), potentially high stability of the urban clutches in *R. arvalis* in favorable conditions represents a consequence of deep adaptive transformations promoted by the reproductive success of populations in changed environmental conditions. Nonselective elimination results in the formation of genetic specificity of new generations that can be displayed in features of color pattern (increased frequency of rare morphs like "striata" and "maculata." in natu-

ral populations) and other phenotypic phenomena. Larger animals survive in the conditions of urban ponds (they have better surface-volume ratios) as well as individuals with a high level of metabolic processes and low skin permeability to sodium.

Along with the listed features, behavioral and physiological specificity is formed in connection to a whole complex of conditions in large industrial cities. The high values of the heart index in froglets in populations from urban areas relates to the process of compensatory hypertrophy developed as a response to decreased contractive properties of the myocardium under anthropogenic environmental changes. This indicates a low activity (high excitation threshold) of the muscle tissue in adult *R. arvalis* (Vershinin and Tereshin, 1989). The larger liver mass in urban populations and its different dynamics in brown frog juveniles in urban areas and in the forest reflect the level of environmental chemistry changes and features of population structure and dynamics. The presence of physiological adaptations in urban populations lead to changes in energy expenditure. The loss of energy increases, in turn, in relation to the presence of physiological specificity. The increase of energy expenditures, as was already mentioned, negatively influences reproductive potential. Thus, general features of structure and functional physiological interrelationships exist in urban populations.

Changes are observed also in the trophic relations of *R. arvalis* juveniles. The large sizes of metamorphosed froglets, low mortality, and the limited habitats area in city promotes an intensive pressure of a new generation of frogs on invertebrates as a whole and on phytophages in particular. Their percentages in the food spectrum increases significantly during the first two weeks of terrestrial life, and this promotes the increase of metabolic rate in urban ecosystems and indicates a shortening of trophic chains. High levels of metabolic processes, primary survivorship of large individuals, and a significant level of pollution promote the appearance of a specific size and age population structure in *R. temporaria*. Maturity comes earlier, and the life span is shorter than in natural populations. Marginal female ages are lower than the marginal male ages, which can be explained by the costs of higher reproductive expenditures. Females prevail in number in the populations of species successfully reproducing in urban areas that are strategically favorable and promotes the increase of the reproductive potential in a population.

Presence of adaptive changes in the genetic structure of *R. arvalis* urban populations and the increase of embryonic tolerance to pollution allow it to reproduce successfully at a reduction of the mean egg number per clutch and reduction of their sizes. These changes promote a decrease of energy expenditure on reproduction. This indicates different reproductive strategy in the urban populations of *R. arvalis* in comparison with the natural population; a deviation from typical r- strategy is observed. Specific features of cytological, physiological and phenotypic levels of populations and species complexes are revealed. They contain adaptive and negative components at all stages of life cycle and cause, on the one hand, the potential opportunity of the increased reproduction and tolerance of populations. On the other, there is high dependence of structures to the stochastic factors of the environment.

Biocenotic specificity of trophic relations, in which amphibians participate in urban areas, prevalence of destructive components, and the rather small amounts of substance and energy put them on the upper trophic levels. The number of predators, in comparison with natural ecosystems, is not enough. The evolution of biogeocenoses is in a w condition. The situation is possible in urban ecosystems when terrestrial vertebrates are represented only by amphibians. In this case, trophic chains are ended by amphibians. Thus, basic biocenotic functions of the animal populations and the regulatory function and the uniform dispersion of the organic substance over the surface of the planet (Vernadsky, 1928; Shvarts, 1980; Chew, 1974; May, 1983) is not carried out. The role of amphibians, as consumers, also undergoes some changes. There is a change in food resources use strategy; populations as a whole influence invertebrates which become food objects more actively. The structure of morphological and/or phenotypic variability reflects deep processes in populations, generate the conditions of transformed environment, and demonstrate their adaptive potential or its absence.

Under varying conditions, there is a redistribution of individuals that are displaced from particular biocenoses, habitats, or the whole territory where they do not undergo competition and maintain their number and distribution. They may expand into others biocenoses, habitats and other territories where the action of the limiting factors appears to be less intense. External factors in relation to species-specific factors delimit its opportunities for reproduction and movement at certain limits and thus determine biocenosis structure and historical changes in this structure. The comparative analysis of amphibian species complexes indicate active processes of their transformation in the conditions of different types of anthropogenic transformation. The direction of observable processes in many respects is determined by distinctions in the evolutionary age of various systematic groups, limits of species reaction norm, range of number of parameters variability, and historically formed specificity of intrapopulation polymorphisms. All the parameters mentioned above, along with character and degree of environmental transformation, influence the future destiny of populations and species in conditions of modern ecosystems. Demographic specificity and age-sexual features indicate an opportunity of various ways of strategy transformation for successful reproduction on urbanized areas (even in sympatric species). These features, on the background of adaptations, arising at different hierarchical levels as well as available preadaptations, make a significant contribution to population resistance to the processes of pollution and urbanization and determine the ability of existence in anthropogenic landscapes.

There is a complex of features in anthropogenic biogeocenoses that promote the maintenance of variety of different structural levels of organization and consequently ecosystems stability. The evolution of communities in anthropogenic conditions results in the appearance of new biogeocenosis that have high stability and effectively perform at high hierarchical levels of structural organization. The mentioned phenomena completely agree with Vernadsky (1965) view about features of biosphere evolution in the modern conditions; there is a break before the establishment of biocenotic relations, simplifica-

tion of food chain structure, soil transformation and microclimate, occurrence of new flows of biogenous elements, and global change in biogeochemical cycles. Thus, the work of the factors of organic evolution has not ceased.

This generated system has a special configuration of energy and substance flow determined by a complex of structurally functional interrelations, other dynamics of numbers, and levels of metabolic processes. I think that the results allow us to consider that the observed general regularities of microevolutionary processes in populations and species communities may be applied to all vertebrates and to many areas changed by human activity. The extreme ecological situations may serve as a tool that reveals biological sense of observed phenomena. Even the traditional directions of research can not be carried out fruitfully without a combination of new methods. It seems logical to use an integrated and interbranch approaches as a methodology of analysis of the biological essence of population specificity. Aspects of reproductive strategy, conditions of morphological and morphophysiological parameters, ecophysiology, anomalies and mutation frequency, faunistics, specificity of ontogeny, potential range of variability, and tolerance in various species and populations should be considered.

The results will allow us to make some conclusions about the status of urban amphibians and microevolutionary processes. A situation with adaptive changes at different hierarchical levels of structural organization, frequency of rare genotypes not characteristic for natural amphibian populations, and also specificity of trophic relations show that the isolated populations have a specific structure and successfully reproducing are formed in urban areas. Long-term reproduction in such populations indicate the presence of certain tendencies in populations dynamics which provide the maintenance of functional integrity and effective and stable maintenance of these populations and species in communities. Microevolutionary changes and their rate are determined by environmental conditions, territorial isolation of urban populations, low number at high local density, high pollution level, and transformation of natural communities. Adaptive changes of behavioral reactions are formed in these conditions, and there are physiological adaptations concerning nervous and muscle tissues which provide advantages for animals with a high level of metabolism, low skin permeability, and the tolerance of embryos and larvae to water pollution. There are data on the dependence of morphogenesis from the coordination of population, physiological and proliferative processes in the conditions of anthropogenically transformed environment. Explanations of differences in the stability of particular species to anthropogenic transformations were found. Features of population dynamics result in the appearance of another genetic structure. A number of phenotypic features (including teratology) allows us to speak about the presence of inbreeding depression in urban populations and about differences in intensity of mutation process in the populations living under different degrees of landscape transformation.

Specificity of the demography of urban populations (e.g., *R. temporaria*) expressed by the prevalence of physiologically functions and fast growing individuals (before the beginning of maturity) with a short life, shortened trophic relations, and intensification of

metabolism. The survival of these individuals in conditions of polluted and transformed environment is allowed by certain changes in their reproductive strategy and use of food resources. Autonomization of spatial groups accompanied with a significant growth of population efficiency on the background of individual decrease is observed. This approach provides a key to understanding real population stability mechanisms and allows us to predict the directions of microevolutionary changes and reveal parameters describing adaptive opportunities of communities. The practical part of research may include the development of competent measures of protection of threatened species based on the discovered patterns and highly objective methods of estimation of environmental quality.

ACKNOWLEDGMENTS

This work was forwarded for publication by the United Council on Biological Sciences of the Urals Branch of the Russian Academy of Sciences, Protocol No. 1 on 16 January 2003 and signed by T.V. Silina, the scientific secretary. I am grateful to specialists from the design bureau at the Uralian Research Institute of Water Management who participated in this work; E.A. Trubetskaya conducted the experimental part of work on survival rate in brown frog, A.V. Ledentsov executed the analysis of *R. arvalis* age, E.V. Volegova analyzed the age of *R. temporaria*, and E.Z. Gatiyatullina executed the processing of materials on egg diameters.

Except for zoological techniques, we made joint physiological investigations with the Ekaterinburg Medical Centre of Sciences and thus are grateful to S. Yu. Tereshin. Finally, I greatly appreciate F.A. Blyachkman and T.F. Shklyar for our joint biophysical investigations of frog myocardium contractability, A.A. Grinko for technical support of the investigations, and N.G. Erokchin for personal communications. Special thanks to all my friends who promoted these investigations.

REFERENCES

- Aebli, H. 1966. Rassenunterschiede in Bezug auf Entwicklungsgeschwindigkeit und Geschlechtsdifferenzierung bei *Rana temporaria* in den Talern des Kantons Glarus (Schweiz). – Rev. Suisse. Zool. 73 (1): 1-36.
- Aitbaeva, B.T., Atakhanova, K.J. and Bigaev A.B. 1991. Morphological and cytogenetic aberrations of the frogs of Central Kazakhstan. – In: Sicietas Eur. Herp. Budapest: 7.
- Alford, R.A. and Harris, R.N. 1988. Effects of larval growth history on anuran metamorphosis. – Amer. Natur. 131 (1): 91-106.
- Alvarez, R. 1995. Skeletal Malformations Induced by the Insecticides ZZ-Aphox and Folidol During Larval Development of *Rana perezi*. – Arch. Environ. Contam. and Toxicol. 28 (3): 349-356.

- Amstyslavskaya, T.S. 1971. [Influence of amphibian larval growth and development regulators on tissue growth]. – *Ekologiya (Sverdlovsk)* (6): 12-14 (in Russian).
- Andren, C. and Nilson, G. 1988. Effects of acidification on Swedish brown frogs. – *Mem. Soc. Fauna et Flora Fenn.* 64 (3): 139-141.
- Andren, C., Marden, M. and Nilson, G. 1989. Tolerance to low pH in a population of Moor Frogs, *Rana arvalis*, from an acid and neutral environment: A possible case of rapid evolutionary response to acidification. – *Oikos*. 56 (2): 215-223.
- Andrushko, A.M. 1973. [Amphibian and reptiles gives distress signal]. – In: *Problems of Herpetology*. Leningrad: 10-12 (in Russian).
- Arano, B., Llorente, G., Garcia-Paris, M. and Herrero, P. 1995. Species translocation menaces Iberian waterfrogs. – *Conserv. Biol.* 9 (1): 196-198.
- Arnold, A. 1983. Zur veränderung des pH-warters lacihgewasser einheimischer amphibien. – *Arch. Naturschutz und Landschaftforsch.* 23 (1): 35-40.
- Astradamov, V.I. 1973. Rol antropogennykh Faktorov v Izmenenii Prirodnykh Kompleksov i Ikh Komponentov (Na Primere Mordovskoi ASSR) [Role of Anthropogenic Factors in Natural Complexes and Their Components Changes (On the Example of Mordovskaya ASSR)]. – Ph. D. Diss. Abstr., Kazan, 24 p (in Russian).
- Avramova, O.S. 1978. [Territorial-ecological determination of reproductive possibilities of semiaquatic amphibians]. – In: *Struktarno-Funktsionalnye Osobennosti Estestvennykh i Iskusstvennykh Biogeotsenozov*. Dnepropetrovsk: 184-185 (in Russian).
- Avramova, O.S., Bobylev, Yu.P. and Bulakhov, V.D. 1977. [Influence of different biochemical features of organism on amphibian reproductive specificity]. – In: *Problems of Herpetology*. Leningrad: 4-5 (in Russian).
- Bakushev, M.K. 1973. [Ecological-physiological mechanisms of tailless amphibian adaptation to mountains]. – Ph.D. Diss. Abstr., Sverdlovsk, 24 p (in Russian).
- Banks, B. and Laverick, G. 1986. Garden ponds as amphibian breeding sites in a conurbation in the north east of England (Sunderland Tyne and Wear). – *Herpetol. J.* 1 (2): 44-50.
- Banks, B. and Beebee, T.J.C. 1986. A comparison of the fecundities of two species of toad (*Bufo bufo* and *B. calamita*) from different habitat types in Britain. – *J. Zool.* 208 (3): 325-337.
- Bannikov, A.G. 1955. [On changes in amphibian distribution of Moscow neighbourhood]. – In: *Uchenye Zapiski Moskovskogo Gorodskogo Pedagogicheskogo Instituta* 38 (3): 219-223 (in Russian).
- Bannikov, A.G. 1977. [Rare amphibian and reptiles species and their protection]. – *Priroda*. (12): 99-102 (in Russian).
- Bannikov, A.G. and Isakov, Yu.A. 1967. [On amphibians in Moscow City]. – In: *Zhivotnoe Naselenie Moskvy i Podmoskovya*. Moscow: 92-96 (in Russian).
- Bannikov, A.G., Darevsky, I.S., Denisova, M.N., Drozdov, N.N. and Iordansky, N.N. 1969. *Zhizn Zhivotnykh [Animal Life]* 4 (2) Moscow: Prosveshchenie Publ., 488 p (in Russian).

- Bannikov, A.G. and Rustamov, A.K. 1974. [Problems of amphibian and reptile conservation]. – In: Okhrana prirody i racionalnoe ispolzovanie dikikh zhivotnykh. Moscow: 164-172 (in Russian).
- Bannikov, A.G., Darevsky, I.S., Ishchenko, V.G., Rustamov, A.K. and Szczerbak, N.N. 1977. Opredelitel Zemnovodnykh i Presmykajushchikhsya Fauny SSSR [Guide to Amphibians and Reptiles of the USSR Fauna]. Moscow: Prosveshchenie Publ., 415 p (in Russian).
- Baranovskii, A.E. and Kudokotsev, V.P. 1988. [Influence of some pollutants on processes of external organs regeneration in aquatic vertebrates and perspectives of widening of the circle of objects for water bioindication]. – In: Racionalnoe Ispolzovanie Okhrana, Vosproizvodstvo Biologicheskikh Resursov i Ekologicheskoe Vospitanie. Zaporozhie: 209 (in Russian).
- Baranovskii, A.E. and Kudokotsev, V.P. 1992. [On the influence of population density on regenerating organism integration in tailless amphibian larvae]. – Ekologiya (Sverdlovsk) (3): 45-50 (in Russian).
- Basarukin, A.M. 1985. [Addition to the morphological anomalies of *Rana chensinensis* on Sakhalin]. – In: 14 Konferentsiya Molodykh Uchenykh i Spetsialistov, Posvyashchennaya 40-letiyu Pobedy Sovetskogo Naroda v Velikoi Otechestvennoi Voine: Tezisy Dokladov. Yuzhno-Sakhalinsk: 43 (in Russian).
- Basarukin, A.M. and Borkin, L.J. 1984. Distribution, ecology and morphological variability of the Siberian salamander, *Hynobius keyserlingii*, of the Sakhalin island. – In: Ecology and Faunistics of Amphibians and Reptiles of the USSR and Adjacent Countries. Leningrad: 12-54 (in Russian).
- Bauer, E.S. 1937. Teoreticheskaya Biologiya [Theoretical biology]. Moscow: VIEHM Publ., 206 p (in Russian).
- Beachy, C.K. 1989. Egg size variation and habitat variability in several species of salamanders. – In: 1st World Congr. Herpetol., Canterbury, 11-19 Sept., 1989: Abstr. Canterbury.
- Beebee, T.J.C. 1973. Observation concerning the decline of the British Amphibia. – Biol. Conserv. 5 (1): 20-24.
- Beebee, T.J.C. 1979. Habitats of the British amphibians (2): suburban parks and gardens. – Biol. Conserv. 15 (4): 241-257.
- Beebee, T.J.C. 1981. Habitats of the British amphibians (II): agricultural lowlands and a general discussion of requirements. – Biol. Conserv. 21 (2): 127-139.
- Beebee, T.J.C. 1983. Habitat selections by amphibians across an agricultural land-heathland transect in Britain. – Biol. Conserv. 27 (2): 111-124.
- Beebee, T.J.C. 1986. Acid tolerance of natterjack toad (*Bufo calamita*) development. – Herpetol. J. 1 (2): 78-81.
- Belimov, G.T. and Sedalishchev, V.T. 1980. [*Rana ridibunda* in water bodies of Yakutsk]. – Vestnik Zoologii. (3): 74-75 (in Russian).
- Bell, G. 1977. The life of the smooth newt (*Triturus vulgaris*) after metamorphosis. – Ecol. Monogr. 47: 279-299.

