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GROWTH OF BROWN FROGS OF FAUNA OF RUSSIA: SOME PROBLEMS OF STUDY OF GROWTH IN AMPHIBIANS

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The growth of some brown frogs (*Rana temporaria*, *R. arvalis*, *R. macrocnemis*, *R. dalmatina*, *R. asiatica*, *R. amurensis*, *R. dybowskii*, *R. pirica*) was studied using skeletochronological method. Comparison of correlations between body size and absolute age evaluated as numbers of wintering has revealed different situations. The curves of growth in the populations of different geographical zones can cross "chaotically," without any obvious geographical regularity: either they coincide, or the growth curves in a population with the greater life time can be a prolongation of a growth curve of population with a shorter lifetime. In some cases growth curves can be parallel or congruent. The interpretation of the results in many cases is difficult as the duration of the period of activity in different populations may differ sharply or, on contrary, may vary and may be overlapped significantly. Therefore, the comparison of growth curves, based on age in months is preferable and it allows obtaining unusual results. The usage of biocoenotic data appears to be more interesting. The comparative analysis of species-specific differences in growth, taking into account geographical and especially various intrapopulation variation is necessary for the assessment of the role of the different factors determining growth in amphibians.

Keywords: amphibians, frogs, growth, skeletochronology.

INTRODUCTION

It is well-known that a study of the growth is of essential interest because many other important traits of life cycles are connected with growth (cost of reproduction, rate of maturity, life-span and, finally, reproductive success of an individual and a population as a whole). The characters of growth are, therefore, among the main traits of a population (Ebenman and Persson, 1988). At present, it is possible to postulate some principal propositions related to population ecology of amphibians on the basis of the study of their growth. Firstly, a higher growth rate is most preferable because it can determine maturation at larger body size and, hence, a comparatively higher fecundity. Secondly, the larger body size provides higher competitiveness, because larger individuals have the wider spectrum of prey.

Till recently, studies of growth and aging of amphibians were curried out in laboratory conditions (Hota, 1994; Kara, 1994), and data on longevity were accumulated by skeletochronological studies. Now there are comparatively few data on the growth character of amphibians in nature, first of all owing to a difficulty of the task itself. From an available arsenal of tools, two are regarded to be the most correct, the individual marking and skeletochronological research (Halliday and Verrell, 1988). These are precisely the methods, which ensure a reliable age determination at the level of an individual and, hence, a possibility of study of growth. Unfortunately an individual marking can result in "additional" mortality rate and, even without that, a low recapture value, owing to migrations and large mortality, from metamorphosis to maturity and alder age. Therefore, skeletochronological studies are more preferable and more widely spread for descriptions of amphibian growth. However, in many cases researchers have dealt with one-time series, and problems arise in interpretation of results. This paper discusses some aspects of the problems.

MATERIAL AND METHODS

This work is based on studying of series the frogs collected in different time. Samples of eight species of brown frogs of Russia and adjacent territories were studied: *Rana arvalis* Nilsson 1842; *R. temporaria* Linnaeus 1758; *R. dalmatina* Bonaparte, 1840; *R. macrocnemis* Boulenger, 1885; *R. asiatica* Bedriaga, 1898; *R. amurensis* Boulenger, 1886; *R. dybowskii* Günther 1876; and *R. pirica* Matsui, 1991. All specimens were fixed in formalin and kept in formalin or ethanol. The specimens were sexed and snout-vent length was measured nearest to 0.1 mm. Age of animals was determined by examination of microscopic cross-sections of the second phalanx of the fourth toe of right hind leg. Data on age structure of all series were published earlier (Ishchenko, 1996). On the basis of data obtained the relations between mean size and age have

