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Geographical variation of sexual size dimorphism in the moor frog (*Rana arvalis*) in East Europe

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Geografische Variation des Geschlechtsdimorphismus beim Moorfrosch (*Rana arvalis*) in Osteuropa

Die geografische Variation des Geschlechtsdimorphismus, der Wachstumsrate und der Körpergröße bei adulten Moorfröschen (*Rana arvalis*) wurde durch einen Vergleich von Alter und Körperlänge an fünf verschiedenen Orten untersucht. Die geschlechtsspezifischen Wachstumsraten und Unterschiede in der Körperlänge und der Altersstruktur verändern sich von Südwest (Minsk und Provinz Chernobyl) nach Nordost (Provinz Kirov). In zwei nördlichen Populationen war das Durchschnittsalter der Weibchen höher als das der Männchen, aber in drei südlichen Populationen war es bei den Weibchen geringer. Solche Unterschiede hängen nicht nur von der Dauer der Aktivitätsperiode ab, sondern auch von den örtlichen Überlebensbedingungen der Weibchen und Männchen. Umgekehrt verursachen diese Bedingungen Unterschiede im Zeitpunkt des Erreichens der Geschlechtsreife, in der Alterszusammensetzung geschlechtsreifer Weibchen und deren Beiträge zur Reproduktion, die selbst zwischen Populationen mit ähnlich langer Aktivitätsperiode auftreten. Die Gründe für die geringeren Wachstumsraten und hohen Überlebensraten bei den Männchen der südlichen Populationen bleiben unklar.

Schlüsselbegriffe: Amphibia, Anura, Ranidae, *Rana arvalis*, Körperlänge, Altersverteilung, Reproduktion, geografische Variation, Geschlechtsunterschiede.

Abstract

Geographical variation of sexual dimorphism in growth rate and body size in mature *Rana arvalis* collected in five distinct localities was studied by comparing body length and age. Sex-specific growth rates and the degree of expression of sexual differences in body length and age composition change from the southwest (Minsk and Chernobyl provinces) to the northeast (Kirov province). The average age was higher in females (than in males) from two northern populations, but lower in females from three southern populations. Such differences depend not only on the duration of the activity season, but also on local conditions that caused differences in female and male survival. These differences, in turn, caused differences in age at maturity, age composition of breeding females, and in their contribution to reproduction even between populations from localities with similar duration of the activity season. The reasons for relatively low growth rates and relatively high survival in males from southern populations remain unclear.

Key words: Amphibia, Anura, Ranidae, *Rana arvalis,* body length, age distribution, reproduction, geographical variation, sexual differences.

Introduction

According to generally accepted hypothesis, sexual size differences in Anura are the evolutionary response not only to sexual selection but also to other forms of natural selection such as female fecundity (for review see MONNET & CHERRY 2002). This assumption is confirmed by females being larger than males in most brown frog species of Eurasian temperate zone (SHINE 1979, MONNET & CHERRY 2002). The widespread common frog (*Rana temporaria*) belongs to such species, for which not only the differences in size between the sexes but also ontogeny of these differences were described. The females became larger than males starting at the age of 3 years, as a result of higher growth rate (LYAPKOV et al. 2004, LYAPKOV 2005). Larger females are typical not only for relatively large but also small brown frog species, such as *R. iberica* (ESTEBAN & SANCHIZ, 2002), *R. latastei* (GUARINO et al. 2003), *R. rugosa* (KHONSUE et al. 2001) and *R. tagoi* (KUSANO et al. 1995), and the North American *R. sylvatica* (BERVEN 1982, SAGOR et al. 1998, LECLAIR et al. 2000). In contrast to all mentioned species, in the moor frog (*R. arvalis*), the most widespread brown frog of Eurasia, the males generally (but not at the western border of the area, see VAN GELDER & OOMEN 1970, HARTUNG 1991, GLANDT 2006) are larger than females (ISHCHENKO 1978). Such dimorphism is uncommon both among brown frogs and Anura as a whole (SHINE 1979). The direction of this size sexual dimorphism is based on the annual growth: males are larger than females in each given age after reaching maturity (LYAPKOV 2005).