- Belova, Z.V. 1964. [Feeding of *Rana ridibunda* tadpoles in Volga delta]. – Byulleten Moskovskogo Obshchestva Ispytatelei Prirody: Otdel Biologicheskii 69 (5): 40-46 (in Russian).
- Belova, Z.V. 1965. [Composition of *Rana ridibunda* tadpoles food in Volga delt]. – In: Trudy Astrakhanskogo Zapovednika 10: 359-374 (in Russian).
- Belova, V.T. and Kostenko, V.A. 1976. [Some data on tailless amphibian biology on the South of Primorye]. – In: Okhrana Prirody i Ratsionalnoe Ispolzovanie Prirodnikh Resursov. Khabarovsk: 58-60 (in Russian).
- Belskii, E.A. 1996. Razmnozhenie i Rannij Ontogenez Vorobinykh Ptits Pri Tekhnogennom Zagryaznenii Sredy Obitaniya [Reproduction and Early Ontogenesis of Passerine Birds under Technogenic Pollution of Environment]. – Ph.D. Diss. Abstr., Ekaterinburg, 18 p. (in Russian).
- Bengtsson, G. and Rundgren, S. 1988. Gusum case: a brass mill and the distribution of soil Collembola. - Can. J. Zool. 66: 1518-1526.
- Berger, L. and Smielowski, J. 1982. Inheritance of vertebral stripe in *Rana ridibunda* Pall. (Amphibia, Ranidae). – Amphibia-Reptilia 3: 145-151.
- Berven, K.A. 1988. Factors affecting variation in reproductive traits within a population of wood frog (*Rana sylvatica*). - Copeia (3): 605-615.
- Beshkov, V. 1978. [Investigation of air industrial pollution influence on amphibians and reptiles in MDC."G. Damyanov" distr. Pirdop]. – Ekologiya (Bulgaria) (4): 4-5 (in Bulgarian).
- Beskrovnyi, M.A. and Burmenskaya, N.M. 1970. [On periodical changes of ranges in some amphibian species, in connection with human activity]. – In: Materialy Chetvertoi Nauchnoi Konferentsii Zoologov Pedinstitutov. Gorky: 32-34 (in Russian).
- Besuglaya, E.Yu., Rastorgueva, G.P. and Smirnova, I.V. 1991. [By what is breathing industrial city]. Leningrad: Gidrometeoizdat Publ., 255 p (in Russian).
- Bikbaeva, E.V. 1987. [Fecundity and egg size of *Salamandrella keyserlingii*]. – In: Ekologicheskie Sistemy Urala: Izuchenie, Okhrana, Ekspluataciya. Sverdlovsk: 8 (in Russian).
- Blaustein, A.R. 1994. Amphibians in a Bad light. What is killing the eggs of Oregon's western toad? – Natur. Hist. 103 (10): 32-37.
- Blaustein, A.R. and Wake, D.B. 1995. The puzzle of declining amphibian populations. – Sci.Amer. 272 (4): 56-61.
- Blyakhman, F.A., Marhasin, V.S. and Shklyar, T.F. [Device for investigation of muscle mechanical properties Autor. Sert. no. 4638591 from 27.07.89.] (in Russian).
- Bobylev, Yu.P. 1980. [Study of the role of digging amphibians forms in recultivation of mining dump of West Donbass]. – In: Biotsenoticheskie Aspekty Lesnoi Rekulivatsii Narushennykh Zemel Zapadnogo Donbassa. Dnepropetrovsk: 132-138 (in Russian).
- Bobylev, Yu.P. 1985. [Habitatat conservation and adaptive specificity of tailless amphibians in anthropogenic landscapes of Pridnestrovie]. – In: Voprosy Stepnogo Lesovedeniya i Nauchnye Osnovy Lesnoi Rekulivatsii Zemel. Dnepropetrovsk: 124-130 (in Russian).

- Bobylev, Yu.P. 1989. [peculiarities of the formation of herpetofauna in technogenic landscapes of steppe Pridneprovie]. – In: Problems of Herpetology. Kiev: 32-33 (in Russian).
- Bogachev, A.V. 1938. [Zoological observations on reptiles and amphibians in Milsk Steppe]. – In: Izvestiya Azerbajjanskogo Filiala Akademii Nauk SSSR (4/5): 89-100 (in Russian).
- Bolotnikov, A.M., Shurakov, A.I. and Haziieva, S.M. 1977. [On species composition, borders of distribution and amphibian fecundity in Permskaya Province]. – In: Problems of Herpetology. Leningrad: 39-40 (in Russian).
- Bolshakov, V.N., Pyastolova, O.A. and Vershinin, V.L. 2001. [Specificity of animal species community formation in technogenic and urbanized landscapes]. – Ekologiya (Sverdlovsk) (5): 343-354 (in Russian).
- Bondarenko, D.A. 1977. [Influence of anthropogenic factor on species variability and reptiles abundance in the Kura River valley]. – In: Problems of Herpetology. Leningrad: 40-41 (in Russian).
- Borkin, Leo. and Pikulik, M.M. 1986. The occurrence of polymely and polydactyly in natural populations of anurans of the USSR. – Amphibia-Reptilia 7 (3): 205-216.
- Boyajiev, V.Ya., Denev, I. and Halageva, L. 1974. [Investigation of pathogenesis of manganese intoxication]. – In: Gigiena Truda i Profzabolevaniya (10b): 35-38 (in Russian).
- Bradford, D.F., Swanson, C. and Gordon, M.S. 1991. Acid deposition in the Sierra Nevada, California: effects of low pH and inorganic aluminum on two declining species of amphibians. – Amer. Zool. 31 (5): 114.
- Breedis, C. 1952. Induction of accessory limbs and of sarcoma in the newt (*Triturus viridescens*) with cancerogenic substances. – Cancer Reseach. 12: 861-866.
- Bretag, A.H. and Stampfl, R. 1975. Differences in action potentials and accommodation of sensory and motor myelinated nerve fibers as computed on the basis of voltage clamp data. – Pflugers Arch. 354: 257-271.
- Breul, M. 1981. Une anomalie de la metamorphose: la persistance dun intestin spirale chez une grenouille verte adulte (Amphibiens, Anoures). - In: Bull. Soc.Linn. Lyon. 50 (10): 322-327.
- Brockelman, W.Y. 1968. Natural regulation of density in tadpoles of *Bufo americanus*. – Ph. D. Tesis. Univ. of Michigan, 78 p.
- Brockelman, W.Y. 1975. Competition, the fitness of offspring and optimal clutch size. – Amer. Natur. 109 (970): 677-699.
- Brooks, J.A. 1981. Otolith abnormalities in *Limnodynastes tasmanensis* to depoles after embryonic exposure to the pesticide dieldrin. – Environ. Pollut. 25 (1): 19-25.
- Browder, L.W. 1975 Frogs of the genus *Rana*. – In: Handbook of Genetics: 19-33.
- Browder, L.W., Underhill, J.C. and Merrell, D.C. 1966. Mid-dorsal stripe in the wood frog. – J. Heredity. 57 (2): 65-67.
- Bugaeva, E.A. 1982. [Influence of chemical substances on growth and development of *Rana arvalis*]. – In: Problemy Ekologii Pribaikalya 5. Irkutsk: 32 (in Russian).

- Bugaeva, E.A. 1983. Vliyanie Khimicheskikh Veshchestv na Rost i Razvitie Ostromordoï Lyagushki [Influence of Chemical Substances on the Growth, Development and Survival of *Rana arvalis* Larvae]. – Ph.D. Diss. Abstr., Sverdlovsk: Institute of Plant and Animal Ecology USSR Academy of Sciences, 24 p. (in Russian).
- Bugaeva, E.A. 1985. [Experimental study of some chemical substances influence on growth and development of *Rana arvalis* larvae]. – In: Ekologicheskie Aspekty Skorosti Rosta i Razvitiya Zhivotnykh. Sverdlovsk: 99-105 (in Russian).
- Burton, J.A. 1976. The decline of the common frog in the London area. – The London Naturalist (55): 16-18.
- Bury, R.B. and Luckenbach, R.A. 1976. Introduces amphibian and reptiles in California. – Biol. Conserv. 10 (1): 1-14.
- Buyanovskaya, A.A. 1973. [On determination of Limited Available Concentrations in water environment]. – In: Vodnye Resursy (4): 124-127 (in Russian).
- Byrne, A.R., Kosta, L. and Stegnar, P. 1975. The occurrence of mercury in Amphibia. – Environ. Lett. 8 (2): 147-155.
- Calef, G.W. 1973. Natural mortality of tadpoles in population of *Rana aurora*. – Ecology 54 (4): 741-758.
- Castanet, J. 1975. Quelques observations sur la presence et la structure des marque squelettiques de croissance chez les amphibiens. – Bull. Soc. Zool. France. 100 (4): 603-620.
- Cecil, S.C., Just, J.J. 1979. Survival rate, population density and development of a natural occurring anuran larvae (*Rana catesbeiana*). – Copeia (3): 447-453.
- Chew, R.M. 1974. Consumers as regulators of ecosystems: an alternative to energetics. – Ohio J.Sci. 74 (6): 359-370.
- Christian, K.A. 1982. Changes in the food niche during postmetamorphic ontogeny the frog *Pseudacris triseriata*. – Copeia (1): 73-80.
- Chugunov, Yu.D. 1974. Eko-fiziologicheskie Adaptatsii Beskhvostykh Amfibii (Adaptatsii k Zhizni na Granitse Vody i Sushy) [Eco-Physiological Adaptations of Tailless Amphibians (Adaptation for Life on the Border of Water and Land)]. – Ph.D. Diss. Abstr. Vladivostok, 42 p. (in Russian).
- Cleinberg, S.E. and Smirina, E.M. 1969. [To the technique of amphibians age determination]. – Zoologichesky Zhurnal 48 (7): 1090-1094 (in Russian).
- Cooke, A.S. 1971. Selective predation by newts on frog tadpoles treated with DDT. – Nature. 229 (5282): 275-276.
- Cooke, A.S. 1972. Indications of recent changes in British Isles of the frog *Rana temporaria* and the toad *Bufo bufo*. – J. Zool. Lond. 167: 161-178.
- Cooke, A.S. 1973a. The effects of DDT, when used as a mosquito larvicide on tadpoles of the frog *Rana temporaria*. – Environ Pollut. (5): 259-273.
- Cooke, A.S. 1973b. Response of *Rana temporaria* tadpoles to chronic doses of p.p.-DDT. – Copeia (4): 647-652.
- Cooke, A.S. 1975a. Spawns clumps of the common frog *Rana temporaria*: number of ova and hatchability. – Brit. J. Herpetol. 5 (5): 505-509.

- Cooke, A.S. 1975b. Spawn site selection and colony size of the frog (*Rana temporaria*) and the toad (*Bufo bufo*). – J. Zool. Lond. (175): 29-38.
- Cooke, A.S. 1977. Effects of field applications of the herbicides diaquat and dichlobenil on amphibians. – Environ. Pollut. 12: 43-50.
- Cooke, A.S. 1978. Neutral red dye as a marker for tadpoles. – Brit. J. Herpetol. 5: 701-705.
- Cooke, A.S. 1981. Tadpoles as indicators of harmful levels of pollution in the field. – Environ. Pollut. Ser. A. 25: 123-133.
- Cooke, A.S. 1985. The deposition and fate of spawn clumps of the common frog *Rana temporaria* at a site in Cambridgeshire, 1971-1983. – Biol. Conserv. 32 (2): 165-187.
- Cooke, A.S. and Frazer, J.F.D. 1976. Characteristics of newt breeding sites. – J. Zool. 178: 223-236.
- Cooke, A.S. and Arnold, H.R. 1982. National changes in status of the commoner British amphibians and reptiles before 1974. – Brit. J. Herpetol. 6 (6): 206-207.
- Crump, M. 1981a. Energy accumulation and amphibian metamorphosis. – Oecologia 49 (2): 167-169.
- Crump, M. 1984a. Ontogenetic changes in vulnerability to predation in tadpoles of *Hyla pseudopuma*. – Herpetologica 40 (3): 265-271.
- Crump, M. 1984b. Intraclutch egg size variability in *Hyla crucifer* (Anura, Hylidae). – Copeia (2): 302-308.
- Crump, M. 1989a. Egg size variability: consequences to tadpoles. – In: 1st World Congr. Herpetol., Canterbury, 11-19 Sept., 1989. Abstr. Canterbury.
- Crump, M. 1989b. Life history consequences of feeding versus non-feeding toad larva. – Oecologia 78 (4): 486-489.
- Crump, M. and Kaplan, R. 1979. Clutch energy partitioning of tropical tree frogs (Hylidae). – Copeia 4 (6): 626-635.
- Cummins, C.P. 1989. Assymetry in the influence of egg size on length of larval period and size at metamorphosis in *Rana temporaria*. – In: 1st World Congr. Herpetol. Canterbury, 11-19 Sept., 1989. Abstr. Canterbury, 1989.
- Cummins, C.P. 1989. Individual growth, survival and breeding site-fidelity in a cohort of common frog (*Rana temporaria* L.). - In: 1st World Congr. Herpetol. Canterbury, 11-19 Sept., 1989. Abstr. Canterbury, 1989.
- Cunningham, M., Moritz K. and McDonald K. 1993. Substitutions, transitions and translocations: a survey of genetic variation for the active management of declining frog populations. - In: Second World Congress of Herpetology. Adelaide, Dec.1993-Jan.1994. Abstr. Adelaide: 65.
- Dabagyan, N.V. and Sleptsova, L.A. 1975. [Common Frog (*Rana temporaria* L.)]. – In: Obiekty Biologii Razvitiya. Moscow: 442-462 (in Russian).
- Danilov, N.N. 1973. [Human influence on a course of biogeocenotic processes]. – Sovremennye Problemy Ekologii. Moscow: 145-163 (in Russian).
- Danilova, M.N. 1992. Eksperimentalnoe Issledovanie Vliyaniya Benzina na Rannie Stadii Ontogeneza Amfibii [Experimental Study of Petroleum Influence on Amphibian Early

