TRICHINELLA INFECTION OF WILD CARNIVORANS IN PRIMORSKY KRAI, RUSSIAN FAR EAST

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Nematodes of the genus *Trichinella* cause trichinosis, which is a zoonotic disease of humans, wild and domestic animals. In the Russian Far East, trichinosis has a natural focal character. Carnivorans (Carnivora), living in natural ecosystems including Protected Areas, are the main hosts of *Trichinella*. The peculiarities of *Trichinella* circulation in natural environment and the parasite prevalence in wild animals of different species remain poorly understood as well as the species composition of the *Trichinella* genus in the studied region. Muscle samples were obtained from 731 specimens belonging to 14 species and four families (Mustelidae, Ursidae, Felidae, and Canidae) in Primorsky Krai (Russia) in 2010–2020 and examined on *Trichinella*. The parasites were found in 124 specimens belonging to 11 species. The highest *Trichinella* prevalence was observed in *Vulpes vulpes* (64%), *Ursus arctos* (57%), and *Lynx lynx* (50%). A relatively high ratio of infected animals (30–50%) was found in *Nyctereutes procyonoides*, *Ursus thibetanus*, and *Prionailurus bengalensis*. The parasite prevalence was relatively low in the representatives of the Mustelidae family. Three species of the genus *Trichinella* (*T. nativa*, *T. spiralis*, and *T. pseudospiralis*) were found for carnivorans inhabiting the study area. *Trichinella nativa* was found the most frequently in natural ecosystems. *Trichinella pseudospiralis* was discovered for the first time both for *P. bengalensis* and for the area of the Primorsky Krai. The Carnivora ecology contributes to a high risk of infection by *Trichinella* species. The parasite prevalence was high in the species that combined different feeding habits, i.e. they acted as predators, scavengers and cannibals. A relatively long life expectancy also contributed to a higher risk of infection. A relatively high parasite prevalence of *Trichinella* in wild animals in the Primorsky Krai was caused by the high biological diversity of carnivorans. Our results are important for understanding the trichinosis circulation in natural communities and the possibility of human infestation. These data are also important for managing the carnivorans' populations in the Russian Far East. The issues of nature conservation in regard to the trichinosis circulation are also important for threatened animals, including *Panthera tigris altaica*.

Key words: animal ecology, nematode, parasite prevalence, parasites, predator, trichinosis

Introduction

Trichinosis is a widespread natural focal disease dangerous to humans (Campbell, 1983; Murrell, 2001; Pozio, 2005). In the wild, invasion circulates among carnivorans, primarily representatives of the order Carnivora (Britov, 1995; Skírnisson et al., 2010; Klun et al., 2019).

The features of *Trichinella* transfer from one host to another have been intensively studied in anthropogenic ecosystems (Beck, 1970; Gottstein et al., 2009; Pozio, 2014). But the range of hosts and the features of their transmission in natural ecosystems have generally not been studied yet.

In the Russian Far East, there were a few studies of *Trichinella* invasion of wild animals (Britov & Sapunov, 1997; Gorodovich & Gorodovich, 2009; Guba, 2009, 2010; Seryodkin, 2015b). These studies were mainly devoted to the description of the parasite prevalence in certain mammal species. In the Primorsky Krai, important studies on trichinosis were previously carried out by Britov (1995), who presented data on the infection of eleven species of wild carnivorans by this parasite. Britov (1995) reported on *Trichinella* infection in humans living in the Primorsky Krai, and listed the species composition of *Trichinella*. The diversity of *Trichinella* species and haplotypes and their distribution in carnivoran populations in the Primorsky Krai were partially addressed in Odoevskaya et al. (2018).

Until now, the features of the trichinosis circulation in the ecosystems of the Primorsky Krai, including Protected Areas (PAs), have not been adequately studied. In particular, the role of carnivorans in the parasite invasion circulation has not been assessed. In addition, the influence of the animal ecology on the *Trichinella* prevalence has not been evaluated.

The study of the species composition and haplotype diversity of *Trichinella* circulating in natural ecosystems is of great interest for fundamental research as well (Mohandas et al., 2014).

The study aimed to identify the wild Carnivora species susceptible i) to *Trichinella* invasion, ii) to estimate the parasite prevalence (PP) for each mammal species, iii) to search for the dependence of the parasite prevalence in carnivorans on the ecology of the latter, iv) to assess the features of the trichinosis circulation in the local ecosystems, and v) to report on the species composition of *Trichinella*.

