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Wildlife and parasitic infections: A One Health perspective in Greece

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A B S T R A C T

While research on the parasitic fauna of wildlife in Greece is currently limited, conducted studies have provided valuable insights into the prevalence of parasitic infections in wild carnivores, omnivores, and herbivores. This review consolidates the existing data on the endoparasites detected in wild animals in Greece, specifically focusing on those that pose established or potential zoonotic risks. Over the last 60 years, various parasite species such as *Leishmania infantum*, *Cryptosporidium* spp., *Toxoplasma gondii*, *Sarcocystis* spp., *Toxocara canis*, *Ancylostoma caninum, Capillaria* spp., *Baylisascaris* spp., *Trichinella* spp., *Thelazia callipaeda, Dirofilaria immitis*, *Echinococcus granulosus*, *Mesocestoides* sp., *Taenia* spp., *Alaria alata*, and *Dicrocoelium dendriticum* have been identified in wildlife in Greece. These findings have become increasingly relevant due to the growing interaction between humans and wild animals, which now extends to urban environments, as well as the increased contact between wild and domestic animals. This is further complicated by the geographical expansion of vector-borne diseases due to global warming and the increased movements of humans and animals. Surveillance and monitoring of parasitic infections in Greek wildlife is warranted, and it should be based on interdisciplinary investigations considering the interconnectedness of human, wild, and domestic animals, as well as environmental health, in line with the One Health approach.

1. Introduction

Greece has different ecosystems and landscapes, rich habitat diversity, and a Mediterranean climate. These conditions provide a nurturing environment for a plethora of Greek fauna species (Koulelis et al., 2023). Today, more than 23,130 animal species have been documented in Greece's terrestrial and freshwater environments (Convention on Biological Diversity, 2016). However, biodiversity in Greece faces numerous threats due to anthropogenic activities, such as forest degradation, habitat fragmentation, unsustainable agricultural practices, climate change, and pollution of soil, water, and air (Koulelis et al., 2023).

Apart from their impact on biodiversity, anthropogenic activities have also brought humans, domestic and wild animals closer (Iliopoulos et al., 2021; Tampakis et al., 2023). Occasionally, this interaction results in human-wildlife conflicts, primarily occurring in rural areas. Nevertheless, in recent years, this conflict has also spread to urban and peri-urban areas with dense human populations due to the expanding distribution and movements of wild animals in human-dominated landscapes (Tampakis et al., 2023). This trend is especially evident with red foxes (*Vulpes vulpes*) and wild boars (*Sus scrofa*), whose population is rising. In addition to other major European cities, wild boars, sometimes in groups, have been observed roaming not only in the metropolitan region of Thessaloniki in Northern Greece but also in other cities, such as the rural area of Trikala in Central Greece, known for its significant agricultural production (Tampakis et al., 2023). Urban areas may offer a secure habitat for various wild animal species, providing protection from predators, ample hiding places, and food sources ranging from discarded waste to pet food left out by residents for stray dogs and cats. The close interaction between humans and wild animals in urban settings in Greece is further emphasised by civilians admitting 54,445 animals, representing 353 species from 104 families, to the Wildlife Rehabilitation Centres ANIMA in Athens over the past 17 years (Vezyrakis et al., 2023).

Greek citizens typically intentionally encounter wild animals when visiting settings such as the ARCTUROS sanctuaries in northern Greece and the Attica Zoological Park in the region of Athens. Nonetheless, unexpected contact may also occur during outdoor activities in mountainous regions. Shepherds monitoring livestock during grazing, workers in abattoirs, veterinarians, and other support staff at Wildlife

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Hospitals and Wildlife Rehabilitation Centres are professional groups that frequently interact with wildlife (Iliopoulos et al., 2021; Vezyrakis et al., 2023). Hunters often encounter and have direct contact with wild animals while handling their game. Furthermore, hunting is a popular activity in Greece, with wild boars and European brown hares (*Lepus europaeus*) being the most hunted species (Sokos et al., 2014). It is worth noting that certain improper practices, such as skinning with bare hands and leaving game carcasses and offal in the field, can significantly contribute to environmental contamination, maintenance, and transmission of pathogens, including parasites, to other cohabiting hosts and pose a future risk for human infection (Tsokana et al., 2020).

The interaction of humans with different animal species and their pathogens is a well-recognised factor linked to an increased risk of spillover and spillback events (Ellwanger and Chies, 2021). Likewise, the escalating loss of biodiversity worldwide is expected to increase the frequency of zoonotic spillover events (Ellwanger and Chies, 2021). In contrast, this risk is reduced in ecosystems with rich biodiversity due to the so-called "dilution effect"; the prevalence of infection in reservoir hosts is reduced when a high diversity of host species exists in a habitat (Civitello et al., 2015). The risk of spillover events is influenced by the prevalence of infection in reservoir hosts, the density of infected hosts, and their distribution in a particular environment. When the barriers and factors that impede the transmission of pathogens from wild animals to the human population are breached, zoonotic spillovers can occur (Plowright et al., 2017).

This review aims to consolidate the existing information on the endoparasitic fauna of wild carnivores, omnivores, and herbivores in Greece, specifically focusing on parasites that pose established or potential zoonotic risks. Therefore, herein, the presence of zoonotic parasites in wildlife in Greece is discussed from a One Health perspective and the scientific areas that necessitate further research are highlighted, considering our current understanding of the involvement of wild animal species in the epidemiology of significant zoonotic parasites.

2. Carnivores

2.1. Red fox (Vulpes vulpes)

The red fox, known for its adaptability as a predator and scavenger, occupies a broad trophic niche. Its expansive home range is primarily influenced by food availability and accessibility (Wooster et al., 2019). This underscores the potential role of red foxes in facilitating interactions with other hosts and transmitting pathogens in diverse ecological settings.

Research conducted on red foxes in Greece revealed that they host a diverse range of parasite species (Table 1), while polyparasitism was common in all studies (Kardasis, 1953; Himonas, 1970; Papadopoulos et al., 1997; Karayiannis et al., 2015; Liatis et al., 2017).

Two of the identified genera of protozoa are of zoonotic significance. *Sarcocystis* spp. was recovered from 6.2% of red foxes admitted to wildlife hospitals and rehabilitation centres (Liatis et al., 2017), and *Leishmania infantum* infection was detected in 59.5% of the red foxes found dead in Central Greece (Karayiannis et al., 2015). The latter study demonstrated *L. infantum* infection through molecular examination of spleen-, lymph node-, and blood samples. Three out of the nine serologically examined individuals showed seroconversion. The researchers reported that the seropositive and 71.4% of the molecularly positive red foxes exhibited clinical signs compatible with canine leishmaniosis (Karayiannis et al., 2015).

Nematodes with zoonotic potential detected in red foxes in Greece include *Eucoleus aerophilus*, *Capillaria plica*, *Trichinella spiralis*, *Ancylostoma caninum*, *Uncinaria stenocephala*, *Toxocara canis*, *Toxascaris leonina*, *Dipetalonema* sp., and *Dirofilaria immitis* (Kardasis, 1953; Himonas, 1970; Papadopoulos et al., 1997; Karayiannis et al., 2015; Liatis et al., 2017).

