ISSN 1022-7954, Russian Journal of Genetics, 2006, Vol. 42, No. 3, pp. 234–246. © Pleiades Publishing, Inc., 2006.
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THEORETICAL PAPERS AND REVIEWS

Unintentional Genetic Processes in Artificially Maintained Populations: Proving the Leading Role of Selection in Evolution

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Received September 1, 2005

Abstract—The review considers studies examining artificially maintained populations as models for understanding biological evolution. The key factors of gene pool evolution—random processes, interspecific hybridization, migration, mutation, and selection—are analyzed. We present evidence indicating that selection is the leading evolutionary factor that regulates the operation of other factors, directly or through genetic systems.

DOI: 10.1134/S1022795406030021

INTRODUCTION

As recently as a century and a half ago, people could allow themselves to overlook the process of biological evolution. To date, changes in the biosphere became one of the most urgent problems of humanity: "good old" species have been vanishing at an astonishing rate, along with the appearance of new forms of pests, weeds, and hazardous infectious agents. These processes are studied by a novel science, conservation genetics [1].

Apparently, clear understanding of evolution of the living matter is essential for preserving the biosphere diversity in its totality. The main factors of evolution are well-known: these are random processes, interspecific hybridization, migration, mutation, and selection. However, no consensus on their contribution to the evolutionary process has been reached yet. The problem formulated by Mayr [2] is still relevant:

"At present, most discussions deal with comparative significance of various interacting factors. We will get very different answers to the following questions asked to modern evolutionists:

What is the evolutionary significance of random events?

How important is the role of hybridization in evolution?

What are the consequences of gene exchange between populations?

What proportion of new mutations is beneficial?

Which part of genetic variation is accounted for by balanced polymorphism?

It seems that answers to these questions must be provided experimentally. But experiments examining genetic processes in populations have serious drawbacks. A too strict experiment with many restrictions yields only a theoretical model, which confirms our views but does not provide comprehensive information on natural populations. On the other hand, in an experimental test of a phenomenon in natural, uncontrolled conditions, the results may be too vague for choosing between the alternative hypotheses [3].

Fortunately for researchers, in addition to the two groups of natural and experimental populations, mentioned above, there is a third group consisting of artificially maintained populations [4]. Apart from the fact that understanding genetic processes in these populations is of great practical significance, we believe that they serve as an ideal "testing ground" for studying gene pool dynamics. Artificial populations include strains maintained in laboratories; groups of individuals of rare species, bred in zoos or botanical gardens; and groups of fish, reproduced in hatcheries. Part of the life cycle of individuals from such populations may pass in a natural environment (for instance, in hatcheries juvenile fish are in many cases released into natural reservoirs to feed).

Here, we analyze only the cases, when the individuals were not purposefully selected by researchers for some traits. However, selection exerts some effect on domestic creatures, irrespective of man's will or even against it [5]. Thus mode of selection was termed *autoselection* [6], or, more aptly, *uncontrolled selection* [7]. In English-language literature, terms *inadvertent selection* or *unintentional selection* are generally used. We will refer as *unintentional* to all genetic processes that occur irrespective of humans in artificial environments.

In the review, we present the factual material on these processes available in literature. The limited space does not allow us to analyze studies on mathematical simulation of these processes and studies on the development of procedures to suppress them (see [8] for review). We also omit from consideration the results of experiments, in which the organisms were reared under clearly adverse conditions [9].

RANDOM PROCESSES: GENE DRIFT AND FOUNDER EFFECT

Gene drift. In recent years, the theory of neutral molecular evolution has gained in importance. According to this theory, the genetic structure of populations of individual species, as well as genetic features of any taxon, are practically totally determined by random processes [10–12]. These processes include primarily gene drift, i.e., unidirectional change of population gene pool, related to the fact that some individuals leave more progeny than others. However, the results of analysis of real evolution in artificial populations reject the neutrality theory.

For instance, phylogeny inferred from allozyme frequencies on the basis of neutrality theory, is in a rather good agreement with the actual phylogeny of the laboratory strains of mice, but this is not so for the trees constructed from the data on immunological allele diversity and the data on proviruses inserted in the mouse genome [13].

