June 1995 *Asiatic Herpetological Research* Vol. 6, pp. 120-131

On the Inheritance of the Mid-dorsal Stripe in the Iranian Wood Frog (*Rana macrocnemis*)

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Abstract. -The frequency of the phenotype *Striata* (presence of a light mid-dorsal stripe) is often used in population investigations of anurans. Simple hereditary nature of this character was established experimentally. Nevertheless, animals with a poorly developed stripe can be found in populations of some species, together with non-striped specimens and clear *Striata*. in the frog, *Rana macrocnemis*, the expression of the mid-dorsal stripe varies continually. Poorly striped frogs prevail in some populations. We examined morph distribution among froglets obtained from seven *R. macrocnemis* pairs whose eggs and larvae developed at 18, 25, and 29°C. Non-striped froglets predominate in the offspring of non-striped parents and striped in the offspring of striped frogs. Non the less, all phenotype spectra, from specimens with a clear stripe to non-striped animals, are represented in almost all groups. The morph distribution is quite continual and the character varies as a quantitative one. When the developmental temperature increases, the frequency of the morph predominating in optimal conditions (18°C) declines with the increasing frequency of poorly striped froglets. Modifications of the character under the influence of thermal conditions shadows genetic specifics of sibling groups. Similar influence of conditions on the morph distribution in froglets was found in natural populations. Morph distribution among newly emerged froglets affects morph distribution of adults in the populations two years later

Key words Amphibia, Anura, Ranidae, *Rana macrocnemis,* inheritance, Georgia

Introduction

Specimens with a high mid-dorsal stripe can be found among a lot of anuran species. This character (phenotype *Striata*) appears in representatives of systematically distant anuran families. Sometimes a light stripe appears as a specific character (e.g. in the frog *Rana amurensis* or among some boreal toads). In other species, *Striata* appears as a morph and within the same population non-striped as well as striped animals can be found. Prevalence of this morph is species-specific. For instance, if among *Discoglossus pictus* or some *Eleutherodactylus* striped animals predominate (Duellman and Trueb, 1986), in *Rana temporaria* they are sparse (Istchenko, 1978) and in *Occidozyga laevis* only a few striped juveniles could be found (our unpublished data).

Anuran species among which a mid-dorsal stripe appears can be divided into two groups independently of their systematic position. The first group includes species in which the mid-dorsal stripe appears as a very clear and discrete character, and striped animals can be divided from non-striped ones easily. There are, for example, some representatives of the genus *Rana*:: *Rana cf. esculenta*, *R. nigromaculata*, brown frogs *R. sylvatica*, *R. arvalis* (Istchenko, 1978). The second group includes species having often or always softened stripe, characterized by the absence of a clear border between the stripe and ground color of dorsal surface. These include some brown frogs (*R. temporaria*, *R. chensinesis*, *R. macrocnemis*) among others. Specimens with a clear mid-dorsal stripe, as well as with a softened stripe, can be found in *R. macrocnemis* only (Istchenko, 1978). Moreover, in populations of these species, the degree of development of the mid-dorsal stripe varies continually. If numerous specimen samples are taken, a range from quite unstriped to very clear *Striata*-s may be constructed. These extreme phenotypes may be connected by animals with softened stripe (*Pseudostriata* phenotype group).

Inheritance of the Striata phenotype was examined experimentally. It was established that, in different anuran families, the hereditary mechanism may be similar and dependent on the effect of the fully-dominant autosomal gene. It was shown, for instance, on *Eleutherodactylus ricordii* (Goin, 1947), *Rana nigromaculata* (Morya, 1952), *R. sylvatica* (Browder et al., 1966), *R. arvalis* (Stchupak, 1977; Stchupak and Istchenko, 1981), *R. ridibunda* (Berger and Imietowski, 1982). Simple hereditary nature was established for the coloration of the mid-dorsal stripe of *Acris crepitans*, as well (Pyburn, 1961). That is the reason of wide exploitation of the character in population-genetic investigations, especially of frogs from the genus *Rana* (Stugren, 1966; Fishbeck and Underhill, 1971; Istchenko, 1978; Pikulik, 1985; Gogoleva, 1985; Shibata, 1988; Kubantsev and Peskova, 1989 etc.). Nonetheless, the frequency of the *Striata* morph has been used as the index of isolation degree (Stugren, 1966; Pikulik, 1985; Shibata, 1988) or as the instrument of the natural selection investigations (Fishbeck and Underhill, 1971; Istchenko, 1978; Vershinin, 1987 etc.). Presence of a poorly expressed stripe in some species made us use mid-dorsal stripe in the phenetical investigations with care. Inheritance of *Pseudostriata* is not clear. For *R. limnocharis*, Moriwaki (1953) supposed polyallelic inheritance; there are no data for other species. In any case, connections between characters *Pseudostriata* and *Striata* must be present. Continual connections between morphs, e.g. in *R. macrocnemis* makes possible modifications of stripe development under environmental conditions, like most other quantitative characters. Variations of mid-dorsal stripe expression during the life span of individual *Rana temporaria* specimens was noted (Heran, 1986). Earlier (Tarkhnishvili and Mamradze, 1989; Mamradze, 1990) we showed that *Striata* and *Pseudostriata* phenotypes frequency in *R. macrocnemis* sibling groups can be modified as a result of temperature variability by which larval development takes place. This present article describes the results of the more detailed experiments and field observations on the Iranian wood frog populations.

