

ANTS TULL

Domesticated and wild mammals
as reservoirs for zoonotic
helminth parasites in Estonia



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UNIVERSITY OF TARTU

Press

Department of Zoology, Institute of Ecology and Earth Sciences,
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LIST OF ORIGINAL PUBLICATIONS

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The author's contribution to the papers (* moderate contribution, ** high contribution, *** very high contribution)

	I	II	III	IV
Original idea	**	**	***	***
Study design	**	***	***	***
Data collection	***	***	**	**
Data analysis	***	***	***	***
Manuscript preparation	***	***	***	***

1. INTRODUCTION

Since the dawn of industrial revolution in the beginning of 18th century, human actions, and policies resulting in urbanization, industrialization and land-use change have consistently boosted the fragmentation and destruction of wildlife habitats. Thus, humans have altered ecosystems on a scale never seen before, which entails problems from high environmental pollution and biodiversity loss to outbreaks of infectious diseases (McMahon et al., 2018; Keys et al., 2019).

Approximately 60% (>800) of pathogens, originating from domesticated animals or wildlife cause human diseases called zoonoses (infectious diseases transmitted between animals and humans). Moreover, it has been estimated that nearly 43% of human infections caused by zoonotic pathogens originate from carnivore hosts (Cleaveland et al., 2001). An overview by Taylor et al. (2001) has identified 1415 species of infectious pathogenic organisms to humans, including 538 bacteria, 307 fungi, 287 helminths, 217 viruses and prions and 66 protozoa. Taken together, these pathogens have a high impact on human health, socio-economics, animals and ecosystems, making parasitic diseases of wildlife a rising One Health concern (Jenkins et al., 2015; Waindok et al., 2021; Casulli et al., 2022).

In 2004, the Wildlife Conservation Society (WCS) forged the term ‘One World, One Health’, partly in response to the understanding of wildlife as the likely cause of the global outbreak of severe acute respiratory syndrome (SARS) (Kruse et al., 2004). As one of the main focus has been on predicting and mitigating the emergence of zoonotic wildlife diseases, much more focus should be paid on preventing zoonotic diseases by taking into account opinions and warnings from scientists (Cheng et al., 2007). So, to mitigate the impacts of these zoonotic diseases to planetary health, the One Health approach is used, which main idea is that animal health, human health and environmental health are basically inter-laced and mutually dependent of each other.

Parasites are globally present among wildlife populations, and the presence of parasites does not directly imply that wildlife is sick. In a naturally functioning ecosystem, parasites can serve as indicators of high biodiversity (Hudson et al., 2006). However, human degraded ecosystems enhance the overlap between domesticated carnivores (primarily dogs and cats) and wildlife species, facilitating transmission of many parasitic infectious diseases (Otranto et al., 2015).

The term helminth applies for parasitic worms, belonging to various taxons: Platyhelminthes (flukes, flat- and tapeworms); Nematoda (roundworms); Nematomorpha (Gordian worms) and Acanthocephala (thorny-headed worms), (Bowman, 2013). These taxa consist of large and diverse group of organisms, some of them are free-living, but most are parasitic, living in, or on most invertebrates as well as vertebrate animals (Bush et al., 2001).

Among these, soil transmitted helminths (STH) or geohelminths are a group of parasitic nematodes (e.g., the roundworm *Ascaris lumbricoides* – the largest intestinal nematode infecting humans and causing ascariasis) infecting both

humans as well as animals via ingestion of viable eggs or through contact with larvae. According to WHO (2022) approximately 1.5 billion people are infected with STHs worldwide, meaning that the main infection route goes by hand-to-mouth contact after exposure to contaminated environment. In general, geohelminths feed on host tissues, including blood, which causes iron and protein loss; hookworms (e.g. *Ancylostomatidae*: *U. stenocephala*, *Ancylostoma* spp.) result in chronic intestinal blood loss, causing anemia. Generally, parasitic worms decrease absorption of nutrients, competing for viable vitamins (e. g. vitamin A) in the intestine and reducing hosts' physical fitness (WHO, 2022).

Other zoonotic parasites, like biohelminths (e.g., the fox tapeworm *Echinococcus multilocularis* – the smallest tapeworm, also capable of infecting humans, causing a disease called alveolar echinococcosis, which is one of the most life-threatening helminthic infections in humans), have more complex life cycles, depending on intermediate (development of larval stages) and definitive hosts (sexual reproduction), but some of them may even grow larger in a reservoir/paratenic host or remain in a dormant stage (Bowman, 2013). As both domestic and wildlife animals can be affected with parasites because of their sympatric populations, potential parasite spillover from wild carnivores to domesticated animals and from the latter to humans may appear. Moreover, while dogs and cats serve as definitive hosts for zoonotic parasites, these zoonotic agents can be directly transmitted to humans via human-pet contact.

The population of Europe is approximately 750 000 000 humans, making nearly 10% of the global world population. It is known that nearly 110 million cats and 90 million dogs live in human households (40%) in Europe (FEDIAF, 2021), excluding stray cats and dogs, probably an additional few million individuals. Since most pet dogs are taken to outdoor activities by their owners or are free-ranging, their territories overlap with wild carnivores of which red foxes are the most abundant followed by raccoon dogs, wolves and golden jackals. The wild canid infection dynamic overlapping with domesticated carnivores is complex, depending mainly on their dietary habits and therefore of enzootic parasites (present at some stable rate in a population) in food objects (paratenic, intermediate or reservoir hosts). As each species occupies its own environmental niche, meaning the concrete spectrum of resources that can be utilized by a species, it very often overlaps with other species. It is therefore beneficial for parasites, as they can expand their own ecological niche which in turn suggests that ecologically plastic parasites maximize their geographical distribution, host diversity and abundance.

1.1. Zoonotic endoparasites of companion animals (dogs, cats)

1.1.1. Cat endoparasites of zoonotic importance

Nematoda

The feline roundworm *Toxocara cati* (syn. *mystax*) is a common cat endoparasite with a worldwide distribution that causes toxocariasis in humans that can cause rheumatic, visceral, neurologic, asthmatic problems and even blindness (Smith and Beaver, 1953; Schantz, 1994). Cat is the definitive host, in which the parasite lives in as adults within the lumen of the small intestine, and rodent, bird, earthworm, ant and soil invertebrate species act as paratenic hosts (Dubinsky, 1994; Despommier, 2003). It is an important zoonotic endoparasite not only because it infects young kittens but it causes human toxocariasis. The disease is associated with poverty, but other risk factors include sex, rural areas and exposure to pets. Ingestion of viable, embryonated eggs from contaminated sources (e.g. soil and earthworms etc.) will trigger the infection or the infection is acquired transplacentally via the female cat. The human acts as an aberrant (abnormal) host, in which after the larvae have hatched from eggs, they do not mature into adults, instead visceral larva migrans (VLM) wander through intestines or damage the eyes' optic nerve caused by ocular larva migrans (OLM) (Despommier, 2003). Moreover, the seropositive status has been associated with asthma and epilepsy, poor neurocognitive function and increased serum lead levels. Among humans, children are at highest risk becoming infected with *T. cati* by accidentally swallowing viable eggs (geophagia) during play in sandboxes or on playgrounds that have been contaminated by infected cats or attached eggs on the animal hair stick on the hand. Children from rural areas have had higher infection risk than children from the urban settlement (Dubinsky, 1994; Shokouhi and Abdi, 2018). Preventing infections with *T. cati* are possible to some extent, e.g. covering sandpits with panels, routine treatment of cats with ivermectin or mebendazole might prove enough effective if the guidance of ESCCAP (2020) is followed. According to studies by Talvik et al. (2006) and Kroten et al. (2016) sandboxes and parks in urban and suburban areas are contaminated with *Toxocara* sp. eggs, showing that free-roaming and stray cats distribute zoonotic *Toxocara* sp. eggs, whereas children are the main risk group for larval toxocariasis.

Protozoa

It is often challenging to determine protozoan endoparasite transmission routes from wild to domestic carnivores because they are described by complex networks within their ecosystems. Some of these endoparasites can be transmitted via contaminated soil or food (e.g., *Toxoplasma* sp.) and water (e.g., *Cryptosporidium* spp.), not to mention direct transmission from cats to humans.

Therefore, knowledge of such transmission cycles is essential to map the hazards which in turn lead to the implementation of possible control methods.

The obligate intracellular parasitic protozoan *Toxoplasma gondii* is another zoonotic ubiquitous endoparasite that can infect cats, humans, livestock (e. g. poultry, cattle and pigs) and a myriad of wildlife species, including marine mammals (Dubey and Jones, 2008; Jokelainen et al., 2015). It causes a disease called toxoplasmosis that is associated with neuropsychiatric and behavioural conditions (Milne et al., 2020). Felids are the key host species in the life cycle of *T. gondii* excreting resistant oocysts to the environment, following sporulation during which infective sporozoites evolve. After swallowing the sporulated oocysts by new intermediate host (e.g., human), sporozoites transform into invasive tachyzoites. Tachyzoites undergo asexual reproduction by penetrating all nucleated cells and replicating rapidly in an intracytoplasmic vacuole. The host cells are disrupted due to the following repeated intravacuolar replication and tachyzoites invade adjacent cells resulting in tissue destruction being thus responsible for the clinical symptoms of the disease. As a result of the immune response, the pathogenic process is terminating with the formation of tissue cysts containing slowly replicating bradyzoites which can persist in the intermediate host for a lifetime. Tissue cysts can be found in the brain, skeletal and cardiac muscles or in the retina that are the infective stages for intermediate and definitive hosts through predation.

Humans get the infection by ingesting (sporulated oocysts) tissue cysts from undercooked meat and/or consuming food or water contaminated with oocysts, or congenital or lactogenic transmission occurs from mother to fetus causing miscarriage or other complications (e.g. hydro- or microcephalus). It is also possible to ingest oocysts from the contaminated environment (e.g. soil), (Dubey and Jones, 2008). Small mammals, mainly rodents (e.g. *Rattus norvegicus*, *Apodemus agrarius*, *Mus musculus*) have been considered as the intermediate hosts of *T. gondii*. Even though it has been estimated by Dubey (1995) that most cats only shed oocysts for only one week in their life, the oocysts show extreme resistance against environmental conditions and may be viable in the soil up to one year but even more in the water environment (VanWormer et al., 2013). Several studies have found that *T. gondii* is highly endemic in Estonian wildlife, showing seroprevalence in nearly a quarter of moose (*Alces alces*) and wild boar (*Sus scrofa*) (Jokelainen et al., 2015; Remes et al., 2018). Even higher (60%) seroprevalence has been found in shelter cats (Must et al., 2015). The seroprevalence in the general human population was 55.8% but even higher in hunters (65%) (Lassen et al., 2016).