The data of DNA nucleotide sequence permitted correct reproduction of the order of divergence of the experimental lines of phage T7, but did not provide a possibility to precisely assess the time of their separate evolution [14]. The phenotype of the ancestral population could not be reconstructed from the results of analysis of quantitative characters in these phages [15]. In another experiment, an integrate phage population was divided into six parts, and then each of the resultant lines was divided in two. The order of these divisions could not be determined by any of the methods used [16].

Note that similar results were obtained also for populations subject to conscious selection. The actual time of divergence of domestic animal breeds is significantly (by one or two orders of magnitude) lower than the time deduced from the genetic distances among them, calculated on the basis of enzyme diversity analysis ([17] and references therein).

All these examples testify to a fact that in actual evolution, the key factor is not gene drift, but a more powerful force, selection (see below).

Indeed, gene drift exercises a considerable impact on very small, artificial populations, but in this case it is coupled with inbred depression (see [18–20] for review), which is accompanied by loss in the ability to adapt [21] and leads the population to extinction. Though inbreeding may promote purging of the population from deleterious mutations, this purging is not efficient in all species and does not work in all environments (review in [22–24]).

Small populations with fixed high-mutability allele may display mutational meltdown. A deleterious mutation, randomly fixed in a population, results in reduction of the size of this population, which mediates fixation of another adverse mutation, and so on, up to extinction ([25] and references therein).

One of the mechanisms counteracting gene drift is sexual process. Recombination was shown to promote viability of small phage populations [26]. Higher organisms have developed mechanisms of selective mating, which also opposes the effects of gene drift (see review in [27]). Drift is also counterbalanced by gene exchange among populations (migration). The said mechanisms are controlled by selection (see below).

Even inbreeding, leading to gene drift, can to some extent neutralize the negative consequences of the latter. For instance, it is known that close inbreeding provokes mobilization of transposable elements, which results in a mutation burst. The genetic diversity within the population increases, providing the possibility for selection ([28] and references therein).

It seems that these and other mechanisms of deceleration of gene drift are very effective in natural populations. Long-term monitoring has shown that gene frequencies in these populations are remarkably constant (reviews in [1, 29]) and a rearrangement of the genetic structure is caused by a drastic change in the environment, e.g., upon anthropogenic impact [30].

The founder effect. This term means an appearance of a new population from several original founders, which carry only a small part of the total genetic variability of the parental population. In this case, significant genetic differences may be observed between the newly arisen and the original population. A dramatic reduction in population size leads to a similar result (the bottleneck effect).

Such events occur both in nature and under artificial conditions. A classical example is island populations, which are characterized by low genetic diversity (review in [31]). A reduction in adaptive potential [32] and additive genetic variation [33]; see also [32] for references) was recorded in experimental populations after passing through a bottleneck.

However, often experimental populations were shown to maintain high variability in heritable adaptive traits [34, 35]. Moreover, in some studies an increase in genetic variation was recorded immediately after the population passed a bottleneck ([34], reviews [35, 36]; see also [32] for references).

As early as in [34], it was suggested that the "striking" behavior of adaptive traits is explained by their polygenic inheritance. It is currently believed that such polygenic systems with nonadditive effect have appeared as a result of stabilizing selection, whose role is discussed below. (Although we employ the term *polygenic* systems, note that in literature such systems are referred to as *coadapted gene complexes, integrated gene systems*, etc.)

A number of authors have suggested that founder effect creates the prerequisites for speciation. Indeed, some experimental studies showed a certain degree of pre- and postcopulative isolation among the *Drosophila* strains derived from one initial population ([37]; review in [36, 38, 39]). However, the role of polygenic systems, formed by selection, is very important in these cases.

Recent reviews, dealing with the founder effect (including experiments modeling this effect) assign to selection even a greater role [40–42]. In particular, it was noted that the level of reproductive isolation among laboratory strains of *Drosophila* considerably increases, if these strains are subjected to selection.

Thus, studies of artificially maintained populations do not provide evidence for random processes as the leading factor of evolution. Rather, they act as a hindrance to it, or, at best, an auxiliary mechanism, operating during speciation.