- Ontogenetic Stages]. – Ph.D. Diss. Abstr., Ekaterinburg: Institute of Plant and Animal Ecology USSR Academy of Sciences, 22 p. (in Russian).
- Dettlaff, T.A. and Vassetzky, S.G. (eds). 1991. Animal Species for Developmental Studies. Volume 2: Vertebrates. Academy of Sciences of the USSR, Moscow. Kluwer Academic/Plenum Publ., 466 p.
- Dinmore, C.E. and Hanken, L. 1986. Native variant limb skeletal patterns in the red-backed salamander, *Plethodon cinereus*, are not regenerated. – J. Morphol. 190 (2): 191-200.
- Dobrinsky, L.N. and Malafeev, Yu.M. 1974. [Technique of carbon dioxide intensity excretion by poikilothermic animals with the help of optic-acoustic gas analyzer]. – Ekologiya (Sverdlovsk) (1): 73-78 (in Russian).
- Dobzhansky, Th. 1954. Evolution as a creative process. – Karyologia V. suppl.: 435-449.
- Dolmen, D. 1987. Hazards to Norwegian amphibians. – In: Proc. 4th Ordinary Gen. Meet. Soc. Eur Herpetol. Nijmegen: 119-122.
- Doms, H. 1916. Über den Einfluss der temperatur auf wachstum und differenzierung der organe während der entwicklung von *Rana esculenta*. – Arch. Mikr. Anat. 87: 60.
- Douglas, R. 1948. Temperature and rate of development of the eggs of British Anura. – Journ. Anim. Ecology. 17 (2): 189-192.
- Drain, A. 1988. Abnormal joints (abj), une nouvelle mutation affectant des membres destetrads de *Xenopus laevis*. – Alytes 7 (2): 45-51.
- Dubinina, V.B. 1954. [Eco-faunistic account of amphibians and reptiles of Havastskii area of Tashkentskaya Province of the Uzbek SSR]. – In: Trudy Instituta Zoologii i Parazitologii. 3: 159-169 (in Russian).
- Dubois, A. 1979. Anomalies and mutations in natural populations of the *Rana "esculenta"* complex (Amphibia, Anura). – Mitt. Zool. Mus. Berlin. (1) 55: 59-87.
- Duellman, W.E. and Trueb, L. 1986. Biology of amphibians. N.Y.: McGraw-Hill Publ., 670 p.
- Dumont, J.N., Schultz, T.W. and Jones, R.D. 1979. Toxicity and teratogenicity of aromatic amines to *Xenopus laevis*. – Bull. Environ. Contam. Toxicol. 22: 159.
- Dumpert, K. 1986. Tests with the South African clawed toad (*Xenopus laevis*) for detecting chemical causes of the decrease of amphibians. – Chemosphere. 15 (6): 807-811.
- Dunson, W.A. and Connel, J. 1982. Specific inhibition of hatching in amphibian embryos by low pH. – J. Herpetol. 15 (6): 807-811.
- Eliseeva, K.G., Voitovich, A.M., Ploskaya, M.V. and Smal, S.E. 1989. [Amphibian usage in genetical monitoring practice]. – In: Dinamika Zoocenozov, Problemy Okhrany i Ratsionalnoe Ispolzovanie Zhivotnogo Mira Belorussii. Minsk: 273-274 (in Russian).
- Epifanova, O.I. 1965. Gormony i Razmnozhenie Kletok [Hormones and Cells Reproduction]. Moscow: Nauka Publ., 243 p (in Russian).
- Etkin, W. 1964. Metamorphosis. Physiology of the Amphibia. N.-Y.: Acad. Press: 427-469.

- Fedoseeva, I.P. 1987. [Activity and dynamics of amphibian population number in the city boundaries of Kurgan (In subterrace part of the Tobol River)]. – In: Tezisy Dokladov Kurganskoi Oblstnoi Mediko-Biologicheskoi Konferentsii Molodykh Uchenykh i Spetsialistov. Kurgan: 61-62 (in Russian).
- Feldmann, R. 1978. Herpetologische bevertungskriterien für denkleingewasser Schutz. – Salamandra 14 (4): 172-177.
- Fischman, J. 1996. Missing metamorphosis. – Science 271 (5246): 148-149.
- Fisher, J.-L. 1976. Loedeme generalise chez la grenouille rousse. – Bull. Mens. Soc. Linn. Lyon 45 (1): 43-46.
- Fejedo, M. 1992. Effects of body size and timing of reproduction on reproductive success in female Natterjack Toads (*Bufo calamita*). – J. Zool. 228 (4): 545-555.
- Flax, N.L. 1986. Influence of acidity and water temperature on the survival of Sakhalin anurans. – In: Systematics and Ecology of Amphibians and Reptiles. Leningrad: 152-166 (in Russian).
- Flindt, R. 1985. Untersuchungen zum Auftreten von misgeildeten wechselkroten (*Bufo viridis*) in einen Steinbruch in Vathingen Roswag. – Jahresh. Ges. Naturk. Wurttemberg (140): 213-233.
- Frazer, J.F.D. 1978. Newts in the New Forest. – Brit. J. Herpetol. 5 (10): 695-699.
- Freda, J. and Dunson, W.A. 1985. The influence of external cation concentration on the hatching of amphibian embryos in water of low pH. – Can. J. Zool. 63 (11): 2649-2656.
- Fryer, G. 1973. Unusal egg spoilage in the common frog. – Naturalist (926): 105-106.
- Gaizhauskene, I.I. and Uselite, S.A. 1977. Vliyanie Pitaniya Golovastikov na Umenshenie Fitoplanktona v Malykh Vodoemakh Litvy [Influence of Tadpole Feeding on Phytoplankton Reduction in Small Wetlands of Lithuania]. – In: Problems of Herpetology. Leningrad: 62-63 (in Russian).
- Ganeev, I.G. 1985. [Results of experimental study of the amount of food consuming by amphibians]. – In: Regionalnye Problemy Ekologii 2. Kazan: 7 (in Russian).
- Ganeev, I.G. 1991. Amfibii kak Entomofagi v Lesnykh Ekosistemakh Volzhsko-Kamskogo Kraya [Amphibians as Entomophages in Forest Ecosystems of Volga-Kama Area]. – Ph.D. Diss. Abstr., Moscow, 24 p. (in Russian).
- Garanin, V.I. 1964. [Material on amphibian distribution and number in Volga-Kama area]. – In: Prirodnye Resursy Volzhsko-Kamskogo Kraya (Zhivotnyi Mir). Moscow: 127-133 (in Russian).
- Garanin, V.I. 1969. [To synanthropization of amphibians and reptiles]. – In: Sinintropizatsiya i Domestikatsiya Zhivotnogo Naseleniya. Moscow: 49-51 (in Russian).
- Garanin, V.I. 1971. K voprosu o dinamike chislennosti zemnovodnykh i presmykajushchikhsya [To the problem of the number of amphibian and reptiles] – In: Prirodnye Resursy Volzhsko-Kamskogo Kraya 3. Kazan: 79-93 (in Russian).
- Garanin, V.I. 1975. [On conservation, reproduction and use of amphibians and reptiles]. – In: Okhrana Prirody i Biogeotsenologiya 1. Kazan: 77-96 (in Russian).

- Garanin, V.I. 1976. [Amphibians and reptiles in vertebrate feeding]. – In: Prirodnye Resursy Volzhsko-Kamskogo Kraya: Zhivotnyi Mir 4. Kazan: 86-111 (in Russian).
- Garanin, V.I. 1977. [On amphibian and reptile place in biogeocenoses of anthropogenic landscape]. – In: Problems of Herpetology. Leningrad: 63-64 (in Russian).
- Garanin, V.I. 1981. O nekotorykh aspektakh roli amfibij i reptilij v antropogennom landshafte [About some aspects of amphibians and reptiles role in an anthropogenic landscape]. – In: Problems of Herpetology. Leningrad: 35-36 (in Russian).
- Garanin, V.I. and Popov, A.Yu. 1958. [Materials on newts ecology of Raifskii Forest (Tatarskaya ASSR)]. – Izvestiya Kazanskogo Filiala Akademii Nauk SSSR, Seriya Biologicheskaya (6): 89-94 (in Russian).
- Garanin, V.I. and Ushakov, V.A. 1970. [Influence of some anthropogenic factors on number and distribution of amphibians and reptiles]. – In: Vliyanie Antropogennykh Faktorov na Formirovanie Zoogeograficheskikh Kompleksov 2. Kazan: 68-70 (in Russian).
- Gatyatullina, E.Z. 1978. [Temperature and experimental populations density influence on mitotic activity and corneal epithelium cell size in amphibians]. – In: Eksperimentalnaya Ekologiya nizshikh pozvonochnykh. Sverdlovsk: 92-111 (in Russian).
- Gatyatullina, E.Z. 1989. [Larval growth and development in *Rana arvalis* in the conditions of technogenic landscape]. – In: Problems of Herpetology. Kiev: 57-58 (in Russian).
- Gatyatullina, E.Z. and Shchupak, E.L. 1992. [Ecophysiological characterization of *Rana arvalis* life cycle under influence of anthropogenic factors]. – In: Zhivotnye Antropogennykh Landshaftov. Ekaterinburg: 54-65 (in Russian).
- Gendron, A., Hontela, A., Bishop, C.A. and Fortin, R. 1994. Multilevel detection of toxic stress in the mudpuppy: an ecotoxicological approach. – In: Second World Congress of Herpetology. Adelaide, Dec. 1993-Jan. 1994. Abstr. Adelaide: 96-97.
- Gershenson, M.S. 1941. [Mobilization resource of infraspecies variability]. – Zhurnal Obshchei Biologii. 2 (1): 85-107 (in Russian).
- Gershenson, M.S. 1985. [Microevolution, polymorphism and dominant mutations]. – Priroda (Moscow) (4): 80-89 (in Russian).
- Giacoma, C., Castellano, S., Marzona, E. and Colombo, L. 1994. Sexual selection in *Rana temporaria*: Seasonal variation in male mating success. – In: Second World Congress of Herpetology. Adelaide, Dec. 1993-Jan. 1994. Abstr. Adelaide: 97.
- Gilmanov, T.G. 1987. Vvedenie v Kolichestvennyu Trofologiyu i Ekologicheskuyu Bioenergetiku Pozvonochnykh v Nazemnykh Ekosistemakh 1. Osnovnye Modeli; Poikilothermnye Zhivotnye [Introduction to Vertebrates Quantitative Trophology and Ecological Bioenergetic in Terrestrial Ecosystems 1. Main Models; Poikilothermic Animals]. Moscow: MGU Publ., 180 p (in Russian).
- Gittins, S.P. 1987. The diet of the Common Toad (*Bufo bufo*) around a pond in Mid-Wales. – Amphibia-Reptilia 8 (1): 13-17.
- Gliwich, I. 1980. [Investigation of animals sinurbization pressing on example of city populations]. – Studia Geographica 71 (1): 121-132 (in Russian).

- Gninenko, Yu.I. [Ants in the settlements of the Urals]. – In: Problemy Promyshlennykh Gorodov Urala. Sverdlovsk: 49-50 (in Russian).
- Godina, L.B. and Sytina, L.A. 1985. [Siberian salamander (*Hynobius keyserlingii*) embryo growth variations]. – In: Problems of Herpetology. Leningrad: 59-60 (in Russian).
- Goin, C.J. and Goin, O.B. 1962. Introduction to Herpetology. San Francisco – Ld., 229 p.
- Gogoleva, N.P. 1985. [Some rules of linear and weight growth of amphibians]. – *Ekologiya* (Sverdlovsk) (1): 61-66 (in Russian).
- Gogoleva, N.P. 1989. [Polymorphism in tailless amphibian populations]. – In: Problems of Herpetology. Kiev: 63-64 (in Russian).
- Golay, N., Starck, C. and Durrer, H. 1995. Das nahrungsspektrum von Kreuzkröten (*Bufo calamita*) in den ersten wochen nach der Metamorphose. – *Z. Feldherpetol.* 2 (1-2): 17-22.
- Gollmann, G., Hodl, W. and Ohler, A. 1984. A tadpole from a *Bombina* hybrid population a hopeless monster. – *Amphibia-Reptilia* 5 (3-4): 411-413.
- Goncharenko, A.E. 1988. [Number and distribution of *Rana temporaria* in the river basin of Southern Bug]. – In: Vid i Ego Produktivnost v Areale. Vilnius: 127-128 (in Russian).
- Gosner, K.L. and Black J.H. 1957. The effects of acidity on the development and hatching of New Jersey frogs. – *Ecology* 38 (2): 256-262.
- Gosseye, M. 1979. L'homme, predateur des des grenouilles dans le Luxemburg belge. – *Natur Belg.* 60 (2-3): 87-95.
- Gossling, J., Loesche, W.J., Ottoni, L.D. and Nace, G.W. 1980. Passage of material throught the gut of hibernating *Rana pipiens* (Amphibia, Anura, Ranidae). – *J. Herpetol.* 14 (4): 407-409.
- Grant, K.P. and Licht, L.E. 1994. Effects of ultraviolet radiation on life history parameters of frog from Ontario, Canada. - In: Second World Congress of Herpetology. Adelaide, Dec.1993-Jan.1994. Abstr. Adelaide: 101.
- Grant, V. 1980. *Evolutsiya Organizmov* [Evolution of organisms]. Moscow: Mir Publ., 470 p (in Russian).
- Gray, R.H. 1984. Effective breeding size and adaptive significance of color polymorphism in the cricket frog (*Acris crepitans*) in Illinois, USA. – *Amphibia-Reptilia* 5 (2): 101-107.
- Grefner, N.M. and Slepyan, E.I. 1989. [The phenomenon of larval development retardation in amphibians and dischemy of fresh waters]. – In: Problems of Herpetology. Kiev: 68-69 (in Russian).
- Griffiths, R.A. 1984. Seasonal behaviour and intrahabitat movements in an urban population of a Smooth newts, *Triturus vulgaris* (Amphibia: Salamandridae). – *J. Zool.* 5 (2): 241-251.
- Griffiths, R.A. 1993. The effects of acidity on newt eggs and larvae. – In: *Ökologie und Stammesgeschichte der Schwanzlurche*. Magdeburg: 11-12.

- Gulve, P.S. 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog *Rana lessonae*. – Ecology 75 (5): 1357-1367.
- Günter, R. and Plotner, J. 1986. On the noxious effects of the household detergents on anuran eggs and tadpoles. – In: Stud. Herpetol. Proc. Eur. Herpetol. Prague: 717-722.
- Gureev, S.P., Kuranova, V.N., Milovidov, C.P., Lyalin, V.G., Moskovitina, A.S. and Dmitrieva, N.G. 1990. [Vertebrate animals population of Tomsk city]. – Prirodnye Kompleksy Tomskoi Oblasti. Tomsk: 118-121 (in Russian).
- Guyetant, R. 1967. Etude de l'alimentation de jeunes batraciens anoures durant la saison estivale. – Ann. Scient. Univ. Besancon Zool. (3): 69-78.
- Hall, H. and Kolbe, F. 1980. Bioconcentrations of organophosphorus pesticides to hazardous levels by amphibians. – J. Toxicol. and Environ. Health 6 (4): 853-860.
- Halliday, T.R. 1993. Declining amphibians in Europe, with particular emphasis on the situation in Britain. – Environ. Rev. 1: 21-25.
- Hanken, J. 1985. Morphological novelty in the limb skeleton accompanies miniaturization in salamanders. – Science 229 (4716): 871-874.
- Harshbarger, J.C. and Rose, F. 1989. Histology of skin, connective tissue, pigment cell and liver neoplasms from a sewage lagoon. – Herpetopathologia 1 (1): 19-27.
- Hazelwood, E. 1970. Frog pond contaminated. – Brit. J. Herpetol. 4 (3): 177-184.
- Hebard, W.B. and Brunson, R.B. 1963. Hind limb anomalies of a western Montana population of the Pacific Tree Frog, *Hyla regilla* Barid and Girard. – Copeia (3): 570-572.
- Hemmer, H. and Kadel, B. 1980. Studien am wasserfrosch - *Rana perezi* (Scoane, 1885) - der Balearen (Amphibia, Anura, Ranidae). - Boll. Soc. Hist. Natur. Balears. 24: 55-70.
- Henderson, C.C. Jr. 1961. Reproductive potential of *Microhyla olivacea*. – Texas J. Sci. (13): 355-356.
- Hensley, F.R. 1993. Ontogenetic loss of phenotypic plasticity of age at metamorphosis in tadpoles. – Ecology 74 (8): 2405-2412.
- Herreid, C.F. and Kinney, S.T. 1966. Survival of Alaskan Woodfrog (*Rana sylvatica*) larvae. – Ecology 47 (6): 1039-1041.
- Herreid, C.F. and Kinney, S.T. 1967. Temperature and development of the wood frog *Rana sylvatica* in Alaska. – Ecology 48 (4): 579-590.
- Hertwig, O. 1898. Ueber den Einfluss der Temperatur auf die Entwicklung von *Rana fusca* und *Rana esculenta*. – Arch. Mikrosk. Anat. und Entwicklungsgesch. 51: 319-381.
- Hickey, J.J. 1960. Death and reproductive rate in relation to flack culing and selection. – New Zealand J. Agric. Res. 3: 332-344.
- Hildmann, C. and Kronshage A. 1988. Verarbeitung und Siedlungsdichte von *Rana temporaria* in Schwelm. – Jahrb. Feldherpetol. 2: 89-107.
- Hileman, B. 1993. Amphibian population loss tied to ozone thinning. – Mitt. Hamburg. Zool. Mus. und Inst. 90: 197-207.

