

A contribution to the ecological genetics of frogs: age structure and frequency of striped specimens in some Caucasian populations of the *Rana macrocnemis* complex

David N. TARKHNISHVILI & Ramaz K. GOKHELASHVILI

Group of Population Ecology, Department of Biology, Tbilisi State University, 380030, Chavchavadze avenue 1, Georgia

Four populations of Caucasian brown frogs (*Rana macrocnemis*) from different elevations and different mountain systems (Great and Minor Caucasus) were studied. In populations from the Minor Caucasus, the percentage of striped frogs increases with elevation, but not in the Great Caucasus. At the same time, age at sexual maturity in Caucasus Minor populations does not differ between forest and subalpine populations. It is suggested that in this region the increasing proportion of genetically striped frogs is the main adaptation preventing a decrease of reproductive potential with elevation. In the brown frogs **metapopulation** inhabiting the Great Caucasus, such a mechanism is **absent**.

INTRODUCTION

Specimens with a light mid-dorsal stripe (phenotype "striata") are found in populations of many anuran species. The inheritance of this character has been studied in several ranid species. Various authors have examined progeny produced as a result of crossings between striped and unstriped frogs collected from populations with different frequencies of the striped phenotype. A bright mid-dorsal stripe has been shown to be determined by a simple dominant gene in *Rana limnocharis* (MORIWAKI, 1953), *R. ridibunda* (BERGER & SMIELOWSKI), *R. syhatica* (BROWDER et al., 1966) and *R. arvalis* (SHCHUPAK, 1977; SHCHUPAK & ISHCENKO, 1981), though it has also been found that isolated striped specimens may appear even among offspring of unstriped parents of *R. limnocharis* (MORIWAKI, 1953) and *R. macrocnemis* (TARKHNISHVILI & MAMRADZE, 1989; TARKHNISHVILI, 1995). The most plausible reason for this appears to be the existence of phenocopies.

At the same time, the proportions of striped specimens in populations of some frog species display clinal variations, following climatic and landscape features. For example, the proportion of striped *R. syhatica* in North America generally increases towards the west and north (FISHBECK & UNDERHILL, 1971; SCHUELLER & COOK, 1980). STUGREN

(1966) has shown that the proportion of striped specimens in populations of *R. arvalis* increases in an eastern direction; at the same time, northern populations of *R. limnocharis* in Japan are characterized by a reduced proportion of striped frogs (MORIWAKI, 1953).

Previous authors have connected clinal changes in the proportion of different colour morphs with genetic-stochastic processes (e.g. STUGREN, 1966) or their adaptive importance (e.g. MERRELL, 1969, 1973; NEVO, 1973; DAPKUS, 1976; ISHCENKO, 1978). In particular, for different colour morphs of the **hylid** *Acris crepitans* (the best studied species in this respect), the hypothesis about the direct adaptive value of different colour morphs (for escaping predation) competes with the hypothesis proposing a correlation of these morphs with important physiological characteristics, i.e. **thermotolerance** and desiccation resistance (NEVO, 1973); however, neither of these hypotheses has been supported experimentally (GRAY, 1977, 1978). A similar situation is observed for a light mid-dorsal stripe in brown frogs: e.g. for *R. sylvatica*, SCHUELLER & COOK (1980) suggest an advantage of striped specimens in open areas with the cryptic character of this pattern. Conversely, ISHCENKO (1978) explains differences in the proportion of striped frogs between different populations of *R. arvalis* on the basis of physiological differences between different morphs. SCHWARZ & ISHCENKO (1968), who compared striped and unstriped froglets emerging from the same breeding site, have shown that striped froglets have a relatively large liver, in comparison with unstriped ones, and that their weight increases more rapidly. L. DOBRINSKY (see ISHCENKO, 1978), who used an optic-acoustic gasanalyser, demonstrated that metabolic exchange of striped froglets of *R. arvalis* is especially high: they excrete up to twice as much CO_2 per gram of body mass than unstriped ones. Tadpoles of striped *R. arvalis* need more time for completing metamorphosis (ISHCHENKO & SHCHUPAK, 1974) but, after metamorphosis, their growth is more* rapid than that of unstriped froglets, as shown by repeated measures of froglets with and without stripes, after their emergence from the breeding pond (ISHCHENKO, 1978). VERSHININ (1987) has shown that in **demes** of *R. arvalis* where striped frogs predominate, froglets grow faster.

An interesting case of polymorphism is observed in populations of Caucasian brown frogs (*Rana macrocnemis* complex). Different forms of brown frogs inhabit the Caucasian Isthmus, Anatolia and mountain plateaus of the Middle East. The most widespread ones, *R. macrocnemis* and *R. camerani*, represent closely related taxa included in the *Rana* (*Rana*) *temporaria* group (DUBOIS, 1992). The taxonomic status of these forms is not very clear. Some authors (e.g. MENSI et al., 1992) accept separate specific status of these frogs, while demonstrating their close relations. BARAN and his co-authors (BARAN, 1969; BARAN & ATATUR, 1986) demonstrated the presence of **numerous** populations with intermediate characters, representing a probable hybrid zone between the two species. ISHCENKO & PYASTOLOVA (1973) obtained hybrids from parents caught in typical "*macrocnemis*" and "*camerani*" populations; their viability, at least before and shortly after metamorphosis, was not lower than in control groups. ISHCENKO (1978, 1987) found no consistent morphometric or coloration characters differentiating these two forms. He showed that the multidimensional distance (based on 20 morphometric indices) between separate populations of "*R. macrocnemis*" and "*R. camerani*" in some cases exceeds the distance between populations composed of the two different forms. He concluded that subdivision of Caucasian brown frogs into two species is artificial.

