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Research Article

Comparative analysis of the helminth fauna of *Apodemus flavicollis* and *Apodemus uralensis* (Rodentia, Muridae) from the protected areas (European Russia)

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Abstract

Closely related animal species living in similar conditions can enter into competitive relationships. The study of parasitic worms of animal hosts living in the same habitats is of great interest. We conducted a comparative analysis of the parasitic worms of cohabiting mice *Apodemus flavicollis* and *Apodemus uralensis* in the Mordovia Nature Reserve and the National Park "Smolny" (European Russia) in 2018–2022. A total of 1457 individuals of the two mouse species were examined by the complete helminthological necropsy: 635 *A. flavicollis* and 822 *A. uralensis*. In total 17 species of parasitic worms were recorded, including five cestodes, four trematodes, and eight nematodes. We found that the species diversity of helminths is higher in *A. uralensis*. All 17 species of parasites were identified in this rodent. The helminth fauna of *A. flavicollis* is less diverse and represented by 10 parasite species, also characteristic of *A. uralensis*, including three tapeworms, two flukes, and five nematodes. *Apodemus flavicollis* and *A. uralensis* inhabit similar forest habitats and are characterized by an average degree of similarity in helminth composition. The identified differences in the helminth fauna may be associated with the food preferences of these mouse species and the features of their microhabitats. Infection of the two mice with shared helminth species varied among the protected areas studied. At some sampling sites, the infection of *A. flavicollis* turned out to be higher, at others – of *A. uralensis*, which is due to changes in the moisture content of the forest floor and a different number of food items (invertebrates) that are intermediate hosts of helminths. The data obtained confirm the partial overlap of ecological niches of sympatric forest rodents, mainly in the spatial and trophic components.

Keywords: myomorph rodents; yellow-necked mouse; ural field mouse; parasitic worms; syntopic species; protected areas.

Introduction

In recent decades, the study of sympatric animal species has become increasingly important (Ribble & Stanley 1998; Ramiez-Bautista & Lemos-Espinal, 2004; Duvernell et al., 2007; Massoud et al., 2021; Sinsch et al., 2021). Closely related species often live in similar ecological conditions and may enter into competitive relationships, especially in syntopic populations (Churchfield, 1984; Carter, et al. 2004; Gorman & Haas, 2011; Heym et al., 2013; Kaicheen, Mohd-Azlan, 2022; Oliveira et al., 2022; Kirillova, et al., 2023; Vasil'ev et al., 2023). An interesting phenomenon is the overlap of ecological niches of sympatric species using the same environmental resources (Pianka, 1981). Emerging competition can be a major biotic factor affecting animal populations and leading to differences in the ecology and behavior of closely related species. The principle of competitive exclusion, also known as Gause's law, applies here, according to which species with the same ecology cannot coexist. In the process of evolution, competition of such species is eliminated due to the divergence of the ecological niche in one of its components (Gause, 1934). Species divergence is most often observed in the spatial niche and, to a lesser extent, in the food and temporal components of the ecological niche. Interspecific competition leads to the division of spatial niches in ecologically similar animal species (Hofer et al., 2004).

Of particular interest to parasitologists is the study of parasitic worms in sympatric animal hosts living in syntopy. The formation of the helminth fauna of such animals is determined by the similarity or difference in their lifestyle, diet, and location of microhabitats (Martínez-Sotelo et al., 2022). It was previously established that the helminth fauna of closely related species of amphibians or reptiles living in syntopy has medium and high similarity in parasite composition. On the contrary, among phylogenetically distant host species the helminth fauna has low similarity, up to the absence of common parasites (Yoder & Coggins, 2007; Mata-Silva et al., 2008; Ruchin & Chikhlyaev, 2013; Zhigileva & Kirina, 2015; Kirillov & Kirillova, 2019; Sinsch et al., 2021). A relationship has been revealed between the composition of helminths and the living conditions of sympatric amphibian hosts, including their food preferences (Bolek & Coggins, 2003). Another example shows that the composition of helminths of sympatric bird species is largely similar and depends mainly on the diet breadth and preferred habitats (Fedynich, et al., 1997; Navarro et al., 2005; Smith & Fedynich, 2012).

