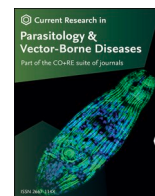












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## Unwelcome guests: Nematodes of zoonotic and animal health importance in native and invasive carnivores of Hungary

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## ARTICLE INFO

## Keywords:

Heartworm

Invasive species

Parasitic nematodes

Zoonoses

## ABSTRACT

Wild carnivores are important reservoirs of parasitic nematodes, several of which have veterinary and zoonotic significance. In Europe, the role of invasive carnivores in parasite circulation remains poorly understood. Here, we screened 371 individuals of six wild carnivore species from Hungary (red foxes, badgers, golden jackals, raccoons, raccoon dogs, and beech martens), using molecular markers (*cox1* and *S12*), and detected five nematode parasites: *Dirofilaria immitis*, *Crenosoma vulpis*, *Angiostrongylus vasorum*, *Thelazia callipaeda*, and *Spirocerca lupi*. The highest prevalence was observed in badgers (32.0%) and red foxes (15.7%), while invasive raccoons also showed a relatively high infection rate (13.2%). *Dirofilaria immitis* was one of the most common nematode species detected: it was found in four host species, including the first confirmed cases in Hungarian badgers and invasive raccoons, extending the known host range of this parasite in central Europe. Importantly, *T. callipaeda* was recorded in red foxes and an invasive raccoon dog, representing the first invasive host records of this zoonotic eyeworm in Hungary. *Crenosoma vulpis* was identified in raccoons, suggesting invasive species may act as incidental carriers of endemic parasites. Both *C. vulpis* and *D. immitis* showed low host specificity. These findings indicate that invasive carnivores, particularly raccoons, may harbour unexpectedly high prevalence and play a greater role in local parasite networks than previously assumed. Our results highlight the epidemiological significance of both native and invasive carnivores in sustaining nematodes of zoonotic and veterinary importance in central Europe, stressing the need for continued surveillance in wild carnivores.

## 1. Introduction

Wild carnivores often play an important role in the maintenance and transmission of various parasitic nematodes, some of which are of considerable veterinary and public health significance (Han et al.,

2021). The diversity and prevalence of nematodes in wild carnivore populations are influenced by several ecological and anthropogenic factors, including host density, host behaviour, environmental conditions, and human-wildlife interactions (Lesniak et al., 2017; Kołodziej-Sobocińska, 2019; Gecchele et al., 2020; Stronen et al., 2021;

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<https://doi.org/10.1016/j.crpvbd.2026.100380>

Received 12 February 2026; Received in revised form 15 April 2026; Accepted 16 April 2026

Available online 16 April 2026

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Arcenillas-Hernández et al., 2024). Understanding the diversity of parasite communities in carnivores is crucial to identifying potential threats to native ecosystems, domestic animals, and human health. In Europe, numerous nematode species have been recorded in wild carnivores, including *Angiostrongylus vasorum* (Baillet, 1866) Kamensky, 1905, *Crenosoma vulpis* (Dujardin, 1845), and *Dirofilaria* spp. (Ionica et al., 2017; Lemming et al., 2020; Veronesi et al., 2023; Szentiványi and Garamszegi, 2024). These parasites differ in their life cycles, transmission modes, and pathogenic potential, but several are known for their zoonotic risk or impact on domestic animals (Veronesi et al., 2023).

Cardiopulmonary nematodes such as *C. vulpis* and *A. vasorum* are increasingly reported in European wild carnivores and domestic dogs (Latrofa et al., 2015; Schug et al., 2018; Fuehrer et al., 2021). Red foxes (*Vulpes vulpes*), which often inhabit peri-urban and urban environments, are considered the primary wildlife reservoirs of both species (Blanch-Lázaro et al., 2018; Deak et al., 2020). In Hungary, *C. vulpis*, which causes crenosomiasis, has been confirmed in foxes (Sréter et al., 2003; Tolnai et al., 2015). Similarly, *A. vasorum*, causing canine angiostrongylosis, is expanding its range in Europe and has been documented in foxes in several central European countries, including Austria, the Czech Republic, Germany, Hungary, Romania, and Slovakia (Sréter et al., 2003; Deak et al., 2017; Fuehrer et al., 2021; Morgan et al., 2021; Mitrea et al., 2025).

*Dirofilaria* spp., particularly *D. immitis* (Leidy, 1856) and *D. repens* Railliet & Henry, 1911, are mosquito-borne nematodes that have been detected in both wild and domestic carnivores in Europe (Genchi and Kramer, 2020; Szentiványi and Garamszegi, 2024). *Dirofilaria repens*, which causes subcutaneous dirofilariosis in dogs and occasionally in humans, is established in many parts of central and southern Europe, with wildlife such as red foxes and golden jackals (*Canis aureus*) implicated in its sylvatic cycle (Ionica et al., 2016; Kravchenko et al., 2016). In Hungary, autochthonous cases of both *D. repens* and *D. immitis* have been reported in domestic and wild hosts, indicating an active transmission cycle in the region (Jacsó et al., 2009; Tolnai et al., 2014; Bacsádi et al., 2016; Farkas et al., 2020; Jerzsele et al., 2025).

Other parasitic nematodes are also showing emerging number of reports, including *Thelazia callipaeda* Railliet & Henry, 1910 and *Spirocerca lupi* (Rudolphi, 1809) (Bertos et al., 2023; Van Hien et al., 2021). Increasing numbers of detections have been reported throughout Europe in both native and invasive hosts, such as *T. callipaeda* in foxes and golden jackals (Nagy et al., 2026), and *S. lupi* in raccoons (Langner et al., 2024).

Native carnivores, particularly generalist mesopredators such as red foxes and badgers (*Meles meles*), are well-established reservoirs of numerous helminths due to their wide distribution, omnivorous diet, and high adaptability (Karamon et al., 2018; Schneider et al., 2023; Veronesi et al., 2023). They often come into contact with urban areas and domestic animals, thereby creating opportunities for cross-species transmission (Plumer et al., 2014; Mackenstedt et al., 2015). Red foxes are considered a key reservoir of *Echinococcus multilocularis* Leuckart, 1863 in central Europe, and have been implicated in the sylvatic cycle of *Dirofilaria* spp. and *Crenosoma* spp. (Sréter et al., 2003; Oksanen et al., 2016; Schug et al., 2018; Fuehrer et al., 2021; Szentiványi and Garamszegi, 2024). In addition, the increasing range of the golden jackal in central Europe, including its recent expansion in Hungary (Bijl et al., 2024), adds another native carnivore with reservoir potential of several pathogens of medical and veterinary importance (Széll et al., 2013; Farkas et al., 2014; Takács et al., 2014; Ionica et al., 2016; Gherman and Mihalca, 2017; Mitková et al., 2017; Sukara et al., 2018; Balog et al., 2021; Nagy et al., 2026).

The emergence and spread of invasive carnivores in Europe further complicate the epidemiological landscape. Species such as the raccoon (*Procyon lotor*) and raccoon dog (*Nyctereutes procyonoides*), introduced during the 20th Century, have successfully established populations in various central and eastern European countries, including Hungary (Kauhala and Kowalczyk, 2011; Beltrán-Beck et al., 2012; Schally et al.,

2024). These species are highly adaptable, often occupying human-modified habitats that overlap with domestic animals and native wildlife (Kauhala and Kowalczyk, 2011). It has been shown that invasive carnivores may act as carriers of both endemic and novel parasites and pathogens (Beltrán-Beck et al., 2012; Sutor et al., 2014; Laurimaa et al., 2016). For instance, studies have highlighted the potential for pathogen spillover and spillback between invasive hosts and native fauna (Clark et al., 2018; Kellner et al., 2018; Roy et al., 2023). In Europe, raccoon dogs have been found to harbour several zoonotic and potentially zoonotic parasites, among others *Trichinella* spp., *Alaria alata* (Goeze, 1792), and *Uncinaria* spp. (Duscher et al., 2017; Kärssin et al., 2017; Pilarczyk et al., 2022; Marin et al., 2023), while raccoons have been found infected with *Baylisascaris procyonis* (Stefanski & Zarnowski, 1951) (Beltrán-Beck et al., 2012; Stope, 2019), raising zoonotic concerns.

Given the ecological overlap between invasive and native carnivores and the growing presence of nematodes of public and veterinary health importance in these populations, it is essential to monitor and compare parasite communities across host species. Understanding the parasite diversity in these animals provides insights into the risks posed to domestic animals and public health, informs disease prevention strategies, and helps reveal the role of wildlife in parasite ecology. Most existing research on zoonotic and wildlife parasites in European carnivores has been focused on western and northern Europe, where long-term wildlife health and pathogen surveillance programmes have generated extensive knowledge (Duscher et al., 2015; Laurimaa et al., 2016; Veronesi et al., 2023). In contrast, central and southeastern Europe, including Hungary, remain comparatively underrepresented, despite their ecological importance as a biogeographical transition zones that host both native and expanding invasive species (Tolnai et al., 2015; Hornok et al., 2022; Szentiványi and Garamszegi, 2024; Nagy et al., 2026).