INTERSPECIFIC HYBRIDIZATION

Recent decades have witnessed the appearance of increasing evidence for an important role of hybridization in evolution of both plants and many animals. Though consequences of hybridization can be negative (nonviability or sterility of the progeny), in some cases it leads to introgression, i.e., transition of adaptive alleles from one to another species or formation of hybrid polyploid species that possess significant evolutionary potential (review in [43]).

Under artificial conditions, hybridization rarely occurs, because measures are usually taken to prevent it. However, these measures can be ineffective in case of morphologically similar species. For instance, hybrids between Atlantic salmon *Salmo salar* and brown trout *S. trutta* [44–47], sturgeons [48], and some other fish species (see [49] for review) periodically appear at hatcheries. Hybrids of two squirrel monkey species, *Saimiri sciureus* and *S. boliviensis,* have been found in captivity [50].

Differences in competitiveness have been experimentally demonstrated among hybrids and pure species of plants from the genera *Abelmoschus, Nicotiana, Secale*, and *Triticum* [51]. It is clear that the distribution of interspecific hybrids in artificial, and probably in natural environments are completely determined by selection. Moreover, the appearance of interspecific hybrids is often controlled by selection. In an artificial population of *Drosophila serrata*, coinhabited by a population of a closely related species, *D. birchii*, the former species was under selection for noncrossability with the latter [52].

If selection does not succeed to develop mechanisms of reproductive isolation in time, the hybridization might end by extinction of one of the species. For instance, in experimental mixed populations of plants *Clarkia biloba* and *C. lingulata,* a massive appearance of poorly fertile hybrids was observed, which resulted in the elimination of the species, whose number was initially lower [53].

In some cases, selection favors interspecific gene transfer (introgression). There are special systems mediating such transfer. For instance, bacteria readily exchange genetic material via plasmids (review in [6]).

Frankham *et al.* [54] pointed out that interspecific hybridization may be problematic for a number of rare animal species bred in captivity. An example is an increase in frequency of alleles, characteristic for domestic horse, in an artificially maintained population of the Przhewalsky horse (*Equus*). This trend seems to be promoted by selection. Note, however, that some authors attribute these horse groups to the same species, in which case it is difficult to distinguish between interspecific hybridization and another factor of evolution, migration occurring within the species.

MIGRATION (AMONG-POPULATION GENE EXCHANGE) AND ITS REGULATION

Shvarts [55] gave a perfectly clear description of migration among populations. “Until the population preserves its viability, it actively imposes restriction on individuals entering from the outside.” “The inflow of individuals from neighboring populations dramatically increases in the periods of local reductions in the population size.” Populations interconnected by gene flow actually become elements (subpopulations) of larger population systems (the term coined by Altukhov and Rychkov).

Altukhov, Bernashevskaya (Imasheva), and Pobedonostseva have designed and studied artificial population systems of *Drosophila* (see [1]). These systems proved to be capable to maintain constant mean allele frequencies, which was not observed in the random-mating artificial control populations. Subsequent experiments have shown that one of the explanations of this was nonrandom migration, which involved mostly flies of the most common genotype [56].

Recently, this phenomenon has been “rediscovered” by Western authors. To maintain genetic variability in artificial populations, they proposed their fragmentation (for minimizing selection) with periodic exchange of individuals between the fragments to remove inbred depression [57, 58].

Examination of migration in viral cultures showed that in homogeneous environments, this migration favors adaptive evolution [59], but in spatially structured, heterogeneous environments, it can cause adverse consequences by prevention of forming local adaptations [60].

In some cases, progeny from crosses of individuals from different populations have low viability. This may be explained either by a disturbance of local genetic adaptations, or by disruption of the polygenic systems that had formed during isolation. Thus phenomenon, known as outbreeding depression, is fairly common in artificial populations. Its analysis in experimental *Drosophila* populations showed that selection typically restores the gene complex, characteristic for one of the parental populations; however, in one case, a new gene complex, whose carriers exhibited high viability, was formed (see [61] for review).

Selection can regulate the level of migration, depending on its beneficial or adverse effects in the particular environment. An illustrative example is spreading of individuals that are unable to fly in *Drosophila* populations that inhabit the environment characterized by strong wind [62, 63].

