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A LOOK AT EVOLUTIONARY ECOLOGY OF YESTERDAY AND TODAY*

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This article discusses the scientific prerequisites, principal problems, current status, and prospects for future development of evolutionary ecology, a special scientific direction founded by Academician S. S. Shvarts in the early 1970s. The significance of the ecological guidepost present in the name "evolutionary ecology" is becoming clear precisely now, when the deep need for enrichment of evolutionary theory with ecological views and methodology has become obvious. It is suggested that, on the strength of the expected acceleration of microevolutionary transformations of animal, plant, and microorganism populations in conditions of intensifying anthropogenic pressure, evolutionary theory may unexpectedly become an applied field.

Academician S. S. Shvarts's last book was published in 1980: "Ecological Patterns of Evolution," which is a significantly supplemented version of his monograph "Evolutionary Ecology of Animals" that contains a number of new concepts and ideas. In these books, he formulated and substantiated a special direction of research that he called evolutionary ecology. In his article "Evolutionary ecology," S. S. Shvarts (1973b) defined the content of this scientific direction as follows: first, study of the origin and development of ecological adaptations of individual species and forms, and secondly, study of ecological patterns of the evolutionary process.

Within the framework of this direction, many works have now been performed on studying ecological adaptations to various environmental conditions, including extreme conditions: subarctic, high-mountain, arid, etc.; however, the basic task of evolutionary ecology consists in studying ecological patterns of the evolutionary process.

In connection with this, we cannot fail to remember the book of the famous ecologist E. Pianka "Evolutionary Ecology," which was republished in Russian (Pianka, 1981). The views developed in it differ fundamentally from domestic ideas about evolutionary ecology. Although the book is quite deep and multifaceted in content, and it covers the ideas of population ecology, community ecology, the theory of insular biogeography, and many others that have been developed for a long time by American ecologists very well, in our view it only deals with solution of evolutionary problems: it gives comparative results of the evolution of population adaptations — statics, not dynamics of evolutionary events. According to E. Pianka's ideas, the content of evolutionary ecology is reduced to using evolutionary concepts to explain population phenomena. On the contrary, S. S. Shvarts believed that evolutionary ecology is aimed at using population phenomena to study the evolutionary process. This shows the fundamental difference in the two directions and the closeness of the problems that they consider. Today these scientific directions closely supplement each other, although they have different aims.

In fact, we can consider a population as an object of investigation in the broad sense of the word. This is undoubtedly a productive and important scientific direction within the framework of population ecology proper and community ecology (when the interaction of populations of different species is considered). However, by itself it is still insufficient for development of evolutionary ideas. It is necessary to consider the population approach as a method of getting to know evolution. According to S. S. Shvarts, population thinking should be a tool for getting to know evolutionary patterns. Consequently, the ecological patterns of evolution are an object of investigation that already lies not within the bounds of population ecology, but evolutionary theory proper. Not so long ago, A. V. Yablokov's book "Population Biology" came out

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(1987), which, along with an abundance of the latest factual data, convincingly showed that the synthesis of population disciplines aimed at studying the evolutionary process, which S. S. Shvarts predicted more than 20 years ago, really does exist. Thus, we can consider that the core of evolutionary ecology has withstood the test of time.

It is important to emphasize that evolution is a deeply ecological process. The thesis about the ecological nature of evolution that evolutionary ecology introduces into the theory of evolution is fundamentally important. The Polish ecologist K. Petrusewicz (a colleague and close friend of S. S. Shvarts) more than once emphasized that the theory of evolution is an ecological theory. We will recall that the basic motivating factor of evolution, natural selection, is exclusively an ecological factor. Acting on phenotypes, it is ecologically mediated. An important factor of evolution, spatial isolation, is already ecological because each habitat on Earth is ecologically unique and forms its own vectorization of the pressure of selection. A factor distinguished by S. S. Chetverikov, population waves, is itself, as a problem of population dynamics, a division of population ecology.

