ISSN 1995-0829, Inland Water Biology, 2022, Vol. 15, No. 4, pp. 464–475.

Comparative Analysis of the Parasite Fauna of *Rana arvalis* in the Environmental Gradients of Ural

A. V. Burakova[a, *], **V. L. Vershinin**[a, b, **], **and S. D. Vershinina**[a, †]

[a] *Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, Russia*
[b] *Department of Biodiversity and Bioecology, Ural Federal University, Yekaterinburg, Russia*
**e-mail: annabios@list.ru*
***e-mail: vol_de_mar@list.ru*

Received June 22, 2021; revised December 7, 2021; accepted December 8, 2021

Abstract—*Rana arvalis* Nilss., 1842 parasitocenoses in the gradients of natural and urban Ural landscapes have been analyzed. Twelve helminth species (Platyhelminthes and Nematoda phyla) have been found. It is demonstrated that the differences in the ratio between parasites belonging to different taxa are caused by the differences in the biology of parasite groups and microbiotopic characteristics of the host's habitat. The transformation of parasitocenoses in the *R. arvalis* populations of the Middle Ural urbocenosis is associated with a decrease in the parasites species diversity and an increase in the proportion of trematodes. At the end of metamorphosis, the species range of macroparasites with different localization expands and rare helminths species appear, which is associated with the amphibians expanding their food spectrum. Thus, the changes in the species diversity and the structure of parasitic communities of the moor frog are largely associated with thermal and moisture supply and their ratio in certain biocenoses.

Keywords: moor frog, parasites, urbanization, natural gradient, ontogenesis

DOI: 10.1134/S1995082922040289

INTRODUCTION

The moor frog *Rana arvalis* Nilsson, 1842 is a tailless amphibian species with broad area and high ecological plasticity (Kuz'min, 1999). The parasite fauna of this species within Russian borders was described for Kaliningrad oblast (Golikova, 1960) and Vologda oblast (Radchenko and Shabunov, 2008). The helminth fauna of *R. arvalis* has been studied in the most detail in the Middle Volga region (Chikhlyaev et al., 2015; Chikhlyaev ad Ruchin, 2021), Republic of Bashkortostan (Yumagulova, 2000; Zaripova et al., 2008; Zaripova et al., 2018), West Siberia (Kuranova, 1988; Burakova, 2012; Zhigileva and Kirina, 2015), Novosibirsk oblast (Zolotarenko and Sous', 1976), Khanty-Mansi Autonomous Okrug–Yugra (Ibragimova and Starikov, 2013; Ibragimova and Nakonechnyi, 2017), and the Republic of Buryatia (Schepina et al., 2009; Baldanova et al., 2010).

In Ural, there is data on the parasitocenoses of the Yekaterinburg urban agglomeration (Vershinin et al., 2017), as well as the Polar (Vershinin et al., 2018) and Southern Ural and Trans-Ural (Danilovaskii, 1997; Burakova and Vershinin, 2016). Since Ural Mountain country extends for an extremely long distance from the north to the south (~2300 km) crossing several landscape and climatic zones and is considered a natural border between Europe and Asia (Chikishev, 1966), the study of *R. arvalis* parasitocenoses in the Urals is of high importance.

The aim of the work was to assess how the parasite complex of *R. arvalis* changes along the environmental gradients of Ural.

MATERIALS AND METHODS

The material for study was collected in the mountainous areas and the Ob River floodlands in the Polar Ural, the western and eastern slopes of the Middle Ural (urban and natural areas), and the East-Southern Ural province of the Southern Ural and Trans-Ural in 2010–2019 (Fig. 1).

Since the Ural Mountains cross eight physicogeographical regions longitudinally (Chikishev, 1966), the climatic differences between its northern and southern parts are profound (Table 1). The distinguishing geochemical feature of spawning water reservoirs in the forest-steppe and steppe zones of the Trans-Ural region is their high natural mineralization (Table 2).

The parasitocenoses in the urban gradient were studied in Yekaterinburg, which is located on the east-

Abbreviations: AI, abundance index, no. of parasites/individual host; P, prevalence, %.
† Deceased.

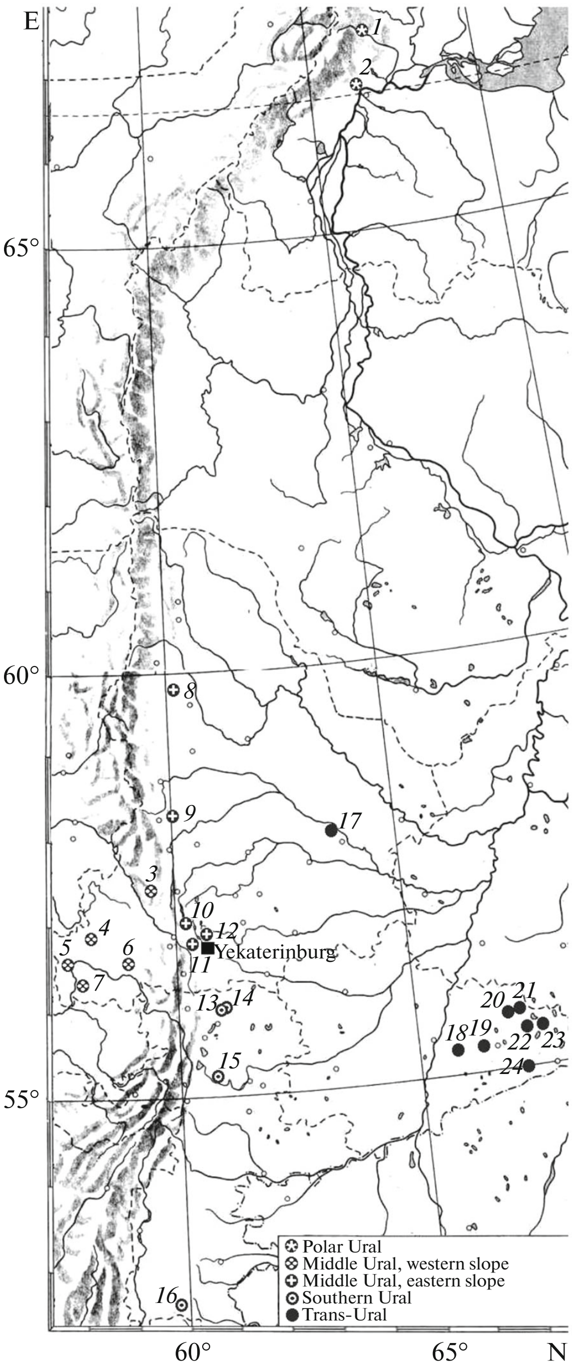

Fig. 1. Schematic map of the material collection sites. (*1*) Krasnyi kamen' ecosite, (*2*) Labytnangi, (*3*) Visimskii natural reserve, (*4*) settlement of Vogulka, (*5*) Krasnorufimsk, (*6*) Olen'i ruch'i Park, (*7*) village of Bugalysh, (*8*) Krasnotur'insk, (*9*) village of Oktyabr'sky, (*10*) village of Sagra, (*11*) Lake Peschanoe, (*12*) Yekaterinburg (black square), (*13*) Lake Berdanish, (*14*) settlement of Metlino, (*15*) settlement of Baydashevo, (*16*) settlement of Arkaim, (*17*) Turinsk, (*18*) settlement of Vargashi, (*19*) Lake Kamyshnoye, (*20*) settlement of Sungurovo, (*21*) Lake Kurtan, (*22*) settlement of Koshelevo, (*23*) settlement of Zhuravlevka, and (*24*) Lake Stepnoe.