MUTATIONS

Advantageous, deleterious, and neutral mutations. Ways of spreading of mutations in populations have been under a heated debate. The neutrality theory assumes that selection eliminates only deleterious mutations, while neutral ones freely spread in populations.

However, the "advantageous" or "deleterious" character of a mutation cannot be regarded as its intrinsic property. As early as in classical works [63–66], the authors pointed that mutations, deleterious in some environments, in others may become advantageous, which was, in particular, demonstrated for experimental populations. Schmalhausen [66] introduced the concept of conditionally deleterious and conditionally advantageous mutations depending on their environmental conditions. Kreslavskii [67] points the existence of pseudoneutral mutations, which under some conditions are neutral and under others, deleterious.

Even the author of the neutrality theory to some extent acknowledged the possibility of changing the status of mutations: "for neutral or nearly neutral mutations, potential possibilities for selection can exist, which are realized under the appropriate conditions" [10]. However, his followers usually disregard this possibility.

Mutation-regulating factors. A number of experiments have shown a dramatic increase in mutability under stressful conditions (review in [68]). Recently, the phenomenon of adaptive mutagenesis was discovered in laboratory microbial cultures: the mutation frequency in genes, controlling resistance to the stressor, was shown to increase in stressful environments (review in [69]).

Furthermore, experiments on model populations of self-pollinating plants have shown that these plants can respond to environmental changes by rapid genome rearrangements ([9, 70], and references therein). Their nature is not quite clear yet: these may be changes in the number of DNA repeats, methylation of various DNA regions, excisions and insertions of transposable genetic elements (TEs, transposons), gene amplification or deletion, and histone acetylation.

Transposons should be considered in more detail. They generate the majority of spontaneous mutations and can cause mutations concurrently in several genes, thus producing diversity for selection to act upon. In some cases, progeny of crossing individuals, whose genomes harbor or lack certain transposons, have low fertility (hybrid dysgenesis; see [71] for review). As noted above, close inbreeding mobilizes transpositions of transposable elements.

The presence of transposons in particular genome regions is not always advantageous for the organism. However, sometimes transposon insertions are maintained by selection and spread in artificial populations. There is evidence documenting a positive effect of transposon insertions on fitness in *Drosophila* [72], *Escherichia coli* ([73]; review in [74]), and yeast *Saccharomyces cerevisiae* (review in [74]).

A number of genes regulating mutation level are known. It has been shown that mutability can be changed by selection. If a mutation-stimulating allele succeeds in "generating" a mutation maintained by selection, it spreads together with it. Until such mutation appears, selection acts against this allele (see [6] for references). An increase in frequency of a mutation-inducing allele occurs in bacterial cultures only if the proportion of carriers of this mutation in the population is high without that increase and the population has a large size. However, in very large populations this allele loses advantage, because beneficial mutations occur in it at a sufficient rate (review in [75]).

However, selection can affect populations even in the case of a fixed mutability allele. For instance, in a highly mutable line of nematode *Caenorhabditis elegans*, the proportion of hermaphrodites is reduced, which seems to promote segregation of deleterious mutations [76]. The results obtained for yeasts also suggest that sexual reproduction mediates selection against adverse mutations [77]. In the absence of recombination, the reproduction ability declines, as well as in cultures of viruses [78] and infusorians [79].

Thus, selection directly or indirectly controls mutation, like other factors of evolution. Its role is diminished only under conditions of flow culturing of organisms, when it simply does not have time to maintain mutations conferring small advantage to their carriers. In this case, the evolution rate increases by treatment with mutagens, which increase the number of mutations, including those with a large effect. In this case, evolution may be saltatory [6, 80].

SELECTION

As a rule, experimenters rarely doubt the fact that exactly selection is the leading force of evolution. However, some theoreticians, in particular, the proponents of the neutrality theory, assign to selection only the role of an "executioner," which is hardly consistent with experimental data.