- Honegger, R.E. 1978. Threatened amphibians and reptiles in Europe. – Collect. Sauvegarde Nature: Cons.Eur. Nature and Environ. Ser. (15): 1-123.
- Houdry, J., Chabot, J.-G., Menard, D. and Hugon J.S. 1979. Intestinal brush border enzyme activities in developing amphibian *Rana catesbeiana*. – Comp. Biochem. and Physiol. A63 (1): 121-125.
- Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. – Ecology 59 (1): 67-77.
- Ilosvay, G. 1977. Effect of urbanization on the herpetofauna of a settlement at the Tisza (Szeged). – Tiscia 12: 123-130.
- Ilyashenko, V.Yu. 1984a. [Influence of the Zeiskoe Storage Lake on herpetofauna]. – In: Vid i Ego Produktivnost v Areale (5) Voprosy Gerpetologii. Sverdlovsk: 20-21 (in Russian).
- Ilyashenko, V.Yu. 1984b. Vliyanie Zeiskogo Vodokhranilishcha na Nazemnykh Pozvonochnykh Zhivotnykh Gornotaezhnykh Ekosistem (na Primere Vostochnoi Chasti Khrebtu Tukuringra) [Influence of Zeya Reservoir on Terrestrial Vertebrates of Mountain Taiga Ecosystems (on the Example of Eastern Part Tukuringira Mountain Ridge)]. – Ph.D. Diss. Moscow (in Russian).
- Ishchenko, V.G. 1961. [Some problems of the biology in *Hynobius keyserlingi*]. – In: Tezisy III Vsesoyuznoi Konferentsii Molodykh Uchenykh-Biologov (1). Moscow: 52 (in Russian).
- Ishchenko, V.G. 1966. [On isolation and role of environmental conditions in formation of the population features in *Triturus vulgaris*]. – In: Chetvertaya Mezhvuzovskaya Zoogeograficheskaya Konferentsiya: Tezisy Dokladov. Odessa. 115-116 (in Russian).
- Ishchenko, V.G. 1968. [On the number of *Hynobius keyserlingi* on Middle Urals]. – In: Optimalnaya Plotnost i Optimalnaya Struktura Populyatsii Zhivotnykh. Sverdlovsk: 56-57 (in Russian).
- Ishchenko, V.G. 1978a. [[On the influence of tree-felling enterprises on the population number of amphibians]. – In: Okhrana i Ratsionalnoe Ispolzovanie Biologicheskikh Resursov Urala (3) Zhivotnyi Mir. Sverdlovsk: 53-54 (in Russian).
- Ishchenko, V.G. 1978. Dinamicheskii Polimorfizm Burykh Lyagushek Fauny SSSR [Dynamic Polymorphism of the Brown Frogs of USSR Fauna]. Moscow: Nauka Publ., 148 p. (in Russian).
- Ishchenko, V.G. 1982. [Chronographic variability of *Rana arvalis* populations spatial structure and its possible ecological consequences]. – In: Dinamika Populyatsionnoi Struktury Mlekopitajushchikh i Amfibii. Sverdlovsk: 23-50 (in Russian).
- Ishchenko, V.G. 1984. [Variability of the growth and developmental rates of the larvae of *Hynobius keyserlingii* and *Triturus vulgaris* in the natural conditions]. – In: Osobennosti Rosta Zhivotnykh i Sreda Obitaniya. Sverdlovsk: 26-36.
- Ishchenko, V.G. 1989a. [Territorial distribution and population number of *Salamandrella keyserlingii* on the Middle Transurals]. – In: Problems of Herpetology. Kiev: 106-107 (in Russian).

- Ishchenko, V.G. 1989. [Reproductive tactics and the demography of populations of amphibians]. – In: Problemy Populatsionnoi Ekologii Zemnovodnykh i Presmykayushchikhsya. Moscow: 5-51 (in Russian).
- Ishchenko, V.G. 1993. Life span and growth in populations of the common frog, *Rana temporaria* L. - In: 7th. Ord Gen. Meet.Eur.Herpetol. Barcelona: 81.
- Ishchenko, V.G. 1994. Ecological mechanisms determinig stability of color polymorphism in the population of moor frog, *Rana arvalis* Nilss. - Russ. J.Herpetol. 1 (2): 117-120.
- Ishchenko, V.G. and Shchupak, E.L. 1974. [About ecological difference of separate genotypes in *Rana arvalis* population]. – Ekologiya (Sverdlovsk) (1): 93-95 (in Russian).
- Ishchenko, V.G. and Shchupak, E.L. 1979. [Intrapopulational variability of growth rate and development in *Rana arvalis* larvae]. – In: Populyatsionnye Mekhanizmy Dinamiki Chislennosti Zhivotnykh. Sverdlovsk: 49-60 (in Russian).
- Ishchenko, V.G. and Skurykhina, E.S. 1981. [On biocenotic role of *Rana arvalis* in subtaiga zone of Transuralian forests]. – In: Fauna Urala i Evropeiskogo Severa. Sverdlovsk: 57-62 (in Russian).
- Ishchenko, V.G. and Ledentsov, A.V. 1985. [Ecological aspects of postmetamorphosis growth in *Rana arvalis*]. – In: Ekologicheskije Aspekty Skorosti Rosta i Razvitiya Zhivotnykh. Sverdlovsk: 11-21 (in Russian).
- Ishchenko, V.G. and Ledentsov, A.V. 1987. [Influence of environmental conditions on the dynamics of age structure of *Rana arvalis* populations]. – In: Vliyanie Uslovii Sredy na Dinamiku Struktury i Chislennosti Populyatsii Zhivotnykh. Sverdlovsk: 40-51 (in Russian).
- Ishchenko, V.G. and Berman, D.I. 1995. Population number and dynamics. – In: The Siberian Newt (*Salamandrella keyserlingii* Dybowski, 1870): Ecology, Behaviour, Conservation. Moscow: 141-156 (in Russian).
- Ivanova, N.L. 1982. [On the use of amphibian larvae as biological indicators of pond conditions]. – In: Problemy Ekologii Pribaikalya. 5. Irkutsk: 79-80 (in Russian).
- Ivanova, N.L. 1995 [Features of ecology in *Rana ridibunda*, introduced in reservoirs-coolers]. – Ekologiya (Sverdlovsk) (6): 473-476 (in Russian).
- Jensen, T.A. 1967. Food habits of the green frog, *Rana clamitans*, before and during metamorphosis. – Copeia (1): 214-218.
- Jorgensen, C.B. 1982. Factors controlling the ovarian cycle in a temperate zone Anuran, the toad *Bufo bufo*: food uptake, nutritional state and gonadotropin. – J. Exp. Zool. 224 (3): 437-443.
- Jung, R.E. and Zafoe, C.H. 1994. Effects of pH and aluminbium on green treefrog (*Hyla cinerea*) tadpoles – In: Second World Congress of Herpetology. Adelaide: 136.
- Kaluste, H. 1968. [Comparative study of the cell nucleuses sizes of two stocks of a winter wheat at different factors use]. – In: Izvestiya Akademii Nauk EHSSR, Seriya Biologicheskaya 17 (1): 15-19 (in Russian).

- Kaplan, R.H. 1980a. The implications of ovum size variability for offspring fitness and clutch size within several populations, of salamanders (*Ambystoma*). – *Evolution* 34: 51-64.
- Kaplan, R.H. 1980b. Ontogenetic energetics in *Ambystoma*. – *Physiol. Zool.* 53 (1): 43-56.
- Kaplan, R.H. 1985. Maternal influences on offspring development in the California Newt, *Taricha torosa*. – *Copeia*. (4): 1028-1039.
- Kaplan, R.H. 1994. Amphibian life histories: a model for the study of the evolution of developmental plasticity and maternal effects - In: *Second World Congr. of Herpetol.* Adelaide: 137-138.
- Kaplan, R.H. and Cooper, W.S. 1984. The evolution of developmental plasticity in reproductive characteristics: an application of the “adaptive coin-flipping” principle. – *Amer. Natur.* 123 (3): 394-410.
- Khodorov, B.I. 1969. *Problema Vozbudimosti*. [Problem of Excitability]. Leningrad: *Meditsina Publ.*, 301 p (in Russian).
- Khodorov, B.I. 1975. *Obshchaya Fiziologiya Vozbudimyykh Membran*. [General Physiology of Excitable Membranes]. Moscow: *Nauka Publ.*, 406 p (in Russian).
- King, P.W. 1979. *Amphibia and Reptilia in the London Area*. – *London. Natur.* (68): 69-70.
- Kleiner, K. 1994. Ozone hole could be killing amphibians. – *New Sci.* 141 (1915): 7.
- Kneitz, S. 1995. An eight-year study of the population dynamics of seven coexisting amphibian species south of Bonn, Germany. – In: *Progr. and Abstr. 8th Ord. Gen. Meet. Soc. Eur. Herpetol.* Bonn: 72-73.
- Kolchinskii, E.I. 1981. [Importance of V.I. Vernadsky works for the evolutionary theory]. – In: *Problemy Noveishei Istorii Evolyutsionnogo Ucheniya*. Leningrad: 85-94 (in Russian).
- Kolodenco, A.I. 1981. [About reptile and amphibian mortality on Turkmenistan roads]. – In: *Problems of Herpetology*. Leningrad: 68 (in Russian).
- Kolyakin, N.N. 1993. *Ekologo-Faunisticheskii Analiz Zhivotnogo Komponenta Ekosistem Promyshlennogo Goroda: (Na Primere g. Volgograda)* [Ecologo-Faunistic Analysis of Animal component in Ecosystems of Industrial City (On the Example of Volgograd)]. – Ph.D. Diss. Abstr., Volgograd, 25 p (in Russian).
- Konstantinova N.F. 1981. [About rare in disappearing amphibian and reptiles species under intensive anthropogenic pressure]. – In: *Problems of Herpetology*. Leningrad: 70 (in Russian).
- Kopein, K.I. 1970. [Tailless amphibian populations of Nort forest-steppe]. – In: *Optimalnaya Plotnost i Optimalnaya Struktura Populyacii Zhivotnykh*. Sverdlovsk: 77-80 (in Russian).
- Kosareva, N.A. and Vasyukov, I.L. 1976. [Changes in *Rana ridibunda* sexual system as a consequence of anthropogenic influence on habitat]. – In: *Antropogennyye Vozeistviya na Prirodnye Kompleksy i Ekosistemy*. Volgograd: 84-93 (in Russian).

- Koshelev, V.V. 1988. [Features of populations adaptive transformations, kinetic of fish communities and change of individual development in different habitat conditions]. – In: *Ekologiya Populyatsii* 2. Novosibirsk: 159-161 (in Russian).
- Kovalchuk, L.A. 1978. [Features of oxidizing metabolism in tailless amphibian (Anura, Amphibia) ontogenesis]. – In: *Ekspperimentalnaya Ekologiya Nizshikh Pozvonochnykh*. Sverdlovsk: 72-85 (in Russian).
- Kubantsev, B.S. 1976. [On the role of the anthropogenic factors in ecological processes]. – In: *Antropogennye Vozdejstviya na Prirodnye Kompleksy i Ekosistemy*. Volgograd: 3-16 (in Russian).
- Kubantsev, B.S. and Zhukova, T.I. 1994. [Anthropogenic influences on amphibian habitats and sexual structure of their populations]. – In: *Ekologicheskaya i Morfologicheskaya Izmenchivost Zhivotnykh pod Vliyaniem Antropogennykh Faktorov*. Volgograd: 64-74 (in Russian).
- Kuranova, V.N. 1980. [Change in the number and distribution of amphibians and reptiles under the influence of anthropogenic factors]. – In: *Problemy Okhrany Prirody Zapadnoi Sibiri*. – Tomsk: 74-77 (in Russian).
- Kuranova, V.N. 1984. [Influence of melioration on distribution and number of *Rana arvalis*]. – In: *Herpetol. Investigations in Siberia and the Far East*. Leningrad: 45-48 (in Russian).
- Kuranova, V.N. 1989. [Features of amphibians and reptiles biology of large city]. – In: *Problems of Herpetology*. Kiev: 132-133 (in Russian).
- Kuranova, V.N. and Grigoriev, O.V. 1980. [Research state and protection of amphibians and reptiles in West Siberia]. – In: *Problems of Biology*. Tomsk: 7-9 (in Russian).
- Kuzmin, S.L. 1984. Rate of food consumption and prey size of the Siberian newt during the ontogenesis. – *Ekologiya (Sverdlovsk)* (5): 42-49 (in Russian).
- Kuzmin, S.L. 1985. [Peculiarities of the larval feeding of *Hynobius keyserlingii* of different micropopulations]. – In: *Problems of Herpetology*. Leningrad: 116-117 (in Russian).
- Kuzmin, S.L. 1986. Oekologie und biozonotische Rolle vom sibirischen Braunfrosch (*Rana amurensis* Pall.) in der Mongolei. – In: *Herpetol. Untersuchungen in der Mongolischen Volksrepublik*. Moskau: 22-59 (in Russian).
- Kuzmin, S.L. 1987. [Comparative feeding ecology of Mongolian amphibians]. – *Ekologiya (Sverdlovsk)* (2): 82-86 (in Russian).
- Kuzmin, S.L. 1995. Amphibian declines and the problem of extinction of taxa. – *Uspekhi Sovremennoi Biologii* 115 (2): 141-155 (in Russian).
- Kuzmin, S.L. 1994. Commercial collecting as a threat for amphibian and reptile species in the former Soviet Union. – *Species*. (23) 47-48.
- Lardner, B. 1995. Larval ecology of *Rana arvalis*: an allopatric island population compared with a sympatric mainland population. – *Amphibia-Reptilia*. 16 (2): 101-111.
- Larionov, L.F. 1923. [Amphibians in the neighbourhood of Tyumen City]. – In: *Izvestiya Tomskogo Universiteta* 72: 1-4 (in Russian).