In recent years, N. V. Glotov (1988) has written about the importance and even the unavoidability of an ecological-genetic synthesis for the further fruitful development of evolutionary theory. It seems to us that this is entirely valid, however we are apparently still far from a genuine, full-fledged synthesis, though there is no doubt that S. S. Shvarts laid one of the first bricks in the foundation of this new evolutionary synthesis. It was he who convincingly showed that population-genetic views on evolution alone are insufficient for description of it, and he believed that the "question of 'species-not species' is solved at the ecological level, not the physiological or genetic level."

The range of problems formulated by S. S. Shvarts within the framework of evolutionary ecology is very great, therefore we will dwell only on some of the most important points.

One of the tools of population analysis is the method of morphophysiological indicators created by S. S. Shvarts and his students (Shvarts et al., 1968). We will recall that it consists in quick evaluation of the physiological condition of animal populations according to the most important morphophysiological indices (relative weight of organs: the heart, kidneys, liver, adrenal gland, etc.), the parameters of which depend on the intensity of their functioning. These morphophysiological traits can serve as distinctive indicators of the condition of population groupings and make it possible to evaluate the reaction to changes in conditions that are not caught by other methods, and at the same time they are more integral than physiological indices.

We will note that the method of morphophysiological indicators immediately found many devotees who saw the next panacea in it. However, as was to be expected, some neophytes' rectilinear interpretation of changes in the relative weight of organs, their not always correct use of statistical methods, and numerous artifacts mostly obtained due to inaccuracy in separating functional age groups led to the appearance of negative and skeptical attitudes toward the method as a whole. The skepticism first showed up among physiologists, in view of certain zoologists' obvious errors in interpreting the results of their own measurements, and then among many ecologists. Of course, this does not mean that the method is not useful. On the contrary, the development of multivariate methods of statistics, and also the rapidly increasing availability of fast computers have made it possible, in a number of cases, not only to completely rehabilitate the method, but also to outline ways of its further use in evolutionary and population ecology.

The widespread use of this method and the enormous amount of data collected on many tens of species of vertebrates from various natural zones of our country have made it possible to formulate many important points of evolutionary ecology. The general fundamental pattern that, according to K. Petrusewicz, can be called Shvarts's ecological rule was revealed. It says that a species specialized in certain conditions is better adapted to the environment in comparison with any specialized intraspecific forms (subspecies, population) of species occurring over a wide range. The theoretical basis for this was the phenomenon known from ecological physiology that any change in environment directly or indirectly leads to a change in the ways in which an organism's energy balance is realized, and also that when it is necessary to intensify metabolism there is a relative (in relation to body weight) change in the weight of the organs that are most closely connected with this process. Consequently, in extreme habitat conditions forms not specialized in adaptation to them will change the ways of realizing their energy balance, and this will be accompanied by intensified metabolism of the organs most connected with it: the heart, kidneys, etc., which will be indirectly expressed in an increase in their relative weight.

Considerable data collected for subarctic populations and populations of moderate latitudes of many tens of species by S. S. Shvartz and his coworkers L. N. Dobrinskii, N. N. Danilov, V. N. Bol'shakov, V. G. Ishchenko, O. A. Pyastolova, V. S. Smirnov, L. M. Syuzyumova, and others confirmed this proposition. Analogous phenomena were found when mountain and plains populations of widespread species were compared with specialized mountain species (Bol'shakov, 1972). Autochthonous species (specialized arctic and mountain ones) are characterized by similar relative parameters of their heart, kidneys, and a number of other organs as are populations of widespread species of birds and mammals from moderate latitudes or plains. On the contrary, subarctic populations of widespread species are distinguished by an increase in the organs' relative weight or index. Thus, V. N. Bol'shakov (1972) showed that in the widespread plains species *Clethrionomys glareolus* and *C. rutilus* a sharp rise in the heart index is observed with an increase in elevation above sea level. However, in *C. frater (centralis)*, typical mountain inhabitants, the heart index is just as low as for individuals of plains populations of *C. glareolus* and *C. rutilus*. The heart index is particularly low for a representative of a genus of high-mountain large-eared voles *Alticola argentata*, silver vole, a typical mountain form close to red-backed voles. It is obvious that typical mountain species have a different way of adapting to high elevations than do widespread species (Bol'shakov, 1972).

