

Role of Recessive and Dominant Mutations in Adaptation the Genus *Rana* to Recent Biosphere

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Abstract—The populations of three anuran amphibian species (Amphibia, Anura) of the genus *Rana* (*R. ridibunda* Pall., *R. arvalis* Nilss. and *R. temporaria* L.) inhabiting the Yekaterinburg urban agglomeration were examined. The frequencies of two traits, morph striata and iris depigmentation, were estimated in these populations. The former trait, so-called morph striata, is phenotypically expressed as a light dorsomedial stripe. It is controlled by a dominant allele of autosomal diallelic gene *striata* in some species of *Rana* genus, exhibiting complete dominance. Striata individuals have a number of physiological features that confer them an advantage under conditions of natural and artificial geochemical anomalies. The second trait, iris depigmentation, is the result of a recessive mutation. The individuals homozygous for this trait have low viability. Thus, the dominant mutations promote rapid adaptation of their carriers. Conversely, the recessive mutations may reduce viability of an individual.

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INTRODUCTION

The orthodox interpretation of microevolution suggests that, due to mutations, recessive alleles accumulate in heterozygous state to serve as a cryptic resource of internal variation [1], which may be used later during adaptation to altered environmental conditions. Conversely, dominant mutations are usually eliminated by natural selection because of immediate phenotypical expression and negative effect on viability of their carriers.

Our long study (1976–2005) of three species of anuran amphibians inhabiting both urban areas and suburbia provided evidence that testifies to different role and fate of some dominant and recessive mutations in adaptation to urbanized areas.

MATERIALS AND METHODS

Our study was performed on the territory of a large industrial city of the Middle Ural (Yekaterinburg) located at the border of Europa and Asia. Zoning of this territory according to the degree of anthropogenic transformation (II, multistorey housing; III, low-rise buildings; IV, forest park; K, suburban population) was conducted in conformity with previous typification and the results of hydrochemical analyses [2, 3].

The populations of three amphibian species (Anura, Ranidae) of the genus *Rana* (*R. ridibunda* Pall., *R. arvalis* Nilss., and *R. temporaria* L.) that inhabit anthropogenically affected territories, were the subject of our study. We have examined this year's brood individuals (yearlings) and adult animals. In total, 15 808

yearlings and 1666 adult individuals of *R. arvalis*, 1120 yearlings and 370 adults of *R. ridibunda*, and 4459 yearlings and 541 adult individuals of *R. temporaria* were studied. The frequencies of two traits, morph striata and iris depigmentation, were estimated. The morph striata is expressed phenotypically in the form of a light dorsomedial stripe in some species of the *Rana* genus. This trait is controlled by a dominant allele of the diallelic autosomal gene *striata* showing complete dominance [4, 5].

The second trait, abnormal iris pigmentation in one or both eyes, is rather widespread among anuran [6] and caudate amphibians [7, 8]. Experiments on *R. esculenta* [9] showed that a recessive mutation is responsible for this trait [10]. The latter was also found to be characteristic of brown frogs *R. temporaria* [10] and *R. arvalis* [11]. Dubois [12] suggests that a single recessive gene is responsible for iris depigmentation, whereas unilateral expression is a result of mosaic inheritance. In fact, this particular feature may be considered as partial albinism.

RESULTS AND DISCUSSION

On the territory of Yekaterinburg, the frequency of morph striata individuals was repeatedly reported to increase with urbanization ($P < 0.01$) (Fig. 1).

This phenomenon is a result of inherited physiological specific properties of this morph. According to our data [13], sodium skin permeability in morph striata of *R. arvalis* is threefold lower than in stripeless animals ($F = 5.39$, $P < 0.0023$). This suggests low effectiveness of the potassium-sodium pump, which is responsible

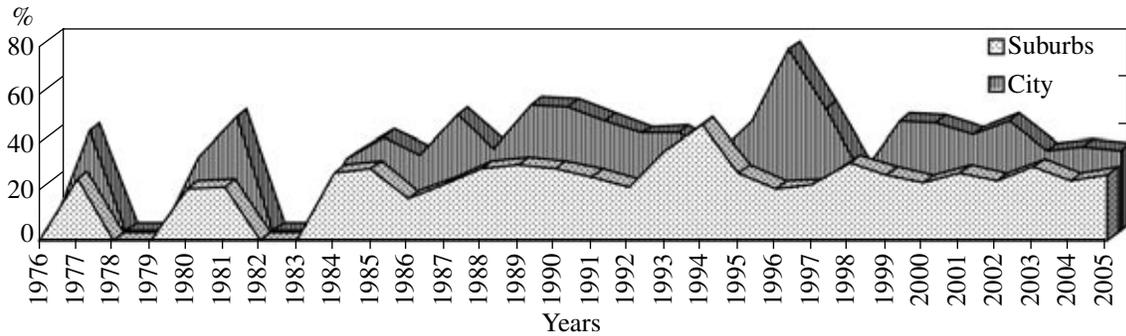


Fig. 1. Frequency of morph striata in juveniles of *R. arvalis* in urban and suburban populations (%).