Material and Methods

Study area

Primorsky Krai is located in the south of the Russian Far East (Fig.). The Sikhote-Alin mountain system covers most of the area. It is a complex system of mountain ranges, river valleys, intermountain depressions, and mountain plateaus. By absolute altitude, the Sikhote-Alin mountain system belongs to the mid-altitude mountains. Part of the Primorsky Krai is represented by plains. The largest area of the region is occupied by the Ussuri-Prikhankaisk plain (Prikhankaisk lowland).

The study area is represented mainly by the natural forest complex. The most common forest formations are mixed broad-leaved and oak (*Quercus mongolica* Fisch. ex Ledeb.) forests of valleys and foothills, pine-broad-leaved forests of the lower and middle mountain zones, pine-spruce forests (*Pinus koraiensis* Siebold & Zucc., *Picea jezoensis* (Siebold & Zucc.) Carrière subsp. *jezoensis*) at an altitude of up to 800 m a.s.l., fir-spruce forests (*Abies nephrolepis* (Trautv.) Maxim., *Picea jezoensis* subsp. *jezoensis*) of the upper mountain zones, larch forests (*Larix gmelinii* (Rupr.) Kuzen. var. *gmelinii*) in swampy areas of river valleys, stony birch (*Betula ermanii* Cham. var. *lanata* Regel) forests of sub-goltsy altitudinal belt, and thickets of *Pinus pumila* (Pall.) Regel (Astafiev, 2006).

This area is characterised by a high diversity of species and natural communities due to the pronounced diversity of climatic, altitude and soil conditions, as well as its location at the junction of various biogeographic regions in Asia. The terrestrial mammal fauna of the Primorsky Krai includes more than 80 species, including 18 species of carnivorans (Pavlinov & Lissovsky, 2012; Darman et al., 2019).

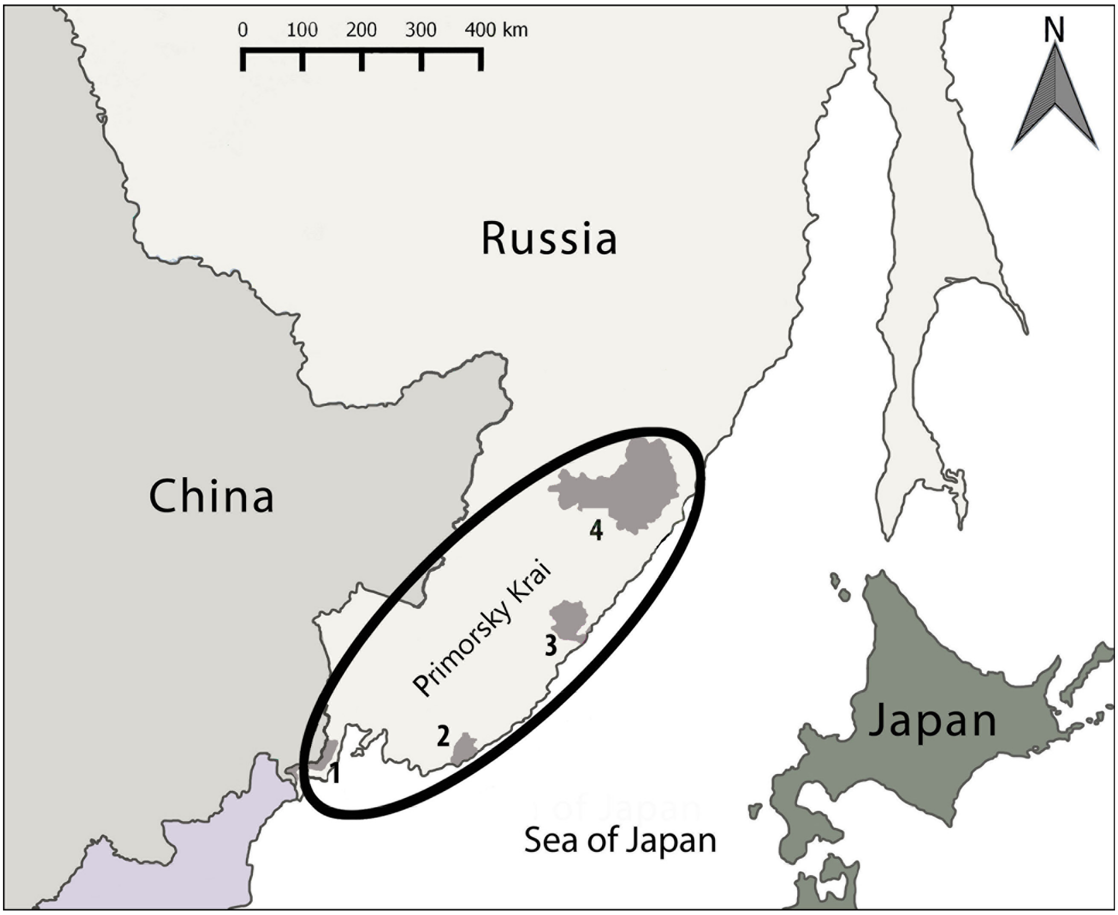

Fig. The study area of *Trichinella* invasion in wild Carnivora in the Primorsky Krai in 2010–2020. The federal-level Protected Areas are indicated in dark grey as: 1 – Land of the Leopard National Park, 2 – Lazovsky State Nature Reserve, 3 – Sikhote-Alin State Nature Reserve, 4 – Bikin National Park.