The high similarity in the helminth fauna of syntopic populations of sympatric bat species is due to the use of the same feeding habitats and a similar diet (Kirillova et al., 2022, 2023a). A high degree of similarity in the helminth fauna and significant differences in infection with common helminth species were also revealed in syntopic populations of closely related rodent hosts (Ondrikova et al., 2010; Simoes, et al., 2011; Dwuznik et al., 2017). In forest ecosystems, the most numerous and widespread mammals are myomorph rodents. The yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834) and the Ural field mouse *Apodemus uralensis* (Pallas, 1811) are among the most abundant and common species of forest rodents in the fauna of Russia. Due to their abundance, these small mammals are the main food source for forest carnivores and birds of prey and are widely involved in the circulation of parasitic worms at higher trophic levels. Considering the abundance and wide distribution of wood mice in forest biocenoses of the Middle Volga region, it is of interest to study their helminth fauna. Moreover, these closely related mouse species often occupy the same habitats. In this regard, the purpose of our study was a comparative analysis of the helminth fauna of syntopic rodent species *A. flavicollis* and *A. uralensis* from the Mordovia Nature Reserve and the National Park "Smolny".

Material and methods

We studied the helminth fauna of wood mouse species in two protected areas of the Republic of Mordovia: the Mordovia State Nature Reserve (MNR) and the National Park "Smolny" (NP "Smolny"). The MNR is located in the northwestern part of the Republic of Mordovia (Figure 1).

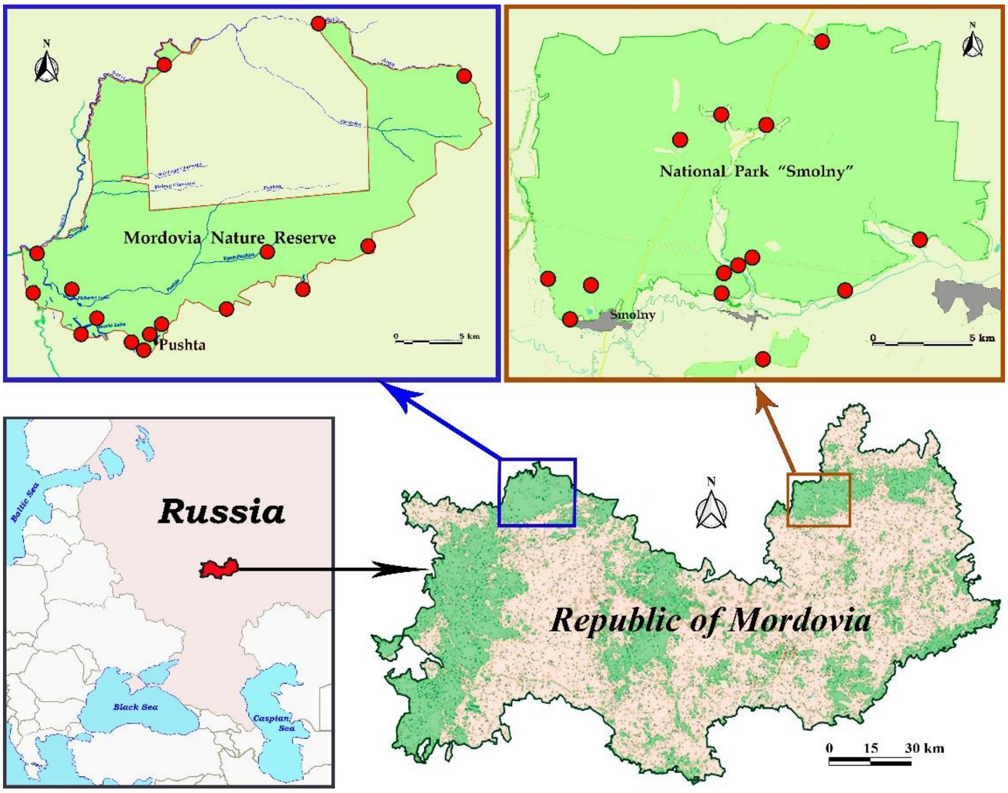

Figure 1. Map of rodent trapping sites in protected areas of the Republic of Mordovia. Red circles on the map indicate the trapping sites.

The territory of the MNR represents the natural ecosystems of southern woodlands (southern taiga), located on the border of mixed and broad-leaved forests, and forest steppe and occupying the right bank of the Moksha River (Artaev et al., 2012). From the north and east, the territory of the reserve is limited by the Satis River (a tributary of the Moksha River) and Arga River, which flows into the Satis. From the south, the forest-steppe directly approaches the border of the reserve. The territory of the reserve is rich in small rivers, streams, and lakes, such as Pushta, Arga, Bolshaya and Malaya Chernaya, Picherki and Inorskoye. In dry years, rivers and streams in the reserve may dry up. The hydrological regime of small rivers often largely depends on beaver dams, which contribute to the flooding of large areas (Grishutkin, 2013; Artaev & Grishutkin, 2014). The fauna of the Mordovia Nature Reserve consists of 299 species, including 22 species of rodents (Artaev et al., 2012; Artaev & Smirnov, 2016).