ern slope of the Middle Ural (Fig. 1). Within the urban agglomeration, a residential area and a forest park area were chosen (Vershinin et al., 2015). The countryside populations of *R. arvalis* were used as a control. The environmental gradient was confirmed by the results of a hydrochemical analysis of spawning reservoirs obtained by the Laboratory of Physical and Chemical Analyses of the Ural State Mining University. The differences between the parasitocenoses of the animals at the 52nd–53rd developmental stages and those that completed metamorphosis (the 54th stage) were studied (Dabagyan and Sleptsova, 1975).

A total of 2468 individual moor frogs were studied, including 30 individuals collected in the Polar Ural and 1833 individuals in the Middle Ural, with 1378 of them collected within the urban agglomeration and 455 in natural areas; 55 individuals were collected in South Ural and 550 in Trans-Ural.

Parasite identification was performed according to the standard method (Ivashkin et al., 1971; Ryzhikov et al., 1980; Sudarikov et al., 2002). Parasite infection rates were assessed based on P(%) and AI (number of parasites/individual host) (Breev, 1976). To test the significance of the differences in P, a χ^2 test with Yates correction was applied, while ANOVA was used in the case of the differences in AI. The domination structure was analyzed using the approach suggested by Kirillov (2011). All calculations, including AI and P calculations and statistical analysis, were carried out using the Statistica software package for Windows 6.0.

RESULTS

In *R. arvalis*, 12 parasite species belonging to the Platyhelminthes (6 species) and Nematoda (6) phyla were registered in the areas under study. Species composition, localization, and parasite infestation level are presented in Tables 3 and 4.

Depending on the mode of entry and developmental cycle, helminths are divided into three ecological groups (Chikhlyaev and Faizulin, 2016): (1) autogenous biohelminths—Trematoda adult stages (marita) circulating along the food chains (*Dolichosaccus rastellus*, *Opisthioglyphe ranae*, *Diplodiscus subclavatus* and *Haplometra cylindracea*); (2) allogenic biohelminths—helminths, actively (percutaneously) entering amphibians from water sources (*Echinoparyphium recurvatum* and *Holostephanus volgensis*); and (3) autogenic geohelminths—sexually mature stages of nematodes with a direct developmental cycle passively (perorally) infecting their hosts while the latter occasionally come into contact with invasive larvae on the shore (*Oswaldocruzia filiformis*, *Aplectana acuminata*, *Neoraillietnema praeputiale*, *Cosmocercoides pulcher*, and *Rhabdias bufonis*) or in water (*Cosmocerca ornata*) (Kirillov and Kirillova, 2016; Kirillov and Kirillova, 2021), i.e., which do not circulate along food chains (Fig. 2a).

Table 1. Climatic conditions of the Ural physicogeographical areas

Region	Climate type	Annual rainfall, mm	Average July temperature, °C	Relative air humidity in summer, %	Reference
Polar Ural	Arctic, cold	650–800 in river valleys	+10 to +12	70–80	Krivtsov and Vodorezhov, 2016
Middle Ural	Moderate Continental	400–700	+16 to +19	60–65	Chikishev, 1966; Dyachenko, 1997; Krivtsov and Vodorezhov, 2016
Western slope	Moderate Continental	600–700			
Eastern slope	Significantly more continental and drier than on the Western slope	400–500			
Southern Ural	More Continental than in the Middle Ural	300–500	+18 to +20, +22 to +40 in the far south	70–76	Chikishev, 1966; Mil'kov and Gvozdetskii, 1976; Dyachenko, 1997
Trans-Ural	Continental	300–400	+19 to +21	30–59	Kuvshinova, 1968; Dyachenko, 1997; Krivtsov and Vodorezhov, 2016

Table 2. Average surface water mineralization and average monthly temperature (April and May)

Region	Parameter	
	mineralization, mg/dm^3	temperature, °C
Middle Ural		
western slope	198.7 ± 102.6 ($n = 4$)	–
eastern slope	142.1 ± 24.9 ($n = 68$)	11.6 ± 0.31 ($n = 223$)
Yekaterinburg		
forest park zone	190.4 ± 18.9 ($n = 117$)	11.5 ± 0.21 ($n = 504$)
residential zones	419.6 ± 18.2 ($n = 128$)	13.7 ± 0.17 ($n = 725$)
Southern Ural	216.0 ± 118.6 ($n = 3$)	–
Trans-Ural	842.3 ± 118.6 ($n = 3$)	–

Mean values and error of mean are provided, n is the sample number; a dash indicates no data.
Mineralization—significant at $F(5, 317) = 27.091$, $p = 0.00001$; temperature—significant at $F(2,1449) = 39.601$, $p = 0.0000$.

In *R. arvalis,* only the *Oswaldocruzia filiformis* nematode was found in the studied areas of the Polar Ural. In the Middle Ural, the *Aplectana acuminata* and *Neoraillietnema praeputiale* nematodes, not found in other regions, were detected. Only the *Cosmocercoides pulcher* nematode was found in the Trans-Ural region. Metacercaria of the *Holostephanus volgensis* trematode have been found everywhere except for the Polar Ural. The relatively small volume of collections from the Polar and Southern Urals did not allow an exhaustive analysis of parasitocenosis structure in these regions (Fig. 2b).