At the same time, two forms of Caucasian brown frogs differ in the extent of altitudinal variation of some characters, in particular the proportion of striped specimens. Traditionally, one of the typical characters separating *R. camerani* from *R. macrocnemis* is a light mid-dorsal stripe (TERENTYEV & CHERNOV, 1940; BARAN, 1969). In frogs inhabiting Caucasus Minor, the proportion of striped specimens rapidly increases with elevation and reaches 80 % in the subalpine belt. This is not observed in the Great Caucasus, though some increase (up to 8 %) in the proportion of striped frogs with elevation can be observed in North Caucasus; in these specimens the stripe is poorly expressed (ISHCHENKO & PYASTOLOVA, 1973).

An increase in the percentage of specimens with a bright stripe at high elevations is clearly expressed in the region of the Trialeti Mountain Ridge (Georgia), bordering the north mountain plateaus of Caucasus Minor. Only a few striped specimens are found in the lowlands and foothills, although they predominate in the subalpine belt, in spite of the short distance between forest and subalpine populations and the very probable inter-population migrations: specimens which had been marked in the forest populations during the breeding period were sometimes caught later near the upper limit of the forest belt (our data), and, thus, the distance between populations does not exceed ranges of individual migrations. There are no barriers preventing interbreeding between frogs inhabiting foothill and subalpine populations. According to our long-term observations, in any population inhabiting the ridge a wide spectrum of phenotypes is found, from typical "*camerani*" with a bright stripe, relatively short legs and sharp snout, to typical "*macrocnemis*", and pair formation among these two forms appears to be totally random. In such conditions, the altitudinal differences we have described must presumably be the result of strong selection favouring striped specimens in the mountains.

The reproductive success of an animal depends on its fecundity, mortality at different stages of its life cycle and the period between successive generations (BEGON et al., 1986). Fecundity, reflected in the number of eggs per clutch, depends directly on body size. Differential mortality of different phenotypes can be estimated from changes in their proportions in consecutive age classes (ISHCHENKO, 1978). The period between generations can be estimated by studying the age distribution of adult animals. In connection with the data on the different growth rates of striped and unstriped frogs, a comparative analysis of the length of generation appears to be especially interesting. We studied the age distribution of five populations of *R. macrocnemis* inhabiting localities at different elevations and including different proportions of striped specimens.

MATERIAL AND METHODS

With the exception of frogs from **Borjomi** Canyon, animals were collected mainly during the period April to July, **1993** and **1994**, from the following localities (fig. 1, Table I).

(1) Borjomi Canyon, western foothills of the Trialeti Mountain Ridge, northern slope. Forested canyon of the river Nedzura. Elevation **900-1100** m. Annual precipitation 1000-1200 mm (VLADIMIROV et al., 1991). Winter mild and wet. Period of activity for amphibians about six months, from the beginning of April to the beginning of October.

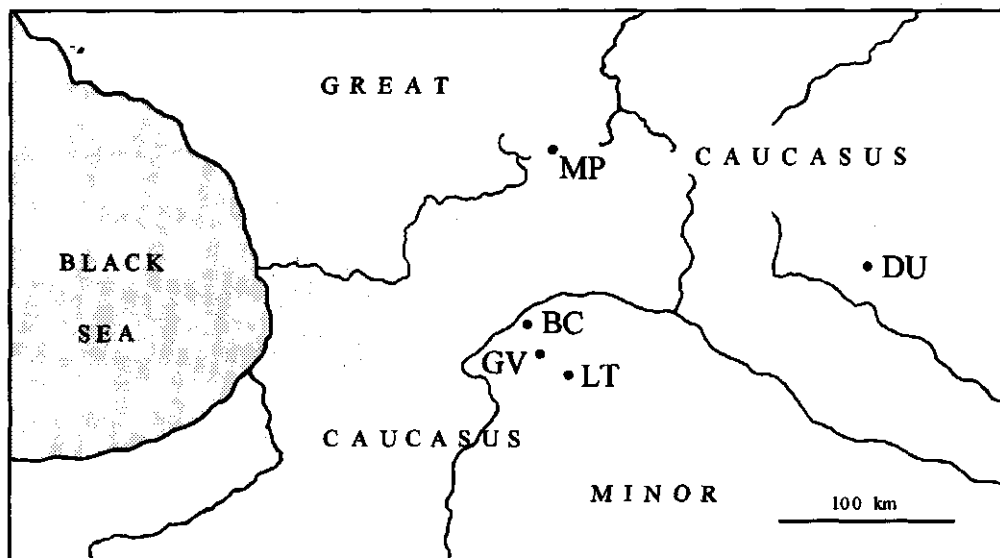


Fig. 1. — Map of Georgia, with indication of studied localities. BC, Borjomi Canyon; GV, Gujareti Village; LT, Lake Tabatskuri; MP, Mamisoni Pass; DU, Duruji Upstreams.

Total number of studied specimens, during two reproductive seasons (1992-1993), 138 adults: 106 males and 32 females.