A comprehensive study conducted on hunter-harvested and dead red foxes revealed a variety of cestodes, with *Mesocestoides* sp. being the most prevalent zoonotic species (Papadopoulos et al., 1997), followed by *Dipylidium caninum*, *Spirometra* sp., *Taenia hydatigena*, *T. crassiceps*, and *Taenia* spp. at a lower frequency (Papadopoulos et al., 1997; Karayiannis et al., 2015; Liatis et al., 2017). Notably, *Echinococcus* spp. were not found in any red foxes tested from rural areas in continental Greece and the islands of Lesbos, Rhodes, Lefkada and Chios (Papadopoulos, 1989).

Trematodes with potential zoonotic transmission were also identified in red foxes, including *Alaria alata* (Papadopoulos et al., 1997; Liatis et al., 2017) and *Brachylaima* spp. (Liatis et al., 2017).

Red foxes may carry a variety of zoonotic parasites, including *Giardia* spp., *Babesia* spp., *Toxoplasma gondii*, *Cryptosporidium* spp., *Echinococcus* spp., *Dirofilaria* spp., *Trichinella* spp., and *Thelazia callipaeda* (Veronesi et al., 2023). Given the distinctive behavioural traits of red foxes, this species has the potential to act as a bridge between the sylvatic and domestic transmission cycles. Future research investigating and monitoring the presence of parasites with zoonotic potential in red fox populations in Greece should be a priority since this species is frequently present in highly populated areas, like urban environments, in search of food (Wooster et al., 2019).

2.2. European wild cat (Felis silvestris)

The European wildcat, a predatory species, serves as a reservoir for parasites that can affect its population and potentially be transmitted to domestic cats and humans (Veronesi et al., 2023). The direct or indirect transmission of parasites at the interface between wild and domestic cats is a scenario frequently observed in rural areas. Shared intermediate and paratenic hosts, such as small rodents and birds, play a crucial role in transmitting these parasites, as they are preyed upon by both wild and domestic cats. Furthermore, the roaming behaviour of domestic cats, which can extend up to 1.1 km from their home range in search of prey, increases the likelihood of interactions with wildcats, especially in rural areas, and facilitates potential parasite transmission between the two populations (Meek, 2003).

The three studies conducted on wildcats in Greece have identified over 20 parasitic genera, with more than ten species with zoonotic potential (Table 1). The researchers have consistently reported mixed infections, highlighting the extensive biodiversity of parasitic fauna in wildcats (Papadopoulos et al., 1997; Liatis et al., 2017; Diakou et al., 2021).

Wild cats were more frequently infected with nematodes. *Toxocara cati* was the predominant species with zoonotic potential, followed by *T. leonina*, *A. caninum*, *A. tubaeforme* and *E. aerophilus*, which also displayed high prevalence rates (Papadopoulos et al., 1997; Liatis et al., 2017; Diakou et al., 2021). *Toxocara canis* and *A. caninum* are established zoonotic parasites causing visceral and ocular *larva migrans* as well as cutaneous lesions. Although *T. cati* has been implicated in zoonotic disease, its significance is likely underestimated since *T. canis* dominates the research attention (Maciag et al., 2022). As for *A. tubaeforme*, it does not appear to cause cutaneous *larva migrans*, as in the case of *A. caninum* (Bowman et al., 2010), and its zoonotic potential warrants further investigation. Other potentially zoonotic nematodes, such as *T. callipaeda* and *D. immitis*, were also identified at a lower frequency (Diakou et al., 2021).

Among cestodes, *T. taeniaeformis*, *Taenia* spp. and *Mesocestoides* sp. were frequently identified in the wild cat populations examined (Papadopoulos, 1989; Diakou et al., 2021). A countrywide study demonstrated *Sarcocystis* spp. as the most prevalent protozoan parasites with zoonotic significance, while *A. alata* and *Opisthorchis felineus* were the most dominant trematodes (Diakou et al., 2021).

Common parasites of major concern for public health, such as *T. gondii* and *Echinococcus multilocularis*, have also been identified in wildcats. Moreover, wildcats serve as reservoirs for parasites like *T. callipaeda* and *E. aerophilus* (Veronesi et al., 2023). Considering the frequent interactions between wild and domestic cats, it is pivotal to

Table 1
Endoparasites reported in carnivores in Greece.

Host/Parasite group	Parasite species	*N*	Positive samples (%)	Reference
Red fox (*Vulpes vulpes*)				
Protozoa	*Cystoisospora canis*	16	6.2	Liatis et al. (2017)
	Leishmania infantum	47	59.5	Karayiannis et al. (2015)
	Sarcocystis spp.	16	6.2	Liatis et al. (2017)
Nematoda	Ancylostomatidae	16	50.0	Liatis et al. (2017)
	Ancylostoma caninum	314	5.1	Papadopoulos et al. (1997)
		47	4.3	Karayiannis et al. (2015)
	Dirofilaria immitis	47	17.0	Karayiannis et al. (2015)
	Eucoleus aerophilus	16	31.2	Liatis et al. (2017)
	Rictularia sp.	314	17.5	Papadopoulos et al. (1997)
	Spirocerca lupi	1	100	Diakou et al. (2012)
	Toxascaris leonina	314	2.5	Papadopoulos et al. (1997)
		47	6.4	Karayiannis et al. (2015)
	Toxocara canis	314	28.6	Papadopoulos et al. (1997)
		16	18.7	Liatis et al. (2017)
	Trichostrongylus sp.	314	0.6	Papadopoulos et al. (1997)
	Trichuris vulpis	314	8.0	Papadopoulos et al. (1997)
		47	8.5	Karayiannis et al. (2015)
		16	31.2	Liatis et al. (2017)
	Uncinaria stenocephala	314	43.9	Papadopoulos et al. (1997)
Cestoda	*Diplopylidium/Joyeuxiella* spp.	16	12.5	Liatis et al. (2017)
	Dipylidium caninum	314	3.2	Papadopoulos et al. (1997)
		47	2.1	Karayiannis et al. (2015)
	Joyeuxiella echinorhynchoides	314	24.5	Papadopoulos et al. (1997)
	Mesocestoides sp.	314	73.2	Papadopoulos et al. (1997)
	Spirometra sp.	314	0.3	Papadopoulos et al. (1997)
	Taenia crassiceps	314	0.3	Papadopoulos et al. (1997)
	Taenia hydatigena	314	0.9	Papadopoulos et al. (1997)
	Taenia spp.	314	1.6	Papadopoulos et al. (1997)
		47	4.3	Karayiannis et al. (2015)
Trematoda	*Alaria alata*	314	1.6	Papadopoulos et al. (1997)
		16	6.2	Liatis et al. (2017)
	Brachylaima spp.	16	31.0	Liatis et al. (2017)
	Trematoda	16	6.2	Liatis et al. (2017)
Acanthocephala	Acanthocephala	16	25.0	Liatis et al. (2017)
	Oncicola canis	314	0.3	Papadopoulos et al. (1997)
	Pachysentis sp.	314	14.6	Papadopoulos et al. (1997)
European wild cat (*Felis silvestris*)				
Protozoa	*Cystoisospora felis*	1	100	Liatis et al. (2017)
		23 animals[a] & 62 fecal samples	26.1 and 12.9	Diakou et al. (2021)
	Cystoisospora rivolta	23 animals[a] & 62 fecal samples	13.0 and 4.8	Diakou et al. (2021)
	Sarcocystis spp.	23 animals[a] & 62 fecal samples	4.3 and 16.1	Diakou et al. (2021)
	Toxoplasma/Besnoitia/Hammondia	23 animals[a] & 62 fecal samples	4.3 and 1.6	Diakou et al. (2021)
Nematoda	*Aelurostrongylus abstrusus*	23 animals[a] & 62 fecal samples	43.5 and 9.7	Diakou et al. (2021)
	Ancylostoma caninum	4	50.0	Papadopoulos et al. (1997)
	Ancylostoma tubaeforme	23 animals[a] & 62 fecal samples	33.8 and 17.7	Diakou et al. (2021)
	Angiostrongylus chabaudi	23 animals[a] & 62 fecal samples	50.0 and 29.0	Diakou et al. (2021)
	Eucoleus aerophilus	23 animals[a] & 62 fecal samples	33.8 and 24.2	Diakou et al. (2021)
	Capillariid eggs	23 animals[a] & 62 fecal samples	13.0 and 9.7	Diakou et al. (2021)
	Cylicospirura spp.	23 animals[a] & 62 fecal samples	17.4 and 6.3	Diakou et al. (2021)
	Dirofilaria immitis	23 animals	4.3	Diakou et al. (2021)
	Oslerus spp.	23 animals	4.3	Diakou et al. (2021)
	Physaloptera spp.	23 animals[a] & 62 fecal samples	4.3 and 1.6	Diakou et al. (2021)
	Thelazia callipaeda	23 animals	8.7	Diakou et al. (2021)
	Toxocara cati	4	100	Papadopoulos et al. (1997)
		1	100	Liatis et al. (2017)
		23 animals[a] & 62 fecal samples	39.1 and 45.2	Diakou et al. (2021)
	Toxascaris leonina	4	25.0	Papadopoulos et al. (1997)
		23 animals[a]	4.3	Diakou et al. (2021)
	Tronglostrongylus brevior	1	100	Liatis et al. (2017)
		23 animals[a] & 62 fecal samples	33.8 and 9.7	Diakou et al. (2021)
Cestoda	Diphyllobothriid eggs	23 animals[a] & 62 fecal samples	21.7 and 12.9	Diakou et al. (2021)
	Mesocestoides sp.	23 animals	17.4	Diakou et al. (2021)
	Spirometra spp.	23 animals	17.4	Diakou et al. (2021)
	Taenia spp.	4	16.6	Papadopoulos et al. (1997)
	Taenia taeniaeformis	4	33.3	Papadopoulos et al. (1997)
		23 animals[a] & 62 fecal samples	17.4 and 1.6	Diakou et al. (2021)
Trematoda	*Alaria alata*	23 animals[a] & 62 fecal samples	17.4 and 8.0	Diakou et al. (2021)
	Opisthorchis felineus	23 animals[a] & 62 fecal samples	13.0 and 1.6	Diakou et al. (2021)
	Trematode eggs	23 animals[a] & 62 fecal samples	8.7 and 13.0	Diakou et al. (2021)
Acanthocephala	*Centrorynchus* spp.	23 animals	4.3	Diakou et al. (2021)