Materials and Methods

Experiment. Adults of *R. macrocnemis* (7 pairs) were obtained in 1989 from a hibernation site in Satovle Mountain ridge (eastern Georgia, surroundings of Tbilisi). Mid-dorsal stripe expression differs in different specimens. We divided frogs conditionally in non-striped ones *(Maculata; M)*, specimens with poor enlightment in the middle-- or hind part of the dorsal surface *(Pseudo-pseudostriata; PPS)*, with poorly developed *(Pseudostriata; PS)* or clear *(Striata; S)* mid-dorsal stripe. The description of the parents (male phenotype/female phenotype) is: pair 1-M/M; 2-M/M; 3-M/PPS; 4-M/PPS; 5-PS/M; 6-M/PS; 7-PS/S. We selected 3 groups of 40 eggs from each of the 7 clutches obtained. Groups were placed in 40-l aquaria with aeration and stable temperature of 18, 25 and 29°C. Tadpoles were fed boiled spinach. Half of the water volume was renewed every second day. After metamorphosis, the complete phenotype of each froglet (M, PS or S) was described. Therefore, 20 experimental sites were elaborated (tadpoles from the 7th clutch developed under 29°C died before metamorphosis had begun).

Field Data. During 1989, 1990 and 1991 in a local population of *R. macrocnemis* from Borjomi Canyon (central Georgia), the ratio of phenotypes M, PPS, PS and S were investigated. We separately analyzed the distribution of different morphs in adult frogs, juveniles, and in 16 groups of froglets emerged from different ponds and pools (each sample included 20-44 froglets). There are more than 60 spawning sites in the population investigated, but every year 2 or 3 water bodies ensure about 90% of the whole generation. Comparative part of each water body was established as well as the number of clutches deposited in each of them (Tarkhnishvili, in press).

For the comparison of morph distribution between different samples, we

TABLE 1. Significance of the differences in morph distribution between experimental groups (values of λ -test).

At 18°C	Sibling group number					
Group No.	1	2	3	4	5	6
2	-					
3	1.56+	-				
4	2.19+++	2.63+++	-			
5	3.00+++	1.83+++	1.43+	-		
6	3.62+++	3.26+++	2.32+++	1.47+	2.10+++	
7	4.55+++	4.36+++	3.33+++	2.40+++	3.08+++	-
At 25°C	1	2	3	4	5	6
2	-					
3	1.53+	1.42+				
4	2.18+++	2.13+++	-			
5	2.53+++	2.42+++	-	-		
6	2.97+++	2.80+++	1.49+	-	-	
7	3.63+++	3.40+++	2.15+++	-	1.79++	-
At 29°C	1	2	3	4	5	6
2	-					
3	-	-				
4	-	-	-			
5	-	1.52+++	-	-		
6	1.99+++	2.07+++	1.61++	-	1.86++	

Note:
+ = P 0.05
++ = P 0.001
+++ = P 0.001

used the Kolmogorov-Smirnov λ-test. We compared the frequency of M, PS (PPS+PS) and S phenotypes in different groups using Fisher's F-test (Zaitsev, 1984).

Results

Experimental data. The distribution of different morphs in the 20 experimental froglet groups, obtained from 7 clutches and developed under the different conditions, is shown in Figure 1. Some main results of the experiment must be noted. Dominance of the S-gene excludes clear-striped animals' appearance among the offspring of non-striped parents; but independently of developmental conditions in offspring of the pair 1 froglets of the S-phenotype present. Morph PS appears in each sample. There are a few non-striped froglets among group 7 (male of S-phenotype) but their frequency is significantly lower than 25 or 50% that could be expected if, in the genotype of parents, the recessive gene M is present. Besides that, the inheritance ability of a mid-dorsal stripe is obvious. After development under the optimal thermal conditions (18°C), differences in the morph distribution between most of the samples, excluding froglet groups with the same or very similar parents' phenotype, are significant (Table 1). Among the offspring of the pairs 1 and 2 (M/M), non-striped specimens predominated; their frequency was significantly higher than even the 3rd or 4th pairs (M/PPS) offspring. Correspondingly, among group 7 (parents PS/S), non-striped morph was significantly lower than in other groups. There is shown the significance of

TABLE 2. Inter-group differences in the frequency of each morph separately (F-test).

