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GEOGRAPHICAL AND LOCAL VARIATION OF REPRODUCTIVE AND DEMOGRAPHIC CHARACTERISTICS IN BROWN FROGS

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INTRODUCTION

The comparative studies of life-history traits in *Rana temporaria* revealed the large scale of variation between geographically removed localities (Ishchenko, 1999; Miaud et al., 1999). The similar studies of reproductive and demographic characteristics in other brown frog species, are scarce (for review see Ishchenko, 1999; Lyapkov et al., 2002b). In addition, the relative value of intrapopulation variation is mostly underestimated. The intrapopulation variation includes the age-specific changes and the differences between generations. So, the long-term study of R. arvalis population allowed to reveal differences in survival and reproductive characteristics of females of distinct ages and generations (Lyapkov et al., 2001a, 2001b). The aim of the present study was to compare the reproductive and demographic characteristics of the populations of *R. temporaria* and *R. arvalis*, inhabiting two different localities. For each species it was necessary to compare the scale of intrapopulation variation with the differences between two localities of the range, basing on long-term and simultaneous studies of populations in both localities. For this purpose the reproducing individuals of these two species have been studied in relatively favorable conditions of their ranges (in Moscow Oblast') as well as in northern part of ranges (in Kirov Oblast').

MATERIAL AND METHODS

For 5 years (1998 – 2002), the amplectant pairs of both species were collected in breeding ponds during reproduction period in two localities: in Moscow Oblast' — near Zvenigorod Biological Station of Moscow State University, 55 km westward of Moscow (55°44′ N 36°51′ E, 50 m above sea level (a.s.l.); the name of this locality is abbreviated to “ZBS”), and in Kirov Oblast' — near Kipenevshchina village, Orlovskii raion, 40 km westward of Kirov (58°40′ N, 49°5′ E, 100 m a.s.l., “Kirov”). The body length and the age were determined in each individual, fecundity and egg diameter (with eyepiece micrometer, accurate to 0.1 mm) — in each female. The fecundity was estimated by mass of whole clutch taken out of dissected females (previously weighted accurate to 0.1 g) and by mass of clutch portion (weighted accurate to 1 mg) in which all eggs were counted. The relative clutch mass, i.e., clutch mass relative to gravid female mass was estimated also. Age was determined by standard skeletochronological method (preparation of cross-sections of tibio-fibula stained by Ehrlich hematoxiline — Smirina, 1994). The survivorship of both sexes was estimated as calculated number of frogs of a given age (based on the percentage of individuals of this age and the total number of frogs reproducing in a given year) relative to initial number of generation (i.e., total egg number laid in a given year divided by 2). To obtain required data the censuses of clutches of both species in all ponds used by each studied population were conducted since 1988.

RESULTS AND DISCUSSION

The age distributions of matured *R. temporaria* differ substantially between two localities (Fig. 1): the proportion of two-year-olds (both females and males) was higher in ZBS population whereas the proportion of older ages was lower than in Kirov population. Contrarily (and surprisingly), ZBS population of *R. arvalis* (Fig. 2) is characterized by lack of two-year-old females and by very low proportion of two-year-old males. Thus, in Kirov Oblast' the females can maturate at age of two years, unlike to those of Moscow Oblast'. The proportion of 3-year-old females and males was also higher in Kirov Oblast'. The only explanation is that in Kirov Oblast' both species are largely syntopic and reproduce in the same ponds. Correspondingly, the proportion of older ages was higher in ZBS population of *R. arvalis*.

In ZBS population of *R. temporaria*, the body length of each age was significantly larger than in Kirov population (Fig. 3), both in males and females (for each age from

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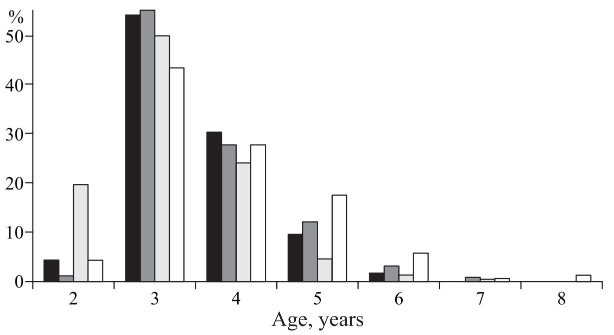

Fig. 1. Age distributions of adult *R. temporaria*, collected in breeding ponds. **Moscow Oblast':** ■, *Rana temporaria* females ($n = 284$); ■, *R. temporaria* males ($n = 326$). **Kirov Oblast':** ■, *R. temporaria* females ($n = 264$); □, *R. temporaria* males ($n = 263$).

