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RESEARCH ARTICLE

Diversity, ecological patterns, and zoogeography of nematodes (Nematoda) in terrestrial vertebrates in the South of the Middle Volga Region, European Russia (a century-long synthesis)

Nadezhda Yu. Kirillova[1], Victoria A. Vekhnik[1], Sofia A. Denisova[2], Sergei V. Shchenkov[2], Roman A. Gorelov[3], Alexander A. Kirillov[1], Igor V. Chikhlyaev[1]

1 *Samara Federal Research Center of RAS, Institute of Ecology of Volga River basin of RAS, Togliatti, 445003, Russia*
2 *Saint Petersburg State University, St. Petersburg, 199034, Russia*
3 *Zhiguli State Nature Biosphere Reserve, Bakhilova Polyana village, 445362, Russia*

Corresponding author: Alexander A. Kirillov (parasitolog@yandex.ru)

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Abstract

This paper presents an overview of the nematode fauna in terrestrial vertebrates from the Samara Oblast (Middle Volga region). We analyzed our own and published literature data on the nematodes of amphibians, reptiles, birds and mammals covering a research period of over a century. To date, 124 nematode species from 33 families are known to infect vertebrates in the Samara Oblast. A total of 117 recorded nematode species use terrestrial vertebrates solely as definitive hosts, while five (*Eustrongylides excisus*, *Spiroxys contortus*, *Streptocara crassicauda*, *Ascarops strongylina*, *Physocephalus sexalatus*) use them only as intermediate and/or paratenic hosts. The remaining two species (*Physaloptera clausa* and *Porrocaecum depressum*) parasitise mammals at the larval and adult stages. Forty-one species of nematodes have an indirect life cycle, while 83 develop directly. Geohelminths predominate in the nematode fauna of mammals, reptiles, and amphibians, with the highest ratio observed in reptiles and mammals. Conversely, biohelminths dominate in birds. The ratio of geo- and biohelminths among nematodes of vertebrates strongly depends on the hosts' lifestyle and diet. The majority of

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nematode species (70) were recorded in mammals. The nematode fauna associated with the avifauna comprises 36 species. The lower number of nematode species recorded in amphibians (15) and reptiles (11) compared with that in birds and mammals likely reflects the smaller number of host species studied in these groups (nine amphibian and nine reptile species vs. 100 bird and 48 mammal species), rather than an inherently poorer parasite fauna. Most of the nematodes identified in vertebrates of the Samara Oblast belong to the Palearctic faunal complex (61 species). Additionally, 34 species are cosmopolitan. The range of 22 nematode species spans the Holarctic. The geographic distribution of seven species is limited to Europe. Among the 124 nematode species found in terrestrial vertebrates in the Samara Oblast, 30 are of medical and veterinary importance as potential pathogens of dangerous helminthiases. Of these, seven species (*Syphacia obvelata*, *Calodium hepaticum*, *Ascaris suum*, *Toxascaris leonina*, *Toxocara canis*, *Ancylostoma caninum*, and *Uncinaria stenocephala*) are zoonotic, capable of infecting humans.

Keywords
Biodiversity, Nematoda, roundworms, Amphibia, Reptilia, Aves, Mammalia, Samara Oblast

Introduction

Gaining knowledge about the biodiversity of a specific territory is crucial for the rational use of natural resources. On the one hand, parasitic organisms are an integral part of natural ecosystems and facilitate nutrient cycling and energy flow within host-parasite systems; on the other, they act as a factor determining biodiversity (Price 1980; Poulin and Morand 2004; Horwitz and Wilcox 2005; Dobson et al. 2008; Cole and Viney 2018).

Nematodes are among the most numerous helminths, parasitizing a wide range of vertebrate and invertebrate animals (Blaxter and Koutsovoulos 2015). Soil contamination with nematodes and other helminth species is a primary source of infection, leading to an increased incidence of severe helminthiases. The importance of studying roundworms of terrestrial vertebrates is determined primarily by the pathogenic significance they may have for humans, as well as for domestic and wild animals (Schlosser-Brandenburg et al. 2023; Chan et al. 2025; Kaminsky and Mäser 2025).

Changes in natural and climatic conditions, increasing anthropogenic pressure, and the deterioration of the region's overall environmental state are leading to the transformation of natural ecosystems, which significantly affects both vertebrates and their helminths. These changes can render hosts more susceptible to existing parasitic nematodes, resulting in more severe infections (Zhang et al. 2008), and a number of nematode species not typically associated with humans and domestic animals may acquire epidemiological significance, becoming new sources of disease (Sakanari et al. 1989; Sorvillo et al. 2002).

The history of helminthological research on vertebrates in the Samara Oblast spans over a century. These surveys in the region were initiated by Palimpsestov (1937) using records from the 5th All-Union Helminthological Expedition (1921),

which contained data on helminths (including nematodes) of domestic animals. Polozhentsev (1936), studying the helminth fauna of shrews, recorded two nematode species in the Samara Oblast. The first information regarding nematodes of bats and rodents in the region was provided by Artyukh (1950). Shlychkov (1968) investigated the helminth fauna of domestic and wild canids in the Samara Oblast and revealed five nematode species in carnivores.

Our studies on the helminth fauna of vertebrates in the Samara Oblast began in 1996; over nearly 30 years of work, we have examined parasites of 166 host species comprising amphibians, reptiles, birds, and small mammals (Kirillov 2000; Chikhlyaev 2004, 2014, 2017, 2024, 2025; Kirillov and Eplanova 2005; Kirillov et al. 2006, 2012; Kirillova and Kirillov 2007, 2011, 2017; Kirillova et al. 2007, 2008; Kirillova 2011; Ruchin and Chikhlyaev 2012; Kirillov and Kirillova 2018a, 2018b; Chikhlyaev and Faizulin 2023). Data on nematodes in vertebrates from the Samara Oblast are contained in several reviews and regional summaries (Rozenberg 2007; Faizulin et al. 2013; Kirillov et al. 2017, 2018, 2019, 2022, 2023, 2025, 2026; Chikhlyaev et al. 2018; Chikhlyaev and Ruchin 2022; Kirillova et al. 2024).

The aim of this study is to provide a comprehensive, systematic overview of the nematode fauna of terrestrial vertebrates in the Samara Oblast, and to analyze the ecological patterns of host-parasite associations, life-cycle strategies, and the zoogeographical structure across different vertebrate classes.

Materials and methods

This review of the nematode fauna in terrestrial vertebrates is based on an analysis of published literature on parasites of amphibians, reptiles, birds, and mammals studied in the Samara Oblast, as well as on the results of the authors' own surveys conducted over the past 30 years.

The Samara Oblast is located in the south-east of European Russia in the Middle Volga region. The territory of the region extends 335 km from north to south and 315 km from west to east, covering an area of 53,565 km^2 (Gorelov et al. 1990; Dmitrieva and Kabytov 1996). The climate of the Samara Oblast is temperate continental. The boundary between two natural zones – forest-steppe and steppe – runs across the region. This factor largely accounts for the diversity of landscapes and the rich regional flora and fauna. The vertebrate fauna of the region comprises 433 species, including 56 fish, 11 amphibians, 11 reptiles, 271 birds, and 84 mammals (Gorelov et al. 1990; Dmitrieva and Kabytov 1996; Gorelov 1996; Faizulin et al. 2013).

Amphibians, reptiles, birds, and small mammals were collected for parasitological study under permits issued by the Ministry of Forestry, Environmental Protection and Nature Management of the Samara Oblast (Nos. 1–6, dated 21 April 2023; Nos. 7–13, dated 23 May 2024) and by Rosprirodnadzor (No. VS-10-34/2646, dated 22 April 2009). Deceased vertebrates provided by staff of the Togliatti Zoo Corner and Bird Shelter, the I.I. Sprygin Zhiguli State Nature Biosphere Reserve and animal

welfare volunteers from Samara and Togliatti, as well as road-killed animals were also used for parasitological analysis. All animal handling and euthanasia procedures were followed in accordance with national or Institutional guidelines for the use and care of wild animals. Our survey was carried out in accordance with the ethical standards for humane treatment of animals in accordance with the recommended standards described in the Directive of the European Parliament and of the Council of the European Union (22 September 2010) "On the protection of animals used for scientific purposes" (EU Directive 2010/63/EU).

