ISSN 1062-3590, Biology Bulletin, 2022, Vol. 49, No. 4, pp. 299–308. © The Author(s), 2022. This article is an open access publication.
Russian Text © The Author(s), 2022, published in Izvestiya Akademii Nauk, Seriya Biologicheskaya, 2022, No. 4, pp. 374–384.

ZOOLOGY

The Age Composition and Postmetamorphic Growth Characteristics of the Moor Frog (*Rana arvalis*) from Habitats with a Short Activity Season

S. M. Lyapkov[a], *, D. V. Ibragimova[b], and N. V. Nakonechnyi[b]

[a] *Faculty of Biology, Moscow State University, Moscow, 119991 Russia*

[b] *Institute of Natural and Technical Sciences of Khanty-Mansii Autonomous Okrug–Yugra, Surgut State University, Surgut, 628412 Russia*

**e-mail: lyapkov@mail.ru*

Received January 13, 2021; revised March 13, 2021; accepted March 13, 2021

Abstract—The between-population and sexual differences in demographic and postmetamorphic growth characteristics were studied in *Rana arvalis* from several habitats of Khanty-Mansiiskii Autonomous Okrug–Yugra (KhMAO) with a relatively short (about 3.5 months) activity season. Skeletochronology was used for age determination. The annual size increments and the rates of these increments were determined on the base of back-calculated body length at each age. In three of four populations, a higher average age in females but not significant sexual differences in the average body length were revealed. In both males and females of all studied KhMAO populations, the rate of the annual size increment between the 1st and 2nd wintering was maximal. The rate of the annual size increment between the 2nd and 3rd wintering was kept relatively high. In comparison with *R. arvalis* populations of Bryansk, Moscow, and Kirov oblasts with a longer activity season (seven, six, and five months, respectively), frogs from KhMAO populations had a relatively small average body length at each age and low population averages of the body length. At the same time, the character of between-age dynamics in the rate of the size increments of KhMAO populations enabled us to reveal the effects of counter-gradient selection not yet mentioned in the literature. These effects represent the maintenance of a relatively high rate of annual increments up to the 5th wintering in *R. arvalis* from KhMAO populations with a short activity season.

Keywords: age composition, body length, postmetamorphic growth, sexual differences, *Rana arvalis*, KhMAO–Yugra

DOI: 10.1134/S1062359022040094

INTRODUCTION

The variability of the life cycle characteristics directed against the gradient of environmental conditions represents interpopulation phenotypic differences, the manifestation of which is opposite to genetic changes that form as an adaptive response in populations located along a given gradient of environmental conditions (for a review, see Laugen et al., 2003; Conover et al., 2009). Already formed adaptive genetic changes can be detected only in field experiments with reciprocal interpopulation transplantations of individuals or under the same conditions of laboratory experiments (Berven et al., 1979). When studying the interpopulation variability of the postmetamorphic growth of amphibians, there is, however, another, indirect way to reveal such genetic changes. Its essence is that data are used not only on the absolute value of the annual increments after metamorphosis during each of the successive seasons of activity, but also on the duration of the season of activity, i.e., the time period during which these annual increases occur (Ishchenko, 1999; Hjernquist et al., 2012). Further, based on these data, estimates of the rate of annual increments are obtained (Lyapkov et al., 2009). Our preliminary study, carried out on two wide range species of Eurasian brown frogs, the moor frog (*Rana arvalis*) and the common frog (*Rana temporaria*), made it possible to reveal in them interpopulation variability in the rate of such annual increments (but not in the average age sizes). This variability was directed against the climatic temperature gradient, which causes differences in the duration of the seasons of activity in the habitats of populations that are geographically distant from each other (Lyapkov et al., 2009). However, in this work, populations from habitats with a duration of the season of activity close to the minimum were not studied. We later obtained such data for the common frog: the growth rates of individuals from populations with an extremely short season of activity were maximum and corresponded to the general pattern of manifestation of variability directed against the gradient of environmental conditions (Lyapkov, 2019).

As a result of our study of moor frog populations in habitats with a short period of activity (~3.5 months) in two different areas of Khanty-Mansiiskii Autonomous Okrug–Yugra (hereinafter for brevity, KhMAO), it was shown that the individuals of these populations are characterized by relatively small sizes at each of the ages and, accordingly, by low annual increments (Matkovsky et al., 2011; Ibragimova and Lyapkov, 2018). A weak expression of size differences between sexually mature females and males was also revealed in these populations of KhMAO.

Later, we studied other populations of the city of Surgut and near it. In this regard, the objectives of this study were the following: (1) Determination of the age of moor frogs of KhMAO populations using the skeletochronology method, a retrospective assessment of body length, and identification of features of their postmetamorphic growth (i.e., body length at each age and the rate of annual growth) under conditions of a severe limitation of the duration of the season of activity. (2) Revealing the relationship of sex differences in body length with the absolute value of annual increments and their rate in each of the populations studied. (3) Comparison of the studied characteristics of populations from urban habitats with a strong anthropogenic load with populations from habitats with a relatively weak anthropogenic impact. (4) Comparison of the results obtained with our earlier data on the growth of moor frogs from populations with a longer season of activity from Bryansk, Moscow, and Kirov oblasts, as well as with the published data.