(*continued on next page*)

Table 1 (*continued*)

Host/Parasite group	Parasite species	*N*	Positive samples (%)	Reference
Gray wolf (*Canis lupus*)				
Protozoa	*Cryptosporidium* spp.	147	25.8	Diakou et al. (2014a)
	Cystoisospora rivolta	147	2.7	Diakou et al. (2014a)
		3	66.6	Liatis et al. (2017)
	Sarcocystis spp.	147	46.9	Diakou et al. (2014a)
		3	33.3	Liatis et al. (2017)
Nematoda	*Ancylostoma caninum*	147	2.7	Diakou et al. (2014a)
	Angiostrongylus vasorum	147	0.7	Diakou et al. (2014a)
	Capillariidae	147	5.4	Diakou et al. (2014a)
	Crenosoma spp.	147	1.4	Diakou et al. (2014a)
	Physaloptera sp.	147	0.7	Diakou et al. (2014a)
	Rictularia sp.	6	16.6	Papadopoulos et al. (1997)
	Spirocerca lupi	147	4.8	Diakou et al. (2014a)
	Thelazia callipaeda	13	100	Papadopoulos et al. (2022)
	Toxascaris leonina	147	3.4	Diakou et al. (2014a)
	Toxocara canis	6	16.6	Papadopoulos et al. (1997)
	Trichuris vulpis	147	6.8	Diakou et al. (2014a)
	Uncinaria stenocephala	6	50.0	Papadopoulos et al. (1997)
		147	15.6	Diakou et al. (2014a)
Cestoda	*Dipylidium caninum*	6	50.0	Papadopoulos et al. (1997)
	Echinococcus granulosus	28	14.3	Papadopoulos (1989)
	Joyeuxiella echinorhynchoides	6	50.0	Papadopoulos et al. (1997)
	Mesocestoides sp.	6	33.3	Papadopoulos et al. (1997)
	Taenia hydatigena	6	16.6	Papadopoulos et al. (1997)
	Taenia sp.	6	50.0	Papadopoulos et al. (1997)
	Taeniidae	147	7.5	Diakou et al. (2014a)
Trematoda	*Alaria* spp.	147	0.7	Diakou et al. (2014a)
Golden jackal (*Canis aureus*)				
Nematoda	*Ancylostoma caninum*	5	20.0	Papadopoulos et al. (1997)
	Ancylostomatidae	1	100	Liatis et al. (2017)
	Eucoleus aerophilus	1	100	Liatis et al. (2017)
	Toxocara canis	5	40.0	Papadopoulos et al. (1997)
		1	100	Liatis et al. (2017)
	Uncinaria stenocephala	5	80.0	Papadopoulos et al. (1997)
Cestoda	*Mesocestoides* sp.	5	60.0	Papadopoulos et al. (1997)
	Rictularia sp.	5	20.0	Papadopoulos et al. (1997)
	Taenia pisiformis	5	20.0	Papadopoulos et al. (1997)
Trematoda	*Alaria alata*	5	20.0	Papadopoulos et al. (1997)
Mink (*Mustela vison*)				
Protozoa	*Leishmania infantum*	200 serum & 95 spleen samples	20 (ELISA) and 2.1 (PCR)	Tsakmakidis et al. (2019)
		14	21.4 (nested PCR)	Filioussis et al. (2018)

Abbreviation: *N*, samples/animals examined.

[a] Fecal samples collected during necropsy from 23 wild cats.

conduct additional research to improve our knowledge of parasite diversity within wildcat populations in Greece.

2.3. Gray wolf (*Canis lupus*)

Wolves in Greece inhabit a wide range of ecosystems, spanning from degraded, hilly areas to densely forested mountains. They are primarily concentrated in mountainous and semi-mountainous regions with low human population density. In these areas, free-ranging wolves coexist with various canids and wild ungulates, which constitute a significant part of their diet. Gray wolves may also be present in human-dominated landscapes, sharing their habitat with livestock, shepherd dogs, and hunting dogs, as well as feral dogs that are often found near human settlements, garbage dumps, slaughterhouses, and even in mountainous terrain (Petridou et al., 2019; Iliopoulos et al., 2021). Additionally, a small population of formerly captivated wolves resides at the ARCTUROS Wolf Sanctuary in northern Greece, in a specially fenced area in natural oak forest (Papadopoulos et al., 2022).

Three studies conducted in Greece investigating the parasitic fauna of gray wolves have identified over 15 genera of parasites with zoonotic potential, encompassing protozoa, nematodes, cestodes, and trematodes (Table 1) (Kardasis, 1953; Himonas, 1970; Papadopoulos, 1989; Papadopoulos et al., 1997, 2022; Diakou et al., 2014a; Liatis et al., 2017).