A total of 1,350 amphibians, 738 reptiles, 590 birds, and 6323 mammals (Eulipothyphla, Chiroptera, Rodentia, and Mustelidae) were examined between 1996 and 2025. Vertebrates were examined by complete and partial parasitological necropsy (Dubinina 1971; Ivashkin et al. 1971; Byhovskaya-Pavlovskaya 1985; Anikanova et al. 2007). The collection and processing of the parasitological material followed standard techniques. The nematodes were collected and preserved in 70% ethanol. Subsequently, under laboratory conditions, the specimens were cleared in lactic acid and mounted in glycerin-jelly (Zander 2014). Morphological identification of nematodes was performed using a light microscope MBI-9 (LOMO, Saint Petersburg, Russia) equipped with a Levenhuk M500 BASE (Levenhuk Inc., Tampa, USA) and measured using LevenhukLite software. Nematode species were identified according to the morphological keys (Ryzhikov 1949; Skrjabin et al. 1952, 1954 1957, 1965; Mozgovoy 1953; Skrjabin and Sobolev 1963, 1964; Ryzhikov and Chertkova 1968, Sonin 1968; Gvozdev et al. 1970; Sharpilo 1976; Smogorzhevskaya 1976; Ryzhikov et al. 1979, 1980; Genov 1984). *Trichuris* spp. were identified according to Feliu et al. (2000). Historical records of nematodes from the early literature were cross-referenced with modern taxonomic databases, including GBIF (https://www.gbif.org/, accessed on 28 August 2026), WoRMS (https://www.marinespecies.org/, accessed on 28 August 2026), and Nemys (https://nemys.ugent.be/, accessed on 29 August 2026) to update synonyms and ensure current nomenclatural accuracy. Records in which the original species identification was deemed doubtful or obsolete were excluded.

Nematodes were classified as geohelminths (direct life cycle) or biohelminths (indirect life cycle requiring intermediate/paratenic hosts) based on Anderson (2000). The following zoogeographical complexes were used to classify the ranges of roundworms: Palearctic (Europe, most of Asia and North Africa); Holarctic (Eurasia and the Nearctic region); European (a part of the western Palearctic); and Cosmopolitan (with a ubiquitous distribution). The morphological keys presented above were used to determine the distribution ranges of the nematode species. To characterize helminth infection in vertebrates, we used the infection coefficient (k), defined as the ratio of the number of helminth species to the number of host species within the considered taxon (Bayanov 1983). Data visualization was performed using the statistical environment (R Core Team 2016) with packages “readxl” (Wickham and Bryan 2025), “ggplot2” (Wickham 2016) and “tidyverse” (Wickham et al. 2019) and Microsoft Excel software. The voucher samples are stored in the parasi-

tological collection of the Institute of the Ecology of the Volga River basin of RAS (Togliatti, Russia).

This study was approved by the Bioethics Committee of the Institute of the Ecology of Volga River Basin of RAS (Registration number: 17/26; 07 September 2026).

Results

At the current stage of research on the vertebrates nematode fauna in the Samara Oblast, 124 species from 33 families have been recorded (Kirillov 2000; Chikhlyaev 2004, 2014, 2017, 2024, 2025; Kirillov and Eplanova 2005; Kirillov et al. 2006, 2012, 2017, 2018, 2019, 2022, 2023, 2025, 2026; Kirillova and Kirillov 2007, 2011, 2017; Kirillova et al. 2007, 2008, 2024; Rozenberg 2007; Kirillova 2011; Ruchin and Chikhlyaev 2012; Faizulin et al. 2013; Chikhlyaev et al. 2018; Kirillov and Kirillova 2018a, 2018b; Chikhlyaev and Ruchin 2022; Chikhlyaev and Faizulin 2023) (Fig. 1).

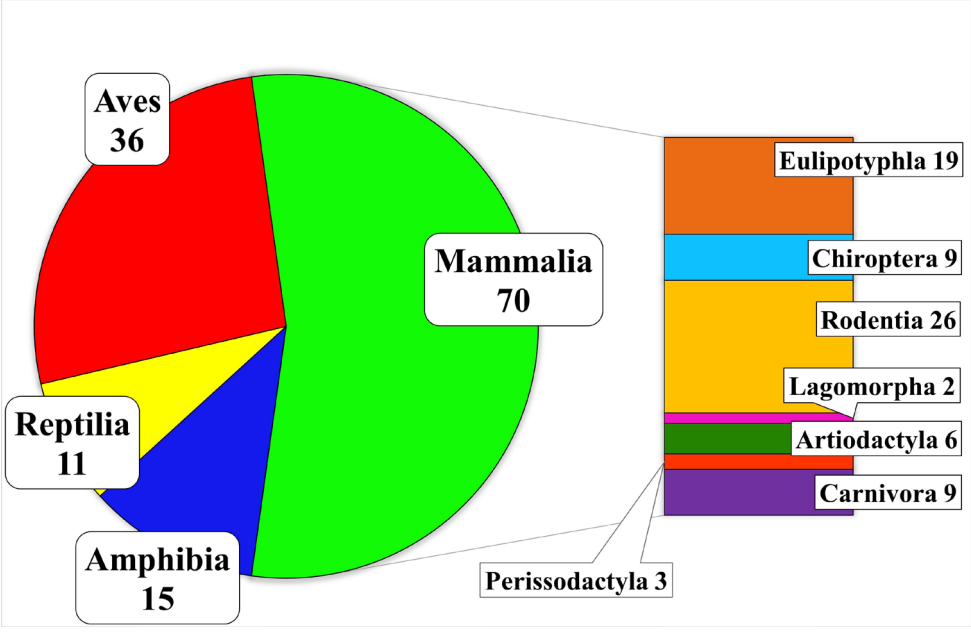


Figure 1. Distribution of nematode species richness among terrestrial vertebrates in the Samara Oblast. Several species of nematodes parasitize several vertebrate classes or orders of mammals.

Amphibian (Amphibia) Nematodes in the Samara Oblast

The list of nematodes that infect amphibians in the Samara Oblast includes 15 species from 10 families (Chikhlyaev 2004, 2014, 2017, 2024, 2025; Kirillov et al. 2018, 2026; Ruchin and Chikhlyaev 2012; Faizulin et al. 2013; Chikhlyaev et al. 2018; Chikhlyaev and Ruchin 2022; Chikhlyaev and Faizulin 2023) (Table 1, Fig. 2).

Table 1. Nematodes of amphibians (Amphibia) in the Samara Oblast

Species	*Pelophylax ridibundus*	*Pelophylax lessonae*	*Pelophylax esculentus*	*Rana arvalis*	*Rana temporaria*	*Bufotes viridis*	*Pelobates vespertinus*	*Bombina bombina*	*Lissotriton vulgaris*
Eustrongylides excisus Jägerskiöld, 1909, larvae	+	-	-	-	-	-	-	-	-
Gyrinicola tba (Dinnik, 1930)	+	-	-	-	-	-	+	-	-
Rhabdias bufonis (Schrank, 1788)	+	+	-	+	-	+	+	+	-
Oswaldocruzia filiformis (Goeze, 1782)	+	+	-	+	+	-	+	-	+
Oswaldocruzia ukrainae Iwanitzky, 1928	-	-	-	-	-	+	-	-	-
Megalobatrachonema terdentatum (Linstow, 1890)	-	-	-	-	-	-	-	-	+
Cosmocerca ornata (Dujardin, 1845)	+	+	+	+	-	+	-	+	-
Cosmocerca commutata (Diesing, 1851)	-	-	-	-	-	+	-	-	-
Aplectana acuminata (Schrank, 1788)	+	-	-	-	-	-	+	-	-
Oxysomatium brevicaudatum (Zeder, 1800)	+	-	-	-	-	-	+	-	-
Strongyloides spiralis Grabda-Kazubska, 1978	+	-	-	+	-	+	-	-	-
Spiroxys contortus (Rudolphi, 1819), larvae	+	-	-	-	-	-	-	-	-
Camallanus truncatus (Rudolphi, 1814)	+	-	-	-	-	-	-	-	-
Icosiella neglecta (Diesing, 1851)	+	+	-	-	-	-	-	-	-
Ascarops strongylina (Rudolphi, 1819), larvae	+	-	-	-	-	-	-	-	-
Total	12	4	1	4	1	5	5	2	2

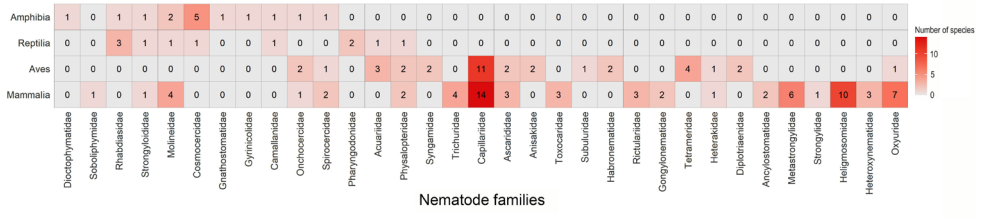


Figure 2. Heatmap showing the distribution of nematode species in vertebrates by family.

Among them, the most represented family is Cosmocercidae (six species). Two species of amphibian nematodes belong to the family Molineidae. The remaining eight families (Dioctophymatidae, Rhabdiasidae, Strongyloididae, Gnathostomatidae, Camallanidae, Onchocercidae, Spirocercidae, and Gyrinicolidae) are represented in amphibians by one species each (Fig. 2). Twelve species of nematodes parasitize amphibians of the Samara Oblast at the adult stage and use them as definitive hosts, whereas three species occur in amphibians at the larval stage. *Cosmocerca commutata* occurs in the green toad *Bufotes viridis* in both adult and larval forms.

