Russian J. Theriol. 21(2): 162–168

Species composition of gastrointestinal nematodes of moose (*Alces alces*) in European Russia

Dmitry N. Kuznetsov*, Natalya B. Romashova & Boris V. Romashov

ABSTRACT. The species of gastrointestinal nematodes found during necropsies of 26 moose from four regions of European Russia (Tver', Smolensk, Ryazan' and Voronezh) were determined. In total, eight species of nematodes were registered: *Aonchotheca bovis, Ashworthius sidemi, Mazamastrongylus dagestanica, Nematodirella alcidis, Ostertagia antipini, Spiculopteragia asymmetrica, Trichostrongylus capricola* and *Trichuris ovis*. Beside this, a minor morph of *O. antipini* ("*Ostertagia lyrataeformis*") was found in seven moose from all of the studied regions. *Ashworthius sidemi*, a blood-sucking nematode, was found in moose in Voronezh region, and this fact indicates the further spreading of this Asian parasite among ruminants in Europe. Apparently, the reason for the relatively low species diversity of nematodes noted in this study is the small number of contacts of moose with other ruminants in the study areas. The intensity of infection was also relatively low and ranged from 87 to 1660 nematodes. The extensity of infection ranged from 3.8% for *Aonchotheca bovis* to 100% for *Mazamastrongylus dagestanica*. No nematode species more typical for domestic ruminants was found, which indicates the absence of contacts between the studied moose and livestock.

How to cite this article: Kuznetsov D.N., Romashova N.B., Romashov B.V. 2022. Species composition of gastrointestinal nematodes of moose (*Alces alces*) in European Russia // Russian J. Theriol. Vol.21. No.2. P.162–168. doi: 10.15298/rusjtheriol.21.2.07

KEY WORDS: wild ruminants, *Alces alces*, digestive tract, parasitic nematodes, European Russia, *Ashworthius sidemi.*

Dmitry N. Kuznetsov [dkuznetsov@mail.ru], Center of Parasitology of A.N. Severtsov Institute of Ecology and Evolution RAS, Mytnaya str., h. 28, build. 1, Moscow 119049, Russia; Natalya B. Romashova [bvnrom@rambler.ru], Voronezh State Nature Biosphere Reserve, Voronezh 394080, Russia; Boris V. Romashov [bvrom@rambler.ru], Voronezh State Agrarian University named after Emperor Peter the Great, Mitchurina str. 1, Voronezh 394087, Russia; Voronezh State Nature Biosphere Reserve, Voronezh 394080, Russia.

Видовой состав нематод желудочно-кишечного тракта у лося (*Alces alces*) в Европейской России

Д.Н. Кузнецов*, Н.Б. Ромашова, Б.В. Ромашов

РЕЗЮМЕ. Определена видовая принадлежность паразитических нематод, обнаруженных при патологоанатомических исследованиях желудочно-кишечного тракта у 26 лосей из четырех областей европейской части России (Тверской, Смоленской, Рязанской и Воронежской). В общей сложности зарегистрировано восемь видов нематод: *Aonchotheca bovis, Ashworthius sidemi, Mazamastrongylus dagestanica, Nematodirella alcidis, Ostertagia antipini, Spiculopteragia asymmetrica, Trichostrongylus capricola* и *Trichuris ovis*. Кроме того, у семи лосей во всех четырех обследованных областях была обнаружена минорная морфа вида *O. antipini* — "*Ostertagia lyrataeformis*". Кровососущая нематода *A. sidemi* была найдена у лосей в Воронежской области, что указывает на дальнейшее распространение этого азиатского паразита среди жвачных Европы. Причиной сравнительно низкого видового разнообразия нематод, отмеченного в рамках данного исследования, является, по-видимому, малое количество контактов лосей с другими жвачными на обследованных территориях. Интенсивность инвазии также оказалась сравнительно низкой и составила от 87 до 1660 экземпляров нематод. Экстенсивность инвазии варьировала в пределах от 3.8% для *Aonchotheca bovis* до 100% для *Mazamastrongylus dagestanica*. Не было обнаружено видов нематод, более типичных для домашних жвачных, что указывает на отсутствие контактов между исследованными лосями и домашним скотом.

КЛЮЧЕВЫЕ СЛОВА: дикие жвачные, *Alces alces*, пищеварительный тракт, паразитические нематоды, Европейская Россия, *Ashworthius sidemi*.