Among them, two zoonotic protozoan parasites, *Cryptosporidium* spp. and *Sarcocystis* spp. and two potentially zoonotic trematodes, *Physaloptera* sp. and *Alaria* spp., were identified (Diakou et al., 2014a; Liatis et al., 2017). The survey by Papadopoulos et al. (1997) showed that all the wolves examined were infected by zoonotic parasites such as *Mesocestoides* sp., *D. caninum*, *T. hydatigena* and *Taenia* sp. (Papadopoulos et al., 1997). Notably, the gray wolve was the only animal species harbouring *E. granulosus* among wild carnivores in an earlier study, suggesting their potential role in the epidemiology of hydatidosis in Greece (Papadopoulos, 1989).

Likewise, the zoonotic nematodes *T. canis*, *T. leonina*, *A. caninum*, *U. stenocephala*, and capillariid nematodes were found in two studies (Papadopoulos et al., 1997; Diakou et al., 2014a), while *Trichinella spiralis* infection had been reported earlier (Kardasis, 1953; Himonas, 1970).

A recent survey involving 12 individuals hosted in the ARCTUROS Wolf Sanctuary and one free-ranging animal showed that all the examined gray wolves were infected with *T. callipaeda*. During ocular examination, various numbers of *T. callipaeda* were recovered (ranging from 6 to 16 worms per animal). The ocular clinical signs recorded were mucus, corneal ulcers, mucopurulent discharge, red eye, blepharospasm, and mild cornea oedema. The prevalence of 100% and the associated clinical signs recorded suggest that thelaziosis may potentially affect the health and welfare of the infected wolves (Papadopoulos et al., 2022).

Given the potential interactions of wolves in Greece with other wild and domestic animals, along with the findings of the abovementioned studies, it is plausible to suggest that the gray wolf population could potentially serve as a source of infection for other animal species and *vice versa*. Their role in parasite transmission is especially relevant in the context of the gray wolf and brown bear populations living in the enclosed areas of the ARCTUROS sanctuaries in the same region of northern Greece. Gray wolves may act as a source of *T. callipaeda* infection, a theory supported by the high thelaziosis prevalence in the brown bear population in the same study (see *Section 3.1*.) (Papadopoulos et al., 2022).

Furthermore, regular surveillance of the gray wolf population is advisable as they may act as reservoirs or maintenance hosts for other zoonotic parasites, including *Giardia duodenalis*, *L. infantum*, *D. immitis* and *E. multilocularis* (Beck et al., 2008; Bindke et al., 2017). The exchange of parasites between wolves and dogs, including feral and shepherd dogs, is a significant concern due to their proximity to other domestic animals and humans. In addition to monitoring and managing potential zoonotic risks associated with gray wolves in Greece, it is also essential to monitor the parasitic fauna of this species for conservation purposes, as some parasitic diseases may impact the health status of the gray wolf population.

2.4. Golden jackal (Canis aureus)

Golden jackals exhibit opportunistic feeding behaviour, with their diet ranging from small mammals and birds to scavenged anthropogenic food sources. Their diverse diet and broad territorial mobility enable them to adapt to various habitats, including suburban and urban areas. This adaptability brings them into contact with animals living near humans, such as dogs, and wild animals like foxes. Notably, jackals harbour several canine and zoonotic parasites (Gherman and Mihalca, 2017).

Data on the parasitic fauna of golden jackals in Greece are limited to three studies involving a small number of animals (Table 1) and reporting the occurrence of *T. spiralis* (Himonas, 1970; Kardasis, 1953), *A. alata*, *Mesocestoides* sp., *T. pisiformis*, *T. canis*, *U. stenocephala*, and *A. caninum* (Papadopoulos et al., 1997). *Echinococcus granulosus* was not detected in golden jackals (Papadopoulos, 1989). Mixed infections have also been demonstrated, with one sheltered golden jackal carrying ancylostomatid nematodes, *E. aerophilus* (syn. *Capillaria aerophila*), and *T. canis* (Liatis et al., 2017).

Studies from other countries have shown that golden jackals harbour zoonotic parasites that have been identified in other wild and domestic animals in Greece, such as *D. immitis*, *D. repens*, *L. infantum*, *Trichinella* spp., and *E. granulosus* (Veronesi et al., 2023). Jackals are regarded as wild reservoirs of *D. immitis* in endemic regions due to frequent adult worm infections, microfilaraemia, and infection rates comparable to those seen in dogs (Otranto and Deplazes, 2019) and natural sylvatic reservoirs of *Trichinella* spp., with *T. britovi* being the predominant species identified. Notably, they can also serve as definitive hosts for both *E. granulosus* and *E. multilocularis* (Veronesi et al., 2023).

The significance of golden jackals lies in their extensive territorial range, which allows them to migrate over long distances (Gherman and Mihalca, 2017). This behaviour can contribute to introducing and disseminating parasites in neighbouring countries, emphasizing their role in the transmission dynamics of zoonotic diseases.

2.5. Mink (Mustela vison)

Minks are opportunistic predators known for their ability to thrive in diverse habitats and present rapid population growth (Kollias and Fernandez-Moran, 2015). In Greece, the first mink farm was established in northwestern Greece back in 1972, with most farms now concentrated in the same region. Over the past decade, the Greek fur industry has experienced significant growth, expanding from 43 mink farms in 2011 to 113 in 2019, making Greece one of the largest fur producers in Europe today. Notably, intentional releases by activists during 2008–2010 have led to the establishment of feral mink populations in Greece, particularly in northwestern Greece, where they are expanding their range into the wild (Galanaki and Kominos, 2022).

Two studies have been carried out in minks in Greece, both reporting *Leishmania*-infected individuals (Table 1). The first study demonstrated *Leishmania* infection in three neonatal minks presenting haemorrhagic pneumonia due to *Pseudomonas aeruginosa*. All the individuals examined originated from a Greek farm (Filioussis et al., 2018). A subsequent study in six farms from the Regional Unit of Kastoria, western Macedonia, reported a seroprevalence of 20% and an infection prevalence of 2.1%. The microscopic examination of spleen imprints yielded negative results in all the animals examined, indicating a possibly low parasitic load. No skin or visceral lesions were found during necropsy, suggesting a limited clinical impact on these animals. These findings suggested that while minks are frequently exposed to *Leishmania* spp., their role in the epidemiology of leishmaniosis is minor in the studied areas (Tsakmakidis et al., 2019).

Considering the potential expansion of feral mink populations towards northeastern and central Greece, as well as neighbouring countries, and their proximity to farmed minks, there is a need to investigate the expansion of their population. This investigation should focus on understanding their impacts on wildlife conservation and their role in the transmission cycle of zoonotic pathogens, including *Giardia* spp., *Sarcocystis* spp., *T. gondii*, *Cryptosporidium* spp., *Trichinella* sp. and *T. canis* that have been identified in minks in other countries (Kollias and Fernandez-Moran, 2015).

3. Omnivores

3.1. Brown bear (Ursus arctos)

The brown bear population in Greece is primarily divided into two main groups: one in the northwestern and the other in the northeastern part (Karamanlidis et al., 2018). Some individuals are also housed in the ARCTUROS Brown Bear Sanctuary in northern Greece, which is frequently visited by people (Papadopoulos et al., 2022). Although epizootiological studies on brown bear populations in Greece are limited (summarized in Table 2), the existing findings raise concerns about the potential role of this species in the transmission of zoonotic parasites, particularly in the rural areas where brown bears are present.