Sampling

In 2010–2020, muscle tissue was sampled from carnivorans killed by predators and hunters, as well as from animals which died from diseases and on the roads by traffic. The sampling was performed in most of the area of the Primorsky Krai, Russia (Fig.). The material was collected in a number of districts (Anuchinskiy, Chuguevskiy, Dalnerechenskiy, Khasanskiy, Khorolskiy, Kirovskiy, Krasnoarmeyskiy, Lazovskiy, Mikhailovskiy, Nadezhdinskiy, Partizanskiy, Pozharskiy, Shkotovskiy, Terneyskiy, and Yakovlevskiy) and in several municipalities (Artemovskiy, Bolshoy Kamen', Dalnegorskiy, Lesozavodskiy, Ussuriiskiy, and Vladivostokskiy) of the Primorsky Krai. The study area included single sites, buffer zones, and the surroundings of the following federal-level PAs: Sikhote-Alin State Nature Reserve, Lazovsky State Nature Reserve, Land of the Leopard National Park, and Bikin National Park (Fig.).

Muscle tissues were sampled and examined for 731 specimens of carnivorans belonging to four families, namely Mustelidae: *Lutra lutra* Linnaeus, 1758 (five individuals), *Martes flavigula* Boddaert, 1785 (three individuals), *M. zibellina* Linnaeus, 1758 (514 individuals), *Meles leucurus* Hodgson, 1847 (three individuals), *Mustela sibirica* Pallas, 1773 (22 individuals), and *Neovison vison* Schreber, 1777 (four individuals); Ursidae: *Ursus arctos* Linnaeus, 1758 (23 individuals), and *U. thibetanus* G. Cuvier, 1823 (16 individuals); Felidae: *Lynx lynx* Linnaeus, 1758 (10 individuals), *Panthera tigris* Linnaeus, 1758 (three individuals), and *Prionailurus bengalensis* Kerr, 1792 (72 individuals); Canidae: *Canis lupus* Linnaeus, 1758 (two individuals), *Nyctereutes procyonoides* Gray, 1834 (40 individuals), and *Vulpes vulpes* Linnaeus, 1758 (14 individuals).

Trichinella larvae detection procedure

In order to identify *Trichinella* larvae, fragments of striated muscle tissue of dead mammals (20–50 g) were studied using standard methods as follows: compression trichinoscopy and biochemical digestion in artificial gastric juice (AGJ), according to state methodology guidelines (MUK 4.2.2747-10, Russia). Each muscle tissue sample was initially examined using light microscopy (microscopes MBS-9 and Zeiss AxioImager.Z1). Digital photography and subsequent processing of images was carried out in the Zeiss Axio Vision program.

Estimation of the parasite prevalence

The parasite prevalence of *Trichinella* was determined for the carnivorans. This number was not less than ten specimens. The parasite prevalence was calculated as the ratio of the number of infected animals to the total number of examined specimens of a certain species, expressed as a percentage. If the total number of specimens of a certain species was less than ten individuals, the possibility of their infection with *Trichinella* was assessed. Our data are accompanied by the data on the infection of carnivorans with *Trichinella* in the Primorsky Krai according to Britov (1995) (Table).

Trichinella species identification

Trichinella larvae were isolated from muscle tissues after peptolysis in AGJ. Then, they were repeatedly washed with water and physiological salt solution.

PCR was used for molecular genetic identification of *Trichinella* samples. Genomic DNA was obtained from 1–12 *Trichinella* larvae by digestion in proteinase K with mercaptoethanol (Holterman et al., 2006). Species identification was carried out by the nucleotide sequence of the mitochondrial genome site (CoxI gene and adjacent tRNA sequences). The sequence was obtained using primers 37F_Tri GCA GTA AAT TTA GAA TTT AAA C and 42R_Tri CCT AAT ATT CAT GGT GTT CAT A (Odoevskaya et al., 2018). After sequencing, the obtained data were compared with the analogous sequences of the representatives of *Trichinella* genus available in the NCBI GenBank. We analysed the obtained alignments using the methods of maximum parsimony, nearest-neighbour algorithm, and maximum likelihood in the MEGA7 program (Kumar et al., 2016).