Trematode P is higher in Trans-Ural, as well as in the amphibian populations in the urban ecosystems of Middle Ural (Table 4), when compared with natural ones, although AI was higher in amphibians from Middle Ural than from Trans-Ural. The rate of infection with *Holostephanus volgensis* trematode metacer-

Table 3. Species composition and invasion indices of *Rana arvalis* in Ural natural ecosystems

Taxon	Polar Ural (n = 30)	Middle Ural (n = 455)	Southern Ural (n = 55)	Transurals (n = 550)	Parasite localization
Phylum Platyhelminthes Claus, 1887					
Class Trematoda Rudolphi, 1808	–	28.35 / 5.84^{d}	29.09 / 1.23	51.09$^{b, c}$ / 3.75	
Dolichosaccus rastellus (Olsson, 1876)	–	6.15 / 0.22	23.63^{b} / 1.05	40.91$^{b, c}$ / 2.19^{b}	Gut
Opisthioglyphe ranae (Frölich., 1791)	–	–	3.63 / 0.05	1.27 / 0.04	The same
Haplometra cylindracea (Zeder., 1800)	–	5.27 / 0.14	5.45 / 0.05	18.00$^{b, c}$ / 0.60$^{b, c}$	Lungs
Echinoparyphium recurvatum (Linstow, 1873), mtc.	–	–	–	2.55 / 0.33	Kidney
Holostephanus volgensis (Sudarikov, 1962), mtc.	–	17.36$^{c, d}$ / 5.48^{d}	1.81 / 0.07	0.73 / 0.57	Visceral cavity
Phylum Nematoda Cobb, 1932					
Class Chromadorea Inglis, 1983	10 / 0.43	31.21^{a} / 1.35	34.54^{a} / 2.03	70.55$^{a, b, c}$ / 7.54$^{a, b, c}$	–
Oswaldocruzia filiformis (Goeze, 1782)	10 / 0.43	20.88 / 0.84	27.27 / 1.18	63.64$^{a, b, c}$ / 4.26$^{a, b, c}$	Gut
Cosmocerca ornata (Dujardin., 1845)	–	14.06$^{c, d}$ / 0.35^{d}	1.81 / 0.01	0.91 / 0.05	The same
Neoraillietnema praeputiale (Skrjabin, 1916)	–	2.42 / 0.05	–	–	"
Aplectana acuminata (Schrank., 1788)	–	0.43 / 0.01	–	–	"
Cosmocercoides pulcher Wilkie., 1930	–	–	–	0.55 / 0.009	"
Rhabdias bufonis (Schrank., 1788)	–	4.40 / 0.09	10.90^{b} / 0.83	35.45$^{b, c}$ / 3.22$^{b, c}$	Lungs
Species number	1	8	7	9	

Here and in Table 4: above the line is prevalence (P), %; under the line is abundance index (AI), no. of parasites/individual host; mtc. is metacercaria; n is number of frogs studied; and a dash indicates the taxon is absent. Significant differences: ^{a} with the Polar region, ^{b} with Middle Ural, ^{c} with Southern Ural, and ^{d} with Transurals.

caria was significantly higher in animals from Middle Ural (Table 3), especially from the eastern slope.

The highest infection rate was observed in Trans-Ural. In the animals in the natural ecosystems of Middle Ural, where infection by *Cosmocerca ornata* makes a significant contribution, nematode P is significantly higher than in the urban ecosystems (Table 4).

Along with the presence of common species (Table 2, Fig. 3), the western slope was unique in the presence of the *Aplectana acuminata* nematode, while the eastern slope was unique in the presence of *Holostephanus volgensis* trematode metacercaria, the invasion rate of which is maximal in *R. arvalis* from the urban ecosystem of Middle Ural. The Middle Ural *R. arvalis* populations inhabiting the western slope are predominated by *Oswaldocruzia filiformis*, with *Cosmocerca ornata* and *Dolichosaccus rastellus* being subdominant. In the natural populations of the eastern slope, the superdomination of *Holostephanus volgensis* was registered. The prevalence of the *Oswaldocruzia filiformis*, *Cosmocerca ornata*, *Rhabdias bufonis*, and *Haplometra*

Table 4. Species composition and invasion indices of *Rana arvalis* in the natural and urban areas of Middle Ural

Species	Middle Ural (n = 1833)		
	western slope (n = 173)	eastern slope (n = 1660)	
		urban ecosystem (n = 1378)	natural areas (n = 282)
Phylum Platyhelminthes Claus, 1887			
Class Trematoda Rudolphi, 1808	$\frac{24.27}{0.73}$	$\frac{40.56^{a}}{9.81}$	$\frac{30.85^{d}}{8.98^{d}}$
Dolichosaccus rastellus (Olsson, 1876)	$\frac{13.87^{c}}{0.52^{c}}$	$\frac{11.17^{a}}{0.70^{a}}$	$\frac{1.42}{0.03}$
Opisthioglyphe ranae (Frölich, 1791)	–	$\frac{1.59}{0.04}$	–
Haplometra cylindracea (Zeder, 1800)	$\frac{10.40^{c}}{0.21}$	$\frac{3.84}{0.22}$	$\frac{2.13}{0.10}$
Echinoparyphium recurvatum (Linstow, 1873), mtc.	–	$\frac{2.24}{0.17}$	–
Holostephanus volgensis (Sudarikov, 1962), mtc.	–	$\frac{26.41}{8.66}$	$\frac{28.01}{8.84}$
Diplodiscus subclavatus (Goeze, 1782)	–	$\frac{0.07}{0.0007}$	–
Phylum Nematoda Cobb, 1932			
Class Chromadorea Inglis, 1983	$\frac{53.17^{c}}{2.48^{c}}$	$\frac{11.53}{0.58}$	$\frac{17.73^{b}}{0.65}$
Oswaldocruzia filiformis (Goeze, 1782)	$\frac{40.46^{c}}{1.76^{c}}$	$\frac{9.57}{0.41}$	$\frac{8.87}{0.27}$
Cosmocerca ornata (Dujardin, 1845)	$\frac{19.65^{c}}{0.42}$	$\frac{3.62}{0.08}$	$\frac{10.64^{b}}{0.30^{b}}$
Neoraillietnema praeputiale (Skrjabin, 1916)	$\frac{5.20^{c}}{0.13^{c}}$	$\frac{0.29}{0.002}$	$\frac{0.35}{0.007}$
Aplectana acuminata (Schrank, 1788)	$\frac{1.15}{0.02}$	–	–
Rhabdias bufonis (Schrank, 1788)	$\frac{6.93}{0.13}$	$\frac{2.53}{0.08}$	$\frac{2.84}{0.07}$
Total number of species	7	10	7

Significant differences: [a] with natural ecosystems, [b] with urban ecosystems, [c] with the Eastern slope, and [d] with the Western slope.

cylindracea trematode is 2.8, 3.13, 0.74, and 1.07%, respectively (Fig. 3).

Nine common parasite species were described in the amphibians of the urban agglomeration (residential and forest park zones) and natural areas. *Diplodiscus subclavatus* (residential zone) and *Echinoparyphium recurvatum* trematodes were found only in the urban area (Table 3 and Fig. 4), while *Aplectana acuminata* was found only in the natural populations. A high degree of domination was demonstrated for *Holostephanus volgensis*, mtc. in the amphibians inhabiting the natural areas (Fig. 4, Table 4). The proportion of the *Dolichosaccus rastellus* trematode and the rate of its infestation in the animals of the residential zone increases in the urban ecosystems.