Most nematodes recorded in amphibians (11 species) are their obligate parasites. Of these, eight species are polyhostal, whereas the other three exhibit strict host specificity. *Icosiella neglecta* is specific to *Pelophylax* spp., while *Megalobatrachonema terdentatum* is a host-specific parasite of newts belonging to the genus *Lissotriton* Bell, 1839. *Oswaldocruzia ukrainae* is host-specific to the European green toad *Bufotes viridis*.

Only *Camallanus truncatus* is an occasional parasite of amphibians, as it is primarily specific to fish. The larval stages of the nematodes *Eustrongylides excisus*, *Spiroxys contortus*, and *Ascarops strongylina* parasitize a wide range of vertebrates, with amphibians serving as their paratenic hosts. Larvae of *E. excisus* parasitize various freshwater fish, while the adult parasite completes its life cycle in piscivorous birds. The range of paratenic hosts for this nematode includes predatory fish, amphibians, and reptiles (Bauer 1987; Bjelic-Cabrilo et al. 2013; Mazzone et al. 2019). The definitive host of *S. contortus* is the European pond turtle *Emys orbicularis* (Linnaeus, 1758). The larvae occur in fish, newts, snakes, and lizards (Bauer 1987; Sharpilo 1976). In its larval stage, the nematode *A. strongylina* parasitizes reptiles, most commonly lizards (Sharpilo 1976). Wild boars serve as definitive hosts for *A. strongylina* (Roepstorff and Nansen 1998).

Ten of the 15 nematode species from amphibians are geohelminths, developing without the involvement of intermediate hosts (Suppl. material 1: Table S1). Infection with *Strongyloides spiralis*, *Gyrinicola tba*, *Aplectana acuminata*, *Cosmocerca ornata* occurs in aquatic environments (Chikhlyaev et al. 2018; Kirillova and Kirillov 2021), whereas *Oxysomatium brevicaudatum*, *Rhabdias bufonis*, *Oswaldocruzia filiformis*, *Oswaldocruzia ukrainae*, *Megalobatrachonema terdentatum*, and *Cos-*

mocerca commutata infect amphibians in moist terrestrial habitats (Hartwich 1975; Hendrikx 1983; Chikhlyaev 2014; Chikhlyaev et al. 2018).

Amphibians become infected with nematodes with an indirect life cycle (*A. strongylina*, *Camallanus truncatus*, *E. excisus*, *S. contortus*) when feeding on invertebrates or through their accidental ingestion with food. Additionally, amphibians can acquire *C. truncatus*, *S. contortus*, and *E. excisus* by preying on small fish. The presence of *C. truncatus* in amphibians appears to be a case of postcyclic parasitism. Regarding other heteroxenous species, such as *Icosiella neglecta*, biting midges (Ceratopogonidae) serve as intermediate hosts, and infection of amphibians occurs through the bites of these insects.

No parasite species common to all amphibians was found in the Samara Oblast. The widest host range is observed for *Rhabdias bufonis*, *Oswaldocruzia filiformis* and *Cosmocerca ornata* (six amphibian species each). *Strongyloides spiralis* was found in three host species. *Icosiella neglecta*, *Aplectana acuminata*, *Oxysomatium brevicaudatum*, and *Gyrinicola tba* were each recorded in two host species. The remaining seven nematode species were recorded in only one amphibian species each (Table 1).

Nematodes were recorded in all nine amphibian species studied in the Samara Oblast. The highest number of nematode species was observed in the marsh frog *Pelophylax ridibundus* (12 species). The nematode fauna is less diverse in *Bufotes viridis* and *Pelobates vespertinus* (five species each), as well as *Pelophylax lessonae* and *Rana arvalis* (four species each). The lowest number of nematode species was recorded in *Bombina bombina* and *Lissotriton vulgaris* (two species each), and in *Pelophylax esculentus* and *Rana temporaria* (one species each) (Table 1).

Only one of the 15 nematode species from amphibians in the Samara Oblast is cosmopolitan. Eight nematode species belong to the Palearctic faunistic complex, while two are distributed across the Holarctic region. The geographic distribution of four nematode species is limited to Europe (Table 1).

Nematodes of reptiles (Reptilia) in the Samara Oblast

Reptiles in the Samara Oblast harbor 11 species of nematodes belonging to eight families (Kirillov 2000; Kirillov and Eplanova 2005; Kirillov et al. 2018, 2019, 2025; Rozenberg 2007; Kirillov and Kirillova 2018b) (Table 2, Fig. 1).

Table 2. Nematodes of amphibians (Amphibia) in the Samara Oblast

Species	*Lacerta agilis*	*Zootoca vivipara*	*Eremias arguta*	*Anguis colchica*	*Natrix natrix*	*Natrix tessellata*	*Vipera berus*	*Vipera renardi*
Rhabdias fuscovenosa (Railliet, 1899)	-	-	-	-	+	+	+	+
Strongyloides mirzai Singh, 1954	-	-	-	-	+	-	-	-

Species	*Lacerta agilis*	*Zootoca vivipara*	*Eremias arguta*	*Anguis colchica*	*Natrix natrix*	*Natrix tessellata*	*Vipera berus*	*Vipera renardi*
Oswaldocruzia filiformis	+	+	-	+	-	-	+	-
Entomelas entomelas (Dujardin, 1845)	-	-	-	+	-	-	-	-
Entomelas dujardini (Maupas, 1916)	-	-	-	+	-	-	-	-
Oxysomatium brevicaudatum (Zeder, 1800)	-	-	-	+	-	-	-	-
Streptocara crassicauda (Creplin, 1829), larvae	-	-	-	-	-	+	-	-
Camallanus truncatus (Rudolphi, 1814)	-	-	-	-	-	+	-	-
Spauligodon lacertae Sharpilo, 1966	+	-	-	-	-	-	-	-
Spauligodon eremiasi Markov et Bogdanov, 1961	-	-	+	-	-	-	-	-
Physaloptera clausa Rudolphi, 1819, larvae	+	-	-	-	-	-	-	+
Total	3	1	1	4	2	3	2	1

The family Rhabdiasidae is represented in reptiles by three species, and Pharyngodonidae by two. Nematodes of the families Strongyloididae, Molineidae, Cosmocercidae, Camallanidae, Acuariidae, and Physalopteridae are represented in reptiles by only one species each (Table 2).

Nine nematode species parasitize reptiles at the adult stage. Moreover, for eight of these species, reptiles serve as obligate hosts. Thus, *Entomelas entomelas* and *Entomelas dujardini* are host-specific parasites of slow worms (*Anguis colchica*); *Rhabdias fuscovenosa* and *Strongyloides mirzai* are specific to colubrid snakes. *Spauligodon lacertae* is a host-specific parasite of lizards, and *Spauligodon eremiasi* is specific to lizards of the genus *Eremias* Fitzinger, 1834. *Oswaldocruzia filiformis* and *Oxysomatium brevicaudatum* parasitize both amphibians and reptiles. For *Camallanus truncatus*, the grass snake (*Natrix natrix*) serves as an accidental host.

Physaloptera clausa and *Streptocara crassicauda* were recorded in reptiles at the larval stage; for these nematodes, reptiles serve as paratenic hosts. It should be noted that the finding of juvenile *Streptocara crassicauda* in the dice snake (*Natrix tessellata*) represents an ecological dead end for the parasite, as the nematode's definitive hosts are waterfowl (Sharpilo 1976; Smogorzhevskaya 1976).

Eight out of eleven nematode species recorded in reptiles are parasites with a direct life cycle (Suppl. material 1: Table S1). Reptiles become infected with them orally by ingesting infective larvae in moist environments. Infection of reptiles with nematodes that have an indirect life cycle (*C. truncatus*, *P. clausa*, and *S. crassicauda*) occurs through feeding on intermediate or paratenic hosts of the parasites. Infection of *N. tessellata* with *S. crassicauda* apparently occurred when the snake preyed

on fish, which serve as paratenic hosts of this parasite (Sharpilo 1976). The presence of *P. clausa* larvae in reptiles indicates that they feed on insects (Sharpilo 1976).

No common parasites were observed in the studied reptile species. Only the nematodes *R. fuscovenosa* and *O. filiformis* were recorded in four host species each. The host range of *P. clausa* larvae includes two reptile species. Eight nematode species have a single reptile host each.

Nematodes were recorded in eight of the nine reptile species studied in the Samara Oblast. No nematodes were detected in *Coronella austriaca*. *Anguis colchica* harbored four nematode species, whereas three species each were found in the sand lizard *Lacerta agilis* and the dice snake *N. tessellata*. Two nematode species were registered in *Vipera berus* and *Natrix natrix*. Only one nematode species was found in *Zootoca vivipara*, *Eremias arguta*, and *Vipera renardi*.

Six nematode species recorded in reptiles of the Samara Oblast belong to the Palearctic faunistic complex. Two species exhibit a Holarctic distribution, and only one species is cosmopolitan. The distribution of two nematode species is limited to Europe.