The NP "Smolny" is located in the northeastern part of the Republic of Mordovia (Figure 1). The territory of the national park is located on the border of mixed and broad-leaved forests, and forest steppe (Grishutkin et al., 2013). The protected area is characterized by a fairly dissected relief with an extensive network of ravines in the northeastern part. The rivers of the park belong to the Sura River basin and include the small rivers Kalysha and Yazovka, and many streams. The lakes are concentrated mainly in the floodplain of the Alatyr River in the south of the NP "Smolny". The national park is inhabited by 282 animal species, including 19 species of rodents (Grishutkin et al., 2013; Smirnov et al., 2022).

Parasitic worms from two mouse species were studied in the 2018–2022 field seasons. Mice were captured at 30 sites in the MNR and the NP "Smolny" (Figure 1). In total, we conducted 15920 trap nights: 7320 in the NP "Smolny" and 8600 in the MNR. A total of 1594 individuals of the two mouse species were trapped: 678 *A. flavicollis* and 916 *A. uralensis* (Kirillova et al., 2024). Of these, 635 *A. flavicollis* and 822 *A. uralensis* were examined for the presence of parasites. Mice were captured using spring metal snap traps. Trap lines with 20 snap traps at 10 m intervals were installed along the edges of forest, the banks of small rivers and streams, and in meadows. Pieces of rye bread fried in sunflower oil were placed in the traps. Mice were captured over five days at each site.

Our research was conducted in compliance with the ethical standards of humane treatment of animals by the recommended standards described by the Directive of the European Parliament and of the Council of the European Union of 22 September 2010, "On the protection of animals used for scientific purposes" (EU Directive 2010/63/EU). The material for the parasitological study was obtained as a result of long-term fieldwork on accounting for the number of small wild animals. Trapping and research of small mammals was carried out by agreements on scientific cooperation with the Federal State Budgetary Institution "Reserved Mordovia" ("Zapovednaya Mordovia") in 2018–2022. The research topics, trapping and handling procedures were approved by the Ministry of Natural Resources and Ecology of the Russian Federation.

The rodents were examined by complete helminthological necropsy (Anikanova, et al., 2007). Parasitic worms were collected and stored in 70% ethanol. Flatworms (trematodes and cestodes) were stained with aceto-carmine, cleared with clove oil, and mounted in Canada balsam. Roundworms (nematodes) were cleared with lactic acid and mounted in Glycerin-Jelly (Anikanova, et al., 2007). Identification of helminths was carried out in the Laboratory of Zoology and Parasitology of the Institute of Ecology of the Volga Basin of the Russian Academy of Sciences (IEVB RAS). The helminth species were identified according to Ryzhikov et al. (1978, 1979), Genov (1984), Kirillov et al. (2012), Feliu et al. (2000), Makarikov and Tkach (2013). Voucher specimens of helminths are deposited in the Parasitological collection of the IEVB RAS (Togliatti, Russia).

To characterize the helminth infection of mice, the following indices were used: infection prevalence (*P*, %), mean abundance (*MA*), and intensity range (*IR*, specimens). To determine the species diversity of helminths in mice, the Shannon index (H'), Margalef diversity index (D_{Mg}), Simpson diversity index (or Simpson dominance index) (d), and Shannon-Pielou evenness (*E*) were calculated. The validity of differences between the values of the Shannon index was assessed using Student′s t-test (Magurran, 2004). Differences were considered to be significant at $P < 0.05$. The dominance of species in the helminth fauna was determined using the Palia-Kovnatsky index (*D*) (Bakanov, 1987). Parasite dominance groups were considered as follows: 10–100 – dominants, 1–10 – subdominants, 0.001–1.000 – adominants. The degree of similarity between the helminth communities of two rodent species was determined using the Jaccard (C_J) (qualitative data) and Sørensen (C_N) (quantitative data) indices (Magurran, 2004). The degree of similarity was assessed as low (0–0.33), medium (0.34–0.66), and high (0.67–1). Mann–Whitney (*U*) tests were used to compare the total infection of mice from different protected areas, as well as to assess the significance of differences in infection of *Apodemus* spp. with shared helminth species. Differences were considered to be significant at $P < 0.05$. The species richness index (bootstrap estimator) was used to standardize rodent sample size (S_B) (Smith & van Belle, 1984; Poulin, 1998). Statistical data processing was performed using the PAST 2.16 software package (Oslo, Norway) (Hammer et al., 2001) and Microsoft Excel 2003 11.5612.5606 (Redmond, USA).

Results

In total, 17 species of helminths were found in *A. flavicollis* and *A. uralensis* from two protected areas of the Republic of Mordovia: four digenean, five cestode, and eight nematode species (Table 1).