Groups Compared	Phenotypes								
	M			PS			S		
	18°C	25°C	29°C	18°C	25°C	29°C	18°C	25°C	29°C
1 and 2	-	-	-	+	-	-	-	-	-
1 and 3	+++	++	-	++	-	-	++	++	-
1 and 4	+++	+++	+	+	-	-	+++	+++	++
1 and 5	+++	+++	+	+++	++	+	++	+++	-
1 and 6	+++	+++	++	+	+	-	+++	+++	+++
1 and 7	+++	+++	?	-	-	?	+++	+++	?
2 and 3	++	++	++	-	-	-	+++	+++	++
2 and 4	+++	+++	++	-	-	-	+++	+++	+++
2 and 5	+++	+++	++	++	+++	+++	+++	+++	-
2 and 6	+++	+++	+++	-	-	-	+++	+++	+++
2 and 7	+++	+++	?	-	-	?	+++	+++	?
3 and 4	-	-	-	-	-	-	-	-	-
3 and 5	++	+	-	+	-	-	-	-	-
3 and 6	+++	+++	-	-	-	?	+++	-	+++
3 and 7	+++	+++	?	-	-	-	+++	+++	-
4 and 5	-	-	-	++	+	+	-	-	+
4 and 6	++	+	-	-	-	-	++	-	+
4 and 7	+++	+++	?	-	-	?	+++	+	?
5 and 6	-	-	-	++	+	++	+++	-	+++
5 and 7	+++	++	?	+++	++	?	+++	+++	?
6 and 7	+	-	?	-	-	?	-	+	?

Note: - = insignificant
\+ = P 0.05
++ = P 0.01
+++ = p 0.001

inter-sample differences in Table 2. In all, along the road of 1-7 groups, frequency of M-phenotype decreases and frequency of S-phenotype increases significantly but gradually. Frequency of (PS)-morphs increases gradually from the 1st to the 5th group (PS/M) and decreases again among the 6th and 7th groups.

Developmental conditions of larvae affect the ratio of different morphs. When temperature increases, especially from 25 to 29°C, in pair 3-6 offspring (information of group 7 absent) frequency of S-morph decreases significantly. These groups are established by frogs with mid-dorsal stripe, even very pale or lightened. This time, a few S-morph froglets among groups 1 and 2 appear independently of the thermal conditions. On the other hand, frequency of non-striped morph in group 1 decreases significantly as a result of high developmental temperature. Inversely, among groups 5 and 6 (parents PS/M and M/PS) part of the non-striped morph increases, especially between 25 and 29°C. At least among most of the groups frequency of PS+PPS morph group slightly increases under high developmental temperature (see Fig. 1 and Table 3). Thus variation of the developmental conditions during the larval period can affect, but in different ways, the ratio of the phenotypes in the froglet groups. We can not conclude

TABLE 3. Significance of the phenotype frequency changes under the thermal conditions.

Sibling Group	Difference of thermal conditions between 18°C to 25°C M	 (PS)	 S	 25°C to 29°C M	 (PS)	 S	 18°C to 29°C M	 (PS)	 S
1	-	-	-	-	-	-	++	++	-
2	-	-	-	-	-	-	-	-	-
3	-	-	-	-	-	++	-	-	-
4	-	-	-	-	-	+	-	-	-
5	-	-	-	+	-	+++	-	-	++
6	-	+	-	++	+	-	+	-	+
7	-	-	-						

Note: -, +, ++ and +++ are significance levels.

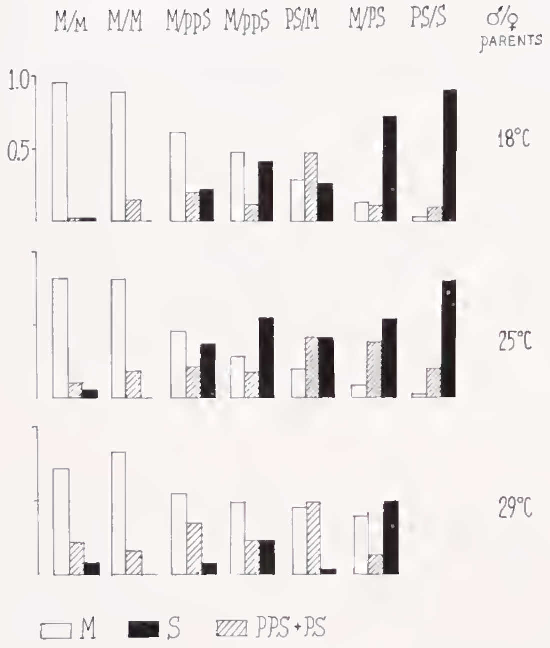

FIG. 1. Frequency distribution of morphs in experimental froglet groups.