The basic propositions of evolutionary ecology were based on a large set of analogous investigations.

Speciation is an adaptive process accompanied by the emergence of a qualitatively new relationship to the environment of the species being formed. The new species is distinguished by a qualitatively different type of metabolism and biochemical processes that is energetically more advantageous and efficient. A specialized subspecies or population does not yet possess these qualities and is adapted within the framework of possibilities of its inherent species. Adaptation of them is expressed in the form of morphofunctional compensation and is energetically more "expensive," and, consequently, less efficient. Therefore, an autochthonous species has no need to resort to intensification of metabolism, which is usually observed in widespread species at the limits of their range in extreme conditions for life.

Any population possesses unique features of adaptation characteristic of it alone. The process of speciation, in contrast to formation of intraspecific adaptations (microevolution), is accompanied by fundamental biochemical and tissue changes and leads to a qualitative change in energy relations with the environment.

One more very important part of evolutionary ecology is the idea of the spatial structure of a species. The main thesis of the synthetic theory of evolution (STE) says that only a population can be the elementary unit of evolution. On the other hand, abundant data provided by population ecology convincingly shows that a population is an elementary, autonomous, ecological, and biochorological unit of a species. According to S. S. Shvarts's definition, "a population is a form of a species' existence" (1980, p. 7). It functions as a unified whole, but this does not mean that it can be considered the smallest biochorological unit. Any intrapopulation grouping (family, aggregation of families, individual colony, etc.) does not possess the main property of a population: ecological independence, and cannot be a relatively autonomous whole commensurable with the time scale of microevolution. Only relatively constant populations meet the requirements imposed by population genetics and the theory of evolution. Understanding the complexity of a species' biochorological structure, one must nevertheless clearly take into account the evolutionarily significant boundary between intrapopulation groupings and populations, and also remember that, although intraspecific groupings themselves are not autonomous, they do create a population proper (a unified, independently functioning system) through interaction with each other. According to S. S. Shvarts's terminology, such intrapopulation groupings are called micropopulations. They are not capable of prolonged existence and function only as part of a whole. Thus, in evolutionary ecology a population acts not only as the elementary unit of evolution, but also as the sole elementary, autonomous, ecological unit. The evolutionary-ecological unity of a population is an important guidepost in creating the basic concept of evolutionary ecology.

A group of morphologically similar adjacent populations constitutes a geographic form. These populations are characterized by common morphological and ecological features that determine the specific nature of reaction of the geographic form or, in other words, subspecies to changes in the environment.

In connection with this, we will dwell on one more important thesis of evolutionary ecology, the idea of the irreversibility of microevolution. Evolutionary ecology proceeds from proposition that not every change in the genetic structure of a population can be equated to a microevolutionary event. Any changes in the environment cause a restructuring of the population, and transformation of its properties and, consequently, genetic structure. On the whole, this is an ordinary phenomenon. For example, the adaptation polymorphism found in the lady beetle *Adalia bipunctata*, and alternating seasonal changes in the frequency of occurrence of dark- and light-colored morphs in common hamster. Seasonal difference between the fall and spring generations of murine ephermeral rodents are widely known and are so contrasting in some cases that they are comparable with the spread of subspecies differences. All of these fairly widespread phenomena are of a pronounced homeostatic nature and reversible. They reflect the interrelation of changes in ecological-genetic structure against the background of which a population is manifested as an ecological-genetic unit.