A recent study reported for the first time that brown bears serve as a host of *T. callipaeda*, providing evidence of a new species in the broad host range of this vector-borne nematode (Papadopoulos et al., 2022). The ocular examination of 28 live animals hosted in the ARCTUROS Brown Bear Sanctuary, the necropsy of two free-ranging individuals that died in car accidents in northern Greece, as well as the subsequent morphological and molecular analysis of the collected nematodes led to the identification of *T. callipaeda* infection in brown bears. The study showed a high prevalence of infection (26.7%) with a varying number of recovered worms (range 2–11 per animal). Most infected individuals presented clinical signs, including conjunctivitis, oedema, epiphora, petechiae, ocular discharge, and keratitis (Papadopoulos et al., 2022).

Heartworm infection with *D. immitis* has also been recently diagnosed in a young male brown bear. The animal died due to severe injuries after a vehicle collision in northern Greece. During necropsy, four nematodes were found in the right ventricle of the heart and the pulmonary arteries but no microfilariae were detected (Papadopoulos et al., 2017).

Another study demonstrated parasitic infection with ten different genera of protozoa, nematodes, cestodes, and trematodes in brown bears. Parasitic elements were found in 55.8% of the bear faecal samples examined, while 31.1% of animals presented mixed infections with two or more parasites. The most frequently found parasite species with zoonotic potential was *Baylisascaris* spp. followed by *Uncinaria* spp. and *D. dentriticum*, while *Sarcocystis* spp., *Taenia* spp., *Linguatula serrata*, and *Toxascaris* spp. were less frequently found (Synapalos et al., 2021). In an

Table 2
Endoparasites reported in omnivores in Greece.

Host/Parasite group	Parasite species	*N*	Positive samples (%)	Reference
Brown bear (*Ursus arctos*)				
Protozoa	*Entamoeba* spp.	8	37.5	Himonas et al. (1998)
	Blastocystis spp.	8	75.0	Himonas et al. (1998)
	Eimeria spp.	103	1.9	Synapalos et al. (2021)
	Sarcocystis spp.	103	2.9	Synapalos et al. (2021)
Nematoda	*Baylisascaris* spp.	103	71.8	Synapalos et al. (2021)
	Eucoleus aerophilus	103	4.8	Synapalos et al. (2021)
	Crenosoma spp.	103	2.9	Synapalos et al. (2021)
	Dirofilaria immitis	1	100	Papadopoulos et al. (2017)
	Thelazia callipaeda	30	26.7	Papadopoulos et al. (2022)
	Toxascaris spp.	103	0.97	Synapalos et al. (2021)
	Uncinaria spp.	103	37.9	Synapalos et al. (2021)
Cestoda	*Taenia* spp.	103	1.0	Synapalos et al. (2021)
Trematoda	*Dicrocoelium dentriticum*	103	18.4	Synapalos et al. (2021)
Wild boar (*Sus scrofa*)				
Protozoa	*Toxoplasma gondii*	94	5.2[a]	Touloudi et al. (2015)
	Neospora caninum	94	1.1[a]	Touloudi et al. (2015)
Nematoda	*Trichinella* spp.	94	6.4[b]	Touloudi et al. (2015)
Cestoda	*Echninococcus granulosus*	273	1.1	Chaligiannis et al. (2015)
European badger (*Meles meles*)				
Protozoa	*Eimeria* spp.	2	50.0	Liatis et al. (2017)
Nematoda	*Dirofilaria immitis*	2	100	Markakis et al. (2024)
Brown rat (*Rattus norvegicus*)				
Protozoa	*Leishmania infantum*	16	6.2[c]	Papadogiannakis et al. (2010)
		19	70.0[b], 0[d]	Tsakmakidis et al. (2017)
Black rat (*Rattus rattus*)				
Protozoa	*Leishmania infantum*	12	50.0[b], 25.0[d]	Tsakmakidis et al. (2017)
House mouse (*Mus musculus*)				
Protozoa	*Leishmania infantum*	66	50.0[b], 24.0[d]	Tsakmakidis et al. (2017)
European hedgehog (*Erinaceus europaeus*)				
Protozoa	*Eimeria* spp.	19	15.7	Liatis et al. (2017)
Nematoda	*Capillaria* spp.	19	36.8	Liatis et al. (2017)
	Crenosoma striatum	19	47.3	Liatis et al. (2017)
	Physaloptera clausa	19	31.5	Liatis et al. (2017)
Cestoda	*Hymenolepis erinacei*	19	5.2	Liatis et al. (2017)
Trematoda	*Brachylaima* spp.	19	5.2	Liatis et al. (2017)
	Trematoda	19	5.2	Liatis et al. (2017)
Acanthocephala	Acanthocephala	19	15.7	Liatis et al. (2017)

[a] IFAT.
[b] ELISA.
[c] Nested PCR.
[d] PCR and real-time PCR.

earlier study, Himonas et al. (1998) showed the occurrence of two protozoan species with zoonotic potential, *Entamoeba* spp. and *Blastocystis* spp. in a small number of brown bears (Himonas et al., 1998).

Free-ranging brown bears share their habitat with wild canids, which act as reservoirs for parasites like *T. callipaeda* in the sylvatic life-cycle (wolves and foxes), final hosts for *D. immitis* (wolves and dogs) or hosts that exhibit microfilaremia, like hunting and shepherd dogs (Otranto and Deplazes, 2019). Moreover, *T. callipaeda* and *D. immitis* vectors are abundant in these rural areas (Papadopoulos et al., 2022; Rodríguez-Escolar et al., 2024). Thus, the involvement of the brown bear in the transmission cycles of these parasites should be considered. Brown bears may also interact with various other wild carnivores, omnivores, and herbivores in the Greek mainland, facilitating the exchange of parasites, some of which may have public health implications.

Studies conducted in other countries have demonstrated that this species can harbour zoonotic parasites such as *Trichinella* spp., *Cryptosporidium* spp., *Babesia* spp., and *T. gondii* (Di Salvo and Chomel, 2020). These parasite species have been identified in different animal species and even in the human population in Greece (Giadinis et al., 2015; Angelou et al., 2019; Papatsiros et al., 2020; Symeonidou et al., 2023). Despite the lack of studies investigating their presence in brown bears in Greece, future research should prioritise this aspect. Even though brown bears are not considered a game species in Greece, they could still serve as maintenance hosts for food-borne parasites in the environment.

3.2. *Wild boar (Sus scrofa)*

Wild boar is a native species in Greece and one of the most popular large game animals. Its population density is high, with an increasing trend in many areas of the country and a wide distribution covering a variety of habitat types (Touloudi et al., 2015; Papatsiros et al., 2020). Despite the importance and wide distribution of this species in Greece, studies of its parasitic fauna are currently limited (summarized in Table 2).

A serological survey conducted by Touloudi et al. (2015) revealed evidence of exposure to *T. gondii* (5.2%), *Neospora caninum* (1.1%), and *Trichinella* spp. (6.4%). Seropositive animals were found in regions where free-range pig farms were located (Touloudi et al., 2015), thus creating concern about the possible interaction of wild boars with free-ranging pigs and the transmission of pathogens between these populations.