Nematodes of Birds (Aves) in the Samara Oblast

In total, 36 species of nematodes from 14 families were recorded from birds in the Samara Oblast (Kirillov et al. 2012, 2018, 2023; Kirillov and Kirillova 2018a) (Tables 3 and 4, Fig. 2). Among them, Capillariidae is the most speciose family, comprising 11 species. The remaining families are less diverse. Thus, the families Tetrameridae and Acuariidae are represented by four and three species, respectively. Seven families (Anisakidae, Ascarididae, Diplotriaenidae, Habronematidae, Onchocercidae, Physalopteridae, and Syngamidae) each include two species. The remaining four families (Heterakidae, Oxyuridae, Spirocercidae, and Subuluridae) are each represented by a single species in birds of the Samara Oblast.

Birds serve as obligate definitive hosts for 33 nematode species. Among these, eight species (*Baruscapillaria carbonis*, *Baruscapillaria obsignata*, *Eucoleus contortus*, *Dispharynx nasuta*, *Hadjelia truncata*, *Microtetrameres inermis*, *Tetrameres fissispina*, and *Cardiofilaria pavlovskyi*) are classified as generalist parasites due to their low host specificity, since they parasitize birds of three or more orders. In contrast, the remaining species exhibit high host specificity and are restricted to particular avian taxa. Two nematodes, *Contracaecum microcephalum* and *Contracaecum spicu-ligerum*, are host-specific to piscivorous birds. Three other species (*Capillaria limi-colae*, *Tetrameres dubia*, *Syngamus palustris*) are characteristic to birds of the order Charadriiformes. Four nematodes (*Aonchotheca exilis*, *Chandlerella sinensis*, *Por-rocaecum ensicaudatum*, *Diplotriaena henryi*) are specific to passerine birds (Pas-seriformes). Six nematode species (*Baruscapillaria falconis*, *Capillaria tenuissima*, *Porrocaecum depressum*, *Synhimantus laticeps*, *Procyrnea leptoptera*, and *Physalop-tera alata*) are specific to diurnal and nocturnal birds of prey. Two species (*Barus-capillaria resecta* and *Diplotriaena tricuspis*) are host-specific parasites of corvids.

Syngamus merulae parasitizes only thrushes (Turdidae). *Capillaria fulicae* is specific to birds of the family Rallidae. *Heterakis gallinarum* is characteristic of galliforms, whereas *Syncuaria decorata* is specific to grebes (Podicipediformes). *Subulura subulata* is host-specific to nightjars (Caprimulgidae) *Capillaria hirundinis* is characteristic of swallows (Hirundinidae). *Capillaria pudendotecta* is a specific parasite of Anseriformes, and *Microtetrameres oshmarini* is specific to owls.

Birds are accidental hosts for *Syphacia petrusecwiczi*. The finding of this host-specific parasite of the bank vole (*Clethrionomys glareolus*) in owls (Strigiformes) represents a case of postcyclic parasitism. Two nematode species (*Physaloptera clausa* and *Physocephalus sexalatus*) were recorded in birds at the larval stage, with birds serving as their paratenic hosts.

The majority of nematode species recorded in birds of the Samara Oblast (21 species) have an indirect life cycle (Suppl. material 1: Table S1). Infection of birds primarily occurs through the consumption of invertebrate prey. An exception is observed for *C. microcephalum* and *C. spiculigerum*, which infect birds upon the ingestion of fish serving as second intermediate hosts. Similarly, *T. fissispina* is transmitted to birds through predation on fish acting as paratenic hosts. Nematodes of the family Onchocercidae have an indirect life cycle, requiring arthropod intermediate hosts (biological vectors) to complete their development and transmission (Ajileye et al. 2025). Therefore, infection of birds with *Cardiofilaria pavlovskyi* and *Chandlerella sinensis* occurs through the bites of blood-sucking insects.

Fifteen species of avian nematodes have a direct life cycle (Suppl. material 1: Table S1). Birds can become infected not only through infective eggs or larvae but also via paratenic hosts, such as invertebrates (primarily earthworms) that may be involved in the nematodes' life cycle.

Among birds, the widest range of hosts is found for *Dispharynx nasuta* (22 avian species). The host range of *Microtetrameres inermis* includes 16 species, *Physocephalus sexalatus* larvae – 13, *Porrocaecum depressum* – nine, *Baruscapillaria falconis* – eight, and *Synhimantus laticeps* – seven. A more restricted host range is observed for *Hadjelia truncata* (five bird species). *Tetrameres fissispina* and *Cardiofilaria pavlovskyi* are each found in four host species. *Baruscapillaria resecta*, *Diplotriaena henryi*, *Diplotriaena tricuspis*, *Physaloptera alata*, and *Porrocaecum ensicaudatum* each parasitize three bird species. Six nematodes (*Aonchotheca exilis*, *Eucoleus contortus*, *Heterakis gallinarum*, *Contracaecum microcephalum*, *Contracaecum spiculigerum*, and *Procyrnea leptoptera*) are each found in two host species. The remaining 16 nematode species were recorded in only a single bird species each.

Nematodes were found in 57 of the 100 studied bird species. Among them, the highest number of parasite species was recorded in the long-eared owl *Asio otus* (seven species). Six nematode species were noted in *Accipiter nisus* and *Strix uralensis*, and five species each in *Turdus merula*, *Corvus frugilegus*, and *Buteo buteo*. Four nematode species were found in eight bird species, and three in three bird species. Two species of roundworms were identified in 15 host species, while 24 species of avifauna serve as hosts to a single nematode species.

Table 3. Nematodes of birds (Aves) of the order Passeriformes in the Samara Oblast

Species	*Turdus philomelos*	*Turdus iliacus*	*Turdus merula*	*Turdus pilaris*	*Sturnus vulgaris*	*Parus major*	*Cyanistes caeruleus*	*Fringilla coelebs*	*Sylvia atricapilla*	*Curruca nisoria*	*Curruca communis*	*Phoenicurus phoenicurus*	*Muscicapa striata*	*Saxicola rubetra*	*Emberiza citrinella*	*Bombycilla garrulus*	*Erithacus rubecula*	*Motacilla alba*	*Luscinia svecica*	*Lanius collurio*	*Anthus trivialis*	*Passer domesticus*	*Passer montanus*	*Sitta europaea*	*Oriolus oriolus*	*Garrulus glandarius*	*Corvus cornix*	*Corvus frugilegus*	*Pica pica*
Aonchotheca exilis (Dujardin, 1845)	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Baruscapillaria resecta (Dujardin, 1845)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+
Eucoleus contortus (Creplin, 1839)	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dispharynx nasuta (Rudolphi, 1819)	+	-	-	+	-	+	-	+	+	-	+	-	+	-	+	+	+	+	+	+	+	+	+	+	-	-	+	+	+
Hadjelia truncata (Creplin, 1825)	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Porrocaecum ensicaudatum (Zeder, 1800)	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Physocephalus sexalatus, larvae	-	-	+	-	-	+	-	-	-	+	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	+	-	+	-
Diplotriaena henryi Blanc, 1919	-	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diplotriaena tricuspis (Fedtschenko, 1874)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+
Microtetrameres inermis (Linstow, 1879)	-	-	+	+	+	-	-	-	-	-	-	+	-	+	-	-	-	+	-	+	+	-	-	-	+	-	+	+	+

Species	*Turdus philomelos*	*Turdus iliacus*	*Turdus merula*	*Turdus pilaris*	*Sturnus vulgaris*	*Parus major*	*Cyanistes caeruleus*	*Fringilla coelebs*	*Sylvia atricapilla*	*Curruca nisoria*	*Curruca communis*	*Phoenicurus phoenicurus*	*Muscicapa striata*	*Saxicola rubetra*	*Emberiza citrinella*	*Bombycilla garrulus*	*Erithacus rubecula*	*Motacilla alba*	*Luscinia svecica*	*Lanius collurio*	*Anthus trivialis*	*Passer domesticus*	*Passer montanus*	*Sitta europaea*	*Oriolus oriolus*	*Garrulus glandarius*	*Corvus cornix*	*Corvus frugilegus*	*Pica pica*
Syngamus merulae Baylis, 1926	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cardiofilaria pavlovskyi Strom, 1937	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Total	4	1	5	2	2	4	1	2	1	1	2	2	1	1	1	2	1	2	1	3	4	1	1	1	1	1	4	5	4

Table 4. Nematodes of non-passerine birds (Aves) in the Samara Oblast

Species	*Buteo buteo*	*Falco subbuteo*	*Falco tinnunculus*	*Accipiter nisus*	*Astur gentilis*	*Circus aeruginosus*	*Pernis apivorus*	*Asio flammeus*	*Asio otus*	*Strix uralensis*	*Strix aluco*	*Dendrocopos major*	*Merops apiaster*	*Apus apus*	*Caprimulgus europaeus*	*Ardea cinerea*	*Ardea purpurea*	*Phalacrocorax carbo*	*Fulica atra*	*Rallus aquaticus*	*Gallinula chloropus*	*Crex crex*	*Scolopax rusticola*	*Cygnus olor*	*Anas platyrhynchos*	*Podiceps cristatus*	*Sterna hirundo*	*Perdix perdix*
Baruscapillaria carbonis (Rudolphi, 1819)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Baruscapillaria falconis (Goeze, 1782)	+	-	-	+	+	-	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Baruscapillaria obsignata (Madsen, 1945)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Eucoleus contortus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-