The difference between homeostatic phenomena maintaining the dynamic equilibrium of a genetic structure and significant microevolutionary shifts in it is of a fundamental nature. Microevolution is the initial stage of the evolutionary process. The microevolutionary process is fundamentally distinguished from homeostatic changes in the genetic structure by the irreversibility of the populations' transformation. According to evolutionary ecology, the irreversibility of intraspecific transformations is determined not by morphophysiological and genetic features of the populations (degree of morphological differences, degree of genetic differentiation), but by their ecological features, i.e., by a change in the normal reaction to a change in the external environment. The specific morphogenetic reactions that make it impossible to return to the original form are created on this basis. According to S. S. Shvarts, microevolution is the process of formation of a population's irreversible adaptive reaction determining the specificity of its evolutionary fate. The forms in which the microevolutionary process materializes are subspecies. It is obvious that not every subspecies can become a species, but all species must pass through the subspecies stage in their individuation.

From these ideas, a scheme of intraspecific differentiation was formulated. It looks like this: directional homeostatic change in the genetic structure of a population — directional change in the population's structure — irreversible change in the population's genetic structure (microevolution or subspeciation) — speciation. This scheme and the propositions set forth above served as the basis for substatiating the theory of an evolutionary-ecological mechanism of speciation. Its general propositions were formulated by S. S. Shvarts. The sequence of speciation from the standpoint of evolutionary ecology is:

1. Development of a population in a distinctive environment.
2. Emergence of irreversible morphophysiological features that alter the population's relationship to the environment.
3. Progressive adaptation. Development of tissue adaptations.
4. Reproductive isolation on the basis of tissue incompatibility.
5. Speciation.

S. S. Shvarts believed that the motive forces of speciation are not fundamentally different from the mechanisms of intraspecific differentiation. These processes differ in their results, but not in their motive forces. In contrast to intraspecific transformations, in the process of speciation selection evaluates not only morphofunctional perfection, but also the energy cost of adaptations. This circumstance leads to formation of a new species. K. Petrusewicz, in discussing the problem, fully supported this point of view: "speciation is a distinct stage of adaptation, formation of a new, energetically more economic adaptation; therefore, specialized species are always better adapted than specialized intraspecific forms" (1979, p. 4).

We have briefly discussed the significant divisions of evolutionary ecology, intentionally not going into detail and not referring to specific sources. The most detailed argumentation, based on an enormous amount of data, is given by S. S. Shvarts himself, the founder of this scientific direction. In thesis form, we will add some important principles of evolutionary ecology, without which the survey would not be complete:

1. Fundamental changes in the ecological structure of populations (age structure, spatial, etc.) are always connected with transformation of adaptive features of their genetic structure.

2. There are diverse ecological mechanisms thanks to which the genetic heterogeneity of a population is maintained in the case of any change in numbers.

3. The development of animals is based on a principle that can be called the principle of the optimum phenotype. The ability of a certain genotype to form different phenotypes does not mean that all possible paths of ontogeny are energetically equivalent. One of them is achieved in an energetically more economical way; another, in a more expensive way. There is an energetically optimum phenotype corresponding to each genotype.

Before we set forth the most important directions of development of modern evolutionary ecology, it seems relevant to us to make a short digression to its sources. There is no need here to go into detail about how the synthesis of classical Darwinism and population genetics led to creation of the STE. The idea of the STE that a population is the elementary evolutionary unit, as is known, in turn led to formation of the population style of thinking. The specific direction of research that uses the population approach as a tool for solving biological problems was born in this stage of the development of biology: population biology (Yablokov, 1987); and within its framework the population ecology of animals and plants originated. In E. Pianka's opinion (1981), there is now no need to distinguish the population ecology of animals and plants; the difference between them only outwardly appears to be fundamental. The fusion of population-ecological ideas with the ideas of population genetics and the theory of evolution led to the creation of evolutionary ecology (Shvarts, 1965, 1969, 1973a, 1980).

At the same time, population morphology was being formed. The development and substantiation of this direction is connected with the name of A. V. Yablokov in our country (1966, 1980, 1987). The fusion of population-morphological and population-genetic views led to development of one of the most productive modern directions of population biology: phenetics (Timofeev-Resovskii and Yablokov, 1973; Timofeev-Resovskii et al., 1973; Yablokov, 1980, 1987). In A. V. Yablokov's definition (1980), phenetics is "the extension of genetic approaches and principles to species and forms the genetic study of which is difficult or impossible" (p. 42). In recent years, other directions of research connected with population analysis of the process of development have formed in the mainstream of population biology: population phenogenetics and quantitative morphogenetics (Zakharov, 1987; Yablokov, 1987; Magomedmirzaev, 1990).