* Corresponding author

Introduction

The present range of the moose (*Alces alces* Linnaeus, 1758) in Russia is from the western to the eastern state borders and associated with forest and forest-steppe ecosystems. In many regions of Russia, including the European part of the country, moose is a common hunting species. By the beginning of the 21st century, the number of moose in Russia had significantly decreased, amounting to 526.47 thousand individuals in 2001 (Kolesnikov, 2014). Subsequently, the number of moose gradually began to grow and reached 720.8 thousand individuals in 2013 (Kolesnikov, 2014). This species of Cervidae has an individual-group lifestyle, moving over considerable distances (Zaitsev, 2002). In natural conditions, due to the peculiarities of the lifestyle and diet, moose is less associated with parasites than other Cervidae and, therefore, is less adapted to them (Maklakova & Rykovsky, 2008). In case of changes in living conditions, such as overpopulation or contacts with other species of ruminants, moose may get parasite infections with high intensity and a noticeable deterioration in health (Maklakova & Rykovsky, 2008). There are only a few recent studies concerning moose parasites in Europe (Shimalov & Shimalov, 2003; Samojlovskja, 2008, 2011; Milner *et al*., 2013; Davidson *et al*., 2015; Filip & Demiaszkiewicz, 2016; Grandi *et al*., 2018; Filip-Hutsch *et al*., 2021). Thus, the addition of data on this issue looks useful.

Gastrointestinal nematodes of wild ruminants are considered as a group of big significance because these helminthes often show high rates of infection and perceptible negative influence for health (Hoberg *et al*., 2001; Stien *et al*., 2002). In moose, the extremely high infection intensities with gastrointestinal nematodes can take place (Grandi *et al*., 2018; Filip-Hutsch *et al*., 2021). The aim of our study was to identify gastrointestinal nematodes found during necropsies of moose from several regions of European Russia, and to determine intensity and extensity of infection. It was also aimed to compare obtained results with the previous data from Russia and other European countries.

Material and methods

Sample collection

Nematodes were collected from 26 moose in four regions of European Russia. The sampling was made in Tver' (56.533° N; 36.583° E), Smolensk (54.567° N; 33.183° E), Ryazan' (54.333° N; 40.833° E) and Voronezh (the territory of Voronezh State Reserve — 51.85° N; 39.667° E) (Fig. 1). Some of the moose were shot licensed hunting, other were died because of accidental traumas. Age of the moose was estimated based on conditions of reproductive system, limb bones, teeth and horns (Klevezal, 2007**)**. The moose were necropsied according to common helminthological methods (Ivashkin *et al*., 1971). In each moose there were separately examined an abomasum, small and large intestine. These parts of the gastrointestinal tract were ligated at the level of pylorus, ileocecal junction and the rectum and then cut from each other. Then these parts of the gastrointestinal tract were dissected and their contents together with washings of mucosa were placed into buckets. Then these matrixes were mixed with water (one part of matrix and 5–10 parts of water). When the sediment has settled, the supernatant was poured out. The sediment was washed in this way 3–5 times and then added with 96% ethanol. After that, the matrixes were studied in the laboratory by small portions using binocular loupe. All of the samples were studied in full volume. Detected nematodes were placed into vials with 96% ethanol.

Taxonomical identification

In most cases an identification of the detected nematodes was based on male's morphology due to big similarity of the females. The nematodes were prepared as temporary whole mounts cleared with glycerol solution (two parts of glycerol and eight parts of water). Then the nematodes were studied using light microscopy at magnification of 40 to 400. The species identification was based on morphological features presented in literature (Skrjabin *et al*., 1954; Drozdz, 1965, 1995; Ivashkin *et al***.,** 1989; Hoberg & Khrustalev, 1996; Demiaszkiewicz *et al*., 2013). The main features used for identification of the detected gastrointestinal strongyles were the shape of spicules and peculiarities of bursa morphology. *Nematodirella* nematodes were identified according to Lichtenfels & Pilitt (1983). *Trichuris* nematodes were identified using the data presented by Yevstafieva *et al.* (2018).

Molecular analysis

Several nematode samples collected during the present study were studied by molecular methods. Molecular study was successful for samples of three nematode species (*A. sidemi* Schulz, 1933, *M. dagestanica* (Altaev, 1953) and *O. antipini* Matschulsky, 1950). Genomic DNA was isolated from single specimens of nematodes using the procedure described by Holterman *et al.* (2006). In all cases, DNA was extracted from individual specimens of the nematodes, previously identified by morphological features.

Polymerase chain reaction (PCR) was performed to obtain the ITS-domain of rDNA using the general primers AB28 and TW81 (Joyce *et al.*, 1994). The PCR was carried out using DNA amplification kit produced by "Sileks" (Russia) in a 25 µl reaction volume. The PCR was conducted according to the following protocol: 3 min at 94°C, then 9 cycles at 94°C for 1 min, 55°C for 1 min 30 s, and 72°C for 1 min 30 s, then 24 cycles at 94°C for 45 s, 57°C for 1 min, and 72°C for 1 min 20 s, followed by a final extension at 72°C for 5 min. The PCR-products were checked in agarose gel and then purified for sequencing using a Wizard SV Gel and PCR Clean-Up System ("Promega", USA) according to the manufacturer's protocol. Obtained PCR-products were sequenced using