Both the causes and the formation process of sexual size differences in size are poorly investigated in Anura. It was supposed that size differences are the consequence of demographic differences: females are larger since their average age is higher than that of males (MONNET & CHERRY 2002). This assumption implies higher survival rates for females, which is demonstrated in only a few studies, and does not take into account the potential sexual differences in growth rate: faster growth in individuals of a given sex can lead to the increase in size despite differences in age. A study on *R. arvalis* (LYAPKOV et al. 2007) demonstrated that males become larger than females due to higher growth rate in males during the period from metamorphosis to first reproduction. These differences were revealed by comparisons of pooled data as well as within each age. Two- and 3-year-old males became mature more often and participated in reproduction earlier. Males also had lower survival rates that resulted in lower frequencies of older ages in males. These sexual differences become apparent despite the gradual increase of male and female sizes, connected with the long-term decrease in mature frogs (see LYAPKOV 2008).

At the same time, the degree of expression of sexual differences in a widespread species indicates that geographic variation is the result of different lengths of the activity (warm) season. Moreover, the reproductive strategies dependent on resource ratio invested in somatic growth and reproduction can also vary with geographic location. Therefore, the aim of this study was the analysis of geographical variation in demographic and reproductive characteristics of a widespread species, the moor frog. For this purpose, we investigated populations along a gradient of the length of activity season from southwest to northeast.

Materials and methods

Adult *R. arvalis* frogs were collected during the breeding season in spawning ponds in five different regions: (1) Belarus, Minsk province, Kopyl' district, in the vicinity of village of Konyukhi (hereafter referred to as Minsk, 21 females and 34 males, 2006–2007), 53° 09′ N, 27° 26′ E; (2) Russia, Bryansk province, in the vicinity of Bryanski Les natural reserve (hereafter Bryansk, 66 females and 86 males, 2001–2007), 52° 27′ N, 33° 53′ E; (3) Russia, Moscow province, Zvenigorod biological station of Moscow State University (hereafter ZBS, 385 females and 382 males, 1998–2006), 55° 44′ N, 36° 51′ E; (4) Russia, Kirov province (hereafter Kirov, 79 females and 115 males, 1998–2006), 58° 40′ N, 49° 5′ E; (5) four moor frog populations were investigated in 1987–1992 in Chernobyl district of Kiev province, Ukraine. In the present study, pooled data are given from one locality (hereafter Chernobyl, 379 females and 380 males). The results of this study are preliminary because the size of the samples with determined age from Minsk population was relatively small.

In all collected individuals, body length was measured and age was determined following skeletochronological method. In females, body mass (FM), clutch mass (CLM) and fecundity were also determined. Relative clutch mass (RCLM) was calculated by the formula RCLM = CLM/FM. Reproductive effort (E) was calculated by the formula $E = F*D^3/SVL^3$, where F is fecundity, D is egg diameter, and SVL is body length (for details see LYAPKOV 2008). During the data collection in Chernobyl, we had no opportunity to weigh frogs and their clutches. Therefore, the index E was used for comparison the Chernobyl population with others populations.

The data were processed using Excel spreadsheets and the STATISTICA 6.0 program package. As even within a population females and males are characterized by different age composition (see results), the significance of sexual differences between average values of each trait was estimated by one-way ANOVA. Differences in age composition among populations was estimated by two-way ANOVA (factors: population and sex) and post-hoc multiple comparisons.

Results and Discussion

Age composition

The earliest maturation and reproduction takes place at the age of two years, after the second hibernation. In three southern populations, the frequency of 2-year-olds was higher than in central (ZBS) and north-east (Kirov) populations (tab. 1). However, in southern populations (with the exception of Minsk) the modal age class was still 3-years. At the same time, the proportion of 4-year-olds increased gradually. The ZBS population (with a modal age class of 4-years) was characterized by maximal average age in females and males (tab. 1). Frogs at the age of 5 years and older were found most frequently in two northern populations.