for skin transport in amphibians. A decrease in skin permeability with respect to various substances (including oxygen) leads to intensification of lung respiration, which in turn increases blood oxygen capacity at the expense of a higher amount of hemoglobin. Because of a high content of hemoglobin significant iron accumulation is observed in organisms of striata individuals. In the latter, intense lung respiration leads to intensification of metabolism and hence, to a reduced life span of morph striata (2.8 ± 0.16 years ($n = 71$) against 3.3 ± 0.19 years ($n = 42$) in stripeless individuals; $F = 4.1$, $P < 0.045$). A shortened life span of striata individuals may lead to changes in the rate of evolutionary transformations.

Similar polymorphism may be characteristic of the genetically related forms because congeneric species may have homologous genes and express identical variation [14]. This is confirmed by significant distinctions in the proportion of neutrophils in yearlings of morph striata *R. arvalis*— 10.1 ± 0.79 versus 7.37 ± 0.56 ($F = 7.995$, $P = 0.005$) and *R. ridibunda*— 18.5 ± 2.4 and 12.2 ± 2.4 ($F = 12.4$, $P = 0.0007$), which testifies to a high phagocytic activity in hemopoietic system of striated animals of both species. This is an important trait under conditions of the human-caused pollution of the environment, which inhibits neutrophil function [15].

The incidence of striata in urban populations somewhat increases among adult animals (Fig. 2). Based on the above, it can be concluded that the carriers of this dominant mutation are preadapted to both natural and artificial geochemical anomalies of the environment [16]. No morph striata is present in *R. temporaria*, which is sympatric with *R. arvalis* [17]. *Rana temporaria* ancestors seem to have lost this morph because hibernating frogs of this species withstand hypoxia using skin respiration [18].

In our view, this explains elimination of *R. temporaria* from the anthropogenic landscape [19–21] and further changes in fate of this species, such as a global decrease of amphibian population in the modern biosphere [22].

Another trait under consideration is a recessive mutation (Fig. 3) that suggests inbreeding depression in

urban populations [11] and intense gene pool transformation on the urbanized territory.

Urbanization is known to induce insulation of amphibian populations and arising of small communities, which results in a higher level of population homozygosity and accelerated gene pool transformation at the expense of gene drift and concomitant inbreeding [23].

The frequency of iris depigmentation in urban populations of *R. arvalis* was higher ($\chi^2 = 28.9$, $P \ll 0.001$) than in the forest population, constituting 1.62 and 0.39%, respectively. The effect of temperature regime at the beginning of individual development seems to be a likely factor responsible for fluctuations in the frequency of this phenotype, because the years, when this phenotype was not recorded, were characterized by the absence) of frost during the period of egg-laying and embryonic development. The spring fall of temperature may promotes the expression of this abnormality [11].

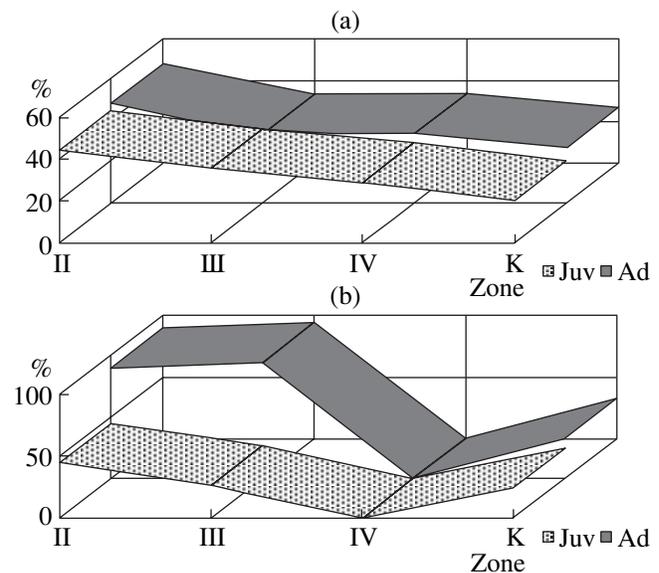


Fig. 2. Age-related changes in morph striata in *R. arvalis* (a) and *R. ridibunda* (b) populations. Juv, juveniles; Ad, adults.