Cestoda

Cats are commonly definitive hosts for three tapeworms in Europe, although they can be infected with *Diphyllobothrium latum* (*syn. Dibothriocephalus latus*) and a few other non-typical species. Typical cat tapeworms are cosmopolitan

Hydatigera (syn. *Taenia*) *taeniaeformis*, *Dipylidium caninum* and *Mesocestoides* spp. (Bowman, 2013) but also *E. multilocularis* (Knapp et al., 2018; Karamon et al., 2019). The intermediate host of zoonotic *H. taeniaeformis* are mainly rodents (rats, mice and muskrats) in which the larvae mature in the liver (Smyth, 1994). One of the most widespread zoonotic tapeworm is *D. caninum* that has fleas and lice (*Pulex irritans*, *Ctenocephalides felis*, *C. canis*, *Trichodectes canis*) as its intermediate hosts, causing dipylidiasis in humans. In most cases, the disease is asymptomatic, albeit diarrhea, anorexia, rectal itching, abdominal colic and pain due to the emerging proglottids may appear (García-Agudo et al., 2014). Definitive hosts get the infection by accidentally ingesting fleas or louse. It has also a very active gravid proglottids, having the capability to frequently exit the anus and moving in the fur in the perianal region of an infected host. If the proglottids dry, the egg packets are released that resemble small rice grains, which will be consumed by fleas. Humans, especially children may become infected by ingesting fleas (Smyth, 1994; Bush et al., 2001). Studies in France and Poland have found *E. multilocularis* in cats that causes alveolar (multilocular) hydatid disease in humans resulting in a multicyst made up of proliferating vesicles that localizes in liver or lungs (Bristow et al., 2012; Knapp et al., 2018; Karamon et al., 2019).

1.1.2. The overall endoparasite prevalence in cats and risk factors

The overall endoparasite prevalence among cats has been found to range from 20.5% in Europe up to 83% in the United States (Kostopoulou et al., 2017; Wyrosdick et al., 2017). The most prevalent nematode helminths in most studies belong to zoonotic *T. cati* ranging from 8.3% up to 36.6% (Kostopoulou et al., 2017; Zottler et al., 2019). In rare cases, *Ancylostoma* spp. with zoonotic potential has been the most prevalent (27.6%) nematode in cats (Wyrosdick et al., 2017). The prevalence of tapeworms is much lower and is ranging between 0.8% up to 11.1% (Kostopoulou et al., 2017; Zottler et al., 2019). Generally, studies have found eggs from family Taeniidae, but some common tapeworm species have been determined at species level like zoonotic *Hydatigera taeniaeformis* and *Dipylidium caninum*; protozoan endoparasite infection prevalence diapason has been ranging from 0.2% up to 12.4%, including infrequently occurring zoonotic *T. gondii*/non-zoonotic *Hammondia hammondi* oocysts, but higher infection prevalences have been found with *Cystoisospora* spp. and zoonotic *Cryptosporidium* spp. and *Giardia* sp. (Mircean et al., 2010; Becker et al., 2012; Kostopoulou et al., 2017; Zottler et al., 2019). The abovementioned zoonotic endoparasites pose a serious threat to human health, especially to children often playing in contaminated areas (e.g. sandboxes, recreational areas) with endoparasite eggs/oocysts (Talvik et al., 2006; Schurer et al., 2013). The main risk factors for high infection predominance with endoparasites is considered straying, living in rural environment and juvenile age (Mircean et al., 2010;

Becker et al., 2012; Nijse et al., 2016; Zottler et al., 2019). In addition, consumption of raw or undercooked meat, hunting and older age have been the key risk factors for *T. gondii* infection, and also originating from multi-cat households, catteries is a risk factor for *Giardia* sp. (Jokelainen et al., 2012; Deksne et al., 2013; Must et al., 2015; Blasco et al., 2017).

1.2. Dog endoparasites of zoonotic importance

Nematoda

Dogs serve as definitive host for zoonotic *Toxocara canis* – one of the most important gastrointestinal helminth in dogs that can affect also human health, causing toxocariasis in humans as described above in *T. cati*. The infection may occur when dogs ingest embryonated eggs from contaminated environment (soil, rodents, birds, earthworms etc.), or the disease is acquired in utero (e.g. transplacentally) or via milk (transmammary) from the infected female dog. *Toxocara* spp. eggs are unembryonated when passed in feces of dogs (and cats) into the environment. Under optimal conditions (25–30 °C, relative humidity of 85–95%) the development into infective larval stage in the egg requires 9–15 days, but it could take time from three to six weeks up to several months, or even one year (Overgaauw, 1997). After ingestion of the eggs, eggs will hatch in the hosts' duodenum (within 2–4 h), then larvae penetrate the mucosal layer of the intestine. Later, when the intestinal wall is penetrated, the larvae invade lymph vessels, migrating to the mesenteric lymph nodes. The next route includes migration to the liver via the portal circulation in venous capillaries. After reaching the liver, most larvae will continue to migrate, exiting the liver via *vena cava*, passing the heart and arriving in the lung through pulmonary artery (Webster, 1958). Some of the larvae are trapped in capillaries and remain in the liver. From the lung alveoli, two different routes are possible, tracheal migration to develop into adult (larvae penetrate alveoli wall continuing their migration via bronchioles and trachea to the pharynx where they are swallowed and can mature into adult worms in the intestine) or a somatic migration during which larvae re-enter the circulatory system via alveoli, being distributed to the somatic tissue and remain arrested as an infected larva (Bowman, 2013). Depending on age, the likelihood of somatic migration progressively increases in older (one or two months old) dogs because of the acquired immunity, and larvae stay in arrested state in the tissues of kidneys, liver, central nervous system and skeletal muscles (Schnieder et al., 2011; Bowman et al., 2013). When paratenic hosts (mice, rats, rabbits, pigs, etc.) become infected with embryonated eggs, the infection occurs directly without tracheal migration, probably because the larvae have already migrated in the tissue of previous host, reaching a stage of maturity (Overgaauw, 1997; Bowman, 2013).

Protozoa

One of the cosmopolitan zoonotic protozoa species is *Giardia doudevalis* (syn. *G. intestinalis* and *G. lamblia*) that can infect gastrointestinal tract (causing giardiasis) of a multitude of mammalian host, including humans, especially children via contaminated food, water or soil. The groups of *Giardia* are discussed as assemblages according to molecular findings of which assemblage A is zoonotic for humans but C and D are host-specific for dogs (Claerebout et al., 2009; Bowman, 2013). Approximately, 7% of the world's human population is infected with *Giardia* in their intestine (Bowman, 2013). The zoonotic disease is usually not life-threatening but it can become severe in young children and immunocompromised humans resulting in diarrhoea which may become chronic for months (Bush et al., 2001). *Giardia* spp. parasitize in the small intestine where trophozoites attach to the mucosal epithelial cells by their adhesive discs (suckers). Trophozoites are passed to the environment and form infective cysts, otherwise they do not persist in the environment and do not cause infections (Bowman, 2013).

Cestoda

There are 18 orders in the tapeworm class, of which two have zoonotic importance. Tapeworms of the order are mainly found in terrestrial animals and Diphylobothriidae have aquatic stages as part of their transmission cycles (Bowman, 2013).

The Cyclophyllidae infect a myriad on animals, e.g. amphibian, reptile, bird and mammal species throughout the world. Most tapeworm species found in bird and mammals belong to this order. Similarly, most common tapeworm species found in humans or domesticated mammals belong also to this taxon. Some of the most hazardous tapeworms belong to the family Taeniidae that can grow up to 10 m (*Taenia saginata*) or only a couple of millimetres (*Echinococcus* spp.) but also cause serious harm to its host (e.g. human). Gravid taeniid proglottids or segments are shed by carnivorous definitive host via the anus containing tens of thousands of eggs in each gravid proglottid. The segments have the ability to move freely around on the surface of faecal samples, emptying themselves of their eggs and are dispersed by flies and other insects. On ingestion from the contaminated environment by a suitable intermediate host (generally prey to the definitive host), the oncosphere penetrates the gut wall of intestine and migrates further into the tissues (liver, skeletal or cardiac muscles) and develops into a cysticercus (bladderworm), which is infectious to the definitive host (Bush et al., 2001; Bowman, 2013). So, once the definitive host swallows the second larval stage within a intermediate host (e.g. rodent), the bladder is digested away and the scolex attaches itself in the mucosa of the small intestine where it begins to grow into an adult stage (Bowman, 2013).

Furthermore, the genus *Echinococcus* comprises mainly of two zoonotically important taxa, *E. multilocularis* and a taxonomically yet unresolved *E. granulosus*

sensu lato (s.l.) complex, that likely contains several species (Thompson, 2008; Saarma et al., 2009). The fox tapeworm *E. multilocularis* is mainly distributed in the northern hemisphere and uses foxes (red fox and arctic fox), but also other canids (wolves and dogs) as definitive hosts, when they have opportunities to prey on rodents, who act as intermediate host. The parasite causes alveolar echinococcosis in liver of rodents, such as voles and lemmings, as well as in humans. In the latter, cysts are typically sterile proliferating and infiltrating surrounding tissue, making surgical intervention very complicated. If not treated timely, the infected human can die (Smith, 1994; Bowman, 2013).

The larval stage of *E. granulosus s.l.* occurs in herbivorous mammals (sheep, swine, cattle, moose, kangaroos, caribou, etc.) who act as intermediate hosts. Human can be an aberrant intermediate host. Infection results in disease called cystic echinococcosis (CE). The adult worm develops in at least 11 species of canids such as dogs, wolves and jackals etc., who act as definitive hosts. Domestic ungulates (sheep, horses and swine) and dogs are a part of the anthropogenic cycle exposing *E. granulosus s.l.* to humans. The CE is starting after ingestion of a small (30–40 µm) egg that eventually can grow to a very large cyst(s) in humans and may become a lethal disease if not treated timely (Smith, 1994; Bush et al., 2001).

1.2.1. The overall endoparasite prevalence in dogs and risk factors

The overall prevalence of dog endoparasites is different in various European countries, depending mainly on origin of the dog (rural, urban, shelter). Generally, infection prevalence is significantly higher in rural regions rather than in urban areas (Fok et al., 2001; Dubna et al., 2007; Papajova et al., 2014). Furthermore, stray and shelter dogs have even higher infection prevalence with endoparasites (Kostopoulou et al., 2017; Regidor-Cerrillo et al., 2020). Tapeworms, having zoonotic potential, are more common in rural settlements than in urban environment, including Taeniidae and *Dipylidium caninum* (Dubna et al., 2007; Papajova et al., 2014). Among nematodes, *T. canis* has been the most prevalent zoonotic parasite in rural areas in Czech Republic and in Hungary (Fok et al., 2001; Dubna et al., 2007). However, higher prevalence of *T. canis* has been revealed in urban areas of Slovak Republic (Papajova et al., 2014). Spanish stray dogs and rural dogs in Portugal have had highest prevalence with zoonotic hookworms (Ancylostomatidea) (Cardoso et al., 2014; Regidor-Cerrillo et al., 2020). Due to the applied antigen test, shelter dogs in Greece had highest prevalence with potentially zoonotic *Giardia* spp., followed by potentially zoonotic *Cryptosporidium* spp. (Kostopoulou et al., 2017), but in most cases, the most prevalent protozoan is *Cystoisospora* spp.

1.3. Red fox, golden jackal and other predator endoparasites of zoonotic importance

The red fox, a highly adaptable (plastic) canid species, has habituated the urban as well as rural settlements in Europe, distributing a myriad of endoparasites that are brought near to humans and their pets (Deplazes et al., 2004; Laurimaa et al., 2015a). In Estonia, a total of 17 endoparasite taxa have been found in red foxes, including 10 of them with zoonotic potential (Laurimaa et al., 2016b). Another canid on the way to colonizing the northern hemisphere is the golden jackal. The species was reported in Estonia in 2013, having naturally migrated to Estonia from the Caucasian population (Rutkowski et al., 2015). It has been reported by Gherman and Mihalca (2017) that a total of 194 parasite species are distributed by golden jackals, a majority of them, including zoonotic (i.e. *Toxocara* spp., *Echinococcus* spp.), are shared with cats and dogs (Bružinskaitė-Schmidhalter et al., 2011; Citterio et al., 2021). In a previous study, Jõgisalu et al. (2019) have found in Estonia that the most prevalent endoparasites of jackals are *A. alata* and *U. stenocephala*, both having zoonotic potential. One of the most abundant and successful canid in Europe and beyond, aside from the red fox, is the raccoon dog, a common definitive host for many zoonotic helminths. Laurimaa et al. (2016a) described a minimum of 32 helminth species of which 19 are zoonotic in raccoon dogs.