(2) Gujareti Village. Western part of the Trialeti Ridge, northern slope. Subalpine meadows. Elevation 1900 m. Annual precipitation 800-1000 mm. Winter cold and dry. Period of activity for amphibians about four months, from the beginning of May to the beginning of September. Total number of studied specimens 47: 13 adult males, 6 adult female, 28 yearlings (body length 20-45 mm).

(3) Lake Tabatskuri, southern slopes of Trialeti Ridge, north-west of Javakheti Plateau, Caucasus Minor. Mountain steppe. Elevation 2000 m. Annual precipitation 1000 mm. Winter cold and dry. Period of activity for amphibians four months, from early May to early September. Total number of studied specimens 63: 27 adult males, 13 adult females, 23 juveniles.

(4) Upstreams of the river Duruji, southern slopes of the eastern part of the Great Caucasus Mountain Ridge, in Kvareli District of Georgia. Subalpine meadows on the upper edge of the forest belt. Elevation 1950-2000 m. Annual precipitation 1500 mm. Period of activity for amphibians about five months, from early May to late September. Total number of studied specimens 22: 21 adult males, 1 adult female.

(5) Surroundings of the Mamisoni Mountain Pass in Racha Province, the central part of the Great Caucasus, southern slopes. Alpine meadows. Elevation 2550 m. Annual precipitation 1500 mm. Period of activity for amphibians about three months, from mid-May to the end of August. Total number of studied specimens 22: 21 adult males, 1 adult female.

Table I. - Climatic conditions of studied locations. E, elevation above sea level (meters); R, sum of sun radiation ($\text{ccal}/\text{cm}^2/\text{year}$); TJA, mean temperature of January ($^{\circ}\text{C}$); TJU, mean temperature of July ($^{\circ}\text{C}$); DWP, duration of the period without freeze (days); **SumT**, sum of temperatures for the period with stable mean temperature above 5°C ; AP, median annual precipitation (mm); DS, duration of the period of stable snow cover (days). BC, Borjomi Canyon; GV, Gujareti Village, subalpine **belt**; LT, Lake Tabatskuri, subalpine belt; **DU**, **upstreams** of the river Duruji, upper limit of forest belt; MP, Mamisoni Pass, Racha. Most of the data are based on the *Atlas of the Georgian SSR* (DJAVAKHISHVILI et al., 1964). Data on the annual precipitation are according to VLADIMIROV et al. (1991). For E, DWP, AP and DS, median values between minimal and maximal average estimations are given; for TJA, maximal average estimations; for R, TJU and SumT, minimal average estimations.

	E	R	TJA	TJU	DWP	SumT	AP	DS
BC	1000	135	-4	+ 18	137	3000	1000	88
GV	1900	>150	-8	+ 14	~100	2000	900	125
LT	2000	>150	-8	+ 12	~100	2000	1000	125
DU	1950	>150	-2	+20	137	3000	1700	125
MP	2550	>150	-10	+ 10	88	1500	1500	>150

Climatic conditions at these localities (according to DJAVAKHISHVILI et al., 1964) are shown in Table I.

Body length (L: **snout-urostyle** length) of each specimen was measured by sliding calipers with the distance between points 0.1 mm. The presence and brightness of the light mid-dorsal stripe was recorded as clear, unclear or absent. Age was estimated by standard skeletochronological methods (SMIRINA, 1989; CASTANET & SMIRINA, 1990).

For skeletochronology, femur (all frogs from Gujareti, Tabatskuri and Mamisoni Pass and 20 specimens from Borjomi Canyon) as well as second phalange of fourth toe of right foot (the remaining frogs from Borjomi Canyon) were used. Sections 25 μ thick were prepared with a cryostat, stained with **Boemer** hematoxylin and examined under a light microscope. The line of the first hibernation is usually resorbed, as in other species of brown frogs (LEDENTSOV, 1990). In most cases, age was estimated as $N + 1$, where N is the number of fully visible lines of arrested growth (LAGs). In frogs collected during early spring, the last LAG is invisible as well. In such cases, age was assumed as $N + 2$. The numbers of visible LAGs in phalanges and femurs of a specimen were always equal. Duplicated or additional LAGs, which can be observed sometimes on the sections of tubular bones of brown frogs together with true ones (e.g. SMIRINA, 1989; LEDENTSOV, 1990) were rare.

Statistical analysis of differences between samples in body length of frogs was conducted using the Student *t* test (ordinary method and modified method for small samples with different dispersions; ZAITSEV, 1984). Differences in age distribution were tested with a nonparametric Kolmogorov-Smirnov X test. Differences in proportion of striped specimens in samples were tested with Fisher's angular method (ZAITSEV, 1984).

RESULTS

OCCURRENCE OF THE "STRIATA" PHENOTYPE

In Borjomi Canyon, only four of 138 examined frogs (2.9 %) had a bright mid-dorsal stripe, and 89 % had not even an unclear stripe. In Gujareti, 35 frogs (74 %) had a bright stripe and only 13 % were unstriped. Among frogs collected near Lake Tabatskuri, 77 % had a bright stripe and 11 % were unstriped. No obviously striped frogs were found in samples from Great Caucasus (Duruji Upstreams and Mamisoni Pass), though in each of these samples a few frogs with very unclear light stripe in the middle part of the back were found (Table II). Differences in the proportion of specimens with bright stripe are significant, not only between "striped" populations from Gujareti and Tabatskuri and all other populations ($P < 0.001$) but also between the population from Borjomi Canyon and the sample from Mamisoni Pass ($P < 0.01$). Therefore, in populations from the Trialeti Ridge an increase in the proportion of striped frogs with elevation was very clear, though it was not observed in the Great Caucasus.