As for *Trichinella* spp. infections, three other studies investigated wild boar populations in Greece (Boutsini et al., 2014; Papatsiros et al., 2012; Dimzas et al., 2021). In total, 360 wild boar samples were examined in the aforementioned studies, but none yielded positive results, suggesting a low infection prevalence for *Trichinella* spp. in the examined wild boar population. Although these findings may seem controversial to the serological data from the study by Touloudi et al. (2015), they are unsurprising due to the short lifespan of *Trichinella* spp. larvae compared to the long lifespan of antibodies, which can be detected for at least two years following infection. As for *T. britovi* larvae, their lifespan is much shorter than *T. spiralis*, as only a small number of larvae can survive for six months (Dimzas et al., 2021).

Importantly, *Trichinella* spp. larvae have been reported in wild-farmed free-range pigs during routine testing at slaughterhouses and the National Reference Laboratory for Parasites. In 2009, two positive samples were reported in two free-ranging pigs from different farms located in northern Greece (Papatsiros et al., 2012). During the years 2009–2012, a total of 37 free-ranging pigs from seven farms tested positive for *Trichinella* spp. larvae. Notably, one of these cases was linked with human trichinellosis cases in five family members who consumed undercooked pork meat from a free-range pig farm. The prevalence of infection was estimated to be 0.29% and showed a positive trend over the four years of investigation. The researchers identified *T. britovi* in 31 out of the 37 positive samples from free-range pigs, which were available for molecular analysis (Boutsini et al., 2014), providing strong evidence of the wild origin of the parasites. Additionally, the serological investigation in 363 farmed free-range pigs during 2009–2010 showed a seroprevalence of 4.1% using enzyme-linked immunosorbent assay (ELISA), indicating that free-range pigs in Greece are exposed to *Trichinella* spp. (Papatsiros et al., 2012), similarly to what Touloudi et al. (2015) demonstrated for wild boar population in Greece (Touloudi et al., 2015).

On top of the above, *T. britovi* was molecularly identified as the causative agent of human trichinellosis in a 47-year-old male in northern Greece. Based on the history and the patient's eating habits, the authors suspected that the source of infection was the consumption of half-cooked domestic pig meat (Dimzas et al., 2019).

To date, all the samples positive for *Trichinella* spp. originated from free-range pigs in various regions of northern-eastern Greece. These regions are close to Bulgaria, where *Trichinella* spp. infection is highly prevalent in wild animals and wild boars specifically. It was suggested that the wild boar population in these areas might come into contact with free-ranging pigs, either directly or indirectly, thus highlighting the potential role of wild boars in transmitting pathogens between neighbouring countries (Papatsiros et al., 2012; Boutsini et al., 2014). Moreover, *T. britovi* is the most common *Trichinella* species infecting European wild carnivores. Improper practices, such as leaving animal carcasses in the field after hunting and skinning game animals, slaughtering pigs without veterinary inspection and biosecurity measures, and feeding pigs with pork scraps, increase the probability of *T. britovi* transmission to new wild and domestic hosts (Papatsiros et al., 2020).

Likewise, the study of Dimzas et al. (2021) yielded negative results for *Alaria* spp. infection in wild boars. However, *Alaria* spp. have been detected in Greece in other wild animal species (wolves, red foxes, jackals and wildcats) and dogs, which are definitive parasite hosts (Papadopoulos et al., 1997; Liatis et al., 2017; Diakou et al., 2021). The negative results of this study do not rule out the presence of infection in wild boars but are indicative of a low infection prevalence in the wild boar population examined (Dimzas et al., 2021).

Another study investigated the incidence of *E. granulosus* in wild boars from northern Greece. During the inspection of slaughtered animals, the researchers examined the viscera for the number and location of cysts, evaluated the hydatid cysts based on their fertility, determined the viability of protoscoleces, and conducted molecular tests to identify the genotypes and species involved. Three cysts were found in the wild boar viscera (1.1%) examined, but none were fertile. *Echinococcus granulosus* (*s.s.*) (G1/G2/G3) genotype complex was predominant among the various intermediate host species studied. These results suggest a low prevalence of infection in the wild boar population. However, the risk of human infection remains, particularly in scenarios such as wild boar hunting or breeding (Chaligiannis et al., 2015).

In recent years, the wild boar population in Greece has experienced an unexpected expansion, mirroring trends observed in other European countries (Papatsiros et al., 2020). This growth has raised concerns within the scientific community regarding the ecological and epidemiological implications of the distribution of wild boars close to humans and domestic animals (Tampakis et al., 2023).

While existing research has primarily focused on bacterial and viral agents in wild boars, there are also many reports on various zoonotic parasites, including *T. gondii*, *Trichinella* spp., *Cryptosporidium* spp., *Blastocystis* spp., *Sarcocystis* spp., *Alaria* spp., and *Echinococcus* spp. (Abrantes and Lopes, 2021). Zoonotic parasites in game species such as wild boar are a concerning issue, especially considering that consuming wild boar meat may occur without prior veterinary inspection (Papatsiros et al., 2020). Continuous monitoring of the wild boar population in Greece through regular surveillance programmes is essential to safeguard public health and animal welfare, particularly under the current expansion of their distribution in human-dominated landscapes.

3.3. European badger (*Meles meles*)

The European badger is an opportunistic omnivore that occupies different habitats and shares the same living space with other mammals, such as red foxes. The parasitic fauna of European badgers in Greece has been little investigated.

Markakis et al. (2024) recently documented the first cases of dirofilariosis in two European badgers from Crete Island (Table 2). While *D. immitis* infection has previously been demonstrated in Romania (Ionică et al., 2017), this study in Greece presented compelling evidence of antigenemia, microfilariemia, and the presence of adult parasites in European badgers accompanied by cardiovascular symptoms. These findings highlighted the role of this species as an additional reservoir host for *D. immitis*. In more detail, this study suggested that dirofilariosis occurs in the indigenous wildlife of Crete Island, an area which, based on the available data, currently, is not regarded as endemic for dirofilariosis (Markakis et al., 2024). Interestingly, a recent ecological niche modeling analysis study for *Culex pipiens*, the main vector of *D. immitis* in Greece, revealed that the environment in Crete is suitable for the mosquito to complete its life-cycle and the future infection risk in that area is high (Rodríguez-Escolar et al., 2024).

The European badger may also be infected with other important zoonotic parasites, including but not limited to *L. infantum*, *Baylisascaris melis*, *Trichinella britovi*, *Cryptosporidium* spp., and *G. duodenalis* (Azami-Conesa et al., 2021; Boros et al., 2021; Maestrini et al., 2022). Consequently, further investigations will provide insights into the role of this wild animal species in the epidemiology of important zoonotic parasites in Greece.

3.4. Rodents

Rodents play a role in the epidemiology of several zoonotic parasites due to their adaptation to human environments and high reproductive rates. Their proximity to humans and dogs establishes them as key players in the life-cycle of various parasites such as *L. infantum*, *T. gondii*, *Giardia* spp., *Cryptosporidium* spp., *Entamoeba* spp., *T. taeniaeformis*, *Hymenolepis diminuta*, *H. nana*, and *Angiostrongylus cantonensis*, as observed worldwide (Mohtasebi et al., 2020; Tijjani et al., 2020).

Two studies in Greece have investigated the occurrence of *L. infantum* infection in rodent species (Table 2). A 2009 study in regions of southern Greece included a small number of brown rats (*Rattus norvegicus*) and showed the presence of a low parasitic load in one animal by PCR (Papadogiannakis et al., 2010). Later, a comprehensive study in northern Greece examined 97 animals belonging to three different rodent species: the house mouse (*Mus musculus*), the brown rat (*R. norvegicus*), and the black rat (*R. rattus*). The findings of this study demonstrated an overall seropositivity rate of 54.5%, prevalence of infection based on molecular methods of 19.6%, and absence of cytological evidence of infection in spleen and liver smears. Poor body condition was recorded in 22 individuals, and there was an absence of external lesions, splenomegaly, or hepatomegaly. Remarkably, all the molecularly positive animals were also seropositive (Tsakmakidis et al., 2017).