Results

Parasite prevalence

Trichinella larvae were found in the muscles of 124 specimens (Table). The highest PP (> 50%) was recorded for *Vulpes vulpes* and *Ursus arctos*. Relatively high *Trichinella* prevalence (> 30%) was observed in *Lynx lynx*, *Nyctereutes procyonoides*, *Prionailurus bengalensis*, and *Ursus thibetanus*. In the Primorsky Krai, a low PP was found in two species of the Mustelidae family, *Martes zibellina* and *Mustela sibirica*. *Trichinella* infestation has also been reported for *Canis lupus*, *Meles leucurus*, and *Neovison vison*.

Compared to our data (Table), Britov (1995) reported a slightly lower PP for *Vulpes vulpes* and *Ursus arctos* and relatively higher values for *Canis lupus*, *Panthera tigris*, and *Martes flavigula* in terms of *Trichinella* invasion in the Primorsky Krai. In general, our study evidenced that *Vulpes vulpes*, *Canis lupus*, *Nyctereutes procyonoides*, *Ursus arctos*, *U. thibetanus*, *Prionailurus bengalensis*, *Lynx lynx*, and *Panthera tigris* are of the highest importance among the studied carnivorans for the circulation of *Trichinella* in the study area.

Trichinella species composition

The following three species of the genus *Trichinella* were found in the studied samples of carnivorans in the Primorsky Krai: *T. nativa* Britov & Boev, 1972, *T. spiralis* (Owen, 1835), and *T. pseudospiralis* Garkavi, 1972. *Trichinella nativa* was observed in most of infected animals. This species was registered for *Ursus arctos*, *U. thibetanus*, *Lynx lynx*, *Prionailurus bengalensis*, *Canis lupus*, *Vulpes vulpes*, *Nyctereutes procyonoides*, *Meles leucurus*, *Martes zibellina*, and *Mustela sibirica*. *Trichinella spiralis* was found in two specimens of *Martes zibellina*, and *Trichinella pseudospiralis* in one specimen of *Prionailurus bengalensis*.

Discussion

Parasite prevalence

Similarly to the Primorsky Krai, a relatively high *Trichinella* prevalence in *Vulpes vulpes* is also observed in the Amur region (Russia), accounting for 43.2% (Gorodovich & Gorodovich, 2009), and in Belarus, for 35.3% (Penkevich & Anisimova, 2013). In some regions of Russia, PP in *V. vulpes* is lower, i.e. 22.3% in the Kursk region (Vagin & Malysheva, 2010), 15% in the central part of Russia (Andreyanov, 2014), 12.2% in Kamchatka (Britov & Sapunov, 1997), 7.5% in the Altaisky Krai (Malkina & Konyaev, 2013), and 3.3% in the Republic of Yakutia (Odnokurtsev et al., 2015).

Trichinella prevalence in *Canis lupus* varies in different parts of the wide range of this predator. Thus, PP comprises 15.2% and higher in the Republic of Yakutia (Odnokurtsev et al., 2015), 19.7% in the Altaisky Krai (Malkina & Konyaev, 2013), 14.3% in Kamchatka (Britov & Sapunov, 1997), and 11% in the central part of Russia (Andreyanov, 2014). In *C. lupus*, PP reaches 22% in the southern regions of the Russian Far East, and up to 50% in the northern regions (Yudin, 1992). High values of PP were noted in Estonia (up to 50%) (Moks et al., 2006), and Latvia (69.7%) (Bagrade et al., 2009).

Nyctereutes procyonoides is characterised by relatively high PP in Belarus (42.8%) (Penkevich & Anisimova, 2013), and in the Amur region (33.3%) (Gorodovich & Gorodovich, 2009). These results are comparable to that observed in the Primorsky Krai. Much lower values were reported in the central part of Russia, 12% (Andreyanov, 2014).

Trichinella prevalence in *Ursus arctos* varies in different regions of the Russian Far East. In particular, PP is the lowest in the Sakhalin region (2.4%), but reaches up to 30.6% in Kamchatka and even up to 61% in the Magadan region (Seryodkin, 2015b). In the Sikhote-Alin mountain range (including Primorsky Krai), it ranges from 45% to 70% (Yudin, 1991). In other Russian regions, PP also varies in *U. arctos* as follows: 13.3% in Altaisky Krai (Malkina & Konyaev, 2013), and 19.7%, in the Republic of Yakutia (Odnokurtsev et al., 2015).