Thus, several directions were formed within the framework of population biology: population genetics, population ecology, population morphology, phenetics, and population developmental biology (Yablokov, 1987). Each of them has its own subject and its own research problems, and the population method and style of thinking can be called their main feature. The interaction of these divisions naturally leads to evolutionary problems. In this regard, the evolutionary-ecological direction has to be recognized as the broadest and most capacious, in our view; it is acutally the evolutionary application of the efforts of all of the directions of population biology.

The current status of population biology can be defined, on the one hand, as the extension of population-genetic views in the broad sense to population ecology and other population-biological disciplines, and, on the other hand, as the reciprocal enrichment of population genetics with the principles and phenomena described by these directions on the basis of natural material. Thus, we are inclined to understand evolutionary ecology as the use of the rich methodological and factological arsenal of population biology (population genetics, population ecology, and other population disciplines) to study the process of evolution and especially its initial stages. The significance of the ecological guidepost that is present in the very name "evolutionary ecology" is becoming clear now, when the deep need for enrichment of evolutionary theory with ecological views and methodology has become obvious. The ecological guidepost in evolutionary theory is also important in our time because, on the strength of expected acceleration of microevolutionary transformations of animal, plant, and microorganism populations in the conditions of intensifying anthropogenic pressure on the environment, evolutionary theory may unexpectedly become an applied field.

In the light of these ideas, we will try to define some characteristics of the development of evolutionary ecology being established in our time. First of all, we will dwell on problems the solution of which leads to a full-fledged ecological-genetic synthesis in evolutionary theory, which will simultaneously indicate the successful development of evolutionary ecology. In this regard, we should pay attention to phenetic research, which performs an important function: it develops indirect genetic methods of investigating natural populations, which, to a certain degree, was formerly lacking in evolutionary ecology. According to A. V. Yablokov (1980), the purpose of phenetics consists in studying questions of microevolution, theoretical taxonomy, practical bioengineering, and other problems connected with population investigations of species in nature. Therefore, it would be no exaggeration to say that many phenetic directions supplement and develop evolutionary ecology and can promote its further development.

We will give a few examples illustrating this point of view. Thus, study of the population structure of various species is an important problem of evolutionary ecology: identification of populations in nature, determination of their boundaries, and comparison of the numerical size of populations and intrapopulation groupings as chorological units. In this regard, investigations performed by phenetic methods are indicative, such as works on isolating intrapopulation groupings by mapping catches of individuals carrying rare phenes (Krylov and Yablokov, 1972; Turutina, 1978; Baranov, 1988), and study of the population structure of a species (Yablokov et al., 1981; Bol'shakov and Vasil'ev, 1975, 1978; Vasil'ev, 1982, 1988; Vasil'ev et al., 1986). For example, in studying the population structure of sand lizard (Yablokov et al., 1981) over the course of many years on stationary plots over a large continuous territory, catches of individuals were mapped, and the frequency of occurrence of more than a hundred marker traits relating to peculiarities of the lizards' coloring pattern and pholidosis was studied.

As a result, biochorological groupings of five levels of the natural hierarchy were isolated. The minimum joining together of individuals is a family, a temporary aggregation with existence lasting 1-2 generations (the level of exchange of individuals between them is more than 50% in a generation). A group of families is combined in a deme and can exist for several generations. A higher level is a group of demes, where exchange amounts to only 3-4% of the individuals in a generation. In the researchers' opinion, such a union can exist for tens of generations. Next comes a combined group of demes, or a population, between which exchange of individuals does not exceed hundredths of a percent in a generation, and the approximate duration of existence is hundreds of generations. An even higher level of structurization is hypothesized: a group of related populations. The authors believe that the third level, a group of demes or a population, can already be considered a sufficiently balanced genetic system, which is confirmed by the presence of intermediate "hybrid" zones at the boundary of such unions (Yablokov et al., 1981). The unusual phenetic diversity in such areas is considered to be the result of disruption of balanced gene systems as a result of their interaction. In our view, this work has important consequences for evolutionary ecology. The natural biochorological groupings revealed not only indicate the reality of the species' population organization, but also the oversimplification of calculations such as clarifying the fate of alleles in a system of Mendelian populations, and they also convincingly show that the latter may not have a biological meaning. This circumstance once again indicates the insufficiency of just a population-genetic basis alone for understanding the process of evolution.