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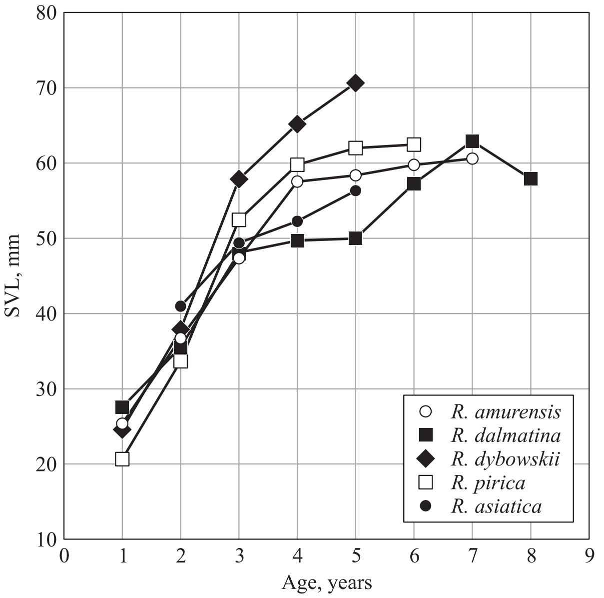

Fig. 1. Relationship SVL – age in some species of brown frogs (*Rana*).

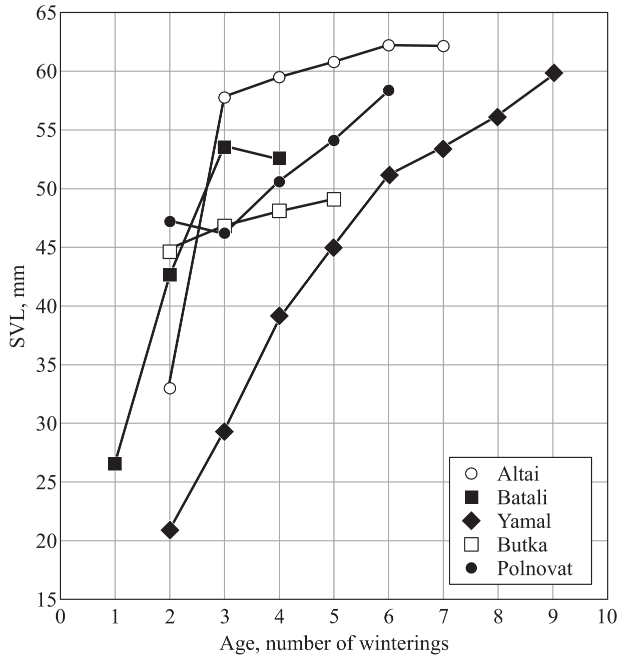

Fig. 2. Relationship SVL – age in some populations of *Rana arvalis*.

been compared. Total numbers of specimens under study counted were 5573 from 41 populations of 8 species. I used statistical software STATISTICA 6.0 and SPSS 11.5.

RESULTS AND DISCUSSION

The results can be considered at some levels, namely, species-specific, population, and intrapopulation. Plotting of the growth curves describing species–specificity in different species of amphibians that can characterize specificity of species is extremely difficult if possible at all. For example, my data can be used for characterization (description) of relations between size and age in some species of frogs (Fig. 1). This result has been obtained on the basis of four samples of *R. amurensis*, two samples of *R. asiatica* and one sample for each of three other species. Therefore it is very difficult to speak in this case of species-specificity. It is possible only to contend that size differences between species at the age of three years contributes of about 10 mm and at the age of five years, 20 mm. It is necessary to remember that in many cases researchers measure SVL nearest to 1 mm, especially in case with living specimens. Therefore, even significant differences in the mean size of 1.5 – 2 mm in many cases can not be regarded as valid.

Intraspecific comparisons of growth curves are much more appropriate and informative.

At the present time, the comparisons of such kind are usual in amphibians and my data permit to suggest various kinds of geographical variability of growth. The comparison of five populations of *R. arvalis* (Fig. 2) based on the series from Altai [560 m above sea level (a.s.l.)], forest-tundra zone (Yamal peninsula), middle taiga of Western Siberia (Polnovat), and forest-steppe of Middle and South Urals (Butka and Batali) does not display a regular (cline) geographical variability in age-size dependencies. In other cases regular geographical differences in growth rates were determined (Hemelaar, 1986). According to our data on age and size in different populations of *R. macrocnemis*, the differences in size-age dependencies can be observed by comparison of mountain and lowland populations (Fig. 3). Nevertheless, it is necessary to keep in mind that conclusions about such differences have some limitations.