BODY LENGTH OF ADULT FROGS

Frogs from Tabatskuri were characterized by the smallest body size (62-63 mm on average; Table II). Frogs from Duruji Upstreams were slightly larger: 62-66 mm. Body length of specimens from other localities showed no significant differences (though frogs from Mamisoni Pass were especially large). In Borjomi Canyon, females were significantly ($P < 0.01$) larger, in comparison with males. Mean body length of specimens from Borjomi Canyon, Gujareti and Mamisoni Pass varied from 67 to 73 mm. Differences between most of samples are significant (Table III).

AGE DISTRIBUTION OF ADULT FROGS

Age distributions of adult frogs are shown in Table IV. In sections of tubular bones of frogs from Trialeti Ridge (Borjomi Canyon, Gujareti, Tabatskuri), as well as from Duruji Upstreams, one to six LAGs were observed (fig. 2) suggesting that the ages of the animals are two to seven years. In the femur sections of frogs from Mamisoni Pass, from four to ten LAGs were seen (i.e., ages five to eleven years). The "youngest" population inhabits Lake Tabatskuri (mean age of adults 2.6-2.8 years). The mean age of frogs

Table II. - Morphological features of *R. macrocnemis* populations from different localities. S, percentage of frogs with clear stripe; PS, percentage of frogs with unclear stripe ("pseudostriata"); N, sample size; *M*, mean; *SE*, standard error. For other abbreviations, see Table I. For Borjomi Canyon, measurements of frogs collected during a five-year study (since 1989) are given.

	Coloration			Body length (mm)					
				♂			♀		
	<i>N</i>	<i>S</i> (%)	<i>PS</i> (%)	<i>N</i>	<i>M</i>	<i>SE</i>	<i>N</i>	<i>M</i>	<i>SE</i>
BC	138	3	8	216	67.1	0.34	88	69.3	0.73
GV	47	74	13	13	70.5	1.98	6	72.6	2.02
LT	63	77	12	27	62.7	0.87	13	62.3	1.09
DU	22	0	4	21	62.4	3.80	1	66.3	-
MP	117	0	4	96	72.3	0.70	20	73.1	1.02

Table III. - Significance of inter-sample differences in body length of *Rana macrocnemis*. Values of Student *t* are given as well as levels of significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. For other abbreviations, see Table I.

♂					♀			
	BC	GV	LT	UD		BC	GV	LT
GV	0.85				GV	1.54		
LT	***	***			LT	***	***	
UD	4.71	4.50				5.33	5.53	
MP	1.94	1.89	0.08					
	***		***	***				***
MP	6.68	0.86	8.59	4.63	MP	2.42	0.28	6.40

