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# Evolutionary ecology

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Evolutionary ecology includes several trends of investigations. The most important are: investigation of the origin and development of ecological adaptations (population dynamics, biology of reproduction, spatial distribution, home range etc.) of different species and forms of investigation of ecological mechanisms of microevolution. The former was developed mainly by Oriens (1962), Lack (1965) and other occidental zoologists. In the Soviet Union this trend in ecology is developing successfully, though its connection with theoretical grounds of evolutionary ecology is usually not specially underlined. In this respect the observations of Poljakov (1964) on the variability of the reproductive cycles in rodents in different life conditions must be mentioned. N. Naumov (Naumov 1964) is mainly interested in investigation of the adaptive importance of different spatial structure of the population. S. Naumov and his collaborators thoroughly investigated the same problem on *Lagomorpha* and some *Carnivora* (Naumov 1966).

Our laboratory represented the above mentioned problem by investigation of ecological adaptations of different animals in extreme life conditions (subarctic, high mountains). Noteworthy is the fact that, for instance, main adaptations of *Amphibia* in the Far North are just ecological adaptations, namely the possibility to use water insects as the main source of nutrition, cold-resistance of embryos, acceleration of larval development (even in cold water), greater life span, and increased activity of adult animals. Accordingly it was shown that ecological adaptability to extreme conditions is of the same importance for small mammals.

These and similar investigations have an important part in scientific plans of many laboratories of the Soviet Union. At the same time our laboratory and some other scientific bodies with which we keep scientific bonds began to pay more attention to the other trend in evolutionary ecology, namely to investigations of ecological mechanisms of microevolution. The main hypothesis upon which these investigations are based is the following: as a matter of fact every change in ecological structure of population inevitably leads to an alteration in its genetical structure and later on to microevolutionary recomposition in the population. In accordance with that hypothesis there are three main routes in investigations, that is: investigation of morphophysiological specificity of different intra-population groups (age groups, seasonal generations, resident animals and migrants, animals on different stages of reproductive cycle, etc), whose ratio is most characteristic for the ecological structure of the population; investigation of populations dynamics (including alteration in population structure); experimental and theoretical investigation of the correlation between ecological structure of population and its genetical composition.

Particular attention was paid to the study of biological peculiarities of seasonal generations of animals (experimentally and in field conditions). It became evident that each generation of small rodents has its unique morphophysiological and ecological peculiarities. Absolutely all available indices of seasonal generations of the same population are different (growth rate, rate of sexual maturation, development of the endocrine system, skull and body proportions, thermoregulatory reactions etc.). The animals with greater life span show similar, though not so clearly expressed differences between generations born in different years. On the grounds of these observations and experimental data a concept of chronographic variability (alteration of the architecture of population in time) was developed (Schwarz 1963).

It was determined that not only the numbers of animals but also the quality of the population is maintained in a state of mobile equilibrium. It is noteworthy that chronographic variability could be

traced on morphophysiological and even on cytological and molecular levels. This fact was noted during an investigation of *Triturus vulgaris* tail tissue thermostability. A generalization of all these observations was published recently (Schwarz, Smirnov, Dobrinsky 1968).

Since animals of different age generations are biologically different, they, it goes without saying, suffer different selection pressure and therefore their genetical composition could not be identical. This was proved on species whose genetical heterogeneity appears in the form of definite polymorphism. For the investigation, representatives of different classes were taken, i.e. insects, amphibians, birds and mammals. As the general pattern depicting differences in genetical structure of intra-population groups is similar, it should be sufficient to give some examples from different groups.

Long-term observation shows that the genetic composition of age groups of *Rana arvalis* is fairly different. The percentage of mutant 'striata' varies from 28.6 (junior age group) to 64.9 (older age group). On the other hand, changes in life conditions call for different changes in genetical structure of different age groups. Thus the dry summer of 1967 decreased numbers of striata frogs in junior age groups (younger than 3 years) and increased numbers in senior age groups from 40 to 60 per cent (Schwarz & Istshenko 1968). Concrete ecological grounds which determine specific reactions of age groups depend on biological peculiarities of genetic variants. The mutants striata and maculata differ in the rate of larval development and in the capability to create energetic reserves in the form of glycogen in the liver. It is clear that in different age groups these peculiarities are of different importance.

