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POPULATION VARIABILITY OF EGG SIZE FOR MOOR FROG DEPENDING ON THE LEVEL OF URBANIZATION*

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On the basis of material collected in populations of moor frog in urban territories with different levels of urbanization, differences were shown in intra- and interpopulation variability, and also average egg size. This article discusses the reasons for the differences that were established and possible negative and positive consequences of the effect of urbanization on indices of the variability of egg diameter and fecundity.

It is known that the volume of egg masses and the size of eggs vary significantly for all species of amphibians. There are a number of hypotheses about adaptive variability of egg diameter for amphibians. For some species, intrapopulation variability in the size of egg masses and eggs is based on the variability of individuals' bodies, but the correlation between these parameters varies in different populations (Banks and Beebee, 1986). Variability of egg size may depend not only on the individual's age; in this case, the size of an individual increases with metamorphosis, and the larval period is reduced with an increase in egg size (Cummins, 1989). A number of researchers (Williamson and Bull, 1989; Crump, 1989; Morin and Johnson, 1988) have shown that individuals that appeared from large eggs possess an undoubted advantage, since they are more competitive in conditions of larval interaction in actual populations. Moreover, large eggs of the same size from egg masses with different average egg size are physiologically inequivalent. Eggs from "large" egg masses grow and develop more rapidly than from "small" ones (Williamson and Bull, 1989a).

In connection with the differences indicated above, the problem of the optimum relationship of the size and number of eggs in amphibians' egg masses arises. Only in ideal conditions do eggs of all sizes survive equally successfully. Consequently, females that produce many small eggs sacrifice their viability (Crump, 1984), while females that produce only large eggs have low fecundity (Crump, 1989). Therefore, the optimum tactic may be the presence in the population of egg masses with a wide range of variability of egg size, which gives eggs of all sizes an equal chance of survival in changing environmental conditions.

It is believed that the presence of interpopulation differences in the variability of egg size reflects adaptations to changes in the habitat (Takahashi and Iwasawa, 1988), which is apparently not valid for all species (Beachy, 1989). Nevertheless, in populations of *R. arvalis* living in conditions of increased acidity, intrapopulation variability of egg size is reliably lower in comparison with populations from relatively clean habitats (Andren et al., 1989). Thus, there is definite interest in interpopulation differences in the variability of egg size in populations subjected to the action of urbanization to different degrees.

The material was collected in the territory of Ekaterinburg and its suburbs in 1990-1991. From fresh egg masses of *Rana arvalis* Nills, we separated 20 eggs each and fixed them with 10% formalin. The diameter of the eggs was measured in laboratory conditions with the help of an ocular micrometer (scale division 0.1 mm). The stage of development was determined according to N. V. Dabagyan and L. A. Sleptsova (1975). We believe that the diameter of the egg adequately reflects its size, since a positive correlation has been established between the average diameter of eggs and their average dry weight (Crump and Kaplan, 1979).

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TABLE 1. Average Egg Size in an Egg Mass of Moor Frog (1990)

Habitat	Stage No. and diameter, mm				
Suburban area					
1. Rezhevskoi tract-2 (RT-2)	9 1,83±0,030 (*n*=7)	8 1,90±0,044 (*n*=8)			
2. Rezhevskoi tract-3 (RT-3)	2 1,72±0,057 (*n*=6)	4 1,80±0,09 (*n*=2)	5 1,77±0,023 (*n*=2)	6 1,74±0,021 (*n*=8)	9 1,79±0,023 (*n*=6)
3. Rezhevskoi tract-4 (RT-4)	4 1,72±0,080 (*n*=3)	5 1,73±0,027 (*n*=13)	6 1,77±0,075 (*n*=3)		
Forest park zone					
4. Kalinovskie profiles-1 (KP-1)	2 1,60±0,034 (*n*=5)	10 1,85±0,036 (*n*=4)			
5. Kalinovskie profiles-2 (KP-2)	2 1,59±0,037 (*n*=6)	3 1,63±0,017 (*n*=3)	4 1,60±0,036 (*n*=5)	9 1,74±0,021 (*n*=3)	
6. Shartash-1 (Sh-1)	2 1,70±0,045 (*n*=10)	7 1,78±0,026 (*n*=5)	10 1,82±0,026 (*n*=2)		
7. Shartash-2 (Sh-2)	1 1,66±0,017 (*n*=10)	2 1,66±0,017 (*n*=10)			
Low-rise development					
8. Samoletnaya Street-5 (S-5)	2 1,65±0,042 (*n*=3)	7 1,58±0,044 (*n*=2)			
9. Samoletnaya Street-4 (S-4)	1 1,58±0,079 (*n*=4)	2 1,62±0,028 (*n*=9)	3 1,64±0,023 (*n*=8)	4 1,68±0,013 (*n*=5)	
10. Patrushikha-1 (P-1)	4 1,73±0,124 (*n*=2)	5 1,70±0,018 (*n*=5)	6 1,59±0,045 (*n*=9)	7 1,81±0,021 (*n*=2)	10 1,64±0,035 (*n*=2)
High-rise development					
11. Ol'khovka River (O)	3 1,73±0,018 (*n*=2)	9 1,84±0,046 (*n*=6)	10 1,83±0,034 (*n*=10)		
12. Central Park (CP)	2 1,51±0,018 (*n*=2)	6 1,55±0,018 (*n*=2)			
13. Krylova-3 (K-3)	7 1,62±0,027 (*n*=10)				
14. Belinskii Street (BL)	3 1,52±0,053 (*n*=2)	10 1,69±0,034 (*n*=3)			
15. Kuibyshev Street (KB)	2 1,58±0,026 (*n*=8)	6 1,58±0,059 (*n*=4)	7 1,67±0,043 (*n*=5)		

