



PERSPECTIVE

Is dirofilariosis an emerging conservation threat in wild carnivores across the Palearctic?

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ABSTRACT

Dirofilaria species are mosquito-borne filarial nematodes, with a high veterinary and public health importance, but growing evidence also indicates their frequent occurrence in wildlife. Wild animals may play an important role in the maintenance, transmission and spread of dirofilariosis, but we have little understanding of the ecological and environmental processes that drive infection dynamics in these hosts. Here, we summarise the current knowledge about the distribution of *Dirofilaria* spp. across carnivore host species and geographic localities in the Palearctic region. This summary highlights that some of these sylvatic species may be important reservoirs of the pathogen, and identifies research trends and biases in the surveillance and monitoring of this host–parasite system in the wild. Furthermore, we provide directions for future research for a better understanding of the threat these parasites may pose to wild mammals.

INTRODUCTION

Mosquito-borne diseases pose significant threats to both human and animal health worldwide. While much attention has been focused on the impact of these diseases on human populations, the effects on animals are equally important, as they can result in substantial economic losses and ecological disruptions that often raise conservational issues (Linthicum et al. 2016, Klug & Drake 2022). Mosquitoes serve as vectors for a wide range of pathogens, including viruses, protozoa and filarial nematodes, transmitting them from infected hosts to susceptible individuals even at the interspecific level. Several mosquito-borne filarial nematodes have shown a rising occurrence both in human and animal populations in the past decades (Szénási et al. 2008, Laaksonen et al. 2010, Traversa et al. 2010, Alsarraf et al. 2021).

Currently, there are 27 recognised *Dirofilaria* species globally, while additional groups with uncertain taxonomic status also exist (Dantas-Torres & Otranto 2013, 2020). However, in the Palearctic region, two species account for most infections in carnivores: *Dirofilaria immitis* and *Dirofilaria repens*.

Dirofilaria immitis, which causes heartworm disease, is globally distributed, and it has long been recognised as a significant health concern for canines worldwide (Simón et al. 2012). This parasite affects domestic and wild carnivores, and occasionally humans (Dantas-Torres & Otranto 2013). In recent years, this pathogen has emerged as a growing threat to dogs (Drake & Wiseman 2018, Alsarraf et al. 2021), leading to increased concern among veterinarians, pet owners and public health officials. The rising incidence of *Dirofilaria immitis* infection in dogs has sparked a renewed interest in understanding its eco-epidemiology, clinical manifestations and preventive measures. The clinical signs of *Dirofilaria immitis* infection can vary depending on the stage of the disease and the number of worms present in the host's body. Early stages may be asymptomatic or show mild symptoms such as coughing, exercise intolerance and weight loss. As the infection progresses, hosts may exhibit more severe signs like difficulty breathing, a persistent cough and a swollen abdomen. In advanced cases, heart failure and life-threatening complications can occur. *Dirofilaria immitis* can also infect humans causing tumour-like lung nodules or conjunctival dirofilariasis (Pampiglione et al. 2009).

Dirofilaria repens, which occurs in Africa, Asia and Europe, is most often found in domestic dogs and cats, where it is responsible for subcutaneous dirofilariosis (Anvari et al. 2020), but it is often asymptomatic in its hosts. *Dirofilaria repens* occasionally infects humans causing ocular dirofilariosis (Szénási et al. 2008, Capelli et al. 2018, Pupić-Bakrač et al. 2021). This infection shows an increasing occurrence in the Eastern Hemisphere both in dogs and in human hosts (Capelli et al. 2018, Alsarraf et al. 2021).

At least two additional *Dirofilaria* species are found in the eastern regions of the Palearctic: *Dirofilaria ailure* (which parasitizes procyonids, e.g. racoons) and *Dirofilaria ursi* (which infects a variety of hosts, including felines, ursids and humans) (Yokohata et al. 1990, Dantas-Torres & Otranto 2013, Masatani et al. 2021). However, these species are rarely detected in the area, therefore we will not focus on them in the current study.

The life cycle of *Dirofilaria* spp. involves several stages, starting with the ingestion of microfilariae by a mosquito during a blood meal from an infected host. The microfilariae develop into infective larvae (L3 stage) within the mosquito, and when the infected mosquito bites a susceptible host, the larvae are released into the host's tissues (Montarsi et al. 2015). Over time, the larvae migrate through the bloodstream and settle either in the right ventricle and pulmonary arteries in the case of *Dirofilaria immitis*, causing severe damage to the cardiovascular system, or in the subcutaneous tissue in the case of *Dirofilaria repens*.

While the presence of some *Dirofilaria* species is showing an increasing occurrence in certain hosts, such as domestic dogs (Capelli et al. 2018, Genchi & Kramer 2020), we currently have little understanding about the role that wild carnivore populations may play in the infection dynamic of this disease. Furthermore, it is unclear which ecological processes drive the occurrence of infection, such as the presence and distribution of sylvatic reservoir species. Nevertheless, evidence in the past years suggests that wild carnivores (e.g. wolves, jackals and foxes) may contribute to the maintenance and spread of this parasitic infection as potential reservoirs (Penezić et al. 2014, Ionica et al. 2016, Alsarraf et al. 2023c).

The order of Carnivora comprises approximately 300 species and subspecies worldwide (Burgin et al. 2018). These species host a wide variety of infectious pathogens (including bacteria, helminths, protozoans and viruses), and thus are important targets of public health research and veterinary practice (Digby et al. 2021, Han et al. 2021). Carnivores exhibit a wide range of biological and ecological characteristics, including morphology and dietary, migratory and social behaviour (Meloro et al. 2015,

Benson-Amram et al. 2016). These traits play important roles in mediating parasite richness and transmission within species (Bordes et al. 2009), and between species (Olival et al. 2017).