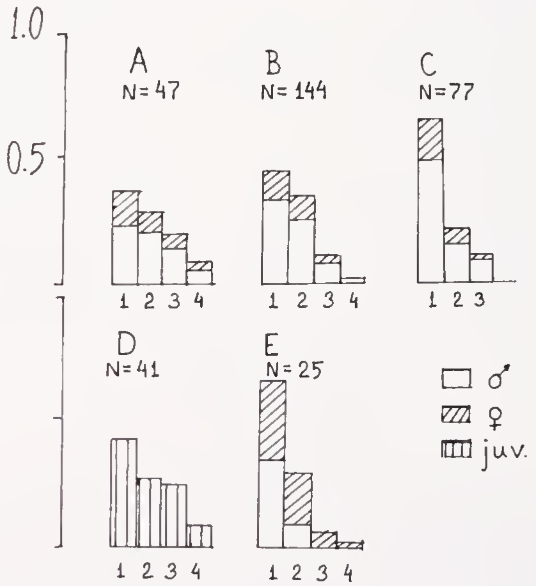

FIG. 2. Frequency distribution of morphs in natural populations. A- adults from Borjomi Canyon in 1989; B- adults from Borjomi Canyon in 1990; C- Adults from Borjomi Canyon in 1991; D- juveniles from Borjomi Canyon in 1989; E- adults from Satovle Mountain ridge in 1989. 1- *Maculata;* 2- PPS; 3- PS; 4- S.

that the rise of temperature always increases or decreases the percentage of striped frogs. Rather it declines frequency of display of the genotype predominating. In other words, the comparative part of heredity in determining the morphological features of the group decreases. This is illustrated in Table 1. Inter-group differences so clear in optimal conditions, after development in warm water often became non-significant. Perhaps the reason for this phenomena is the changing in expression of the stripe. In warm water, the part of genetically striped specimens processes determining the appearance of stripe are delayed and only non-clear stripes develop. Inversely, the

TABLE 4. Significance of the differences in morph distribution between groups emerged from the sites 9, 11 (1989) and 12 (1990), and that which emerged from another site (values of the λ-test).

	1a	2a	3a	4a	5a	6a	7a	8a	9a	10a	11a	12b	13b	14b	11c	12c	15c
	+++	+++	-	++	-	++	-	-	-	-	+++	-	-	+	+	-	+
9a	2.00	1.97		1.90		1.88					2.39			1.60	1.46		1.86
	-	-	-	-	+	-	-	+	+	-	-	++	-	-	-	-	-
2a					1.60			1.58	2.39			1.82					
	+	+	-	+	-	-	+	-	-	-	-	-	-	-	-	-	+
12b	1.44	1.45		1.36			1.43										1.42

Note: Numbers 1-15 are the pond number from which the froglets emerged.
a = generation of 1989
b= generation of 1990
c = generation of 1991
+, ++, and +++ are significance levels

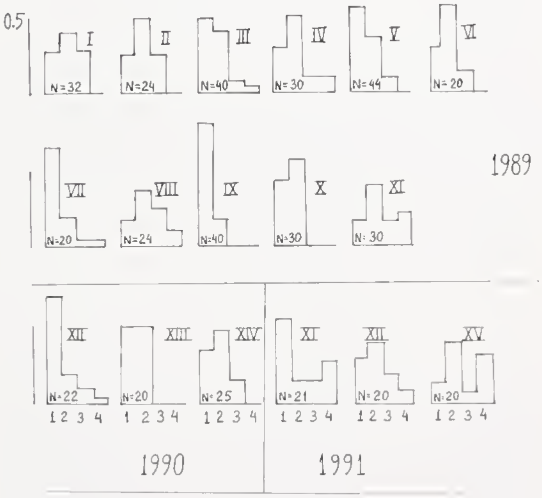

FIG. 3. Frequency distribution of morphs in frogs that emerged from natural ponds and pools in Borjomi Canyon. I-XV- number of the water body; N- sample size; Phenotypes: 1- M; 2- PPS; 3- PS; 4- S.

part of genetically non-striped frogs can be turned into the PS-category.

Field data. Morph frequency distribution among the adult frogs from the natural population is shown in Fig. 2. The sexual differences are not significant. The differences between these samples are the sample collected in 1991: λ= 1.51 (1989-1991) - 1.41 (1990-1991) (P<0.05). It correlates with an increase of non-striped frogs to 65% in this year ($F=10.11^{xx}$) and the disappearance of the froglets with a clear mid-dorsal stripe ($F=13.34^{xxx}$). Interestingly, morph distribution in the investigated population became similar to morph distribution in the population from the Satovle Mountain ridge (this is a drier habitat distant from the former by 100-150 km) (Fig. 2e). Note that in both population, S-morph frequency is lower than in other populations of *R. macrocnemis* investigated earlier (Istchenko, 1978), but the frequency of the frogs with poorly developed stripes remain very high. Phenotypic distribution of sub-adults and juveniles in 1989 (Fig. 2d) is similar to those of adults during 1989-1990.

A great part of animals in brown frog populations begins to breed after the 2nd to 3rd hibernation (Istchenko and Ledentsov, 1987; Ledentsov, 1990). We can not exclude the fact that froglets which emerged in 1989 could participate in the formation of the generation that emerged during 1991. Therefore, analysis of their phenotypic distribution appears interesting. During 1989, froglet groups that emerged from 11 small water bodies were described. Results are shown on Fig. 3. Because of the small volume of sample differences between them, it appears non-significant in most cases. Only froglets from the water bodies 9 and 11, moreover from 12 (1990) are significantly different from most other groups (Table 4). Spawning sites 9 and 12 are well warmed pools, filled with vegetation. Daily temperature during the developmental period often exceeds 30°C. Among the froglets that emerged from these pools, the non-striped morph predominates. The percent of the S-morph (in site 9, this morph is absent), as well as PS and even PPS, is low. Inversely, site 2 is self-flowing and shadowed. Vegetation is absent and the water temperature do not exceed 20°C, even during the warmest days. PS and PPS morphs predominate here, and the percent of the S-morph exceeds 20.