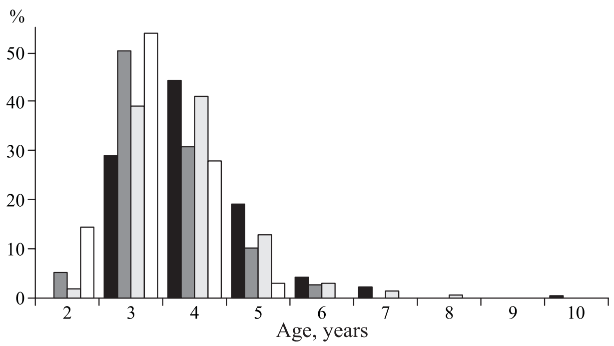

Fig. 2. Age distributions of adult *R. arvalis*, collected in breeding ponds. **Moscow Oblast':** ■, *Rana arvalis* females ($n = 280$); ■, *R. arvalis* males ($n = 280$). **Kirov Oblast':** ■, *R. arvalis* females ($n = 77$); □, *R. arvalis* males ($n = 103$).

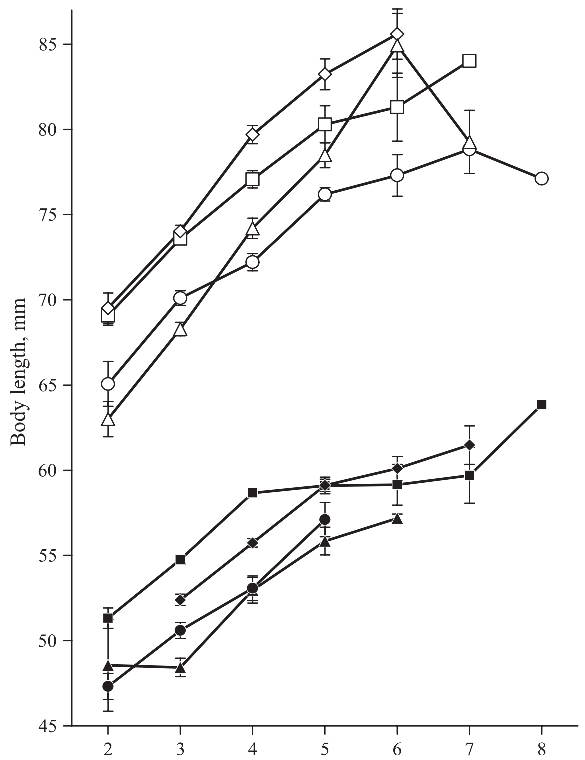

Fig. 3. Dependence of body length on age in *R. temporaria* and *R. arvalis*. The average values and standard errors are given. **Moscow Oblast':** ◇, *Rana temporaria* females; □, *R. temporaria* males; ◆, *R. arvalis* females; ■, *R. arvalis* males. **Kirov Oblast':** △, *R. temporaria* females; ○, *R. temporaria* males; ▲, *R. arvalis* females; ●, *R. arvalis* males.

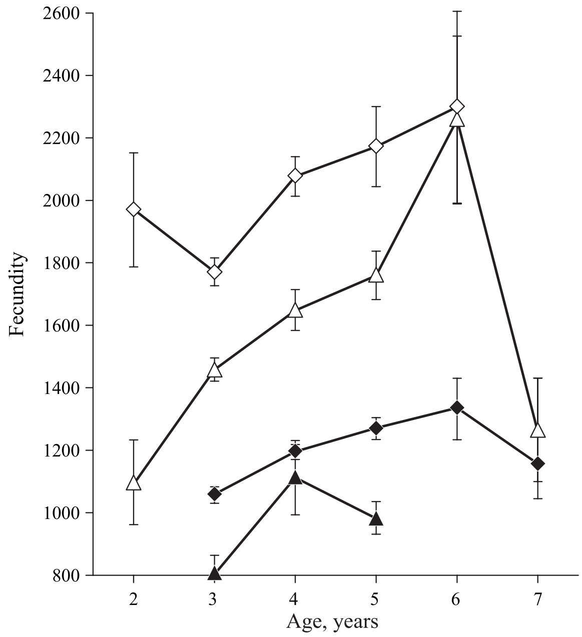

Fig. 4. Dependence of fecundity on age in *R. temporaria* and *R. arvalis*. For designations see Fig. 3.

2 to 5, $p < 0.01$, accordingly to results of 1-way ANOVA). It indicates on lower annual growth rate in Kirov population, though males maturated at the same age as in Moscow Oblast' (after second or third wintering). In ZBS population of *R. arvalis*, the body length at each given age was also considerably larger than in Kirov population, both in males (at the ages from 2 to 5) and females (at the ages from 3 to 5; $p < 0.01$, accordingly to results of one-way ANOVA).