Table 1. Helminth fauna of *Apodemus flavicollis* and *Apodemus uralensis* in protected areas of Mordovia (European Russia).

Helminth species	**Mordovia Nature Reserve**		**National Park "Smolny"**	
	A. flavicollis	***A. uralensis***	***A. flavicollis***	***A. uralensis***
Spasskijela lobata (Baer, 1925)	4.8/1–6/0.11[1]	8.4/1–54/0.3	5.3/1–14/0.2	4.2/1–13/0.2
Hymenolepis apodemi Makarikov et Tkach, 2013	–	0.2/1/0.002	0.8/1–2/0.01	0.3/1/0.003
Hydatigera taeniaeformis (Batsch, 1786) s. l., larva	1.1/1/0.01	2.6/1–3/0.04	1.5/1/0.02	1.3/1/0.01
Taenia martis Zeder, 1803, larva	–	0.2/2/0.004	–	–
Taenia laticollis Rudolphi, 1819, larva	–	2.3/1–28/0.08	–	–
Plagiorchis elegans (Rudolphi, 1802)	–	1.4/1–7/0.04	3.4/1–6/0.1	7.4/1–51/0.4

Corrigia vitta (Dujardin, 1845)	–	0.4/13–46/0.12	–	1.3/1–2/0.02
Macyella apodemi Jourdane & Triquell, 1973	–	0.2/3/0.01	–	–
Skrjabinoplagiorchis polonicus (Soltys, 1957)	0.8/1–3/0.01	0.8/1–5/0.02	–	–
Aonchotheca murissylvatici (Diesing, 1851)	–	0.4/4– 47/0.1	–	–
Trichuris muris (Schrank, 1788)	–	–	–	0.3/1/0.003
Heligmosomoides polygyrus (Dujardin, 1845)	28.8/1–93/2.7	41.6/1–180/4.9	49.8/1–83/4.7	31.1/1–71/2.7
Mastophorus muris (Gmelin, 1790)	0.8/1–4/0.02	0.2/4/0.01	–	0.3/1/0.003
Heterakis spumosa Schneider, 1866	–	0.2/1/0.002	–	0.3/2/0.01
Syphacia obvelata (Rudolphi, 1802)	11.8/3–200/4.3	24.5/1–200/8.1	13.3/1–189/5.2	21.5/2–341/8.0
Syphacia stroma (Linstow, 1884)	56.5/4–400/29.1	12.0/1–570/3.7	51.3/1–449/21.6	8.3/1–110/1.1
Rictularia proni Seurat, 1915	0.3/3/0.01	0.4/4/0.02	–	–
Total	8(8.1)[2]	16	7(7.1)	11(11.1)
Cestoda	2	5	3	3
Trematoda	1	4	1	2
Nematoda	5	7	3	6

Note: [1] – prevalence of infection (*P*, %)/intensity range (*IR*)/mean abundance (*MA*); [2] – species richness index in parentheses.

The majority of helminths found in mice were represented by adult forms of 14 species. The larval stages of three species of tapeworms were also observed since the intermediate hosts of these cestodes are rodents. Ten recorded helminth species are host-specific parasites of rodents from the Murinae subfamily: *Spasskijela lobata*, *Hymenolepis apodemi*, *Macyella apodemi*, *Skrjabinoplagiorchis polonicus*, *Trichuris muris*, *Heligmosomoides polygyrus*, *Syphacia obvelata*, *S. stroma*, *Heterakis spumosa* and *Rictularia proni*. The six identified species of parasitic worms (metacestodes *Hydatigera taeniaeformis* s.l., *Taenia martis*, *Taenia laticollis*, trematode *Corrigia vitta*, nematodes *Aonchotheca murissylvatici* and *Mastophorus muris*) parasitize a wide range of rodent hosts. The identified trematode *Plagiorchis elegans* is an accidental parasite of rodents found in a variety of vertebrates (reptiles, birds, and mammals).

Seventeen species of helminths were found in *A. uralensis* (Table 1). In A. flavicollis, 10 parasite species were detected, also characteristic of the Ural field mouse. Seven species of parasitic worms were found only in *A. uralensis*: metacestodes *Taenia martis* and *Taenia laticollis*, trematodes *Corrigia vitta* and *Macyella apodemi*, nematodes *Aonchotheca murissylvatici*, *Trichuris muris* and *Heterakis spumosa*.