There is the question of whether the differences noted above can reflect non-random distribution of the parent's morphs along the different spawning sites. On the one hand, the displacement of warmed and shadowed sites are irregular in the habitat examined, and striped frogs have equal possibility of spawning in different water bodies. On the other hand, only a few clutches (4 and 7 correspondingly) were deposited in sites 9 and 11 during 1989. Morph distribution in the froglets could be the consequence of random processes as a result. But, as many as 93 clutches were deposited in site 12 (1990). It is quite a representative sample of the population, numbering 1037 adult females in all (1990). This time, the frequency of non-striped froglets emerged from site 12 (68%) is instantly higher than M-morph frequency among adult frogs (45%). Moreover, during 1991 in site 2, already 37 clutches were deposited, but the frequency of S-morph among froglets even slightly increased. Therefore, we can suppose non-random reasons of the morph distribution in the groups of froglets emerged from different spawning sites. The frequency of one or another morph depends on the physical conditions under which larval development takes place. This is argued by the significant differences in phenotypic structure between froglets that emerged from different water bodies as well as between the young generation and adult animals. The stability of the morph composition of groups emerging from the same site, but in different waters, is additional evidence.

Above, we told about the increase of the non-striped morph in 1991 to 65%. It may be connected with the increasing of the comparative part of warmed pools during previous years. For instance, spawning site 5 produced at least 45% of the total number of the 1989 generation (about 20,000). In that time, the frequency of M-morph approached 55% and not one froglet with a clear stripe was found. Most of the other sites producing metamorphosis in 1989 were warmed. Shadowed site 2 (17% M and 23% S) produced not more than 25% of the generation. In 1990, the situation changed in *Maculata's* favor still more. There were 68% of froglets of this phenotype that emerged from site 12 (site 12 produced about 70% of the generation numbering 44,000 froglets). Perhaps in the future, we can suppose still more increase of non-striped morph's comparative part and a decline of the striped animals' frequency in the investigated population.

Discussion

Two directions of the S-morph frequency investigations in amphibian population can be noted. The first is the analysis of geographic variations of morph frequency in populations of different species. The second one is to study the dynamics of polymorphism of separate populations including age-dependent changes of morph distribution. The summarizing bibliography following must be noted.

Geographic variation. There is no good evidence of clear clinal variations of frequency of the morph *Striata* in a single species. Stugren's conclusion (1966) about increasing of frequency of striped frogs in *Rana arvalis* toward the east was refuted by Istchenko (1978). In some cases (i.e. *R. arvalis* and *R. temporaria* in Belorussia), the percent of striped frogs increase toward the north (Istchenko, 1978; Pikulik, 1985), but in the populations of *R. arvalis* from the Urals or of *R. semiplicata* from the Russian Far East, the inverse situation was noted (Toporkova, 1965; Istchenko, 1978). On the other hand, irregular but clear interpopulational differences in S-morph frequency are common in different species' populations (Masalikin, 1985; Panchenko, 1985; Shibata, 1988 etc.). The frequency of the S-morph in *R. arvalis* may increase under the hardening of antropogenous pressing (Vershinin, 1987). Therefore, frequency distribution of phenotypes in the separate populations of some species depend highly on the climatic or microhabitat conditions but not on historical reasons. Interestingly, when the coexistence of *R. temporaria* and *R. arvalis* populations takes place (in the Middle Volga) the same environmental conditions ensure parallel variations in population morphology (Lebedinski et al., 1989)

Intrapopulation dynamics.
Comparative frequency of different morphs may vary between years and separate generations (Istchenko, 1978). Influence of the pond conditions on the morph distribution in *R. macrocnemis* froglet groups was described by this author. Besides, morph distribution in the generation could be changed in relation to animal age. For some *R. arvalis* populations, decreasing of S-morph frequency in adult animals was established in comparison to juveniles (Pikulik, 1985; Vershinin, 1987). Inversely, in the same species, increasing of the comparative part of striped animals was recorded for the older age groups (Istchenko, 1978). Therefore, the morphological features of the population may be changed rapidly and instantly by environmental conditions. There is the mean adaptation on the population level. Istchenko (1978) supposes that rapid reactions of morph distribution on the environmental conditions take place because of the elective elimination of animals. Rapid modifications of the genotypes' distribution is the result of this process. Selection may be connected not only with preferences of striped or non-striped frogs but also with elective elimination of larvae accordingly to their genotypes. For instance, larvae of *Striata* genotype are more vulnerable to the high density and shortage of the oxygen because of the abnormally high metabolic rates (Schvarz and Istchenko, 1968). On the other hand, the adult *Striata*-s are less susceptible than other frogs to drying and are characterized by high migration ability. Correspondingly, in some ecosystems with unfavorable conditions, striped specimens predominate (Istchenko, 1978; Vershinin, 1987).