Species	*Buteo buteo*	*Falco subbuteo*	*Falco tinnunculus*	*Accipiter nisus*	*Astur gentilis*	*Circus aeruginosus*	*Pernis apivorus*	*Asio flammeus*	*Asio otus*	*Strix uralensis*	*Strix aluco*	*Dendrocopos major*	*Merops apiaster*	*Apus apus*	*Caprimulgus europaeus*	*Ardea cinerea*	*Ardea purpurea*	*Phalacrocorax carbo*	*Fulica atra*	*Rallus aquaticus*	*Gallinula chloropus*	*Crex crex*	*Scolopax rusticola*	*Cygnus olor*	*Anas platyrhynchos*	*Podiceps cristatus*	*Sterna hirundo*	*Perdix perdix*
Capillaria fulicae Pavlov & Borgarenko, 1959	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Capillaria hirundinis (Rudolphi, 1819)	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Capillaria limicolae (Gubanov & Mamajev, 1964)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Capillaria pudendotecta Lubimova, 1947	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Capillaria tenuissima (Rudolphi, 1803)	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Porrocaecum depressum (Zeder, 1800)	+	-	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Syncuaria decorata (Cram, 1927)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Dispharynx nasuta	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Synhimantus laticeps (Rudolphi, 1819)	+	-	+	+	+	+	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Microtetrameres inermis	+	+	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Microtetrameres oshmarini Sobolev, 1963	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tetrameres dubia Travassos, 1917	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Tetrameres fissispina (Diesing, 1861)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	+	-	-	-

Species	*Buteo buteo*	*Falco subbuteo*	*Falco tinnunculus*	*Accipiter nisus*	*Astur gentilis*	*Circus aeruginosus*	*Pernis apivorus*	*Asio flammeus*	*Asio otus*	*Strix uralensis*	*Strix aluco*	*Dendrocopos major*	*Merops apiaster*	*Apus apus*	*Caprimulgus europaeus*	*Ardea cinerea*	*Ardea purpurea*	*Phalacrocorax carbo*	*Fulica atra*	*Rallus aquaticus*	*Gallinula chloropus*	*Crex crex*	*Scolopax rusticola*	*Cygnus olor*	*Anas platyrhynchos*	*Podiceps cristatus*	*Sterna hirundo*	*Perdix perdix*
Heterakis gallinarum (Schrank, 1788)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+
Contracaecum microcephalum (Rudolphi, 1809)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-
Contracaecum spiculigerum (Rudolphi, 1809)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+	-
Syngamus palustris Ryjikov, 1949	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Subulura subulata (Rudolphi, 1819)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Hadjelia truncata	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Procyrnea leptoptera (Rudolphi, 1819)	-	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Physaloptera alata Rudolphi, 1819	+	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Physaloptera clausa, larvae	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Physocephalus sexalatus, larvae		+	-	+	-	-	-	-	-	+	-	-	+	+														
Diplotriaena henryi	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chandlerella sinensis Li, 1933	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cardiofilaria pavlovskyi	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Syphacia petrusewiczii Bernard, 1966	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total	5	3	2	6	4	2	2	2	7	6	1	1	3	4	1	1	1	2	1	1	1	2	4	1	2	2	1	2

Cosmopolitan parasites account for 13 species of the avian nematode fauna in the Samara Oblast. Twelve species of avian nematodes have a Holarctic distribution. Eleven nematode species belong to the Palearctic faunal complex.

Nematodes of mammals (Mammalia) in the Samara Oblast

The known nematode fauna of mammals in the region comprises 70 species belonging to 19 families (Kirillov et al. 2006, 2017, 2018, 2022; Kirillova and Kirillov 2007, 2011, 2017; Kirillova et al. 2007, 2008, 2024; Rozenberg 2007; Kirillova 2011; Kirillov and Kirillova 2018a) (Figs. 1, 2). The families Capillariidae (14 species) and Heligmosomidae (10 species) are the most speciose. The families Oxyuridae and Metastrongylidae are represented by seven and six species, respectively. The families Trichuridae and Molineidae (four species each), as well as Ascarididae, Heteroxynematidae, Rictulariidae, and Toxocaridae (three species each), are less diverse among mammals. The families Ancylostomatidae, Gongylonematidae, Physalopteridae, and Spirocercidae are each represented by two species in the region, while the remaining five families are represented by only one species each (Fig. 2).

For the majority of nematodes (67 species), mammals serve as obligate definitive hosts. Their degree of host specificity varies. Nineteen nematode species were recorded in insectivores of the Samara Oblast (Polozhentsev 1936; Kirillov et al. 2017, 2018, 2022; Kirillova and Kirillov 2007, 2011, 2017; Kirillova et al. 2024; Rozenberg 2007; Kirillova 2011) (Table 5). Of these, 16 species parasitize only insectivores.

Nematoideum talpae, *Tricholinstowia linstowi*, and *Tricholinstowia talpae* are host-specific parasites of moles, while *Paracrenosoma skrjabini* parasitizes only shrews of the genus *Sorex*. Three species of nematodes (*Aonchotheca erinacei*, *Crenosoma striatum*, and *Physaloptera clausa*) are specific to hedgehogs. *Aonchotheca exigua*, *Aonchotheca kutorii*, *Longistriata codrus*, *Longistriata paradoxi*, and *Soboliphyme soricis* are specific to mammals of the family Soricidae. Four nematodes (*Calodium soricicola*, *Eucoleus oesophagicola*, *Liniscus incrassatus*, and *Pseudophysaloptera soricina*) are classified as generalist parasites of insectivores. *Eucoleus aerophilus* is a facultative parasite of insectivores (specifically hedgehogs).

Nine nematode species were recorded in bats (Chiroptera) (Kirillov et al. 2006, 2017, 2018; Kirillova and Kirillov 2011, 2017; Kirillova et al. 2007, 2008) (Table 6), seven of which are found exclusively in these mammals. For instance, *Molinostrongylus alatus* and *Molinostrongylus skrjabini* are host-specific parasites of bats belonging to the families Vespertilionidae and Rhinolophidae. *Molinostrongylis vespertilionis*, *Pterothominx neopulchra*, and *Pterygodermatites bovieri* are specific to vespertilionid bats. *Molinostrongylus skrjabini* is restricted to *Myotis* bats. *Litomosa filaria* acts as a generalist parasite found in various bat species.

Twenty-six nematode species were recorded in rodents (Rodentia) (Kirillov et al. 2017, 2018; Kirillova and Kirillov 2011, 2017; Rozenberg 2007; Kirillova 2011) (Table 7), 25 of which occur exclusively in members of this order.

Table 5. Nematodes of insectivores (Eulipotyphla) in the Samara Oblast

Species	*Erinaceus roumanicus*	*Talpa europaea*	*Sorex araneus*	*Sorex minutus*	*Crocidura suaveolens*
Aonchotheca erinacei (Rudolphi, 1819)	+	-	-	-	-
Aonchotheca exigua (Dujardin, 1845)	-	-	-	+	-
Aonchotheca kutorii (Ruchljadeva, 1964)	-	-	+	-	-
Calodium soricicola (Yokogava et Nishigori, 1924)	-	-	+	-	-
Eucoleus aerophilus (Creplin, 1839)	+	-	-	-	-
Eucoleus oesophagicola (Soltys, 1952)	-	+	+	-	-
Liniscus incrassatus Diesing, 1851	-	-	+	-	-
Longistriata codrus Thomas, 1953	-	-	+	-	-
Longistriata paradoxi Schaldybin, 1964	-	-	+	+	-
Nematoideum talpae Siebold, 1850	-	+	-	-	-
Tricholinstowia linstowi Travassos, 1918	-	+	-	-	-
Tricholinstowia talpae (Morgan, 1928)	-	+	-	-	-
Soboliphyme soricis Baylis et King, 1932	-	-	+	-	-
Paracrenosoma skrjabini (Pologentsev, 1935)	-	-	+	+	-
Crenosoma striatum Zeder, 1800	+	-	-	-	-
Physaloptera clausa Rudolphi, 1819	+	-	+	-	-
Pseudophysaloptera soricina Baylis, 1934	-	-	+	+	-
Physocephalus sexalatus (Molin, 1860), larvae	+	-	-	-	+
Porrocaecum depressum (Zeder, 1800), larvae	+	+	+	+	-
Total	6	5	11	6	1