The total infection of *A. uralensis* with helminths was 59.3%, *MA* = 15.5; *A. flavicollis* – 72.4%, 34.1. The helminth fauna of both mouse species was dominated by nematodes (Table 1). The infection rate of *A. flavicollis* with roundworms was 71.8%, 33.9; of *A. uralensis* – 56.0%, 14.9. The highest infection rates of *A. uralensis* with nematodes were observed for *Heligmosomoides polygyrus*; among nematodes in *A. flavicollis* – for *Syphacia stroma* (Table 1).

Infection of mice with cestodes was significantly lower: *A. flavicollis* – 6.3%, 0.2; *A. uralensis* – 9.9%, 0.3. Among cestodes, *S. lobata* was the most common in both rodent species (Table 1). Trematodes in mice were rare: *A. flavicollis* – 1.9%, 0.1; *A. uralensis* – 4.8%, 0.3.

On the territory of the MNR, 16 species of helminths were found in mice, eight parasites were common to both rodent species (Table 1). All 16 parasite species were detected in *A. uralensis*. The total infection of the Ural field mouse with helminths was 63.5%, 17.4. According to the Palia-Kovnatsky dominance index (*D*), the helminth fauna of *A. uralensis* was dominated by nematodes *Heligmosomoides polygyrus* (*D* = 11.7) and *Syphacia obvelata* (11.4). The nematode *Syphacia stroma* (2.5) was subdominant. The remaining 13 species of parasites were classified as adominants. Eight species of helminths were detected in *A. flavicollis*. The total infection rate of the yellow-necked mouse was 68.8%, 35.7. In the helminth fauna of *A. flavicollis*, the dominant species was the nematode *S. stroma* (44.6); subdominants were *H. polygyrus* (2.2) and *S. obvelata* (1.4). Five species of parasites were adominants.

In the NP "Smolny", 11 species of helminths were registered in the mouse hosts studied (Table 1). All of these parasite species were found in *A. uralensis*, with seven helminths being common to both mouse species. The total infection of rodents with helminths was 52.2%, 12.5. Among the helminths of *A. uralensis*, the nematode *S. obvelata* (14.2) dominated; subdominants included *H. polygyrus* (5.7) and *S. stroma* (1.0). The remaining eight species of parasites were adominants. Seven species of parasites were found in *A. flavicollis*. The total infection rate of *A. flavicollis* with helminths was 77.6%, 31.8. The helminth community was dominated by the nematode *S. stroma* (34.7); subdominants – *H. polygyrus* (7.2) and *S. obvelata* (2.1). The remaining four species of helminths belong to adominants (Table 1).

In both protected areas of Mordovia, only five parasite species were found in A. flavicollis and *A. uralensis* (*S. lobata*, *H. taeniaeformis* (larva), *H. polygyrus*, *S. obvelata*, *S. stroma*) (Table 1). Only in the MNR, six species of helminths were recorded in mice (metacestodes *Taenia martis* and *Taenia laticollis*, trematodes *Macyella apodemi* and *Skrjabinoplagiorchis polonicus*, nematodes *Aonchotheca murissylvatici* and *Rictularia proni*). The nematode *Trichuris muris* was found only in *A. uralensis* from the NP "Smolny".

The remaining six species of parasitic worms (*Hymenolepis apodemi*, *Plagiorchis elegans*, *Corrigia vitta*, *Mastophorus muris*, *Heterakis spumosa*) were recorded in one or both mouse species from both protected areas (Table 1).

In helminth communities of *A. flavicollis* and *A. uralensis* from both protected areas, the structure of dominant and subdominant species was similar. Thus, in both protected areas, three species of helminths are background for mice: *H. polygyrus*, *S. obvelata*, and *S. stroma*.

A comparison of the helminth fauna of two rodent species from two protected areas of Mordovia showed high similarity for mice from the NP “Smolny” according to the Sørensen index (Table 2). An average degree of similarity in helminth communities was noted for mice from the NP “Smolny” according to the Jaccard index, as well as for mice from the MNR according to both similarity indices (Table 2).

Table 2. Indices of helminth species diversity in *Apodemus flavicollis* and *Apodemus uralensis* from two protected areas of Mordovia (European Russia).

Index	**Mordovia Nature Reserve**		**National Park “Smolny”**	
	A. flavicollis	***A. uralensis***	***A. flavicollis***	***A. uralensis***
D_{Mg}	0.736	1.650	0.666	1.090
H'	0.667	1.276	0.896	1.018
d	1.518	2.967	1.969	2.088
E	0.321	0.460	0.460	0.442
C_J	0.50		0.64	
C_N	0.64		0.79	

Analysis of the helminth species diversity in two mouse species showed that the parasite community of *A. uralensis* differs significantly from that of *A. flavicollis* both in the MNR and in the NP “Smolny” (Table 2). The differences between the Shannon index (H') values are statistically significant ($P < 0.001$) for the helminth fauna of mice in both protected areas.