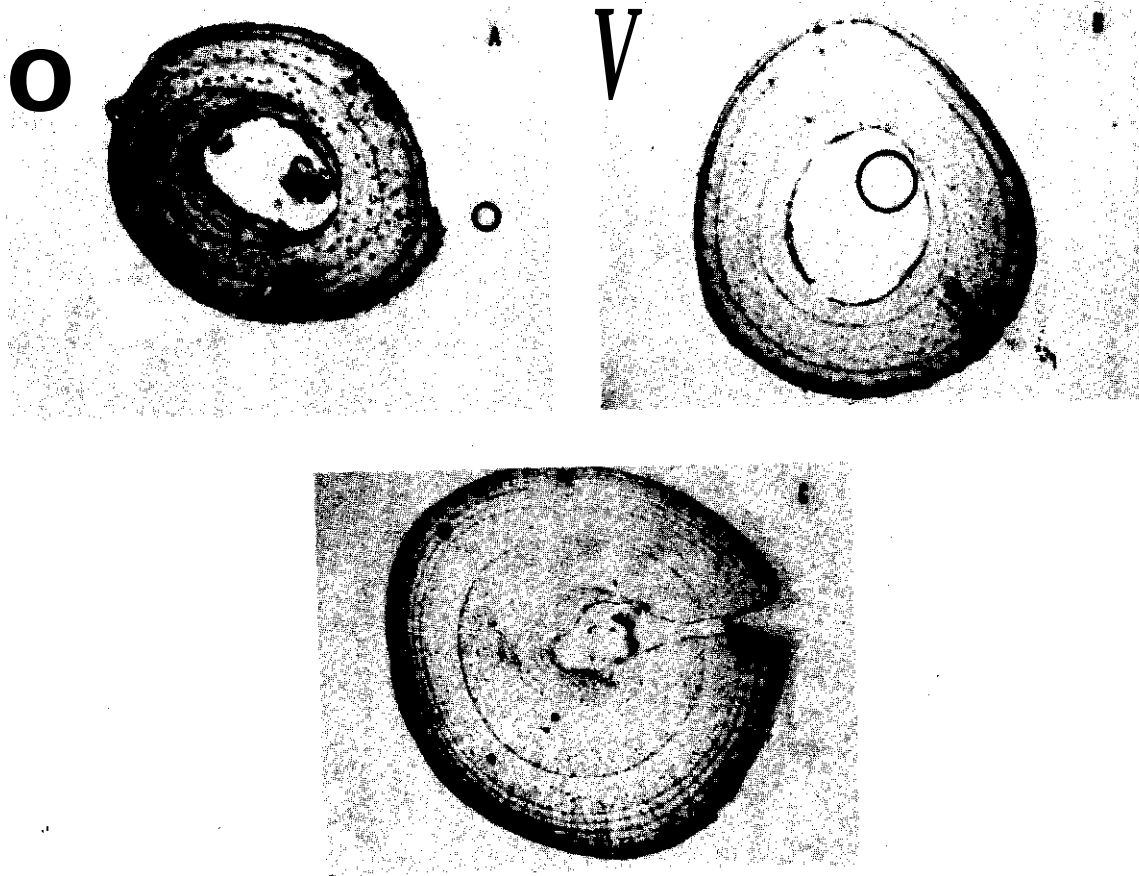


Fig. 2. — Femur sections of *R. macrocnemis* from different populations. A, Borjomi Canyon, female, three full LAGs (four years of age); B, Gujareti Village, female, three full LAGs (four years of age); C, Mamisoni Pass, male, eight full LAGs (nine years of age).

Table IV. - Age distribution of *Rana macrocnemis* from different localities. *N*, sample size; *MA*, mean age in years; *SE*, standard error. For other abbreviations, see Table I.. Percentage of frogs of different age classes is indicated.

		N	MA	SE	Age in years (%)										
					2	3	4	5	6	7	8	9	10	11	
BC	♂	92	2.95	0.10	36	45	11	8	1						
	?	30	3.60	0.22	17	33	33	10	3	3					
GV	♂	13	3.39	0.31	8	69	15			8					
	♀	6	3.50	0.22		50	50								
LT	♂	27	2.63	0.14	52	33	15								
	♀	13	2.84	0.18	31	54	15								
DU	♂	21	3.57	0.68	5	38	52	5							
	♀	1	4.00	-			100								
MP	♂	76	7.75	0.33				8	13	21	31	14	8	5	
	?	19	7.47	-				10	16	21	27	21	5		

Table V. - Significance of inter-sample differences in age distribution of *Rana macrocnemis*, using Kolmogorov-Smirnov λ test. For abbreviations, see Tables I and III.

♂					♀			
	BC	GV	LT	UD		BC	GV	LT
GV	0.93				GV	0.38		
LT	0.73	1.30			LT	1.05	0.71	
UD	1.54*	0.96	1.61*					
MP	*** 6.45	*** 3.06	*** 4.46	*** 3.98	MP	*** 3.21	*** 2.14	*** 2.78

Table VI. - Index of absolute growth rate ($IG = L \times MA^{-1}$) and weighted index ($TIG = IG \times \Sigma t^{-1} \times 1000$, where t is the sum of effective temperatures for the warm period: average twenty-four-hour temperature + 5°C and more) for different populations of *Rana macrocnemis*. For abbreviations, see Tables I and III.

	BC		GV		LT		DU		MP	
	♂	\$	♂	?	♂	?	♂	♀	♂	?
IG	22.74	19.25	20.80	20.74	23.84	21.9	17.48	16.58	9.01	8.04
TIG	7.6	6.4	10.4	10.4	11.9	11.0	5.8	5.5	6.0	5.4

inhabiting Borjomi Canyon, Gujareti and Duruji Upstreams varied from 3.2 to 4.2 years, but the mean age of frogs from Mamisoni was much higher and reached about eight years. Differences in the age distributions of frogs from Mamisoni Pass, on the one hand, and all other populations, on the other, are significant. Frogs from Duruji Upstreams are significantly older than those from Borjomi Canyon (Table V). In all localities females were slightly older than males, but differences are significant only for Borjomi Canyon ($P < 0.05$).

POST-METAMORPHIC GROWTH RATES

The ratio $IG = L \times MA^{-1}$ of mean body size of adults (L , mm) to their mean age (MA , years) can be assumed to be a good index of absolute growth rate. This index varied between 19 and 24 in animals from Borjomi Canyon, Gujareti and Tabatskuri; it was less (about 17) in Duruji Upstreams, and did not exceed 9 at Mamisoni Pass. No differences in the growth rates of the sexes were detected.

Obviously, growth rates depend on the climatic conditions of the location. We cannot detect genetic interpopulation differences in growth rates based only on observed growth rates, but we have to take into account climatic differences between locations. Sum of temperatures for the activity period of frogs (which more or less coincides with the period when stable temperature exceeds 5°C), seems to be the most important quantitative climatic variable affecting the growth rates of frogs. The modified index of growth, more available for interpopulation comparisons than IG , was calculated in the following manner: $TIG = IG \times \Sigma t^{-1} \times 1000$, where t represents the sum of temperatures for the activity period. Calculated values are given in Table VI. Judging from estimated values of TIG , similarity between different populations where unstriped frogs predominated (Duruji Upstreams, Mamisoni Pass and Borjomi Canyon) was higher than between any of these populations and populations with striped frogs (Gujareti and Tabatskuri).