On one end of the scale, among predators that harbour zoonotic helminths, dominate domesticated animals (primarily dog and cats) with their helminths, but on the other end of the scale, wildlife predators can be found with their diverse parasite communities, often with infection rates ranging from 90% up to 100%. Wildlife taxa (e.g. Carnivora, Artiodactyla) keep wildlife diseases endemic in natural ecosystems that often interlace with anthropogenic rural and urban environments.

Thus, the main aims of the present study were to:

- 1) Identify endoparasites with zoonotic potential in Estonian domesticated and wildlife animals, mainly in cats and dogs, but also in wildlife species (red fox, golden jackal), (I, II, III, IV);
- 2) Determine endoparasite transmission routes in the urban environment and factors impacting the cycle, (I, II);
- 3) Compare urban and rural endoparasite fauna among dogs and cats, (I, II, III);
- 4) Assess the effect of diet on the infection risk among mammalian predators, and to evaluate the overlap between helminth fauna of domesticated (dog) and wildlife canids (red fox, golden jackal), (III, IV).

2. MATERIAL AND METHODS

2.1. Methods used to study endoparasites of domesticated and wild mammals

2.1.1. Sample collection

In order to study the helminth burden of domesticated and wild carnivores, faecal samples of 657 urban dogs, 290 shelter cats, 84 rural dogs, 131 red foxes, 65 golden jackals, 19 pine martens, 5 American minks, 2 grey wolves, a rural cat and an otter were analysed (**I**, **II**, **III**, **IV**). Fieldworks for sampling were carried out during 2013–2019: (**I**) autumn 2013 till winter 2014, (**II**) August 2015 till October 2016 and (**III** and **IV**) April till June of 2019. The sample collection originated from various towns and rural areas. The urban dog samples ($n = 657$) were collected from smaller towns (Elva, $n = 102$; Kunda, $n = 89$ and Rakvere, $n = 29$) and larger towns (Pärnu, $n = 37$ and Tartu, $n = 400$), (**I**); whereas the rural dog samples ($n = 84$) originated from Western Estonia (Häädemeeste, $n = 13$; Hiiumaa, $n = 3$ and Matsalu National Park, $n = 68$) as well as did the wild mammal samples (Häädemeeste, $n = 31$; Hiiumaa, $n = 15$ and Matsalu National Park, $n = 239$), (**III**, **IV**). The sample data of **I** and **III** were summed up ($n = 741$) to compare findings among rural ($n = 84$) and urban ($n = 657$) dogs. Since shelter cat faecal samples were collected from Tartu Animal Shelter, these samples were further divided into rural ($n = 160$) and urban ($n = 130$) cats according to their original capture location (**II**).

The study design used only non-invasive methods meaning that none of the studied vertebrate (host) animals were handled or their welfare risked. Samples were held at -80°C for a minimum period of seven days to inactivate highly pathogenic zoonotic parasites, for example *Echinococcus* spp. and *Toxocara* spp. that are endemic in Estonia (Moks et al., 2006; 2008; Laurimaa et al., 2015a, b).

2.1.2. Parasite identification and prevalence

Prior to the analysis, samples were thawed, then concentration flotation technique was applied using sodium chloride [$[\text{NaCl}$, specific gravity = 1.2 g/cm^3 (**I–III**) or $\text{NaCl} + \text{glucose}$ solution, specific gravity = $1.2\text{--}1.3 \text{ g/cm}^3$ (**IV**)], (Roepstorff and Nansen 1998). The glucose was added to further increase the detection rate of taeniid ova. All the helminth eggs and oocysts were counted up in the McMaster chamber per helminth taxa (at species, genus or family level), (**I–II**) or up to 100 per taxa in a sample to prevent large time consumption (**III–IV**), therefore, this is considered as relative intensity. The endoparasite prevalence was determined as the proportion of all eggs/oocysts of all eggs in scats. Endoparasite eggs and/or oocysts were determined based on their morphological characteristics (**I–IV**) or genetically (**III**) (Pavlásek and Ryan 2007; Bowman, 2013; Khatat et al., 2016; Dubey, 2018; Tokiwa et al., 2018; Greenwood, 2020).

Molecular methods were applied to distinguish between similar tapeworm (genus *Taeniidae*) and nematode eggs. For this, single eggs were pipetted on microslides into distilled water droplets and subsequently isolated with a pipette into 1.5 ml tubes for genetic analysis. Genomic DNA was extracted from the isolated eggs and a 506 bp (base pair) for Cestoda or 917 bp fragment for Nematoda of mtDNA COI gene were amplified as described in **II**.

2.1.3. Molecular identification of dogs

Scats of different canid species are sometimes difficult to distinguish and to avoid mixing the data of various species, a genetic analysis was conducted to identify predator species (III–IV). Genomic DNA was isolated from scats using the QIAamp Fast DNA Stool Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. A hypervariable fragment of the mitochondrial DNA (mtDNA) control region that enables to distinguish between wolves and dogs in Estonia, was polymerase chain reaction (PCR)-amplified and sequenced as described in Plumer et al. (2018) The same mtDNA fragment allows also distinguishing other canids (IV). In brief, a 351 base-pair (bp) fragment of the mtDNA control region was PCR-amplified using 0.25 pmol of primers Canis1F and Canis3R. The reaction mixture (20 µl in total), contained 2 µl of DNA, 4 µl of 5× Phusion HF buffer, 0.4 mM deoxynucleoside triphosphate (dNTP) and 0.2 µl Phusion HS II polymerase (Thermo Fisher Scientific, Waltham, USA). The following PCR cycling parameters were used: 30 s at 98 °C, then 10 cycles: 10 s at 98 °C, 30 s at 68 °C (with touchdown of –0.8 °C per cycle), 45 s at 72 °C; then 35 cycles: 10 s at 98 °C, 30 s at 60 °C, 45 s at 72 °C, and finally 2 min at 72 °C. PCR products were purified with 1 U of both FastAP and ExoI (Thermo Fisher Scientific). Purified PCR products were sent for sequencing to the core laboratory of the Institute of Genomics at the University of Tartu. Sequences of both DNA chains were aligned with CodonCode Aligner v.5.0.2 (CodonCode Corp.) to produce consensus sequences and corrected using BioEdit v.7.2.5 (Hall, 1999). The length of the final alignment was 245 bp and the dataset was further aligned with homologous wolf and dog sequences (Hindrikson et al., 2012; Plumer et al., 2018), red fox, and golden jackal (III–IV) sequences from Estonia.

2.1.4. Molecular identification of food objects

For the identification of birds, mammals, reptiles and fish, a 303 bp fragment of mtDNA *cox1* gene was PCR-amplified with primers AVS2F and AVS3R as described in **III** and **IV**. PCR reactions were carried out in a total volume of 20 µl with 1x Phusion HF Buffer (Thermo Fisher Scientific), 0.2 mM dNTP, 0.25 µM of each primer and 0.4 U Phusion Hot Start II DNA Polymerase and 2 µl of purified DNA. The PCR mixture was initially denatured at 98 °C for 30 s, followed by 10 touchdown cycles for 10 s at 98 °C, 20 s at 60 °C (reducing the temperature 1 °C per cycle) and 30 s at 72 °C, followed by 30 cycles of 10 s at

98 °C, 20 s at 50 °C and 30 s at 72 °C. In case the PCR was negative due to highly degraded DNA, we performed a second analysis by PCR-amplifying a shorter, 183 bp fragment of mtDNA 12S rRNA gene, using primers Ave12F and Ave12R, described in Oja et al. (2017). PCR products were checked using 2% 1xTAE gel-electrophoresis and visualized under UV radiation using ethidium bromide.

PCR products were purified, sequenced and nucleotide BLAST (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) was used to identify various taxa, such as reptiles, fish and birds in **III** and **IV**.

2.1.5. Morphological analyses of food objects

The morphological analysis of food object is described in Valdmann & Saarma (2020). Shortly, faecal samples were processed according to standard laboratory procedures (Reynolds & Aebischer, 1991). Non-mammal remains (e.g., birds) recovered in predator scats were identified in comparison with reference materials. Mammal remains were identified by examining the cuticular pattern and the medulla of the hairs using reference manuals (Teerink, 1991; Toth, 2017) and hairs collected from hunted animals (**III**, **IV**).

2.1.6. Spatial analyses

The spatial analyses included descriptive maps created with the Free & Open Source QGIS (3.24). The aim was to visualize the geographical locations of predator scats and to measure the average distance between private houses and the collected scat samples (**III**, **IV**). Further, the buffer distance around faecal samples was considered as the average free-ranging or straying area of mammalian predators from detached houses. Another buffer was generated in **IV** by adding together the first buffer with the infected faecal samples layer situated inside the buffer zone to count detached houses in the potential hazard zone. The map layers originated from public WMS services (Land Board, 2022).

2.1.7. Statistical analyses

Proportions were compared in **II–IV** using Chi-squared tests of independence (PROC FREQ) to determine independent variables associated with overall (co)infection and single taxa (species, genus, family) prevalence. If one or more cells in the 2 X 2 contingency tables had expected values of less than 5, Fisher's exact test was used. The non-parametric Mann-Whitney U test was used to compare the mean parasite richness between three larger canid (red fox, golden jackal, dog) groups (**IV**). Chi-squared and non-parametric tests were performed using software of SAS Studio v9.04 (SAS Institute, Cary NC, 2021).

In general, all statistical models contained dependent (response) variables determined as (co)infection risk (0 – uninfected; 1 = infected) or infection intensity (the sum of counted ova/oocysts), (**I–IV**). The same aforementioned analogy

applied for a specific endoparasite taxa (species, genus, family) infection or intensity (**II–IV**). Various predictor variables were formed to identify factors impacting infection intensity and co(infections) with endoparasites. Generalized linear mixed models (**I**) or generalized linear models (package ‘glmmTMB’, Brooks et al., 2017 or ‘logistf’, Heinze & Ploner, 2018) with a binomial error distribution were used for evaluating overall and single endoparasite prevalence (**II–IV**). Models with a negative binomial error distribution were used for assessing the factors influencing endoparasite intensity (**I–IV**). Models were compared using the Akaike’s information criterion corrected for small samples (AICc) (Burnham & Anderson, 2004). Package “MuMIn” (Barton, 2019) was used for conducting model selection and model averaging. Only models with the highest Akaike weight w_i (AIC), ($\Delta AICc < 2$) were described as the model with the highest Akaike weight provides a continuous measure of strength of evidence. It is especially important to assess the weight of evidence in favor of the best model when a binary decision is made and the other candidate models (with higher AIC values) are simply discarded (Wagenmakers et al., 2004). Furthermore, the weights (w_i) of the same factors presented in one model set were summed for calculating the relative variable importance (RVI), (**I, III, IV**). All statistical modeling was performed in R (R Development Core Team, 2022).

To estimate the infection risk and intensity of urban dogs (**I**), the following independent variables: ‘excrement size’ (excrement were classified according to their diameter: <15 mm as ‘small’, 15–20 mm ‘medium’, >20 mm as ‘large’), ‘town size’ (small towns – less than 20,000 inhabitants or large towns – more than 40,000 inhabitants), ‘housing type’ (detached individual houses or densely populated apartment-houses), ‘season’ (autumn, winter, spring, summer) and ‘potential hazard zone’ (sidewalk or potential hazard zones consisting of green areas and recreational zones near public playgrounds, schools or nurseries). The random variable included location (town).