In *A. uralensis* from the NP “Smolny”, a lower species diversity of helminths was revealed. Here, species diversity indices turned out to be lower than in the MNR (H', E, D_{Mg} and d). A greater diversity of helminths was found in *A. flavicollis* from the NP “Smolny”. In this study area, only the Margalef diversity index (D_{Mg}) value for *A. flavicollis* is lower than that in the MNR. A comparison of the two rodent species from different protected areas using the Mann-Whitney test showed significant differences in the helminth infection of *A. flavicollis* and *A. uralensis* (Table 3).

Table 3. Reliability of differences in the infection of *Apodemus flavicollis* and *Apodemus uralensis* with shared helminth species in two protected areas of Mordovia (European Russia).

Helminth species	**Mordovia Nature Reserve**		**National Park “Smolny”**	
	U	***P***	***U***	***P***
Spasskijela lobata	91430.0	0.037	40560.0	0.525
Plagiorchis elegans	–	–	39420.0	0.041
Heligmosomoides polygyrus	82320.0	0.00001	33580.0	0.00001
Syphacia obvelata	82980.0	0.00001	37700.0	0.012
Syphacia stroma	49970.0	0.00001	22410.0	0.00001
Total	76104.0	0.00001	26817.0	0.00001

Note: insignificant differences are shown in gray.

A pairwise comparison of the infection of *A. flavicollis* and *A. uralensis* with shared helminth species using the Mann-Whitney test showed that the Ural field mouse was significantly more infected with the nematode *S. obvelata* in both protected areas. Separately, in the MNR, *A. uralensis* was more infected with the cestode *S. lobata* and the nematode *H. polygyrus*, and in the NP "Smolny" – with the trematode *P. elegans* (species of single parasites were not included in the analysis). *Apodemus flavicollis* was significantly more infected with *H. polygyrus* in the NP "Smolny", and with *S. stroma* in both protected areas (Table 3). Significant differences were revealed in the abundance of helminths of different systematic groups in two species of mice (Table 4).

Table 4. Infection of mice with helminths of different taxonomic groups.

Helminth taxa	Mordovia Nature Reserve				National Park "Smolny"			
	Apodemus flavicollis		*Apodemus uralensis*		*Apodemus flavicollis*		*Apodemus uralensis*	
	P,%	*MA*	*P,%*	*MA*	*P,%*	*MA*	*P,%*	*MA*
Trematoda	0.8	0.01	2.6	0.2	3.4	0.1	8.3	0.4
Cestoda	5.7	0.1	12.6	0.5	7.2	0.2	5.5	0.1
Nematoda	68.3	35.5	60.0	16.7	76.8	31.5	49.4	11.9
Total	68.8	35.7	63.5	17.4	77.6	31.7	52.2	12.5

In both protected areas studied, *A. flavicollis* was significantly more infected with nematodes (MNR – 74680.0, NP "Smolny" – 26310.0, P < 0.0001), and *A. uralensis* was more infected with trematodes and cestodes. Moreover, the differences in the infection of the two rodent species were significant: infection with trematodes in NP "Smolny" – 39030.0, P = 0.015 and with cestodes in MNR – 88260.0, P = 0.0006. The total mean abundance of all parasites in *A. flavicollis* was significantly higher than in *A. uralensis* (Tables 3, 4).

Discussion

A comparative analysis of the helminth species composition in *A. flavicollis* and *A. uralensis* from two protected areas of Mordovia showed that the helminth fauna of the Ural field mouse is more diverse. The helminth fauna of *A. flavicollis* represents a species-poor parasite community characteristic of *A. uralensis*. Differences in the helminth fauna of the two mouse species are associated mainly with the presence/absence of rare and single parasites (Table 1). Analysis of the infection of mice revealed differences in infection rates both for separate helminth species and for taxonomic groups of parasites (Tables 1, 3, 4). Thus, *A. uralensis* is highly infected with cestodes, trematodes, and the nematode *S. obvelata*. *Apodemus flavicollis* is characterized by a higher infection with nematodes, mainly *S. stroma* (Tables 1, 4). In general, *A. flavicollis* carries the highest parasitic load in wood mouse populations in two protected areas of Mordovia, both in the MNR and in the NP "Smolny" (Table 4).

Among the 17 helminth species found in *A. flavicollis* and *A. uralensis*, 10 species are host-specific for mice. Only these two mouse species participate in the life cycle of *S. polonicus*, *R. proni*, *S. obvelata*, and *S. stroma* in the studied protected areas of Mordovia. Moreover, only *A. uralensis* participates in the circulation of the trematode *M. apodemi*, the cestode *T. laticollis*, and the nematode *T. muris*. *Apodemus flavicollis* and *A. uralensis* are also the main hosts of *S. lobata* and *H. polygyrus*.

