Russian Journal of Herpetology Vol. 1, No. 2, 1994, pp. 117 – 120

ECOLOGICAL MECHANISMS DETERMINING STABILITY OF COLOR POLYMORPHISM IN THE POPULATION OF MOOR FROG, *Rana arvalis* NILSS

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Submitted June 1, 1994.

The distribution and frequency of various color morphs were determined in the population of moor frog, *Rana arvalis* Nilss, on the Middle Ural. The color polymorphism has been established to correlate with some demographic traits such as migration and the life-span. The relative stability of polymorphism within the population is assumed to be determined by ecological mechanisms, i.e., the dynamics of numbers and spatial and age structure of the population.

Key words: ecology, polymorphism, amphibians, brown frogs.

INTRODUCTION

A prevalence of color polymorphism in Amphibians (see the review, Ishchenko, 1978) constantly attracts the attention of herpetologists in its relation to the fitness and the mode of inheritance. The Mendelian inheritance is described for at least fifteen species of Anura (Blouin, 1989; Ishchenko, 1978; Shchupak and Ishchenko, 1981). At the same time the mechanisms ensuring the maintenance of polymorphism in amphibian populations are not fully investigated. In most cases the polymorphism is believed to be controlled directly by selection due to various cryptic value of the morphs in respect to the predators (Fishbeck and Underhill, 1971; Merrell, 1965; Milstead et al., 1974) but the experimental tests did not always yield adequate result (Blouin, 1989). One of the main questions to be decided is whether the polymorphism is correlated with any traits of the life history. As a result of the study of polymorphism in Iranian long-legged wood frog (*Rana macrocnemis* Blgr.) it was suggested that the polymorphism in the population might be stable because of the variation of its age structure and migration (Ishchenko and Shchupak, 1975). However, in that study the age determination was based on the body size of the frogs and therefore it is more correct to speak about the correlation of the body size of the frogs and the frequency of morphs. As soon as the correct age determination became possible, especially with a progress in the method of the investigation of layered structures (Klevezal and Kleinenberg, 1969) and its application well known as skeletochronology (Castanet et al., 1977), the long-term demographic studies without marking became possible, too. For a long time we conducted one of such investigations on the population of the moor frog, *Rana arvalis* Nilss, in the Middle Urals. The species under study is characterized by polymorphism described in the last century by Schreiber (1875) and by Dely (1964) in detail. The present paper contents some results of the long-term studies of numbers, age structure and polymorphism of the moor frog populations.

MATERIAL AND METHODS

The investigations of the population of *Rana arvalis* were started in 1977 but the main part of the work was carried out in 1983 – 1993. The population monitored inhabits pine-birch forests near the town of Talitsa, 210 km to the east of Ekaterinburg, Middle Urals. During the spawning period the population occupies various water bodies, mostly originated as a result of logging along the forest roads and the natural lowerings of relief flooded by thawed water. In different years the number and the area of the water bodies vary significantly, and usually are equal to about 100. During 1983 – 1993, every year we counted all egg masses on the territory occupied by

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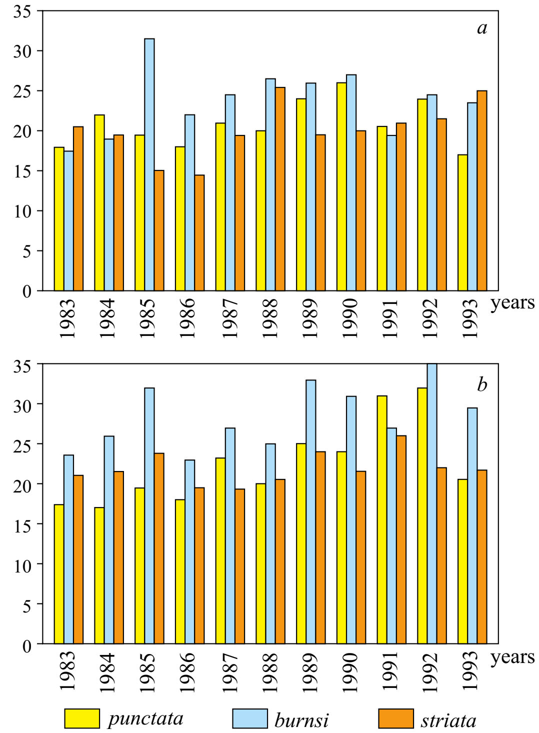

Fig. 1. Yearly variation in frequencies of morphs in males (*a*) and females (*b*) of the moor frog.