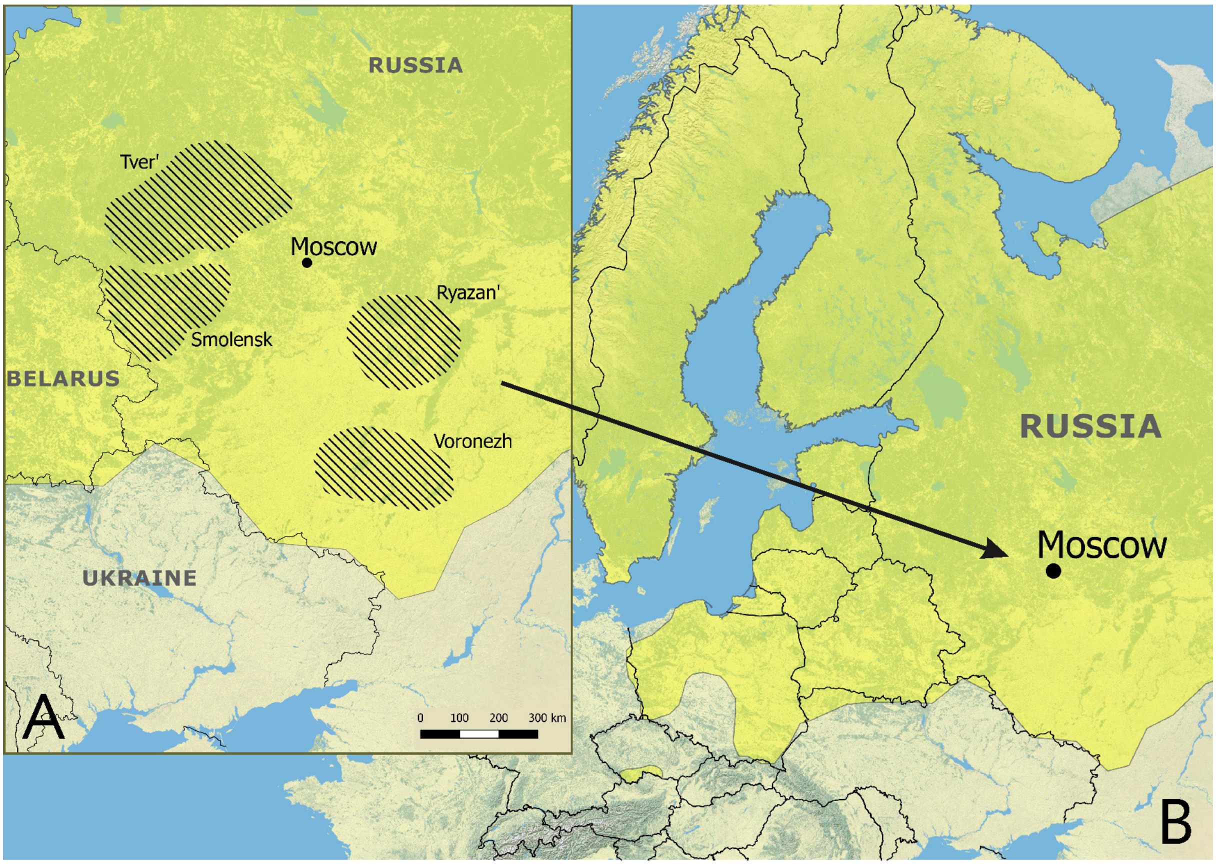

Fig. 1. The area of collection of *Alces alces* nematodes (hatching) (A) within the distribution range of *A. alces* in Europe (B). The distribution range of *A. alces* in Europe is given according to IUCN (Henttonen *et al*., 2007).

Table 1. The sequences of ITS-region rDNA of gastrointestinal nematodes obtained in the course of the present study.

Species of nematodes	Region of sampling	GenBank accession number
Ashworthius sidemi	Voronezh	OM443078
Ashworthius sidemi	Voronezh	OM443079
Mazamastrongylus dagestanica	Tver’	OM451216
Mazamastrongylus dagestanica	Tver’	OM451217
Mazamastrongylus dagestanica	Smolensk	OM445252
Mazamastrongylus dagestanica	Smolensk	OM445253
Mazamastrongylus dagestanica	Smolensk	OM445254
Mazamastrongylus dagestanica	Ryazan’	OM444202
Mazamastrongylus dagestanica	Ryazan’	OM444203
Mazamastrongylus dagestanica	Voronezh	OM451427
Mazamastrongylus dagestanica	Voronezh	OM451428
Mazamastrongylus dagestanica	Voronezh	OM451429
Ostertagia antipini	Smolensk	OM509875
Ostertagia antipini	Smolensk	OM509876
Ostertagia antipini	Ryazan’	OM509877
Ostertagia antipini	Voronezh	OM509878
Ostertagia antipini	Voronezh	OM509879

ABI PRISM Big Dye Terminator v 3.1 kit (Applied Biosystems, USA) with an analysis of the reaction products using automatic sequencer Applied Biosystems 3730 DNA Analyzer. Obtained sequences were compared with the NCBI GenBank nucleotide database using the BLASTn 2.8.1+ program (Morgulis *et al*., 2008). The sequences were deposited in GenBank (Tab. 1).