In this study, we investigated the occurrence of parasitic nematodes in invasive and native carnivores in Hungary. The country's central biogeographical position between both western and eastern and southern and northern Europe, combined with its heterogeneous habitats, makes it a key region for understanding wildlife-domestic-human interfaces and the ecological processes shaping disease dynamics. The region supports high carnivore diversity and overlap among native, invasive, and domestic hosts, creating unique opportunities for pathogen exchange. We aimed to explore the diversity and infection patterns of nematodes, reveal differences between host species, and assess their potential role in maintaining and transmitting parasites of zoonotic or veterinary relevance. Our goal was to improve understanding of parasite dynamics in central European wildlife and their implications for disease transmission at the wildlife-domestic-human interface.

## 2. Materials and methods

### 2.1. Sample collection

Native mammals were collected voluntarily by professional hunters between 2022 and 2025 (legalisation details: <https://zenodo.org/records/15645626>). Invasive species were also collected by hunters via shooting, along with the processing of roadkill specimens. While most invasive species samples were collected between 2022 and 2024, our study also included a limited number of older samples dating from 2002 to 2018. Blood and spleen samples from native mammals were obtained by hunters immediately after culling, using pre-distributed sampling swabs and/or collection tubes and stored at  $-20^{\circ}\text{C}$  until DNA extraction. In the case of invasive mammals, only spleen samples were used for DNA extraction and were stored at  $-80^{\circ}\text{C}$  beforehand.

### 2.2. DNA extraction and processing

Sample extractions were performed individually using a pre-manufactured protocol and DNA extraction kit (DNeasy Blood & Tissue Kit, Qiagen, Germany). To detect parasite DNA, we targeted the

mitochondrial cytochrome *c* oxidase subunit 1 (*cox1*) gene and the ribosomal S12 protein (S12) gene, using conventional PCR. For molecular identification, specific primers were employed to amplify mitochondrial and ribosomal gene regions. The *cox1* region was amplified using the primers COLintF (5'-TGA TTG GTG GTT TTG GTA A-3') and COLintR (5'-ATA AGT ACG AGT ATC AAT AT-3'), while the ribosomal S12 gene was targeted using the primers 12SF (5'-GTT CCA GAA TAA TCG GCT A-3') and 12SR (5'-ATT GAC GGA TGA GTT TGT ACC-3') as described previously (Casiraghi et al., 2001, 2004).

Polymerase chain reactions (PCR) were performed in a total volume of 20 µl. For reactions with the *cox1* primers, 4 µl of extracted DNA was added; for those with the S12 primers, 3 µl was used. The PCR mix in both cases contained 0.25 µl DreamTaq DNA Polymerase (5 U/µl), 1 µl of each primer (10 mM), 1 µl dNTP mix (10 mM), 2.5 µl MgCl<sub>2</sub>, 2.5 µl DreamTaq Green Buffer, and nuclease-free water was added to reach a final volume of 20 µl. Thermal cycling conditions for *cox1* amplification began with an initial denaturation step at 95 °C for 2 min, followed by 40 cycles consisting of denaturation at 94 °C for 30 s, annealing at 47 °C for 30 s, and extension at 72 °C for 50 s. A final extension was carried out at 72 °C for 5 min. For the S12 gene, the cycling protocol started with a 1-min denaturation at 94 °C, followed by 40 cycles of 98 °C for 10 s, 50 °C for 15 s, and 68 °C for 1 min. The reaction concluded with a final extension step at 68 °C for 5 min.

Amplified products were run on a 1.5% agarose gel and visualised under UV light. Each PCR reaction was replicated at least twice to confirm the consistency of the results. Positive samples were purified using a Zymo Research extraction kit (USA) and then submitted for sequencing (Eurofins, Germany). Nematode species were subsequently identified using GenBank (NCBI, BLAST). The newly generated sequences were submitted to the GenBank database under the accession numbers PZ252551-PZ252561 (*cox1*), PZ254718-PZ254734 (S12), and PZ267076-PZ267088 (S12).

### 2.3. Data analysis

Data visualisation was performed using RStudio software version R 4.4.3, with the packages *ggplot2* and *ggalluvial* (Wickham and Chang, 2016; Brunson and Read, 2018; R Core Team, 2023). Maps were generated using QGIS software version 3.40.4 (QGIS Development Team, 2023).

### 3. Results

Samples were collected from across Hungary from multiple carnivore species ( $n = 371$ , 6 species) (Fig. 1). The highest prevalence of nematodes was found in European badgers and red foxes, with infection rates of 32.0% and 15.7%, respectively (Table 1, Fig. 2). In golden jackals, a single infected individual was identified, showing 1.3% infection prevalence (Table 1). Nematodes were also detected in invasive carnivore species: raccoons showed a prevalence of 13.2%, and raccoon dogs 3.7% (Table 1, Fig. 2). No infection was detected in beech martens.

Several parasitic nematodes were detected in the examined hosts, including *Angiostrongylus vasorum* (family Angiostrongylidae), *Crenosoma vulpis* (family Crenosomatidae), and *Dirofilaria immitis* (family Onchocercidae). In addition, *Thelazia callipaeda* and *Spirocerca lupi* belong to the families Thelaziidae and Spirocercidae, respectively, reflecting the broad taxonomic diversity of parasitic fauna identified in the studied hosts (Table 1).

The most frequently detected parasite, *Angiostrongylus vasorum* ( $n = 15$ ), was found in red foxes, with a prevalence of 7.6% (Table 1). *Dirofilaria immitis* ( $n = 13$ ) was present in red foxes, badgers, raccoons, and one golden jackal. Its prevalence was 8.0% in badgers, 4.0% in red foxes, 1.3% in golden jackals, and 5.3% in raccoons (Table 1). Another nematode was *Crenosoma vulpis* ( $n = 11$ ), detected in five foxes, three badgers, and three raccoons, with prevalences of 2.5%, 12.0%, and

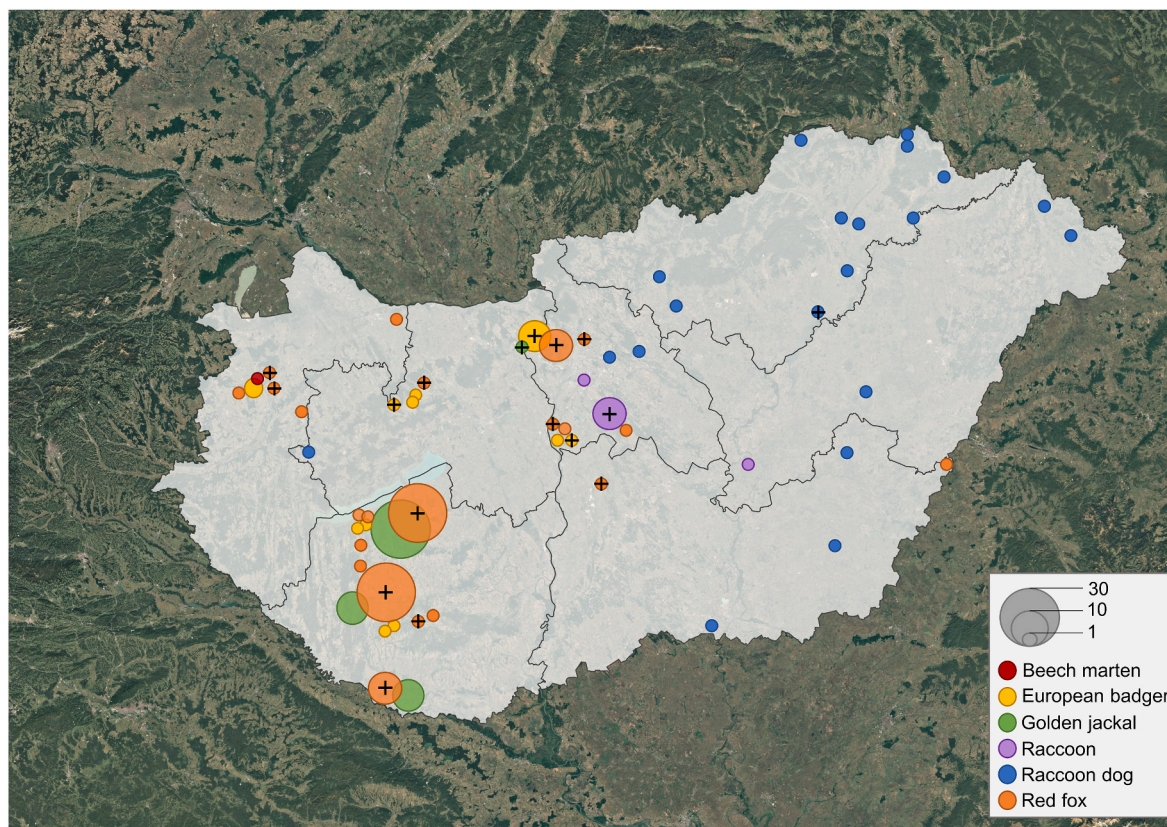


Fig. 1. Geographical distribution of collected samples. Circles of different colours indicate sampled carnivore species. Infected individuals are indicated with a positive sign. Scale: 1:4,000,000.