It follows that host population density is important for maintaining the number of parasites that have one or two species of definitive hosts in a certain area. According to our data, the number of *A. flavicollis* is relatively lower than that of *A. uralensis* (Kirillova, 2024). Thus, the relative abundance of *A. flavicollis* in the MNR was 4.8 individuals per 100 trapping nights, and of *A. uralensis* – 7.2 individuals per 100 trapping nights. In the NP "Smolny", the same trend was revealed: the relative abundance of *A. flavicollis* was 3.6 individuals per 100 trapping nights, and of *A. uralensis* – 4.1 individuals per 100 trapping nights. Analysis of the helminth fauna of mice showed that the more numerous species, *A. uralensis*, has a greater species diversity of helminths both in the MNR and in the NP "Smolny". At the same time, the infection rates of *A. flavicollis* with helminths were significantly higher than those of *A. uralensis*. More numerous *A. uralensis* inhabit most habitats of the biocenosis, thereby increasing the likelihood of helminth infection. As a result, the range of rodent diets is expanding due to new food items. This leads to an expansion of the helminth composition, mainly due to the appearance of rare parasite species that make up the majority of the helminth fauna of *A. uralensis*. It has previously been shown that the degree of infection with helminths that have a direct life cycle is related to the population density of the host (Arneberg et al., 1998; Arneberg, 2002; Kirillova et al., 2009; Dwuznik et al., 2017). Despite the presence of a certain relationship between the number of hosts and their infection with helminths, the density of the host population is not a determining factor for the degree of infection of mice with parasites. Infection of animals with helminths that have a complex life cycle occurs regardless of the host population density, as a result of the implementation of its main trophic relationships.

More than half of helminths (11 species) found in the studied wood mice are para-sites with an indirect life cycle. Only six nematode species are geohelminths. The intermediate hosts of the cestode *S. lobata* are oribatid and thyroglyphoid mites (Ryzhikov et al., 1979; Genov, 1984). Infection of rodents with this cestode occurs through accidental ingestion of intermediate hosts along with plant food or when digging burrows. The life cycle of *H. apodemi* has not been studied. Apparently, rodents become infected with this parasite by eating millipedes and insects, which serve as intermediate hosts for another species from the genus *Hymenolepis* (Genov, 1984).

Infection of rodents with larval stages of cestodes *H. taeniaeformis* s.l. and *T. laticollis* occurs during the oral penetration of invasive helminth eggs along with food [Genov, 1984; Anikanova et al., 2007). Findings of metacestodes in mice indicate their important role in the circulation of helminths of carnivores. Mice become infected with trematodes from the genera *Plagiorchis* and *Skrjabinoplagiorchis* mainly by eating semi-aquatic insects, the second intermediate hosts of these parasites (Genov, 1984; Kirillov et al., 2012). Infection of mice with the trematode *C. vitta* occurs when eating woodlice of the genera *Philosophia* and *Porcellio* (Quentin, 1970). The life cycle of the trematode *M. apodemi* has not been studied. Rodents become infected with the nematode *M. muris* by eating dung beetles of the genus *Geotrupes*, locusts, grasshoppers, crickets, earwigs and cockroaches – the intermediate hosts of this parasite (Quentin, 1970; Ryzhikov et al., 1978; Shaykenov, 1981). Infection of rodents with *R. proni* probably occurs by eating centipedes, which serve as intermediate hosts for other representatives of the genus *Rictularia* (Ryzhikov et al., 1978). Infection of rodents with geohelminths occurs through accidental ingestion of larvae (*H. polygyrus*) and eggs of nematodes (*A. murissylvatici, T. muris, S. obvelata, S. stroma,* and *H. spumosa*) in close contact with the soil litter. Thus, for the infection of mice with helminths, herbivore diet and close contact with the forest soil litter are of greater importance. In this way, mice become infected with 10 species of parasites. Somewhat less important is the consumption of animal food. In this way, rodents acquire rare or accidental parasites (7 species).

The helminth fauna of two mouse species from different protected areas has an average degree of similarity according to the Jaccard index (without taking into account the abundance of parasites). The Sørensen index (taking into account the abundance of helminths) showed a high degree of similarity only for the NP "Smolny"; for the MNR, an average degree of similarity was revealed (Table 2). The values of species diversity indices showed a greater diversity of helminths in *A. uralensis* from the MNR and the NP "Smolny" (Table 2). In the helminth fauna of *A. flavicollis* from both protected areas, high abundance and dominance of one species (*S. stroma*) leads to a decrease in species diversity.