The greatest diversity of nematodes was found in the *R. arvalis* populations in the natural areas and the forest park zone. The proportion of *Oswaldocruzia filiformis* and *Rhabdias bufonis* decreases along the urbanisation gradient (Fig. 4). The western slope of Middle Ural is predominated by *Oswaldocruzia filiformis,* whereas the proportion of this species is low on

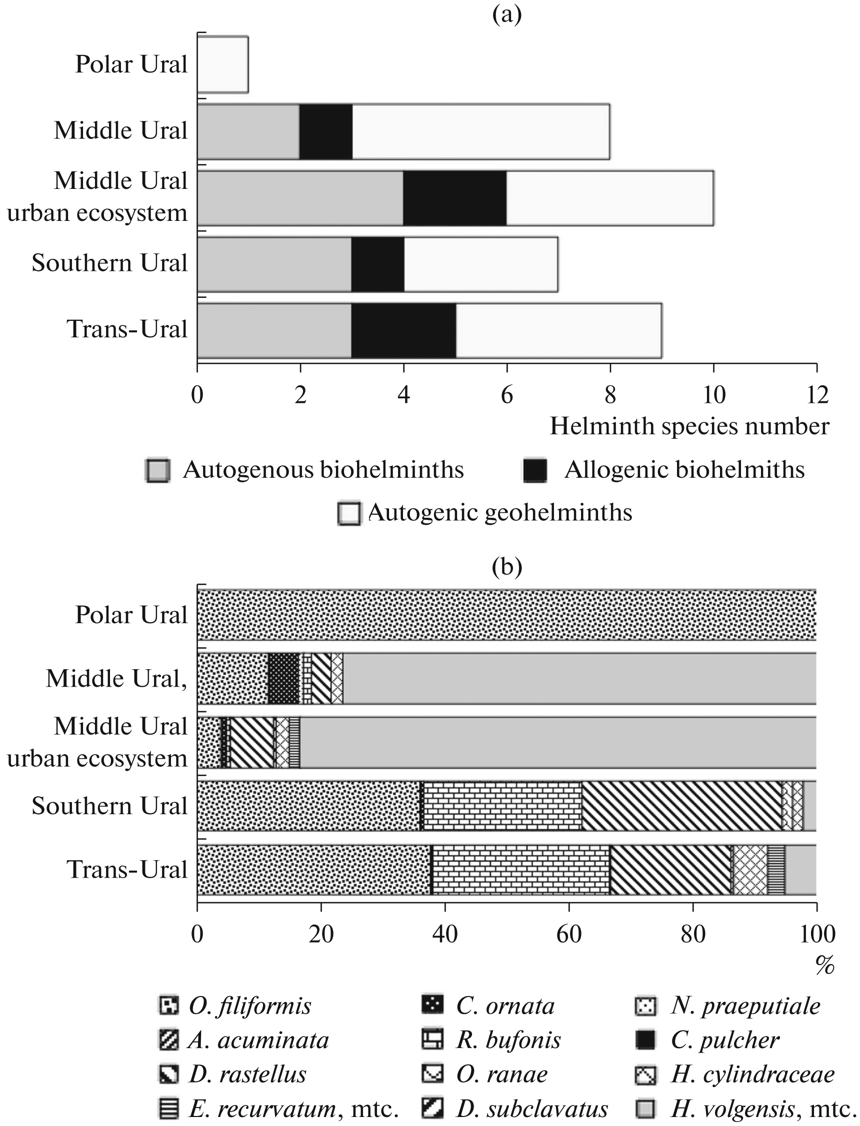

Fig. 2. Ecological groups (a) and parasite species ratio (b) in *R. arvalis* in the studied regions.

the eastern slope (Fig. 3). This is probably why there is a decrease in its presence in urban areas compared to the European part of the habitat.

Of particular interest is a study of the parasitocenoses of amphibians completing metamorphosis (Fig. 5). Two trematode species, *Holostephanus volgensis* and *Dolichosaccus rastellus*, were detected in *R. arvalis* at the 52–53 stages of development in the natural areas of the eastern slope of the Middle Urals, with the rate of infection by *Holostephanus volgensis* metacercaria being considerably higher here that in the urban ecosystem. By the end of metamorphosis, the amphibians are invaded by the *Diplodiscus subclavatus* trematode and *Oswaldocruzia filiformis*, *Cosmocerca ornata*, *Neoraillietnema praeputiale*, and *Rhabdias bufonis* nematodes, whose invasion rates are low (Table 5). The helminthocenoses of *R. arvalis* frogs that have completed metamorphosis in the natural ecosystems are characterized by greater nematode diversity than at the preceding stages.

At stages 52–53, the parasitocenosis of *R. arvalis* inhabiting the residential zone proved to be the most abundant, with four trematode species and the *Oswaldocruzia filiformis* nematode. By the 54th stage, species diversity increases to encompass eight helminth species. Gut nematodes *Cosmocerca ornata* and *Neoraillietnema praeputiale* are absent in the amphibia at the final stages of morphogenesis in urban areas, with the proportion of *Opisthioglyphe ranae* decreased. The *Diplodiscus subclavatus* trematode was registered in the amphibians that completed morphogenesis only in the residential zone. The *Rhabdias bufonis* nematode was detected in the animals with complete metamorphosis

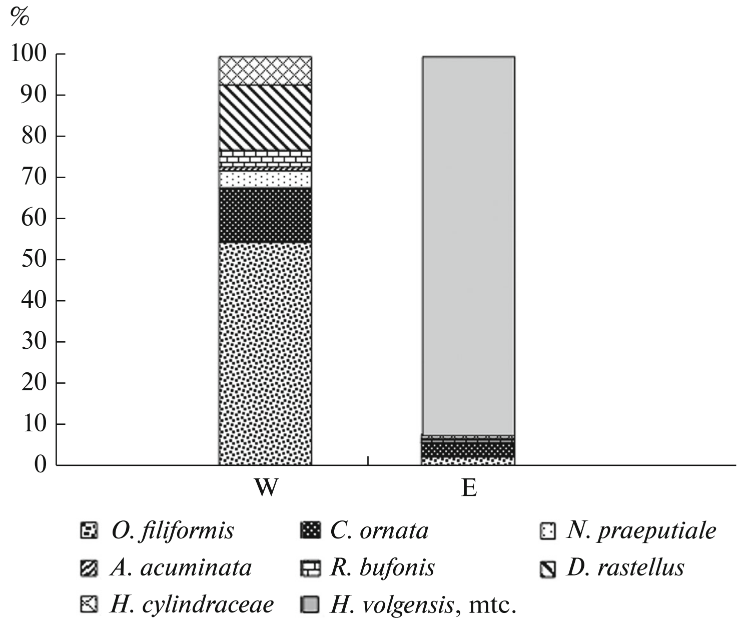

Fig. 3. Parasite species ratio in *Rana arvalis* on the Western (W) and Eastern (E) slopes of the Middle Ural.