MATERIALS AND METHODS

The material was collected in the habitats of several populations of moor frogs in the Khanty-Mansiiskii Autonomous Okrug. The habitat of the first of the urban populations was in the industrial zone of the city of Surgut (61°15′35″ N, 73°32′45″ E), near the dam of Surgutskaya GRES-2. The habitat of the second urban population was in the forest park (mixed small-leaved–coniferous forest and raised bog, 61°14′38″ N, 73°25′06″ E), and the third habitat was in the Ob floodplain (willow reed grass–sedge water meadows, 61°14′04″ N, 73°25′44″ E). The data for all these urban populations, with high or medium anthropogenic loads, were pooled (hereinafter for brevity, Surgut). The control population, the anthropogenic load in the habitat of which was practically absent, was located 28 km northeast of Surgut (hereinafter, for brevity, Control, 61°38′35″ N, 73°48′35″ E). A more detailed description of the habitats of the populations of Surgut and Control was given earlier (Ibragimova and Starikov, 2013). The capture of animals in the habitats of these populations was carried out using trapping cylinders, from May to September 2011, and the duration of the season of activity in the habitats of a given population was 3.7 months, The habitat of another studied population, also characterized by low anthropogenic pressure, was located 50 km south of Surgut, in the vicinity of the village of Yugan (hereinafter for brevity, Yugan, 60°52′41″ N, 73°41′20″ E). This habitat includes forest and floodplain plant communities, with activity season duration also of 3.7 months. The material was collected at the end of May 2017 and 2018, manually, on land during the period of migration of adults to spawning water bodies, as well as in spawning water bodies. In addition, we used our data on three populations of the northern part of the Khanty-Mansiiskii Autonomous Okrug (hereinafter, NKhMAO). The age and size composition of these three populations does not differ significantly from each other (for more details, see Matkovsky et al., 2011), so we combined the data on them into one sample. The duration of the season of activity in the habitats of populations NKhMAO was 3.5 months.

Postmetamorphic growth was studied using data on the age and calculated body length of immature and adult moor frogs from the populations studied. In each individual, the body length was measured and the age was determined by making sections of the middle of the diaphysis of the shin, stained with Ehrlich's hematoxylin. A few immature individuals were also used to determine the age and assess the rate of resorption of the endosteal bone. The main problem of accurate age determination is the estimation of the number of resorbed lines of stunting (otherwise referred to as "lines of arrested growth") corresponding to the first and second (rarely) wintering (Hemelaar, 1985; Smirina and Makarov, 1987). According to the measurements, in individuals from the populations of Surgut, Control, and Yugan, the diameter of the line of arrested growth corresponding to the first wintering did not exceed 0.87 mm, respectively. When determining the age, we assumed that in individuals with a bone marrow cavity diameter of more than 0.87 mm, complete resorption of this first line occurred. Similar data (0.77 mm) were used to determine the number of individuals with a resorbed first line of population of NKhMAO.

Since the transverse sections of the shin usually have a shape close to an ellipse (rather than a regular circle), the value of the outer diameter of the transverse sections and each of the lines of arrested growth was determined as half the sum of the minimum and maximum values of the measured diameters (for details, see Smirina, 1983). A retrospective assessment of the body length was performed using the most commonly used Dahl–Leo equation (Marunouchi et al., 2000): $L_i = LD_i/D_{external}$, where L_i is the calculated body length at a given age i, D_i is the diameter of the corresponding line of arrested growth, $D_{external}$ is the outer diameter of the section measured in the caught

Table 1. Average values of body length (mm) and age in the moor frog of the studied populations of Khanty-Mansiiskii Autonomous Okrug

Population	Sex	*n*	Age	Body length, mm
NKhMAO (a)	♀	75	**3.80**	48.24
	♂	74	**3.41**	47.80
Surgut (b)	♀	32	3.28	45.21
	♂	48	3.19	46.27
Control (c)	♀	14	3.50	45.27
	♂	14	3.57	45.90
Yugan (d)	♀	30	4.60	51.10
	♂	33	4.27	52.88

Significant differences in the mean values of females and males are marked in bold ($p < 0.05$). Significant differences between populations (letter designations of populations are in the left column of the table): age, females: a–b, a–d, b–d, c–d; age, males: a–d, b–d, c–d; body length, females: a–b, a–c, a–d, b–d, c–d; body length, males: a–d, b–d, c–d.

individual, and L is the length of the body of the caught individual. According to the calculated body lengths before this one (L_{i+1}) and the previous one (L_i) overwintering, the annual increments were calculated: $L_{i+1} - L_i$, and according to them, the growth rate for a given season: $V(i \rightarrow i + 1) = (L_{i+1} - L_i)/t$, where t (months) is the duration of the season of activity in the habitat of a given population. For comparison with the KhMAO populations, the same calculations were carried out using our unpublished data on the populations of Bryansk, Moscow, and Kirov oblasts, for which the duration of the active season was seven, six, and five months, respectively. It should be noted that the need to use a retrospective assessment of body length is explained by the fact that, since the majority of individuals in the KhMAO populations become sexually mature not earlier than after the 3rd wintering (see the Results section), the calculated values allow us to estimate the body length before the 1st and 2nd wintering using larger samples, in comparison with a few samples of immature individuals with a measured body length.

During the statistical processing of the material, a two-way analysis of variance was used (factors: sex and population, fixed effects model) and subsequent multiple comparisons of means using the STATISTICA 8.0 statistical software package.

RESULTS

Age Composition and Qualitative Features of Post-Metamorphosis Growth and the Structure of Growth Layers

In the Yugan population, a relatively small part of individuals bred for the first time already after the 3rd wintering, the rest after the 4th wintering, and the maximum identified age was ten years (Fig. 1). In other populations, i.e., NKhMAO, Surgut, and Control, at the age of three years, a large proportion of individuals bred, not only males, but also females, and, correspondingly, a smaller proportion of four-year-old individuals (Fig. 1). In contrast to the Yugan population, the maximum age of individuals in these three populations was seven years old (NKhMAO) and five years old (Surgut and Control).