Therefore, the influence of the developmental conditions on the ratio of striped and non-striped morphs in the generation may be considered well-grounded. The role of the developmental sites' type is obvious and our data are in accordance with this fact. All the researchers agree that the phenomena depends on the elective elimination.

It is not possible in practice to only conduct field investigations. What is the part of individual modifications in the process of morph distribution changing? High natural mortality, especially during the larval stages, does not allow us to exclude the effect of natural selection. Thus, each explanation depends on a prior opinion of the concrete researcher. For instance, in field conditions, information principally similar to our experimental data was obtained by Stchupak (1975). Increasing the frequency of genotype S or M has inverse reaction of larval grouping as the result: the comparative part of the dominant phenotype decreases by the completion of metamorphosis. The author explains this fact as the result of frequency-dependent selection.

Part of the phenotypic modification during the early development can be established only in experiments where larval mortality can be neglected. The experiment described above illustrates the main part of modifications taking place during larval development. We conclude that in some specimens displacement of the characters in the road of alternative variants could be changes as a result of temperature changes.

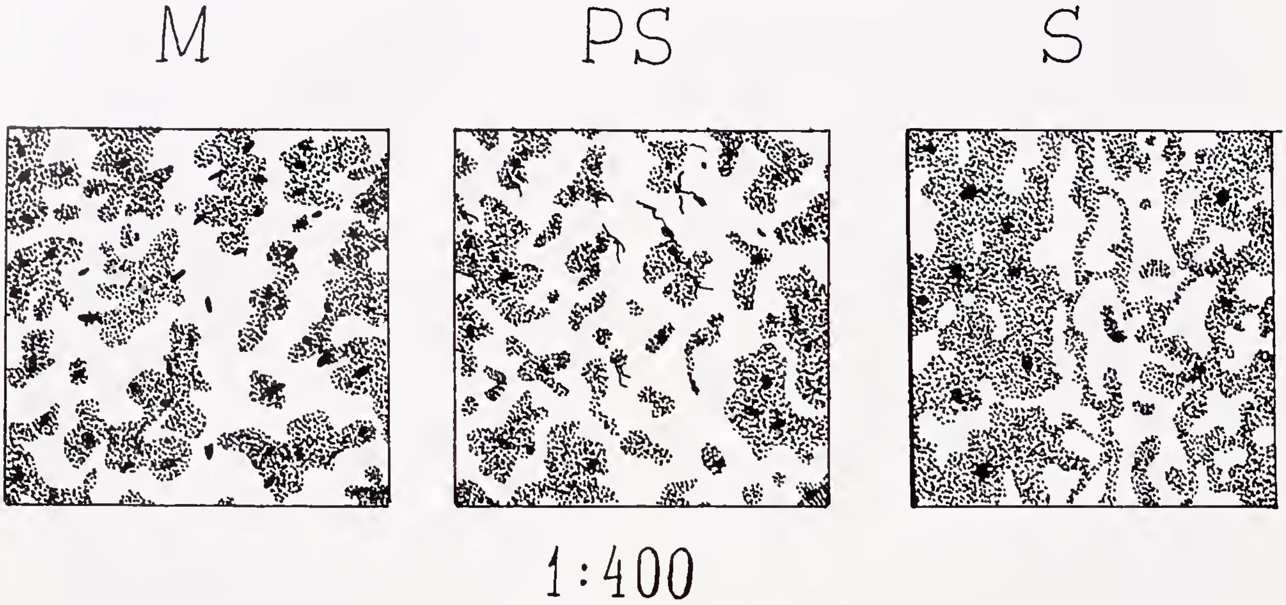

FIG. 4. Distribution of the pigmental cells in the mid-dorsal area of froglets that have different phenotypes. Magnification is X400.

It brings us to suppose that morphological specifics of froglet groups is provided not only by elective elimination but by phenotypic modifications as well. What is the comparative part of this latter could be shown by further investigations.

Experimental results described here and evidence in favor of the main part of phenotypic modifications are obtained namely for *R. macrocnemis*, not surprisingly. This is the only boreal brown frog in which non-striped and striped morphs are connected by continual intergradations (Istchenko, 1978) and practically the character "presence of the mid-dorsal stripe" varies as the quantitative one. On the one hand, it may be connected with the specific nature of the character inheritance in this species; but it is less possible. More realistic is taking in our opinion that every character, both quantitative and qualitative, are determined by quantitative morphogenetic processes. Thus development of coloration of the mid-dorsal stripe in *Acris crepitans* is determined by the size of pigmental cells and genetical specifics of morphs may be shaded (Gray, 1972). We observed the dorsal surface of *R. macrocnemis* froglets with different coloration patterns under a binocular. Presence of the mid-dorsal stripe depends on the rate of pigment concentration declining toward the dorso-medial line (Fig. 4). The lower density of the pigmental cells along the mid-dorsal line in all froglets can be observed. But to distinguish the stripe with the naked eye, the gradient of pigmental cells concentration must be expressed enough or exceed a certain threshold. Morphogenetically, the presence of the gradient is determined by the kinds of melanophorisation of the dorsal surface before metamorphosis: the mid-dorsal surface is filled in by pigmental cells at the end. The phenotype of the froglet: S, PS, PPS or M which appears to correspond with the degree of filling in the mid-dorsal surface by melanophores just before metamorphic climax has begun. The hereditary mechanisms keep the main part of this process but regulation of morphogenesis by the environment is important, too. Perhaps comparative significance of the environment increases in non-optimal conditions.