the population, i.e., the number of mature females in the population. we believe the number of mature males to be the same. Simultaneously, the mature frogs were sampled every year at three different spawning sites where the major part of the adults breeds regularly. Sex, SVL and phenotype were registered in each specimen. The fourth toe of the right hind leg was cut for the age determination in laboratory conditions. Then, in the overwhelming majority of cases, frogs were released to their breeding sites. The age structure of the population was based on age determination for 300 – 400 specimens, in 1983 – 1990, and for 600 – 1000 specimens, in 1991 – 1993. The age structure of the animals from different sites was determined separately, and the total age structure was evaluated on the basis the contribution of each site to the number of mature population. Simultaneously, the frequency of morphs was determined for each breeding site and for each age group. As a result, the absolute numbers of different morphs were determined for each year and each age group, both at different breeding sites and in the population as a whole. On the basis of these data the mortality of different morphs was determined as well.

TABLE 1. Dynamic of the Number of the Egg Masses in the Population of *Rana arvalis* Nills

Year	Breeding sites			Total
	1	2	3	
1983	8431	3698	6727	18856
1984	11477	3859	6588	22024
1985	7931	3907	6143	17981
1986	3642	3912	11963	19517
1987	2955	2618	8527	14100
1988	2073	2145	7774	11992
1989	1794	1917	8070	11781
1990	3489	1922	16200	21611
1991	8189	2817	14712	25718
1992	2930	1785	11017	15792
1993	3338	3250	14009	20597

RESULTS AND DISCUSSION

According to Dely (1964) and Ishchenko (1978), several morphs were found in populations of *Rana arvalis*. The morph "*striata*" has a light dorsal stripe and the morph "*maculata*" has a certain number of black spots on a back. The specimens that have no spots are unicolor and dotted specimens are named as "*punctata*." We name the unicolor specimens "*burnsi*" by the analogy with polymorphism of *Rana pipiens*. Since many specimens may have various combinations of traits we studied their frequencies separately.

The population monitored is characterized by high dynamics of the total numbers; and the changes of numbers at different breeding sites are not synchronous (Table 1). Simultaneously, the frequencies of different morphs fluctuate in different years (Fig. 1*a* and *b*). Therefore, it is very essential to determine whether the distribution of different morphs on the territory occupied by population is accidental or not. We used the next method to answer this question. The quota contributed into the number of adults by each breeding site was compared with appropriate quota to the absolute numbers of different morphs. In the case of even distribution of morphs over the territory a correlation between two quotas has to be linear and all the points have to lie on the same line. Some results (Fig. 2) permit to assert that the distribution of morphs over the territory, when being analyzed together with the evaluation of the number of animals is not always even. Particularly, we have observed a sit-

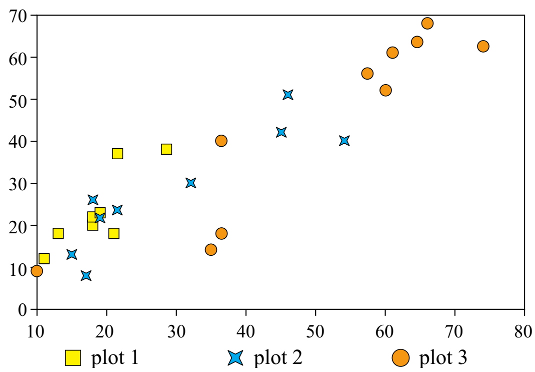

Fig. 2. Correlation between the input of the breeding site into the reproductive part of population and the phonetic structure. Abscissa) Quota of breeding site in the total number of the population (%); Ordinate) quota of burnishes in the breeding site in the total number of "*burnsi*" (%). Data for 9 years.

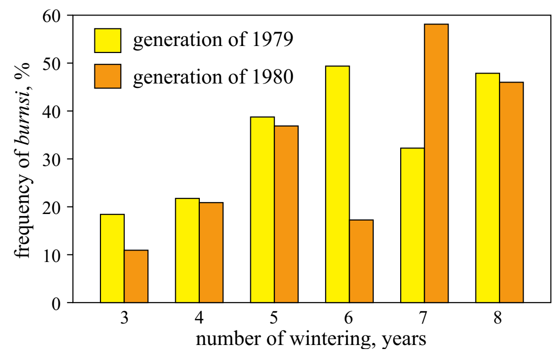

Fig. 3. Variation in the frequency of "*burnsi*" (%) in two generation of moor frog as they are ageing.