DISCUSSION

Despite previous studies (see Introduction), the *Rana macrocnemis* complex remains poorly known and more work is needed before a clear taxonomy of this group can be proposed. Pending such studies, we here adopt a conservative attitude, and we use for the Caucasian brown frogs the oldest available name for frogs of this complex, i.e. *Rana macrocnemis* Boulenger, 1885.

Taking into consideration the great **intra-population** variability in all three localities from Trialeti Ridge (**Borjomi** Canyon, Gujarati Village and Lake Tabatskuri), as well as the free interbreeding that occurs between different phenotypes, we could unify them in the same metapopulation system ("Trialeti"). The most important question appears to be why there is such marked morphological differences between different populations within this system.

At the intraspecific level, growth rates of specimens are related to two main factors: climatic conditions at the locality and genetically determined growth rates. Moreover, actual growth rate of each individual depends on the attained body size: growth slows down in animals reaching definitive species-specific size. Populations from Trialeti Ridge differed one from another in each of these three characteristics. Borjomi Canyon, situated at an elevation of about **1000 m** in a forested gorge, is characterized by a relatively mild climate (sum of effective temperatures about 3000, January temperature -4°C , etc.; see Table I) in comparison with the other two localities. Attained body size is especially **small** in the population at Lake Tabatskuri. At the same time, judging from the proportion of striped frogs, the genetic composition of populations from Gujarati and Lake Tabatskuri clearly differ from that of the population at Borjomi Canyon (though the distance between populations from Borjomi Canyon and Gujarati is less than 18 km and the only natural barrier between them is a small ridge of about 2000 m maximum elevation).

We considered the role of climatic conditions and weighted the indices of growth rates according to the sum of effective temperatures (reflecting the period of activity of frogs) at different elevations. Weighted growth index was especially high for frogs inhabiting the vicinity of Lake Tabatskuri. This may have resulted in especially early maturation, at the expense of decreased mean adult body size, in this population. However, frogs from Gujarati, which mature at the same age and the **same** body size as frogs from Borjomi Canyon, also grow much more rapidly than frogs **from** the latter locality. Thus, we propose that post-metamorphic growth rates for Trialeti metapopulation are due to genetic differences between local populations, reflected in the different frequencies of striped specimens. The growth index of frogs from the populations where striped animals predominate is about 1.5 times more than in the "unstriped" population inhabiting Borjomi Canyon. Accelerated growth in the mountain populations of Trialeti Ridge has an adaptive value. If frogs from Gujarati had the same growth index as in the Borjomi Canyon, they would mature 1.5 times later (taking into account differences in the period of activity and sum of effective temperatures). If mean age of females from the Borjomi Canyon reaches 3.6 years, in Gujarati it would reach about 5.4 years.

Intrinsic growth rate of a population, in accordance with well-known demographic models (e.g. WILLIAMSON, 1972), is described by the equation $\sqrt[\tau]{b - d + 1} = \sqrt[\tau]{\lambda}$, where b is the mean value of fecundity, d the mean mortality rate for adult animals and T the mean age of adult frogs. If the animals from two populations have the same fecundity and mortality rates, the ratio of their productivities would be $k = \lambda^{(1/\tau_1 - 1/\tau_2)}$, where τ_1 and τ_2 are the mean ages of animals in populations where animals mature at a younger and older age, respectively.

Genetically fixed rapid growth of frogs from Gujareti prevents displacement of local genotypes by the genotypes predominating in Borjomi Canyon, in spite of the latter breeding in more favourable climatic conditions.

Frogs from Lake Tabatskuri grow and mature even faster than in Gujareti. If fecundity and mortality of these two populations were equal, the reproductive success of frogs inhabiting the surroundings of Tabatskuri would be higher. However, the fecundity of females with a body length of about six centimeters (mean size in Tabatskuri population) is 1.5 times lower than that of females of the same species with a body length of seven centimeters (TARKHNISHVILI, 1993). The small size of frogs inhabiting surroundings of Tabatskuri is probably the cost of advantages associated with rapid maturation. The productivities of frogs from different populations on Trialeti Ridge appear to be similar. This allows the stable coexistence of populations dominated by different **morphs** without the displacement of morphological characters as a result of interbreeding.

The results presented in this study enable the high proportion of striped specimens in some populations to be explained. However, the inverse situation, the very low proportion of striped frogs in Borjomi Canyon, remains to be explained. The hypothesis that in forested canyons selective pressure works against striped frogs cannot be excluded. In particular, it may be connected with the very unstable breeding sites in this habitat (see TARKHNISHVILI, 1993), taking into account the longer larval period of genetically striped brown frogs, demonstrated in *Rana arvalis* (ISHCHENKO & SHCHUPAK, 1974). However, this question requires further study.

In both populations from Great Caucasus, frogs with a bright stripe are absent, independently of the elevation and the climatic conditions. Overall, the climate in the Great Caucasus is more humid and mild, in comparison with Caucasus Minor localities situated at the same elevations (Table I): the sum of effective temperatures in the upper reaches of streams in Duruji (elevation 1900 m) is similar to that in Borjomi Canyon (1000 m). At the same time, the growth rates of frogs from this population are slightly lower than those of unstriped frogs from Borjomi Canyon and markedly lower than in "striped" populations from Gujareti Village and Lake Tabatskuri. The growth rates of frogs from Mamisoni Pass are lowest; even the growth index (TIG), which takes into account the coldest climate in this locality (Table I), shows a low value (Table IV). As a result, the actual productivity of frogs from Great Caucasus clearly declines with elevation. The only reason that can be hypothesized for this situation is an absence of a genotype, correlated with rapid growth, in the gene pool of the metapopulation of brown frogs inhabiting Great Caucasus.