Perhaps in the base of phenotype formation in species characterized by severe alternative variation of the character (e.g. *R. arvalis* or *R. ridibunda)* the same morphological processes occur. But, in these species, inter-gradations between S- and M- morphs are absent. It may depend either on greater part of hereditary in stripe determination among these species or on a more expressed threshold level. It must be explained. Developmental processes which form the ground of coloration pattern formation may finish in some developmental stage before metamorphosis has began. One or another phenotype could be formed depending on if the process exceeds some threshold level or not. Depending on the expression of this threshold or prolongation of final stage of color formation (when basic processes are completed) takes place either in continual distribution of morphs (as in *R. macrocnemis*) or in bi-modal distribution (as in *R. arvalis*).

The scheme described above, as we can see, does not exclude identity of the inheritance nature of the *Striata* in *R. macrocnemis* to those in *R. arvalis* or other anurans. But, it does not allow us to neglect the modification ability of this character in the population investigations, especially in species with continual distribution of the stripe expression. Perhaps in some cases, the quantitative value of pigment cell density along the mid-dorsal line can be a more adequate index of the mid-dorsal-strip development.

We took into consideration the evidence data of differential survival ability of S- and M- genotypes (Schvarz and Istchenko, 1968). In part, a higher mortality of tadpoles with S-genotype was established when a high density or an oxygen shortage takes place. Increasing the developmental temperature could have the same effect. But, not only the death of S- tadpoles can be a result of the worsening of environmental conditions: they can modify their genotype without lacking of survival ability. Perhaps, the character *Striata* correlates with the intensification of metabolism, not at a genetical but rather at an epigenetical level. Processes which take part in the mid-dorsal stripe formation also affect intensification of energetic exchange. If intensity of these processes change, neither their morphological nor physiological results appear. There is an interesting example of the phenomena when modifications during the separate animal's life results similarly to a short-term selection at the population level. It appears as one of the hard moments in micro-evolutional investigations but would not be neglected.

Acknowledgments

I greatly appreciate my wife, R. Mamradze, for her help in the elaboration of the experiment. I also appreciate J. Manukjan and S. Tzabadze for their help in the experimental and field work, and to J. Ilieva for reading the manuscript.

Literature Cited

BERGER, J. AND J. IMIETOWSKI. 1982. Inheritance of vertebral stripe in *Rana ridibunda* Pall. Amphibia-Reptilia 3,(2-3):145-151.

BROWDER, L. W., J. C. UNDERHILL AND D. J. MERREL. 1966. Mid-dorsal stripe in the wood frog. Journal of Heredity 57(2):65-67.

DUELLMAN, W. E. AND L. TRUEB. 1986. Biology of amphibians. McGraw-Hill Book Company. i-xvii + 1-670.

FISHBECK, D. W. AND J. D. UNDERHILL. 1971. Distribution of stripe polymorphism in wood frogs, *Rana sylvatica*. Le Conte, from Minnesota. Copeia 1971(2):253-259.

GOGOLEVA, N. P. 1989. [Polymorphism in anuran populations]. Pp. 26-29. *In* N.N. Szczerbak (Ed.) (Proc. 7th Sov. Herpetol. Symp.). Kiev, Naukova dumka. (In Russian).

GOIN, C. J. 1947. Studies in the life history of *Eleutherodactylus ricordii planirostris* (Cope) in Florida. Univ. Florida publ. Biol. Sci. 4(2):1-56.

GRAY, R. H. 1972. Metachrosis of the vertebral stripe in the cricket frog *Acris crepitans*. American Midland Naturalist 87(2):549-551.

HERAN, I. 1986. Comments on coloration and color changes in *Rana temporaria* L. Pp. 267-270.

In Z. Rocek (Ed), Proc. Eur. Herpetol. Meet, Prague.

ISTCHENKO, V. G. 1978. [Dynamic polymorphism of brown frogs of the USSR fauna]. Moscow, Nauka. 148pp. (In Russian).

ISTCHENKO, V. G. AND A. V. LEDENTSOV. 1987. [Environmental influence on the age structure dynamics in the moor frog populations]. Pp. 40-51. *In* L. M. Suzumova (Ed), Vlijanie sredi na dinamiku structuri I chislennosti populacij zhivotnih. Sverdlovsk, Ural Sci. Cent. Acad. Sci. USSR. (In Russian).

KUBANTSEV, B. S., T. J. PESKOVA AND I. GORODNICHEVA. 1989. [On the variation of some tailless amphibian species' coloration]. Pp. 126-127. *In* N.N. Szczerbak (Ed.), Voprosi gerpetologii. Kiev, Naukova Dumka. (In Russian).