Selection upon collecting animals. When the founders of an artificial population are collected (caught), selection is inevitable, because they are different in migration activity, preferred habitats, with regard to the catching equipment, and so on. A number of

The effect of unintentional directional selection on artificial populations

Taxon	Result of selection	Source
Viruses	Increase in competitiveness	[59, 60] and references therein
	Appearance of viral particles with truncated genome; decline in infectivity	Review [102]
Colibacillus *Escherichia coli*	Increase in competitiveness	[103]
	Increase in rate of growth and cell volume	Review [89]
Bacterium *Photobacterium leiognathi*	Increase in glucose uptake by the population	[6], p. 64
Yeast *Saccharomyces cerevisiae*	Increase in competitiveness	[25]
Yeast *Candida tropicalis*	Increase in growth rate	[6]
Cereal crops	Increase in competitiveness	[63], p. 434–437
	Increase in grain yield, morphological changes	[104] and references therein
	Increase in proportion of polyploids	[105]
Amoeba *Amoeba discoides*	Increase in resistance to pathogenic bacterium	[106]
Nematode *Caenorhabditis elegans*	Increase in proportion of hermaphrodites	[76, 107]
Drosophila melanogaster	Increase in competitiveness	[108] and references therein; [63]
Drosophila subobscura	Increase in maturation rate, fertility, resistance to starving	[109] and references therein
	Increase in mating activity	[110]
Drosophila serrata	More effective utilization of resources (increase in population size)	[111] and references therein
	Increase in reproductive isolation upon cohabitation with a close species	[52]
Screw-worm *Cochliomia hominivorax*	Increase in ability to reproduce in culture	[112]
Guppy *Poecilia reticulata**	Increase in growth, decrease in maturation rate. Reduction in viability and growth rate at high population density	[113]
Atlantic salmon *Salmo salar*	Increase in growth and maturation rate	See [114] for references
Pacific salmonids *Parasalmo* and *Oncorhynchus*	Reduction in egg size; increase in growth rate; altered aggressiveness (decreased after emergence, enhanced at later developmental stages)	[115, 116]; review in [117]
Hybrids of wild and domestic turkey *Meleagris gallopavo*	Selection for low wildness, against individuals with nervous temperament and violent reactions	[118]
Lemming *Lemmus* sp.	Increase in reproduction intensity	[119]
Norway rat *Rattus norvegicus*	Increase in stress resistance, ability to reproduce in captivity, body size, fertility, duration of reproduction period; reduction in willingness to bite and escape	[120]; review in [121]
True otter *Lutra lutra*	Increase in proportion of animals with positive response to humans	[122]

* The wild guppy population of the Moscow River originated from aquarium fish.

examples of selectivity in commercial catching of animals and fish are known (see [81] for references); cases of unintentional selection of salmonid spawners for hatchery by size and maturation time have been described [82, 83].

Increase and decrease of stabilizing selection. Artificial *Drosophila* populations may accumulate mutations that are rapidly eliminated in nature [21, 84]. In particular, some populations lose their sensitivity to poisons (see [63] for references), reduce stress resistance [85]; in parthenogenetic lines, courting behavior is disrupted [86].

Courting behavior was also distorted in a laboratory strain of mosquito *Anopheles albitarsis* subjected to artificial crossing [87]. In the absence of selection, laboratory strains of *Caenorhabditis elegans* also displayed defective behavior [88]. Cultures of *Escherichia coli* lost their ability to grow on some substrates [89], virulence decreased in pathogenic bacteria [90], hydrobionts lost their capacity to diapause [91], and the sense of smell was deteriorated in males of codling moth *Laspeyresia pomonella* [92]. As mentioned above, ability for reproduction declines in cultures of viruses and infusorians.

However, an increase in stabilizing selection on a set of wing traits was recorded in laboratory populations of *Drosophila* [93, 94]. In some cases, an accumulation of mutations in *Drosophila* laboratory populations is associated with the adaptive advantage of individuals, carrying these mutations in heterozygous state (see review in [63, 95]). Below, we consider other examples of adaptive advantage of heterozygotes.

Selection fin favor of heterozygotes has been aptly termed a Sisyphean cycle [96]: each generation selection maintains the optimal genotype combination, which is destroyed in mating. However, just as physical exercises help maintaining physical fitness, such selection preserves genetic diversity in the population. Moreover, it promotes the appearance of polygenic systems [97].