**Table 1**

Molecularly tested carnivore species and prevalence (%) per parasite species. Nematoda fam. gen. sp. represents nematode species of unknown identity, as no matching sequences were found in GenBank.

Host species	n	Parasite species, n (%)					Nematoda fam. gen. sp.
		<i>D. immitis</i>	<i>C. vulpis</i>	<i>T. callipaeda</i>	<i>A. vasorum</i>	<i>S. lupi</i>	
Red fox (N = 198)	31	8 (4.0)	5 (2.5)	2 (1.0%)	15 (7.6)	1 (0.5)	–
European badger (N = 25)	8	2 (8.0)	3 (12.0)	–	–	–	3 (12.0)
Golden jackal (N = 77)	1	1 (1.3)	–	–	–	–	–
Beech marten (N = 6)	–	–	–	–	–	–	–
Raccoon (N = 38)	5	2 (5.3)	3 (7.9)	–	–	–	–
Raccoon dog (N = 27)	1	–	–	1 (3.7%)	–	–	–

Abbreviation: N, total number of specimens studied; n, number of infected individuals.

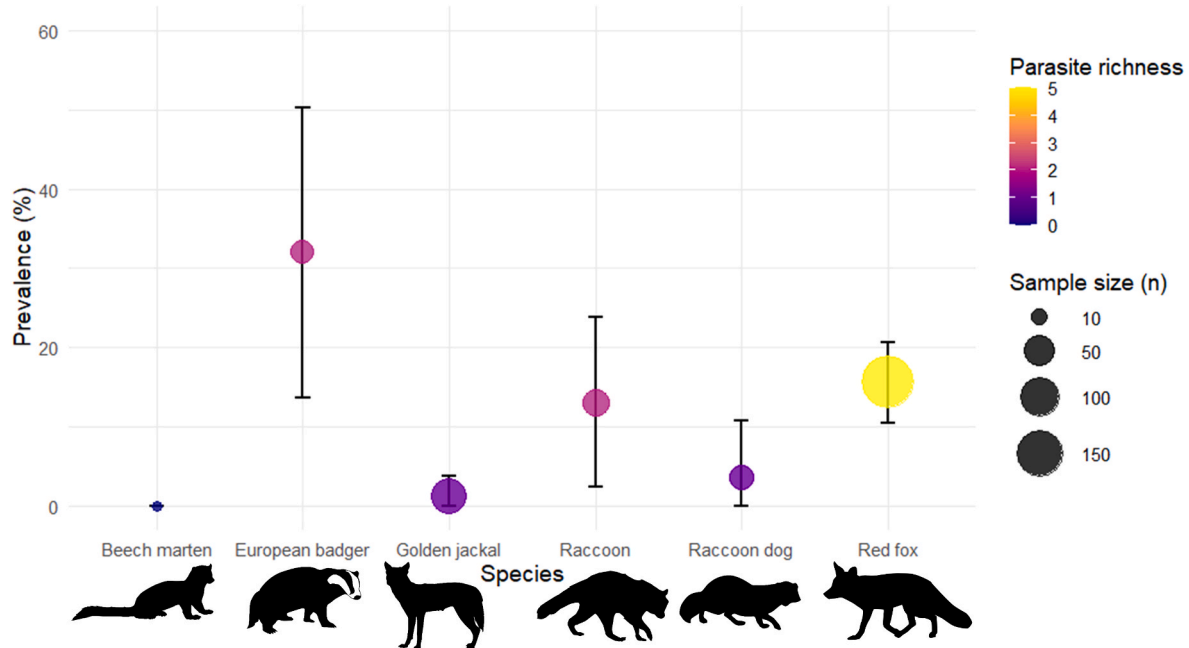


Fig. 2. Infection prevalence among screened carnivore species. Circle size is proportional to sample size, and circle colour refers to the number of parasite species identified per host species. Error bars represent 95% confidence intervals. Icons are licensed under CC0 via PhyloPic ([www.phylopic.org](http://www.phylopic.org)).

7.9%, respectively (Table 1, Fig. 3).

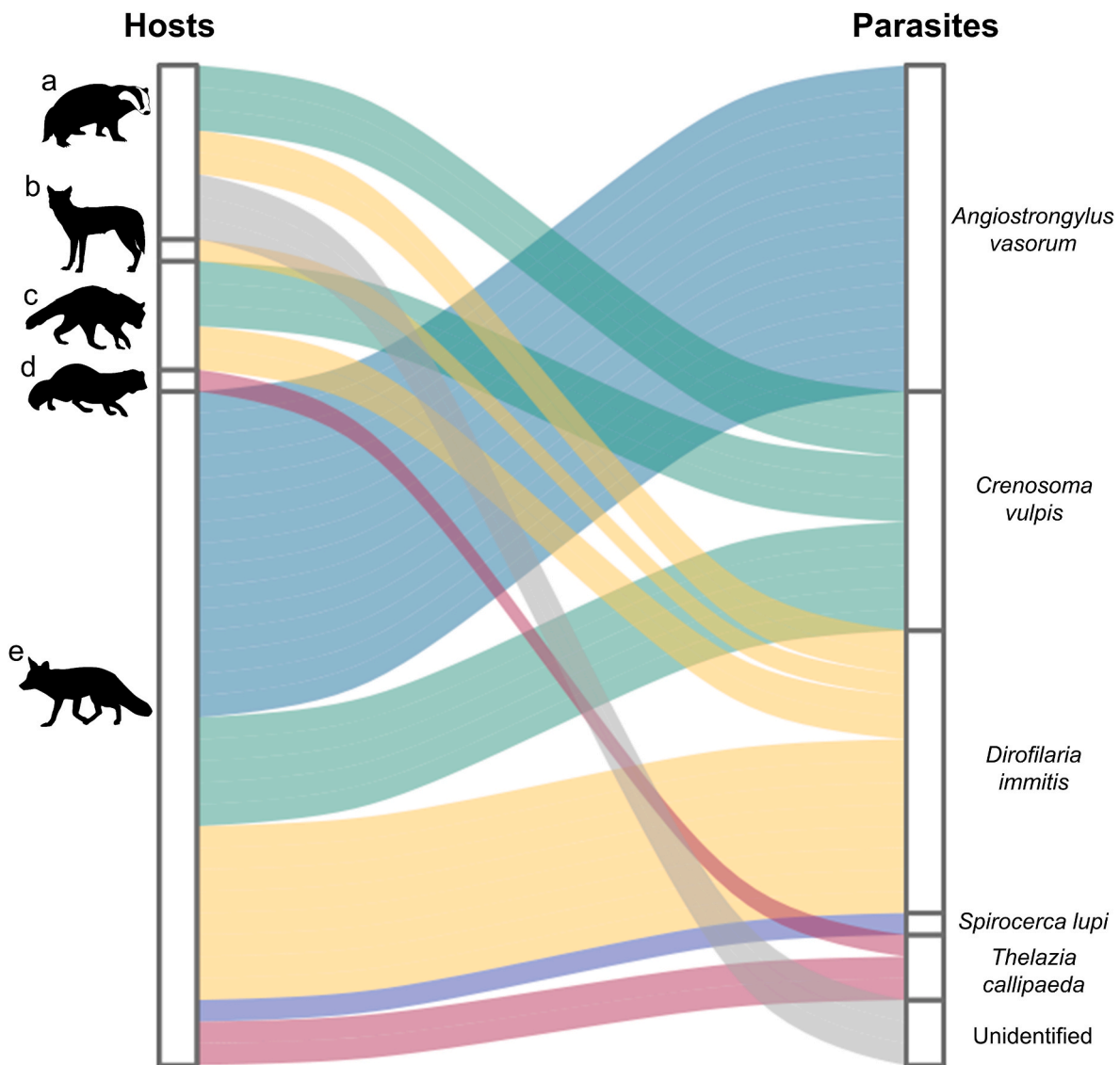
*Thelazia callipaeda* (n = 3) infection was also detected, two infections were found in red foxes and one in a raccoon dog, corresponding to prevalences of 1.0% and 3.7%, respectively (Table 1). Additionally, *Spirocerca lupi* (n = 1) was found in a single red fox, representing 0.5% infection rate. Three more positive samples were detected, all originating from badgers, which did not match any sequences in GenBank. No co-infections were observed in any of the samples.