- Larionov, P.D. 1976. [Reproduction of *Hynobius keyserlingi* in the neighbourhood of Yakutsk]. – Zoologichesky Zhurnal. 55 (8): 1259-1261 (in Russian).
- Lebedeva, G.D. 1970. [Determination of pollution toxicity of fresh waters concerning some hydrobionts]. – In: Voprosy Vodnoi Toksikologii. Moscow: 61-66 (in Russian).
- Lebedinsky, A.A. 1981. [Features of amphibian distribution on urbanized territory]. – In: Nazemnye i Vodnye Ekosistemy. Gorky: 49-56 (in Russian).
- Lebedinsky, A.A. 1984a. Amfibii v Usloviyakh Urbanizirovannoi Territoriy (na Primere g. Gorkogo) [Amphibians in the Conditions of Urbanized Territory (Example of Gorky City)]. – Ph.D. Diss. Abstr., Moscow, 23 p. (in Russian).
- Lebedinsky, A.A. 1984b. [On amphibian adaptations to conditions of urbanized territory]. – In: Problemy Regionalnoi Ekologii Zhivotnykh v Tsikle Zoologicheskikh Distiplin Pedvuza. Vitebsk: 106 (in Russian).
- Lebedinsky, A.A. 1995. [Some morphophysiological frogs adaptations to anthropogenic influence]. – Ekologiya i Okhrana Okruzhayushchei Sredy 2. Perm: 78-79 (in Russian).
- Ledentsov, A.V. 1990. Dinamika Vozrastnoi Struktury i Chislennosti Polovozreloi Chasti Populyatsii *Rana arvalis* [Dynamics of Age Structure and Number in the Mature Part of *Rana arvalis* Population]. – Ph.D. Diss. Abstr., Sverdlovsk: Institute of Plant and Animal Ecology, USSR Academy of Sciences, 24 p. (in Russian).
- Leuven, R.S.E.W., Hartog, C. den, Christians, M.M.C. and Heijligers, W.H.C. 1986. Effect of water acidification on the distribution pattern and reproductive success of amphibians. – Experientia 42 (5): 495-503.
- Leontjeva, O.A. 1987. [Soil invertebrates in amphibian food]. – In: Pochvennaya Fauna Severnoi Evropy. Moscow: 149-152 (in Russian).
- Leontjeva, O.A. 1990. Beskhvostye Zemnovodnye kak Bioindikatory Antropogennykh Izmenenii v Ekosistemakh Podmoskovya [Tailless Amphibians as Bioindicators of Anthropogenic Changes in ecosystems of Moscow Neighbourhood]. – Ph.D. Diss. Abstr., Moscow, 24 p. (in Russian).
- Lesnikov, L.A. 1970. [Features of pollution influence on populations of water organisms]. – In: Voprosy Vodnoi Toksikologii. Moscow: 61-66 (in Russian).
- Levchenko, V.F. 1990. [Evolutionary ecology and evolutionary physiology – what is common?]. – Zhurnal Evolyutsionnoi Biokhimii i Fiziologii 26 (4): 455-461 (in Russian).
- Li, J.C. and Lin, C.S. 1935. Studies of the “rain frog” *Kaloula borealis*, 2. The food and feeding of the embryos and adults. – Peking Nat. Hist. Bull. 10 (1): 45-53.
- Licht, L.E. 1967. Growth inhibition in crowded tadpoles: intraspecific and interspecific effects. – Ecology. 48 (5): 736-745.
- Licht, L.E. 1974. Survival of embryos tadpoles and adult of the frogs *Rana aurora aurora* and *Rana prettiosa prettiosa* sympatric in southwestern British Columbia. – Can. J. Zool. 52 (5): 613-627.
- Linnenbach, M. and Gebhart, H. 1987. Untersuchungen zu den Auswirkungen der Gewässerversauerung auf die Ei und Larvalstadien von *Rana temporaria* Linnaeus, 1758 (Anura; Ranidae). – Salamandra. 23 (2-3): 153-158.

- Linnenbach, M., Marthaler, R. and Gebhardt, H. 1987. Effects of acid water on gills and epidermis in brown trout (*Salmo trutta* L.) and in tadpoles of the common frog (*Rana temporaria* L.). – Ann. Soc. Roy. Zool. Belg. 117 (1): 365-374.
- Liosner, L.D. 1975. [Newts *Triturus vulgaris*, *Triturus cristatus*]. – In: Obiekty Biologii Razvitiya. Moscow: 324-341 (in Russian).
- Loman, J. 1979. Food, feeding rates and prey-size selection in juvenile and adult frogs, *Rana arvalis* Nilss. and *R. temporaria* L. – Ecologia Polska 27 (4): 581-601.
- Loman, J. 1994. Metamorphosis strategy in tadpoles (*Rana temporaria*) from different ponds - microevolutionary effects. – In: Second World Congr. of Herpetol. Adelaide: 157.
- Lubashevsky, N.M, Sadykov, O.F. Popov, B.V. et al. 1985. [Technogenic fluoride in forest ecosystems of Ural]. – Biokhimicheskaya Ekologiya i Medicina 2. Sverdlovsk: 234-272 (in Russian).
- Lukyanova, L.E. 1990. Ekologicheskaya Kharakteristika i Osobennosti Naseleniya Melkikh Mlekopitajushchikh v Usloviyakh Tekhnogenogo Vozdejstviya [The Ecological Characteristic and Peculiarities of Small Mammals Populations in Conditions of Technogenic Influence]. – Ph.D. Diss. Abstr., Sverdlovsk: Institute of Plant and Animal Ecology, USSR Academy of Sciences, 24 p. (in Russian).
- Lyapkov, S.M. 1986. [Factors determining variability of sizes of juveniles of *Rana temporaria* and *R.arvalis* during metamorphosis]. – Zoologichesky Zhurnal 65 (1): 88-89 (in Russian).
- Lyapkov, S.M. 1987. [Preying of the red-tooth shrew and green frogs on *Rana temporaria* juveniles in the conditions of experiment]. – In: Problemy Sovremennoj biologii 3. Moscow: 27-31 (in Russian).
- Lyapkov, S.M. 1988. [Brown frogs (*Rana temporaria* and *R.arvalis*) juveniles survivorship in the beginning of terrestrial life]. – Zoologichesky Zhurnal 67 (10): 1519-1529 (in Russian).
- Lyapkov, S.M. 1989. [Brown frogs juveniles eating by green frogs]. – In: Zemnovodnye i Presmykajushchiesya Moskovskoi Oblasti. Moscow: 156-162 (in Russian).
- Lyapkov, S.M. 1992. Factory, Opredelyayushchie Dinamiku Chislennosti Segoletok Burykh Lyagushek [Factors Determining Dynamics of Brown Frogs Juvenile Number]. – Ph.D. Diss. Abstr., Moscow, 24 p. (in Russian).
- Lyapkov, S.M. 1994. [Influence of initial number of generation on the number of metamorphosed animals, their sizes and metamorphosis duration in *Ran temporaria* and *R.arvalis* frogs]. – Zoologichesky Zhurnal 74 (1): 97-111 (in Russian).
- Lynch, J.F. 1985. The feeding ecology of *Aneides flavipunctatus* and sympatric plethodontid salamanders in Northwestern California. – J.Herpetol. 19 (3): 328-352.
- MacArthur, R.H. and Wilson, E.O. 1967. The theory of island biogeography. N.Y.: Princeton Univ. Press, 203p.
- Malone, B. 1994. The impact of anuran larvae on temporary pond communities: An experimental approach. – In: Second World Congr. of Herpetol. Adelaide: 164.

- Martof, B. 1953. Territoriality in the green frog *Rana clamitans*. – Ecology. 34 (3): 529-544.
- Mathias, J.H. 1975. A survey of amphibians in Leicestershire gardens. – Transactions of the Leicestershire Literary and Philosophical Society. 6 (11): 61-62.
- May, R.M. 1983. The structure of food webs. – Nature. 301 (5901): 566-568.
- Mayr, E. 1974. Populyatsii, Vidy i Evolyutsiya [Populations, Species and Evolution]. Moscow: Mir Publ., 460 p. (in Russian).
- Mazing, V.V. 1987. [Problems of city ecology]. – In: Goroda i Ekologiya 1. Moscow: 145-150 (in Russian).
- Menon, J.G., Ren Ken and Drews, R.C. 1996. Cisplatin inhibits metamorphosis of Bull frog tadpoles, via thyroid suppression. – Amer. Zool. 36 (5): 117.
- Meyer-Rochow, B.V. and Asashima, M. 1988. Naturally occurring morphological anomalies in wild populations of the Japanese Newt *Cynops pyrrhogaster* (Salamandridae; Urodela; Amphibia). – Zool.Anz. 221 (1-2): 70-80.
- McCoid, M.J. and Fritts, T.H. 1989. Growth and fatbody cycles in feral populations of the african clawed frog, *Xenopus laevis* (Pipidae), in California with comments on reproduction. – Southwest. Natur. 34 (4): 499-505.
- McCue, R.W. 1989. Simulated nitric and sulfuric acid precipitation: the effects on the development of *Rana pipiens*. – Trans. Kans. Acad. Sci. 92: 12-17.
- Meleshina, N. 1975. [Influence of atmosphere pollution of cold asphalt factory on lichens flora of Urals State University Botanical Garden]. – In: Problemy Promyshlennykh Gorodov Urala. Sverdlovsk: 57-58 (in Russian).
- Menshikov, G.I. 1975. [On recultivation of drags waste lands in settlements area and in suburban green zones]. – In: Problemy Promyshlennykh Gorodov Urala. Sverdlovsk: 32-33 (in Russian).
- Mezhzherin, V.A. 1988. [Two approaches to study of energetics of populations]. – In: Ekologicheskaya Energetika Zhivotnykh. Pushchino: 109-110 (in Russian).
- Milkov, N.F. 1973. Chelovek i Landshafty [The Man and Landscapes]. Moscow: Mysl Publ., 224 p (in Russian).
- Milkov, N.F. 1978. Rukotvornye Landshafty [Man-Made Landscapes]. Moscow: Mysl Publ. (in Russian).
- Misyura, A.N. 1981. [Ecologo-biochemical parameters of *Rana ridibunda* in the conditions of industrial pollution of aquatic ecosystem]. – In: Problems of Herpetology. Leningrad: 128-136 (in Russian).
- Misyura, A.N. 1982. [Comparison of some parameters of substances exchange in *Rana ridibunda* as a parameter of ecological condition of this species in anthropogenic systems]. – In: Problemy Ekologii Pribajkalya 5. Irkutsk: 53 (in Russian).
- Misyura, A.N. 1985. [Some ecological and biochemical aspects of *Rana ridibunda* adaptation to technogenic factors]. – In: Problems of Herpetology. Leningrad: 143-144 (in Russian).
- Misyura, A.N. 1989. Ekologiya Fonovogo Vida Amfibii Tsentralnogo Stepnogo Pridneprovya v Usloviyakh Promyshlennogo Zagryazneniya Vodoemov [Ecology of

- Widespread species of Amphibians in Central Steppes Pridneprovye in the Conditions of Industrial Pollution of Wetlands]. – Ph.D. Diss. Abstr., Moscow, 16 p (in Russian).
- Misyura, A.N., Chernyshenko, S.V. and Varenko, N.I. 1990. [Preservation and use of *Rana ridibunda* populations in conditions of influence of industrial waste water on ecosystems]. – In: Zookultura amfibij. Moscow: 112-119 (in Russian).
- Mitskevich, M.S. 1978. Gormonalnye Regulyacii v Ontogeneze Zhivotnykh [Hormonal Regulations in Animals Ontogenesis]. Moscow: Nauka Publ., 222 p (in Russian).
- Mittermeier, R.A. and Carr, J.L. 1994. Conservation of reptiles and amphibians: a global perspective. – In: Captive Manag. and Conserv. of Amphibians and Reptiles. Ithaca (NY): 27-35.
- Mizgirev, I.V., Flax, N.L., Borkin, L.J. and Khudoley, V.V. 1984. Dysplastic lesions and abnormalities in amphibians associated with environmental conditions. – Neoplasma. 31 (2): 175-181.
- Morin, D.J. and Johnson, E.A. 1988. Experimental studies of asymmetric competition among anurans. – Oikos. 53 (3): 398-407.
- Moriwaki, T. 1952. The inheritance of the dorsal-median stripe in *Rana limnocharis* Wiegmann. – J. Sci. Hiroshima Univ. Ser. B. Div.1 (Zool.) 14 Art.1-19: 159-164.
- Motkova, M.Yu. 1977. [On the feeding and ecology of anuran larvae]. – In: Problems of Herpetology. Leningrad: 148-149 (in Russian).
- Moyle, P.B. 1973. Effects of introduced Bullfrogs, *Rana catesbeiana*, on the native frogs of San Joaquin Valley, California. – Copeia (1): 18-22.
- Munkhbayar, H. 1987. Khoir Nutagtan, Mulkhugchid [Amphibians and reptiles]. – In: BNMAU Ulaan Nom. Ulaan Baatar: 63-69 (in Mongolian).
- Neff, A.W., Briggs, F. and Chung, H-M. 1987. Cranio-fascial development mutant pi (pinhead) in the axolotl (*Ambystoma mexicanum*) which exhibits reduced interocular distance. – J. Exp. Zool. 241 (3): 309-316.
- Obuchova, H.Yu. 1984. [Influence of cooling on developing eggs of *Hynobius keyserlingii*]. – In: Vid i Ego Produktivnost v Areale 5: Voprosy Gerpetologii. Sverdlovsk, 30 (in Russian).
- Odum, E. 1975. Osnovy Ekologii [Fundamentals of Ecology]. Moscow: Mir Publ., 740 p. (in Russian).
- Ogieska, M. 1991. Abnormal eye development in the progeny of the natural hybridogenetic frog *Rana esculenta* L. (Amphibia, Anura). – Zool. Anz. 226 (3-4): 174-184.
- Okawa, H. 1994. Hachu ryoseirugaku zasshi. – Yap. J. Herpetol. 15 (4): 147-148.
- Oplinger, C.S. 1966. Sex ratio, reproductive cycles, and time of ovulation in *Hyla crucifer* Wied. – Herpetologica 22 (4): 276-283.
- Orser, P.N. and Shure, D.J. 1972. Effects of urbanization on the salamander *Desmognathus fuscus fuscus*. – Ecology 53 (6): 1148-1154.
- Osborn, O., Cooke, A.S. and Freestone, S. 1981. Histology of a teratogenic effect of DDT on *Rana temporaria* tadpoles. – Environ. Pollut. Ser. A 25: 305-319.

- Papanyan, S.B. 1949. [The data on importance of *Bufo viridis* in agriculture of Armenian SSR]. – *Izvestiya Akademii Nauk Armyanskoi SSR* 11 (6): 587-595 (in Russian).
- Pavlov, B.K. 1982. [Genetics-poulational aspects of populations reactions on anthropogenic factors]. – *Problemy Ekologii Pribaikalya* 1. Irkutsk: 122 (in Russian).
- Pawlowska-Indyk, 1980. A. Effect of temperature on the embryonic development of *Bombina variegata* L. – *Zoologica Poloniae* 27 (3): 397-408.
- Peskova, T.Yu. 1995. Krasnobryukhaya Zherlyanka ka Test-Obiekt dlya Bioindikatsii Pestitsidnogo Zagryazneniya Vodoemov Zapadnogo Predkavkazya [*Bombina bombina* as the Test Object of Bioindication of Pesticide Pollution of Ponds in Western Precaucasia]. – Ph.D. Diss. Abstr., Krasnodar, 24 p. (in Russian).
- Petersen, C.G.J. 1896. The yearly immigration of young plaice into Limfjord from the German sea. – In: *Rept. Danish Biol. Srn.* 6: 1-48.
- Petrov, V.S. and Sharygin, S.A. 1981. [On the opportunity of amphibian and reptile usage for indication of environmental pollution]. – In: *Nazemnye i Vodnye Ekosistemy*. Gorky: 41-48 (in Russian).
- Petrova, L.A. 1995. [Tailless amphibians variability in the conditions of Tulskaaya Province]. – In: *Ekologiya i Okhrana Okruzhayushchei Sredy* 2. Perm: 97-98 (in Russian).
- Pianka, E.R. 1970. On “r” and “k” selection. – *Amer. Natur.* (104): 592-597.
- Pierce, B.A. 1985. Acid tolerance in amphibians. – *Bio Science* (4): 239-243.
- Pikulik, M.M. 1976. [Growth rate and development of *R. esculenta* and *R. arvalis* larvae at coexistence with *R. temporaria* larvae]. – *Doklady Akademii Nauk Belorusskoi SSR* 20 (11): 1048-1050 (in Russian).
- Pikulik, M.M. 1977. [Experimental study of larval growth and development in nature]. – In: *Problems of Herpetology*. Leningrad: 169-170 (in Russian).
- Pikulik, M.M. 1978. [On some morphological features of anuran froglets depending on density at larval development]. – In: *Voprosy Estestvoznaniya*. Minsk: 55-58 (in Russian).
- Pliss, G.B. and Khudolei, V.V. 1979. [Oncogenesis and cancerogenous factors in primitive vertebrates and invertebrate animals]. – In: *Ekologicheskoe Prognozirovanie*. Moscow: 167-185 (in Russian).
- Popov, Yu.K. 1967. [On the influence of forest chemical treatment on birds and shrews]. – *Uchenye Zapiski Permskogo Pedagogicheskogo Instituta* 1: 34-41 (in Russian).
- Porter, K.R. 1972. *Herpetology*. Philadelphia-London-Toronto. 524p.
- Pramoda, S. and Saidapur, S.K. 1986. Effect of cadmium chloride on the ovary of the frog *Rana tigrina*. – *Curr. Sci. (India)*. 55: 206-208.
- Preest, M.R. 1992. Feeding performance of acid-exposed larval salamanders: mechanism of growth rate reduction. – *Amer. Zool.* 32 (5) 43.
- Prestt, I., Cooke, A.S. and Corbett, K.P. 1974. *British amphibians and reptiles*. – In: *Chang. Flora and Fauna Brit. Ld.* – NY: 229-254.
- Pyastolova, O.A. 1985. [Amphibians as indicators of industrial pollution of environment]. – In: *Problems of Herpetology*. Leningrad: 174 (in Russian).