In 1990, egg size was determined in early stages of development: the beginning of cleavage to late epithelial blastula. The eggs were measured in samples from 294 egg masses (Table 1). Unfortunately, the data for 1991 are not very comparable with the results from 1990, since the rapid onset of spring, which caused practically simultaneous spawning in all of the populations being observed, did not permit collection of material in early stages of the egg's development. Moreover, the severe cold spell that followed led to the death of a large number of eggs, which also complicated collection of material. Comparison of egg size was done in the tenth-eighteenth stages of development from 240 egg masses (Table 2).

The data given in Table 1 indicate insignificant differences in average egg size in bodies of water in the forest park belt and the suburban zone. Reliable differences in egg size were noted only in the ninth stage between bodies of water RT-1 and KP-2 ($t = 2.31$).

The variability of the eggs' average diameters was significantly higher between egg masses within bodies of water, especially in the first four stages of the egg's development (up to the stage of eight blastomeres). The coefficient of variation

TABLE 2. Average Egg Size in an Egg Mass of Moor Frog (1991)

Habitat	Stage No. and diameter, mm			
	Suburban area			
1. Rezhevskoi tract-2 (RT-1)	16 1,88±0,067 (n=3)	17 1,83±0,084 (n=4)		
2. Rezhevskoi tract-3 (RT-2)	16 2,04±0,039 (n=6)	17 2,00±0,039 (n=7)		
3. Rezhevskoi tract-4 (RT-4)	11 1,91±0,023 (n=7)	12 1,89±0,067 (n=4)	16 2,00±0,147 (n=3)	
	Forest park zone			
4. Kalinovskie profiles-1 (KP-1)	10 1,80±0,44 (n=9)	11 1,84±0,020 (n=8)	12 1,87±0,038 (n=9)	13 1,96±0,05 (n=5)
5. Kalinovskie profiles-2 (KP-2)	13 1,89±0,034 (n=3)	16 1,91±0,025 (n=4)	17 2,00±0,019 (n=11)	18 1,99±0,03 (n=7)
6. Shartash-1 (Sh-1)	16 1,94±0,020 (n=7)	17 2,00±0,021 (n=5)		
7. Shartash-2 (Sh-2)	16 2,02±0,013 (n=3)	17 2,02±0,058 (n=6)		
	Low-rise development			
8. Samoletnaya Street-4 (S-4)	16 1,98±0,035 (n=7)	17 1,98±0,032 (n=6)	18 1,97±0,039 (n=4)	
	High-rise development			
9. Central Park (CP)	16 1,64±0,013 (n=3)	17 1,60±0,014 (n=4)		
10. Belinskii Street (BL)	17 1,95±0,043 (n=5)			
11. Ol'khovka River (O)	6 1,93±0,035 (n=2)	10 1,94±0,088 (n=2)	11 1,98±0,106 (n=2)	
12. Kuibyshev Street (KB)	5 1,87±0,034 (n=3)	10 1,88±0,029 (n=11)		

of egg size between egg masses within bodies of water is greater in the initial stages of cleavage than in later ones and reaches 0.44 mm (1.84-1.40 mm) in the second stage (first cleavage division), and 0.33 mm (2.11-1.78 mm) in the tenth stage (late blastula).

Differences in egg size within egg masses are expressed to an even greater degree than between egg masses. The size in individual egg masses varies by 0.4 to 0.7 mm. As a rule, the eggs' average diameters increase in successive stages of development in a body of water, but within a body of water their variability is insignificant in different egg masses; the maximum egg size increases for the most part.

These features of the variability of moor-frog eggs in the vicinity of the city almost absolutely coincide with data obtained for the Talitsa population of this species in 1983 (Shchupak and Gatiyatullina, 1987).

The egg size is significantly smaller in bodies of water in the urban territory proper (see Table 1). The differences are reliable when we compare the diameters of eggs in individual stages in bodies of water RT-3 and KB (t = 2.26), CP, and P-1; RT-4 and K-3 (t = 2.89); and RT-2 and BL (t = 3.75). This is connected with the fact that the frequency of occurrence of egg masses with small eggs is noticeably higher in populations from the most polluted and urbanized areas, which also showed up in the average egg size. The average egg size is also reliably smaller in most of the populations from zones of high- and low-rise development. The variability of average egg size between egg masses in urban bodies of water is lower in comparison with suburban ones, which may indicate the presence of selection in such populations. For example, at the first cleavage division, differences in the egg's average diameters between egg masses varied from 1.46 to 1.70 mm (body of water S-4).