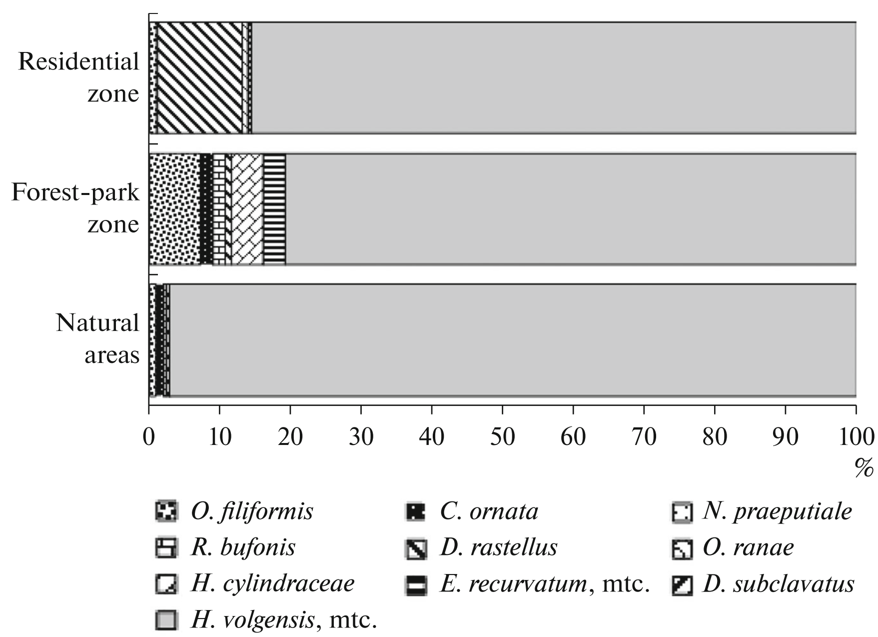

Fig. 4. Parasite species ratio in *Rana arvalis* from the urbanized and natural areas of the eastern slope of the Middle Ural.

in both urban ecosystems and natural areas (Table 5, Fig. 5).

DISCUSSION

The parasitocenoses of moor frogs in the areas under study are characterized by both common and specific features. The trematodes detected in *R. arvalis* from the Middle and Southern Ural and Trans-Ural were not found in the animals inhabiting the Polar Ural, which may be due to the limited sample size, but is more likely due to the extreme environmental conditions. It is generally known that, in natural ecosystems, parasite transmission is regulated by the ambient temperature conditions (Marcogliese, 2001; Morley and Lewis, 2013) and, in some regions with the arctic climate, parasitocenoses are absent or are depleted of trematodes (Galaktionov, 2017).

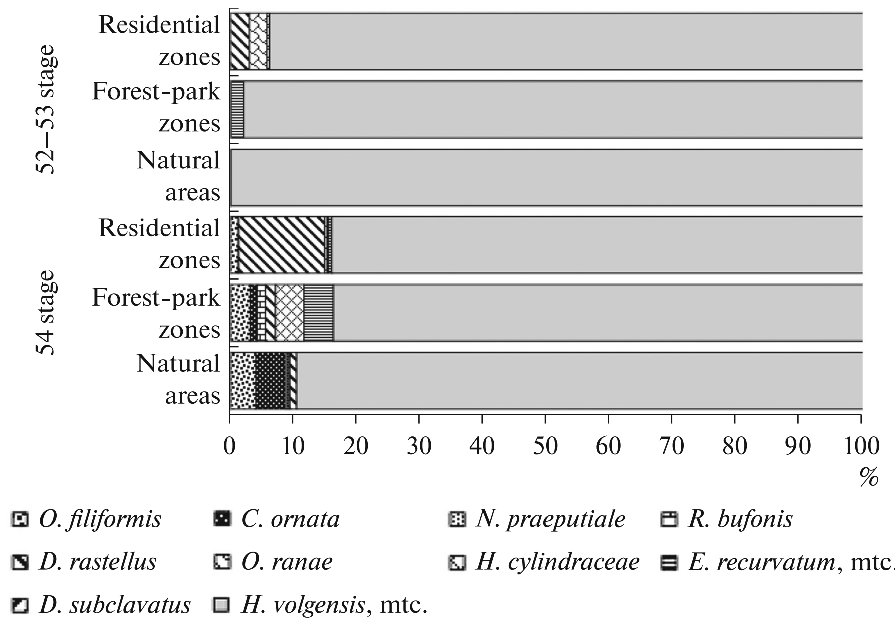

Fig. 5. Parasite species ratio in *Rana arvalis* at different stages of development in the natural populations of the Middle Ural and urban ecosystems.

Trematode species abundance and P are higher in the Trans-Ural region. This may be due to the characteristics of the habitat with open forest-steppe spaces abundant in well-heated lakes and with a wide distribution and high abundance of intermediate and definitive hosts (mollusks and aquatic and semi-aquatic birds with rich trophic links). The spawning water reservoirs of the Trans-Ural region are highly mineralized (Table 2) when compared with those of Middle and Southern Ural. High levels of insolation (Titi et al., 2014) and mineralization (Vershinin et al., 2015) contribute to algae biomass accumulation and the growth of intermediate host populations as well as, as a consequence, the increase in the amounts of cercariae produced by them.

The absence of the *Aplectana acuminata* nematode (Table 4) in the *R. arvalis* populations in Southern Ural (despite its presence in the Middle Ural) is probably due to the small sample size, since it is has been described for this species in the Republic of Bashkortostan (Yumagulova, 2000).

The higher infestation by nematodes on the western slope of Middle Ural than on the eastern slope is determined by differences in temperature and precipitation affecting the completion of the life cycle by nematodes and trematodes. The nematodes described for the western and eastern macroslopes of the Middle Ural are geohelminths, whose eggs and larvae mature in soil at sufficient moisture levels (Barton, 1998) and appropriate temperatures (Griffin, 1988). The high level of precipitation on the western slope of the Middle Ural probably causes a greater infection of animals with nematodes compared with the eastern slope. *Rhabdias bufonis* and *Oswaldocruzia filiformis* AI and P significantly decrease in the eastward direction and the rates of infection with the intestinal nematode *Cosmocerca ornata* decrease.

The distinguishing feature of the eastern slope of the Middle Ural is the high rate of moor frog infection by *Holostephanus volgensis*, which explains the high levels of trematode infestation in the populations of *R. arvalis* observed on this territory. In other regions, *Holostephanus volgensis* was described in *Pelophylax ridibundus* (Pallas, 1771) (Indiryakova, 2011; Chikhlyaev et al., 2012). The putative definitive host of *Holostephanus volgensis* is probably the hooded crow *Corvus cornix* (L., 1758), which is present in large numbers in the anthropocenoses of the Middle Ural (Lyakhov, 2012), including in areas near the spawning reservoirs of *R. arvalis*. The migration routes of the hooded crow (Ryzhanovsky, 2019) make the introduction of the *Holostephanus volgensis* trematode into the Middle Ural highly possible. The maximum invasion of *R. arvalis* by *Holostephanus volgensis* metacercariae in the urban ecosystem may be associated with the high numbers of its intermediate host, the *Bithinia tentaculata* mollusk (L., 1758), which is the dominant species in urban reservoirs (Filippenko, 2011; Romashkova, 2015; Suvorova and Shmakova, 2016).