The general trend in populations of both species studied in both localities was the significant increase of fecundity, egg diameter and relative clutch mass with the age of females. At the same time, in Kirov females of both species the age-specific changes of fecundity and egg diameter occur at lower level that corresponds to smaller body length at each age (Figs. 4 and 5). It in turn is determined by stronger restriction of activity season. The number of

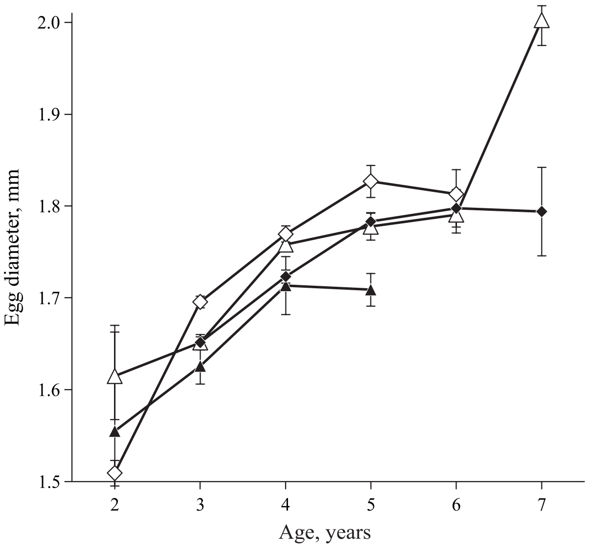

Fig. 5. Dependence of egg diameter on age in *R. temporaria* and *R. arvalis*. For designations see Fig. 3.

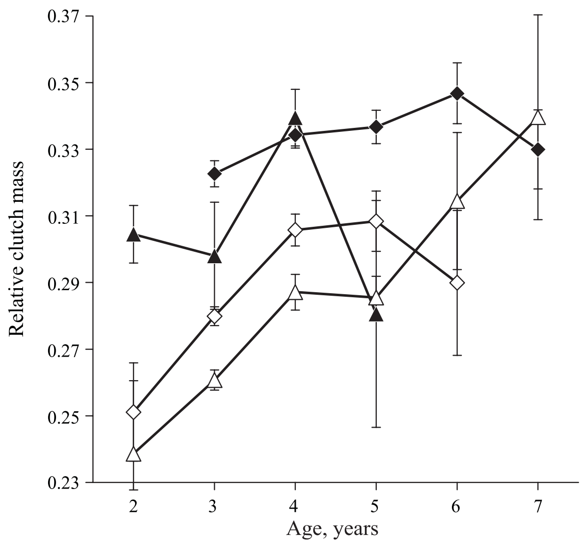

Fig. 6. Dependence of relative clutch mass on age in *R. temporaria* and *R. arvalis*. For designations see Fig. 3.

TABLE 1. Mean Annual Survivorship (%) in *Rana temporaria* and *R. arvalis* in Two Localities

Year	*Rana temporaria*				*Rana arvalis*			
	Moscow Oblast’		Kirov Oblast’		Moscow Oblast’		Kirov Oblast’	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
1998	0.1704	0.0752	0.0181	0.0071	0.1149	0.1042	0.0376	0.0407
1999	0.0893	0.0576	0.0342	0.0071	0.1165	0.0751	0.0418	0.0403
2000	0.1708	0.0776	0.0690	0.0021	0.0609	0.0620	0.1165	0.0123
2001	0.0546	0.0354	0.0261	0.0279	0.0533	0.0334	0.1944	0.1590
2002	0.0155	0.0094	0.0255	0.0000	0.0146	0.0200	0.0695	0.0000

days with air temperature above +5°C in Moscow Oblast’ is on an average on 15 higher than in Kirov Oblast’. In *R. arvalis*, the differences in relative clutch mass between two localities within each age were non-significant (with the exception of 3- and 5-year-old females). In addition, the mean values of relative clutch mass were significantly higher in *R. arvalis* than in *R. temporaria* in each locality (Fig. 6) despite of smaller body size in this species.

The survivorship of separate generations differed between species, localities and sexes. So, in ZBS populations the survivorship of *R. temporaria* females was higher than in the same generations of *R. arvalis*. Survivorship of many ZBS generations in *R. arvalis* females was higher than in Kirov generations. Survivorship of many ZBS generations in *R. temporaria* females was higher than in males. In *R. temporaria*, mean annual survivorship (i.e., average over all generation in a given year, Table 1) of females was higher than in males; mean survivorship in ZBS population was higher than in Kirov population, both in females and males. In *R. arvalis* (Table 1), mean survivorship of females was usually higher than in males, but the differences between two localities were not as distinct as in *R. temporaria*.