Table. Parasite prevalence of *Trichinella* spp. in wild carnivorans inhabiting the Primorsky Krai, Russia

Host species	Original data			According to Britov (1995)		
	Number of studied specimens	Number of infected specimens	PP, %	Number of studied specimens	Number of infected specimens	PP, %
Vulpes vulpes	14	9	64.29	71	15	21.13
Canis lupus	2	1	scarce data	33	15	45.45
Nyctereutes procyonoides	40	17	42.50	78	28	35.90
Ursus arctos	23	13	56.52	211	58	27.49
Ursus thibetanus	16	6	37.50	–	–	–
Prionailurus bengalensis	72	25	34.72	26	8	30.77
Lynx lynx	10	5	50.00	8	4	scarce data
Panthera tigris	3	0	scarce data	15	8	53.33
Meles leucurus	3	1	scarce data	33	9	27.27
Martes zibellina	514	42	8.17	–	–	–
Martes flavigula	3	0	scarce data	11	8	72.73
Mustela sibirica	22	4	18.18	40	1	2.50
Neovison vison	4	1	scarce data	–	–	scarce data
Lutra lutra	5	0	scarce data	1	0	scarce data

Comparing to our data, a lower *Trichinella* prevalence (5.9%) was reported for *Ursus thibetanus* in the Russian Far East (Britov & Sapunov, 1997). This evidences that PP may change over time and may vary in different areas of the same region.

Our data on the PP in *Prionailurus bengalensis* in comparison to Britov (1995), obtained earlier in the Primorsky Krai, were comparable (34.7% and 30.8%, respectively). A serological study indicated a presence of antibodies to *Trichinella* in 10% of *P. bengalensis* animals in the south of Primorsky Krai (Naidenko et al., 2019).

In the Primorsky Krai, the PP in *Lynx lynx* is higher than in the Amur region, another region of the Russian Far East, where *Trichinella* PP accounts for 21.1% (Guba, 2010). However, in other parts of *L. lynx* range, the PP is higher. Its values are 50% in Estonia (Malakauskas et al., 2007), up to 70% in Finland (Airas et al., 2010), and 88.9% in Latvia (Malakauskas et al., 2007).

Despite not having found *Trichinella* in *Panthera tigris*, caused by a small sampling, the PP was apparently quite high in these carnivorans in the Russian Far East. *Trichinella* infection was reported in 53.3% of studied specimens (Britov, 1995). In the Amur region, all examined *P. tigris* (four individuals) were infected (Gorodovich & Gorodovich, 2009). In the south of the Primorsky Krai, a serological study reported on the antibodies to *Trichinella* in 72% of *P. tigris* individuals (Naidenko et al., 2019).

In *Meles leucurus*, *Trichinella* prevalence ranged as 13.2–17.4% in the Amur region (Gorodovich & Gorodovich, 2009; Solovieva et al., 2017), and 6.7% in the Altaisky Krai (Malkina & Konyaev, 2013). These values are lower than we observed in the Primorsky Krai. In the closely related species *Meles meles* Linnaeus, 1758, inhabiting Europe, the prevalence of this parasite also varied in different regions, for example, from 6.2% in the Balkans (Klun et al., 2019) and up to 25% in the central part of Russia (Andreyanov, 2014).

In *Martes flavigula*, the high PP compared to other Mustelidae species in the study area may be caused by the small sampling size. Other Mustelidae species are characterised by lower *Trichinella* prevalence than observed for *M. flavigula* in Primorsky Krai as well as in other Russian regions. For example, for *Martes zibellina*, it was 1.9% in Kamchatka (Britov & Sapunov, 1997), 2.2% in the Amur region (Gorodovich & Gorodovich, 2009), and 4.3% in the Altaisky Krai (Malkina & Konyaev, 2013). In *Mustela sibirica*, PP varied from 5.2% to 11.1% in the Amur region (Gorodovich & Gorodovich, 2009; Guba, 2009; Solovieva et al., 2017). *Neovison vison* was characterised by PP of 1.1% in the Amur region (Gorodovich & Gorodovich, 2009), 3% in the northern part of the Russian Non-Chernozem Zone (Maslennikova & Strelnikov, 2017), while it comprised 16.6% in the Altaisky Krai (Malkina & Konyaev, 2013). The only exceptions were relatively high PP in the Republic of Yakutia (24.9%) for *Martes zibellina* (Kokolova, 2014), and in the Kursk region (36.6%) for *Neovison vison* (Vagin & Malysheva, 2010). Despite not having found *Trichinella* in *Lutra lutra*, Britov & Sapunov (1997) indicated that 3% of population of this species was infected by *Trichinella* in the Russian Far East.