It is known, the duration of the period of frog activity is very important for attaining of certain size (Licht, 1975) but in some cases this duration is unknown. At least, it is unknown usually whether the duration of period of activity of frogs coincides with a duration of period of growth or not. Therefore, interpretation of observed differences is often difficult, but in some cases it is quite possible. Comparison of populations of *R. temporaria* can be an example (Fig. 4). It is known that populations of amphibians inhabiting the subarctic zone, in particular, at the Polar Urals, are active usually during two months and rarely, during 2.5 months (Schwarz and Ishchenko, 1971), and all phenological events go on with large intensity. In southern popula-

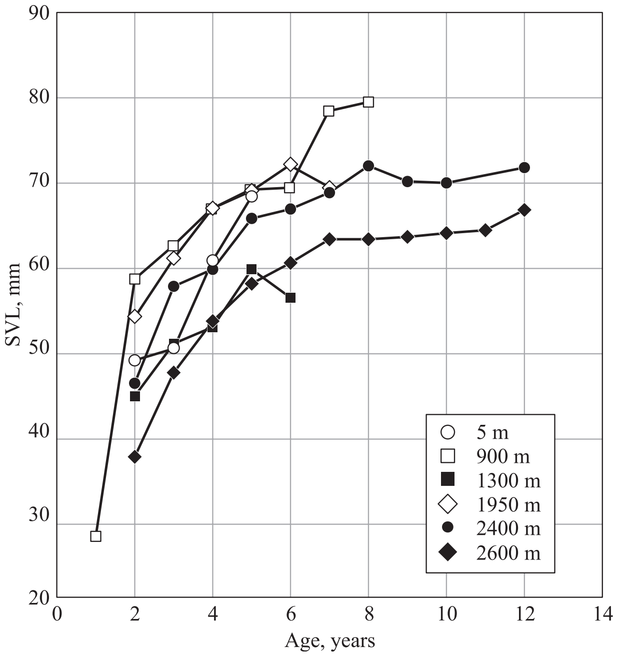

Fig. 3. Relationship SVL – age in some populations (elevations) of *Rana macrocnemis*.

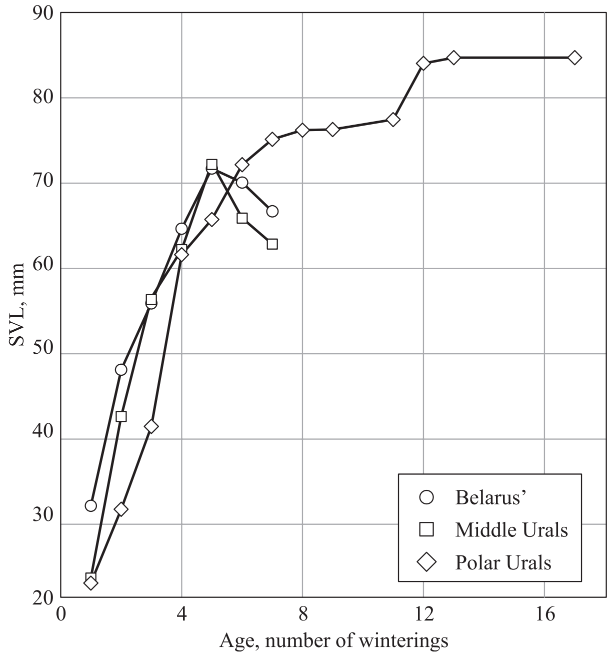

Fig. 4. Relationship SVL – age (number of winterings) in *Rana temporaria*.

tions of the temperate zone duration of the period of activity and potential growth is not less than 4 months and usually it is equal to 5 months. It is quite possible to estimate age of animals in number of months of active life but not in number of winterings. Results obtained in such way for *R. temporaria* (Fig. 5) permit to conclude that northern common frogs are not characterized by comparatively larger life-span, but they are characterized by a more intensive growth. The reasons of this phenomenon seem to be unknown but some explanations can be given. Firstly, long photoperiod (in summer) in the Subarctic can result in increasing of growth rate of juvenile specimens (Richards and Lehman, 1980) and this specificity may be retained at older age. Secondly, according to the data of Olschwang (1992), total biomasses of aboveground invertebrates produced in summer in Polar Urals and Middle Urals are almost equal, therefore middle daily abundance and availability of potential food in northern amphibians is at least twice as large as that in frogs from southern populations. Growth of amphibians is often determined by conditions of feeding (Claussen and Layne, 1983; Seale, 1987).