Similar observations were carried out on ruffs (Dobrinsky 1968). Enormous data (about 1000 anatomized birds) was employed and it was found that black coloured birds (melanists) weigh heavier, have bigger hearts and kidneys than any other variety (with respect to allometric growth).

Worthy of note is Pavlov's work on trapped animals (Pavlov 1965), who found that in different age groups of squirrels the per-

centage of colour variants (genetical markers of population) varies from 14.8 to 86.5%. As with frogs, squirrels of different age generations display different chronographic variation.

More important though fairly similar irregularities were detected by the observation of the variability of polygenic characters (body and skull proportions, allometric growth curves). Age generations in a single population (and of the same age) often differ more than well differentiated intraspecific forms whose independent development has taken place over many thousands of years. The whole complex of all these observations depicts that changes in population age structure inevitably lead to their genetic alteration. Of course, natural selection and insufficiently studied mechanisms of population homeostasis restore the disturbed equilibrium and help population keep its optimal genetic structure despite all possible changes in life conditions and fluctuations in animal numbers. In particular this phenomenon was demonstrated by Novozhenov (1968). During several years he studied three cockchafer populations and found that despite enormous fluctuations in the abundance of the beetles the genetic composition (the ratio of 'red' and 'black' specimens, who differ in size as well) of the generations of different years (the author calls them 'populations divided by time', chronopopulations) remain approximately at the same level. In different populations the percentage of red chafers numbers 12.9–18.74, 1.8–5.2 and 70.2–79.2%.

Such observations show that a population is able to adjust its genetical structure despite immense numbers of obstacles arising during the ontogenesis of a population. However, when environmental conditions change so much that a population cannot come to its original state or when a restoration of former population structure is ecologically disadvantageous the population falls out from a state of mobile equilibrium. It leads to an irreversible alteration in ecological structure of a population and consequently to an alteration in its genetic composition (the first stage of microevolution). According to calculations microevolution based on such mechanisms might develop incomparably quicker than under the influence of classical form of natural selection or individual selection.

We call this mechanism age selection. Sometimes it has a perplexing outcome. In particular it changes the evolutionary role of inselective elimination. A powerful disastrous ecological (abiotic or biotic) factor causes the destruction of a population; most of the animals die out. Only accidental specimens may survive the catastrophe. Therefore this form of elimination is called inselective. An ecological analysis shows that such point of view is far from being indisputable. For example floods might destroy all the animals of younger age, but only some of the adults. Inevitably it would change the age structure of the population and the elimination would be selective, directly recomposing the ecological structure of the population and accordingly its genetic composition.

Sometimes the age selection changes the very action of selective forces. For example theoretical analysis of possible selective forces in populations of *Arvicola terrestris* to 'cold resistance' showed that the mean increase of cold-resistance depends upon the ratio of specimens who survived two winters. Therefore mild and not cold winters provide cold resistant populations. These observations, based on imposing experimental data, are eloquent enough to show that ecological mechanisms of population transformation determine efficiency of natural selection (Schwarz 1965).

Another important manifestation of ecological mechanisms of microevolution comes from spatial and not age structure of population. As a matter of fact, populations practically consist of smaller groups (I call them micropopulations) which exist independently for a certain period and afterwards form a single whole, a single population. Well known ethological variations might lead to temporal isolation of intrapopulation groups even without any visible physical barriers. All this leads to origination of genetic differences between neighbouring groups of animals.

As an example the investigations of Beregovoy (1966) on spittlebug (*Philemus spumarius*) may be cited. He studied the distribution of 9 colour variants (used as genetic markers) and found that differences between isolated populations are statistically significant even if the space separating them scarcely numbers several metres, and

they keep their genetic composition despite a considerable (up to 60 fold) fluctuation in numbers. Thus the mentioned work is similar to the investigations on cockchafers by Novozhenov (op. cit.) but detailed analysis showed that genetical structure of different populations depends upon migrations between different groups of insects.