In general, *Trichinella* prevalence in the carnivorans is predictably higher than in other taxonomic groups, including omnivores, due to their ecological peculiarities. In *Sus scrofa* Linnaeus, 1758, PP was 0.65% in the Russian Far East (Britov, 1995). It reaches up to 2.2% in the Amur region (Solovieva et al., 2017). It is known that rodents (Rodentia) and insectivores (Eulipotyphla) have low values of *Trichinella* prevalence in all the regions studied so far (e.g. Pozio, 2005; Malkina & Konyaev, 2013; Penkevich & Anisimova, 2013; Andreyanov, 2014).

The influence of animal ecology on Trichinella prevalence

In nature, the most carnivorans (e.g. *Panthera tigris*, *Lynx lynx*, *Prionailurus bengalensis*, *Canis lupus*, and *Vulpes vulpes*) with high PP values are characterised by a long life expectancy, that may exceed ten years (Tumanov, 2003; Yudin & Yudina, 2009; Yudin, 2015), while it may exceed up to 20 years or even more in *Ursus arctos* and *U. thibetanus* (Tumanov, 2003; Seryodkin et al., 2017). Undoubtedly, a longer life span increases the chances of a carnivoran to eat an animal infected with *Trichinella*.

The prey spectra of large carnivorans include smaller carnivorans. In addition, cannibalism is a characteristic of such species as *Ursus arctos*, *U. thibetanus*, *Vulpes vulpes*, and *Prionailurus bengalensis* (Yudin, 1986; Seryodkin et al., 2012; Seryodkin, 2015a; Seryodkin & Burkovskiy, 2019). In the Primorsky Krai, the diet of all large carnivorans includes *Sus* *scrofa*, which is also susceptible to *Trichinella* infection (Britov, 1995).

In addition to predation, some species with a relatively high degree of *Trichinella* infection are also characterised by necrophagy. Therefore, they are also able to eat any mammal species potentially carrying *Trichinella* larvae. *Ursus arctos* and *U. thibetanus* are potential scavengers (Seryodkin, 2015a), as well as *Vulpes vulpes* (Yudin, 1986), *Nyctereutes procyonoides* (Krivosheev, 1984), and *Prionailurus bengalensis* (Yudin, 2015).

Ursus thibetanus and especially *U. arctos* have high risks to be infected by *Trichinella*. As they are characterised by the highest life expectancy among all the carnivorans in the study area, they consume animal corpses more often than any other species. In addition, they are characterised by both cannibalism and predation. *Ursus arctos* feeds on all mammalian species, including *U. thibetanus*, *Panthera tigris*, *Nyctereutes procyonoides*, and *Meles leucurus*. Moreover, the occurrence of mammal remains in the scats in *U. arctos* is 4.3 times higher than that in *U. thibetanus* and amounts to 18.4% and 4.3%, respectively (Seryodkin, 2015a). *Ursus arctos* is able to hunt actively. But *Ursus thibetanus* may be characterised by a lower degree of predation. Thus, the lower infection of *U. thibetanus* by *Trichinella* compared with *U. arctos* is explained by the peculiarities of their feeding behaviour.

Panthera tigris, *Lynx lynx*, and *Canis lupus* are specialised predators, which hunt mainly on ungulates. However, they are able to catch several mammals infected with *Trichinella*. *Ursus thibetanus*, *Meles leucurus*, *Nyctereutes procyonoides*, *Vulpes vulpes*, *Canis lupus familiaris* Linnaeus, 1758 and others are in the list of their prey (Yudin, 1992; Matyushkin et al., 2003; Kerley et al., 2015; Seryodkin, 2015a). In the wild, *Panthera tigris*' lifespan may reach 19 years (Yudin & Yudina, 2009). It is known that *Canis lupus* may live up to 17 years (Tumanov, 2003).

Seven-year-old to eight-year-old *Vulpes vulpes* are usually found in natural habitats. Nevertheless, it is known that they may live up to 11 years (Tumanov, 2003). Despite small rodents and birds being the basis of the *Vulpes vulpes* diet in the Far East they eat any animal food (Krivosheev, 1984). It was reported that *V. vulpes* ate domestic dogs, while *Nyctereutes procyonoides*, *Mustela sibirica* may hunt on representatives of their own species (Yudin, 1986). Such diet contributes to *Trichinella* infection of *Vulpes vulpes*. Dead animals are also a part of the *Nyctereutes procyonoides* diet (Krivosheev, 1984), similarly as it is observed for *Vulpes vulpes*.

Small rodents, birds, and, to a lesser extent, other animals, are of the highest importance in *Prionailurus bengalensis*' diet (Yudin, 2015). The diet of this species includes insectivores, *Vulpes vulpes*, *Nyctereutes procyonoides*, and individuals of the same species (Seryodkin & Burkovskiy, 2019). Together with necrophagy, this promotes *Trichinella* infection. *Prionailurus bengalensis* lives up to 12–14 years in nature (Yudin, 2015).