Table 6. Nematodes of bats (Chiroptera) in the Samara Oblast

Species	*Myotis daubentonii*	*Myotis dasycneme*	*Myotis brandtii*	*Myotis nattereri*	*Vespertilio murinus*	*Eptesicus serotinus*	*Eptesicus nilssonii*	*Nyctalus noctula*	*Nyctalus lasiopterus*	*Nyctalus leisleri*	*Pipistrellus nathusii*	*Pipistrellus pygmaeus*	*Plecotus auritus*
Pterothominx neopulchra (Babos, 1954)	+	+	-	+	+	-	+	+	+	+	-	-	-
Molinostrongylus alatus (Ortlepp, 1932)	-	-	-	+	-	-	-	-	-	-	-	-	-
Molinostrongylus skrjabini Skarbilovitsch, 1934	-	-	-	-	+	-	-	+	+	-	-	-	+
Molinostrongylis spasskii Andrejko, Pintschuk et Skvorzov, 1968	+	-	-	-	-	-	-	-	-	-	-	-	-
Molinostrongylis vespertilionis Morosov et Spassky, 1961	-	-	-	-	-	-	-	-	-	+	-	+	-
Litomosa filaria Beneden, 1873	-	-	-	-	+	-	-	-	-	-	-	-	-
Physaloptera clausa, larvae	-	-	-	-	-	+	-	-	-	-	+	-	-
Physocephalus sexalatus, larvae	-	+	+	-	-	-	-	+	+	-	+	-	+
Pterygodermatites bovieri (Blanchard, 1886)	-	+	+	-	-	-	-	-	-	-	-	-	-
Total	2	3	2	2	3	1	1	3	3	2	2	1	2

Table 7. Nematodes of rodents (Rodentia) and lagomorphs (Lagomorpha) in the Samara Oblast

Species	*Spalax microphthalmus*	*Arvicola amphibius*	*Microtus cf arvalis*	*Microtus oeconomus*	*Clethrionomys glareolus*	*Apodemus flavicollis*	*Apodemus uralensis*	*Apodemus agrarius*	*Mus musculus*	*Micromys minutus*	*Rattus norvegicus*	*Dryomis nitedula*	*Ochotona pusilla*
Aonchotheca murissylvatici (Diesing, 1851)	-	-	-	-	+	+	+	+	-	-	-	-	-
Calodium hepaticum (Bancroft, 1893)	-	-	-	-	+	+	-	+	-	-	-	-	-
Eucoleus baccilatus (Eberth, 1863)	-	-	-	-	+	-	-	-	-	-	-	-	-
Eucoleus lemmi (Retzius, 1841)	-	-	+	-	-	-	-	-	-	-	-	-	-
Trichuris arvicolae Feliu, Spakulova, Casanova, Renaud, Morand, Hugot, Santalla et Durand, 2000	-	-	+	-	+	-	-	-	-	-	-	-	-

Species	*Spalax microphthalmus*	*Arvicola amphibius*	*Microtus cf arvalis*	*Microtus oeconomus*	*Clethrionomys glareolus*	*Apodemus flavicollis*	*Apodemus uralensis*	*Apodemus agrarius*	*Mus musculus*	*Micromys minutus*	*Rattus norvegicus*	*Dryomis nitedula*	*Ochotona pusilla*
Trichuris muris (Schrank, 1788)	-	-	-	-	-	+	+	+	-	-	-	-	-
Trichuris spalacis (Petrov et Potechina, 1953)	+	-	-	-	-	-	-	-	-	-	-	-	-
Spalacina spalacis (Sharpilo, 1973)	+	-	-	-	-	-	-	-	-	-	-	-	-
Heligmosomoides polygyrus (Dujardin, 1845)	-	-	-	-	-	+	+	+	+	-	-	-	-
Heligmosomoides glareoli (Baylis, 1928)	-	-	-	-	+	-	-	-	-	-	-	-	-
Heligmosomoides laevis (Dujardin, 1845)	-	+	+	+	-	-	-	-	-	-	-	-	-
Heligmosomum mixtum Schulz, 1954	-	-	-	-	+	+	+	+	-	-	-	-	-
Heligmosomum costellatum (Dujardin, 1845)	-	-	+	-	-	-	-	-	-	-	-	-	-
Gongylonema problematicum Schulz, 1924	-	-	+	-	-	-	-	-	-	-	-	-	-
Gongylonema neoplasticum (Fibiger et Ditlevsen, 1914)	-	-	-	-	-	+	+	+	-	-	+	-	-
Syphacia agraria Sharpilo, 1973	-	-	-	-	-	-	-	+	-	-	-	-	-
Syphacia obvelata (Rudolphi, 1802)	-	-	-	-	-	+	+	-	+	-	-	-	-
Syphacia nigeriana Baylis, 1928	-	-	+	+	-	-	-	-	-	-	-	-	-
Syphacia stroma (Linstow, 1884)	-	-	-	-	-	+	+	-	+	-	+	-	-
Syphacia petrusewiczii	-	-	-	-	+	-	-	-	-	-	-	-	-
Syphacia vanderbrueli Bernard, 1966	-	-	-	-	-	-	-	-	-	+	-	-	-
Mastophorus muris (Gmelin, 1790)	-	-	-	-	+	-	-	-	-	-	-	-	-
Rictularia proni Seurat, 1915	-	-	-	-	-	+	+	+	-	-	-	-	-
Rictularia cristata Frolich, 1802	-	-	-	-	-	-	-	-	-	-	-	+	-
Aspiculuris tetraptera (Nitsch, 1821)	-	-	-	-	-	+	-	-	-	-	-	-	-
Heterakis spumosa Schneider, 1866	-	-	-	-	-	-	-	-	-	-	+	-	-
Cephaluris andrejevi Schulz, 1948	-	-	-	-	-	-	-	-	-	-	-	-	+
Labiostomum vesicularis Gvosdev, 1956	-	-	-	-	-	-	-	-	-	-	-	-	+
Total	2	1	6	2	8	10	8	8	3	1	3	1	2

Rodent nematodes exhibit a high degree of host specificity. Thus, *Heligmosomoides glareoli* and *Syphacia petrusewiczii* are host-specific parasites of *Clethrionomys* voles, while *Spalacina spalacis* and *Trichuris spalacis* are specific to molerats. Four nematode species (*Heligmosomoides laevis*, *Heligmosomum costellatum*, *Syphacia nigeriana*, and *Trichuris arvicolae*) are specific to voles of the subfamily Arvicolinae. *Heligmosomoides polygyrus*, *Rictularia proni*, *Syphacia stroma*, and *Trichuris muris* are host-specific parasites of mice. Five parasites (*Aonchotheca murissylvatici*, *Eucoleus baccilatus*, *Eucoleus lemmi*, *Syphacia obvelata* and *Heterakis spumosa*) are host-specific to rodents of the families Muridae and Cricetidae. *Rictularia cristata* parasitizes members of the families Muridae and Gliridae. Only two nematode species are strictly monoxenous, restricted to a single host species: *Syphacia agraria* (striped field mouse) and *Syphacia vanderbrueli* (the harvest mouse). Generalist parasites, such as *Aspiculuris tetraptera*, *Gongylonema neoplasticum*, *Gongylonema problematicum*, *Heligmosomum mixtum*, and *Mastophorus muris* parasitize various rodents. Only *Calodium hepaticum* has a wide host range, infecting rodent species across multiple orders. Only two nematode species were identified in the steppe pika (*Ochotona pusilla*), a member of the order Lagomorpha (Table 7); both are host-specific parasites of *Ochotona* pikas.

Nine nematodes specific to ungulates were recorded (Palimpsestov 1937; Kirillov et al. 2018) (Table 8). For instance, *Strongyloides westeri*, *Oxyuris equi* and *Parascaris equorum* are specific to perissodactyls, whereas *Dictyocaulus viviparus* is a host-specific parasite of artiodactyls. The remaining five nematodes (*Ascaris suum*, *Metastrongylus elongatus*, *Metastrongylus pudendotectus*, *Oesophagostomum dentatum*, and *Trichuris suis*) are host-specific parasites of mammals of the family Suidae.

Table 8. Nematodes of artiodactyls (Artiodactyla) and perissodactyls (Perissodactyla) in the Samara Oblast

Species	***Sus scrofa domesticus***	***Equus caballus***	***Bos taurus taurus***
Trichuris suis (Schrank, 1788)	+	-	-
Strongyloides westeri Ihle, 1917	-	+	-
Metastrongylus elongatus (Dujardin, 1845)	+	-	-
Metastrongylus pudendotectus (Wostokow, 1905)	+	-	-
Dictyocaulus viviparus (Bloch, 1782)	-	-	+
Oesophagostomum dentatum (Rudolphi, 1803)	+	-	-
Ascaris suum Goeze, 1782	+	-	-
Parascaris equorum (Goeze, 1782)	-	+	-
Oxyuris equi (Schrank, 1788)	-	+	-
Total	5	3	1

Nine species of nematodes were recorded in carnivores studied in the Samara Oblast, eight of which are host-specific parasites of these mammals (Table 9).

Toxascaris leonina is a host-specific parasite of carnivores of the families Canidae and Felidae, while *Toxocara mystax* is specific to felids. *Ancylostoma caninum* and *Uncinaria stenocephala* parasitize members of the family Canidae. *Skrjabingylus petrowi* is a host-specific parasite of mustelids. In contrast, *Eucoleus aerophilus*, *Toxocara canis*, and *Aonchotheca putorii* have a wide host range and are classified as generalist parasites.