Line of arrested growth, corresponding to the first wintering, was completely (or almost completely, which excluded the possibility of measuring its diameters) resorbed in 40.9% of individuals of the Surgut population, in 64.1% of individuals of the Control population, in 46.9% of individuals of the Yugan population (Fig. 2), and in 85.3% of individuals populations of the NKhMAO. Line of arrested growth, corresponding to the second wintering, was completely resorbed in 5.1, 20.5, 3.1, and 27.7% of individuals, respectively.

Interpopulation and Sex Differences in the Mean Values of the Age and Body Length

Comparison of the studied populations of NKhMAO within the same sex revealed the maximum average population age values (significantly differing from all other populations) in both females and males of Yugan and the minimum values in both females and males of the Surgut population (Table 1).

Both females and males of the Yugan population were characterized by maximum average body lengths (all differences are significant, see Table 1), which corresponded to the maximum value of their average age. In comparison with the other two populations, the females of the Surgut and Control populations were characterized by significantly lower values of the average body length and did not differ from each other. Males of the populations studied were characterized by the same ratio of the average population sizes (Table 1).

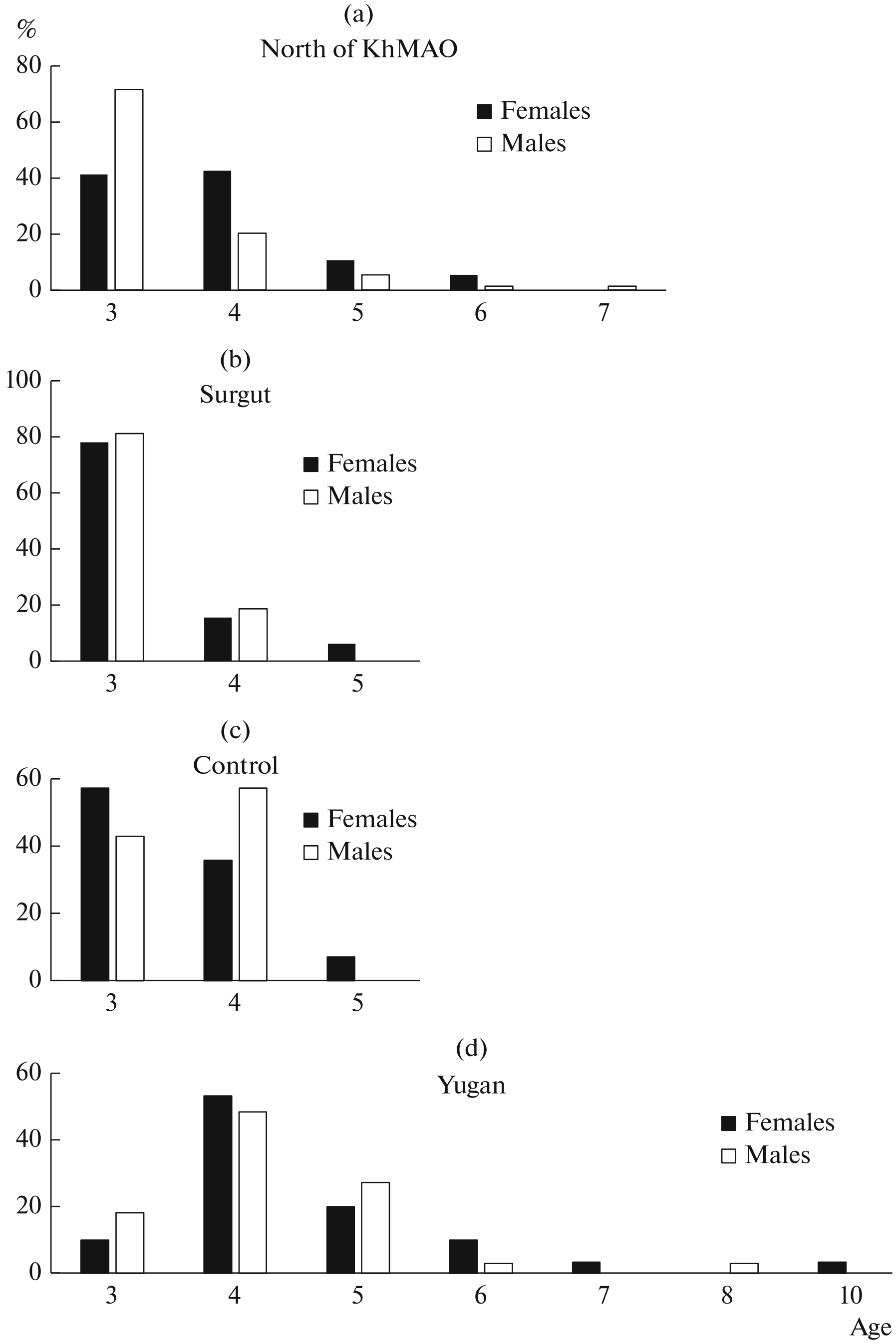


Fig. 1. Distribution (%, vertical axis) of ages (horizontal axis) of mature individuals of the studied populations of KhMAO. (a) NKhMAO, (b) Surgut, (c) Control, (d) Yugan.

The general trend of sex differences in all populations, except for Control, was higher average values of the age of females (significant differences in the NKhMAO population). In accordance with the revealed differences in age, the females of the NKhMAO population were slightly (non-significantly) larger than the males; however, in the three remaining populations, the average body length of males was slightly larger (also non-significantly) than that of females.