Meles leucurus is an omnivore animal. Small animals, fruits, and sappy rhizomes of plants form the basis of its diet. Besides, insects form a considerable proportion in its diet. *Meles leucurus* feeds on frogs and small rodents. It destroys bird nests and consumes dead animals (Krivosheev, 1984). In nature, the maximal life expectancy of this species does not exceed 12–15 years (Tumanov, 2003). Thus, *M. leucurus* is also susceptible to *Trichinella* infection, but to a lesser extent than species of Ursidae, Canidae, and Felidae.

The relatively low *Trichinella* prevalence in *Martes zibellina* and *Mustela sibirica* is explained by the predominance of small rodents, birds, and amphibians in their diet (Krivosheev, 1984), as well as by a short life span (Tumanov, 2003). In the Primorsky Krai, PP in small rodents, the main prey of the mentioned animal species, is small and amounts to 0.65% (Britov, 1995).

Mustelidae species leading a semi-aquatic lifestyle (*Lutra lutra* and *Neovison vison*) have the lowest chance of *Trichinella* infection. The food spectra of these species include primarily fish, amphibians, various other aquatic animals, rodents, and birds (Krivosheev, 1984). Life expectancy of *L. lutra* and *N. vison* often does not exceed six years in the wild (Tumanov, 2003).

Trichinella species composition

In general, *Trichinella nativa* is the most common *Trichinella* species in the Russian Far East, and in the Primorsky Krai, in particular. This nematode usually parasitises in wild carnivorans. And it is distributed over the wide area of the temperate, subarctic and arctic zones in the Eurasia and North America (Gottstein et al., 2009).

Trichinella spiralis is the most widespread *Trichinella* species, because it is adapted to synanthropic animals, including *Sus scrofa domesticus* Erxleben, 1777 and *Rattus* spp. (Gottstein et al., 2009). The wide distribution of this *Trichinella* species is the result of the anthropogenic dissemination of this invasion along with *Sus s. domesticus* (Rosenthal et al., 2008). However, the infection of sables by the larvae of *T. spiralis* is possible since this parasite has been found in these Mustelidae species in the present study.

In our study, *T. pseudospiralis* was found for the first time in the Primorsky Krai, as well as for *Prionailurus bengalensis* as a host. Earlier, in the Russian Far East, this *Trichinella* species was recorded among wild animals in *Vulpes vulpes*, *Nyctereutes procyonoides*, and *Sus scrofa* in the Amur region (Gorodovich & Gorodovich, 2009). *Trichinella pseudospiralis* is often recorded in birds (Pozio, 2005; Garkavi, 2007). Since in the Primorsky Krai birds are one of the main food sources of *P. bengalensis* (Yudin, 2015; Seryodkin & Burkovskiy, 2019), infection may occur when they are eaten. In addition, small rodents and insectivores (Garkavi, 2007), also consumed by *P. bengalensis*, being the links for spreading of *T. pseudospiralis* in the study area.

Trichinosis circulation in ecosystems

Nowadays, there is a generally accepted concept that divides the foci of trichinosis invasion into synanthropic (*Trichinella* circulates mainly between *Rattus* spp. and *Sus scrofa domesticus*) and natural (circulation occurs between wild animals). However, over the past few decades, an analysis of the epidemic and epizootic conditions indicates an increasingly important role of wild animals in the transmission of invasion to people and domestic animals, including PAs (Britov, 1995; Britov & Nivin, 2009; Solovieva et al., 2017). Generally, trichinosis has a natural focal character both in the Primorsky Krai and in the Russian Far East (Britov, 1995; Britov & Sapunov, 1997).

The area of Primorsky Krai, including PAs, is characterised by a high biodiversity level, including carnivorans represented by predators and scavengers. This determines the widespread occurrence of trichinosis, which is relatively large compared with PP in the wild animals in other regions. Carnivora species play the largest role in the trichinosis circulation in the forest ecosystems prevailing in the Primorsky Krai. *Vulpes vulpes*, *Canis lupus*, *Nyctereutes procyonoides*, *Ursus arctos*, *U. thibetanus*, *Prionailurus bengalensis*, *Lynx lynx*, and *Panthera tigris* are the most considerable hosts of *Trichinella*. Their predation on other carnivorans widely known in literature, as well as cannibalism, play an important role in the *Trichinella* circulation. Other mammals, which are able to consume animals, such as *Sus scrofa* and small rodents, are involved in the spread of this invasion to a lesser extent.