To model the conjunction between (co)infection prevalence and intensity among shelter cats (**II**), a set of explanatory variables were included: age (young or adult), location (rural or urban) and the time spent in the animal shelter (1–14 days, ≥ 15 days), (see further details of variables in Table 1 in **II**). Furthermore, a distinct group of potentially directly transmittable zoonotic endoparasites was formed consisting of *T. gondii*/*H. hammondi*, *Cryptosporidium* spp., *Giardia* sp., *Cystoisospora* spp., *T. cati* and *E. aerophilus* (**II**, Online Resource 4).

Last but not least, the (co)infection prevalence and intensity among predators, mainly dogs, red foxes and golden jackals was analysed in Western Estonian rural areas (**III, IV**). The independent variable (food object) was divided into five categorical variables: rodent, game, bird, dog food and plant material. Aside from the food objects, urban dog (co)infection prevalence data (**I**) was compared to rural dog (co)infection prevalence (**II**) to compare infection risk of endoparasites in these areas.

To measure the overlap of helminths between various host species (dog, red fox and golden jackal), the Pianka’s Index (Pianka, 1973) was calculated (0 – no overlap, 1 – total overlap), (**IV**).

3. RESULTS

3.1. Endoparasites of urban and rural animals and possible transmission patterns

3.1.1. General zoonotic endoparasite fauna

In rural areas (**III**, **IV**), out of the 315 genetically identified predator scat samples 84 belonged to dogs, 131 to red foxes, 65 to golden jackals, 19 to pine martens, 7 to raccoon dogs, 5 to American minks, 2 to grey wolves, 1 to a cat and 1 to an otter. Of these hosts six helminth taxa (Taeniidae, 265; *Eucoleus* spp./*Trichuris* spp., 158; *U. stenocephala*, 64; *T. canis*, 28; *T. leonina*, 4 and *T. cati*, 1) were determined with a total frequency of 520 helminth specimen.

In total, 657 and 84 faecal samples of urban and rural dog were analysed, respectively (**I**; **III**). Urban dog faecal samples included five endoparasite species or genera with an overall prevalence of nearly 10% (**I**; Table 1). The most abundant endoparasites among urban dogs were *U. stenocephala* (3.5%) and *Toxocara* spp. (3.4%). In comparison with urban dogs, the overall helminth prevalence differed nearly nine times between urban and rural dogs (9.8% and 87%, respectively), (**I**, **III**). However, the rural dog scat samples contained in total 116 helminth specimen: Taeniidae (65.5%), followed by *Trichuris* spp./*Eucoleus* spp. (15.5%), *U. stenocephala* (14.7%) and *T. canis* (4.3%), (**III**, Fig. 2). The general parasitological examination of shelter cats indicated that nearly half (47.6%; 138/290) were infected with endoparasites (**II**, Table 3). The highest prevalence rate was assessed for *T. cati* (36.6%), followed by *Cystoisospora* spp. (12.4%), Taeniidae (4.1%), *T. gondii*/*H. hammondi* (3.4%), *E. aerophilus* (2.1%), *Cryptosporidium* spp. (2.1%), *Ancylostoma* sp. (0.7%) and *Giardia* sp. (0.7%) (**II**, Fig. 1). Genetic analyses revealed two potentially zoonotic helminth species among shelter cats, namely *Ancylostoma tubaeforme* and *Hydatigera taeniaeformis*.

Among wild predators, 92.4% (121/131) of red fox environmental scat samples were infected with endoparasites. The most prevalent infection included *Eucoleus* spp./*Trichuris* spp. (80.2%; 105/131), followed by Taeniidae (76.3%; 100/131) and *U. stenocephala* (24/131, 18.3%) (**IV**, Table 1). The golden jackal scat samples had comparably high proportion of infected scats (90.8%; 59/65) with the red fox scats containing most frequently eggs of Taeniidae (87.7%; 57/65), followed by *U. stenocephala* (18/65; 27.7%) and *Eucoleus* spp./*Trichuris* spp. (21.5%; 14/65), (**IV**, Table 1). The niche overlap of helminth taxa revealed highest result for golden jackals and dog (0.99) and slightly lower results were found between red foxes and golden jackals (0.84) as well as between dogs and red foxes (0.84), (**IV**).

3.1.2. Rural and urban zoonotic endoparasite (co)infections among domesticated and wild animals

Considering the non-invasive coprological study methods applied (I–IV), it was not possible to detect all endoparasites. The main focus was on determining helminth (tape- and roundworm) parasite taxa at species, genus or at least family level. Thus, the detected species richness might be an underestimation of the real species abundance. In III and IV genetic methods were applied to determine helminth species but most likely due to high UV-radiation in spring season the ova were too degraded for DNA isolation compared to II where endoparasite eggs were isolated from fresh faecal material.

Coinfections in domesticated animals were significantly lower among urban cats ($\beta_{\text{URBAN}} = -1.3$; SE = 0.4; P = 0.0005) and dogs (P < 0.0001) than among rural cats and dogs, (II, III). Rural dogs (73/741; 9.9%) had significantly higher (P < 0.0001) (co)infection prevalence with biohelminths (Taeniidae), while urban dogs were significantly (co)infected with geohelminths (P < 0.0001), mainly with zoonotic *U. stenocephala* and with *Toxocara* spp. (P = 0.5), (III, Fig. 4). Moreover, rural dogs preying on rodents had significantly (3.7 times) higher odds to be coinfecting than rural dogs who had not preyed on rodents ($\beta_{\text{RODENT}} = 1.3$; SE = 0.6; P = 0.02). The model also indicated a 63% of reduction in rural dogs' coinfection with helminths, if they consumed dog food ($\beta_{\text{DOGFOOD}} = -1.0$; SE = 0.6; P = 0.1), (III).

Furthermore, shelter cats had also significant difference in infection prevalence between rural and urban cats (P = 0.0006). Namely, over half of rural cats (56.7%; 91/160) were infected with endoparasites compared to the 1/3 of infected urban cats (36.2%; 47/130), (II, Table 3). In resemblance with dogs, urban cats had significantly lower endoparasite infection prevalence with Taeniidae ($\beta_{\text{URBAN}} = -2.1$; SE = 1.1, P = 0.04) but also with *T. cati* ($\beta_{\text{URBAN}} = -1.0$; SE = 0.3; P < 0.001) and overall helminths ($\beta_{\text{URBAN}} = -1.0$; SE = 0.3; P < 0.001) than rural cats (II, Table 2). Rural cats in quarantine up to 14 days had significantly higher endoparasite infection prevalence with directly transmittable zoonotic endoparasites than urban cats in quarantine ($\chi^2 = 5.5$; P = 0.01), (in II Online Resource 4).

Of the wild predators, the highest coinfection prevalence (80.2%) was found among red foxes being the most coinfecting with Taeniidae and *Eucoleus* spp./*Trichuris* spp. (62.9%) (IV; Table 2). The golden jackal had much lower coinfection prevalence (46.2%) of which the most prominent coinfection occurred between Taeniidae and *U. stenocephala* (36.7%). Furthermore, diet affects the coinfection prevalence with multiple helminths among predators, preying on rodents increased the risk of coinfection with multiple helminth taxa 2.5 times than not preying on rodents ($\beta_{\text{RODENT}} = 0.9$; SE = 0.3; P < 0.001), (IV).

3.1.3. Main infection models and main zoonotic endoparasite transmission patterns and dynamics among domesticated pets

Main infection prevalence models revealed lower infection with endoparasites among larger urban dogs ($\beta_{\text{Large}} = -1.0$, SE = 0.4) than among small dogs. Depending on the housing type, higher endoparasite prevalence was predicted in apartment-house districts ($\beta_{\text{ApartmentHouse}} = 0.9$, SE = 0.3) than in private house regions. The infection gradient between large and small towns implied higher endoparasite infection prevalence ($\beta_{\text{SmallTown}} = 0.8$; SE = 0.3) as well as intensity ($\beta_{\text{SmallTown}} = 1.5$, SE = 0.8) towards smaller towns (I). However, while comparing urban areas with rural areas, higher endoparasite infection prevalence shifts from larger and smaller towns towards rural areas where helminth prevalence between urban and rural dogs differs approximately 9 times (I, III) reaching ~ 90% in rural areas (III, IV). Similar findings were acquired for zoonotic roundworms (*Toxocara* spp., *U. stenocephala* and *Capillaria* spp.) infections with one exception, meaning that urban dogs have higher infection prevalence in potential hazard zones than on streets ($\beta_{\text{PotentialHazardZone}} = 0.6$; SE = 0.3). Also, spatial analyses confirmed for rural areas that at least 160 private houses were situated in the buffer zone of ≤ 578 m in which the average distance of an infected environmental scat to a private reached as far as 59 meters (IV). Analogous patterns apply for infection intensity models with endoparasites and roundworms. Infection intensity models imply for both groups (endoparasites and roundworms) higher infection intensity in apartment-house districts than near detached houses ($\beta_{\text{ApartmentHouse}} = 2.3$; SE = 0.7). Large-sized dogs tend to have lesser intensity with both parasite groups than small-sized dogs ($\beta_{\text{Large}} = -1.5$; SE = 0.8). Different seasons have an important impact on the endoparasite infection dynamics, mainly the infection prevalence and intensity increased in spring and autumn but decreased in summer season compared to winter season (IV).

Age of shelter cats determined the infection risk and intensity with endoparasites. Juvenile cats had significantly higher infection prevalence with helminths ($\beta_{\text{YOUNG}} = 0.5$; SE = 0.3; P = 0.04) as well as 2.7 times higher infection intensity ($\beta_{\text{YOUNG}} = 1.0$; SE = 0.4; P = 0.02) and with zoonotic *T. cati* ($\beta_{\text{YOUNG}} = 0.7$; SE = 0.3; P = 0.01) than adult cats. On the other hand, compared to adult cats, young ones had significantly lower infection prevalence with *T. gondii/H. hammondi* ($\beta_{\text{YOUNG}} = -2.8$; SE = 1.5; P = 0.003) (II, Table 2). In quarantine cats, some endoparasite [*Cystoisospora* spp. ($\beta_{\text{QUARANTINE}} = -1.3$; SE = 0.4; P = 0.001)] and with total protozoa ($\beta_{\text{QUARANTINE}} = -0.8$; SE = 0.3; P = 0.01)] infection prevalence decreased, but the opposite effect applied for cats ready to be adopted. On the contrary, other endoparasites (*Cryptosporidium* spp. [$\beta_{\text{QUARANTINE}} = 2.3$; SE = 1.5; P = 0.03] and with *E. aerophilus* ($\beta_{\text{QUARANTINE}} = 2.3$; SE = 1.4; P = 0.03)] were more common in quarantine cats and less found among cats ready for adoption (see in II Table 2).