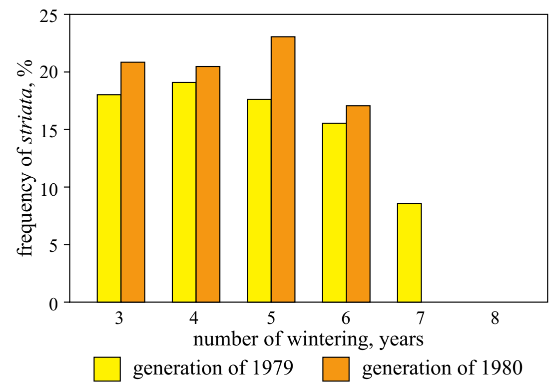

Fig. 4. Variation of frequency of "*striata*" (%) in two generations of moor frog as they are ageing.

uation when males are characterized by an uneven distribution of the "*burnsi*" morph. This result can be a consequence of different activity in of males and females. For example, in 1985 – 86, the male-female ratio in summer was found to vary from 2:1 to 3:1 when animals were sampled by ditches with cylinders. At the same time, the ratio was about 1:1 in the case of sampling by overall catching with a help of the displacement of the litter. Therefore, the different activity and ability for migration of males and females can result in different frequencies of their morphs in different parts of population area.

The yearly variations in frequencies of morphs in a population (Fig. 1) can be a consequence of the fact that every generation has different frequencies of morphs immediately after metamorphosis. Therefore, a study of polymorphism of a single generation during its life can give a more correct answer to our question. we analyzed the changes of the frequencies of morphs "*striata* " and "*burnsi*" during the life-span of two generations — of 1979 and 1980. The results received (Figs. 3 and 4) testify to the fact that the frogs with a dorsal stripe are rare amongst the animals older than 6 years, while the frogs without dorsal spots are more usual in the oldest age groups. In that way, as a generation is ageing the frequency of one morph increases and the frequency of another one decreases. This result may be a consequence of the different mortality in different morphs. On the basis of my data we could estimate it. Earlier, it had been established that a sexual maturity in the population under the study usually takes place at the age of 3 – 4 years. After maturation the mortality is expected to increase. Some results permit me to suggest a different situation. If all frogs of a single generation mature at the age of 4 years their number can be estimated as 100%. The number of this generation must be less than 100% at the age of 5 years and older. we compared such data for morphs "*burnsi*" and "*striata*" separately for the generation of 1980. The results received are shown in Fig. 5. As the generation is ageing the number of frogs with a dorsal stripe decreases essentially and specimens older than 7 years with a dorsal stripe are not found at all. At the same time the number of "*burnsi*" frogs at the age of 5 years are not less abundant in comparison with their number at the age of 4 years. This result can be a consequence either of the migration of other frogs into population from outside or of a different time of maturation of a part of "*burnsi*" frogs. The immigration of new frogs into population seems to be practically impossible because the territory occupied by the pop-

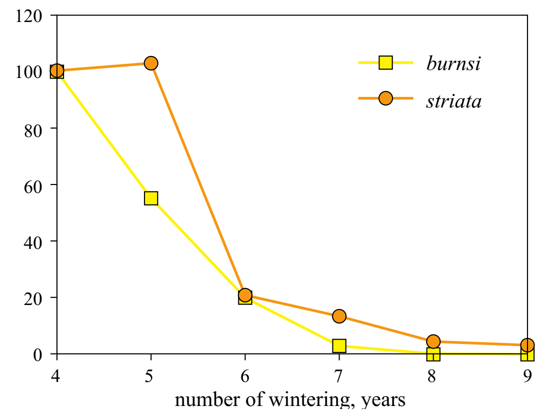

Fig. 5. Mortality of two morphs in the population of the moor frog. Abscissa) Age (number of wintering); Ordinate) mortality.

ulation is isolated by vast tilled fields, on the east and the west, and by the forests without ponds, on the north and the south. Therefore we believe that a large number of the 5 years old animals are the result of the tardy maturation of "*burnsi*" frogs. As the time of maturation and the life-span are correlated (Stearns and Koela, 1986), the longevity of "*burnsi*" frogs is higher than that of other morphs.

CONCLUSION

The results obtained permit us to think that in the population under study the different morphs are characterized by different ecological features. These differences concern such traits as migration and settling, the rate of maturation and the longevity. Since the specimens of a single generation may reproduce during their life in different water bodies with a different probability of drying up, in the case of their settlement at the borders of the population area there arises a risk of spawning in unstable water bodies where the risk of not producing and offspring increases. However, this risk is compensated by an increase of the life-span and of the number of reproductive periods per specimen respectively. It is not clear how usual such situations are because we have not sufficient data on many generations. Nevertheless, the obtain results permit us to assert that the combined investigations of demography and polymorphism are promising enough.

Acknowledgments. I am grateful to Dr. A. Ledentsov and Dr. E. Shchupak for their help during the field seasons.

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