The maximum coefficient of variation of egg size for moor frog in the second stage (first cleavage division) reached 5.18% (body of water S-4), while in suburban bodies of water it exceeded 8% for the most part.

The limits of variations in the eggs' diameter within egg masses in urban populations are close to what was observed in the suburbs, i.e., fairly high variability of average egg size within egg masses is preserved. Researchers usually correlate stability of the mean values of egg size between bodies of water with characteristics of the populations, including the absence of the females' confinement to specific bodies of water during breeding, and inconstancy of functioning bodies of water in different years. Significant variability of moor frog's egg size determines the population's flexibility in its interrelations with the environment and provides for successful reproduction in unstable conditions.

Within the bounds of urban isolates suitable for breeding of frogs, the variability of average egg size between bodies of water is lower, and the egg's average diameters are smaller than in the suburbs.

If we accept that the relationships between egg size and the age of the female established for *Hyla crucifer* (Crump, 1989) and *Rana temporaria* (Cummins, 1989) are also true of moor frog, then we consider one of the reasons for a reduction in average egg size in moor-frog egg mass recorded in 1990 in populations from urban territories to be the small size of females: high-rise development - 46.2 ± 1.6 mm ($n = 32$), low-rise development - 46.4 ± 1.8 ($n = 13$), the forest park zone — 48.6 ± 1.1 ($n = 40$), suburban population — 53.3 ± 1.6 ($n = 12$). Another possible factor may be a rise in breeders' energy expenditures in conditions of pollution of their habitat. It is known that the action of chemical substances causes a decrease in the amount of yolk and granule cells in follicles (Pramoda and Saidapur, 1986).

In "ideal" conditions of an experiment, large larvae hatched from large eggs of *Hyla crucifer* (Crump, 1984), but these individuals did not have a subsequent advantage either in their rate of development or in their size after metamorphosis, and their survival rate also did not increase. In natural bodies of water, during embryogenesis the egg is subjected to the action of a large number of diverse factors, primarily abiotic ones (temperature, the chemical composition of the water, location and number of egg masses in the body of water, etc.). After hatching from the egg, during the period of larval development, when the larvae interact with predators and competitors, and the possibility that the body of water will dry up increases, large tadpoles do have an advantage (Shchupak and Gatiyatullina, 1987).

In urban bodies of water, in the process of embryogenesis, in vulnerable stages of the zygotes' development (gastrula) differential death is possible. In our case, in later stages of embryogenesis differences in egg size between urban and suburban bodies of water were smoothed out. For example, in the body of water KB (Kuibyshev Street) this difference already disappears in the sixth stage. Differences existing in early stages of development can be leveled out in the course of growth and development (Godina and Sytina, 1985), since the egg's diameter begins to change from the time of gastrulation (Surova and Cherdantsev, 1987). This is apparently due to the fact that in 1991, in most cases, we did not manage to reveal significant differences in the egg's diameter between populations (see Table 2), with the most complete material being collected for stages 16, 17, and 18. In these stages of embryogenesis, the least egg size was noted in the Central Park body of water. In the rest of the bodies of water, the eggs' average diameters are comparable with each other.

Thus, in 1990-1991, no reliable correlation was revealed between the diameter of an egg and fecundity.

An increase in the portion of small eggs in egg masses of urban moor-frog populations, along with a reduction in the number of eggs in an egg mass, probably may present a danger for normal reproduction of these populations, since in conditions of pollution embryos survive only in the central part of the clump (Linnenbach and Gebhardt, 1987), while large embryos and larvae are less vulnerable. Our data indicate high mortality in early stages of development in urban moor-frog populations (Vershinin, 1985a) and preferential survival of large frogs in their first year of life (Vershinin, 1985b). It has been shown on common-frog tadpoles that mortality during metamorphosis is higher for larvae that emerged from small eggs, and morphological anomalies are more often found in metamorphosed individuals (Surova and Cherdantsev, 1987).

Nevertheless, larvae that emerged from small eggs are more capable of changing their intial rate of growth and development (for example, on account of more active feeding or a rise in the level of metabolism), which leads to equal final outcomes, i.e., it enables them, by the time of metamorphosis, to be comparable in all regards to individuals of the large morph (Surova and Cherdantsev, 1987). Consequently, the positive point of an increase in the portion of small eggs in urban populations is a rise in the population's adaptive possibilities in the rapidly changing conditions of urbanized landscapes.

It has been shown experimentally that removal of the effect determined by pollution of bodies of water led to a significant increase in the embryonic survival rate, exceeding the value for egg masses from a suburban population, which, in our opinion, indicates the presence of adaptive changes in the urban population (Vershinin and Trubetskaya, 1991). Mortality during metamorphosis is significantly lower in populations in the zone of high-rise development. Thus, successful reproduction with a change in the average number of eggs in an egg mass, and also the presence of a number of adaptive features for embryos, larvae, and frogs in their first year of life, may indicate that two strategies are present in the reproduction of amphibians in urban areas: R and K (with the latter being found more often). A change in the reproduction strategy and its diversity provide for the existence of limited small isolates with low average fecundity and small egg size.

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