Diet preferences also shape the endoparasite fauna among rural predators. Indeed, preying on various intermediate, reservoir/paratenic hosts increases significantly infection risk with helminth taxa (III, IV). When predators preyed

on reptiles or rodents, the infection risk with *Eucoleus* spp./*Trichuris* spp. increased 5.5 ($\beta_{\text{REPTILE}} = 1.7$; SE = 0.7; $P < 0.01$) and 3 ($\beta_{\text{RODENT}} = 1.1$; SE = 0.3; $P < 0.0001$) times, respectively (**IV**). Among golden jackals, the infection prevalence ($\beta_{\text{RODENT}} = 2.6$; SE = 0.7; $P < 0.001$) and intensity ($\beta_{\text{RODENT}} = 4.1$; SE = 1.3; $P < 0.001$), ($\beta_{\text{GAME}} = 2.6$; SE = 1.2; $P = 0.03$) with helminths *Eucoleus* spp./*Trichuris* spp. increased significantly, if preying on rodents or game. Notably, red foxes had up to 4 times higher odds to be infected with *T. canis*, if they feed on plant material ($\beta_{\text{PLANT}} = 1.4$; SE = 0.6; $P = 0.02$), (**IV**).

4. DISCUSSION

4.1. Endoparasites with zoonotic potential

Our results indicate clearly that domesticated animals, dogs and cats, as well as sympatric wildlife predators distribute endoparasites with zoonotic potential (I–IV). It has been shown that dogs can transmit over 60 zoonotic parasites infecting humans (Macpherson et al., 2013), originating from wildlife species like red foxes and golden jackals (Gherman and Mihalca, 2017). Over a third of examined shelter cats in the II study (36.6%) excreted parasitic stages of zoonotic *Toxocara cati* which is one of the most prevalent zoonotic gastrointestinal helminth worldwide (Gracenea et al., 2009; Becker et al., 2012; Loftin et al., 2019; Tull et al., 2021), (Table 1), causing toxocariasis in humans, mainly in young children (Despommier, 2003). Also, helminths that only in rare cases have infected humans such as *Hydatigera taeniaeformis*, *Ancylostoma tubaeforme* and *Eucoleus aerophilus* were found. It has been suspected, that their zoonotic potential is probably not well studied or known (Rossin et al., 2004; Altreuther et al., 2005; Lalošević et al., 2008), (Table 1). Genetic analysis confirmed the presence of *H. taeniaeformis* (II), which can cause severe illness in humans (Ekanayake et al., 1999), (Table 1). Formerly, Valdmann et al. (2004) have demonstrated infections with *H. taeniaeformis* (3%) in Estonian Eurasian lynx. The tapeworm *H. taeniaeformis* has a cosmopolitan distribution and it uses felines as definitive hosts. The findings of the II study imply that high infection rates of *T. cati*, *A. tubaeforme*, *E. aerophilus* and *H. taeniaeformis* in cats, originating from various areas, especially from rural areas, indicate coexisting sylvatic and synanthropic cycles, and imply a simple transmission route of zoonotic parasites between sympatric intermediate and definitive or reservoir hosts in the environment. Thus, domestic cats, rather than wild carnivores, could pose a greater risk for human's health because of their close contacts with people. The lack of accurate diagnostics or infrequent diagnosis of the aforementioned endoparasites may result in higher numbers of infected humans. Hence, health workers and officials need to consider the possibility that stray cats distribute zoonotic endoparasites that are a threat to human health.

Table 1. Main cat endoparasites in studies in Europe and in the US.

Method	Switzerland (Zotoller et al., 2019)	Germany (Becker et al., 2012)	Romania (Mircean et al., 2010)	US (Wyrosdick et al., 2017)	Greece (Kostopoulou et al., 2017)	Estonia (Tull et al., 2021)
Sample size	scat+morphology+d uplex PCR n = 664	scat+morphology+ antigen n = 837	scat+ morphology n = 414	scat+ morphology n = 76	scat+morphology+ antigen+PCR n = 264	scat+morphology+P CR n = 290
Cat status	stray, shelter, owned	shelter	household	shelter	shelter, household	shelter, rural, urban
Cestoda						
<i>Taenia</i> -type*	11.1% (74/n)	2.0%			0.8%	2.4% (7/n)
<i>Hydatigera taeniaeformis</i> *			2.7% (11/n)			1.7% (5/n)
<i>Dipylidium caninum</i> *	0.6% (4/n)		0.2% (1/n)			
<i>Dipyllobothrium latum</i> *	0.2% (1/n)					
<i>Mesocostoides</i> spp.*				1.3% (1/n)		
Nematoda						
<i>Toxocara cati</i> *	18.5% (123/n)	27.1%	20.3% (84/n)	6.6% (5/n)	8.3%	36.6% (106/n)
<i>Capillaria</i> sp.	4.7% (31/n)	5.0%			4.2%	
<i>Eucoleus aerophilus</i> *			3.1% (13/n)			2.1% (6/n)
<i>Ancylostoma tubaeforme</i> *						0.3% (1/n)
<i>Ancylostoma</i> spp.*			10.1% (42/n)	27.6% (21/n)		0.3% (1/n)
<i>Aelurostrongylus abstrusus</i>	2.3% (15/n)	1.0%	5.6% (23/n)			

	Switzerland (Zotzler et al., 2019)	Germany (Becker et al., 2012)	Romania (Mircean et al., 2010)	US (Wyrosdick et al., 2017)	Greece (Kostopoulou et al., 2017)	Estonia (Tull et al., 2021)
Hookworms*	1.1% (7/n)	1.1%			7.6%	
<i>Strongyloides</i> spp.*			3.4% (14/n)			
<i>Anchotheca putorii</i>				1.3% (1/n)		
<i>Spirometra</i> sp.*				7.9% (6/n)		
Protozoa						
<i>Cryptosporidium</i> spp.*				6.6% (5/n)	6.8%	2.1% (6/n)
<i>Giardia</i> sp.*	0.8% (5/n)	0.7%; 6.8 (cysts vs antigen)	0.7% (3/n) D	3.9% (3/n)	9.5%	0.7% (2/n)
<i>Cystoisospora</i> sp./ <i>Isospora</i> sp.	8.1% (54)	7.5%	5.3% (22/n) IF; 8.9% (37/n) IR	1.3% (1/n) CF; 13.2% (10/n) CR		12.4% (36/n)
<i>Toxoplasma gondii</i> */ <i>Hammondia hammondi</i>	0.6% (4/n)	0.1%	1.2% (5/n)		0.4%	3.4% (10/n)
<i>H. hammondi</i>	0.5% (3/n)					
<i>Toxoplasma</i> -type*	0.3% (2)					
<i>Sarcocystis</i> sp.*	0.2% (1)		1.0% (4/n)	1.3% (1/n)		
overall prevalence ^e	31.3% (208/n)	33.6% (281/n)	34.3% (142/n)	83.0%	20.5%	47.6% (138/n)

* – potentially zoonotic endoparasites; ^e – including all parasites in the study; ^D – *Giardia doudeinalis*; ^{IF} – *Isospora felis*; ^{IR} – *Isospora rivolta*; ^{CF} – *Cystoisospora felis*; ^{CR} – *Cystoisospora rivolta*

Among dogs, the difference between rural and urban dog's endoparasite prevalence differed significantly, nearly 9 times (87.0% vs 9.8%, respectively; **III**, **IV**), (Table 2). In Estonia, stray dogs are uncommon, whereas free-ranging dogs are abundant in rural areas. In larger towns, dog owners are obliged to remove pet excrements from public areas, while it is uncommon to remove faecal scats in rural areas. Faecal material collected in public areas is, thus, a useful tool for determining environmental contamination with endoparasites, often with zoonotic potential. In **I** it was revealed that the most common zoonotic helminths in urban settlements are geohelminths, namely *U. stenocephala* and *Toxocara* spp. (Table 2), which was also demonstrated by Talvik et al. (2006) over a decade ago. In the study **III**, a very low prevalence of *T. canis* among rural dogs was found, although previous studies have shown that *T. canis* was one of the most prevalent helminth species in rural areas in Hungary and the Slovak Republic (Fok et al., 2001; Antolová et al., 2004; Papajova et al., 2014). The low prevalence of *T. canis* may be likely due to the high prevalence of taeniid species that have taken over or displaced *T. canis* in competition for nutrients in the intestine.

The most prevalent endoparasites among rural dog and cats were biohelminths of family Taeniidae, which consists of zoonotic tapeworms (e. g. *Echinococcus* spp., *Taenia* spp.), in lieu of geohelminths in urban areas (**II–IV**). It is known that most of the taeniid species that occur in dogs have zoonotic potential (e. g., *Dipylidium caninum*, *Dibothriocephalus latus*, *Taenia* spp. and *Echinococcus* spp.). In the case of rural cats, they had significantly higher infection with *T. cati* and Taeniidae than urban cats (Table 2). In study **III**, a higher prevalence of taeniids was revealed than in most other studies in Europe (Dubná et al., 2007; Soriano et al., 2010; Schurer et al., 2013; Papajová et al., 2014; Tull et al., 2020 and 2021), (Table 2). The high prevalence (65.5%) of taeniids may result from coastal effect where more opportunities are presented to prey on raw fish. Fish remnants or raw fish can be fed to rural dogs by humans or can be found in coastal areas during roaming. The occurrence of *D. latus* in grizzly and black bears and in wolves has been linked to seasonality when hosts' diet shifts to salmon (Frechette & Rau, 1978; Gau et al., 1999; Bryan et al., 2012).

Table 2. Potentially zoonotic endoparasites in dogs in European studies.

Parasite	Czech Republic (Dubna et al. 2007)	Portugal (Cardoso et al. 2013)	Slovak Republic (Papajova et al. 2014)	Hungary (Fok et al. 2001)	Spain (Regidor-Cerrillo et al. 2020)	Greece (Kostopoulou et al. 2017)	Estonia (Tull et al. 2020 and 2021)
Method	rural urban scat+ morphology	rural urban scat+ morphology+ PCR	rural urban scat+ morphology	rural urban scat+ morphology	rural stray scat+ morphology+ PCR	shelter house-hold shepherd/rural scat+ morphology+ antigen+PCR	rural urban scat+ morphology
Sample size	n = 540 n = 3780	n = 301	n = 70 n = 508	n = 206 n = 284	n = 131 n = 102	n = 278 n = 529	n = 84 n = 657
Cestoda							
<i>Taenia</i> -type*	3.5% 1.0%	1.7%	11.4% 3.0%	2.4% 2.8%	3.0%	6.9%	65.5% 0.5%
<i>Dipylidium caninum</i> *	1.3% 0.7%	0.3%	0.0% 0.2%	1.0% 0.4%			
<i>Spirometra</i> sp.							
Nematoda							
<i>Toxocara</i> spp.*	13.7% 6.2%	8.0%	12.9% 13.8%	30.1% 24.3%	6.1% 18.6%	5.1% 8.3%	4.3% 3.4%
<i>Toxascaris</i> sp.	1.7% 0.9%		0.0% 4.1%	0.0% 2.1%	2.3% 13.7%	0.9% 2.8%	
<i>Trichuris</i> sp.*	1.7% 1.1%	29.9%	0.0% 10.0% ^{TV}	23.3% ^{TV} 20.4% ^{TV}	31.3% 40.2%		15.5% ^k 15.5% ^k
<i>Trichuris</i> spp./ <i>Eucoleus</i> spp.*	0.6%		1.2%	12.9%			
<i>Capillaria</i> spp.*	0.6%	0.7%	0.0% 1.2%	7.3% 0.0%	29.7% 43.1%	0.7% ^f 1.9% ^f	0.3%
<i>Ancylostomatidae</i> /hookworm*		40.9%	8.6% 9.1%	13.1% 8.1%		9.7% 5.3%	