Another aspect of study of the population organization of a species is study of intraspecific differentiation, its scale, and actual pattern. In revealing the degree of differentiation of populations, comprehensive analysis of ecological, morphological, and indirect genetic (phenetic) characteristics of populations acquires great significance (Bol'shakov and Vasil'ev, 1978; Vasil'ev, 1982). Comparison of the ecological structure of populations (age structure, spatial arrangement, rate of propagation, population density, etc.) makes it possible to evaluate their specific population-ecological nature. Multivariate morphometric comparison provides the opportunity to reveal the distinctiveness of the populations' phenotypic appearance, while comparison of populations with respect to the frequencies of occurrence of phenes of nonmetric threshold traits, as shown in a number of works on phenetics performed abroad and in our country (Berry, 1963, 1964; Hartman, 1980; Sikorski, 1982; Vasil'ev et al., 1986) makes it possible to genetically interpret the differences obtained. All of these approaches, supplementing each other, lead to a fairly completely evolutionary-ecological idea of the degree of population differentiation. For example, on a continuous section of floodplain forests of the Ural River in Orenburg Oblast, A. G. Vasil'ev took representative samples from six approximately equally remote colonies of bank vole in a short time. The total extent of the comparison area was about 150 km. Study of these samples showed that two sets possessing specific features are distinguished with respect to ecological structure and morphological characteristics. One set includes the first and second samples, and the other combines samples from the third through the sixth colonies. Differences are found between the sets in age structure, level of relative population density, and in the overall dimensions and certain proportions of the skull.

Determination of the phenetic differences between the samples (according to the frequencies of 23 phenes of nonmetric cranial traits) revealed that the first and second samples are close, and the difference between them is comparable with the level of intrapopulation differences. No sharp differences were established between the second and third samples, or in general between adjacent samples. However, between the most remote samples (first-sixth, second-fifth) the order of differences is great and comparable with the phenetic distance between neighboring populations of the species known to be isolated for a long time. On the continuous area of the strip range we were unable to find rigid boundaries between the populations. We can only talk about a large transitional zone between them. Nonetheless, one fact that was obtained is important: the combination of analysis of the ecological structure, morphometric peculiarities, and phenetic distances showed that the given segment of floodplain forest is inhabited by no fewer than two populations of bank vole. In our view, development of such research can be fruitful in studying the population organization of a species, intraspecific differentiation, and microevolution.

Modern evolutionary ecology is deeply historical, since it studies the problem of transformation of populations in space and in time. However, this aspect is not always reflected in neontology, which justifies turning to paleontological, subfossil material and archeozoological data. The pioneer works in this direction were performed by K. L. Paaver (1976), who was responsible for the development of ideas about secular variability. N. G. Smirnov called this direction of evolutionary ecology historical ecology (Smirnov et al., 1990). As a result of studying the variability of morphological traits in modern and subfossil (2500-3000 years ago) populations of common hamster, N. G. Smirnov not only showed the presence of secular variability of the traits, but also established a change in the traits' normal reaction from the ancient population to the contemporary one. Another example is B. A. Kalabushkin's investigation (1976) revealing genetic differentiation in modern and Middle-Holocene populations of one of the species of gastropods from the Busse lagoon in the coastal zone of Sakhalin. It is noteworthy that the author not only established the phenomenon of genetic differentiation of the population in the process of adaptation to different habitat conditions, but also showed changes in structure connected with an increase in ecological differentiation in the lagoon's aquatory [underwater territory] over the course of 4500-5000 years. The important fact was revealed that with respect to the investigated traits subpopulations (micropopulations) of the contemporary lagoon differ from each other to a greater degree than the ancient population does from the contemporary one as a whole. It is hard to overestimate the evolutionary-ecological significance of such works.