The detection of *L. infantum* infection in various rodent species indicates their potential contribution to the transmission cycle of this parasite. However, further xenodiagnosis investigations are essential to gain deeper insights into the specific role the different rodent species play in transmitting and maintaining *L. infantum* (Alcover et al., 2021).

3.5. European hedgehog (Erinaceus europaeus)

Hedgehogs are small insectivorous mammals that also feed on a wide variety of food, including eggs and nestlings of ground-nesting birds, mice, and frogs (Rautio et al., 2016), which is suggestive of their opportunistically omnivorous nature. This species is prevalent in Europe, commonly found in suburban environments near humans and domestic animals. Individuals involved in hedgehog rescue and rehabilitation activities are particularly vulnerable to exposure to infected hedgehog faeces, providing a pathway for zoonotic infections by enteric pathogens (Ruszkowski et al., 2021).

There is only one study involving 19 hedgehogs sheltered in wildlife hospitals and rehabilitation centres in Greece (Table 2). This study reported infection by potentially zoonotic parasites, including *Capillaria* spp., Acanthocephala, *Brachylaima* spp., *H. erinacei* and Trematoda (Liatis et al., 2017). In other studies, hedgehogs were found infected with enteric zoonotic protozoa like *Blastocystis* sp., *Cryptosporidium* spp., *G. duodenalis* (Gomes-Gonçalves et al., 2024) and *L. infantum* (Azami-Conesa et al., 2023). The encroachment of humans into hedgehog habitats has disrupted the delicate balance of the human-animal-environment interface, further emphasizing the importance of understanding and managing zoonotic risks associated with hedgehog populations.

4. Herbivores

4.1. European brown hare (Lepus europaeus)

Lepus europaeus, a key game animal in Europe, is widely distributed and abundant across its range due to its adaptability to various habitats. With individual home ranges spanning 10–300 ha and overlapping on preferred feeding grounds with the habitat of other animal species, hares may play a significant role in the epidemiology of pathogens in a particular area (Tsokana et al., 2020).

In 2016, the occurrence of *Leishmania* spp. infection in European brown hares in Greece was documented for the first time (Tsokana et al., 2016). The study involved the analysis of spleen samples obtained from hares harvested by hunters in northern Greece during 2007–2011. Molecular testing revealed a notable prevalence of *Leishmania* spp. infection, with 23.5% of the examined hares testing positive. Phylogenetic investigation indicated that the detected parasites belonged to the *Leishmania donovani* complex and exhibited a high sequence similarity (98.9%) to *Leishmania* sequences found in dogs from the same areas. Furthermore, the researchers conducted a geographical information system (GIS) analysis, demonstrating that seasonal precipitation patterns influenced the presence of *Leishmania*-infected hares. The likelihood of infection was found to increase with rising precipitation levels, possibly due to the impact of this factor on the activity period of sand flies, their survival, the promotion of adult emergence, and the determination of appropriate oviposition sites. The authors, based on their results, suggested a potential overlap between sylvatic and domestic transmission cycles in certain regions (Tsokana et al., 2016).

A subsequent study in hunter-harvested hares in northern Greece during 2014–2016 revealed a lower infection prevalence of 3.6% in the examined population using molecular analysis (Tsakmakidis et al., 2019). All the infected hares were from the same Regional Units where positive hares had been previously reported (Tsokana et al., 2016). Notably, no external lesions, splenomegaly or hepatomegaly were observed in any of the animals included in the study, and microscopic examination of the spleen imprints was negative for *Leishmania* spp. amastigotes in all the examined samples (Tsakmakidis et al., 2019).

A 2019 study reported *Leishmania* infection in hares from other regions of Greece, including the central part of the country - a highly endemic area for human and canine leishmaniosis. This study documented a 9.6% positivity rate in hares from central and northern Greece (ranging from 7.4% to 20% based on the Regional Unit) using molecular tests, with a sequence homology of 99% with *L. infantum* (Tsokana et al., 2019).

Serological investigations of the abovementioned hare populations indicated a 6.7% seroprevalence in hares from northern Greece *via* ELISA (Tsakmakidis et al., 2019) and an overall 12.4% seroprevalence in central and northern Greece (with ranges from 9.7% to 13.9% according to the Regional Unit) using IFAT (Tsokana et al., 2019).

The widespread prevalence of *Leishmania* infection in hares is a significant concern, as observed in other countries where specific conditions, such as an unusual surge in hare population, high sand fly density, and low human immunity levels, may lead to hares acting as reservoir hosts (Molina et al., 2012).

The study by Tsokana et al. (2019) also provided evidence of the hare population exposure to *T. gondii* since a total of 5.7% seropositivity was recorded. Still, the molecular analysis failed to detect the parasite DNA in the liver samples examined (Tsokana et al., 2019).

Another study investigated the endoparasitic fauna of European brown hares hunted in northern Greece (Table 3) and showed that 73.8% of the examined individuals were parasitised by at least one parasite species. Potentially zoonotic parasites and parasitic elements were identified in the gastrointestinal tracts examined, including eggs of the trematode *D. dendriticum* and larvae of *L. serrata*. At the same time, no *Cryptosporidium* oocysts were found in the stained faecal smears (Diakou et al., 2014b). Similarly, Liatis et al. (2017) found adults of *D. dendriticum* and larvae of *L. serrata* in the post-mortem examination of the gastrointestinal tract and liver of one hare admitted to wildlife hospitals and rehabilitation centres (Liatis et al., 2017).

Hares can also harbour other zoonotic parasites such as *E. granulosus*, *E. multilocularis*, *Strongyloides* sp. (Panayotova-Pencheva, 2022), and *T. callipaeda* (Cotuțiu et al., 2022). The cohabitation of hares with definitive hosts of parasites such as gray wolves, red foxes, dogs, and cats suggests a potential for pathogen transmission. Moreover, their movements across borders and long distances, interactions with vectors, and predation by carnivores and omnivores further bring them into contact with domestic, wild animals, and humans. Finally, given their short lifespan, hares serve as valuable indicators of recent pathogen circulation in a habitat (Ezio and Anna, 2003; Tsokana et al., 2019, 2020). Considering all these factors and the significance of this game species in Greece, monitoring parasites and other pathogens in hare populations in Greece is crucial.

4.2. Wild rabbit (Oryctolagus cuniculus)

Oryctolagus cuniculus, a highly prevalent lagomorph species, thrives in many ecosystems due to its moderate size and abundant presence. Wild rabbits share the same habitat with small to medium-sized predators like foxes, cats, and civets, while domestic rabbits are bred for various purposes, such as meat and fur, and as a popular pet choice (Ferrand, 2008). Interestingly, in the islands in the northern part of the Aegean Sea, Greece, specifically on the Island of Lemnos, wild rabbits are overpopulated and have caused significant ecosystem disruption and crop damage since 1995. There are only three studies in Greece investigating the occurrence of parasitic pathogens in this wild rabbit population (Table 3), with two of them reporting infection with parasites with zoonotic potential (Tsakmakidis et al., 2019; Athanasiou et al., 2021, 2023).