Parasite	Czech Republic (Dubna et al. 2007)	Portugal (Cardoso et al. 2013)	Slovak Republic (Papajova et al. 2014)	Hungary (Fok et al. 2001)	Spain (Regidor-Cerrillo et al. 2020)	Greece (Kostopoulou et al. 2017)	Estonia (Tull et al. 2020 and 2021)
<i>Uncinaria</i> sp.*	0.9%						14.7%
<i>Ancylostoma</i> sp.*	0.4%						3.5%
<i>Spirocerca</i>	0.2%						
Protozoa							
<i>Cystoisospora</i> spp./ <i>Isospora</i> spp.	8.0%	4.0%		3.4%	3.8%	7.6%	8.3%
<i>Cryptosporidium</i> spp.*	1.4%				0.8%	14.7%	1.9%
<i>Sarcocystis</i> sp.*	0.6%						2.1%
<i>Neospora</i> */ <i>Hammondia</i>	0.5%						
<i>Giardia</i> spp.*	0.1%				2.3%	54.3%	12.9%
<i>Coccidia</i> *			0.0%				
overall prevalence	41.7%	58.8%	31.4%	56.3%	58.8%	62.9%	87.0%
	17.6%	2.2%	29.7%	50.7%	72.5%	23.8%	9.8%

* – zoonotic or potentially zoonotic parasites; f – family Capillariidae; TV – *Trichuris vulpis*; k – no differentiation in the study

Over the recent years, toxocarasis has gained a lot of attention, while this disease was listed as one of the five most neglected parasitic infections according by the Centers for Disease Control and Prevention (CDC) in the United States. In Estonia, Remm & Remm (2014) demonstrated that dog owners have a significantly higher risk for infection with *Toxocara* spp. Last but not least, a study by Lassen et al. (2016) found higher *T. canis* seroprevalence in animal caretakers than in the general population. The epidemiology of *T. canis* is also largely affected by the age of the host. The highest infection rates with *T. canis* were found among puppies of four weeks old, but the infection decreased in older dogs (Barutzki & Schaper, 2013). The results in **I** stated smaller dogs to have more infections with endoparasites than larger dogs, which is in accordance with previous studies, where endoparasite transmission by puppies is described (Fontanarrosa et al., 2006; Barutzki & Schaper, 2011). However, small-sized dogs may also pose a serious hazard in towns by contaminating the environment with endoparasites as an infected dog with *T. canis* can shed 10 000 eggs in each gram of faecal material (Ahmad et al., 2011). In the last decade, small dogs have become increasingly popular pets in the US, and the situation appears similar in Estonia (Ferdman, 2015; Teng et al., 2016; Tull et al., 2020). Although it was not possible to differentiate between puppies and small dogs (**I**), the result is alarming, as both puppies and small dogs are highly attractive to children and probably have a higher degree of physical contact with humans (e.g. face licking, sharing bed with owner, petting etc.) than larger dogs. Elderly people may also prefer small dogs, as they are more affordable and easier to handle than medium- or large-sized dogs. Thus, it is likely that people underestimate the risk of disease transmission and zoonotic infections associated with small dogs (**I**).

In addition to helminths, in **I** and **II**, protozoan species were also determined with morphological methods. However, thawing of the samples could have had reduced the detection rate of oocysts. Additionally, the small dimensions of oocysts or intermittent stages could have impaired the detection rate of protozoan parasites by morphology (McGlade et al., 2003). As it was not possible to identify all endoparasite taxa at species level, it is likely that some cats and dogs had infections with zoonotic *Cryptosporidium parvum*, *Giardia duodenalis* assemblage A or *Cryptosporidium felis/canis* (Cacciò et al., 2002; Tzannes et al., 2008; Heyworth, 2016). Although the prevalence of *Giardia* sp., *Cryptosporidium* spp. and *Cystoisospora* spp. was not high, these parasites can rapidly spread during dogs walking on the same areas, as shown by Bugg et al. (1999) in Australia, where dogs only treated with anthelmintics targeting roundworms were infected by *Giardia* sp. Therefore, further studies are needed in order to determine protozoan infections at species level. Although, *Cystoisospora* spp. do not have zoonotic potential, they can cause gastrointestinal diseases in cats and dogs (Palmer et al., 2008). In future studies, it is crucial to distinguish between zoonotic parasite taxa at species level to estimate their composition in various hosts (dogs, cats and wildlife predators) and how predator-prey dynamics impact the distribution and infection routes of these zoonotic helminths.

4.2. Main zoonotic endoparasite transmission patterns and dynamics among domesticated pets

The infection gradient with endoparasites in shifting from large towns to smaller towns and from smaller towns to rural areas (I, III, IV). Despite of the above pattern, there have evolved evident continuous endoparasite transmission routes (infection hotspots) in towns as indicated by I and II. In towns, contamination with zoonotic parasites is concentrated in areas of high human density, in areas dominated by multi-stored apartment blocks and in potentially hazardous zones, including playgrounds, recreational areas near schools/nurseries, whereas adopted shelter cats can act as zoonotic disease distributors. The study I demonstrated that parasite infection prevalence is higher in smaller than in larger towns. There may be restricted availability of areas in smaller towns that are suitable for dog walking, and, conversely, easier access to rural trails. In addition, opportunistic mesocarnivores, like the red fox, raccoon dog, pine marten and badger (*Meles meles*), may occur more frequently in and around smaller towns, presenting a potential source of infection with zoonotic parasites (Deplazes et al., 2004; Bateman & Fleming, 2012). Moreover, the II and III study suggests that rural areas are in comparison with urban areas by far more contaminated with helminths and the infection risk among dogs is nine times higher in rural areas than in towns. Free-ranging rural dogs and cats preying on various reservoir, paratenic or intermediate hosts boost their infection risk with parasites, including zoonotic. Rural cats had more coinfections with multiple endoparasites than urban cats, which is related to their ability to roam freely, encountering more contacts with other feral or free-ranging cats, and thus facilitating parasite transmission between them. Rural areas also offer a wide variety of hosts to prey on. Further, rural dogs preying on rodents had higher coinfection risk with helminths than rural dogs consuming other food objects. In rural and suburban areas, rodents such as *Arvicola terrestris*, *Microtus arvalis*, *Myodes glareolus* and *Apodemus agrarius* can be paratenic or intermediate hosts for *E. multilocularis* and *Toxocara* spp. (Antolová et al., 2004; Reperant et al., 2009). Another serious problem displayed is access to raw meat and offal of domestic and wild animals in rural areas. It is known, for example, that dogs scavenging internal organs of wild game infected with *E. granulosus s.l.* can become a direct source of infection to humans and domestic animals (Baneth et al., 2016). What is more, contamination of pastures or coastal meadows with scats of infected wild carnivores, as implied in IV, also results in *E. granulosus s.l.* infection of domestic ruminants. The establishment of a pastoral cycle may then result from the feeding of uncooked offal from these domestic animals to dogs (Bowman, 2013). In Estonia *E. granulosus s.l.* has been found in dogs (Laurimaa et al., 2015b), grey wolves (Moks et al., 2006), but also in moose (*Alces alces*; Moks et al., 2008) and roe deer (*Capreolus capreolus*; Marcinkutė et al., 2015). It is therefore important to highlight the high possibility that rural dogs may be infected with zoonotic *E. granulosus s.l.*

A second infection route of zoonotic endoparasites includes shelter cats in quarantine and young kittens (<1 year), (II). So, in the II study, it was discovered that the composition of endoparasite species as well as infection trend was different for quarantine (1–14 days in shelter) and cats ready for adoption (≥15 days in the shelter). During the stay in the shelter, some parasites (*Cystoisospora* spp. and total protozoan species) flourished, meaning that their infection prevalence was significantly higher among cats ready for adoption but decreased among quarantine cats. The opposite effect applied to infection prevalence with *Cryptosporidium* spp. and *E. aerophilus*, namely these parasites were more common in quarantine cats than in the ready for adoption

group. Another seriously infected cat group included juvenile cats who had significantly higher endoparasite infection prevalence with zoonotic *T. cati* and nearly three times higher infection intensity with endoparasites than adult cats. The II study suggests that more attention should be paid to infection with protozoa and *T. cati* because infected cats may pose a threat not only to other shelter cats, but also to the shelter staff and new owners. Some shelter cats may experience stress-induced appetite loss and may not consume enough anthelmintics that is mixed with food, facilitating endoparasite spread in the shelter. Thus, animal shelters with high endoparasite prevalence and intensity should re-evaluate their parasite control procedures (Spain et al., 2001; Villeneuve et al., 2015; Blasco et al., 2017; Zottler et al., 2019), (Table 1). Faecal samples should be taken frequently from quarantine cats and measures undertaken for adequate isolation, environmental hygiene and, in indicated cases, treatment to prevent parasite spread (ESCCAP, 2018).

The potential hazard zones formulated in study I included recreational sites and green areas near schools and nurseries, functioning as infection hotspots. These are mainly sites where people tend to walk their dogs, resulting in higher environmental contamination and an increased amount of contacts between dogs as well as with overlapping wild canid scats. Thus, the infection cycle may be ‘closed’ in the apartment-house region. Poor excrement-removal practice also supports higher endoparasite prevalence in soil. The finding is important from an epidemiological perspective and is consistent with theoretical models, linking host density to the opportunity of a parasite to invade a population of hosts (Morand & Poulin, 1998). Dubná et al. (2007) also suggested that the occurrence of *Toxocara* eggs was high in public parks of urban areas because of the growing dog population and due to the relatively small dog walking areas. Moreover, the overlap between urbanized red foxes and dog scats can cause direct (zoonotic) endoparasite transmission, e.g. Gecchele et al. (2020) showed in UK that areas with higher greenspace ratios contained more red fox scats, and indeed, these scats were more likely infected with endoparasites, as well as had more parasite richness. Contradictory to the results of Talvik et al. (2006) who found more endoparasites near detached houses, in the study I, higher endoparasite prevalence and intensity dominated near apartment blocks. It is likely that dogs living in detached houses are kept in yards, with less access to streets, compared to dogs from apartments that are walked more widely by their owners at least once a day. As the density of humans and pets is probably highest in areas dominated by apartment blocks, it is also likely that endoparasites are also concentrated in the green areas surrounding apartment blocks.

4.3. Other endoparasites of mammalian predators and possible host-parasite link with diet

Scats collected during field work provide little background information about the investigated hosts. Previously, only excrement location has been used to identify risk factors for parasite transmission in different areas (Antolová et al., 2004; Dubná et al., 2007; Dado et al., 2012). However, if genetic methods are applied, much more information can be obtained about host species and their dietary habits as well as parasites (III, IV). In studies III and IV genetic methods were used to distinguish between various mammal predators, also their food objects were determined by genetic as well as morphological methods. The most abundant canids were according to genetic analyses the red fox, golden jackal and dog.

In IV, a very high endoparasite overlap between golden jackals and rural dogs (99%) was revealed. Moreover, all three canid species had very high infection prevalence, around or more than 90%. The environmental scat samples of red foxes, golden jackals and dogs were highly parasitized with Taeniidae, followed by *Eucoleus* spp./*Trichuris* spp., *U. stenocephala* and *T. canis* (Table 3 and Table 4). Furthermore, households, situated near to the infected environmental scats were mapped, and a total of 160 private houses (probably even more, since all living land areas cannot be found in the register) located on average up to 59 m from an infected scat. These findings are alarming due to the fact that rural dogs provide a direct transmission link of zoonotic helminths from sympatric wildlife predators to dogs and from dogs to humans, meaning that the sylvatic endoparasite cycle is deeply interlaced with synanthropic endoparasite cycle. Therefore, these findings are important from the aspect of One Health, providing viable evidence that rural areas are under continuous helminth contamination and relevant healthcare institutions should focus more on rural areas to diagnose helminth infections among companion animals (especially dogs) and in general human population. Otherwise, these diseases remain neglected, posing health risks for children.