- Pyastolova, O.A. 1990. [Some problems of zoological control of natural environment on the Urals]. – In: Zhivotnye v Usloviyakh Antropogenogo Landshafta. Sverdlovsk: 3-9 (in Russian).
- Pyastolova, O.A. and Shvarts, S.S. 1975. [New data describing ecophysiological specificity of the Arctic amphibians]. – Doklady Akademii Nauk SSSR. 223 (1): 216-217 (in Russian).
- Pyastolova, O.A. and Ivanova, N.L. 1978. [Growth and development of amphibians larvae in experimental conditions]. – In: Eksperimentalnaya Ekologiya Nizshikh Pozvonochnykh. Sverdlovsk: 13-31 (in Russian).
- Pyastolova, O.A., Bugaeva, E.A. and Bolshakov, V.N. 1981. [Amphibian larvae as bioindicators of environmental pollution]. – In: Problems of Herpetology. Leningrad: 112 (in Russian).
- Pyastolova, O.A. and Trubetskaya, E.A. 1988 [Some features of metamorphic energetics of *Rana arvalis* in technogenic landscape]. – In: Ekologicheskaya Energetika Zhivotnykh. Sverdlovsk: 105-117 (in Russian).
- Pyastolova, O.A. and Trubetskaya, E.A. 1989. [Some morphological and cytological features of *Rana arvalis* froglets liver in conditions of technogenic landscape]. Ekologiya (Sverdlovsk) (5): 57-63 (in Russian).
- Pyastolova, O.A., Vershinin, V.L., Trubetskaya, E.A. and Gatiyatullina, E.Z. 1996. [Use of amphibians in bioindication researches of territory of the East-Uralian radioactive trace]. – Ekologiya (Ekaterinburg) (5): 378-382 (in Russian).
- Pyastolova, O.A. and Vershinin, V.L. 1999. [Some cytological features of *Rana arvalis* on the territory of East-Uralian radioactive trace]. – Ekologiya (Ekaterinburg) (1): 30-35 (in Russian).
- Rahmel, U. and Eikhorst, R. 1988. Untersuchungen an der Laichplätzen von Moorfrosch (*Rana arvalis*) und Grassfrosch (*Rana temporaria*) auf den Nordfriesischen Geestinseln Amrum, Fohr und Sylt. – In: Jahrb. Feldherpetol. 2. Duisburg-Rheinhausen: 47-65.
- Ravkin, Yu.S. and Lukyanova, I.V. 1976. Geografiya Pozvonochnykh Zhivotnykh Yuzhnoi Taigi Zapadnoi Sibiri: Ptitsy, Melkie Mlekopitayushchie, Zemnovidnye [Geography of Vertebrates of the Southern Taiga of West Siberia: Birds, Small Mammals, Amphibians]. Novosibirsk: Nauka Publ., 360 p (in Russian).
- Reeder, W.G. 1964. The digestive system. Physiology of the Amphibia. NY – London: 99-149.
- Rengel, D. and Pisano, A. 1989. Mercuric chloride effect during *Bufo arenarum* development. – Comun. Biol. 8 (1): 49-64.
- Reynolds, T.D. and Stephens, T.D. 1984. Multiple ectopic limbs in a wild population of *Hyla regilla*. – Great Basin Natur. 44 (1): 166-169.
- Richards, C.M. 1962. The control of tadpole growth by alga-like cells. – Physiol. Zool. 31: 138-151.
- Richards, C.M., Tartof, D.T. and Nace, G.W. 1969. A melanoid variant in *Rana pipiens*. – Copeia (4): 850-852.

- Richards, S.J., McDonald, K.R. and Alford, R.A. 1994. Declines in populations of Australia's endemic tropical rainforest frogs. – In: Second World Congress of Herpetology. Adelaide: 215-216.
- Roberts, J.M. and Verrel, P.A. 1984. Physical abnormalities of the limbs of Smooth Newts (*Triturus vulgaris*) (short note). – Brit. J. Herpetol. 6 (11): 416-418.
- Robertson, J.G.M. 1989. Predation by a carabid beetle on Australian frogs. – Herpetol. Rev. 20 (1): 7-8.
- Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M.L., Fitch, H.S. and Martinco, E.A. 1992. Diverse and contrasting effects of habitat fragmentation. – Science 257 (5069): 524-526.
- Rose, F.L. and Harshbarger, J.C. 1977. Neoplastic and possibly related skin lesions in neothenic Tiger salamanders from a sewage lagoon. – Science 196 (4287): 315-317.
- Roskin, G.I. and Levinson, L.B. 1957. Mikroskopicheskaya Tekhnika [Microscopic Engineering]. Moscow: Sovetskaya Nauka Publ., 476 p (in Russian).
- Rostand, J. and Darre, P. 1970. Une mutation de *Rana esculenta*: la grenouille aux yeux noirs. – C.R. Acad. Sci. (D) 217: 1414-1415.
- Runkova, G.G. 1975. [Experience of some methods of mathematical experiment planning application in ecological and biochemical researches]. – In: Matematicheskoe Planirovanie Eksperimenta V Biologicheskikh Issledovaniyakh. Sverdlovsk: 18-104 (in Russian).
- Ruth, S. 1987. Flukes produce legs in profusion. – New Sci. 113 (1551): 24.
- Ruzskii, M. 1894. [Results of amphibian and reptile study in Kazan and adjacent areas]. – In: Prilozheniya k Protokolam Zasedanii Obshchestva Estestvoispytatelei pri Imperatorskom Kazanskom Universitete (139): 1-8 (in Russian).
- Sabaneev, L.P. 1874. Pozvonochnye Srednego Urala i Geograficheskoe Rasprostraneniye ikh v Permskoi i Orenburgskoi Guberniyakh. [Vertebrates of Middle Urals and Their Geographical Distribution in Perm And Orenburg Provinces]. Moscow, 183 p (in Russian).
- Saidapur, S.K. and Prasadmurthy, Y.S. 1988. Effects of feeding and starvation on follicular development (ovarian cycle) in the frog *Rana cyanophlyctis* (Schn.). – Indian J. Exp. Biol. 26 (7): 520-524.
- Seale, D.B. 1982. Amphibia. – In: Anim. Energetics 2: 467-552.
- Seale, D.B. and Beckvar, N. 1980. The comparative ability of anuran larvae (Genera: *Hyla*, *Bufo* and *Rana*) to ingest suspended blue-green algae. – Copeia (3): 495-503.
- Semlitsch, R.D., Scott, D.E. and Pechmann, J.H.K. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. – Ecology 69 (1): 184-192.
- Serov, S.I. and Tereshin, S.Yu. 1984. [Influence of sapropel and its fractions from Moltaevo Lake on nerve and muscle accommodation]. – In: Tezisy Dokladov 4-go Vserossiiskogo Siezda Fizioterapevtov i Kurortologov. Moscow: 39-40 (in Russian).
- Severtsov, A.S. 1986. [On the causes of evolutionary stability of populations in nature]. – Zhurnal Obshchei Biologii 47 (6): 723-734 (in Russian).

- Severtsov, A.S. 1987. *Osnovy Teorii Ehvolyucii*. [Fundamentals of Evolutionary Theory]. Moscow: Moscow State Univ. Publ., 320 p (in Russian).
- Severtsov, A.S. and Surova, G.S. 1979a. [*Rana temporaria* larval mortality and factors determining it]. – *Zoologichesky Zhurnal* 58 (3): 393-403 (in Russian).
- Severtsov, A.S. and Surova, G.S. 1979b. [Influence of predators on *Rana temporaria* population]. – *Zoologichesky Zhurnal* 58 (9): 1374-1379 (in Russian).
- Severtsov, A.S. and Surova, G.S. 1988. [Factors limiting brown frogs population number]. – In: *Ekologiya Populyacii*. Novosibirsk: 109-110 (in Russian).
- Severtsov, A.S. and Surova, G.S. 1989. [Dynamics of brown frogs population number in Moscow Province]. – In: *Zemnovodnye i Presmykayushchiesya Moskovskoi Oblasti*. Moscow: 110-120 (in Russian).
- Scheller, W.G. 1995. The sky above and the mud below. – *Sanctuary* 34 (4): 18-20.
- Schlue, W.R. 1976. Sensory neurons leech central nervous system: changes in potassium conductance and excitation threshold. – *J. Neurophysiol.* 39 (6): 1184-1192.
- Schmid, T.D. 1982. Survival of frogs in low temperature. – *Science* 215 (4533): 697-698.
- Schabetsberger, R. 1994. Gastric evacuation rates of adult and larval alpine newts (*Triturus alpestris*) under laboratory and field conditions. – *Freshwater Biol.* 31 (2): 143-151.
- Schreiber, E. 1912. *Herpetologia Europaea: Eine Systematische Bearbeitung der Amphibien und Reptilien, welche bisher in Europa Aufgefunden sind*. Jena: von G. Fisher Verl., 960 p.
- Shagaeva, V.G., Semenov, D.V. and Sytina, L.A. 1981. [On reproduction and development of *Hynobius keyserlingii*]. – In: *Problems of Herpetology*. Leningrad: 152-153 (in Russian).
- Shamanayev, Sh.Sh. and Brayalovsky, B.S. 1975. [Synthetic surface-active substances - specific pollutants of urban water pools]. – In: *Problemy Promyshlennykh Gorodov Urala*. Sverdlovsk: 115-116 (in Russian).
- Sharleman, E.V. 1917. [Notes about reptiles and amphibian fauna of Kiev vicinities]. – In: *Materialy k Poznaniyu Fauny Yugo-Zapadnoi Rossii* 2. Kiev: 1-17 (in Russian).
- Sharygin, S.A. 1980a. *Mikroelementy v Organizme Nekotorykh Amfibii i Reptilii i Ikh Dinamika pod Vliyaniem Antropogennykh Faktorov* [Microelements in Organisms of Some Amphibians and Reptiles and Their Dynamics Under Influence of Anthropogenic Factors]. – Ph.D. Diss. Abstr. Sverdlovsk: Institute of Plant and Animal Ecology USSR Academy of Sciences, Sverdlovsk, 24 p. (in Russian).
- Sharygin, S.A. 1980b. [The contents of microelements in *Rana arvalis* organism]. – In: *Vid i Ego Produktivnost v Areale*. Vilnius: 78-80 (in Russian).
- Sharygin, S.A. and Ushakov, V.A. 1979. [Amphibians and reptiles in large cities]. – In: *Ekologo-Faunisticheskie Issledovaniya v Nechernozemnoi Zone RSFSR* 2. Saransk: 83-96 (in Russian).
- Shchupak, E.L. 1970a. *Ekologiya i Biologicheskaya Produktivnost Populyatsii Ostromordoi Lyagushki Rana arvalis Nilss.* [Ecology and Biological Productivity *Rana arvalis*

- Populations]. – Ph.D. Diss. Abstr., Sverdlovsk: Institute of Plant and Animal Ecology, USSR Academy of Sciences, 21 p (in Russian).
- Shchupak, E.L. 1970b. [Dynamics of biological productivity in *Rana arvalis* populations]. – *Ekologiya* (Sverdlovsk) (1): 83-86 (in Russian).
- Shchupak, E.L. 1973. [Experimental study of moor frog population ecological structure]. – *Ekologiya* (Sverdlovsk) (1): 54-59 (in Russian).
- Shchupak, E.L. 1977. [Mid-dorsal stripe inheritance of *Rana arvalis*]. – In: *Informatsionnye Materialy Instituta Ekologii Rastenii i Zhivotnykh*. Sverdlovsk: 36 (in Russian).
- Shchupak, E.L. and Ishchenko, V.G. 1981. [To the genetics of colour polymorphism in *Rana arvalis* 1. Light dorso-medial stripe]. – In: *Herpetol. Investigations in Siberia and the Far East*. Leningrad: 128-132 (in Russian).
- Shchupak, E.L. and Gatiyatullina, E.Z. 1987. [Intrapopulation variability of *Rana arvalis* egg size]. – In: *Vliyaniye Usloviy Sredy na Dinamiku Struktury i Chislennosti Populyatsii Zhivotnykh*. Sverdlovsk: 65-73 (in Russian).
- Shitova, E.G. 1981. [Influence of car transport on fauna of Pushchino vicinities]. – In: *Ekologiya Malogo Goroda. Pushchino*: 118-124 (in Russian).
- Shklyar, T.F., Blyakhman, F.A. and Vershinin, V.L. 1999. [Specificity of miocard contractility in amphibians populations of urbanized territories]. – In: *Novoe v Ekologii i Bezopasnosti Zhiznedeyatel'nosti 3*. St. Petersburg: 52 (in Russian).
- Shklyar, T.F. and Vershinin, V.L. 2000. [Physiological specificity of amphibians populations in urbanized territories]. – In: *Ekopolis-2000. Ekologiya i Ustojchivoe Razvitiye Goroda*. Moscow: 182-183 (in Russian).
- Shvarts, S.S. 1948. [On the amphibians specific role in forest biocenosis in connection with the problem on their estimation from the point of view of their importance for man]. – *Zoologichesky Zhurnal* 27 (5): 441-445 (in Russian).
- Shvarts, S.S. 1954. [Microelement influence on animals in natural conditions of ore deposit field]. – *Trydy Biogeokhimmicheskoi Laboratorii Akademii Nauk SSSR* 10: 76-81 (in Russian).
- Shvarts, S.S. 1967. [Modern problems of the evolutionary theory (On the change of relative role of leading evolutionary factors during the organic world development)]. – *Voprosy Filosofii* (10): 143-153 (in Russian).
- Shvarts, S.S. 1969. *Ehvoljucionnaya Ekologiya Zhivotnykh*. [Evolutionary Ecology of Animals]. Sverdlovsk, 200 p (in Russian).
- Shvarts, S.S. 1972a. [Metabolic regulation of animal growth and development at population and organism levels]. – *Izvestiya Akademii Nauk SSSR, Seriya Biologicheskaya* (6): 822-835 (in Russian).
- Shvarts, S.S. 1973. [Ecological bases of biosphere conservation]. – *Vestnik Akademii Nauk SSSR* (9): 35-45 (in Russian).
- Shvarts, S.S. 1973. [Evolutionary biology]. – *Vestnik Akademii Nauk SSSR* (9): 11-21 (in Russian).