Results

Gastrointestinal nematodes were found in all of the studied moose. At the same time, there were not

Table 2. The intensity of infection with gastrointestinal nematodes in studied individuals of *Alces alces* and the list of detected species. A — abomasum, SI — small intestine, LI — large intestine; major and minor morphs are listed via slash.

Sequence number of the studied moose	Region of sampling	Month and year of sampling	Sex and age of hosts	Number of detected nematodes			Species of detected nematodes, localization and number of males (in brackets)
				Total	Males	Females	
1	Tver’	January 2013	male, 3 years	140	31	109	*Mazamastrongylus dagestanica* (A 19), *Nematodirella alcidis* (SI 5), *Ostertagia antipini* (A 3) / “*Ostertagia lyrataeformis*” (A 1), *Trichuris ovis* (LI 3)
2	Tver’	October 2015	male, 4 years	592	251	341	*M. dagestanica* (A 199), *N. alcidis* (SI 31), *O. antipini* (A 18) / “*O. lyrataeformis*” (A 1), *T. ovis* (LI 2)
3	Tver’	February 2016	male, 4 years	136	59	77	*M. dagestanica* (A 45), *N. alcidis* (SI 14)
4	Tver’	October 2017	male, 2 years	196	86	110	*M. dagestanica* (A 69), *O. antipini* (A 14) / “*O. lyrataeformis”* (A 1), *T. ovis* (LI 2)
5	Tver’	October 2018	male, 3 years	157	41	116	*M. dagestanica* (A 32), *N. alcidis* (SI 3), *O. antipini* (A 6)
6	Tver’	November 2018	female, 3 years	137	47	90	*M. dagestanica* (A 38), *N. alcidis* (SI 6), *O. antipini* (A 2), *T. ovis* (LI 1)
7	Tver’	October 2019	female, 3 years	130	42	88	*M. dagestanica* (A 31), *N. alcidis* (SI 11),
8	Smolensk	November 2013	male, 2 years	149	49	100	*M. dagestanica* (A 46), *O. antipini* (A 3)
9	Smolensk	November 2014	female, 4 years	199	65	134	*M. dagestanica* (A 49), *O. antipini* (A 16)
10	Smolensk	January 2015	male, 4 years	209	77	132	*M. dagestanica* (A 69), *O. antipini* (A 8)
11	Smolensk	December 2015	female, 4 years	1175	437	738	*M. dagestanica* (A 389), *O. antipini* (A 41) / “*O. lyrataeformis”* (A 7)
12	Smolensk	October 2016	male, 3 years	109	32	77	*M. dagestanica* (A 29), *O. antipini* (A 3)
13	Smolensk	November 2016	female, 3 years	141	32	109	*M. dagestanica* (A 28), *O. antipini* (A 4)
14	Smolensk	January 2018	male, 5 years	98	29	69	*M. dagestanica* (A 29)
15	Ryazan’	January 2009	male, 1 year	127	46	81	*M. dagestanica* (A 38), *O. antipini* (A 8)
16	Ryazan’	October 2013	female, 3 years	187	60	127	*M. dagestanica* (A 55), *O. antipini* (A 5)
17	Ryazan’	February 2014	male, 1 year	176	55	121	*M. dagestanica* (A 48), *O. antipini* (A 7)
18	Ryazan’	October 2015	female, 4 years	198	55	143	*M. dagestanica* (A 49), *O. antipini* (A 6)
19	Ryazan’	January 2016	male, 3 years	150	40	110	*M. dagestanica* (A 37), *O. antipini* (A 3)
20	Ryazan’	February 2017	female, 3 years	178	63	115	*M. dagestanica* (A 53), *O. antipini* (A 10)
21	Ryazan’	December 2018	male, 5 years	1229	527	702	*M. dagestanica* (A 489), *O. antipini* (A 32) / “*O. lyrataeformis”* (A 6)
22	Ryazan’	February 2019	male, 3 years	87	15	72	*M. dagestanica* (A 15)
23	Voronezh	December 2016	male, 7 years	1660	770	890	*Aonchotheca bovis* (SI 1), *Ashworthius sidemi* (A 4), *M. dagestanica* (A 364), *N. alcidis* (SI 126), *O. antipini* (A 266) / “*O. lyrataeformis*” (A 9)
24	Voronezh	July 2017	male, 2 years	1279	573	706	*M. dagestanica* (A 360), *O. antipini* (A 207) / “*O. lyratae-formis*” (A 3), *Spiculopteragia asymmetrica* (A 3)
25	Voronezh	February 2021	female, 3 years	1188	295	893	*A. sidemi* (A 47), *M. dagestanica* (A 175), *N. alcidis* (SI 1), *O. antipini* (A 66), *S. asymmetrica* (A 4), *T. ovis* (LI 2)
26	Voronezh	May 2021	female, 4 years	540	155	385	*A. sidemi* (A 43), *M. dagestanica* (A 61), *N. alcidis* (SI 5), *O. antipini* (A 40), *Trichostrongylus capricola* (SI 2), *T. ovis* (LI 4)

pronounced lesions in gastrointestinal tracts of the moose. All of the studied moose were not emaciated. The intensity of infection and the list of detected species are presented in Tab. 2. The species names of detected nematodes are given in alphabetical order. In total, eight species of nematodes were found in this study. There were detected five species from the family Trichostrongylidae (*Ashworthius sidemi*; *Mazamastrongylus dagestanica*; *Ostertagia antipini*; *Spiculopteragia asymmetrica* (Ware, 1925); *Trichostrongylus capricola* Ransom, 1907) and one species each from the families Molineidae (*Nematodirella alcidis* (Dikmans, 1935)), Capillariidae