#### 4. Discussion

The infection patterns of invasive carnivores like raccoons and raccoon dogs have so far been insufficiently documented in Hungary; our study offers the first evidence contributing to their characterisation. We found no evidence that raccoon dogs are involved in the transmission of *Dirofilaria* spp., although the presence of these nematodes has been confirmed in their native range (Kido et al., 2011). In contrast, two raccoon individuals were found infected with *D. immitis*, even though this infection has not previously been documented in European raccoon populations. One of the positive samples dates back to 2002, whereas the first autochthonous case of *D. immitis* infection in Hungary was not observed until 2007 in a domestic dog (Bacsádi et al., 2016). This suggests that the infected raccoon may have been an imported individual of unknown origin, particularly since raccoons were being imported and kept as pets in Europe during that period without regulation. In the

southern USA and Mexico, *Dirofilaria tenuis* infection is frequently found in raccoons (Hernández-Núñez et al., 2024). It is therefore plausible that genetic similarities between *D. tenuis* and *D. immitis* facilitate molecular compatibility in these hosts (Hernández-Núñez et al., 2024). Based on our results, the role of raccoons as reservoirs or definitive hosts remains uncertain; they are likely to function as dead-end hosts, suggesting that transmission through them is probably limited, but further studies are needed.

Among native carnivore species, *D. immitis* showed the highest prevalence in red foxes and badgers, suggesting these species may play roles in the sylvatic cycle of this parasite, and in both intra- and inter-species transmission. A previous study reported a 3.7% prevalence of *D. immitis* in red foxes (Tolnai et al., 2014), a result consistent with our data. The first record of *D. immitis* in badgers in Europe (excluding imported cases) was in Romania in 2022, followed by two additional cases in Greece in 2024 (Ionică et al., 2022; Markakis et al., 2024). Our study identified two more infected badgers, documenting the first such cases in Hungary. Although the raccoon dog is a known reservoir of *D. immitis* in its native range in East Asia (Nakagaki et al., 2000), we found no evidence of infection in this species in Hungary. Compared with previous prevalence data, it is evident that *Dirofilaria* infections are increasing in both individual numbers and geographical spread among wild mammal populations in Hungary and Europe. Based on our findings, *D. immitis* was present in four of the six mammal species examined, suggesting some of these species may contribute to its maintenance and



**Fig. 3.** Host-parasite associations. Relationship between mammal host species (a: European badger; b: golden jackal; c: raccoon; d: raccoon dog; e: red fox) and parasite species. The height of the white bars indicates the relative frequency among infected individuals and identified parasites. Different colours are assigned to parasite species. The unidentified data represent nematode species of unknown identity, as no matching sequences were found in GenBank. Icons are licensed under CC0 via PhyloPic ([www.phylopic.org](http://www.phylopic.org)).

circulation in nature (Szentiványi and Garamszegi, 2024). However, until these hosts are confirmed as definitive or reservoir hosts, further studies are needed to substantiate this hypothesis. *Dirofilaria immitis* is transmitted by mosquitoes, with microfilariae circulating in the host's bloodstream and infective larvae transmitted during blood-feeding. In Hungary, several mosquito species are implicated as potential vectors, particularly *Culex pipiens*, *Aedes vexans*, and the invasive *Aedes albopictus* and *Aedes koreicus* (Szentiványi et al., 2025; Varga et al., 2025). Recent studies indicate that both the abundance and distribution of these vectors have expanded in Europe, including Hungary, likely driven by climatic warming, increased precipitation variability, and anthropogenic environmental changes (Morchón et al., 2012; Garamszegi et al., 2025). It is important to note that positive samples in vertebrate hosts indicate the presence of microfilariae, which confirms active infection (Ionica et al., 2017). However, the absence of microfilariae does not necessarily indicate the pathogen is absent, as negative results can be influenced by factors such as the host's immune response, single-sex worm infections, the prepatent period, or the parasite not being present in the sampled tissue (Simón et al., 2007; Pietrzak et al., 2024). *Dirofilaria repens* was

not found in any tested carnivore samples.

The detection of *Thelazia callipaeda* in the invasive raccoon dog in Hungary is a significant finding with both epidemiological and ecological implications. This parasite has been present in western Europe for nearly 30 years (Farkas et al., 2018; Do Vale et al., 2020). In neighbouring countries, infections in red foxes have been reported in Serbia, Romania, and Slovakia, whereas in Hungary the pathogen has recently been detected in red foxes and jackals; however, the majority of cases have occurred in domestic dogs, with a single reported case in a cat (Cabanová et al., 2018; Farkas et al., 2018; Ionica et al., 2019; Nagy et al., 2026). To date, only one documented case exists in raccoon dogs (in Korea), although another species in the same genus, the Japanese raccoon dog or tanuki (*Nyctereutes viverrinus*), has shown higher prevalence in Japan (Doi et al., 2023; Jang et al., 2025). The observation that a raccoon dog in Hungary hosts this nematode species suggests that this newly introduced carnivore may serve as a novel reservoir host for the zoonotic eyeworm, hence supporting its persistence and facilitating its spread in new areas. Given the species' ongoing expansion across central and eastern Europe, their potential involvement in the life cycle of

*T. callipaeda* could contribute to the further geographical spread of this parasite. This is of particular concern as *T. callipaeda* infects domestic animals and humans, raising potential public health risks (Otašević et al., 2014). However, it is important to note that only a single infected raccoon dog was identified in our study, which suggests that, at present, this species may play only a minor or incidental role in the parasite's transmission dynamics. Nonetheless, the identification of *T. callipaeda* in an invasive mammal highlights the importance of monitoring such species, as they may influence the emergence and maintenance of vector-borne zoonoses in changing ecosystems (Farkas et al., 2018; Doi et al., 2023; Jang et al., 2025).

In Hungary, *Crenosoma vulpis* is one of the most widespread lungworms in foxes, with particularly high prevalence in the Northern Hungarian Mountains and Transdanubia (Tolnai et al., 2015). It was present in three species, including foxes, badgers, and invasive raccoons. The latter two are rarely reported as hosts, suggesting they may serve as incidental hosts of *Crenosoma* spp. (Deak et al., 2023). Prior to our findings, *C. vulpis* has not been reported in raccoons, but in the USA, a related species, *C. goblei*, frequently infects wild raccoons (Groves et al., 2020). The detection of *C. vulpis* in invasive mammals in Hungary highlights the expanding host range of this lungworm, suggesting that invasive species may act as new reservoirs or carriers. This finding could indicate potential changes in parasite transmission dynamics, which may impact both wildlife and domestic animals. Monitoring *C. vulpis* in invasive hosts is therefore crucial for understanding its spread and managing parasitic infections in the region.

The presence of *A. vasorum* has been documented in domestic dogs, red foxes and golden jackals, with early reports dating back to 1960 in Hungary (Majoros et al., 2010). Our work has also revealed the presence of this parasite in red foxes, showing similar patterns to previous studies. Previous work has examined 567 red foxes in Romania and found a 4.2% prevalence of *A. vasorum* infection, with no significant differences regarding host sex, age, or county of origin (Deak et al., 2017). In Hungary, a large-scale serological survey involving 1247 dogs revealed that 1.36% were positive for *A. vasorum*, indicating an endemic presence of the parasite in domestic canid populations (Schnyder et al., 2015). The distribution of *A. vasorum* appears to be influenced by environmental factors, particularly annual precipitation and temperature, which affect the survival of intermediate hosts such as slugs and snails (Tolnai et al., 2015). Monitoring the prevalence and distribution of *A. vasorum* in wild canid populations is essential for understanding the spread of the disease and implementing effective control measures to protect both wildlife and domestic animals.

Lastly, *Spirocerca lupi* was also found in a single red fox individual. This parasitic nematode primarily infects canids, especially domestic dogs and wild carnivores such as red foxes and golden jackals. In Europe, *S. lupi* has been reported sporadically, with higher prevalence in southern and southeastern countries (Mylonakis et al., 2001; Ferrantelli et al., 2010). In Hungary, sporadic cases in domestic dogs have been reported; however, these remain rare in comparison to endemic regions (Psáder et al., 2017).