The first study reported an overall seropositivity of 7.6% and an infection rate of 2.6% for *L. infantum* in both domestic rabbits from northern Greece and wild rabbits from the Island of Lemnos (Tsakmakidis et al., 2019). These authors did not detect *Leishmania* amastigotes in spleen imprints nor external lesions, splenomegaly or hepatomegaly

Table 3
Endoparasites reported in herbivores in Greece.

Host/Parasite group	Parasite species	*N*	Positive samples (%)	Reference
European brown hare (*Lepus europaeus*)				
Protozoa	*Eimeria* spp.	84	64.3	Diakou et al. (2014b)
		3	33.3	Liatis et al. (2017)
	Leishmania infantum	166	23.5[a]	Tsokana et al. (2016)
		90	6.7[b] and 3.6[c]	Tsakmakidis et al. (2019)
		105 serum & 52 liver samples	12.4[d] and 9.6[a]	Tsokana et al. (2019)
	Neospora caninum	105 serum & 52 liver samples	0.9[d] and 3.8[a]	Tsokana et al. (2019)
	Toxoplasma gondii	105 serum & 52 liver samples	5.7[d] and 0[a]	Tsokana et al. (2019)
Nematoda	*Dirofilaria scapiceps*	84	1.2	Diakou et al. (2014b)
	Passalurus ambiguus	84	4.8	Diakou et al. (2014b)
	Protostrongylus spp.	84	1.2	Diakou et al. (2014b)
	Trichostrongylus retortaeformis	84	50.0	Diakou et al. (2014b)
	Trichostrongylys spp.	3	66.6	Liatis et al. (2017)
	Trichuris leporis	84	21.4	Diakou et al. (2014b)
Trematoda	*Dicrocoelium dentriticum*	84	9.5	Diakou et al. (2014b)
		3	33.3	Liatis et al. (2017)
Wild rabbit (*Oryctolagus cuniculus*)				
Protozoa	*Eimeria stiedae*	60	13.3	Athanasiou et al. (2023)
	Babesia spp.	72	9.7[d]	Athanasiou et al. (2021)
	Leishmania infantum	101	7.6[b] and 2.6[c]	Tsakmakidis et al. (2019)
		72	4.2[d]	Athanasiou et al. (2021)
	Toxoplasma gondii	72	5.5[d]	Athanasiou et al. (2021)
European ground squirrel (*Spermophilus citellus*)				
Protozoa	*Cryptosporidium* spp.	125	23.2	Diakou et al. (2015)
	Eimeria callospermophili	125	73.6	Diakou et al. (2015)
	Eimeria citelli	125	60.8	Diakou et al. (2015)
	Eimeria cynomysis	125	32.8	Diakou et al. (2015)
	Eimeria spp.	125	17.6	Diakou et al. (2015)
	Entamoeba spp.	125	25.6	Diakou et al. (2015)
Trematoda	*Brachylaima* spp.	125	5.6	Diakou et al. (2015)
Wild ruminants				
Roe deer (*Capreolus capreolus*)				
Trematoda	*Dicrocoelium dendriticum*	6	33.3	Liatis et al. (2017)
Fallow deer (*Dama dama*)				
Protozoa	*Eimeria* spp.	1	100	Liatis et al. (2017)
Nematoda	*Capillaria bovis*	1	100	Liatis et al. (2017)

[a] Nested PCR.
[b] ELISA.
[c] PCR.
[d] IFAT.

in the examined animals (Tsakmakidis et al., 2019). Later, Athanasiou et al. (2021) demonstrated that 4.2%, 5.5%, and 9.7% of the wild rabbits examined from the Island of Lemnos were exposed to *L. infantum*, *T. gondii*, and *Babesia* spp., respectively. Studies on the occurrence of *L. infantum* infection in wild rabbits across various countries have revealed varying seropositivity rates ranging from 0% to 75.4% and infection rates from 0% to as high as 100% (Cardoso et al., 2021). These results have led to conflicting interpretations regarding the potential role of rabbits in the epidemiology of leishmaniosis, underscoring discrepancies in research methodologies and sample selection. Nevertheless, *Leishmania* infection demonstrates spatial and temporal clustering at a local level (Martín-Sánchez et al., 2021).

Monitoring of the wild rabbit population in Greece is essential since it is abundant and lives close to humans and domestic animals in Greece. Likewise, this species serves as a valuable sentinel for assessing pathogen circulation in its immediate surroundings due to its narrow home range (Ferrand, 2008).

4.3. European ground squirrel (*Spermophilus citellus*)

The only study investigating the parasitic fauna of European ground squirrels in Greece demonstrated a high prevalence of parasitic infection in 94.4% of the animals examined (summarized in Table 3). Interestingly, high infection rates with the potentially zoonotic parasites *Cryptosporidium* spp. (23.2%), and *Entamoeba* spp. (25.6%) were detected, followed by a lower prevalence of infection with *Brachylaima* spp. (5.6%) (Diakou et al., 2015). The authors suggested further research on *S. citellus* populations, including parasite genotyping, to better clarify the role of this species in the epidemiology of the identified parasites.

4.4. Wild ruminants

Research on wild ruminants in Greece is scarce. The conducted studies involved one fallow deer (*Dama dama*) and six roe deer (*Capreolus capreolus*) admitted to wildlife hospitals and rehabilitation centres (Liatis et al., 2017) and 15 red deer (*Cervus elaphus*) reared in free-ranging farms (Chaligiannis et al., 2015).

Dicrocoelium dendriticum was the parasite with zoonotic potential detected in two out of the six roe deer examined (Liatis et al., 2017), while no hydatid cysts were detected in the free-range red deer included in the study, during inspection in abattoirs (Chaligiannis et al., 2015).

5. Conclusions

Despite the rich wildlife biodiversity in Greece, there remains a significant gap in research on its parasitic fauna. Nevertheless, the existing studies have offered valuable insights into the occurrence of parasite species that could impact wild animal populations, as well as those that could be transmitted to domestic animals at the interface with their wild counterparts.

Notably, carnivores, omnivores, and herbivores in Greece are infected with various zoonotic parasites, underscoring the need for further investigation into their role in transmission dynamics and the necessity for ongoing surveillance and monitoring of wild animal populations.

Particularly, predators and prey were found to be infected and/or exposed to species of 22 and 12 genera of zoonotic parasites, respectively. Nematodes with zoonotic potential were more frequently detected in predators while prey species exhibited a higher prevalence of zoonotic protozoan parasites.

The literature presents numerous examples of wild animal species that may act as sources of infection, natural reservoirs, or potential bridge hosts in spillover events (Plowright et al., 2017). These findings have gained increased relevance due to the escalating interaction between humans, domestic and wild animals, which now extends to urban environments (Bradley and Altizer, 2007; Tampakis et al., 2023). Moreover, domestic animals such as dogs and cats readily move between domestic and forest environments, facilitating the transmission of parasites from wild animals to humans, particularly in urban areas near forested landscapes (Plowright et al., 2017).

Considering the above, it is reasonable to recommend that surveillance and monitoring of parasitic infections in Greek wildlife should encompass interdisciplinary investigations that acknowledge the interconnectedness of human, wild, and domestic animals, as well as environmental health, in line with the One Health approach. Further research on the epidemiology of parasitic infections in Greek wildlife is essential for developing evidence-based interventions that can mitigate the risks of zoonotic spillovers.

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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.

Data availability

The data supporting the conclusions of this article are included within the article.

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