A similar situation was observed at comparison of populations of *R. macrocnemis* living at different altitudes in various localities of the Caucasus. It is easy to see (Fig. 3) significant distinctions in growth of frogs from various populations and they are retained at comparison

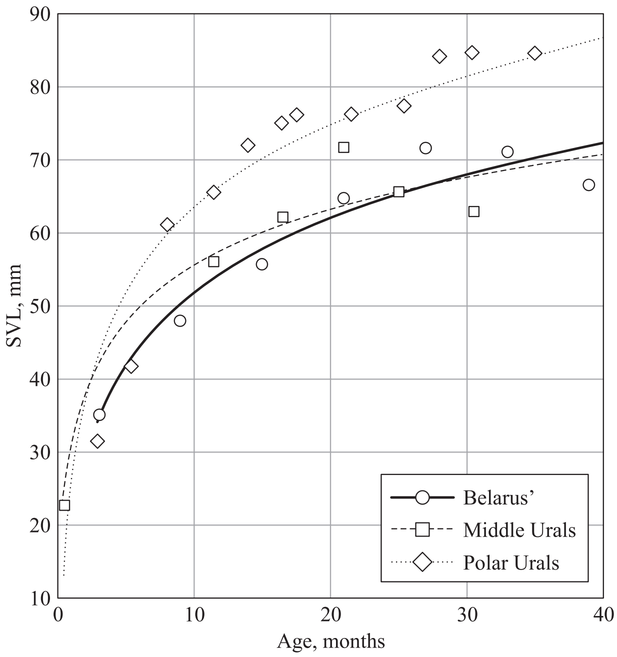

Fig. 5. Relationship SVL – age in *Rana temporaria*.

when their age is expressed in months. High-mountain frogs grow more slowly than those from moderate altitudes. However, it is interesting to note, that the frogs in

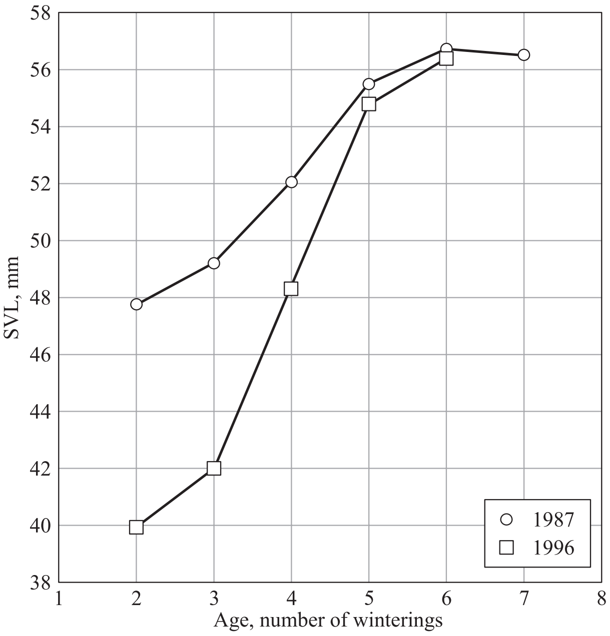

Fig. 6. Relationship SVL – age in *Rana arvalis* in various years.