The presence of the *Opisthioglyphe ranae, Echinoparyphium recurvatum,* mtc., and *Diplodiscus subclavatus* trematodes and an increase in the infection rate and the proportion of *Dolichosaccus rastellus* in the amphibians of the residential zone is associated with the accumulating nature of urbanized ecosystems, an increase in mineralization and temperature of

Table 5. Species composition and invasion indices of *Rana arvalis* at different ontogenetic stages along the urbanization gradient

Species	Residential zone (n = 642)		Forest-park zone (n = 643)		Natural area (n = 242)	
	stages 52, 53 (n = 159)	stage 54 (n = 483)	stages 52, 53 (n = 171)	stage 54 (n = 472)	stage 52, 53 (n = 65)	stage 54 (n = 177)
Phylum Platyhelminthes Claus, 1887						
Class Trematoda Rudolphi, 1808	42.76 / 7.35	$44.09^{d, e}$ / $13.13^{d, e}$	50.29^{b} / 15.63^{b}	33.68 / 6.73	$82.08^{b, c, d}$ / $31.17^{b, c, d}$	14.44 / 2.29
Dolichosaccus rastellus (Olsson, 1876)	8.17^{d} / 0.22	$24.22^{d, a}$ / $1.81^{a, d, e}$	1.16 / 0.02	3.81 / 0.11	1.49 / 0.04	1.66 / 0.02
Opisthioglyphe ranae (Frölich, 1791)	7.54^{b} / 0.20^{b}	2.7 / 0.05	–	–	–	–
Haplometra cylindracea (Zeder, 1800)	2.51 / 0.03	0.62 / 0.006	–	2.54 / 0.31^{c}	–	–
Echinoparyphium recurvatum (Linstow, 1873), mtc.	–	1.24 / 0.06	4.09 / 0.30	3.81^{c} / 0.32^{c}	–	–
Diplodiscus subclavatus (Goeze, 1782)	–	0.20 / 0.002	–	–	–	–
Holostephanus volgensis (Sudarikov, 1962), mtc.	30.18 / 6.89	23.18 / $11.18^{d, e}$	47.95^{c} / 15.30^{b}	26.05 / 5.97	$82.08^{b, c, d}$ / $31.13^{b, c, d}$	13.33 / 2.26
PhylumNematoda Cobb, 1932						
Class Chromadorea Inglis, 1983	0.62 / 0.006	7.24^{a} / 0.18	–	9.74^{c} / $0.40^{c, e}$	–	12.77^{c} / 0.23
Oswaldocruzia filiformis (Goeze, 1782)	0.62 / 0.006	6.83^{a} / 0.17	–	6.56 / $0.22^{c, e}$	–	6.66 / 0.10
Cosmocerca ornata (Dujardin, 1845)	–	–	–	4.02 / 0.07	–	5.55^{d} / 0.11
Neoraillietnema praeputiale (Skrjabin, 1916)	–	–	–	–	–	0.55 / 0.01
Rhabdias bufonis (Schrank, 1788)	–	0.62 / 0.01	–	2.54^{c} / 0.10	–	0.55 / 0.005
Total number of species	5	8	3	7	2	6

Above the line, P, %; below the line, AI, no. of parasites/individual host; the rest is the same as in Table 4.
Significant differences within each zone: [a] with stage 53; [b] with stage 54; significant differences for each developmental stage: [c] with residential zone, [d] with forest-park zone, and [e] with natural area.

spawning reservoirs, and an increase in the intermediate host (gastropods and insects) numbers and the abundance of cercariae produced by them (Vershinin et al. al., 2015; Vershinin et al., 2017). The intermediate hosts of *Diplodiscus subclavatus* are mollusks in the genera *Planorbis* Müller, 1774 (Ryzhikov et al., 1980), as well as *Anisus* Studer, 1820 and *Viviparus* Montfort, 1810, which predominate in urban reservoirs (Mingazova et al., 2008).

Thus, the proportion of trematodes infecting *R. arvalis* increases and the proportion of nematodes decreases on the urban territory, with the emergence of rarely occurring parasite species not registered in natural populations; i.e., these indices show a clear southward trend. This trend can also be noted along the time gradient at the end of metamorphosis.

R. arvalis from the urban and natural territories at the 52nd and 53rd stages of development is invaded by metacercaria forms of trematodes. Early infection by trematodes and their high species diversity in amphibians in residential zones are associated with the ecological features of spawning reservoirs. Infection with

Holostephanus volgensis metacercariae commonly decreases by the 54th stage of development due to the mortality of the most infected individuals (Vershinin et al., 2017). A high proportion of underyearlings (30.4%), who start feeding before the completion of metamorphosis (Vershinin, 1995), in the residential zones of the city leads to their early infestation by soil-inhabiting nematode forms. By the 54th stage, *R. arvalis* frogs inhabiting natural territories are characterized by maximum infestation rates and species diversity, which decrease with the increasing degree of urbanization due to the deep transformation of soils in urban areas.

CONCLUSIONS

Twelve parasite species belonging to the Platyhelminthes (6) and Nematoda (6) phyla were identified in *Rana arvalis* inhabiting the studied areas. The change in the structure of parasitocenoses of *R. arvalis* populations observed along the environmental gradients is due to the differences in the biology of parasite groups and microbiotopic features of host habitats. The distinguishing feature of *R. arvalis* parasite complexes is high rates of infection by the metacercariae of the *Holostephanus volgensis* trematode observed in the animals inhabiting the eastern slope of the Middle Ural. In the urban ecosystems of the Middle Ural, *R. arvalis* parasite species composition is depleted with the increase in the proportion of trematodes and the occurrence of rare parasite species. This is due to the specific features of urban habitats: increased temperatures and a changed chemistry of spawning reservoirs. In the initial period of *R. arvalis* terrestrial life, in the animals completing metamorphosis, colonization by host biotope parasites is determined by the expansion of the spectrum of food objects associated with an increase in the radius of food activity and the continued growth of underyearlings. When moving from the north to the south, infection rates increase, which is due to an increase in heat supply and in the biodiversity of intermediate and definitive hosts. Trematode infection rates increase from west to east. The opposite trend is observed with respect to nematodes, which is associated with a decrease in the moisture supply on the western slope, namely, differences in the hydrothermal coefficient between the western (1.5–1.6) and eastern (1.26) slopes of the Ural mountains, which means an increase in the continentality of the climate.

ACKNOWLEDGMENTS

The authors are grateful to anonymous reviewers for instructive comments that significantly improved the quality of the manuscript, as well as to I.V. Brattseva for her help in preparing the references list.

FUNDING

The work was carried out as part of the State Task for the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, state registration topic no. 122021000082-0.

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.