LEBEDINSKI, A. A., T. B. GOLUBEVA AND V. I. ANISIMOV. 1989. [Polymorphism among brown and green frogs under the antropogenic pressure]. Pp. 139-140. *In* N.N. Szczerbak (Ed.), Voprosi gerpetologii. Kiev, Naukova Dumka. (In Russian).

LEDENTSOV, A. V. 1990. [Dynamics of the age structure and number of the reproductive part of the moor frog *(Rana arvalis* Nilss.) population]. Reph. Dissertation Cand. Biol. Sci. Sverdlovsk, Ural Sci. Center Acad. Sci. USSR. 23pp. (In Russian).

MAMRADZE, R. G. 1989. [Effect of the thermal conditions on the frequency of the phenotype *Striata* in Iranian wood frog]. Pp. 151-152. *In* N.N. Szczerbak (Ed.), Voprosi gerpetologii. Kiev, Naukova Dumka. (In Russian).

MASALIKIN, A. I. 1985. [Populational-phenetic analysis of the fire-bellied toad in the Voronezh reserve]. P. 169. *In* Phenetica populacij (Proceedings of the 3rd Soviet Phenetic meeting, Saratov). Moscow, Nauka. (In Russian).

MELKUMJAN, L. S. AND K. E. VARDANJAN. 1985. [Polymorphism in the transcaucasian populations of lake frog]. Biol. Journ. Armenia 38(3):267-270. (In Russian).

MORIWAKI, T. 1953. The inheritance of the dorso-madian stripe in *Rana limnocharis* Wiegmann. J. Sci. Hiroshima Univ., Ser. Biol. 1(14):159-164.

MORIYA, K. 1952. Genetical study of the pond frog *Rana nigromaculata*.. 1. Two types of *Rana nigr. nigromaculata* found in Tokata district. J. Sci. Hiroshima Univ., Ser. Biol. 1(13):189.

PANCHENKO, I. M. 1985. [Phenotypic variation of moor frog coloration in the flood-lands of Oka River]. Pp. 171-173. *In* Phenetica populacij (Proceedings of the 3rd Soviet Phenetic meeting, Saratov). Moscow, Nauka. (In Russian).

PIKULIK, M. M. 1985. [Amphibians of Belorussia]. Minsk, Nauka i technica. 192pp. (In Russian).

PYBURN, W. F. 1961. The inheritance and the distribution of vertebral stripe color in the cricket frog. Pp. 235-261. *In* Vertebrate speciation. University of Texas Press, Austin.

SCHVARZ, S. S. AND V. G. ISTCHENKO. 1968. [Dynamics of the genetic structure of the moor frog population]. Bull. Mosc. Soc. Nat. Res. Ser. Biol. 73(3)127-134. (In Russian).

SHIBATA, Y. 1988. [Mid-dorsal stripe type of a frog, *Rana limnocharis*, in northwestern islands of Kyushu, Japan (Amphibia: Ranidae)]. Shizenzhi-Kenkyu. (Proc. Osaka Mus. Nat. Hist.) 2(4):69-71. (In Japanese).

STCHUPAK, E. L. 1975. Populational mechanisms of conservation of the genetical structure in the *Rana arvalis* Nilss. population. Bull. Acad. Sci. USSR 222(1):220-222. (In Russian).

STCHUPAK, E. L. 1977. Inheritance of the mid-dorsal stripe in moor frog. Pp. 36-37. *In* Inform. Materials Inst. Plant and Anim. Ecol. Sverdlovsk. (In Russian).

STCHUPAK, E. L. AND V. G. ISTCHENKO. 1981. On the hereditary base of color polymorphism in moor frog *(Rana arvalis* Nilss.). 1: light mid-dorsal stripe. Pp. 128-132. *In* Herpetological researches in Siberia and Far East. Leningrad, Nauka.

STUGREN, B. 1966. Geographic variation and distribution of the Moor frog, *Rana arvalis* Nilss. Ann. Zool. Fenn. 3(1):29-39.

TARKNISHVILI, D. N. In press. Embryonic and larval mortality of the caucasian brown frog in the Borjomi Canyon: peculiarities and the main reasons. Varan, St. Petersburg.

TARKNISHVILI, D. N. AND R. G. MAMRADZE. 1989. Modification of caucasian brown frog's phenotype under the influence of high temperature. Bull. Acad. Sci. Georgia. 135(2):437-440.

TOPORKOVA, L. J. 1965. Geographical variation of the morphological features in amphibians. 1. *Rana terrestria* Andrz. Nauchnie dokladi visshey scholi, Ser. Biol. 1:31-36.

VERSHININ, V. L. 1987. Some features of the phenetical structure of the moor frog groupings in the industrial city. Pp. 74-79. *In* L. M. Süzümova (Ed), Vlijanie sredi na dinamiku structuri I chislennosti populacij zhivotnih. Sverdlovsk, Ural Sci. Cent. Acad. Sci. USSR.