Table 3. The extensity of infection with gastrointestinal nematodes in studied individuals (*n*=26) of *Alces alces*.

Nematode species	Regions of detection	The number of infected animals	Extensity of infection (%)
Aonchotheca bovis	Voronezh	1	3.8
Ashworthius sidemi	Voronezh	3	11.5
Mazamastrongylus dagestanica	Tver', Smolensk, Ryazan', Voronezh	26	100.0
Nematodirella alcidis	Tver', Voronezh	9	34.6
Ostertagia antipini	Tver', Smolensk, Ryazan', Voronezh	22	84.6
Spiculopteragia asymmetrica	Voronezh	2	7.7
Trichostrongylus capricola	Voronezh	1	3.8
Trichuris ovis	Tver', Voronezh	6	23.1

(*Aonchotheca bovis* (Schnyder, 1906)) and Trichuridae (*Trichuris ovis* (Abildgaard, 1795)). Beside this, a minor morph of *Ostertagia antipini* ("*Ostertagia lyrataeformis*") was also found in seven moose from all of the studied regions (Tab. 2).

Thus, we found rather low species diversity of gastrointestinal nematodes in studied moose. The intensity of infection was also quite low and ranged from 87 to 1660 nematodes (Tab. 2). Two nematode species (*M. dagestanica* and *O. antipini*) were recorded in all four regions studied (Tab. 3). As well as, the highest intensity of infection levels was noted for these two species: 489 males of *M. dagestanica* in moose from Ryazan' and 266 males of *O. antipini* in moose from Voronezh (Tab. 2). Four out of eight detected nematode species were found in Voronezh region only (Tab. 3), and besides in low numbers (Tab. 2). And two species (*N. alcidis* and *T. ovis*) were found in two of the four regions studied, in most cases in few specimens (Tabs 2, 3).

For three of the detected species they taxonomic affiliation was confirmed by molecular analysis. Obtained sequences of *A. sidemi*, *M. dagestanica* and *O. antipini*, contained ITS-region of rDNA, were compared with the GenBank nucleotide database using the BLAST. All of the sequences obtained during the present study showed 99% identity to the sequences of the corresponding species from the GenBank nucleotide database. Namely, *A. sidemi* sequences are identical to *A. sidemi* sequence EF467325, *M. dagestanica* sequences are identical to JQ925868 and *O. antipini* sequences are identical to JQ925869.

Discussion

In the present study, the number of gastrointestinal nematodes found in moose was not very high compared to data from other countries (Davidson *et al*., 2015; Grandi *et al*., 2018; Filip-Hutsch *et al*., 2021). As well as the species diversity of nematodes was relatively low. Eight species was found in the present study in total, but only one species (*M. dagestanica*) was registered in all of the studied moose (Tab. 2). In two moose we registered single-species infection with *M. dagestanica* (Tab. 2). *Ostertagia antipini* was found in 22 moose in all of the studied regions (Tabs 2, 3)**.** The coinfection with *M. dagestanica* and *O. antipini* is very common in moose (Kuznetsov, 2013; Grandi *et al*., 2018; Filip-Hutsch *et al*., 2021) and was noted in European roe deer as well (Kuznetsov *et al*., 2020). Grandi *et al.* (2018) and Wyrobisz-Papiewska *et al.* (2018) consider *A. alces* as a principal host for *M. dagestanica* and *O. antipini*. In the present study the intensity of infection with *M. dagestanica* is higher than with *O. antipini*. Interestingly, the study of moose from other regions of European Russia showed that the intensity of infection with *O. antipini* prevailed over *M. dagestanica* or was almost equal (Kuznetsov, 2013). Filip-Hutsch *et al.* (2021) noted that *O. antipini* predominated in the most intensively infected animals, but our data does not confirm this (Tab. 2). Thus, *M. dagestanica* showed the highest rates of the intensity and extensity of infection in the present study (Tabs 2, 3). A minor morph of *O. antipini* ("*O. lyrataeformis*") was found in few specimens, which apparently correlates with the detected small amount of the major morph.