Several infection prevalence models indicated, that among predators, preying on paratenic or intermediate hosts (rodents, reptiles) increases significantly the infection risk with helminths, mainly with *Eucoleus* spp./*Trichuris* spp. (IV). The latter are geohelminths and mammalian predators become infected by ingesting eggs of *E. aerophilus* or *T. vulpis* from the environment (attached to plants or distributed in water and soil), but infection may also occur when consuming invertebrates (earthworms), Norway rats (*Rattus norvegicus*) or reptiles (Rataj et al., 2011; Rothenburger et al., 2014; Traversa et al., 2014; Wolf et al., 2014). Similarly, in dogs (III), the infection intensity was higher among rural dogs preying on rodents and game. However, feeding dogs dog food, decreased the infection risk with helminths, especially with *Eucoleus* spp./*Trichuris* spp. In paper IV, a surprising relationship between consumed plant material and infection with *T. canis* among red foxes indicated that infection prevalence with *T. canis* increased when diet consisted of plants, referring to potential self-medicating behaviour as suggested also for raccoon dogs by Laurimaa et al. (2016a), or possible geohelminth infection route via plant material.

Table 3. Helminth infections in red foxes in European countries.

Parasites of red foxes	Italy (Citterio et al., 2021)	United Kingdom (Gecchele et al., 2020)	Slovak Republic (Míterpáková et al., 2009)	Lithuania (Bružinskaitė-Schmidhalter et al., 2011)	Denmark (Saeed et al., 2006)	Estonia (Laurimaa et al., 2016)	Estonia (Tull et al., 2022)
Method	scat+ multiplex PCR	scat+ morphology	scat+ morphology	intestines+ morphology+ PCR	intestines, organs+morphology+PCR	intestines+ morphology+ PCR	scat+ morphology
Sample size	n = 2872	n = 224	n = 1198	n = 310	n = 1040	n = 111	n = 131
Cestoda							
<i>Taenia</i> -type		12.6% vs 4.7% (summer vs autumn)	12.2% (146/n)				76.3% (100/n)
<i>Taenia crassiceps</i>	35% (76/217)			26.4% (71/269)	0.2%		
<i>Taenia polyacantha</i>	26.2% (57/217)			61.7% (166/269)			
<i>Echinococcus multilocularis</i>	13.8% (30/217)			58.7% (158/269)	0.3%	31.5% (34/108)	
<i>Taenia krabbei</i>	0.9% (2/217)						
<i>Taenia taeniaeformis</i>	0.9% (2/217)			3.7% (10/269)	1.0%		
<i>Dipylidium caninum</i>	0.9% (2/217)		0.5% (5/n)				
<i>Taenia serialis</i>	0.5% (1/217)						
<i>Mesocestoides litteratus</i>	2.3 (5/217)						
<i>Mesocestoides</i> spp.	5.1 (5/217)		5.8% (70/n)	78.4% (211/269)	35.6%	77.8% (84/108)	
<i>Taenia</i> spp.	1.4 (3/217)				21.5%	70.4% (76/180)	
<i>Hymenolepis diminuta</i>			0.6% (7/n)				

Parasites of red foxes	Italy (Citterio et al., 2021)	United Kingdom (Gechele et al., 2020)	Slovak Republic (Míterpáková et al., 2009)	Lithuania (Bružinskaitė- Schmidhalter et al., 2011)	Denmark (Saeed et al., 2006)	Estonia (Laurimaa et al., 2016)	Estonia (Tull et al., 2022)
Nematoda							
<i>Toxocara canis</i>		14.3% vs 13.1%	12.5% (150/n)	40.5% (109/269)	59.4%	29.6% (32/108)	13.7% (18/n)
<i>Toxascaris leonina</i>			42.9% (514/n)		0.6%	5.6% (6/108)	0.8% (1/n)
<i>Trichuris</i> spp./ <i>Eucoileus</i> spp.							80.2% (105/n)
<i>Capillaria</i> spp.			22.4% (268/n)		80.5% ^p	91.5% (97/106)	
<i>Eucoileus aerophilus</i>		52.1% vs 32.7%		97.1% (101/104)	74.1%	87.6% (92/105)	
<i>Trichuris vulpis</i>			33.5% (401/n)		0.5% ^d		
<i>Ancylostomatidae</i>							
<i>Uncinaria stenocephala</i>		47.1% vs 42.0%	6.9% (83/n)	76.9% (207/269)	68.6%	84.3% (91/108)	18.3% (24/131)
<i>Ancylostoma caninum</i>			18.1% (217/n)		0.6%		
overall prevalence ^e	7.6%	83.9%	83.3%	NE	92.4%	93.8%	92.4%

NE – not estimated; ^d– *Trichuris vulpis*; ^p– *Capillaria plica*; ^e– including all parasites in the study

Table 4. Helminth infections in golden jackals in European countries and Iran.

Parasites of golden jackals	Bulgaria (Kirkova et al. 2011)	Serbia (Ćirović et al. 2015)	Serbia (Ilić et al. 2016)	Serbia (Lalošević et al. 2016)	Iran (Dalimi et al. 2006)	Iran (Meshgi et al. 2009)	Switzerland (Frey et al. 2022)	Hungary (Balog et al. 2021)	Estonia (Tull et al. 2022)
Method	intestines+ morphology	intestines+ morphology	intestines+ morphology	intestines+ morphology	intestines+ morphology	intestines, organs+ morphology	intestines+ morphology+ multiplex PCR	intestines+ morphology+ multiplex PCR	scat+ morphology
Sample size	n = 56	n = 447	n = 60	n = 28	n = 10	n = 79	n = 5	n = 173	n = 65
Cestoda									
<i>Taenia</i> -type									87.7% (57/n)
<i>Echinococcus multilocularis</i>				14.3% (4/n)			40% (2/n)	15.6% (27/n)	
<i>Echinococcus granulosus</i>	1.9%					8.9% (7/n)		1.7% (3/n)	
<i>Taenia hydatigena</i>		0.9%			10% (1/n)	2.5%–5% (2;4/n)			
<i>Dipylidium caninum</i>	3.8%	1.6%			20% (2/n)	10.1% (8/n)			
<i>Mesocestoides litteratus</i>		4.7%							
<i>Mesocestoides</i> spp.	34.6%	5.8%			70% (7/n)	15.2%–21.5% (12;17/n)			
<i>Taenia</i> spp.	23.0%								

Parasites of golden jackals	Bulgaria (Kirkova et al. 2011)	Serbia (Ćirović et al. 2015)	Serbia (Ilić et al. 2016)	Serbia (Lalošević et al. 2016)	Iran (Dalimi et al. 2006)	Iran (Meshgi et al. 2009)	Switzerland (Frey et al. 2022)	Hungary (Balog et al. 2021)	Estonia (Tull et al. 2022)
Nematoda									
<i>Toxocara canis</i>	7.7%	1.6%	23.3% (14/n)		10% (1/n)	5% (4/n)			4.6% (3/n)
<i>Toxascaris leonina</i>	5.8%				30% (3/n)				4.6% (3/n)
<i>Trichuris</i> spp./ <i>Eucoleus</i> spp.									21.5% (14/n)
<i>Capillaria</i> spp.	16.4%								
<i>Trichuris vulpis</i>	30.7%		11.7 (7/60)						
<i>Ancylostomatidae</i>			33.3% (20/n)						
<i>Uncinaria stenocephala</i>	84.6%					6.3% (5/n)			27.7% (18/n)
<i>Ancylostoma caninum</i>	11.5%	0.2%				2.5% (2/n)			
overall prevalence ^e	100%	10.3%	12.2%	14.3%	100%	33.3%	40%		90.8% (59/n)

^e – including all parasites in the study

SUMMARY

Nowadays, the human-animal bond is beneficial for human physical and mental health as domesticated animals are raised (besides for food, work etc.) for companionship and therapy. However, companion animals (mostly dogs and cats) also pose potential hazards to our health as they are hosts for agents of zoonotic diseases, transmitted between animals and humans. In the light of zoonotic diseases, a worldwide concept of One Health has been established based on collaboration in all aspects of health care for humans, animals, and the environment. However, the importance of companion animals, such as cats and dogs, as disease distributors is often underestimated, whereas potential threats related to wild mammals is largely neglected. Therefore, to assess environmental contamination with zoonotic parasites and potential threats, it is necessary to understand the abundance and taxonomic composition of zoonotic parasites in pets and wild mammals in both urban and rural environments.

The aims of the study were to identify endoparasites with zoonotic potential in domesticated and wildlife animals in Estonia, mainly in cats and dogs, but also in wildlife species (red fox, golden jackal etc.), (I, II, III, IV). Furthermore, one of the goals was to determine endoparasite transmission routes in the urban environment and factors impacting the parasite cycles (I, II), and to compare urban and rural endoparasite fauna among dogs and cats (I, II, III). Last but not least, the effect of diet was assessed to evaluate the infection risk among mammalian predators, and to evaluate the overlap between helminth fauna of domesticated (dog) and wildlife canids such as the red fox and golden jackal (III, IV).

Our results indicate clearly that domesticated animals (dogs and cats) as well as sympatric wildlife predators distribute endoparasites with zoonotic potential (I–IV). Over a third of examined shelter cats (36.6%) excreted parasitic stages of zoonotic *Toxocara cati*. Moreover, among cats, helminths (*Hydatigera taeniaeformis*, *Ancylostoma tubaeforme* and *Eucoleus aerophilus*) with zoonotic potential were found. In dogs, it was revealed that the most common group of zoonotic helminths in urban settlements are geohelminths, namely *U. stenocephala* and *Toxocara* spp., both zoonotic (I, II). The comparison of helminth prevalence between rural and urban dogs and cats revealed alarming results (I, II, III). Namely, rural areas are in comparison with urban areas by far more contaminated with helminths, revealing a 9-fold difference between urban (~10%) and rural (~90%) dog`s endoparasite fauna. Territories of wildlife canids (red fox and golden jackal) often overlap with rural dogs, which poses a direct threat to human health. Our studies have shown that in addition to very high helminth prevalence, there is also a high overlap of helminth fauna between rural dogs, golden jackals and red foxes. All these predators were highly infected with zoonotic helminths of the family Taeniidae, but also with zoonotic roundworms. Moreover, the environmental scats, contaminated with endoparasite ova, were situated on average 60 m from nearest living lands, where, in total 160 households (private property) could be found, which places the infected scats to human`s backyards (IV).

Over half of rural cats (56.7%) were infected with endoparasites compared to the 1/3 of infected urban cats (36.2%). Rural cats in quarantine (up to 14 days) had significantly higher endoparasite infection prevalence with directly transmittable zoonotic endoparasites than urban cats in quarantine. The most prevalent endoparasites among rural dogs and cats were biohelminths, rather than geohelminths in urban areas (II, III).

The general infection gradient of endoparasites is shifting from large towns towards smaller towns and from smaller towns to rural areas (I, III, IV). However, towns have

their own endoparasite transmission routes (infection hotspots), whereas the infection risk and prevalence are higher in smaller than in larger towns. So, the potential hazard zones formulated in **I** included recreational sites and green areas near schools and nurseries, functioning as important infection hotspots compared to streets. Apartment-house region had also higher endoparasite prevalence risk in lieu of the detached-house region, supporting a ‘closed’ infection cycle in the apartment-house region where the soil may have permanent geohelminth contamination throughout the year (**I**).