Frequency-dependent and cyclic selection. Frequency-dependent selection, which generally acts in favor of carriers of rare genotypes, has been found in model populations of a number of animals and plants (reviews in [62, 63, 98, 99]). Polymorphism maintained via interaction of bacteria from different clones was reported for *E. coli* (review in [74, 100]). When carriers of one genotype promote conditions, beneficial for another genotype, cyclic selection may appear in the population.

For example, in experimental population of meadow moth *Loxostege sticticalis* [101] and *Drosophila* [99], cyclic fluctuations of population size were observed, which were accompanied by cyclic selection for particular genotypes. In populations of *Drosophila,* animals with low migration activity gain advantage at high population density, and vice versa [99].

Cyclic selection can probably operate even in constant environments. In experimental population of yeast and *E. coli*, mutations regularly appear, whose carriers reproduce faster than other members of the population and gradually replace the latter. Change of carriers of different mutations can occur in culture repeatedly. However, in some cases the mutants prove to have lower competitive ability than individual that composed the population at a previous stage of evolution (review in [74]). This situation is similar to the “stone, scissors, paper” game.

It would seem that cyclic selection works in vain, but this is not so: it promotes optimization of the population size [99] and in extreme environmental conditions transforms into directional selection (a widely known example is provided by population of insects having lost their ability to fly). In some cases, cyclic selection is difficult to distinguish from local adaptation. For instance, a situation was described, when upon viral infection of two different hosts (in nature, the virus can move from one host to another), carriers of one genotype gained advantage in one host, and of another genotype, in the other [78].

Directional selection. Artificial populations of various organisms are characterized by high competitiveness as compared to their wild ancestors, high rates of growth and sexual maturation, high fecundity or productivity, changed behavior (table). Apparently, in nature selection in this direction was suppressed by environmental conditions, lack of food or its different composition.

Many of these properties are also characteristic for domesticated forms. Thus, it seems likely that uncontrolled selection played a significant role in forming many traits of domestic animals and cultured plants. In particular, Vavilov [123] noted that rye *Secale cereale* was originally a weed that contaminated fields of cultured wheat. It may well be that rye acquired many properties of a cultured plant through unintentional selection. Possibly, many characters in weeds and meadow plants are explained by similar selection ([124] and references therein).

A special case of directional selection is spreading of compensatory mutations in a population with a fixed deleterious allele. Examples of such situations are presented in [63, 125] and references therein; a case with a compensation of the effect of a mutability gene was considered above. This process leads to the formation of polygenic systems. Such systems have been repeatedly designed experimentally, but their analysis is beyond the scope of the present review.

Close inbreeding inevitably results in segregation of alleles that are adverse in the given environmental conditions, but these genotypes can be preserved, if an allele neutralizing the adverse effect is fixed in another gene. Such gene complexes were found in experimental parthenogenetic strains of *Drosophila* (review in [61]). This phenomenon is of interest from the evolutionary viewpoint, as an early stage of postcopulative reproductive isolation.

Furthermore, this phenomenon demonstrates that an individual can be favored by selection, if it carries a favorable combination of alleles of several genes. This largely lifts restrictions imposed on evolution by the so-called "Haldane's dilemma," according to which selection can operate simultaneously only on a few loci, otherwise the cost of this selection would be too high [126].

Rapid selection, appearing upon lifting the pressure of some environmental factors, supports the view on an important role of opposite selection vectors in maintaining polymorphism in natural populations (reviews in [96, 127]). This counterbalancing of selection vectors is vividly manifested in the cases, when the artificial population has to counteract "selfish" trends of some individuals (parasitism, sexual selection) or alleles (meiotic drive).

In laboratory virus cultures, forms with truncated genome persistently appear, which cannot reproduce themselves and parasitize on viruses with full-size genomes. In response, the viruses acquire traits protecting them against such parasitism (review in [102]).

As noted above, in laboratory cultures of codling moth, sense of smell in males deteriorates in the course of culturing. At the same time, the attraction of a sexual attractant, released by females, increases [92].

Holland and Rice [128] analyzed the consequences of a transfer from random mating to monogamy (which is often the case in artificial reproduction). *Drosophila* males from an experimental population, in which sexual selection was excluded for 47 generation, proved to have lower competitive ability, than males from the control group, and females from that population more often died after mating, although the experimental population exceeded the control one in rates of reproduction and individual development [128]. Thus, a negative effect of sexual selection on population viability was demonstrated.