The direction of sexual differences also depended on geographical location: in all southern populations, the proportion of 2-year-olds was higher in females than in males

Tab. 1: Geographic and age variation of body length and reproductive characteristics in the moor frog. % ♂ or ♀ – the proportion (%) of males or females of a given age, in column »total«, the population average values of age are given. The characteristic abbreviations see in text.
Geografische und altersbezogene Variation der Körperlänge und reproduktiver Merkmale beim Moorfrosch.

		Age, years					
Population	Character	2	3	4	5	6	total
Minsk	% ♂ (n = 34)	44.1	41.2	11.8	2.9		2.74
	% ♀ (n = 21)	57.1	23.8	19.0			2.62
	SVL ♂, mm	49.4	55.1	57.5	60.0		53.0
	SVL ♀, mm	48.0	53.2	50.8			49.8
	Fecundity	763	945	655			800
	RCLM	0.320	0.355	0.278			0.324
	E	0.027	0.028	0.014			0.027
Chernobyl	% ♂ (n = 380)	14.7	50.5	22.4	10.8	1.6	3.34
	% ♀ (n = 379)	29.8	54.1	13.2	2.6	0.3	2.89
	SVL ♂	46.0	50.3	56.7	59.5	60.3	52.3
	SVL ♀	42.4	48.3	56.3	59.0	64.0	47.9
	Fecundity	617	960	1460	1849	1839	932
	E	0.028	0.033	0.037	0.038	0.036	0.032
Bryansk	% ♂ (n = 86)	15.1	58.1	19.8	4.7	1.2	3.22
	% ♀ (n = 66)	24.2	42.4	25.8	7.6		3.17
	SVL ♂	53.0	57.9	62.4	66.3	60.0	58.5
	SVL ♀	49.6	56.0	62.4	64.4		56.7
	Fecundity	1082	1689	2153	1967		1692
	RCLM	0.322	0.375	0.399	0.403		0.371
	E	0.029	0.038	0.041	0.039		0.037
ZBS	% ♂ (n = 382)	1.6	38.7	42.6	13.5	2.3	3.81
	% ♀ (n = 385)	0.3	33.8	45.3	15.7	3.1	3.94
	SVL ♂	50.4	54.4	57.9	59.3	59.4	56.6
	SVL ♀	47.0	52.3	56.0	59.3	60.1	55.5
	Fecundity	684	1057	1193	1267	1332	1176
	RCLM	0.290	0.323	0.334	0.336	0.351	0.332
	E	0.025	0.033	0.035	0.035	0.036	0.034
Kirov	% ♂ (n = 115)	13.9	53.9	27.8	4.4		3.23
	% ♀ (n = 79)	3.8	53.2	30.4	10.1	2.5	3.54
	SVL ♂	47.4	50.5	53.6	58.7		51.4
	SVL ♀	48.3	48.4	53.0	55.8	57.2	50.9
	Fecundity	1063	847	1111	981		988
	RCLM	0.305	0.2984	0.3395	0.2806		0.310
	E	0.037	0.031	0.037	0.029		0.033

(tab. 1). As a result, in southern populations the males were on an average older than females (in Bryansk and Chernobyl, these differences were significant), whereas in two northern populations (ZBS and Kirov), females were significantly older than males.

The sexual differences in growth rate after reaching maturity

In Minsk (tab. 1), the average body length of 3- and 4-year-old males was considerably larger than in females of corresponding age, but connected with a small sample size

Fig. 1: That females are larger than males represent a rare case in East European *Rana arvalis* population, including the population of the Bryansky Les natural reserve.
Dass Weibchen größer als Männchen werden, ist eine große Ausnahme in osteuropäischen Populationen von *Rana arvalis* und gilt auch für die Tiere aus dem Naturreservat Bransky Les.

Fig. 2: In East European populations of *Rana arvalis* males are usually larger than females.
In osteuropäischen *Rana arvalis*-Populationen sind Männchen normalerweise größer als Weibchen.

these differences were not significant. Males from Bryansk population were significantly larger compared to females at the age of two and three years. Males from Chernobyl were significantly larger than females at the ages of 2 and 3 years, but not from 4 to 6 years. In ZBS, average male body length was significantly larger than in females at the age of 3 and 4 years, but did not differ significantly between sexes at older ages. In Kirov, average male body length was significantly larger than in females at the age of 3 years only.