Another endoparasite transmission cycle is linked with cats and a shelter (**III**) where young (< 1 year) cats and cats ready for adoption (≥ 15 days in the shelter) had heavy endoparasite burdens with also zoonotic parasites. During the stay in the shelter, some endoparasites (*Cystoisospora* spp. and total protozoan species) flourished, meaning that their infection prevalence was significantly higher among cats ready for adoption but decreased among quarantine cats (1–14 days in shelter). The opposite effect applied to infection prevalence with *Cryptosporidium* spp. and *E. aerophilus*, namely these parasites were more common in quarantine cats than in the ready for adoption group. Juvenile cats had seriously higher endoparasite infection prevalence with zoonotic *T. cati* and nearly three times higher infection intensity with overall endoparasites than adult cats (**III**).

Since the parasite infection occurrence is closely related to predator-prey relations in food webs, the studied diet among predators enabled to distinguish relationships between parasites and consumed food objects (**III**, **IV**). In nature, prey objects (rodents, reptiles, birds, earthworms etc.) serve as intermediate, reservoir or paratenic hosts where parasites mature or stay dormant. We demonstrated that if rural dogs preyed on rodents and game, the infection rate increased. On the other hand, if people cared for their dogs and fed them dog food, there was a (63%) reduction of coinfection with helminths (**III**). For predators (red fox, golden jackals, dogs, raccoon dogs etc.), preying on rodents increased the coinfection rate with multiple endoparasites. Several infection prevalence models indicated among predators that preying on paratenic or intermediate hosts (rodents, reptiles) significantly increases the infection risk with helminths, mainly with *Eucoleus* spp./*Trichuris* spp. A surprising relationship between consumed plant material and infection with *T. canis* among red foxes indicated that infection prevalence with *T. canis* increased when diet consisted of plant material, referring to potential self-medicating behaviour or possible higher geohelminth infection via plant material (**IV**).

To conclude, domesticated companion animals such as dogs and cats can act as transmitters of zoonotic parasites capable of affecting human health, and are therefore of One Health concern. The overlap between free-ranging companion animals and wildlife predators ensures an enzootic parasite cycle in an anthropogenic landscape. Therefore, it is of utmost importance to highlight possible parasite transmission routes and species compositions in wild and domesticated animals. It is equally important to educate and counsel people by experts to minimize zoonotic disease transmissions. One of the main concluding messages of my PhD work is that a regular monitoring of zoonotic parasites among wildlife and domesticated animals should be implemented to reduce the burden of zoonotic diseases.

SUMMARY IN ESTONIAN

Kodu- ja metsloomadega levivad zoonootilised siseparasiidid Eestis

Inimese ja lemmiklooma vaheline suhe on muutunud tänapäeval väga oluliseks, pakkudes mitmeid hüvesid nii füüsilisele kui ka vaimsele tervisele, ent teisalt on koduloomad (nagu koerad ja kassid) mitmete zoonootiliste haiguste levitajad, võimaldades haiguste levikut loomadelt inimestele ja vastupidi. Zoonootiliste haiguspuhangute ärahoidmiseks on pandud alus *One Health* (Üks Tervis) kontseptsioonile (üks tervis, üks maailm), mis hõlmab interdistsiplinaarset koostööd kogu maailmas, sidudes ühtseks tervikuks inimese tervishoiu koos loomade ning keskkonnaga. Parasiitide edasikandumist loomade vahendusel inimesele on sageli alahinnatud, mistõttu on oluline uurida mets- ja lemmikloomade parasiteeritust, eriti zoonootiliste parasiitidega. Nakkusriski hindamine aitab vältida inimeste nakkumist, seda eriti väikelaste puhul, kes on oluliselt suurema nakkusriskiga kui täiskasvanud.

Töö eesmärkideks oli kindlaks teha Eestis lemmikloomade (koer, kass) ja kiskjatega (punarebane, harilik šaakal jt) levivad zoonootilised siseparasiidid (**I, II, III, IV**). Uurida, millised on linnakeskkonnas peamised siseparasiitide levikuteed ning millised tegurid seda mõjutavad (**I, II**); ühtlasi oli üheks eesmärgiks võrrelda kasside ja koerte nakatumist siseparasiitidega linna- ja maapiirkonnas (**I, II, III**). Samuti hinnati, kuidas kiskjaliste toitumine mõjutab nende nakkusriski siseparasiitidega ning võrreldi kodu (koer)- ja metsloomade (punarebane, harilik šaakal) parasitofauna kattuvust; (**III, IV**).

Uuringud kinnitavad üheselt, et nii Eesti lemmikloomad (koerad ja kassid) kui ka metsloomad (punarebane, harilik šaakal, jt.) on nakatunud zoonootiliste siseparasiitidega (**I–IV**). Varjupaiga kassidest olid enam kui kolmandik (36,6%) nakatunud zoonootilise nematoodi kassisolkmega (*Toxocara cati*). Samuti leiti varjupaiga kassidelt mitmeid teisi zoonootilisi helminte (nt *Hydatigera taeniaeformis*, *Ancylostoma tubaeforme* ja *Eucoleus aerophilus*), kes nakatavad inimesi, kuid kelle epidemioloogiast on seni vähe teada. Linnadest leiti koertelt enim geohelminte, kellest on zoonootilised untsinaaria (*Uncinaria stenocephala*) ja kutsikasolge (*Toxocara canis*) (**I, II**). Linna- ja maapiirkonna kasside ja koerte siseparasiitide uuringute tulemused näitasid kõrget nakatumise taset (**I, II, III**). Tuvastasin, et maapiirkonna koerad olid üheksa korda enam nakatunud helmintidega kui linnakoerad (vastavalt 90% ja 10%). Maapiirkondades elavate koerte kõrget nakkustaset soosivad arvatavasti ulukkiskjalised, kellest 90% olid nakatunud ning kelle territoorium kattub suuresti koduloomadega. Põhiliselt olid ulukoerlased nakatunud zoonootiliste paeluslastega (*Taeniidae*), aga võrdlemisi sageli esines ka mitmeid teisi zoonootilisi helminte nagu nematoodid *Eucoleus spp./Trichuris spp.*, untsinaariat (*U. stenocephala*) ja kutsikasolget (*T. canis*). Murettekitav on ka leid, et enamik nakkunud väljaheidetest asusid keskmiselt vaid 60 m kaugusel elamu- maadest, kus paiknes vähemalt 160 majapidamist.

Üle poole maapiirkondades elavatest kassidest (56,7%) olid nakatunud siseparasiitidega, veidi vähem esines nakkust linnades elavatel kassidel (36,2%). Kusjuures maapiirkondade kassidel, kes olid varjupaigas karantiinis (kuni 14 päeva), esines märkimisväärselt rohkem otsesel teel edasikanduvaid zoonootilisi siseparasiite kui karantiinis linnapiirkonna kassidel. Nii maapiirkonna koertel kui -kassidel esines siseparasiitidest märksa enam biohelminte kui linnapiirkonna koertel ja -kassidel (**II, III**).

Töös leiti, et Eestis on välja kujunenud üldine siseparasiitide levimus, kus nakkusrisk on väikseim suurlinnades, seejärel järgnevad väikelinnad ning suurim nakkustase

on maapiirkondades (**I**, **III**, **IV**). Vaatamata linnade madalamale nakkustasemele, on siiski linnakeskkonnas välja kujunenud konkreetsed nakkusteid (nn nakkuse tulipunktid), kusjuures nakkusrisk on kõrgem väikelinnades kui suurlinnades. Mainitud tulipunktides puhke- ja rohealadel, millest osad paiknesid ka lasteaedade ja koolide läheduses esines oluliselt rohkem siseparasiitidega saastunud väljaheiteid kui rohealadel tänavaservades. Samuti oli nakkusrisk kõrgem paneelmajade ümbruskonnas, võrreldes eramajade piirkonnaga. Arvatavasti on tekkinud paneelmajade läheduses suletud nakkusring, kus pinnas on alaliselt nakkusvõimeliste geohelmintide munadega saastunud (**I**).

Veel üks oluline siseparasiitide levikuteekond on seotud varjupaiga kassidega, kus pea pooled kassid (ca 50%) on nakatunud vähemalt ühe parasiidiliigiga. Enim olid zoonootiliste siseparasiitidega nakatunud noored (< 1 a) ja koduootel kassid (olnud varjupaigas ≥ 15 päeva ehk läbinud karantiini perioodi). See tähendab, et varjupaigas veedetud aja jooksul suutsid mõned siseparasiidid plahvatuslikult vohama hakata (nt *Cystoisospora* spp.) võrrelduna karantiini kassidega (1–14 päeva karantiinis). Erandi moodustasid zoonootilised parasiidid algloom *Cryptosporidium* spp. ja ümaruss *Eucoleus aerophilus* – koduootel kassid olid vähem nakatunud kui karantiini kassid. Noortel kassidel esines oluliselt enam nakkust kassisolkmega ning nende nakkuse intensiivsus oli kolm korda suurem kui täiskasvanud kassidel (**III**).

Kuna parasiitide esinemine on tihedalt seotud toiduahelaga, st kiskja-saakloom suhtega, siis uuriti kiskluse ja söödud toiduobjektide seoseid parasiteeritusega (**III**, **IV**). Looduses võivad saakliigid (nt närilised, herbivoorid, roomajad, linnud, vihmaussid jne) olla parasiitidele kas vahe-, säilitus- või lisaperemeesteks, kelles parasiidid arenevad mitesuguliselt või püsivad aastaid mitteaktiivses staadiumis. Uuring näitas, et kui maapiirkondade koerad toitusid närilistest ja jahiulukitest, siis nakkusrisk suurenes, samas kui koertel, kes olid söönud koeratoitu, oli parasiidiliike vähem (**III**). Kiskjaliste (punarebane, harilik šaakal, koer, metsnugis jt) puhul selgus, et närilistest toitumine suurendas oluliselt enamate parasiidiliikidega nakatumist. Mitmed nakkuse mudelid näitasid, et kui kiskjalised toitusid vahe- või säilitusperemeestest (närilised, roomajad), siis tõsis nakatamine helmintidega (nt *Eucoleus* spp./*Trichuris* spp.). Üllataval kombel tuvastati uuringus seos punarebase taimedest toitumise ja parasiteerituse vahel. Nimelt leiti, et mida rohkem esines toidus taimset komponenti, seda enam oldi nakkunud kutsikasolkmega, mis viitab kas potentsiaalsele tervenemiskäitumisele seedekulglast siseparasiitide väljutamiseks (taimede abil) või hoopis suuremale võimalusele nakatuda geohelmintidega (**IV**).

Kokkuvõtteks saab öelda, et lemmikloomad (koerad-kassid) võivad olla paljude zoonooside levitajad ja võivad nakatada inimesi parasiitidega, kellest osad on eluohtlikud. Mets- ja koduloomade kattuvad areaalid inimtekkelises maastikus võimaldavad parasiitaarsetel nakkushaigustel püsida mõlemas populatsioonis. Lisaks sellele, et on äärmiselt vajalik uurida võimalikke zoonooside levikuteid ning määrata kindlaks zoonooside tekitajad, on võrdväärset oluline ka harida ja nõustada inimesi eriala ekspertide poolt, et vähendada zoonootilistesse haigustesse nakatumist. Võimalike nakkusriskide hindamiseks oleks vaja püsivalt seirata looduskeskkonnas levivaid ohtlikke zoonootilisi parasiite nii mets- kui koduloomadel.

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