In laboratory populations of *Drosophila*, in which one of the sex chromosomes carries an allele favoring its transfer to progeny (meiotic drive), either alleles suppressing meiotic drive appear, or a mechanism is developed that promoted aneuploidy for sex chromosomes, which normalizes the sex ratio in the population (review in [129]).

Local genetic adaptations. It has been shown for many species that individuals taken from different habitats but reared under the same conditions produce the progeny differing in a number of traits. Based on these observations, Turesson has formulated a concept of the ecotype, i.e., a hereditary form, created by natural selection whose operation is directed by the local environment (review in [63]).

Moreover, the process of the appearance of local adaptations has been simulated in artificial populations. Genetic differences appeared at different culturing conditions between experimental populations of viruses [60, 78], bacteria (review in [100]), plants ([130], see also [131] for references), *Drosophila* ([132] and references therein), and sheep [133]. In addition, it has been shown that environmental heterogeneity determines the presence of a wide or a narrow adaptation spectrum, as well as a level of genetic diversity within the population (review in [134]). This evidence conforms to the results of numerous experiments on adaptation to a particular environmental factor, but their discussion is beyond the scope of this article.

Local adaptations appear due to conditionally advantageous mutations. Experiments with artificially reared salmon juveniles have shown that the survival of fish is the highest, if they are released in the river from which the spawners had been derived (i.e., in their native river) and decreases with increasing the distance of the site of release from the native river [135, 136]. Apparently, the water reservoirs have a gradient of environmental conditions with corresponding gradient of frequencies of conditionally advantageous alleles in population. The results of the introduction of alien juveniles of chum salmon *Oncorhynchus keta* in rivers showed that the degree of similarity of the introduced fish to the aboriginal ones was directly proportional to their survival [137].

This probably involves a process of stepwise adaptation: after having colonized the river and genetically adapted to it, the population becomes more adapted to the neighboring river with close, but not identical environmental conditions. The process of spreading, in its turn, models adaptation to a gradual change of an environmental factor in a distinct river (spreading northward is analogous to climatic cooling). Thus, the very existence of polymorphism is determined by environmental factors: particular alleles appear and are fixed in the population, existing in certain environmental conditions.

Adaptive value of genetic polymorphism. Selection at some loci has been demonstrated in many cases, including experiments in artificial populations (reviews in [138–142].

We would like to emphasize the cases, in which genotype frequencies at the majority of the genes examined were shown to be under selection in particular environmental conditions. These results were obtained for pink salmon *Oncorhynchus gorbuscha* ([143] and references therein; [144]), Atlantic salmon *Salmo salar* ([114] and references therein), as well as for microsatellites in chinook salmon *Oncorhynchus tshawytscha* [145] and Atlantic salmon [146]. Similar data are available also for groups of animals and plants, subjected to artificial selection (e.g., [147]), but their analysis is beyond the scope of this article.

Conclusive evidence for the adaptive nature of molecular evolution is provided by artificially maintained phage cultures, for which all genomic changes can be traced ([148] and references therein). For instance, marked parallel evolution of different lines in similar environments serves as such evidence.

Under artificial conditions, selection for traits that are adaptive in natural environments can cease, which explains the results of *Drosophila* experiments, in which no adaptive significance of allozyme polymorphisms was found. Nevertheless, these experiments were presented as supporting the neutrality theory [149].

Thus, the adaptive significance of polymorphism is undoubted. This polymorphism provides a reserve ensuring population survival upon environmental change. There are three forms of this reserve: Sisyphean cycle, cyclic selection, and counteraction of differently directed selection vectors. As noted by several authors [67, 144, 150], the distribution of allele frequencies at loci, potentially subject to selection in natural populations, may correspond to the distribution expected for neutral alleles.

GENETIC SYSTEMS AS A MECHANISM FOR EVOLUTION REGULATION

Classical works [1, 63, 66, 151, 152] have shown that populations, including those maintained artificially, are not a passive field for operation of evolutionary factors. The process of evolution is largely determined by the already existing in the population genetic systems, many of which were mentioned above.