A limitation of this study is that only blood and/or spleen samples were screened as only these were available, which are not the primary tissues for several of the parasites detected. For instance, *T. callipaeda* is generally not present in blood or spleen, as it can be found in the conjunctival sac. Hence, the detection of its DNA likely reflects either a microtrauma causing these parasites to enter blood or circulating cell-free DNA from worms. Consequently, some infections may have been missed, potentially leading to an underestimation of prevalence for certain species.

## 5. Conclusions

We found that several parasitic species, including potentially zoonotic ones, infect multiple hosts, including invasive species, suggesting that interspecies host switching may be more common than previously

assumed. The presence of *D. immitis* and *C. vulpis* in invasive raccoons further stresses their importance in disease networks and highlights the need for additional research on these rapidly spreading host species. Host spectrum and infection patterns of filarial nematodes in wild mammals often remain understudied, and the role of wild carnivores in interspecific transmission is also unclear. Monitoring both invasive and native carnivore species for nematodes is essential for understanding and mitigating the risks they pose to animal and human health. The spread of these parasites among wild carnivores can sustain their life cycles in nature, increasing the likelihood of transmission to domestic animals and humans, particularly in areas where human and wildlife habitats overlap. Equally important are nematodes like *C. vulpis*, which, while not zoonotic, can cause serious respiratory disease in domestic dogs. The presence of such parasites in wildlife indicates environmental circulation and highlights the risk of infection to companion animals, especially in rural or peri-urban settings where contact with wild hosts or their habitats is possible. Additionally, reverse spillover from domestic carnivores to wildlife is a growing concern. In areas with high densities of domestic dogs and cats, especially those not treated regularly with antiparasitic drugs, parasites can be introduced into wild populations. This can alter parasite-host dynamics, establish new reservoirs, and potentially threaten native wildlife health and conservation efforts. Thus, regular surveillance of both wild and domestic carnivores is essential for understanding parasite transmission dynamics, predicting outbreaks, and implementing effective control strategies.

## Ethical approval

Not applicable. Legislative background of mesocarnivore control is detailed in the following document: <https://zenodo.org/records/15645626>.

## CRediT authorship contribution statement

**Tamara Szentiványi:** Conceptualisation, Formal analysis, Investigation, Methodology, Project administration, Supervision, Visualisation, Writing - original draft, Writing - review & editing. **Borbála Bruszniczky:** Conceptualisation, Formal analysis, Investigation, Methodology, Visualisation, Writing - review & editing. **Zsolt Bíró:** Investigation, Methodology, Writing - review & editing. **Krisztián Katona:** Investigation, Methodology, Writing - review & editing. **Ágnes Klein:** Investigation, Writing - review & editing. **Attila Bende:** Investigation, Writing - review & editing. **László Bánáti:** Investigation, Writing - review & editing. **Gábor Vass:** Investigation, Writing - review & editing. **Pál Lehotzky:** Investigation, Writing - review & editing. **Dorottya Kovács:** Investigation, Writing - review & editing. **Gábor Földvári:** Investigation, Methodology, Project administration, Writing - review & editing. **Ágnes Csinicsik:** Investigation, Methodology, Project administration, Writing - review & editing. **Gábor Nagy:** Investigation, Methodology, Project administration, Writing - review & editing. **Rebeka Ráhel Nagy:** Investigation, Methodology, Writing - review & editing. **Máté Miklós:** Investigation, Methodology, Writing - review & editing. **Kriszta Lilla Szabadi:** Investigation, Methodology, Writing - review & editing. **Éva S. Szabó:** Investigation, Methodology, Writing - review & editing. **László Z. Garamszegi:** Conceptualisation, Investigation, Writing - review & editing.

## Funding

Tamara Szentiványi was supported by the AXA Research Fund and by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences. Our work was supported by funds from the Hungary's National Research, Development and Innovation Office (K-135841, FK-138563, PD-135143, ADVANCED 152427), and the Sustainable Development and Technologies National Programme of the Hungarian Academy of Sciences (László Z. Garamszegi: FFT NP FTA).

## Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments

The authors gratefully acknowledge the hunters for their valuable assistance in collecting samples, without which this study would not have been possible. We are grateful to the reviewers for their time and constructive feedback.

## Data availability

The dataset supporting the conclusions of this article is included within the article.