Predatory birds are of high importance in the dispersion of *Trichinella* larvae. Birds are active destructors of organic waste in natural ecosystems, including dead animals (Odoyevskaya, 2010; Bukina, 2013). Previous studies showed that alimentary contact of predatory birds with *Trichinella* has developed historically. It plays a considerable role in the epizootology of trichinosis (Garkavi, 2007; Odoyevskaya, 2010). Only *T. pseudospiralis* parasitises and completely passes all ontogenesis stages in the muscle tissues of birds. Larvae of capsule-forming *Trichinella* species (*T. nativa* and *T. spiralis*), passing through the digestive tract of birds, can also enter both invertebrate animals (Insecta, Mollusca, Crustacea) and herbivorous and omnivorous mammals (Odoevskaya, 2011; Krapivin & Odoyevskaya, 2019).

Necrophagous insects can be mechanical vectors of *Trichinella* larvae (Andreyanov, 2014; Riva et al., 2015). The fundamental possibility for mammal infection with *Trichinella* by eating crustaceans, which consumed infected meat for the last 24 h., was experimentally confirmed (Krapivin & Odoevskaya, 2019).

Conclusions

In the Primorsky Krai, the highest PP of *Trichinella* larvae is observed in mammals (both predators and scavengers) having a relatively long lifespan. The PP of particular species is preconditioned both by the host diet and a set of preferred prey species. That is why large carnivorans and species characterised by cannibalism were the most infected compared to other animals.

In the Primorsky Krai, carnivorans have relatively high *Trichinella* prevalence compared to other regions. This is ensured by the high biodiversity in the study area, including a large number of carnivorans. Carnivorans, mostly species of the Canidae, Ursidae, and Felidae, play a leading role in the *Trichinella* circulation in ecosystems. Its PP in some species of these orders reaches 64%, 57%, and 50%, respectively. In fact, natural trichinosis is widely distributed. The *Trichinella* infestation is promoted not only by mammals, but also by birds and mechanical hosts (i.e. invertebrates).

Three *Trichinella* species (*T. nativa*, *T. spiralis*, and *T. pseudospiralis*) circulate in the natural ecosystems of the Russian Far East, including PAs. Carnivorans are infected mostly by *Trichinella nativa*.

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ЗАРАЖЕННОСТЬ ТРИХИНЕЛЛАМИ ДИКИХ ХИЩНЫХ МЛЕКОПИТАЮЩИХ В ПРИМОРСКОМ КРАЕ, ДАЛЬНИЙ ВОСТОК РОССИИ

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Нематоды рода *Trichinella* являются возбудителями трихинеллеза – зоонозной инвазии, заражающей человека, диких и домашних животных. На Дальнем Востоке трихинеллез имеет природно-очаговый характер, а резервуарами трихинелл являются в основном хищные млекопитающие (Carnivora), обитающие в природных биоценозах, в том числе на особо охраняемых природных территориях. Особенности циркуляции трихинелл в естественной среде, доля зараженных диких животных разных видов и видовой состав трихинелл в регионе остаются недостаточно изученным. В 2010–2020 гг. в Приморском крае на наличие трихинелл обследованы пробы мышц от 731 экземпляра хищных млекопитающих 14 видов из четырех семейств (Mustelidae, Ursidae, Felidae, Canidae). Положительными были пробы от 124 млекопитающих 11 видов. Наибольшая экстенсивность инвазии трихинеллами была у *Vulpes vulpes* (64%), *Ursus arctos* (57%) и *Lynx lynx* (50%). Относительно высокая доля зараженных животных (30–50%) была у *Nyctereutes procyonoides*, *Ursus thibetanus* и *Prionailurus bengalensis*. У представителей семейства Mustelidae зараженность была относительно низкой. У хищных млекопитающих на территории исследования обнаружено три вида рода *Trichinella*: *T. nativa*, *T. spiralis* и *T. pseudospiralis*. При этом наибольшее распространение в природных биоценозах имеет *T. nativa*. У *P. bengalensis*, а также на территории Приморского края впервые обнаружена *T. pseudospiralis*. Экология хищных млекопитающих обуславливает вероятность их заражения. Высокую экстенсивность инвазии имеют животные, для которых характерны одновременно хищничество, падальничество и каннибализм и при этом имеющие относительно большую продолжительность жизни. Относительно высокие показатели зараженности диких животных трихинеллами в Приморском крае обусловлены высоким биологическим разнообразием плотоядных животных. Полученные результаты важны для понимания особенностей циркуляции трихинеллеза в естественных биоценозах и возможности заражения человека, а также имеют ценность для управления популяциями хищных млекопитающих на Дальнем Востоке России. Природоохранный аспект имеет участие в циркуляции трихинеллеза редких и охраняемых видов животных, включая *Panthera tigris altaica*.

Ключевые слова: нематода, трихинеллез, хищник, экология животных, экстенсивность инвазии