It should also be noted that the populations from the urban habitats of Surgut with a strong anthropogenic load were most similar in terms of the average body length and age to the suburban population closest to it (Control), and all of them (i.e., both Surgut and Control) differed from the more remote populations of Yugan and NKhMAO.

Age Dynamics of Body Length and the Rate of Annual Growth

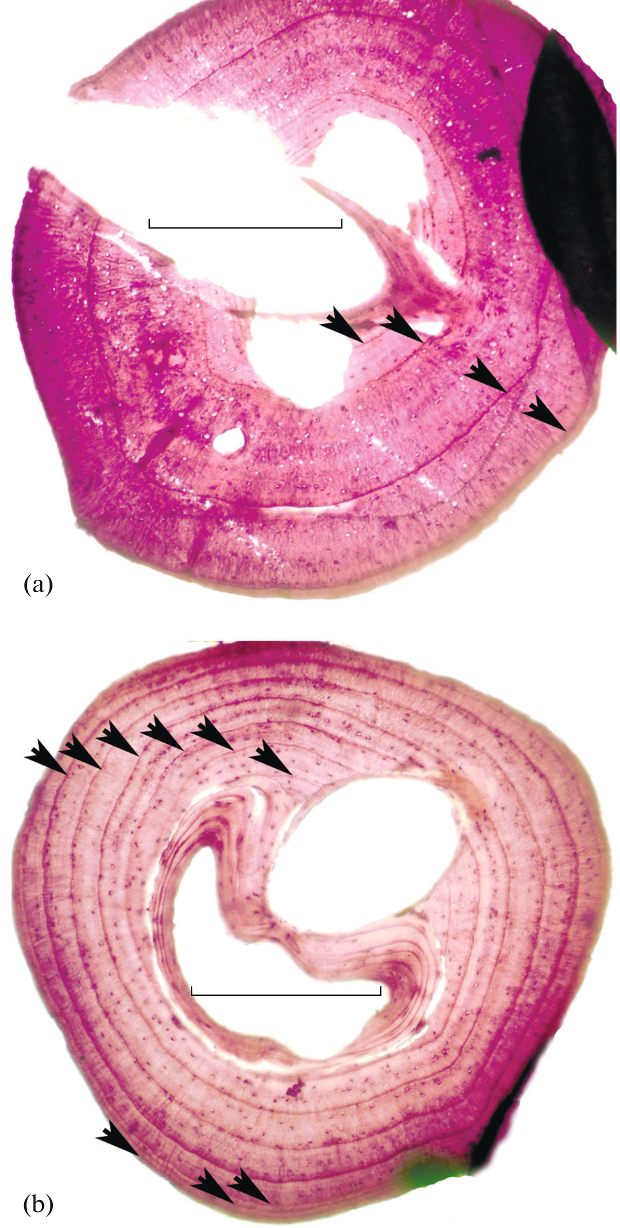
According to the obtained retrospective assessment of the body length (Table 2), individuals of the Yugan population were characterized by the minimum size before the first wintering (in males, they were significantly different from all other populations, see Table 2), as well as before the 2nd wintering (in females, it was significantly different from all other populations; see Table 2). Subsequently, their growth accelerated, and before the 4th wintering they were already larger than the individuals of the other three populations. At the same time, no sex differences in the average body size were found in any of the populations and in any of the ages (the exception is individuals of the Yugan population before the 1st wintering, see Table 2).

Both males and females of each of the four populations of Khanty-Mansiiskii Autonomous Okrug were characterized by the maximum rate of annual increments in the interval between the 1st and 2nd wintering (Fig. 3). Between the 2nd and 3rd wintering, the growth rate remained the same in the Yugan population and slowed down in the three remaining populations. Between the 3rd and 4th wintering, the growth rate in the Yugan population began to slow down, but remained higher than in other populations. Such features of the change in the rate of annual increments of the Yugan population determined the above-mentioned predominance in the size of individuals of this population at the ages of four and five years (Table 2).

Sex differences in the rate of annual increments were not revealed in any of the populations or in any of the ages (the only exception is the increment rate between the 2nd and 3rd wintering in the population of the NKhMAO, Fig. 3).

We also note that the populations from urban habitats (Surgut) were most similar, both in terms of the average age values of the body length and in the rate of annual growth and their age dynamics, with the nearest suburban population (Control), and both of these populations differed significantly from the Yugan population spatially distant from them. As noted above, the same direction of interpopulation differences was also observed in the average values of the body length and age. On this basis, we can conclude that all the demographic and growth characteristics considered are most affected by the spatial disunity and the corresponding climatic differences, and not by the anthropogenic load itself.

Compared with the populations of Bryansk, Moscow (Zvenigorod biostation, hereinafter referred to as ZBS), and Kirov oblasts, the individuals of the Khanty-Mansiiskii Autonomous Okrug populations were characterized by a relatively high average rate of annual growth over a wider range of ages (Fig. 3). In the period between the 1st and 2nd wintering, almost all the studied populations were characterized by a high growth rate, regardless of the duration of the active season. However, already in the next warm season (between the 2nd and 3rd wintering), the rate of growth in individuals from the population of Bryansk oblast was significantly lower than the year before. Further, between the 3rd and 4th wintering, the growth rates also decreased in the two more northern



(a)

(b)

Fig. 2. Microphotographs of sections of the shin of sexually mature moor frogs. Length scale, 1 mm. (a) Yugan, male, body length 54 mm, five winterings; (b) Yugan, female, body length 57 mm, ten winterings. Arrows point to lines of arrested growth corresponding to wintering areas. In both individuals, the line corresponding to the first wintering is not completely resorbed, and the line of the last wintering is not marked, since it has not moved away from the outer edge of the section.