## References

- Čabanová, V., Miterpáková, M., Oravec, M., Hurníková, Z., Jerg, S., Nemčíková, G., et al., 2018. Nematode *Thelazia callipaeda* is spreading across Europe. The first survey of red foxes from Slovakia. *Acta Parasitol.* 63, 160–166. <https://doi.org/10.1515/ap-2018-0018>.
- Arcenillas-Hernández, I., Ruiz de Ybáñez, M.R., Tizzani, P., Pérez-Cutillas, P., Martínez-Carrasco, C., 2024. Influence of environmental factors on the occurrence of gastrointestinal and cardiopulmonary nematodes in the red fox in the semi-arid Mediterranean areas of the Iberian Peninsula. *Res. Vet. Sci.* 171, 105199. <https://doi.org/10.1016/j.rvsc.2024.105199>.
- Bacsadi, Á., Papp, A., Szeredi, L., Tóth, G., Nemes, C., Imre, V., et al., 2016. Retrospective study on the distribution of *Dirofilaria immitis* in dogs in Hungary. *Vet. Parasitol.* 220, 83–86. <https://doi.org/10.1016/j.vetpar.2016.03.001>.
- Balog, T., Nagy, G., Halász, T., Csányi, E., Zomborszky, Z., Csivicsik, Á., 2021. The occurrence of *Echinococcus* spp. in golden jackal (*Canis aureus*) in southwestern Hungary: should we need to rethink its expansion? *Parasitol. Int.* 80, 102214. <https://doi.org/10.1016/j.parint.2020.102214>.
- Beltrán-Beck, B., García, F.J., Gortázar, C., 2012. Raccoons in Europe: disease hazards due to the establishment of an invasive species. *Eur. J. Wildl. Res.* 58, 5–15. <https://doi.org/10.1007/s10344-011-0600-4>.
- Bertos, E., Sánchez-Cerdá, M., Virgós, E., Gil-Sánchez, J.M., Moleón, M., 2023. *Thelazia callipaeda* as a potential new threat to European wildcats: insights from an eco-epidemiological study. *Vet. Res. Commun.* 47, 2153–2160. <https://doi.org/10.1007/s11259-023-10071-8>.
- Bijl, H., Schally, G., Márton, M., Heltai, M., Csányi, S., 2024. From invaders to residents: the golden jackal (*Canis aureus*) expansion in Hungary since the mid-1990s. *PLoS One* 19, e0306489. <https://doi.org/10.1371/journal.pone.0306489>.
- Blanch-Lázaro, B., Mitton, Z., Tudor, C., Hindle, J., Martineau, H., Fox, M., et al., 2018. Genetic diversity and population structure of *Angiostrongylus vasorum* parasites within and between local urban foxes (*Vulpes vulpes*). *Vet. Parasitol.* 262, 42–46. <https://doi.org/10.1016/j.vetpar.2018.09.008>.
- Brunson, J.C., Read, Q.D., 2018. Package “ggalluvial”. <https://cran.r-project.org/web/packages/ggalluvial/index.html>.
- Casiraghi, M., Anderson, T.J.C., Bandi, C., Bazzocchi, C., Genchi, C., 2001. A phylogenetic analysis of filarial nematodes: comparison with the phylogeny of *Wolbachia* endosymbionts. *Parasitology* 122, 93–103. <https://doi.org/10.1017/S0031182000007149>.
- Casiraghi, M., Bain, O., Guerrero, R., Martín, C., Pocacqua, V., Gardner, S.L., et al., 2004. Mapping the presence of *Wolbachia pipientis* on the phylogeny of filarial nematodes: evidence for symbiont loss during evolution. *Int. J. Parasitol.* 34, 191–203. <https://doi.org/10.1016/j.ijpara.2003.10.004>.
- Clark, N.J., Seddon, J.M., Ślapeta, J., Wells, K., 2018. Parasite spread at the domestic animal-wildlife interface: anthropogenic habitat use, phylogeny and body mass drive risk of cat and dog flea (*Ctenocephalides* spp.) infestation in wild mammals. *Parasites Vectors* 11, 8. <https://doi.org/10.1186/s13071-017-2564-z>.
- Deak, G., Gherman, C.M., Ionică, A.M., Péter, Á., Sándor, A.D., Mihalca, A.D., 2020. Biotic and abiotic factors influencing the prevalence, intensity and distribution of *Eucoleus aerophilus* and *Crenosoma vulpis* in red foxes, *Vulpes vulpes* from Romania. *Int. J. Parasitol. Parasites Wildl.* 12, 121–125. <https://doi.org/10.1016/j.ijppaw.2020.05.009>.
- Deak, G., Gherman, C.M., Ionică, A.M., Vezendan, A.D., D’Amico, G., Matei, I.A., et al., 2017. *Angiostrongylus vasorum* in Romania: an extensive survey in red foxes, *Vulpes vulpes*. *Parasites Vectors* 10, 330. <https://doi.org/10.1186/s13071-017-2270-x>.
- Deak, G., Ionică, A.M., Gherman, C.M., Mihalca, A.D., 2023. Diversity of *Crenosoma* species in mustelids with the first molecular characterization of *C. melesi* and *C. petrowi*. *Front. Vet. Sci.* 10, 1094554. <https://doi.org/10.3389/fvets.2023.1094554>.
- do Vale, B., Lopes, A.P., da Conceição Fontes, M., Silvestre, M., Cardoso, L., Coelho, A.C., 2020. Systematic review on infection and disease caused by *Thelazia callipaeda* in Europe: 2001–2020. *Parasite* 27, 52. <https://doi.org/10.1051/parasite/2020048>.
- Doi, K., Tokiwa, T., Imoto, M., Chou, S., Yamasaki, F., Kato, T., et al., 2023. Molecular characterization of oriental eyeworm (*Thelazia callipaeda*) detected from raccoon (*Procyon lotor*) and Japanese raccoon dog (*Nyctereutes viverrinus*) in Kanto region, Japan. *Parasites Vectors* 16, 116. <https://doi.org/10.1186/s13071-023-05736-x>.
- Duscher, G.G., Leschnik, M., Fuehrer, H.P., Joachim, A., 2015. Wildlife reservoirs for vector-borne canine, feline and zoonotic infections in Austria. *Int. J. Parasitol. Parasites Wildl.* 4, 88–96. <https://doi.org/10.1016/j.ijppaw.2014.12.001>.
- Duscher, T., Hodžić, A., Glawischnig, W., Duscher, G.G., 2017. The raccoon dog (*Nyctereutes procyonoides*) and the raccoon (*Procyon lotor*) - their role and impact of maintaining and transmitting zoonotic diseases in Austria, Central Europe. *Parasitol. Res.* 116, 1411–1416. <https://doi.org/10.1007/s00436-017-5405-2>.
- Farkas, R., Mag, V., Gyurkovszky, M., Takács, N., Vörös, K., Solymosi, N., 2020. The current situation of canine dirofilariosis in Hungary. *Parasitol. Res.* 119, 129–135. <https://doi.org/10.1007/s00436-019-06478-5>.
- Farkas, R., Solymosi, N., Takács, N., Hornyák, Á., Hornok, S., Nachum-Biala, Y., et al., 2014. First molecular evidence of *Hepatozoon canis* infection in red foxes and golden jackals from Hungary. *Parasites Vectors* 7, 303. <https://doi.org/10.1186/1756-3305-7-303>.
- Farkas, R., Takács, N., Gyurkovszky, M., Henszelmann, N., Kisgergely, J., Balka, G., et al., 2018. The first feline and new canine cases of *Thelazia callipaeda* (Spirurida: Thelaziidae) infection in Hungary. *Parasites Vectors* 11, 338. <https://doi.org/10.1186/s13071-018-2925-2>.
- Ferrantelli, V., Riili, S., Vicari, D., Percipalle, M., Chetta, M., Monteverde, V., et al., 2010. *Spirocerca lupi* isolated from gastric lesions in foxes (*Vulpes vulpes*) in Sicily (Italy). *Pol. J. Vet. Sci.* 13, 465–471.
- Fuehrer, H.P., Morelli, S., Unterköfler, M.S., Bajzer, A., Bakran-Lebl, K., Dwuznik-Szarek, D., et al., 2021. *Dirofilaria* spp. and *Angiostrongylus vasorum*: current risk of spreading in central and northern Europe. *Pathogens* 10, 1268. <https://doi.org/10.3390/pathogens10101268>.
- Garamszegi, L.Z., Soltész, Z., Szentiványi, T., Kurucz, K., Nagy, G., Bede-Fazekas, Á., 2025. Identifying ecological factors mediating the spread of three invasive mosquito species: citizen science-informed prediction. *J. Pest. Sci.* 98, 913–928. <https://doi.org/10.1007/s10340-024-01841-7>.
- Gecchele, L.V., Pedersen, A.B., Bell, M., 2020. Fine-scale variation within urban landscapes affects marking patterns and gastrointestinal parasite diversity in red foxes. *Ecol. Evol.* 10, 13796–13809. <https://doi.org/10.1002/ece3.6970>.
- Genchi, C., Kramer, L.H., 2020. The prevalence of *Dirofilaria immitis* and *D. repens* in the Old World. *Vet. Parasitol.* 280, 108995. <https://doi.org/10.1016/j.vetpar.2019.108995>.
- Gherman, C.M., Mihalca, A.D., 2017. A synoptic overview of golden jackal parasites reveals high diversity of species. *Parasites Vectors* 10, 419. <https://doi.org/10.1186/s13071-017-2329-8>.
- Groves, B.A., Yabsley, M.J., Swanepoel, L., Garner, M.M., 2020. Lungworm (*Crenosoma goblei*) infection in unweaned free-ranging raccoons (*Procyon lotor*) in Washington state, USA. *J. Wildl. Dis.* 56, 419–423. <https://doi.org/10.7589/2019-03-060>.
- Han, B.A., Castellanos, A.A., Schmidt, J.P., Fischhoff, I.R., Drake, J.M., 2021. The ecology of zoonotic parasites in the Carnivora. *Trends Parasitol.* 37, 1096–1110. <https://doi.org/10.1016/j.pt.2021.08.006>.
- Hernández-Núñez, A., Vidal-Martínez, V.M., Aguirre-Macedo, M.L., 2024. New distribution record, morphological and molecular characterization of *Dirofilaria (Nochiella) tenuis* (Nematoda: Onchocercidae) in raccoons (*Procyon lotor*) from the Yucatan Peninsula, Mexico. *Int. J. Parasitol. Parasites Wildl.* 25, 100981. <https://doi.org/10.1016/j.ijppaw.2024.100981>.
- Hornok, S., Boldogh, S.A., Takács, N., Kotschán, J., Szekeres, S., Sós, E., 2022. Molecular epidemiological study on ticks and tick-borne protozoan parasites (Apicomplexa: *Cytauxzoon* and *Hepatozoon* spp.) from wild cats (*Felis silvestris*), Mustelidae and red squirrels (*Sciurus vulgaris*) in central Europe, Hungary. *Parasites Vectors* 15, 174. <https://doi.org/10.1186/s13071-022-05271-1>.
- Ionică, A.M., Deak, G., Boncea, R., Gherman, C.M., Mihalca, A.D., 2022. The European badger as a new host for *Dirofilaria immitis* and an update on the distribution of the heartworm in wild carnivores from Romania. *Pathogens* 11, 420. <https://doi.org/10.3390/pathogens11040420>.
- Ionică, A.M., Deak, G., D’Amico, G., Stan, G.F., Chieamera, G.B., Constantinescu, I.C., et al., 2019. *Thelazia callipaeda* in mustelids from Romania with the European badger, *Meles meles*, as a new host for this parasite. *Parasites Vectors* 12, 370. <https://doi.org/10.1186/s13071-019-3631-4>.
- Ionică, A.M., Matei, I.A., D’Amico, G., Ababii, J., Daskalaki, A.A., Sándor, A.D., et al., 2017. Filarioid infections in wild carnivores: a multispecies survey in Romania. *Parasites Vectors* 10, 332. <https://doi.org/10.1186/s13071-017-2269-3>.
- Ionică, A.M., Matei, I.A., D’Amico, G., Daskalaki, A.A., Juránková, J., Ionescu, D.T., et al., 2016. Role of golden jackals (*Canis aureus*) as natural reservoirs of *Dirofilaria* spp. in Romania. *Parasites Vectors* 9, 240. <https://doi.org/10.1186/s13071-016-1524-3>.
- Jacsó, O., Mándoki, M., Majoros, G., Pétsch, M., Mortarino, M., Genchi, C., et al., 2009. First autochthonous *Dirofilaria immitis* (Leidy, 1856) infection in a dog in Hungary. *Helminthologia* 46, 159–161. <https://doi.org/10.2478/s11687-009-0030-y>.
- Jang, J., Park, Y.S., Yun, Y.M., Eom, K.S., Choe, S., 2025. *Thelazia callipaeda* (Nematoda: Spirurida) infections in 2 wildlife species, *Prionailurus bengalensis* and *Nyctereutes procyonoides*, in Korea. *Parasites Hosts Dis.* 63, 95–101. <https://doi.org/10.3347/PHD.24079>.
- Jerzsele, Á., Kovács, D., Fábíán, P., Fehérvári, P., Paszerbovics, B., Bali, K., et al., 2025. New insights into the prevalence of *Dirofilaria immitis* in Hungary. *Animals* 15, 1198. <https://doi.org/10.3390/ani15091198>.
- Karamon, J., Dąbrowska, J., Kochanowski, M., Samorek-Pieróg, M., Sroka, J., Różycki, M., et al., 2018. Prevalence of intestinal helminths of red foxes (*Vulpes*