REFERENCES

Baldanova, D.R., Shchepina, N.A., and Dugarov, Zh.N., Parasite fauna of tailless amphibians of Transbaikalia and its dependence on ecological conditions, *Trudy Mezhdunarodnoi konferentsii "Ekologicheskie Posledstviya biosfernykh protsessov v ekotonnoi zone Yuzhnoi Sibiri i Tsentral'noi Azii"* (Proc. Int. Conf. "Ecological Consequences of Biospheric Processes in the Ecotone Zone of Southern Siberia and Central Asia"), Ulan-Bator: Bembi, vol. 2, 2010.

Barton, D.P., Dynamics of natural infections of *Rhabdias* cf. *hylae* (Nematoda) in *Bufo marinus* (Amphibia) in Australia, *Parasitology*, 1998, vol. 117, no. 5, pp. 505–513. https://doi.org/10.1017/s0031182098003199

Breev, K.A., Application of mathematical methods in parasitology, in *Problemy izucheniya parazitov i boleznei ryb* (Problems of Studying Parasites and Diseases of Fish), Leningrad: Nauka, 1976.

Burakova, A.V. and Vershinin, V.L., Analysis of parasitofauna in syntopically cohabitating representatives of Anura, *Vestn. S.-Peterb. Univ. Ser. 3.: Biol.*, 2016, vol. 3, pp. 31–36.

Burakova, A.V., Ecological analysis of the helminth fauna of moor frog (Rana arvalis Nilsson, 1842) populations in the urbanization gradient, *Extended Abstract of Cand.* (*Biol.*) *Dissertation*, Perm, 2012.

Chikhlyaev, I.V. and Faizulin, A.I., Materials for the helminth fauna of the edible frog *Pelophylax esculentus* (Linnaeus, 1758) in the Volga basin, *Vestn. S.-Peterb. Univ., Ser. 3: Biol.*, 2016, pp. 175–180. https://doi.org/10.21638/11701/spbu03.2016.329

Chikhlyaev, I.V. and Ruchin, A.B., An overview of the helminths of moor frog *Rana arvalis* Nilsson, 1842 (Amphibia: Anura) in the Volga basin, *Diversity*, 2021, vol. 13, no. 2, art. ID 61. https://doi.org/10.3390/d13020061

Chikhlyaev, I.V., Kirillov, A.A., and Kirillova, N.Yu., Trematodes (Trematoda) of Amphibia from the Middle Volga region. 1. Orders Fasciolida, Hemiurida, Paramphistomida and Strigeida, *Parazitologiya*, 2012, vol. 46, no. 3, p. 171–192.

Chikhlyaev, I.V., Ruchin, A.B., and Faizulin, A.I., Helminths of tailless amphibians (Anura, Amphibia) of the Mordovia Reserve, *Tr. Mord. Gos. Prir. Zapoved.*, 2015, no. 14, p. 376–388.

Chikishev, A.G., 1966. Physical – geographic zoning of the Urals, in *Problemy fizicheskoi geografii Urala* (Problems of physical geography of the Urals), Moscow: Mosk. Gos. Univ., 1966, p. 7.

Dabagyan, N.V. and Sleptsova, L.A., Common frog *Rana temporaria* L., in *Ob"ekty biologii razvitiya* (Objects of Developmental Biology), Moscow: Nauka, 1975.

Danilovskii, G.A., *Kharakteristika klassa zemnovodnykh i ikh parazitofauna na territorii Chelyabinskoi oblasti* (Characteristics of the Class of Amphibians and their Parasite Fauna on the Territory of the Chelyabinsk Region), Chelyabinsk: Chelyabinsk. Gos. Pedagog. Univ., 1997.

D'yachenko, A.P., *Flora listostebel'nykh mkhov Urala* (The Moss Flora of the Urals), Yekaterinburg: Ural, 1997.

Filippenko, D.P., Species composition biotopic groups of gastropod mollusks in pond reservoirs of Kaliningrad, *Vestn. Ross. Gos. Univ. im. I. Kanta*, 2011, no. 1, p. 55–63.

Galaktionov, K.V., Patterns and processes influencing helminth parasites of Arctic coastal communities during climate change, *J. Helminthol.*, 2017, vol. 91, no. 4, pp. 387–408. https://doi.org/10.1017/s0022149x17000232

Golikova, M.N., Ecological and parasitological study of biocenoses of some lakes in the Kaliningrad region, *Parazitologiya*, 1960, vol. 39, no. 7, p. 984.

Griffin, C.T., The effect of constant and changing temperatures on the development of the eggs and larvae *Oswaldocruzia filiformis* (Nematoda: Trichostrongyloidea), *J. Helminthol.*, 1988, vol. 62, no. 4, pp. 281–292.

Ibragimova, D.V. and Nakonechnyi, N.V., Comparative analysis of helminths invasion of *Rana arvalis* Nilss, 1842 of the Middle Ob, *Vestn. Nizhnevartovsk. Gos. Univ.*, 2017, no. 1, p. 49–54.

Ibragimova, D.V. and Starikov, V.P., *Amfibii v ekosistemakh goroda Surguta: problema optimizatsii gorodskoi sredy* (Amphibians in the Ecosystems of Surgut city: the Problem of Optimizing the Urban Environment), Surgut: Bibliografiya, 2013.

Indiryakova, T.A., Comparative characteristics of the helminth fauna of aquatic ecosystems in the Ulyanovsk region, *Vestn. Ul'yanovsk. Gos. S-kh. Akad.*, 2011, no. 1, p. 70–75.

Ivashkin, V.M., Kontrimavichus, V.M., and Nazarova, N.S., *Metody sbora i izucheniya gel'mintov nazemnykh pozvonochnykh mlekopitayushchikh* (Methods for Collecting and Studying Helminths of Terrestrial Vertebrate Mammals), Moscow: Nauka, 1971.

Kirillov, A.A. and Kirillova, N.Y., Analysis of the reproductive structure of the hemipopulation of the *Cosmocerca ornata* (Dujardin, 1845) (Nematoda: Cosmocercidae) in marsh frogs of different ages, *Inland Water Biol.*, 2016, vol. 9, no. 3, pp. 310–318.
https://doi.org/10.1134/S199508291603007X

Kirillov, A.A., Helminth communities of grass snake *Natrix natrix* L. (Reptilia: Colubridae) from south of Middle Volga area, *Izv. Samar. Nauchn. Tsentra Ross. Akad. Nauk*, 2011, vol. 13, no. 1, p. 127–134.

Kirillova, N.Yu. and Kirillov, A.A., Life cycle of *Cosmocerca ornata* (Nematoda: Cosmocercidae), a parasite of Amphibians *Inland Water Biol.*, 2021, vol. 14. no. 3, pp. 316–330.
https://doi.org/10.1134/S1995082921020061

Krivtsov, V.A. and Vodorezov, A.V., *Fizicheskaya geografiya i landshafty Rossii* (Physical Geography and Landscapes of Russia), Rjazan': Rjazansk. Gos. Univ., 2016.