Table 2. Back-calculated body length (mm) in each of the ages in the moor frog of the studied populations

Population		NKhMAO (a)		Surgut (b)		Control (c)		Yugan (d)	
age	sex	♀	♂	♀	♂	♀	♂	♀	♂
1	X	22.23	23.24	23.03	22.65	23.93	24.48	**21.98**	**19.34**
	n	10	3	68	73	13	9	19	14
	min	16.58	21.34	15.41	15.00	19.87	20.85	15.84	16.60
	max	24.82	24.19	29.37	28.38	27.23	29.96	27.51	23.00
2	X	33.17	33.24	33.27	32.92	33.98	34.75	30.96	31.17
	n	68	64	65	77	22	16	30	31
	min	23.83	22.31	23.10	19.85	24.68	29.61	21.43	23.41
	max	44.18	43.14	43.78	47.52	40.72	39.37	41.36	41.20
3	X	40.54	41.81	42.29	42.85	41.16	41.61	42.08	43.88
	n	72	73	21	29	11	13	30	33
	min	27.50	25.22	32.30	32.30	31.86	35.94	31.42	33.20
	max	55.00	53.77	50.78	52.36	47.98	46.46	51.72	52.00
4	X	46.67	46.97	48.24	49.79	47.40	46.51	**49.16**	**52.06**
	n	44	22	2	3	3	3	28	28
	min	36.77	39.87	46.97	48.41	45.40	40.70	40.51	46.61
	max	56.62	52.93	49.52	50.49	50.66	49.91	57.00	59.09
5	X	51.88	49.56	51.87				52.85	55.25
	n	13	6	2	0	0	0	9	11
	min	45.30	46.02	51.64				44.99	52.00
	max	57.07	52.13	52.10				58.00	62.00

X is the average, *n* is the sample size, min is the minimum value, and max is the maximum value. Significant differences in the mean values of females and males are marked in bold ($p < 0.05$). Significant ($p < 0.05$) differences between populations (letter designations of populations are in the heading of the table): age one year, males: a–d, b–d, c–d; age two years, females: a–d, b–d, c–d; age two years, males: c–d; age four years, females: a–d; age four years, males: a–d, c–d; age five years, males: Yugan-NKhMAO.

(than the population of Bryansk oblast) populations of the ZBS and Kirov oblast, while the growth rates remained relatively high in individuals from all four populations of KhMAO (with one exception, males of the Surgut population). The most likely explanation for the revealed age dynamics is that, in the southern populations, most individuals (and not only males, but also females) reach maturity and then grow much more slowly (because they annually allocate a significant proportion of resources for reproduction) already before the 2nd wintering. In more northern populations, this occurs before the 3rd wintering, and only in populations of Khanty-Mansiiskii Autonomous Okrug with the shortest season of activity does it occur before the 4th wintering.

In contrast to the KhMAO populations, sex differences in the growth rate between the 1st and 2nd and 2nd and 3rd wintering were revealed in most of the more southern populations (Fig. 3). In all these cases, males grew faster than females, which corresponds to the general trend of sex differences in the size of annual increments that we revealed, which is manifested in the fact that males are usually larger than females at each age (Lyapkov et al., 2007).

DISCUSSION

There are no data on the annual increment rates in moor frogs (except for our data on several populations (Lyapkov et al., 2009)) in the literature, and therefore we can compare populations of the species from different regions only by the age-specific size dynamics. The most complete set of such published data is contained in our review (Lyapkov, 2013). Let us clarify that the average age values of the body length presented in the review are not a retrospective estimate based on "back-calculation," but data obtained directly from the measurement of frogs. This age-specific body size dynamics is the result of age-related growth dynamics, which, as we have shown, are specific for populations from regions that differ greatly in the duration of the activity period. Record-breaking low average body length values for each of the ages were found in the extreme northern population of the species in Yamal (Ishchenko, 2005). When compared with the populations of other regions with a longer season of activity, the individuals of the studied four populations of Khanty-Mansiiskii Autonomous Okrug were also characterized by relatively small average body length values at each of the ages and average body length values of the population (cf. Lyapkov, 2013, Table 3 and Figs. 3 and 4). The similarity in the average size of KhMAO populations was observed only with populations from habitats with a duration of the season of activity close to the maximum (more than seven months) (Lyapkov et al., 2010), which is explained by the significantly higher contribution to the reproduction of southern populations (Lyapkov et al., 2008) and, correspondingly, by relatively slow growth upon reaching sexual maturity. It is also possible that in some southern populations the humidity regime is not close to the optimum during the entire season of activity.

In addition to a decrease in the size of annual increments with a strong reduction in the duration of the season of activity, a decrease in the average population sizes is also facilitated by a relatively high mortality (primarily from unfavorable abiotic factors), which causes a decrease in the proportion of older ages among mature individuals, which is probably typical for many populations with a short activity season. Thus, in all the populations of the Khanty-Mansiiskii Autonomous Okrug studied by us, relatively high age values were not revealed, which are characteristic, for example, of some mountain populations of the species (Altai with up to 17 winterings and, at the same time, relatively large sizes, Ishchenko, 1996).

The proposed explanation for the decrease in the average population sizes does not contradict the compensation of relatively low growth rates in populations of moor frogs with the short period of activity that we revealed. This compensation cannot be complete, primarily because of the need to allocate a significant proportion of resources not to growth, but to the storage of reserve substances necessary to survive a long winter (for a review, see Berman et al., 2017; Berman and Bulakhova, 2019). It is also likely that, in the complete absence of such compensation, all sexually mature individuals of populations with a short period of activity would be relatively small, despite the higher average population age values, which is not observed in reality (Lyapkov, 2013, Figs. 1, 2).