Only three nematode species (*Physocephalus sexalatus*, *Physaloptera clausa* and *Porrocaecum depressum*) were recorded in mammals at the larval stage (Tables 5, 6, 9), with mammals acting as paratenic hosts for these parasites. It should be noted that bats represent an ecological dead end for *P. sexalatus* (the definitive hosts of which are wild boars and domestic pigs) and *P. clausa* (for which hedgehogs serve as definitive hosts), since transmission to their definitive hosts is highly unlikely.

Table 9. Nematodes of carnivores (Carnivora) in the Samara Oblast

Species	*Canis lupus*	*Canis familiaris*	*Vulpes vulpes*	*Nyctereutes procyonoides*	*Meles meles*	*Martes martes*	*Mustela nivalis*
Aonchotheca putorii (Rudolphi, 1819)	-	-	-	-	+	-	-
Ancylostoma caninum (Ercolani, 1859)	+	+	-	+	-	-	-
Uncinaria stenocephala (Railliet, 1884)	-	+	-	+	-	-	-
Eucoleus aerophilus	-	-	-	-	-	+	-
Toxocara canis (Werner, 1782)	+	+	+	-	-	-	-
Toxocara mystax (Zeder, 1800)	-	-	+	-	-	-	-
Toxascaris leonina (Linstow, 1902)	+	+	+	-	-	-	-
Physocephalus sexalatus, larvae	-	-	-	-	+	-	+
Skrjabingylus petrowi Bageanov in Petrow, 1941	-	-	-	-	-	+	-
Total	3	4	3	2	2	2	1

The majority of nematodes (53 species) recorded in mammals are geohelminths (Suppl. material 1: Table S1). Infection occurs directly through the ingestion of infective eggs and/or larvae, either accidentally from the environment or along with food. Additionally, the development of capillariids can involve paratenic hosts, such as earthworms and other invertebrates.

Seventeen nematode species parasitizing mammals in the Samara Oblast have an indirect life cycle (Suppl. material 1: Table S1). Infection occurs when mammals feed on intermediate and/or paratenic hosts, specifically various invertebrates. An exception is observed for *Litomosa filaria*, which is transmitted via the bites of ectoparasites.

The host range of more than half of the nematode species (41 out of 70) is limited to a single mammal species. Eleven nematode species have two host species each, whereas eight are associated with three host species each. Another eight nematode species have been recorded in four host species each. The broadest host range was observed for *Physocephalus sexalatus* (10 vertebrate species) and *Pterothominx neopulchra* (eight host species) (Tables 5–9).

Nematodes were found in 41 of the 48 mammal species studied in the Samara Oblast. Among them, the nematode fauna is most diverse in *Sorex araneus* (11 species) and *Apodemus flavicollis* (10 species). Eight nematode species have been recorded in each of *Clethrionomys glareolus*, *Apodemus agrarius*, and *Apodemus uralensis*. The nematode fauna is less diverse in *Erinaceus roumanicus*, *Sorex minutus*, and *Microtus* cf. *arvalis* (six species each), *Sus scrofa domesticus* and *Talpa europaea* (five species each), and *Canis familiaris* (four species). Three nematode species were recorded in nine mammal species each, whereas two were found in 12 host species each. A single nematode species was recorded in nine mammal species each.

Nematodes recorded in mammals are widely distributed. Twenty-one species of roundworms are cosmopolitan, nine belong to the Holarctic faunal complex, and 39 exhibit a Palearctic distribution. Only one nematode species (*Spalacina spalacis*) is limited to Europe in its distribution.

Thus, 124 species of nematodes belonging to 33 families have been recorded in the studied terrestrial vertebrates in the Samara Oblast to date. The family Capillariidae is the most speciose (25 species). The families Heligmosomidae (10 species), Oxyuridae (seven species), Metastrongylidae and Molineidae (six species each), and Cosmocercidae (five species) exhibit lower diversity. The families Acuariidae, Ascarididae, Onchocercidae, Rhabdiasidae, Tetrameridae, and Trichuridae are each represented by four species, whereas another six families (Heteroxynematidae, Physalopteridae, Rictulariidae, Spirocercidae, Strongyloididae, and Toxocaridae) are represented by three species each in vertebrates of the region. Eight families (Ancylostomatidae, Anisakidae, Diplotriaenidae, Gongylonematidae, Habronematidae, Heterakidae, Pharyngodonidae, and Syngamidae) are represented by two species each. The families Camallanidae, Dioctophymatidae, Gnathostomatidae, Gyrinicolidae, Soboliphymidae, Strongylidae, and Subuluridae are each represented by a single nematode species in vertebrates of the Samara Oblast.

Since terrestrial vertebrates occupy the top of food webs, most of the recorded nematode species (117) parasitize them solely at the adult stage (Suppl. material 1: Table S1). Five species of nematodes (*E. excisus*, *S. contortus*, *S. crassicauda*, *A. strongylina*, and *Ph. sexalatus*) use vertebrates only as intermediate and/or paratenic hosts, whereas *P. depressum* and *P. clausa* parasitize various vertebrates at both the adult and larval stages (Suppl. material: Table S1). *Cosmocerca commutata* undergoes both larval and adult developmental stages in the European green toad (*Bufotes viridis*), which serves as an amphixenic host for this parasite (Chikhlyaev 2014). This phenomenon represents an adaptive strategy of the nematode aligned with the host's ecology, ensuring stable transmission of *C. commutata* in the steppe and

forest-steppe zones. The success of the nematode's life cycle depends neither on the presence or absence of invertebrate intermediate hosts in the biocenosis, nor on climatic fluctuations such as droughts or temperature swings. This independence is crucial for the helminth's persistence in arid and semi-arid landscapes, where environmental instability and the scarcity of potential intermediate hosts often disrupt indirect life cycles.

The majority of nematode species (70 out of 124) were recorded in mammals. The nematode fauna associated with the avifauna comprises 36 species. Fewer nematode species were recorded in amphibians and reptiles of the Samara Oblast. Although mammals lead in the number of nematode species among vertebrates, the infection coefficient *k* is higher in amphibians (Table 10). In birds, this value is the lowest (0.36), even though avifauna harbor more nematode species than amphibians and reptiles (Table 10).

Table 10. Nematode infection patterns across vertebrate classes

Class	*N*	Direct life cycle	Indirect life cycle	Ratio, %	*k*
Amphibia	15	10	5	66.7/33.3	1.67
Reptilia	11	8	3	72.7/27.3	1.22
Aves	36	15	21	41.7/58.3	0.36
Mammalia	70	53	17	75.7/24.3	1.46

Note: N – number of nematode species.

Accordingly, amphibians exhibit the greatest richness in terms of the ratio of nematode species to host species. This group is followed by mammals and reptiles, whereas birds demonstrate the lowest diversity (Table 10). The lower number of nematode species recorded in amphibians and reptiles compared with that in birds and mammals likely reflects the smaller number of host species studied in these groups (nine amphibian and nine reptile species vs. 100 bird and 48 mammal species). Geohelminths (83 species) predominate among the nematodes of terrestrial vertebrates, whereas biohelminths are represented by 41 species.

Geohelminths predominate in the nematode fauna of mammals, reptiles, and amphibians, with the highest ratio observed in reptiles and mammals (Table 10). In contrast, biohelminths dominate in birds. The ratio of geo- and biohelminths in the nematode fauna of vertebrates strongly depends on the hosts' lifestyle and diet. It is known that the more diverse the animals' diet, the more diverse their helminth fauna (Poulin and Morand 2004; Thieltges et al. 2013). The birds' diet encompasses a wide range of invertebrates and vertebrates that can serve as intermediate and/or paratenic hosts for nematodes with an indirect life cycle. Bird mobility and seasonal migrations also play a significant role, as they can lead to the acquisition of new parasites. Mammals have a terrestrial lifestyle (with the exception of bats).

Consequently, geohelminths predominate among the nematodes that infect them. Furthermore, many mammals are herbivores, which increases the likelihood of infection with nematodes with a direct life cycle. While feeding on plant matter, these animals ingest infective eggs and larvae of nematodes.

In the case of geohelminth infections, factors such as a sedentary lifestyle, herd behavior (in ungulates), and high population density (e.g., in rodents) are of great importance, as they allow the infective stage to be preserved and accumulated in the environment. For amphibians and reptiles, ambient temperature and humidity are crucial. Most of these animals are closely associated with aquatic habitats or moist forest litter – conditions that favor the development of nematodes with a direct life cycle.

The nematode fauna in vertebrates of various classes in the region is heterogeneous and comprises parasites from different zoogeographical regions (Fig. 3). The geographical range of the helminths depends on the distribution range of their hosts. Seven nematode species are found in vertebrates (amphibians, reptiles, and mammals) exclusively in Europe (Suppl. material 1: Table S1). These nematodes are typically host-specific, and the distribution ranges of their hosts are likewise limited to Europe. The nematode fauna of vertebrates in the Samara Oblast is mainly composed of parasites from the Palearctic faunal complex (61 out of 124 species). The predominance of nematodes with a Palearctic distribution is characteristic of mammals, amphibians, and reptiles (Fig. 3). Nematodes of these taxonomic groups exhibit a higher degree of specificity at the species, genus, and subfamily host levels. The Holarctic faunal complex in vertebrates of the Samara Oblast comprises 22 nematode species, 19 of which parasitize birds and mammals. Additionally, 34 species of roundworms found in vertebrates have a cosmopolitan distribution, the majority of which (32 species) parasitize birds and mammals as well (Suppl. material 1: Table S1). In these cases, the nematodes demonstrate broader specificity, primarily at the order level. Notably, nematode species with broad zoogeographic distributions (cosmopolitan and Holarctic) tend to infect members of various vertebrate classes, indicating a generalist strategy. In contrast, European nematode species largely display host specificity. This observation underscores the link between geographic range and host range, suggesting that dispersal capacity and host availability may drive host plasticity in nematodes.