A significant role in the study of evolutionary-ecological problems is played by comparative karyological and electrophoretic investigations, which are not only aimed at solving taxonomic problems, but also have a clearly expressed evolutionary direction (Vorontsov et al., 1972; Orlov, 1974; Gileva et al., 1982; Malygin, 1983). Works combining karyological, electrophoretic, and morphological analysis are interesting. Investigations studying intrapopulation chromosomal polymorphism and the phenomenon of geographic variability of chromosome sets have great significance for evolutionary ecology (Gileva, 1990).

Development of the evolutionary-ecological direction is also promoted by experimentally hybridizing representatives of different intraspecific and taxonomically debatable forms, and raising them in similar conditions. The experience of research of this kind was generalized by A. V. Pokrovskii and V. N. Bol'shakov in the monograph "Experimental Ecology of Voles" (Pokrovskii and Bol'shakov, 1979). The importance of the development of such research was emphasized more than once by S. S. Shvarts (1973a, 1980). Transfer of animals belonging to different intraspecific forms to relatively equal laboratory conditions and study of their reaction to these conditions can be considered a distinctive morphogenetic test. By revealing the specific nature of morphogenetic and other reactions to similar conditions for representatives of different intraspecific forms, it is possible to establish not only the fact itself of the irreversible specific nature of given forms, but also the direction of microevolutionary transformations (Bol'shakov et al., 1980). Use of the method of provocation environments and study of the effects of genotype-environment interaction from an ecological-genetic standpoint are in the same vein (Glotov and Tarakanov, 1985). Quite recently, thanks to the combination of electrophoretic, morphological, and phenogenetic methods with ecological ones, there has been renewed interest in ecological-genetic investigations of natural populations and, consequently, in further development of evolutionary ecology.

We will recall that back in the 1920's B. L. Astaurov (1974) revealed a special form of variability, which is due to natural stochastic errors in development and leads to the now well known phenomenon of asymmetry (Zakharov, 1981, 1987; Soule', 1979; Palmer and Strobeck, 1986; Parsons, 1992). Most bilateral morphometric and nonmetric traits are subject to fluctuating asymmetry. This phenomenon of unequal realization of the trait on different sides of an individual is due to malfunctions (errors) in development (epigenetic factors), since the individual's genotype and the conditions of its development are practically the same for both sides. Fluctuating asymmetry (FA), the independent and often unequal realization of bilateral traits on different sides of an individual, is a generalized epigenetic measure of stress (Parsons, 1990) that makes it possible to evaluate the stability of a group of individuals' development and, consequently, can be used for biomonitoring of populations (Zakharov, 1981, 1987; Palmer and Strobeck, 1986). The use of FA indices will make it possible to evaluate the stability of development of various functional groups of animals in a population, to reveal individual levels of FA, and also to compare the stability of development of animals from populations living in different conditions (in the optimum and pessimum of a range, in different phases of the population's dynamics, in regions of technogenic pollution, etc.). In 1992, the I International Symposium on ecological genetics of mammals was held in Poland, which brought together specialists from different fields of population biology, including population genetics, ecology, and developmental biology. The approach connected with use of fluctuating asymmetry in ecological-genetic investigations was recognized as one of the main directions at this symposium.

Everything that has been said above confirms the validity of the direction of research chosen almost 25 years ago by S. S. Shvarts, which he, somewhat ahead of his time, called evolutionary ecology. Only now is the ecological paradigm beginning to show up in all directions of biology, and the ecological-genetic view of the evolutionary process is gradually becoming dominant in population-biological research. For this reason, we must once again emphasize the importance and timeliness of the problems raised by evolutionary ecology for formation of modern fundamental ideas about the evolutionary process.

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