Separately, the absence of significant sex differences in the size in each of the studied populations of KhMAO should be noted. Despite the higher average values of the age of females (in the population of the NKhMAO, the differences are significant, see Table 1), females and males did not differ significantly in body length, although the trend of larger males remained in the three other populations. Such weak sex differences

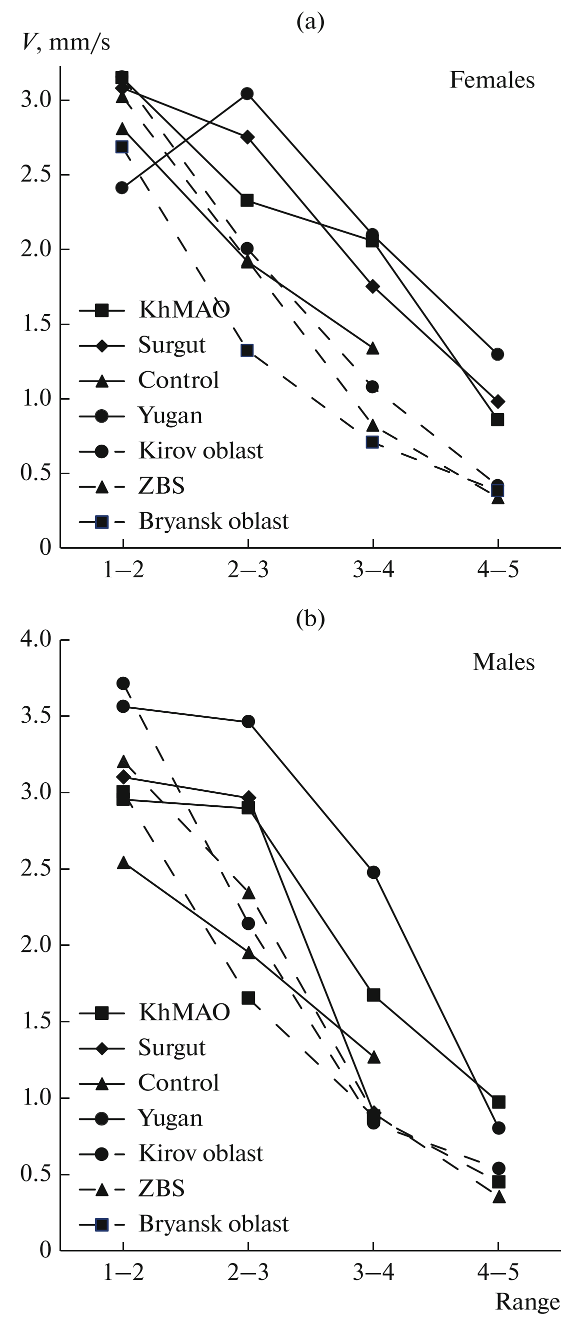


Fig. 3. Annual growth rate (mm/month) during the first four years of life on land after the first wintering (1–2, from leaving the 1st wintering to leaving for the 2nd wintering, 2–3, from leaving the 2nd wintering to leaving for the 3rd wintering, 3–4, from the exit from the 3rd wintering to leaving for the 4th wintering, 4–5, from the exit from the 4th wintering to the leaving to the 5th wintering) in the moor frog of the studied populations of Khanty-Mansiiskii Autonomous Okrug, and from other, geographically remote populations with a longer season of activity. (a) Females; (b) males. Note: significant differences between males and females were revealed: in the interval 1–2, in the populations of Kirov oblast, ZBS, and Bryansk oblast; in the interval 2–3, in the populations of the NKhMAO, Kirov oblast and ST; in intervals 3–4 and 4–5, there were no significant differences between males and females revealed. For the significance of differences between populations, see Table 3.

Table 3. Significance levels of differences between the average population values of the rate of annual growth (V) during the first five years of life on land (1–2, from leaving the 1st wintering to leaving for the 2nd wintering, 2–3, from leaving the 2nd wintering to leaving for the 3rd wintering, etc.)

Population	North KhMAO	Surgut	Control	Yugan	Kirov oblast	ZBS	Bryansk oblast
				V(1–2)			
NKhMAO	×	0.803	0.301	0.015	0.982	0.618	0.061
Surgut	0.845	×	0.279	0.002	0.620	0.668	0.002
Control	0.612	0.141	×	0.164	0.146	0.346	0.580
Yugan	0.437	0.136	0.020	×	0.000	0.002	0.153
Kirov oblast	0/309	0.002	0.001	0.611	×	0.207	0.000
ZBS	0.735	0.558	0.065	0.207	0.001	×	0.000
Bryansk oblast	0.950	0.557	0.196	0.044	0.000	0.080	×
				V(2–3)			
NKhMAO	×	0.045	0.126	0.000	0.023	0.001	0.000
Surgut	0.794	×	0.006	0.212	0.000	0.000	0.000
Control	0.004	0.004	×	0.000	0.737	0.969	0.018
Yugan	0.020	0.072	0.000	×	0.000	0.000	0.000
Kirov oblast	0.000	0.000	0.538	0.000	×	0.438	0.000
ZBS	0.001	0.004	0.179	0.000	0.074	×	0.000
Bryansk oblast	0.000	0.000	0.303	0.000	0.000	0.000	×
				V(3–4)			
NKhMAO	×	0.465	0.036	0.768	0.000	0.000	0.000
Surgut	0.075	×	0.428	0.412	0.102	0.022	0.012
Control	0.351	0.520	×	0.030	0.439	0.119	0.064
Yugan	0.000	0.000	0.005	×	0.000	0.000	0.000
Kirov oblast	0.000	0.870	0.298	0.000	×	0.012	0.004
ZBS	0.000	0.997	0.365	0.000	0.588	×	0.242
Bryansk oblast	0.000	0.958	0.345	0.000	0.737	0.838	×
				V(4–5)			
NKhMAO	×	0.656		0.004	0.004	0.000	0.009
Surgut		×		0.262	0.047	0.015	0.045
Control			×				
Yugan	0.388			×	0.000	0.000	0.000
Kirov oblast	0.057			0.188	×	0.521	0.852
ZBS	0.000			0.001	0.285	×	0.777
Bryansk oblast	0.007			0.029	0.650	0.425	×