- vulpes*) in central Europe (Poland): a significant zoonotic threat. *Parasites Vectors* 11, 436. <https://doi.org/10.1186/s13071-018-3021-3>.
- Kauhala, K., Kowalczyk, R., 2011. Invasion of the raccoon dog *Nyctereutes procyonoides* in Europe: history of colonization, features behind its success, and threats to native fauna. *Curr. Zool.* 57, 584–598. <https://doi.org/10.1093/czoolo/57.5.584>.
- Kellner, A., Carver, S., Scorza, V., McKee, C.D., Lappin, M., Crooks, K.R., et al., 2018. Transmission pathways and spillover of an erythrocytic bacterial pathogen from domestic cats to wild felids. *Ecol. Evol.* 8, 9779–9792. <https://doi.org/10.1002/ece3.4451>.
- Kido, N., Wada, Y., Takahashi, M., Kamegaya, C., Omiya, T., Yamamoto, Y., 2011. Prevalence of *Dirofilaria immitis* infection in living raccoon dogs assessed by hematological examination. *J. Vet. Med. Sci.* 73, 845–847. <https://doi.org/10.1292/jvms.10-0512>.
- Kotodziej-Sobocińska, M., 2019. Factors affecting the spread of parasites in populations of wild European terrestrial mammals. *Mammal. Res.* 64, 301–318. <https://doi.org/10.1007/s13364-019-00423-8>.
- Kravchenko, V., Itin, G., Kartashev, V., Ermakov, A., Kartashov, S., Diosdado, A., et al., 2016. *Dirofilaria immitis* and *D. repens* in sylvatic reservoirs of Krasnodar Krai (Russian Federation). *Vet. Parasitol. Reg. Stud. Reports* 6, 35–38. <https://doi.org/10.1016/j.vprsr.2016.08.004>.
- Kärssin, A., Häkkinen, L., Niin, E., Peik, K., Vilem, A., Jokelainen, P., et al., 2017. *Trichinella* spp. biomass has increased in raccoon dogs (*Nyctereutes procyonoides*) and red foxes (*Vulpes vulpes*) in Estonia. *Parasites Vectors* 10, 609. <https://doi.org/10.1186/s13071-017-2571-0>.
- Langner, T., Otranto, D., Bezerra-Santos, M.A., Franzen, J., Johne, A., Tonanzi, D., et al., 2024. Detection of *Spirocerca lupi* and an unknown *Trichinella*-like nematode in raccoon (*Procyon lotor*). *Int. J. Parasitol. Parasites Wildl.* 23, 100911. <https://doi.org/10.1016/j.ijppaw.2024.100911>.
- Latrofa, M.S., Lia, R.P., Giannelli, A., Colella, V., Santoro, M., D'Alessio, N., et al., 2015. *Crenosoma vulpis* in wild and domestic carnivores from Italy: a morphological and molecular study. *Parasitol. Res.* 114, 3611–3617. <https://doi.org/10.1007/s00436-015-4583-z>.
- Laurimaa, L., Süld, K., Davison, J., Moks, E., Valdmann, H., Saarma, U., 2016. Alien species and their zoonotic parasites in native and introduced ranges: the raccoon dog example. *Vet. Parasitol.* 219, 24–33. <https://doi.org/10.1016/j.vetpar.2016.01.020>.
- Lemming, L., Jørgensen, A.C., Nielsen, L.B., Nielsen, S.T., Mejer, H., Chriél, M., et al., 2020. Cardiopulmonary nematodes of wild carnivores from Denmark: do they serve as reservoir hosts for infections in domestic animals? *Int. J. Parasitol. Parasites Wildl.* 13, 90–97. <https://doi.org/10.1016/j.ijppaw.2020.08.001>.
- Lesniak, I., Heckmann, I., Heitlinger, E., Szentiks, C.A., Nowak, C., Harms, V., et al., 2017. Population expansion and individual age affect endoparasite richness and diversity in a recolonising large carnivore population. *Sci. Rep.* 7, 41730. <https://doi.org/10.1038/srep41730>.
- Mackenstedt, U., Jenkins, D., Romig, T., 2015. The role of wildlife in the transmission of parasitic zoonoses in peri-urban and urban areas. *Int. J. Parasitol. Parasites Wildl.* 4, 71–79. <https://doi.org/10.1016/j.ijppaw.2015.01.006>.
- Majoros, G., Fukár, O., Farkas, R., 2010. Autochthonous infection of dogs and slugs with *Angiostrongylus vasorum* in Hungary. *Vet. Parasitol.* 174, 351–354. <https://doi.org/10.1016/j.vetpar.2010.09.012>.
- Marin, A.M., Popovici, D.C., Dărăbuș, G., Marian, C., Nițușcă, D., Mederle, N., 2023. The first identification of *Trichinella britovi* in the raccoon dog (*Nyctereutes procyonoides*) in Romania. *Pathogens* 12, 1132. <https://doi.org/10.3390/pathogens12091132>.
- Markakis, G., Sioutas, G., Bitchava, D., Komnenou, A., Ganoti, M., Papadopoulos, E., 2024. Is the European badger a new host for *Dirofilaria immitis*? The first records in Greece. *Parasitol. Res.* 123, 118. <https://doi.org/10.1007/s00436-024-08141-0>.
- Mitková, B., Hrazdilová, K., D'Amico, G., Duscher, G.G., Suchentrunk, F., Forejtek, P., et al., 2017. Eurasian golden jackal as host of canine vector-borne protists. *Parasites Vectors* 10, 183. <https://doi.org/10.1186/s13071-017-2110-z>.
- Mitreă, I.B., Iani, A.D., Gherman, C.M., Cazan, C.D., Ionică, A.M., Deak, G., et al., 2025. Golden jackals (*Canis aureus*) as novel hosts for *Angiostrongylus vasorum* in Romania. *Vet. Parasitol. Reg. Stud. Reports* 64, 101335. <https://doi.org/10.1016/j.vprsr.2025.101335>.
- Morchón, R., Carretón, E., González-Miguel, J., Mellado-Hernández, I., 2012. Heartworm disease (*Dirofilaria immitis*) and their vectors in Europe - new distribution trends. *Front. Physiol.* 3, 196. <https://doi.org/10.3389/fphys.2012.00196>.
- Morgan, E.R., Modry, D., Paredes-Esquivel, C., Foronda, P., Traversa, D., 2021. Angiostrongylosis in animals and humans in Europe. *Pathogens* 10, 1236. <https://doi.org/10.3390/pathogens10101236>.
- Mylonakis, M.E., Koutinas, A.F., Liapi, M.V., Saridomichelakis, M.N., Rallis, T.S., 2001. A comparison of the prevalence of *Spirocerca lupi* in three groups of dogs with different life and hunting styles. *J. Helminthol.* 75, 359–361. <https://doi.org/10.1017/S0022149X01000555>.
- Nagy, E., Nagy, R.R., Miklós, M., Szekeres, S., Abdalrahman, B.M., Földvári, G., et al., 2026. Eye to eye with *Thelazia*-infected canids in Central European forests. *Curr. Res. Parasitol. Vector-Borne Dis.* 9, 100353. <https://doi.org/10.1016/j.crpvbd.2026.100353>.
- Nakagaki, K., Suzuki, T., Hayama, S.I., Kanda, E., 2000. Prevalence of dirofilarial infection in raccoon dogs in Japan. *Parasitol. Int.* 49, 253–256. [https://doi.org/10.1016/S1383-5769\(00\)00049-0](https://doi.org/10.1016/S1383-5769(00)00049-0).
- Oksanen, A., Siles-Lucas, M., Karamon, J., Possenti, A., Conraths, F.J., Romig, T., et al., 2016. The geographical distribution and prevalence of *Echinococcus multilocularis* in animals in the European Union and adjacent countries: a systematic review and meta-analysis. *Parasites Vectors* 9, 519. <https://doi.org/10.1186/s13071-016-1746-4>.
- Otašević, S., Božinović, M.T., Tasić, A., Petrović, A., Petrović, V., 2014. *Thelazia callipaeda* and eye infections. *Acta Fac. Med. Naiss.* 31, 171–176. <https://doi.org/10.2478/afmna-2014-0021>.
- Pietrzak, D., Łuczak, J.W., Wiśniewski, M., 2024. Detecting *Dirofilaria immitis*: current practices and novel diagnostic methods. *Pathogens* 13, 950. <https://doi.org/10.3390/pathogens13110950>.
- Pilarczyk, B.M., Tomza-Marciniak, A.K., Pilarczyk, R., Rząd, I., Bąkowska, M.J., Udała, J. M., et al., 2022. Infection of raccoon dogs (*Nyctereutes procyonoides*) from northern Poland with gastrointestinal parasites as a potential threat to human health. *J. Clin. Med.* 11, 1277. <https://doi.org/10.3390/jcm11051277>.
- Plumer, L., Davison, J., Saarma, U., Cameron, E.Z., 2014. Rapid urbanization of red foxes in Estonia: distribution, behaviour, attacks on domestic animals, and health-risks related to zoonotic diseases. *PLoS One* 9, e115124. <https://doi.org/10.1371/journal.pone.0115124>.
- Psáder, R., Balogh, M., Pápa, K., Sterczler, Á., Lukács, Z., Harnos, A., 2017. Occurrence of *Spirocerca lupi* infection in Hungarian dogs referred for gastroscopy. *Parasitol. Res.* 116, 99–108. <https://doi.org/10.1007/s00436-017-5496-9>.
- QGIS Development Team, 2023. QGIS Geographic Information System. Open Source Geospatial Foundation Project. <https://qgis.org>.
- R Core Team, 2023. R: A Language and Environment for Statistical Computing (version 4.3.1). R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org>.
- Roy, H.E., Tricarico, E., Hassall, R., Johns, C.A., Roy, K.A., Scalera, R., et al., 2023. The role of invasive alien species in the emergence and spread of zoonoses. *Biol. Invasions* 25, 1249–1264. <https://doi.org/10.1007/s10530-022-02978-1>.
- Schally, G., Bijl, H., Kashyap, B., Márton, M., Bóti, S., Katona, K., et al., 2024. Analysis of the raccoon (*Procyon lotor*) and common raccoon dog (*Nyctereutes procyonoides*) spatiotemporal changes based on hunting bag data in Hungary. *Diversity* 16, 532. <https://doi.org/10.3390/d16090532>.
- Schneider, C., Kratzer, W., Binzberger, A., Schlingeloff, P., Baumann, S., Romig, T., et al., 2023. *Echinococcus multilocularis* and other zoonotic helminths in red foxes (*Vulpes vulpes*) from a southern German hotspot for human alveolar echinococcosis. *Parasites Vectors* 16, 425. <https://doi.org/10.1186/s13071-023-06026-2>.
- Schnyder, M., Schaper, R., Lukács, Z., Hornok, S., Farkas, R., 2015. Combined serological detection of circulating *Angiostrongylus vasorum* antigen and parasite-specific antibodies in dogs from Hungary. *Parasitol. Res.* 114, 145–154. <https://doi.org/10.1007/s00436-015-4520-1>.
- Schug, K., Krämer, F., Schaper, R., Hirtzmann, J., Failing, K., Hermsilla, C., et al., 2018. Prevalence survey on lungworm (*Angiostrongylus vasorum*, *Crenosoma vulpis*, *Eucoleus aerophilus*) infections of wild red foxes (*Vulpes vulpes*) in central Germany. *Parasites Vectors* 11, 85. <https://doi.org/10.1186/s13071-018-2672-4>.
- Simón, F., Kramer, L.H., Román, A., Blasini, V., Morchón, R., Marcos-Atxutegi, C., et al., 2007. Immunopathology of *Dirofilaria immitis* infection. *Vet. Res. Commun.* 31, 161–171. <https://doi.org/10.1007/s11259-006-3387-0>.
- Sréter, T., Széll, Z., Marucci, G., Pozio, E., Varga, I., 2003. Extraintestinal nematode infections of red foxes (*Vulpes vulpes*) in Hungary. *Vet. Parasitol.* 115, 329–334. [https://doi.org/10.1016/S0304-4017\(03\)00217-6](https://doi.org/10.1016/S0304-4017(03)00217-6).
- Stope, M., 2019. Wild raccoons in Germany as a reservoir for zoonotic agents. *Eur. J. Wildl. Res.* 65, 94. <https://doi.org/10.1007/s10344-019-1339-6>.
- Stronen, A.V., Molnar, B., Ciucci, P., Darimont, C.T., Grotto, L., Paquet, P.C., et al., 2021. Cross-continental comparison of parasite communities in a wide-ranging carnivore suggests associations with prey diversity and host density. *Ecol. Evol.* 11, 10338–10352. <https://doi.org/10.1002/ece3.7837>.
- Sukara, R., Chochlakis, D., Čirović, D., Penezić, A., Mihaljica, D., Čakić, S., et al., 2018. Golden jackals (*Canis aureus*) as hosts for ticks and tick-borne pathogens in Serbia. *Ticks Tick. Borne Dis.* 9, 1090–1097. <https://doi.org/10.1016/j.ttbdis.2018.04.003>.
- Sutor, A., Schwarz, S., Conraths, F.J., 2014. The biological potential of the raccoon dog (*Nyctereutes procyonoides* Gray, 1834) as an invasive species in Europe - new risks for disease spread? *Acta Theriol.* 59, 49–59. <https://doi.org/10.1007/s13364-013-0138-9>.
- Szentiványi, T., González, L.V., Klein, Á., Soltész, Z., Garamszegi, L.Z., 2025. Complementing community science with xenomonitoring: understanding the eco-epidemiology of *Dirofilaria immitis* infection in dogs and mosquitoes. *Parasites Vectors* 18, 233. <https://doi.org/10.1186/s13071-025-06882-0>.
- Szentiványi, T., Garamszegi, L.Z., 2024. Is dirofilariosis an emerging conservation threat in wild carnivores across the Palearctic? *Mamm. Rev.* 54, 427–440. <https://doi.org/10.1111/mam.12353>.
- Széll, Z., Marucci, G., Pozio, E., Sréter, T., 2013. *Echinococcus multilocularis* and *Trichinella spiralis* in golden jackals (*Canis aureus*) of Hungary. *Vet. Parasitol.* 197, 393–396. <https://doi.org/10.1016/j.vetpar.2013.04.032>.
- Takács, A., Szabó, L., Juhász, L., Takács, A., Lanszki, J., Takács, P., et al., 2014. Data on the parasitological status of golden jackal (*Canis aureus* L., 1758) in Hungary. *Acta Vet. Hung.* 62, 33–41. <https://doi.org/10.1556/AVet.2013.058>.