- Shvarts, S.S. 1974b. [Problems of human ecology]. – Voprosy Filosofii (9): 102-110 (in Russian).
- Shvarts, S.S. 1975. The flow of energy and matter between trophic levels (with special reference to the higher levels). – In: Unifying concepts in ecology. Publishers, The Hague and Centre for agricultural publishing and documentation, Wageningen. Ed. van Dobben W.H. et al.: 50-60.
- Shvarts, S.S. 1976a. [Evolution of biosphere and ecological forecasting]. – Vestnik Akademii Nauk SSSR (2): 61-71 (in Russian).
- Shvarts, S.S. 1976b. [Theoretical fundamentals of global ecological forecasting]. – Vsestoronniy Analiz Okruzhayushchei Prirodnoi Sredy. Leningrad: 181-191 (in Russian).
- Shvarts, S.S. 1977. The evolutionary ecology of animals. Studies in Soviet science. New York and London. Consultant Bureau, 292 p.
- Shvarts, S.S. 1980. Ekologicheskie Zakonomernosti Ehvolutsii [Ecological Regularities Of Evolution]. Moscow: Nauka Publ., 277 p (in Russian).
- Shvarts, S.S., Smirnov, V.S. and Dobrinskii, L.N. 1968. Metod Morfofiziologicheskikh Indikatorov v Ekologii Nazemnykh Pozvonochnykh [Method of Morphophysiological Indicators in Terrestrial Vertebrates Ecology]. Sverdlovsk, 387 p (in Russian).
- Shvarts, S.S. and Ishchenko, V.G. 1968. [Genetic structure dynamics in moor frog populations]. – Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii 73 (4): 127-134 (in Russian).
- Shvarts, S.S. and Pyastolova, O.A. 1970a. [Regulators of amphibian larvae growth and development]. – Ekologiya (Sverdlovsk) (1): 77-82 (in Russian).
- Shvarts, S.S. and Pyastolova, O.A. 1970b. [Regulators of amphibian larval growth and development]. – Ekologiya (Sverdlovsk) (2): 38-54 (in Russian).
- Simberloff, D. 1983. What a species needs to survive. – Nature Conserv. News. 33 (6): 18-22.
- Simms, C. 1969. Indications of the decline of breeding amphibians at an isolated pond in marginal land 1954-1967. – Brit. J. Herpetol. 4 (4): 93-96.
- Sinsch, U., Sommersberg, W. and Neumann, D. 1980. Die Amphibien der Sudlichen Drever Heide im Kreis Duren. – Decheniana. 133: 144-148.
- Skokova, N.N. and Lobanov, V.A. 1973. [Influence of 2,4 D butil ether on amphibians]. – In: Nauchnye Osnovy Okhrany Prirody 2. Moscow: 79-86 (in Russian).
- Smirina, E.M. 1980. [On growth rate and survival in *Rana temporaria* during the first years of life]. – Zoologicheskyy Zhurnal 59 (12): 1831-1840 (in Russian).
- Smith, D.C. 1983. Factors affecting tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. – Ecology 64 (3): 501-510.
- Smith, D.C. 1987. Adult recruitments in chorus frogs: effects of size and dose at metamorphosis. – Ecology 68 (2): 344-350.
- Smith, D.C. and Fretwell, S.D. 1974. The optimal balance between size and number of offspring. – Amer.Natur. 108: 499-506.

- Smith-Gill, S.J. and Berven, K.A. 1979. Predicting amphibian metamorphosis. – *Amer. Natur.* 113: 563-585.
- Straalen, N.M.van and Wensen, J.van 1986. Heavy metal content of forest litter arthropods as related to body size and trophic level. – *Environ. Pollut.* 42: 209-221.
- Strelkov, E.I. 1964. [On the ecology and significance of amphibians and reptiles of West Siberian plain taiga]. – In: *Uchenye Zapiski Tomskogo Gosudarstvennogo Pedagogicheskogo Instituta* 21: 93-105.
- Surova, G.S. 1988. [Ontogenetic mechanisms of brown frogs larval populations stability maintenance]. – In: *Problemy Evolyutsii*. Moscow: 40-41.
- Surova, G.S. 1988. [Environmental and hereditary components in the ontogenetic rates in *Rana temporaria* and *R. arvalis* larvae]. – *Zoologicheskyy Zhurnal* 67 (3): 396-405 (in Russian).
- Surova, G.S. and Cherdantsev, V.G. 1987. [Embryonic morphs in populations of brown frogs: egg sizes and larval growths rates in *Rana temporaria* and *R. arvalis* in the suburbs of Moscow]. – *Zoologicheskyy Zhurnal* 66 (12): 1864-1872 (in Russian).
- Surova, G.S. and Svertsov, A.S. 1988. [Influence of predators on brown frogs larvae in conditions of experiment]. – *Zoologicheskyy Zhurnal* 67 (10): 1509- 1518 (in Russian).
- Syuzumova, L.M. 1978. [Influence of ecological factors on amphibian larval stability to poisons]. – In: *Eksperimentalnaya Ekologiya Nizshikh Pozvonochnykh*. Sverdlovsk: 57-71 (in Russian).
- Syuzumova, L.M. 1979. [On the problem of the role of population mechanisms in formation of group morphophysiological features in amphibians]. - In: *Populyatsionnye Mekhanizmy Dinamiki Chislennosti Zhivotnykh*. Sverdlovsk: 75-88 (in Russian).
- Syuzumova, L.M. 1985. [Influence of the ecological factors on development and limb regeneration of *Rana arvalis* larvae on the background of thyroid function inhibition by vitamin A]. – In: *Ekologicheskie Aspekty Skorosti Rosta i Razvitiya Zhivotnykh*. Sverdlovsk: 85-98 (in Russian).
- Syuzumova, L.M., Ivanova, N.L. and Grebennikova, S.I. 1987. [The role of larval feeding and group density in formation of morphophysiological specificity of *Rana arvalis* groups]. – In: *Vliyanie Uslovii Sredy na Dinamiku Struktury i Chislennosti Populyatsii Zhivotnykh*. Sverdlovsk: 26-39 (in Russian).
- Taban, C.H., Cathieni, M. and Burcard, P. 1982. Changes in newt brain caused by Zinc water pollution. – *Experientia* 38 (6): 683-685.
- Tagirova, V.T. 1978. [Amphibians and reptiles of Preamuria cultural landscapes]. – In: *Gerpetofauna Dalnego Vostoka i Sibiri*. Vladivostok: 31-33 (in Russian).
- Takahashi, H. and Iwasawa, H. 1989. Clutch size and egg size variations in salamanders: traits of the variations in some levels of biological organization. – In: *Curr. Herpetol. East Asia*. Kyoto: 282-291.
- Talvi, T. 1993. Naturally occurring limb abnormalities in anurans of the Estonia. – In: 7-th Ord. Gen. Meet.Soc. Eur Herpetol. Progr. and Absr. Barcelona: 124.

- Tarasenko, S.N. 1981. [Haematological aspects of adaptation of *Rana ridibunda* to extreme conditions of industrial pollution of environment]. – In: Problems of Herpetology. Leningrad: Nauka: 129-130 (in Russian).
- Tarasenko, S.N. and Tarasenko, S.V. 1988. [Comparative characterization of tailless amphibian blood parameters in relation to the degree of anthropogenic transformation of ecosystem]. – In: Vid i Ego Produktivnost v Areale. Vilnius: 137-138 (in Russian).
- Tarkhnishvili, D.N. and Kuzmin, S.L. 1989. [On hierarchical structure of the ecological niche: seasonal and age variability of salamander food spectra]. – Ekologiya (Sverdlovsk) (1): 28-34 (in Russian).
- Taylor, D.H., Steele, C.W. and Strickler-Shaw, S. 1990. Responses of green frog (*Rana clamitans*) tadpoles to lead-polluted water. – Environ. Toxicol. and Chem. 9 (1): 87-93.
- Terentjev, P.V. 1950. Lyagushka. [The Frog]. Moscow: Sovetskaya Nauka Publ., 354 p (in Russian).
- Terentjev, P.V. and Chernov, S.A. 1949. Opredelitel zemnovodnykh i presmykajushchikhsya [Guide to Amphibians and Reptiles]. Moscow: Sovetskaya Nauka Publ., 339 p (in Russian).
- Tereshin, S. Yu. 1979. [Comparative characteristic of Moltaevo Lake components]. – In: Aktualnye Voprosy Fizioterapii i Kurortologii v Usloviyakh Zapadnoi Sibiri. Tyumen: 41-42 (in Russian).
- Tereshin, S. Yu., Datsun, L.B. and Volkova, N.A. 1981. [Problems of sapropel biological activity]. – In: Problemy Ispolzovaniya Sapropeli v Narodnom Khozyaistve. Minsk: 32-34 (in Russian).
- Tereshin, S. Yu. and Vershinin, V.L. 1989. [Influence of urban environmental pollution on Sodium balance at amphibians]. – In: Aktualnye Problemy Ekologii: Ekologicheskie Sistemy v Estestvennykh i Antropogennykh Usloviyakh. Sverdlovsk: 91-92 (in Russian).
- Testov, B.V. 1993. Vliyanie Radioaktivnogo Zagryazneniya na Populyatsii Myshevidnykh Gryzunov [Influence of Radioactive Pollution on Mice Rodents Populations]. – Dr. Sc. Diss. Abstr., Perm, 48 p. (in Russian).
- Thatcher, T. 1992. Thoughts on animals in captivity and other and other related matters. – Brit.J.Herpetol. Soc. Bull. (40): 5-6.
- Timofeev-Ressovsky, N.V. 1958. [Microevolution, elementary phenomena: material and factors of evolutionary process]. – Botanicheskii Zhurnal 43 (3): 317-336 (in Russian).
- Timofeev-Ressovsky, N.V., Yablokov, A.V. and Glotov, N.V. 1973. Ocherk Ucheniya o Populyatsii. [Account of the Population Doctrine]. Moscow. Nauka Publ., 278 p (in Russian).
- Tokar, V.I., Zhavoronkov, A.A. and Shcherbakov, S.V. 1991. Ftor i Ehndokrinnaya Sistema [Fluoride and Endocrine System]. Novosibirsk: Nauka Publ., 193 p (in Russian).
- Toporkova, L. Ya. 1966. [Note on amphibian ecology of Southern Transuralia]. – In: Uchenye Zapiski Uralskogo Universiteta, Seriya Biologicheskaya 3: 90-102 (in Russian).

- Toporkova, L. Ya. 1973. [Amphibians and reptiles of the Urals]. – In: Fauna Evropeiskogo Severa, Urala i Zapadnoi Sibiri. Sverdlovsk: 84-117 (in Russian).
- Toporkova, L. Ya. 1977. [Influence of human activity on amphibian distribution]. – In: Problems of Herpetology. Leningrad: 204-205 (in Russian).
- Toporkova, L. Ya. 1978. [New element in herpetofauna of the mountain taiga zone of Middle Urals]. – In: Fauna i Ekologiya Zhivotnykh UASSR i Prilezhashchikh Raionov 2. Izhevsk: 63-65 (in Russian).
- Toporkova, L. Ya. 1985. [Formation of *Rana ridibunda* population]. – In: Problems of Herpetology. Leningrad: 212 (in Russian).
- Toporkova, L. Ya., Bogolyubova, T.V. and Khafizova, R.G. 1979. [To the ecology of *Rana ridibunda*, introduced in the ponds of mountain-taiga zone of the Middle Urals]. – In: Fauna Urala i Evropeiskogo Severa. Sverdlovsk: 108-115 (in Russian).
- Travis, J. 1984. Anuran size at metamorphosis: experimental test of a model based on intraspecific completion. – Ecology 65 (4): 1155-1160.
- Trubetskaya, E.A. 1994. [Experimental study of embryonic and larval survival in two brown frog species in the environment polluted by detergents]. – Ekologiya (Ekaterinburg) (3): 87-93 (in Russian).
- Tyler, M.J. 1989. Australian Frogs. Penguin Books Australia Ltd.: 163-187.
- Uehlinger, V. and Beauchemin, M.L. 1968. Loedeme sous-cutane, oedema (oe), une maladie hereditaire de la pre- et post- metamorphose chez le batracien *Xenopus laevis*. – Rev. Suisse Zool. 75: 697-706.
- Usachev, V.L., Tarasov, O.V. and Semenov, D.V. 1993. [Amphibian and reptile populations on the territory of East Uralian Radioactive trace]. – In: Ekologicheskie Posledstviya Radioaktivnogo Zagryazneniya na Yuzhnom Urale. Moscow: 192-194 (in Russian).
- Ushakov, V.A. and Garanin, V.I. 1973. [Amphibians and reptiles in settlements]. – In: Problems of Herpetology. Leningrad: 185-187 (in Russian).
- Ushakov, V.A., Lebedinsky, A.A. and Grefner, N.M. 1982. [The analysis of size and age structure in *Rana temporaria* population on urbanized territory]. – Vestnik Zoologii. (2): 67-68 (in Russian).
- Van Gelder, J.J. 1973. A quantitative approach to the mortality resulting from traffic in a population of *Bufo bufo*. – Oecologia. 13 (1): 93-95.
- Van Gelder, J.J. and Grooten, P.H. 1992. The use of small landscape elements by newts. – In: Proc. Sixth Ord. Meet. Eur. Herpetol. Budapest: 177-181.
- Van Valen, L. 1974. A natural model for the origin of some higher taxa. – J. Herpetol. 8: 109-121.
- Vavilov, N.I. 1967. Zakon Gomologichnykh Ryadov v Nasledstvennoi Izmenchivosti: Linneevskij Vid kak Sistema [Law of Homological Rows in Hereditary Variability: Linnaean Species as a System]. Leningrad: Nauka Publ., 1-92 (in Russian).
- Vernadsky, V.I. 1928. Eholjuciya vidov i zhivoe veshchestvo [Species evolution of and alive substance]. – Priroda (Moscow) (3): 227-262.

- Vernadsky, V.I. 1931. [On the conditions of life appearance on the Earth]. – *Izvestiya Akademii Nauk SSSR* 7 (5): 633-653 (in Russian).
- Vernadsky, V.I. 1965. *Khimicheskoe Stroenie Biosfery Zemli i Ee Okruzheniya* [Chemical Structure of the Earth and Its Surroundings]. Moscow: Nauka Publ., 374 p (in Russian).
- Vernadsky, V.I. 1977. *Razmyshleniya Naturalista*. (Kn.2: Nauchnaya Mysl kak Planetarnoe Yavlenie) [Thoughts of Naturalist. (Book 2: Scientific Thought as Planetary Phenomenon)]. Moscow: Nauka Publ.: 18-63 (in Russian).
- Vernadsky, V.I. 1978. *Zhivoe Veshchestvo* [Live Substance]. Moscow, 358 p. (in Russian).
- Vershinin, V.L. 1980a. [Distribution and amphibians species composition of Sverdlovsk city area]. – In: *Informatsionnye Materialy Instituta Ekologii Rastenii i Zhivotnykh*. Sverdlovsk: 5-6 (in Russian).
- Vershinin, V.L. 1980b. [Preliminary estimation of anthropogenic factors influence on amphibians of Sverdlovsk]. – In: *Problemy Ekologii, Racionalnogo Ispolzovaniya i Okhrany Prirodnykh Resursov na Urale*. Sverdlovsk: 117-118 (in Russian).
- Vershinin, V.L. 1981. [*Rana ridibunda* in a city boundaries of Sverdlovsk]. – In: *Problems of Herpetology*. Leningrad: 32-33 (in Russian).
- Vershinin, V.L. 1982a. [Urban amphibian groups as criterion of the estimation of small ponds condition]. – In: *Problemy Ekologii Pribaikalya 1*. Irkutsk: 19-22 (in Russian).
- Vershinin, V.L. 1982b. [The status of the groups of Amphibia in Sverdlovsk]. – In: *Voprosy Ekologii*. Sverdlovsk: 34 (in Russian).
- Vershinin, V.L. 1983a. [Larval and froglets mortality in brown frogs *Rana arvalis* and *R. temporaria* depending on a degree of urbanization]. – In: *Ekologiya, Chelovek i Problemy Okhrany Prirody*. Sverdlovsk: 89 (in Russian).
- Vershinin, V.L. 1983b. *Vidovoi Sostav i Biologicheskie Osobennosti Amfibii Ryada Promyshlennykh Gorodov Urala* [Species Composition and Biological Peculiarities of Amphibia in Some Industrial Cities of Ural]. – Ph. D. Diss. Sverdlovsk: Inst. Plant and Anim. Ecol. Uralian Sci. Center Acad. Sci. USSR, 199 p. (in Russian).
- Vershinin, V.L. 1984. [Feeding of *Rana temporaria* and *R. arvalis* juvenile during the metamorphosis]. – In: *Vid i Ego Produktivnost v Areale 5: Voprosy Gerpetologii*. Sverdlovsk: 9-10 (in Russian).
- Vershinin, V.L. 1985a. [Materials on growth and development of amphibians in conditions of a large city]. – In: *Ekologicheskie Aspekty Skorosti Rosta i Razvitiya Zhivotnykh*. Sverdlovsk: 61-75 (in Russian).
- Vershinin, V.L. 1985b. [Dynamics of *Rana arvalis* larvae and froglets number in the conditions of industrial city]. – In: *Problems of Herpetology*. Leningrad: 46-47 (in Russian).
- Vershinin, V.L. 1987a. [Adaptive peculiarities of *Rana arvalis* groups in the conditions of a large city]. – *Ekologiya (Sverdlovsk)* (2): 56-50 (in Russian).
- Vershinin, V.L. 1987b. [Some features of phenetic structure of *Rana arvalis* groups in the conditions of industrial city]. – In: *Vliyanie Uslovij Sredy na Dinamiku Struktury i Chislennosti Populyatsii Zhivotnykh*. Sverdlovsk: 74-79 (in Russian).