The greater diversity of helminth communities of *A. uralensis* is due to the fact that the values of dominance indices for one or two dominant parasite species do not differ significantly (in both protected areas) from those for subdominant helminth species. This leads to an increase in the Shannon and Simpson indices. Accordingly, the Shannon-Pielou evenness index will also be higher. The values of the Margalef index, which takes into account both species abundance and number of species, are also higher for *A. uralensis* in both protected areas (Table 2).

The decrease in species diversity of helminths of mice from one study area is associated either with the loss of the dominant parasite species from the helminth fauna (in the case of *A. uralensis*), or with an increase in the abundance of the dominant species (*S. stroma*), as in *A. flavicollis* (Tables 1, 2). Differences in the helminth fauna of *A. flavicollis* and *A. uralensis* are determined primarily by the lifestyle and feeding habits of these mice. *Apodemus flavicollis* avoids open spaces, preferring to live in deciduous forests. This rodent is a typical stenophage and feeds mainly on seeds with a limited amount of other food (Zablotskaya, 1957; Averin et al., 1979; Vekhnik et al., 2019). A characteristic feature of *A. flavicollis* is the ability to climb trees. The rodent willingly settles in hollows at various heights and can collect acorns, nuts and seeds directly from trees (Vekhnik, et al., 2019; Gromov & Erbaeva, 1995; Rossolimo et al., 2004).

Unlike *A. flavicollis*, *A. uralensis* lives in both forests and open habitats and feeds on a wide variety of food items. A wide range of food allows the rodent to settle in different habitats. In addition to plant food, *A. uralensis* readily eats invertebrates – probable intermediate and paratenic hosts of helminths (Zablotskaya, 1957; Kozlov & Tukhsanova, 1966). *Apodemus uralensis* is more associated with the forest floor, which increases the likelihood of infection with helminth eggs or larvae. Thus, the determining factors for infection of both mouse species with helminths are the width of the trophic niche occupied by *A. flavicollis* and *A. uralensis* and the close contact of mice with the forest litter.

The species diversity of helminths of mice from different protected areas is deter-mined by the characteristics of the natural ecosystems. The structure of the helminth fauna is influenced by the structure of the fauna of vertebrates and invertebrates, which can serve as intermediate, paratenic and definitive hosts of parasites in the biocenosis. To the same extent, the influence is exerted by the microclimatic conditions of habitats, the hydrological conditions of the biocenosis, the host population density and several other factors. In our case, there are different degrees of influence of anthropogenic activities on the ecosystems of two protected areas. The greater diversity of helminths found in both mouse species from the MNR is due to the undisturbed biocenoses of this protected area and less human influence over the past 100 years. Therefore, six species of helminths were found in mice only in the MNR (Table 1). The lower diversity of helminths of both mouse species from the NP "Smolny" may be explained by the short history of this protected area. The NP "Smolny" was created only in 1995. Several decades ago, this territory was under anthropogenic pressure, and the forest was actively cut down. The decrease in the diversity of helminths in mice from the NP "Smolny" is due to anthropogenic impact on the ecosystems of the protected area, which, as a rule, leads to a decrease in biodiversity and disruption of the living conditions of invertebrates and vertebrate animals, and also changes the historical connections between the parasites and their hosts.

Conclusions

A comparative analysis of the helminth fauna of syntopic populations of *Apodemus flavicollis* and *A. uralensis* in two protected areas of the Republic of Mordovia showed that the species diversity of helminths is higher for *A. uralensis*. Differences in the species structure of helminths are mainly due to the presence/absence of single or rare parasite species. However, *A. flavicollis* carries the main parasitic load in the biocenoses of both protected areas. The helminth fauna of *Apodemus flavicollis* represents a poor helminth community of *A. uralensis*. In general, *A. uralensis* is characterized by high infection with cestodes, trematodes, and the nematode *S. obvelata*, while *A. flavicollis* is more heavily infected with other species of nematodes. *Apodemus flavicollis* and *A. uralensis*, occupying close ecological niches, live in similar habitats and have an average degree of similarity in helminth fauna. The revealed differences in the helminth fauna are explained, on the one hand, by the food preferences of the two species of mice, and on the other, by the characteristics of the microhabitats of *A. flavicollis* and *A. uralensis*. Our data confirm the partial overlap of ecological niches of the sympatric mouse species *A. flavicollis* and *A. uralensis* in spatial and trophic components of forest ecosystems of protected areas of Mordovia, which indirectly indicates possible competition for food between the two rodent species.

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