The rate of population turnover of each species differs between two localities. As the measures of these differences we can use the values of R_0 (net rate of reproduction) and T (generation time) calculated according to formulas (Pianka, 1978):

$$T = \frac{\sum_{x=0}^{T_{max}} x l_x m_x}{\sum_{x=0}^{T_{max}} l_x m_x}; \; R_0 = \sum_{x=0}^{T_{max}} l_x m_x,$$

where T_{max} is the maximal age, m_x is the average female fecundity of age class x, l_x is the proportion of individuals that have survived till age x.

TABLE 2. Net Rate of Reproduction (R_0) and Generation Time (T) in *Rana temporaria* and *R. arvalis*

Year of birth	R_0				T			
	Rana temporaria		*Rana arvalis*		*Rana temporaria*		*Rana arvalis*	
	Moscow Oblast'	Kirov Oblast'	Moscow Oblast'	Kirov Oblast'	Moscow Oblast'	Kirov Oblast'	Moscow Oblast'	Kirov Oblast'
1994	0.860	2.460	2.978	2.013	4.222	3.687	4.279	3.725
1995	4.401	0.943	5.046	1.406	3.610	4.437	4.048	4.074
1996	2.732	2.797	3.657	1.475	3.616	3.712	4.389	3.811
1997	4.688	3.891	2.460	4.181	3.608	3.836	4.228	3.798

In *R. temporaria*, relatively high proportion of younger ages among breeding adults (Fig. 1) corresponds to lower value of T in most generations of ZBS population (in comparison with Kirov one); in *R. arvalis*, the converse relationship was revealed (Table 2). The variation of R_0 depends not only on age structure and survivorship but on the fecundity. Therefore, the values of R_0 in both localities did not differ distinctly between two species. The values of R_0 in both species are usually higher in Moscow Oblast' than in Kirov Oblast'.

CONCLUSIONS

1. In both species, the variation between localities was comparable with intrapopulation variation that is due to age and belonging to given generation. Therefore, long-term studies are necessary for evaluation of interrelation between geographical and local variation.

2. The constraints, associated with unfavorable climatic conditions in northern locality, influence on both species in the same way.

3. Within each locality, the differences between species in fecundity and egg diameter correspond to larger body length of *R. temporaria* females. The higher values of relative clutch mass in *R. arvalis* females are due to other reasons.

4. The values of R_0 in most generations of both species are usually higher in Moscow Oblast' than in Kirov Oblast'.

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REFERENCES

Ishchenko V. G. (1999), *The Population Ecology of Brown Frogs of Russia and Adjacent Areas. Author's Abstract of Doctoral Thesis*, Zoological Institute, Russian Academy of Sciences, St. Petersburg.

Lyapkov S. M., Cherdantsev V. G., and Cherdantseva E. M. (2001a), "Structure of relationship between fitness components in life history of *Rana arvalis*: 1. Dynamics of reproductive effort and its components," *Entomol. Rev.*, **81**(Suppl. 1), S161 – S169 {Translated from *Zool. Zh.*, 2001, **80**(4), 438 – 446 [in Russian]}.

Lyapkov S. M., Cherdantsev V. G., and Cherdantseva E. M. (2001b), "Structure of relationship between fitness components in life history of *Rana arvalis*: 2. Dynamics of fitness components," *Entomol. Rev.*, **81**(Suppl. 1), S170 – S179. {Translated from *Zool. Zh.*, 2001, **80**(5), 567 – 575 [in Russian]}.

Lyapkov S. M., Kornilova M. B., and Severtsov A. S. (2002a), "Variation structure of reproductive characteristics in *Rana temporaria* and its relationship with size and age of the frogs," *Zool. Zh.*, **81**(6), 719 – 733 [in Russian].

Lyapkov S. M., Kornilova M. B., and Severtsov A. S. (2002a), "Demographic characteristics and number dynamics of *Rana temporaria* population," *Zool. Zh.*, **81**(10), 1251 – 1259 [in Russian].

Miaud C., Guyetant R., and Elmberg J. (1999), "Variations in life-history traits in the common frog *Rana temporaria* (Amphibia: Anura): a literature review and new data from the French Alps," *J. Zool. Lond.*, **249**, 61 – 73.

Pianka E. (1978), *Evolutionary Ecology*, Harper and Row, New York.

Smirina E. M. (1994), "Age determination and longevity in amphibians," *Gerontology*, **40**(4), 133 – 146.