Nematodirella alcidis was found in 34.6% of the studied moose, in Tver' and Voronezh regions (Tab. 3). The number of detected males of *N. alcidis* ranged from 1 to 126 (Tab. 2). This species is very common parasite of *A. alces*, registered in several countries (Lichtenfels & Pilitt, 1983; Grandi *et al*., 2018; Filip-Hutsch *et al*., 2021). Maklakova & Rykovsky (2008) believe that *A. alces* is the principal host for only three species of gastrointestinal nematodes: *O. antipini*, *M. dagestanica* and *N. alcidis*. It worth to mention, that *A. alces* was also often recorded as a host for *Nematodirella longissimespiculata* (Romanovich, 1915), but Lichtenfels & Pilitt (1983) proved that some reports of *N. longissimespiculata* from *A. alces* was erroneous and corrected that as parasitizing of *N. alcidis*.

Trichuris ovis was noted in few specimens for 23.1% of the studied moose from two regions (Tabs 2, 3). This nematode is widespread in domestic and wild ruminants. *Trichuris ovis* was reported from *A. alces* in Belorussia (Shimalov & Shimalov, 2003) and Poland (Filip & Demiaszkiewicz, 2016). In European Russia, *T. ovis* was recently found in moose from Moscow region (Samojlovskja, 2011).

We found a blood-sucking nematode *A. sidemi* in 11.5% of the studied moose, in Voronezh region only (Tab. 3). Previously, in Russia, *A. sidemi* was found in moose in Tver (former Kalinin) and Moscow regions (Nazarova & Starodynova, 1974; Samojlovskja, 2008).

Demiaszkiewicz *et al.* (2013) reported *A. sidemi* in moose in Poland. The detection of *A. sidemi* in moose in Voronezh region confirms the further spreading of this Asiatic nematode among ruminants in European Russia. Recently, *A. sidemi* was found in European roe deer in Voronezh and Tver' regions (Kuznetsov *et al*., 2018, 2020), as well as in fallow deer in Smolensk (Kuznetsov, 2022). Probably, *A. sidemi* was brought to Voronezh region in 1938 with sika deer introduced in Khopyor Nature Reserve from Sidemi peninsula of Russian Far East (Izmailov, 1940). And the Sidemi peninsula is a place of the first description of *A. sidemi* (Schulz, 1933). Subsequently, *A. sidemi* could enter from Khopyor Nature Reserve (51.183° N; 41.717° E) to Voronezh State Reserve (51.85° N; 39.667° E) during the migration of various wild ruminants. Beside these, over the past thirty years, several game-farms have been established near the Voronezh State Reserve. Various wild ruminants sometimes escape from these game-farms because of insufficient control. The origin, as well as the health status of these animals is not clear. Thus, *A. sidemi* could also have been introduced from these game-farms.

Small numbers of *S. asymmetrica* were found in two moose from Voronezh (Tabs 2, 3). Previously, *S. asymmetrica* was found in a small amount in moose from Moscow region (Kuznetsov, 2013). Wyrobisz-Papiewska *et al.* (2018) consider fallow deer as a principal host of *S. asymmetrica*. This nematode was reported from fallow deer even in North America (Doster & Friend, 1971). At the same time, *S. asymmetrica* was reported from European roe deer in Tver' and Voronezh, were fallow deer do not inhabit (Kuznetsov *et al.,* 2020). During the present study *S. asymmetrica* was registered in moose from the same area (the territory of Voronezh State Reserve) as this parasite was previously found in European roe deer (Kuznetsov *et al*., 2020).

Aonchotheca bovis was found in one of the studied moose from Voronezh (Tab. 3). In Russia, this nematode was previously detected in moose, both in the European and Asian parts of the country (Maklakova & Rykovsky, 2008). *Aonchotheca bovis* was also registered in several European countries in various species of wild ruminants, as well as in cattle and sheep (Govorka *et al.,* 1988). Filip-Hutsch *et al.* (2021) detected the eggs of *Aonchotheca* sp. during examination of fecal samples from *A. alces* in Poland. Few specimens of *T. capricola* were found in one of the studied moose from Voronezh (Tabs 2, 3). Recently, this nematode was reported from 78% of the examined moose in Sweden (Grandi *et al*., 2018) and from 31% of the examined moose in Poland (Filip-Hutsch *et al*., 2021). Grandi *et al.* (2018) noted that *T. capricola* was more prevalent and abundant in *A. alces* with lesions of gastrointestinal tract, than in *A. alces* without these lesions. But we did not observe any pronounced lesions of the gastrointestinal tract of the studied moose, possibly due to the rather low intensity of infection.

It is believed that most part of the helminth species ever reported from *A. alces* was obtained as a result of sharing of pastures with other species of ruminants, both wild and domestic (Maklakova & Rykovsky, 2008). Thus, the relatively low species diversity of gastrointestinal nematodes detected in our study reflects a small number of contacts of the moose with other ruminants in the studied areas. The biggest species diversity of nematodes, as well as the intensity of infection, we noted in moose from the relatively compact territory of Voronezh State Reserve inhabited by European roe deer and red deer as well. We did not find any nematode species more typical for domestic ruminants, and this fact indicates that there were no contacts between the studied moose and livestock.