Among-population variability of the degree of expression of sexual differences in body length

As shown above, sexual differences in the three southern populations were largest in relatively young frogs, and in ZBS in frogs at the age of 3 and 4 years, i. e. the largest part of mature frogs. As a result, in these four populations the sexual differences in average body length were considerable and significant (tab. 1). The reason for sexual differences in southern populations could not only be the higher growth rate in males, but also their higher average age. At the same time, in the northern population (Kirov) the significant sexual differences were not revealed, as a result of the low male growth rate in comparison with females. According to the literature from other parts of the *R. arvalis* range (ISHCHENKO 1978), including southern populations (e. g. Ukraine – TARASHCHUK 1984), the male advantage in body length was significant. The lack of sexual size dimorphism in several central European populations of Poland, Hungary and Romania (BABIK & RAFINSKI 2000) can be explained by the addition of immature frogs to samples of adults during collecting away from the breeding season (but HARTUNG 1991, only took adult moor frogs in his computations, caught at a drift fence during breeding migration and could not found a statistical difference of SVL between the two sexes, see GLANDT 2006).

Among-population variation in growth rate

The considerable differences in age composition in three southern, central and northern populations indicate a necessity of among-population comparisons of body length in adult frogs of the same sex within each age. The highest growth rate was revealed in Bryansk population (tab. 1), where at each age the average body length in males and females were significantly larger than the corresponding values in frogs from ZBS. At the same time, individual growth rates up to the age of 5 years from two other southern populations (Minsk and Chernobyl) were lower than in frogs from ZBS. Non-significantly larger body lengths were revealed for females at the age of 6 years from Chernobyl compared with ZBS. The relatively low growth rate in females from Minsk and Chernobyl can be explained by earlier involvement in reproduction (see next section). However, the reasons for lower growth rates in males remain unclear.

Among-population variation in female investment in reproduction

In females, average fecundity and RCLM, a trait characterizing the resource allocation for reproduction (tab. 1), increased with age. The maximal average values of fecundity and RCLM were observed in females from Bryansk. In females from Minsk popula-

tion, the average value of fecundity was lowest, and RCLM was also low. This »retardation« in reproductive characteristics of females from Minsk population corresponds to their low growth rate.

Taking into account the among-population differences in age composition, one can assume that female reproductive strategies depend not only on the length of the activity season. Females from two southern populations had similar values of RCLM, but due of different reasons: in Bryansk it is the result of fecundity (i. e. clutch mass) increase, whereas in Minsk it is the result of constraints in female body size due to lower growth. Apparently, these differences are connected with the relatively low survival that corresponds to minimal average age in females from Minsk (tab. 1).

The long-term study of ZBS population (LYAPKOV 2008) enables to demonstrate that the higher average age in females than in males corresponds to higher female survival. The same relationship between the higher average age and the higher female survival was revealed in frogs from Kirov (for preliminary results see LYAPKOV 2005). In turn, the lower average values of female age in all three southern populations indicate a lower survival in these females, as compared both with males from the same populations and with females from northern populations. It should be noted that the reasons for relatively low survival in females from southern populations remain unclear. It is accepted that survival during breeding period in males should be lower as a result of their visible position and prolonged staying in spawning ponds (PECHMANN et al. 1997), but our study contradict this assumption.

The evolutionary response on low female survival should be earlier maturation and reproduction at early age, which is revealed in all southern populations. The sexual size differences compared to males in southern populations also demonstrate earlier involvement of the part of females in reproduction. The southern populations were remarkable for this distinction and differed from well-studied ZBS population in which the frequencies of 2- and 3-year-old frogs were higher in males than in females (see LYAPKOV 2008). The difference in reproductive strategies is the best explanation of the fact that growth rate after maturity was the most variable trait among all studied parameters, demonstrating large variation even among the populations inhabiting localities with similar climatic conditions.

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