An interesting conclusion can be outlined. In spite of the high external similarity between populations from Borjomi Canyon and Great Caucasus, they belong to different

metapopulation systems. The first system (western part of the Trialeti Ridge) includes **genotypes** connected with rapid growth. This facilitates the rapid redistribution of genotypes when the population is exposed to new climatic conditions and the appearance of specific "mountainous" populations, composed almost exclusively of striped frogs. In the gene pool of the second system (southern slopes of Great Caucasus) such genotypes are simply absent.

In *R. macrocnemis* populations from Armenia, inhabiting elevations of 1900-3000 m, frogs of one to three years of age predominate (LEDENTSOV & MELKUMYAN, 1986). The situation is similar to that in localities from Trialeti Ridge, which belong to the same mountain system of Caucasus Minor.

This point of view requires further studies. Expected difficulties could be outlined. For instance, the presence of striped frogs in the population does not necessarily prove the presence of the genotype "striata" in its gene pool, because under changed developmental conditions they can appear even in the descendants of genetically unstriped parents.

ACKNOWLEDGEMENTS

The authors are obligated to the Georgian-German Organization CUNA Georgica and Dr. Udo HIRSCH, founder of this organization, which supported our field work for 1993 and 1994. We are greatly thankful to Dr. Alain DUBOIS, Dr. Tim HALLIDAY and Dr. Sergius KUZMIN for helpful comments and remarks on the first draft of the manuscript. We greatly appreciated the efforts of Mr. Boris ARDABIEVSKY and Mr. Alexander GAVASHELISHVILI who accompanied and helped us in the field work.

LITERATURE CITED

- BARAN, I., 1969. — Anadolu dag kurbagalari uzerindeki sistematik arastirma. [A study on the taxonomy of the mountain frogs of Anatolia]. *Sci. Rep. Fac. Sci. Ege Univ.*, 80 (54): 1-78. [In Turkish, with English Summary].
- BARAN, I. & ATATUR, M. K., 1986. — A taxonomical survey of the mountain frogs of Anatolia. *Amphibia-Reptilia*, 7: 115-133.
- BEGON, M., HARPER, J. L. & TOWNSEND, C. R., 1986. - *Ecology: individuals, populations and communities*. Part II. Blackwell Scientific Publications.
- BERGER, L. & SMIELOWSKI, J., 1982. - Inheritance of vertebral stripe in *Rana ridibunda* Pall. (Amphibia, Ranidae). *Amphibia-Reptilia*, 3: 145-151.
- BROWDER, L. W., UNDERHILL, J. C. & MERRELL, D. J., 1966. — Mid-dorsal stripe in the wood frog. *J. Hered.*, 57 (2): 65-67.
- CASTANET, J. & SMIRINA, E., 1990. — Introduction to the skeletochronological method in amphibians and reptiles. *Ann. Sci. nat., Zool.*, (13), 11: 191-196.
- DAPKUS, D., 1976. — Differential survival involving the Burns phenotype in the northern leopard frog, *Rana pipiens*. *Herpetologica*, 32: 325-327.
- DJAVAKHISHVILI, A. N., ASLANIKASHVILI, A. F., DZOTSENIDZE, G. S. et al., 1964. - *Atlas Gruzinskoj Sovetskoy Sozialisticheskoy Respubliki*. [Atlas of the Georgian Soviet Socialist Republic]. Tbilisi and Moscow, Main Department of Geodesy and Cartography: 1-269.
- DUBOIS, A., 1992. — Notes sur la classification des Ranidae (Amphibiens Anoures). *Bull. Soc. linn. Lyon*, 61 (10): 305-352.