Conclusion

The study of the species composition of gastrointestinal nematodes found in *A. alces* from four regions of European Russia showed rather low species diversity. This fact, apparently, indicates a small number of contacts of the moose with other ruminants (wild and domestic) in the studied areas. At the same time, the detection of Asiatic nematode *A. sidemi* in moose in Voronezh region confirms the further spreading of this potentially dangerous parasite among ruminants in European Russia. Since moose are able to move over big distances, they can spread parasites in new areas and among other ruminants.

ACKNOWLEDGMENTS. The authors express their gratitude to Alexander Khutoryanskiy, Anton Aksyonov and Oleg Andrejanov for the big help in collecting the samples of nematodes from moose. Our gratitude also goes to the reviewers for valuable comments regarding the manuscript.

References

Davidson R.K., Licina T., Gorini L. & Milner J.M. 2015. Endoparasites in a Norwegian moose (*Alces alces*) population — Faunal diversity, abundance and body condition // International Journal for Parasitology: Parasites and Wildlife. Vol.4. P.29–36.

Demiaszkiewicz A.W., Kuligowska I., Lachowicz J., Pyziel A.M. & Moskwa B. 2013. The first detection of nematodes *Ashworthius sidemi* in elk *Alces alces* (L.) in Poland and remarks of ashworthiosis foci limitations // Acta Parasitologica. Vol.58. No.4. P.515–518.

Doster G.L. & Friend M. 1971. *Spiculopteragia* (Nematoda) from Deer in North America // Journal of Parasitology. Vol.57. No.3. P.468–470.

Drozdz J. 1965. Studies on helminths and helminthiases in Cervidae. I. Revision of the subfamily Ostertagiinae Sarwar, 1956 and an attempt to explain the phylogenesis of its representatives // Acta Parasitologica Polonica. Vol.13. No.44. P.445–481.

Drozdz J. 1995. Polymorphism in the Ostertagiinae Lopez-Neyra, 1947 and comments on the systematics of these nematodes // Systematic Parasitology. Vol.32. P.91–99.

Filip K.J. & Demiaszkiewicz A.W. 2016. Internal parasitic fauna of elk (*Alces alces*) in Poland // Acta Parasitologica. Vol.61. No.4. P.657–664.

Filip-Hutsch K., Czopowicz M., Barc A. & Demiaszkiewicz A.W. 2021. Gastrointestinal helminthes of European Moose population in Poland // Pathogens. Vol.10. No.4. P.456.

Govorka I., Maklakova L.P., Mitukh I., Pelgunov A.N., Rykovskii A.S., Semenova M.K., Sonin M.D., Erkhardova-Kotrla B. & Iurashek V. 1988. [Helminths of Wild Ungulates of Eastern Europe]. Moscow: Nauka. 208 p. [in Russian].

Grandi G., Uhlhorn H., Agren E., Morner T., Righi F., Osterman-Lind E. & Neimanis A. 2018. Gastrointestinal parasitic infections in dead or debilitated moose (*Alces alces*) in Sweden // Journal of wildlife Diseases. Vol.54. No.1. P.165–169.

Henttonen H., Kranz A., Stubbe M., Maran T. & Tikhonov A. 2007. *Alces alces* ssp. *alces*. // The IUCN Red List of Threatened Species. P.e.T41782A10539156.

Hoberg E.P. & Khrustalev A.V. 1996. Re-evaluation of *Mazamastrongylus dagestanica* (Trichostrongylidae) with descriptions of the synlophe, genital cone, and other structural characters // Journal of Parasitology. Vol.82. No.5. P.778–787.

Hoberg E.P., Kocan A.A. & Rickard L.G. 2001. Gastrointestinal strongyles in wild ruminants // Samuel W., Pubis M. & Kocan A.A. (eds.). Parasitic Diseases of Wild Mammals. Ames: Iowa State University Press. P.193–227.

Holterman M., Wurff A., Elsen S., Megen H., Bongers T., Holovachov A., Bakker J. & Helder J. 2006. Phylum-wide analysis of SSU rDNA reveals deep phylogenetic relationships among nematodes and accelerated evolution towards crown clades // Molecular Biology and Evolution. Vol.23. No.9. P.1792–1800.

Ivashkin V.M., Kontrimavichus V.I. & Nazarova N.S. 1971. [Methods of Terrestrial Mammals' Helminths Collection and Study]. Moscow: Nauka. 124 p. [in Russian].

Ivashkin V.M., Orypov A.O. & Sonin M.D. 1989. [Keys to the Helminths of Small Cattle]. Moscow: Nauka. 255 p. [in Russian].

Izmailov I.V. 1940. [Fauna of birds and mammals of the Khopyor State Reserve] // Trudy Khoperskogo Gosudarstvennogo Zapovednika. No.1. P.89–173 [in Russian].