Among the 124 nematode species recorded in terrestrial vertebrates of the Samara Oblast, 30 are of epidemiological and epizootiological significance as potential causative agents of severe helminthiases in humans, as well as in wild, domestic, and farm animals: *Eustrongylides excisus*, *Streptocara crassicauda*, *Physaloptera clausa*, *Tetrameres fissispina*, *Hadjelia truncata*, *Heterakis gallinarum*, *Aonchotheca putorii*, *Eucoleus aerophilus*, *Crenosoma striatum*, *Contracaecum microcephalum*, *Contracaecum spiculigerum*, *Calodium hepaticum*, *Oxyuris equi*, *Parascaris equorum*, *Strongyloides westeri*, *Metastrongylus elongatus*, *Metastrongylus pudendotectus*, *Oesophagostomum dentatum*, *Trichuris suis*, *Dictyocaulus viviparus*, *Ascaris suum*, *Ancylostoma caninum*, *Uncinaria stenocephala*, *Skrjabingylus petrowi*, *Physocephalus*

sexalatus, *Ascarops strongylina*, *Toxascaris leonina*, *Toxocara canis*, *Toxocara mystax*, and *Syphacia obvelata* (Suppl. material 1: Table S1). Of these, 17 nematode species are classified as soil-transmitted helminths. Infection of vertebrates with these species is determined by the spatial relationship between host and parasite and occurs via the ingestion of infective eggs or larvae, – either during feeding or accidentally from the environment. Infection with the remaining 13 nematode species is driven by trophic relationships between host and parasite; these nematodes enter the host's body through the consumption of other organisms that serve as intermediate or paratenic hosts. Of the 30 nematode species, seven (*S. obvelata*, *C. hepaticum*, *A. suum*, *T. leonina*, *T. canis*, *A. caninum*, and *U. stenocephala*) are zoonotic, capable of infecting humans, particularly when personal hygiene practices are neglected. The study of the helminth fauna of wild vertebrates, and specifically their nematodes, aligns with the One Health concept, helping to elucidate the interconnections between human, animal, and environmental health. The data obtained will facilitate the development and implementation of preventive measures and control strategies for zoonotic helminthiases with natural foci, where wild vertebrates play a key role in their maintenance.

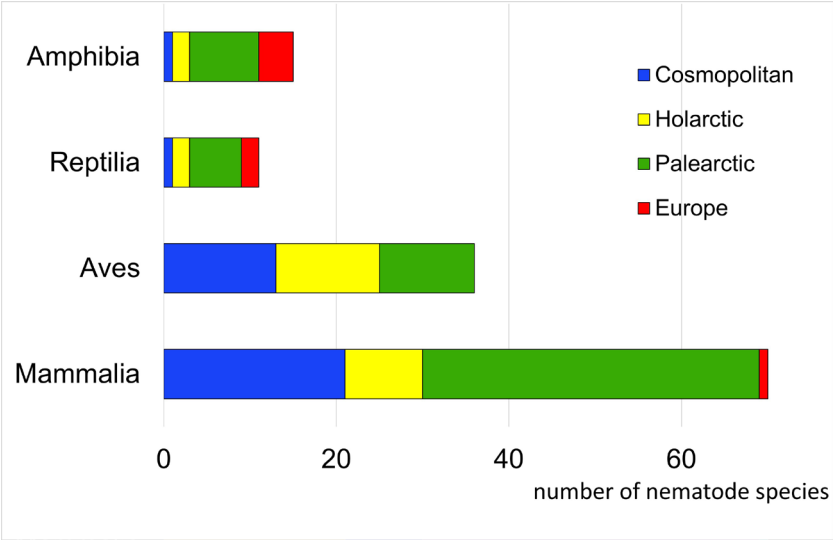


Figure 3. Zoogeographical structure of nematode fauna in terrestrial vertebrates of the Samara Oblast.

Climate change and the increasing anthropogenic impact on natural ecosystems, coupled with the decline of the environmental situation in the Middle Volga region, exert a significant influence on vertebrates and their helminth fauna. The disruption of natural habitats of both invertebrates and vertebrates leads to the transformation of historically established parasite–host relationships and to the in-

volvement of humans in parasite–host associations that were previously atypical for them. Particular attention should be given to the expansion of the geographic ranges of biohelminths, driven by climate warming, which creates favorable conditions for the development of their invertebrate intermediate hosts. Furthermore, the northward range expansion of helminth species typically found in southern regions may lead to certain nematode species, previously unassociated with humans and domestic animals (e.g., *Dirofilaria repens*, *Dirofilaria immitis*), becoming epidemiologically significant. Additional factors capable of significantly altering the epidemiological situation include increasing population migration, the intentional or accidental introduction of animals and plants, and the importation of agricultural products. These factors may contribute to the expansion of the nematode fauna in vertebrates and the possible emergence of new helminth infections in humans, domestic animals, and wild fauna in the Samara Oblast.

Conclusion

This comprehensive long-term study provides the first systematic overview of the nematode fauna in terrestrial vertebrates of the Samara Oblast. Our findings reveal a highly diverse parasite community comprising 124 nematode species. Of these, 41 species have an indirect life cycle, whereas 83 develop directly. The ratio of geo- and biohelminths in the nematode fauna of vertebrates strongly depends on the hosts' lifestyle and diet. A total of 117 recorded nematode species use terrestrial vertebrates solely as definitive hosts, while five (*Eustrongylides excisus*, *Spiroxys contortus*, *Streptocara crassicauda*, *Ascarops strongylina*, and *Physocephalus sexalatus*) use them only as intermediate and/or paratenic hosts. The remaining two species (*Physaloptera clausa* and *Porrocaecum depressum*) parasitize vertebrates (mammals) at the larval and adult stages. *Cosmocerca commutata* undergoes both the larval and adult stages in *Bufotes viridis*, which serves as an amphixenic host for this parasite. The structure of these parasite assemblages is tightly linked to the ecological traits of their hosts. While the majority of the recorded nematodes exhibit high host specificity, frequently restricted to a single host taxon, a significant portion consists of generalists. The lower number of nematode species recorded in amphibians (15) and reptiles (11) compared to birds (36) and mammals (70) likely reflects the smaller number of host species studied in these groups, rather than an inherently poorer parasite fauna.

From a zoogeographical perspective, the majority of the nematode species (61) recorded in land vertebrates of the Samara Oblast belong to the Palearctic faunal complex, while 34 species have a cosmopolitan distribution. The ranges of 22 species cover the Holarctic region, and the distribution of seven nematode species is limited to Europe. Nematode species with broad distribution ranges (cosmopolitan and Holarctic) tend to infect multiple vertebrate classes, indicating a generalist strategy. Conversely, nematode species with a narrower distribution range (Europe and the

Palearctic) largely display host specificity. This observation underscores the link between geographic range and host range, suggesting that dispersal capacity and host availability may drive host plasticity in nematodes. Notably, 30 of 124 nematode species found in terrestrial vertebrates of the Samara Oblast are of medical and veterinary importance as potential pathogens of severe helminthiases. Moreover, seven species (*Syphacia obvelata*, *Calodium hepaticum*, *Ascaris suum*, *Toxascaris leonina*, *Toxocara canis*, *Ancylostoma caninum*, and *Uncinaria stenocephala*) can parasitize humans, particularly when personal hygiene practices are neglected. The study of the nematode fauna in wild vertebrates aligns with the One Health concept, helping to elucidate the interconnections between human, animal, and environmental health.

The number of nematode species currently recorded does not reflect the true diversity of nematodes associated with terrestrial vertebrates, as a significant portion of the regional vertebrate fauna remains unsurveyed. Thus, of the 377 terrestrial vertebrate species inhabiting the Samara Oblast, the helminth fauna of only 166 species has been studied to varying degrees. In particular, data on the helminths of the avifauna, lagomorphs, and carnivores remain insufficient. From the perspective of further research, the primary focus should be, on the one hand, on studying the nematode fauna of vertebrates that have not yet been investigated, and, on the other hand, on expanding the study areas, which will significantly supplement our knowledge of nematodes of vertebrates in the region.

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Supplementary material 1

Table S1. List of nematodes of vertebrates in the Samara Oblast

Authors: Nadezhda Yu. Kirillova, Victoria A. Vekhnik, Sofia A. Denisova, Sergei V. Shchenkov, Roman A. Gorelov, Alexander A. Kirillov, Igor V. Chikhlyaev

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