In cases where isolation between groups exists only during definite stages of population ontogenesis the importance of spatial structure of population could be traced in evolution of interpopulation forms, including subspecies. That was shown on the mentioned *Rana arvalis*. Genetical composition of the newly born animals in neighbouring habitats is fairly different but in time they become widely dispersed and so the representatives from different micropopulations are mixed. At last the genetical composition of elder generations becomes practically uniform and no differences between micropopulations could be observed (Schwarz & Istchenko 1968). Theoretical analysis of all the consequences grounded on observations of such kind proves that the more complex population spatial structure is, so much the higher its stability and it suffers less influence from accidental disasters (including genetic drift as well), so that the effectiveness of natural selection increases.

Some accidental disasters (such as a decrease in numbers) might change genetical structure of separate micropopulations, but the coincidence of after-effects of accidental events in a few or in a number of isolated communities is hardly probable. A reunion of micropopulations leads to a restoration of population optimal structure; the results of accidental disturbances in the structure of separate micropopulations becomes insignificant. Therefore the more complex the spatial distribution of a population the more its stability.

When the neighbouring micropopulations fuse into a single whole it may call out a real revolution in gene pool. It is evident now that in many cases the same morphophysiological effect appearing in populations under the influence of similar selective forces might be based on different genetical grounds. 'Achievements' of different populations might be summarized by crossing (additive gene action).

In other cases hybridization leads to the appearance of animals with new patterns. From the genetical point of view everything is clear in that case. The task of evolutionary ecology is to trace definite sequences of consolidation of temporarily isolated subpopulations into a panmixing whole.

We were investigating the problem experimentally during a number of years. Let us confine ourselves to the result of experimental crossings carried out on different intraspecific forms of *Microtus arvalis*, *M. oeconomus* and *M. gregalis*.

It is well known that one of the most important indexes in vole taxonomy is the interorbital breadth. Two geographic forms of *M. oeconomus* were crossed. In one form the increase in skull length was connected with important increase of interorbital breadth. In the other form this correlation was less pronounced; in the hybrids an increase in skull length was not accompanied by any change in interorbital breadth. It was proved that the differences between parent forms and the hybrids are of great morphological importance, and are significant from the evolutionary point of view. Quite analogous results were obtained by crossing different forms of species listed above.

It should however be noted that for the due estimation of the evolutionary role of interpopulation hybridization particular attention should be paid to investigation of interpopulational differences. Under investigation were morpho-physiological indices of animals, metabolic rate, vitamin contents in tissues, endocrinological differences, tissue respiration, protein thermostability, immunological reactions, haematological indices, electrophoresis of blood serum, etc. It was found that with respect to all these indices interpopulation differences could be observed. It leads to the conclusion that interpopulation hybridization and consequently all the factors causing temporary separation and the succeeding amalgamation of sub-populations are of immense though not always investigated importance in population evolution. Dynamics of spatial organization of populations is, beyond any doubt, the most important ecological mechanism of microevolution.

It must be especially underlined that between ecological mechanisms of microevolution there exists a strong inner correlation. Change of genetic composition of the population by an alteration of its age ratio arouses sufficient genetic differences between subpopulations which were isolated only during several reproductive cycles. The subsequent amalgamation of subpopulations leads to outcomes which are typical for intraspecific hybridization.

These variations of population transformation are of interest from the point of view of biocenology and especially in prey-predator problems. In the limits of his home-range a predator creates a certain vacuum in the prey population. The vacuum is to be filled from neighbouring habitats, so that, according to the law of population homeostasis (reproduction rate is reversely proportional to population density), the predator may give rise to an increase in prey population. If we assume that migrating animals represent a specific ecological group, then in accordance with our hypothesis, a predator provides for genetic heterogeneity in the prey population and indirectly increases its biological stability. Fine evidence of this effect was obtained by N. Sjusjumova (in press). By the means of immunogenetical methods she proved that ground squirrel populations on the territories where they were destroyed (pest control) display better genetical heterogeneity than on untoured territories.

It goes without saying that ecological mechanisms of population transformation should not oppose natural selection. Selection originates differences between generations and micropopulations which are mobilized by ecological mechanisms of evolution. Ecological mechanisms of population recomposition make as it were, quick, but rough adaptation, which is corrected by selection. This determines the most important task of evolutionary ecology. It confines the most possible detailed examination of mutual dependence to ecological and genetical composition of populations of different species in different conditions of environment.

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