Joyce S.A, Reid A., Driver F. & Curran J. 1994. Application of polymerase chain reaction (PCR) methods to identification of entomopathogenic nematodes // Burnell A.M., Ehlers R.U. & Masson J.P. (eds.). COST 812 Biotechnology: Genetics of Entomopathogenic Nematode–Bacterium Complexes, Proceedings of Symposium & Workshop. Maynooth: St Patrick's College. P.178–187.

Klevezal G.A. 2007. [Principles and Methods of Age Determination of Mammals]. Moscow: KMK Scientific Press. 283 p. [in Russian, with English summary].

Kolesnikov V.V. 2014. [The population dynamics of moose in the Russian Federation in the XXI century] // Vestnik Okhotovedeniya. Vol.11. No.2. P.139–141 [in Russian, with English summary].

Kuznetsov D. 2022. The first detection of abomasal nematode *Ashworthius sidemi* in fallow deer (*Dama dama*) in Russia // Acta Parasitologica. Vol.67. P.560–563.

Kuznetsov D., Romashova N. & Romashov B. 2018. The first detection of *Ashworthius sidemi* (Nematoda, Trichostrongylidae) in roe deer (*Capreolus capreolus*) in Russia // Veterinary Parasitology: Regional Studies and Reports. Vol.14. P.200–203.

Kuznetsov D.N. 2013. [The study of gastrointestinal nematodes species composition in wild ruminants from European Russia] // Vestnik Okhotovedeniya. Vol.10. No.2. P.204–207 [in Russian, with English summary].

Kuznetsov D.N., Romashova N.B. & Romashov B.V. 2020. Gastrointestinal nematodes of European roe deer (*Capreolus capreolus*) in Russia // Russian Journal of Theriology. Vol.19. No.1. P.85–93.

Lichtenfels J.R. & Pilitt P.A. 1983. Cuticular ridge patterns of *Nematodirella* (Nematoda: Trichostrongyloidea) of North American ruminants, with a key to species // Systematic Parasitology. Vol.5. P.271–285.

Maklakova L.P. & Rykovsky A.S. 2008. [Parasites of Palearctic elk] // Trudy Tsentra Parazitologii. Vol.45. P.100–115 [in Russian, with English summary].

Milner J.M., Wedul S.J., Laaksonen S. & Oksanen A. 2013. Gastrointestinal nematodes of moose (*Alces alces*) in relation supplementary feeding // Journal of Wildlife Diseases. Vol.49. No.1. P.69–79.

Morgulis A., Coulouris G., Raytselis Y., Madden T., Agarwala R. & Schaffer A. 2008. Database indexing for production MegaBLAST searches // Bioinformatics. Vol.24. P.1757–1764.

Nazarova N.S. & Starodynova A.K. 1974. [Helminths of wild ungulates in forests of Kalinin and Moscow regions] // Trudy Gosudarstvennogo Zapovednika "Zavidovo". Vol.3. P.173–180 [in Russian].

Samojlovskja N.A. 2008. [Infection of moose of national park "Losinyi island" by parasites] // Rossiiskii Parazitologicheskiy Zhurnal. No.3. P.29–31 [in Russian, with English summary].

Samojlovskja N.A. 2011. [Fauna of parasites of elks in National park "Losinyj Island" and the Kostroma elk farm] // Rossiiskii Parazitologicheskiy Zhurnal. No.3. P.20–25 [in Russian, with English summary].

Schulz R.S. 1933. [*Ashworthius sidemi* n.sp. (Nematoda, Trichostrongylidae) from a deer (*Pseudaxis hortulorum*)] // Zeitschrift fur Parasitenkunde. Vol.5. P.735–739 [in German].

Shimalov V.V. & Shimalov V.T. 2003. Helminth fauna of cervids in Belorussian Polesie // Parasitology Research. Vol.89. P.75–76.

Skrjabin K.I., Shikhobalova N.P. & Shults R.S. 1954. [Essentials of Nematodology. Vol.3. Trichostrongylids of Animals and Man]. Moscow: Izdatel'stvo Akademii nauk SSSR. 683 p. [in Russian].

Stien A., Irvine R.J., Ropstad E., Halvorsen O., Langvatn R. & Albon S.D. 2002. The impact of gastrointestinal nematodes on wild reindeer: experimental and cross-sectional studies // Journal of Animal Ecology. Vol.71. P.937–945.

Wyrobisz-Papiewska A., Kowal J., Nosal P., Chovancová G. & Rehbein S. 2018. Host specificity and species diversity of the Ostertagiinae Lopez-Neyra, 1947 in ruminants: a European perspective // Parasites & Vectors. Vol.11. No.369. P.1–10.

Yevstafieva V.A., Yuskiv I.D., Melnychuk V.V., Yasnolob I.O., Kovalenko V.A. & Horb K.O. 2018. Nematodes of the genus *Trichuris* (Nematoda, Trichuridae), parasitizing sheep in Central and South-Eastern regions of Ukraine // Vestnik Zoologii. Vol.52. No.3. P.193–204.

Zaitsev V.A. 2002. Structure of moose (*Alces alces*) population in Russia with special reference to communication distances // Alces. No.2. P.137–141.