- Vershinin, V.L. 1987c. [Influence of isolation on morphological aberrations frequency in urban amphibians]. – In: *Ekologicheskie Sistemy Urala: Izuchenie, Okhrana, Eksploatatsiya*. Sverdlovsk: 11 (in Russian).
- Vershinin, V.L. 1987d. [Dynamics of brown frog juveniles trophic relations in natural and anthropogenic communities]. – In: *Ekologicheskie Mekhanizmy Preobrazovaniya Populyatsii Zhivotnykh pri Antropogennykh Vozdeistviyakh*. Sverdlovsk: 15 (in Russian).
- Vershinin, V.L. 1988. [Iris depigmentation frequency in moor frogs urban groupings]. – In: *Ekologiya Populyatsii 1*. Novosibirsk: 89-91 (in Russian).
- Vershinin, V.L. 1989a. [Morphological anomalies in urban amphibians]. – *Ekologiya (Sverdlovsk)* (3): 58-66 (in Russian).
- Vershinin, V.L. 1989b. [Variability of eggs number in *Hynobius keyserlingii* clutches in recreation zone]. – In: *Problems of Herpetology*. Kiev: 45-46 (in Russian).
- Vershinin, V.L. 1990. Features of amphibian populations of an industrial city. – In: *Urban Ecological Studies in Central and Eastern Europe*. Warszawa: 112-121.
- Vershinin, V.L. 1990a. [Level of recreation pressure and status of populations of *Hynobius keyserlingii*]. – In: *Zhivotnye v Usloviyakh Antropogennogo Landshafta*. Sverdlovsk: 10-18 (in Russian).
- Vershinin, V.L. 1990b. [Abnormal amphibians spawns in territory of urban agglomeration]. – *Ekologiya (Sverdlovsk)* (3): 61-66 (in Russian).
- Vershinin, V.L. 1990c. [On frequency of striata morph in *Rana ridibunda* in urban territory]. – In: *Fenetika Populyatsii*. Moscow: 44-45 (in Russian).
- Vershinin, V.L. 1990d. [*Rana ridibunda* distribution in Sverdlovsk]. – *Ekologiya (Sverdlovsk)* (2): 67-71 (in Russian).
- Vershinin, V.L. 1990e. [Methodology of bioindication characteristics of amphibians]. – In: *Bioindikatsiya Nazemnykh Ekosistem*. Sverdlovsk: 3-15 (in Russian).
- Vershinin, V.L. 1991. [Intensity of *Rana arvalis* juveniles pressure on invertebrate animals depending on the level of anthropogenic influence]. – In: *Problemy Ratsionalnogo Ispolzovaniya, Vosproizvodstva i Ekologicheskogo Monitoringa Lesov*. Sverdlovsk: 25-26 (in Russian).
- Vershinin, V.L. 1992. [Morphophysiological features of brown frogs juveniles in urban territories]. – In: *Zhivotnye Antropogennykh Landshaftov*. Ekaterinburg: 3-11 (in Russian).
- Vershinin, V.L. 1995a. [Complex of amphibian species in ecosystems of a big industrial city]. – *Ekologiya (Ekaterinburg)* (4): 299-306 (in Russian).
- Vershinin, V.L. 1995b. [*Rana arvalis* fecundity depending on a degree of anthropogenic influence]. – In: *Ustojchivoe Razvitie: Zagryaznenie Okruzhayushchei Sredy 1 Ekologicheskaya Bezopasnost 2*. Dnepropetrovsk: 50 (in Russian).
- Vershinin, V.L. 1995c. [Feeding dynamics of one-summer-old brown frogs during the end of metamorphosis]. – *Ekologiya* (1): 68-75 (in Russian).
- Vershinin, V.L. 1996. [*Triturus vulgaris* in urban ecosystems]. – *Ekologiya (Ekaterinburg)* (2): 58-62 (in Russian).

- Vershinin, V.L. 1997. *Ekologicheskie Osobennosti Populyatsii Amfibii Urbanizirovannykh Territorii* [Ecological Features of Amphibian Populations on Urbanized Territories]. – Dr. Sc. Diss. Abstr., Ekaterinburg, Institute of Plant and Animal Ecology, Russian Academy of Sciences, 47 p. (in Russian).
- Vershinin, V.L. and Gatiyatullina, E.Z. 1994. [Population variability of egg size in *Rana arvalis* depending on the level of urbanization]. – *Ekologiya* (Ekaterinburg) (5): 95-100 (in Russian).
- Vershinin, V.L. and Kamkina, I.N. 2001. [Proliferative activity of corneal epithelium and specific features of morphogenesis in postmetamorphic *Rana arvalis* in urbanized areas]. – *Ekologiya* (Ekaterinburg) (4): 297-302 (in Russian).
- Vershinin, V.L. and Krinitsyn, S.V. 1985. [Density in moor frog groupings under urbanization degree]. – In: *Problemy Ekologicheskogo Monitoringa i Nauchnye Osnovy Okhrany Prirody na Urale*. Sverdlovsk: 9-10 (in Russian).
- Vershinin, V.L. and Tereshin, S.Yu. 1989. [On the opportunity of test on a functional condition of excitable tissues of amphibians for environmental quality estimation]. – In: *Aktualnye Problemy Ekologii: Ekologicheskie Sistemy v Estestvennekh i Antropogennykh Usloviyakh*. Sverdlovsk: 15-16 (in Russian).
- Vershinin, V.L. and Tereshin, S.Yu. 1991. [Features of *Rana arvalis* excitable tissues in the conditions of urbanization]. – In: *Ocherki po Ekologicheskoi Diagnostike*. Sverdlovsk: 60-67 (in Russian).
- Vershinin, V.L. and Tereshin, S.Yu. 1992. [Influence of urban environmental pollution on the oxygen consumption by amphibians]. – In: *Novye Metody Teoreticheskoi i Prakticheskoi Fiziologii*. Ekaterinburg: 9-10 (in Russian).
- Vershinin, V.L. and Tereshin, S.Yu. 1996. [Use of physiological parameters of amphibians in ecological monitoring]. – In: *Strategicheskie Napravleniya Ekologicheskikh Issledovaniy na Urale i Ekologicheskaya Politika*. Ekaterinburg: 10 (in Russian).
- Vershinin, V.L. and Tereshin, S.Yu. 1999. [Physiological parameters of amphibians in ecosystems of urbanized territories]. – *Ekologiya* (Sverdlovsk) (4): 283-287 (in Russian).
- Vershinin, V.L. and Toporkova, L.Ya. 1981. [Amphibians of urban landscapes]. – In: *Fauna Urala i Evropejskogo Severa*. Sverdlovsk: 48-56 (in Russian).
- Vershinin, V.L. and Trubetskaya, E.A. 1992. [Brown frog mortality in embryonic, larval and postmetamorphic period at different levels of anthropogenic influence]. – In: *Zhivotnye v Usloviyakh Antropogenogo Landshafta*. Ekaterinburg: 12-20 (in Russian).
- Vershinin, V.L. and Volegova, E.V. 1993. [The analysis of size-age structure of mature *Rana temporaria* on the territory of industrial city]. – In: *Zooindikatsiya i Ekotoksikologiya Zhivotnykh v Tekhnogennykh Landshaftakh*. Dnepropetrovsk: 113 (in Russian).
- Viegas, A.M., Rei, M.A., Vasconcolos, S., Andrade, V., Paulo, O.S., Rosa, H. and Crespo, E.G. 1993. Lipids and their relationship with the reproductive cycles in two species of *Rana*. – In: 7-th Ord. Gen. Meet.Soc. Eur.Herpitol. Barcelona: 130.

- Voigt, M. 1991. On the effects of crowding and pollution in tadpoles of the brown-striped marshfrog (*Lymnodynastes peroni*). – Herpetofauna 21 (1): 25-34.
- Voitkevich, A.A. 1961. Le development des extremitaires sunumeraires chez les amphibiens. – Bull. Biol. France Belgique. 95: 569-600.
- Voronov, A.G. 1968. [Role of the animal population in formation of biocenosis structures]. – Byulleten Moskovskogo Obshchestva Ispytatelei Prirody: Otdel Biologicheskii 73 (1): 85-92 (in Russian).
- Voronova, L.D., Golichenkov, V.A., Popov, D.V., Kalistratova, E.N. and Sokolova, Z.A. 1983. [Reactions of amphibian larvae pigment system on small concentration of some pesticides]. – In: Problemy Ekologicheskogo Monitoringa i Modelirovaniya Ekosistem. Leningrad 6: 77-90 (in Russian).
- Wassersug, R.J. 1994. Ecological versus endocrinological factors influencing amphibian metamorphosis. – In: Second World Congr. of Herpetol. Adelaide: 267-268.
- Wassersug, R.J. and Seibert, E.A. 1975. Behavioral responses of amphibia larvae to variation in dissolved oxygen. – Copeia. (1): 86-103.
- Werner, E.E. 1986. Amphibian metamorphosis growth rate, predation risk, and optimal size at transformation. – Amer.Natur. 128 (3): 319-341.
- Wheater, C.P. 1986. Prey-size and parasite relationship in the common toad *Bufo bufo*. – Herpetol. J. 1 (2): 62-66.
- Whitaker, J.O., Maser, Ch., Storm, R.M. and Beatty, J.J. 1986. Food habits of Clouded Salamanders (*Aneides ferreus*) in Curry County, Oregon (Amphibia: Caudata: Plethodontidae). – Gr. Basin. Natur. 46 (2): 81-86.
- Wilbur, H.M. 1977a. Propagule size, number and dispersion pattern in *Ambistoma* and *Asclepias*. – Amer. Natur. 111: 43-68.
- Wilbur, H.M. 1977b. Interaction of food level and population density in *Rana sylvatica*. – Ecology 58 (1): 206-209.
- Wilbur, H.M. 1980. Complex life cycles - Ann. Rev. Ecol.Syst. 11: 67-93.
- Williamson, I. and Bull, C.M. 1989a. The significance of egg size variation in a population of the frog *Ranidella signifera*. – In: 1st World Congr. Herpetol. Abstr. Canterbury.
- Williamson, I. and Bull, C.M. 1989b. Life history variation in a population of the Australian frog *Ranidella signifera*: Egg size and early development. – Copeia. (2): 349-356.
- Wittouck, P. 1980. Lcedeme sous-cutane, cedema (CE), une malade de la postmetamorphose, observe chez tetrards de *Rana esculenta*. - Bull. Soc. zool. France. 105 (4): 545-550.
- Wright, S. 1964. Evolution organic. – In: Encyclop. Brit. Ld. 8: 917-929.
- Yablokov, A.V. 1987. Populyatsionnaya Biologiya [Population Biology]. Moscow: Vysshaya Shkola Publ., 303 p (in Russian).
- Yablokov, A.V. and Yusufov, A.G. 1989. Evolyutsionnoe Uchenie (Darvinizm) [The Evolutionary Doctrine (Darwinism)]. Moscow: Vysshaya Shkola Publ., 335 p (in Russian).

- Yacobs, J. 1975. Diversity, stability and maturity in ecosystems influenced by human activities. – In: *Unifying Concepts in Ecology*. Wageningen: 187-207.
- Yakovlev, V.A. 1990. [On the ecology of *Rana ridibunda* on Altai]. – *Ekologiya (Sverdlovsk)* (1): 67-71 (in Russian).
- Yanitsky, O.N. 1987. *Ekologicheskaya Perspektiva Goroda*. [Ecological Perspective of City]. Moscow, 278 p (in Russian).
- Zaffaroni, N.P., Zavanella, T.E. and Arias, E. 1989. Spontaneous skeletal malformation of the forelimbs in the adult crested newt. – *Herpetopathologia* 1 (1): 49-50.
- Zakharov, V.M. 1987. *Asimetriya Zhivotnykh*. [Animal Asymmetry]. Moscow: Nauka Publ., 216 p (in Russian).
- Zakharov, V.M. and Sergievskii, C.O. 1984. [Populational melanism in *Adalia bipunctata* as an example of technogenic evolution]. – In: *Vliyanie Promyshlennykh Predpriyatii na Okruzhayushchuyu Sredu*. Pushchino: 74-76 (in Russian).
- Zavadsky, K.M. 1973. *Razvitie Evoljucionnoi Teorii Posle Darvina (1859 – 1920-e Gody)* [Development of the Evolutionary Theory after Darwin (1859-1920 Years)]. Leningrad: Nauka Publ., 423 p (in Russian).
- Zavanella, T., Zaffaroni, N.P. and Arias, E. 1984. Abnormal limb regeneration in adult newts exposed to the fungicide Maneb 80. A histological study. – *J. Toxicol. and Environ. Health* 13 (4-6): 735-745.
- Zhukov, V.S. 1984. [Anthropogenic transformation of amphibian population in building area of KATEK]. – In: *Vid i Ego Produktivnost v Areale 5: Voprosy Gerpetologii*. Sverdlovsk: 17-18 (in Russian).
- Zhukov, V.S. 1989. *Antropogennaya Transformatsiya Naseleniya Nazemnykh Pozvonochnykh Lesostepi Nazarevskoi Kotloviny (Pticy, Melkie Mlekopitayushchie i Zemnovodnye)* [Anthropogenic Transformation of Forest Steppe Terrestrial Vertebrates of Nazarevskaya Hollow (Birds, Small Mammals and Amphibians)]. – Ph.D. Diss. Abstr., Novosibirsk, 22 p. (in Russian).
- Zhukova, T.I. 1978. [Influence of anthropogenic factors on number and structure of *Rana ridibunda* populations]. – In: *Antropogennoe Vozdeistvie na Prirodnye Kompleksy i Ekosistemy*. Volgograd: 93-104 (in Russian).
- Zhukova, T.I. 1979. [Green Toad juveniles feeding]. – In: *Gerpetologiya*. Krasnodar: 52-62 (in Russian)
- Zhukova, T.I. and Kubantsev, B.S. 1980. [Differences in *Rana ridibunda* gonads condition depending on a degree of anthropogenic influences on habitat]. – In: *Antropogennye Vozdeistviya na Prirodnye Kompleksy i Ekosistemy*. Volgograd: 51-56. (in Russian)
- Zhukova, T.I., Kubantsev, B.S. and Burlachenko, T.L. 1986. [Reaction in some *Rana ridibunda* populations on pesticide pollution of ponds]. – In: *Antropogennoe Vozdeistvie na Populyatsii Zhivotnykh*. Volgograd: 61-81 (in Russian).
- Zhukova, T.I., Kubantsev, B.S. and Peskova, T.Yu. 1990. [Morphological characterization of *Bombina orientalis* in Western Precaucasia in connection with anthropogenic

influence on its habitat]. – In: Fauna i Ekologiya Pozvonochnykh Zhivotnykh v Antropogennykh Usloviyakh. Volgograd: 38-45 (in Russian).

Zubakin, V.A., Abonosimova, E.V., Lavrinovich, T.E., Mishchenko, A.L., Oshanin, S.D. and Shitova, E.G. 1981. [Fauna of terrestrial vertebrates of Pushchino and its vicinities]. – In: Ekologiya Malogo Goroda. Pushchino: 118-124 (in Russian).