Genetic systems can be arbitrarily classified in five hierarchical levels: a chromosome (polygenic systems), an individual (mating systems), subpopulations, population systems, and, finally, superspecific level, at which species that can exchange genes interact (for example, a system of closely related species that readily produce viable fertile hybrids). The fields of operations of different evolutionary factors largely correspond to different levels of this hierarchy.

The central position in it is occupied by subpopulation, because adaptation to environmental conditions occurs mainly exactly at this level, which accounts for survival of any species. These adaptation processes, as shown in the previous section, are controlled by selection. Maintenance of genetic diversity, i.e., adaptive potential, is ensured by the Sisyphean cycle, cyclic selection, and counteraction of opposite selection vectors.

The action of another important evolutionary factor, mutation, occurs mainly at the chromosomal level. However, the appearance of mutations is in most cases strictly controlled by repair systems, which, in their turn, are controlled by selection.

Negative consequences of random processes primarily affect separate individuals (inbreeding depression), but ultimately this factor decreases the effective size of the population. Selection opposes this scenario, controlling complex mating systems that hinder gene drift.

Migration is a process that connects individual subpopulations in population systems, and this factor of evolution is also under the strict control of selection.

And, finally, interspecific hybridization. Generally alien genes are deleterious or useless for the species. Thus, it is not surprising that selection successfully suppress interspecific crosses. Consequently, stable systems of gene exchange among different species are fairly rarely established.

As we have seen, selection directly shapes adaptation processes, occurring at the subpopulation level, as well as creates and controls the mechanisms, regulating evolution on other levels of the hierarchy of genetic systems. This provides subpopulations with considerable stability in stable environmental conditions and promotes rapid evolution upon their change.

This supports the following assumption by Schmalhausen ([66]): “Usually populations are in the state of some genetic equilibrium, and after a change in the environmental conditions proceed from one stationary state to another at the expense of mobilization of inner reserves of variability.”

CONCLUSIONS

How would we then answer the questions, posed by Mayr more than three decades ago?

What is the evolutionary significance of random events? Random events decelerate evolution, thy lead to maladaptive changes and population extinction. Hence, these events cannot promote progressive evolution, but they can affect survival of relic groups on limited areas. In many organisms, selection developed special mechanisms, restricting effects of random events.

How important is the role of hybridization in evolution? Interspecific hybridization plays a significant role in the evolution of plants and many groups of animals.

What are the consequences of gene exchange between populations? Gene exchanger connects populations in population systems, which mediate genetic homeostasis. As a result, the population remains stable in stable environment over many generations.

What proportion of new mutations is beneficial? A large part of mutations can be assigned to conditionally advantageous. Advantage, neutrality, or disadvantage of a mutation is determined in relation to the environment, in which dwell its carriers.

Which part of genetic variation is accounted for by balanced polymorphism? A significant proportion of genetic variation (more precisely, diversity), existing in populations, is due to balanced polymorphism: the Sisyphean cycle, cyclic selection, and counteraction of differently directed selection vectors.

Moreover, selection creates genetic systems that regulate all of the remaining factors of evolution.

ACKNOWLEDGMENTS

We are grateful to Yu.P. Altukhov, I.A. Zakharov, and E.A. Salmenkova for comprehensive support; A.N. Kuz'mina and M.N. Perfil'eva, for invaluable assistance in selecting the literature; A.G. Imasheva, A.G. Kreslavskii, M.L. Arnold, N.H. Barton, I. Fleming, R. Frankham, E. Garcia-Vazquez, L. Laikre, L.M. Meffert, D.H. Reed, R.R. Reisenbichler, J. Ringo, A.R. Templeton, F. Utter, and C. Zeyl kindly provided copies of their papers.

The work was supported by the foundation for Support of Russian Science, the Russian Foundation for Basic Research (project no. 05-04-49232), the programs "Dynamics of Plant, Animal, and Human Gene Pools," "Scientific Bases off Preserving Biodiversity of Russia," "Fundamental Bases of Managing Biological Resources," "Evolution of Life on the Earth," and "Fundamental Bases of Management of Biological Resourses."

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