- Tolnai, Z., Széll, Z., Sproch, Á., Szeredi, L., Sréter, T., 2014. *Dirofilaria immitis*: an emerging parasite in dogs, red foxes and golden jackals in Hungary. *Vet. Parasitol.* 203, 339–342. <https://doi.org/10.1016/j.vetpar.2014.04.004>.
- Tolnai, Z., Széll, Z., Sréter, T., 2015. Environmental determinants of the spatial distribution of *Angiostrongylus vasorum*, *Crenosoma vulpis* and *Eucoleus aerophilus* in Hungary. *Vet. Parasitol.* 207, 355–358. <https://doi.org/10.1016/j.vetpar.2014.12.008>.
- Van Hien, H., Phuc, P.T.H., Lan, N.T.K., Doanh, P.N., 2021. Morphological and molecular characterization of *Spirocerca lupi* (Nematoda: Spirocercidae) from domestic dogs in Vietnam with reference to *Spirocerca vulpis*. *Parasitol. Int.* 84, 102381. <https://doi.org/10.1016/j.parint.2021.102381>.
- Varga, Z., Csiba, R., Ábrahám, Á., Pásztor, D., Németh, C., Kemenesi, G., et al., 2025. Investigating the impact of endemic mosquitoes and invasive *Aedes* species on the circulation of *Dirofilaria* nematodes. *Parasites Vectors* 18, 266. <https://doi.org/10.1186/s13071-025-06901-0>.
- Veronesi, F., Deak, G., Diakou, A., 2023. Wild mesocarnivores as reservoirs of endoparasites causing important zoonoses and emerging bridging infections across Europe. *Pathogens* 12, 178. <https://doi.org/10.3390/pathogens12020178>.
- Wickham, H., Chang, W., 2016. *ggplot2: Create elegant data visualisations using the grammar of graphics*. Springer, Cham, Switzerland. <https://ggplot2.tidyverse.org/>.