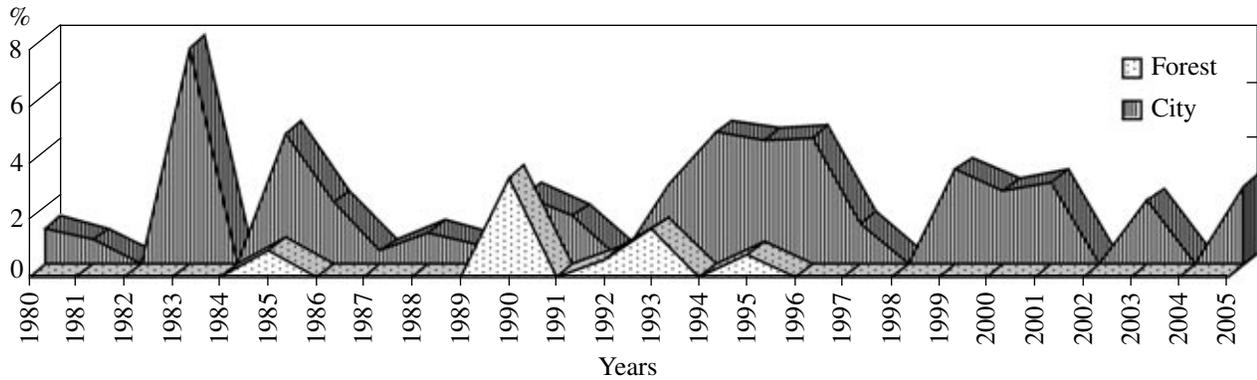


Fig. 3. The frequency of iris depigmentation in juveniles of *R. arvalis* in the urban and suburban populations (%).

In the urban and forest populations of *R. arvalis*, the frequency of this phenotype decreases in the adults as compared to the yearlings (Fig. 4).

In general, the trait frequency is 4.9 times ($\chi^2 = 12.39$; $P < 0.001$) higher in the yearlings than in the adult individuals. In our view, homozygosity of the latter may have a negative effect on their viability. A single phenotypically expressed trait is apparently accompanied by a complex of homozygous recessive parameters leading to low viability because of inbreeding depression [24–26].

For the entire period of our observations, the above abnormality was recorded in *R. temporaria*, which is related to *R. arvalis*, only in two yearlings (0.045%, $n = 4459$) and in a single adult (0.19%, $n = 531$) on the urban territory and was not observed in suburban population. Such rare incidence of this deviation in *R. temporaria* may be explained by more important role in ontogeny of the hereditary component as compared to *R. arvalis*, as well as by ecological plasticity [27] and high cold resistance [28, 29] of the former species.

Rana arvalis and *R. ridibunda* are the species that have such a genetic variant as morph striata and they display a high tolerance to anthropogenic transforma-

tion of the environment. Phenotypic expression of the dominant striata trait differs from that of the recessive trait, iris depigmentation (Figs. 1, 3), by high penetrance independent of seasonal factors.

Thus, the dominant mutations promote rapid adaptation of their carriers. Conversely, the recessive mutations potentially reduce viability of an individual.

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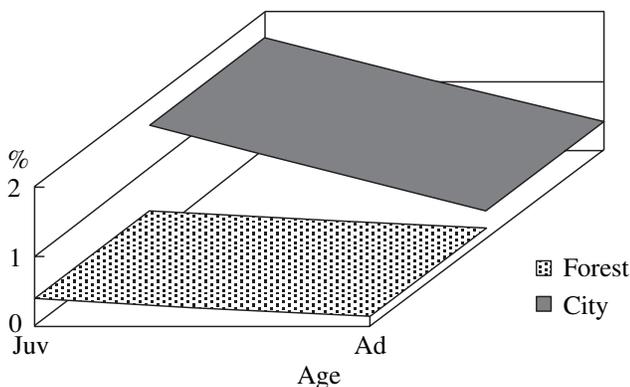


Fig. 4. Age-related changes in the frequency of iris depigmentation in urban and suburban populations of *R. arvalis*. Juv, juveniles; Ad, adults.

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