Kuranova, V.N., *Helminth fauna of tailless amphibians of the Ob floodplain, its sex, age and seasonal dynamics, Vopr. Ekol. Bespozvon., Tomsk*: Tomsk. Univ., 1988.

Kuvshinova, K.V., *Climate, Ural i Priural'e: prirodnye usloviya i estestvennye resursy SSSR* (*The Urals and the Urals: Natural Conditions and Natural Resources of the USSR*), Moscow: Nauka, 1968.

Kuz'min, S.L., *Zemnovodnye byvshego SSSR* (Amphibians of the Former USSR), Moscow: KMK, 1999.

Lyakhov, A.G., Corvids of Yekaterinburg, *Mater. Rasprostr. Ptits Urale*, 2012, no. 17, pp. 98–110.

Marcogliese, D.J., Implications of climate change for parasitism of animals in the aquatic environment, *Can. J. Zool.*, 2001, vol. 79, no. 8, p. 1331.
https://doi.org/10.1139/cjz-79-8-1331

Mil'kov, F.N. and Gvozdetskii, N.A., *Fizicheskaya geografiya SSSR* (Physical Geography of the USSR), Moscow: Mysl', 1976.

Mingazova, N.M., Derevenskaya, O.Yu., Palagushkina, O.V., et al., Biodiversity of Kazan water objects, *Uch. Zap. Kazan. Univ., Ser. Estestv. Nauki*, 2008, vol. 150, no. 5, pp. 252–260.

Morley, N.J. and Lewis, J.W., Thermodynamics of cercarial development and emergence in trematodes, *Parasitology*, 2013, vol. 140, pp. 1211–1224.

Radchenko, N.M. and Shabunov, A.A., Ecological and helminthological studies of amphibians in the Vologda region, in *Materialy IV s"ezda Parazitol. obshchestva pri RAN "Parazitologiya v XXI veke—problemy, metody, resheniya"* (Proc. IV Congr. Parasitol. Soc. Russ. Acad. Sci. "Parasitology in the XXI Century—Problems, Methods, Solutions"), St. Petersburg: Lema, 2008, vol. 3.

Romashkova, Yu.A., Small lakes of urban areas in Tolyatti: taxonomic composition, structure of benthic communities, *Samarskaya Luka: Probl. Reg. Glob. Ekol.*, 2015, vol. 24, no. 4.

Ryzhanovsky, V.N., The phenology of seasonal phenomena and the territorial distribution of gray crow (*Corvus cornix*) from the Lower Ob region, *Russ. J. Ecol.*, 2019, vol. 50, no. 1, pp. 88–92.
https://doi.org/10.1134/S1067413618060103

Ryzhikov, K.M., Sharpilo, V.P., and Shevchenko, N.N., *Gel'minty amfibii fauny SSSR* (Helminths of Amphibians of the Fauna of the USSR), Moscow: Nauka, 1980.

Shchepina, N.A., Borisova, N.G., Baldanova, D.R., et al., *Zemnovodnye Buryatii* (Amphibians of Buryatia), Ulan-Ude: Buryat. Nauchn. Tsentr Sib. Otd. Ross. Akad. Nauk, 2009.

Sudarikov, V.E., Shigin, A.A., Kurochkin, Yu.V., et al., *Metatserkarii trematod - parazity presnovodnykh gidrobiontov Tsentral'noi Rossii* (Trematode Metacercariae – Parasites of Freshwater Hydrobionts in Central Russia), Moscow: Nauka, 2002, vol. 1.

Suvorova, A.A. and Shmakova, E.V., The fauna of freshwater gastropod mollusks in Ulyanovsk city, in *Materialy V Vserossiiskoi studencheskoi nauchnoi konferentsii "V mire nauchnykh otkrytii"* (Proc. All-Russ. Student Sci. Conf. "In the World of Scientific Discoveries"), Ul'yanovsk: Ul'yanovsk. Gos. S-kh. Akad., 2016, vol. 6, part 2, p. 297.

Titi, A., Rondelaud, D., Mekroud, A., et al., Natural light influences cercarial emergence of *Calicophoron daubneyi* but not that of *Haplometra cylindracea* from temperature-challenged *Galba truncatula, Parasitol. Res.*, 2014, vol. 113,

no. 10, pp. 3557–3563.
https://doi.org/10.1007/s00436-014-4021-7

Vershinin V.L., Vershinina S.D., Trofimov A.G., and Burakova A.V., Morphological anomalies in *Rana arvalis* Nilsson, 1842 from Subarctic Urban Areas, *Russ. J. Ecol.,* 2018, vol. 49, no. 3, pp. 274–276. https:// doi.org/
https://doi.org/10.1134/S1067413618030116

Vershinin, V.L., Burakova, A.V., and Vershinina, S.D., Comparative analysis of the parasitocenoses of amphibians from the family Ranidae (Anura) in the urbanization gradient, *Russ. J. Ecol.*, 2017, vol. 48, no. 5, pp. 466–475.
https://doi.org/10.1134/S1067413617050149

Vershinin, V.L., Dynamics of nutrition of brown frog leverets during the completion of metamorphosis, *Ekologiya*, 1995, no. 1, p. 68–75.

Vershinin, V.L., Vershinina, S.D., Berzin, D.L., et al., Long-term observation of amphibian populations inhabiting urban and forested areas in Yekaterinburg, Russia, *Sci. Data*, 2015, vol. 2, art. ID 150018.
https://doi.org/10.1038/sdata.2015.18

Yumagulova, G.R., Helminths of amphibians of the Southern Urals, *Extended Abstract of Cand. Sci.* (*Biol.*) *Dissertation*, Ufa, 2000.

Zaripova, F.F., Bairamgulova, G.R., Yumagulova, G.R., et al., Helminth fauna of amphibians in the environment of the Bashkir Trans-Urals, *Vestn. Orenb. Gos. Univ.*, 2008, no. 12, p. 86–88.

Zaripova, F.F., Faizulin, A.I., and Mikhailov, R.A., The fauna of helminths Anurans South Ural region, *Izv. Samar. Nauchn. Tsentra Ross. Akad. Nauk*, 2018, vol. 20, nos. 5–4, p. 559–563.

Zhigileva, O.N. and Kirina, I.Yu., Heminths infestation of the moor frog (*Rana arvalis* Nilsson, 1842) and the siberian tree frog (*Rana amurensis* Boultnger, 1886) in Western Siberia, *Sib. Ekol. Zh.*, 2015, vol. 22, no. 2, p. 287–292.

Zolotarenko, G.S. and Sous', S.M., 1976. Food relations and endoparasites of moor frog (*Rana terrestris* Andr.) in Northern Kulunda, in *Okhrana i preobrazovanie prirody lesostepi Zapadnoi Sibiri* (Protection and Transformation of Forest-Steppe Nature in Western Siberia), Novosibirsk: Nauka.

Translated by E. Martynova