Above the diagonal are females, and below the diagonal are males.

in the KhMAO populations correspond to the revealed direction of sex differences in size (males are larger in general and for each of the ages) in most of the range, except for the regions with the shortest period of activity (Lyapkov, 2013).

Thus, the most obvious effect of countergradient selection, i.e., a higher growth rate in the same periods in populations from regions with a shorter season of activity, was revealed by comparing a number of populations of the species whose habitats cover a wide range of the duration of the season of activity. Such differences are revealed, for example, when comparing the population of Bryansk oblast with the more northern population of Kirov oblast (between the 1st and 2nd wintering, as well as between the 2nd and 3rd wintering; Fig. 3). At the same time, there is a great similarity when comparing the average age values of the body length, for example, the same population of Kirov oblast with other populations of the species from habitats with a similar duration of the season of activity (Baitimirova and Vershinin, 2017). Less obviously, but no less important for local adaptations, is the effect of countergradient selection manifested in the fact that in populations with the shortest season of activity (in our work, these are the KhMAO populations; Fig. 3), there is not such a strong slowdown in the growth rate between the 2nd and 3rd, as well as between the 3rd and 4th and between the 4th and 5th, winterings as in southern populations. This growth rate dynamics is a partial compensation for the relatively small sizes before the first and subsequent winterings, due to the relatively short season of activity. Note that we were unable to find in the literature other examples of such an effect of countergradient selection, at least among ectothermic vertebrates. Known cases of secondary growth acceleration of some fish species (Alekseyev et al., 2013; Fig. 4) are explained by migration from small rivers to lakes and the transition to feeding on larger prey, and such an acceleration of growth occurs after reaching sexual maturity. It should also be noted that sometimes the authors of amphibian skeletochronological studies mistakenly interpret the border between the endosteal and periosteal bones, or even lines in the endosteal bone located close to each other, as the first few periosteal lines of arrested growth (Kumbar and Lad, 2017, Fig. 2C; Yilmaz et al., 2005, Fig. 2). This explains the cases of apparent violation of the pattern of rapid growth from the 1st to the 2nd wintering and slower further growth.

CONCLUSIONS

(1) The severe limitation of postmetamorphic growth of the moor frog from populations with the shortest season of activity leads to relatively small sizes at the end of each growth season and usually to low average body lengths of adults, as well as to a weak expression of sexual differences by body size.

(2) Despite the strong anthropogenic impact, the urban populations of the city of Surgut were most similar both in terms of the average body length and the age, and in the rate of annual growth and their age dynamics with the suburban population closest to them, and both of these populations differed more strongly from other, spatially remote from them, KhMAO populations.

(3) When comparing the populations of moor frogs from a number of regions that differ in the duration of the season of activity, only in populations from habitats with the shortest season of activity was the effect of countergradient selection, which was not previously noted in the literature, revealed, which is manifested in the fact that a relatively high rate of annual increments persists up to 5th wintering.

FUNDING

This work was supported by the Russian Foundation for Basic Research (project no. 16-04-01771) and within the framework of a State Assignment (Part 2 no. CITIS AAAA-A16-116021660031-5).

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

OPEN ACCESS

REFERENCES

Alekseyev, S.S., Gordeeva, N.V., Samusenok, V.P., Matveev, A.N., Andreev, R.S., Yur'ev, A.L., and Smirina, E.M., Extant and extinct forms of arctic charr *Salvelinus alpinus* (L.) complex from the Leprindo Lake system (Transbaikalia): differentiation in life history, morphology, and genetics, *J. Ichthyol.*, 2013, vol. 53, no. 10, pp. 792–803.

Baytimirova, E.A. and Vershinin, V.L., Interpopulation variability in growth and puberty rates in male moor frogs (*Rana arvalis* Nilsson, 1842), *Comtemp. Probl. Ecol.*, 2017, vol. 10, no. 1, pp. 9–16.

Berman, D.I. and Bulakhova, N.A., Border closed, or what does not let the common frog from Europe to Asia?, *Priroda* (Moscow, Russ. Fed.), 2019, no. 7, pp. 12–26.

Berman, D.I., Bulakhova, N.A., and Meshcheryakova, E.N., Adaptive strategies of brown frogs (Amphibia, Anura, *Rana*) in relation to winter temperatures in the northern Palearctic, *Zool. Zh.*, 2017, vol. 96, no. 11, pp. 1392–1403.

Berven, K.A., Gill, D.E., and Smith-Gill, S.J., Countergradient selection in the green frog, *Rana clamitans, Evolution*, 1979, vol. 33, no. 2, pp. 609–623.