- FISHBECK, D. W. & UNDERHILL, J. C., 1971. — Distribution of stripe polymorphism in wood frogs, *Rana sylvatica* LeConte, from Minnesota. *Copeia*, **1971** (2): 253-259.
- GRAY, R. H., 1977. — Lack of physiological differentiation in three color morphs of the cricket frog (*Acris crepitans*) in Illinois. *Trans. Ill. State Acad. Sci.*, **70** (1): 73-79.
- 1978. — Nondifferential predation susceptibility and behavioral selection in three color morphs of Illinois cricket frogs, *Acris crepitans*. *Trans. Ill. State Acad. Sci.*, **71** (4): 356-360.
- ISHCHENKO, V. G., 1978. — *Dinamicheskij polimorfizm* burikh lyagushek fauni SSSR. [Dynamic polymorphism of the brown frogs of USSR fauna]. Moscow, Nauka: 1-148. [In Russian].
- 1987. — The level of morphological similarity between the populations of the Caucasian brown frog, *R. macrocnemis* Blgr. In: L. J. BORKIN (ed.), *Herpetological investigations in the Caucasus*, USSR Academy of Sciences, *Proc. zool. Inst. Leningrad*, **158**: 100-104. [In Russian, with English summary].
- ISHCHENKO, V. G. & PYASTOLOVA, O. A., 1973. — A contribution to the taxonomy of Caucasian brown frogs. *Zool. Zhurnal*, **52** (11): 1733-1735. [In Russian, with English summary].
- ISHCHENKO, V. G. & SHCHUPAK, E. L., 1974. — Ecological differences of individual genotypes in a moor frog population. *Soviet J. Ecol.*, **5** (4): 379-380.
- LEDENTSOV, A. V., 1990. — *Prostranstvennaya i vozrastnaya struktura reproduktivnoj chasti populyatsii ostromordoj lyagushki (Rana arvalis)*. [Spatial and age structure of the reproductive part of population of moor frog (*Rana arvalis*)]. Ph.D. Thesis, Sverdlovsk: 1-24. [In Russian].
- LEDENTSOV, A. V. & MELKUMYAN, L. S., 1987. — On longevity and growth rate in amphibians and reptiles in Armenia. *Proc. zool. Inst. Leningrad*, **158**: 105-110. [In Russian, with English summary].
- MENSI, P., LATTES, A., MACARIO, B., SALVIDIO, S., GIACOMA, C. & BALLETTTO, E., 1992. - Taxonomy and evolution of European brown frogs. *Zool. J. linn. Soc.*, **104**: 293-311.
- MERRELL, D. J., 1969. — Limits on heterozygous advantage as an explanation of polymorphism. *J. Hered.*, **60**: 180-182.
- 1973. — Ecological genetics of anurans as exemplified by *Rana pipiens*. In: J. L. VIAL (ed.), *Evolutionary biology of the anurans*, Columbia, Missouri, University of Missouri Press: 329-335.
- MORIWAKI, T., 1953. — The inheritance of the dorso-median stripe in *Rana limnocharis* Wiegmann. *J. Sci. Hiroshima Univ.*, Sec. 3, Div. 1 (Zool.), **14**: 159-164.
- NEVO, E., 1973. — Adaptive color polymorphism in cricket frogs. *Evolution*, **27** (3): 353-367.
- SCHUELLER, F. W. & COOK, F. R., 1980. — Distribution of the middorsal stripe dimorphism in the wood frog, *Rana sylvatica*, in eastern North America. *Canad. J. Zool.*, **58** (9): 1643-1651.
- SCHWARZ, S. S. & ISHCHENKO, V. G., 1968. — [Dynamics of genetical composition of populations of moor frog]. *Bulleten MOIP, Otdel biologicheskij*, **73** (3): 127-134. [In Russian].
- SHCHUPAK, E. L., 1977. — [Inheritance of the mid-dorsal stripe in moor frog]. *Informacionnie Materiali Instituta Ekologii Rastenij i Zhivotnikh*, Sverdlovsk: 36-37. [In Russian].
- SHCHUPAK, E. L. & ISHCHENKO, V. G., 1981. — On the hereditary base of colour polymorphism in moor frog (*Rana arvalis* Nilss). I. Light mid-dorsal stripe. In: *Herpetological researches in Siberia and Far East*, Leningrad, Nauka: 128-132. [In Russian, with English summary].
- SMIRINA, E. M., 1989. — [The method of determination of the age in amphibians and reptiles with bone layers]. In: SHCHERBAK, N. N. (ed.), *Rukovodstvo po izucheniyu zemnovodnikh i presmikhayushchikhsya*, Kijev: 143-153. [In Russian].
- STUGREN, B., 1966. — Geographic variation and distribution of the moor frog, *Rana arvalis* Nilss. *Ann. zool. fern.*, **3** (1): 29-39.
- TARKHNISHVILI, D. N., 1993. — Anurans of Borjomi Canyon: clutch parameters and guild structure. *Alytes*, **11** (4): 140-154.
- 1995. — On the inheritance of the mid-dorsal stripe in the Iranian wood frog (*Rana macrocnemis*). *Asiat. herpet. Res.*, **6**: 120-131.
- TARKHNISHVILI, D. N. & MAMRADZE, R. G., 1989. - Modification of the phenotype of Caucasian brown frogs under the influence of high temperature. *Bull. Acad. Sci. Georgia*, **135** (2): 437-440. [In Russian, with English summary].
- TERENTYEV, P. V. & CHERNOV, S. A., 1949. - *Opredelitel zemnovodnikh i presmikhayushchikhsya SSSR*. [Guide for amphibians and reptiles of the USSR]. Moscow, Sovetskaya Nauka. [In Russian].

- VERSHININ, V. L., 1987. - Some features of the phenetical structure of groupings of the moor frog in the industrial city. In: *Vliyanie sredi na dinamiku strukturi i chislennosti zhivotnikh*, Sverdlovsk: 74-79. [In Russian].
- VLADIMIROV, L. A., GIGINEISHVILI, G. A., DJAVAKHISHVILI, A. I. & ZAKHARASHVILI, N. N., 1991. — *Vodny balans Kavkaza i ego geograficheskie zakonomernosti*. [Water balance of Caucasus and its geographic conformity to natural laws]. Tbilisi, Metsniereba. [In Russian].
- WILLIAMSON, M., 1972. — *The analysis of biological populations*. London, Edward Arnold.
- ZAITSSEV, G. N., 1984. — *Matematicheskaya statistika v eksperimentalnoy botanike*. [The mathematical statistics in experimental botany]. Moscow, Nauka: 1-424. [In Russian].

Corresponding editors: Alain DUBOIS & Tim R. HALLIDAY.