Kolkhida lowland (5 m a.s.l.) are characterized by the slower growth and minimum body size. In spite of the fact that a period of activity and potential growth in this population is maximum (6.5 – 7 months), growth rate is evidently insignificant. The reasons of this can be presumably biocoenotic. In this site the total biomass of aboveground invertebrates produced through a season of vegetation is similar to it in the Polar Urals, however, in each time unit it is very small. In the habitats of frogs (mainly boggy small-leafed woods) an abundance of invertebrates is always lower than anywhere else. Moreover, a plenty of days with intensive precipitation, typical of humid subtropics zone, make a feeding of frogs complicated, i.e., the factor of actual availability of food resource takes place. It is difficult to prove these assumptions, but it is possible to speculate about them. Moreover, relatively small size of northern *R. arvalis* (Fig. 2) does not confirm to this hypothesis. On the other hand one must not exclude an influence of the size at metamorphosis that can determine size at maturity and at older age (Camp et al., 2000). Additionally, there is one other factor, which is almost impossible to measure comparing populations of frogs. This factor is a certain "phylogenetic variable" determining evolutionary specificity of populations. Any compared populations can differ, but the exact reasons of these differences cannot be comprehended.

There are some more circumstances, which do not permit us to study amphibians' growth more accurately. Firstly, it is necessary to remember about replications of results at sampling of animals for a study. They can be obtained at long-term studies, which results cannot be always satisfactory. For example, at comparison of dependence of the body size on age in moor frogs collected in the same population in different years (Fig. 6) we notice a great difference.

I have got some explanations. Summer of 1995 was very dry season, and the most part of frogs lived in a shore zone of non-dried shallow ponds in conditions of high density (5 – 7 specimens per 1 m^2), thus failing to feed successfully. Therefore the growth of young individuals was strongly inhibited. In addition, the differences of such kind in dependencies between size and age of animals collected in various parts of large spatially structured population can be observed, too. Further, zoologists usually diligently overlook that relations between body size and the age are not growth *sensu stricto*, because a growth is a vectorial change of the size or mass of an individual or a group of individuals of the same time of birth in time continuum. Usually, when we compare the average body size in different age groups of the same population, we are dealing not only with individuals of different age, but also with individuals of different generations born in different years and this can be a good reason for differences in size (Ishchenko, 1989). Differences between generations can be determined by conditions of larval growth, and genetically, and by the fact that in different years a population can be invaded by immigrants from the other neighbor populations, which can differ in growth (Augert and Joly, 1993). Many of the factors listed above practically were not defined in descriptions of the growth of amphibians in nature unless their marking was done. Thus, we usually do not know an impact of information noise on the results of our studies. There are ways of studying the growth allowing to avoid some restrictions. Besides of being used for individual marking, skeletochronological studies can be highly promising. Similar problems are resolved in dendrochronology at studying of tree growth. Dendrochronologists do not measure the height of trees for studying growth, but use diameter and width of annual rings. Amphibians appear to be a beneficial object in this aspect because of an insignificant increase of length can be imperceptible, because of natural errors of measurement; however studying cross-sections of a bone (and phalanx) permits registering any growth precisely. Moreover, it is well known the correlations between body size and diameter of a phalanx are quite often high and the calculation of body length is available. Thus one can work with this material and can easily find out an individual variability of growth. However, this method has some minor restrictions. As a matter of fact a line of the first wintering is often resorbed, and the animals keeping this line can be characterized by specific growth type, in comparison with individuals with resorption. Nevertheless, studies on variability of curves of growth obtained on the basis of analysis of microscope sections of bones are very promising. It is difficult, however, to imagine a mathematical tool allowing for, e.g., a cluster analysis of many hundreds or thousands of curves. In my opinion, there is one more comprehensible way for studying of variability of growth. It consists of determining the variants components of body size.

Analysis of variance of body length has shown that the most part of variability (63.54%) of 41 populations of 8 species of frogs is determined by age, while species or population specificity plays a smaller role (13.19 and 3.65%, respectively). The part of "sex" factor is about 4.4% of variance of SVL. Thus, distinctions in character of growth can be rather insignificant, and observed differences in it between populations seem to be determined mainly by distinctions in life-span (in years!). This conclusion does not contradict the plots because in the analysis of variance all the individuals have been taken into account. The author use not only average sizes in the plots, but also the intragroup variance of body size. However such an approach can only be used in search analysis.

Now, when skeletochronological data are available for more than 110 species of amphibians (in my database), it is quite possible to do a comparison of various kind between the growth curves (more correctly — curves of dependencies of the size on age). Despite of the abundant evidence available, the studies on growth of amphibians in nature, in my opinion, are only beginning.

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