Conover, D., Duffy, T., and Hice, L., The covariance between genetic and environmental influences across ecological gradients, *Ann. N.Y. Acad. Sci.*, 2009, vol. 1168, pp. 100–129.

Hemelaar, A.S.M., An improved method to estimate the number of year rings resorbed in phalanges of *Bufo bufo* (L.) and its application to populations from different latitudes and altitudes, *Amphibia-Reptilia*, 1985, vol. 6, pp. 323–341.

Hjernquist, M.B., Soderman, F., Jonsson, K.I., Herczeg, G., Laurila, A., and Merila, J., Seasonality determines patterns of growth and age structure over a geographic gradient in an ectothermic vertebrate, *Oecologia*, 2012, vol. 170, no. 3, pp. 641–649.

Ibragimova, D.V. and Lyapkov, S.M., Demographic and morphometric characteristics of the moor frog *Rana arvalis* from a transformed habitat in the Khanty-Mansi Autonomous Region—Yugra, *Biol. Bull.* (Moscow), 2018, vol. 45, no. 8, pp. 831–838.

Ibragimova, D.V. and Starikov, V.P., *Amfibii v ekosistemakh goroda Surguta: problema optimizatsii gorodskoi sredy* (Amphibians in the Ecosystems of the City of Surgut: The Problem of Optimization of the Urban Environment), Surgut: OOO Bibliografika, 2013.

Ishchenko, V.G., Problems of demography and declining populations of some Euroasiatic brown frogs, *Russ. J. Herpetol.*, 1996, vol. 3, no. 2, pp. 143–151.

Ishchenko, V.G., Population ecology of brown frogs in Russia and adjacent countries, *Doctoral (Biol.) Dissertation*, St. Petersburg: Zool. Inst. Ross. Akad. Nauk, 1999.

Ishchenko, V.G., Growth of brown frogs of fauna of Russia: some problems of study of growth in amphibians, *Russ. J. Herpetol.*, 2005, vol. 12, suppl., pp. 153–157.

Kumbar, S.M. and Lad, S.B., Determination of age and longevity of road mortal Iindian common toad *Duttaphrynus melanostictus* by skeletochronology, *Russ. J. Herpetol.*, 2017, vol. 24, no. 3, pp. 217–222.

Laugen, A.T., Laurila, A., Rasanen, K., and Merila, J., Latitudinal countergradient variation in the common frog (*Rana temporaria*) development rates—evidence for local adaptation, *J. Evol. Biol.*, 2003, vol. 16, pp. 996–1005.

Lyapkov, S.M., Geographical variability and sex differences in body length and age composition in moor frogs: formation and patterns of manifestation, *Pratsi Ukr. Gerpetol. Tov.*, 2013, no. 4, pp. 64–86.

Lyapkov, S.M., Age composition and features of postmetamorphic growth of common frog (*Rana temporaria*) from populations with an extremely short season of activity, *Izv. Vyssh. Uchebn. Zaved., Povolzh. Reg., Estestv. Nauki*, 2019, no. 1, pp. 96–104.

Lyapkov, S.M., Cherdantsev, V.G., and Cherdantseva, E.M., Sexual differences in growth rates and survival in the moor frog (*Rana arvalis*) after completion of metamorphosis, *Zool. Zh.*, 2007, vol. 86, no. 4, pp. 475–491.

Lyapkov, S.M., Cherdantsev, V.G., and Cherdantseva, E.M., Geographical variation as a result of differences in the rates of evolution of traits with a wide and narrow reaction norm in the moor frog (*Rana arvalis*), *Zh. Obshch. Biol.*, 2008, vol. 69, no. 1, pp. 25–43.

Lyapkov, S.M., Kornilova, M.B., Serbinova, I.A., Korzun, E.V., and Novitskii, R.V., Formation of directed geographic variation of features of the life cycle of brown frogs, *Sovr. Gerpetol.*, 2009, vol. 9, no. 3/4, pp. 103–121.

Lyapkov, S.M., Kornilova, M.B., Marchenkovskaya, A.A., Misyura, A.N., and Gasso, V.Ya., Peculiarities of age composition, dimensional sex differences, and reproductive characteristics of moor frogs in the southern part of the range, in *Gerpetologicheskie issledovaniya v Kazakhstane i sopredel'nykh stranakh* (Gerpetological Research in Kazakhstan and Adjacent Countries), Almaty, 2010, pp. 150–165.

Marunouchi, J., Kusano, T., and Ueda, H., Validity of back-calculation methods of body size from phalangeal bones: an assessment using data for *Rana japonica, Curr. Herpetol.*, 2000, vol. 19, pp. 81–89.

Matkovskii, A.V., Lyapkov, S.M., and Starikov, V.P., Rates of post-metamorphic growth and age composition of moor frog populations near the northern border of the range according to skeletal chronology data, *Sovr. Gerpetol.*, 2011, vol. 11, no. 3/4, pp. 143–156.

Smirina, E.M., Intravital age determination and retrospective assessment of the body size of the common toad (*Bufo bufo*), *Zool. Zh.*, 1983, vol. 62, no. 3, pp. 437–444.

Smirina, E.M. and Makarov, A.N., On establishing the correspondence between the number of layers in the tubular bones of amphibians and the age of individuals, *Zool. Zh.*, 1987, vol. 66, no. 4, pp. 599–603.

Yilmaz, N., Kutrup, B., Çobanoğlu, Ü., and Özoran, Y., Age determination and some growth parameters of a *Rana ridibunda* population in turkey, *Acta Zool. Acad. Sci. Hung.*, 2005, vol. 51, no. 1, pp. 67–74.