Vector-borne diseases are common in both wild and domestic carnivores, and different parasites show different degrees of specificity. Vector-borne diseases in carnivores are typically grouped according to vectorial organisms, such as the sandfly-borne *Leishmania*, the tick-borne *Anaplasma*, *Borrelia*, *Ehrlichia*, *Rickettsia* and the mosquito-borne *Dirofilaria* species (Millán et al. 2016, Battisti et al. 2020, Han et al. 2021). Some of these vector-borne diseases pose a particularly high zoonotic threat to humans (Otranto et al. 2009). For instance, helminth parasites such as *Dirofilaria immitis* and *Dirofilaria repens* are increasingly observed to infect humans in the Americas and Europe, respectively (Dantas-Torres & Otranto 2013, Capelli et al. 2018). As mosquitoes thrive in various geographical regions and their populations are influenced by climate change and global travel, the spread of *Dirofilaria* infection has become a global concern.

In the present study, our goal was to review currently known patterns of *Dirofilaria* occurrence and distribution, and to understand surveillance patterns in *Dirofilaria* detection that may exist in sylvatic hosts. Furthermore, we summarise suspected and known drivers of dirofilariosis spread, which include climate change, urbanisation, presence of invasive species and host ecology, to help identify factors that shape infection dynamics in the wild that could lead to a better understanding about the extent of the veterinary and public health threat posed by dirofilariosis. Additionally, assessing current knowledge gaps will help allocate research efforts in the future.

HOST RANGE, PHYLOGENETIC AND GEOGRAPHIC DISTRIBUTION OF *DIROFILARIA* ACROSS CARNIVORA

Although some parasites tend to infect closely related host species (Braga et al. 2015, Albery et al. 2020), the host range can vary across taxa, depending on environmental and ecological factors (Poulin et al. 2011). Closely related helminth species generally infect hosts within a restricted phylogenetic range (Huang et al. 2014). Shared biological and ecological traits and overlapping geographical distributions are also important factors in mediating host switch that results in shared pathogen communities among host species (McKee et al. 2019).

Dirofilaria immitis is most often found in canids. Nevertheless, data shows its occurrence in 18 species within carnivora, across seven families, including Ailuridae, Canidae, Felidae, Mustelidae, Phocidae, Procyonidae and Ursidae (Fig. 1), indicating that a wide range of species

Table 1. Prevalence and number of tested hosts of *Dirofilaria immitis* and *Dirofilaria repens* across the Palearctic region between 1998 and 2022, including different diagnostic tests. Additional data and references are found in Appendix S1

Host	<i>Dirofilaria immitis</i>		<i>Dirofilaria repens</i>	
	Infected individuals/ tested individuals	Country	Infected individuals/ tested individuals	Country
<i>Ailurus fulgens</i> *	21/50	China	–	–
<i>Canis aureus</i> †	241/1470	Bulgaria, Hungary, Iran, Iraq, Romania, Russia, Serbia, Uzbekistan	30/551	Macedonia, Romania, Russia, Serbia, Uzbekistan
<i>Canis lupus</i> † (incl. <i>Canis lupus signatus</i>)	18/616	Bulgaria, Italy, Iran, Kazakhstan, Portugal, Romania, Serbia, Slovakia, Spain, Uzbekistan	15/296	Macedonia, Poland, Romania, Serbia, Slovakia, Ukraine, Uzbekistan
<i>Felis chaus</i> †	7/82	Uzbekistan	8/124	Uzbekistan
<i>Felis lybica</i> †	Present†/11	Uzbekistan	Present†/11	Uzbekistan
<i>Felis silvestris</i>	10/151	Bulgaria, Italy, Romania, Serbia, Slovakia	0/2	Romania, Slovakia
<i>Halichoerus grypus</i> *	0/2	Portugal	–	–
<i>Lutra lutra</i> *	6/176	Italy, Portugal, Romania, Serbia, Slovakia, Spain, South Korea, Uzbekistan	0/15	Romania, Slovakia, Uzbekistan
<i>Lynx lynx</i>	0/21	Romania, Uzbekistan	0/9	Romania, Uzbekistan
<i>Lynx pardinus</i> *	8/191	Spain		
<i>Martes foina</i>	0/100	Romania, Serbia, Slovakia, Uzbekistan	3/58	Poland, Romania, Slovakia, Uzbekistan
<i>Martes martes</i>	0/38	Bulgaria, Romania, Serbia, Slovakia	0/11	Poland, Romania, Slovakia
<i>Meles meles</i>	2/283	Bulgaria, Italy, Romania, Russia, Serbia, Slovakia, Uzbekistan	8/225	Poland, Romania, Russia, Slovakia, Uzbekistan
<i>Mustela erminea</i>	0/4	Romania	0/3	Romania
<i>Mustela eversmanii</i>	0/1	Romania	–	–
<i>Mustela lutreola</i>	0/5	Romania	0/4	Romania
<i>Mustela nivalis</i>	0/41	Romania, Uzbekistan	1/38	Romania, Uzbekistan
<i>Mustela putorius</i>	2/93	Hungary, Japan, Romania, Serbia, Slovakia	0/7	Romania, Slovakia
<i>Mustela vison</i>	0/26	Uzbekistan	0/26	Uzbekistan
<i>Nyctereutes procyonoides</i> * (incl. <i>Nyctereutes procyonoides viverrinus</i>)	53/296	Japan, Romania, Russia	0/138	Germany, Poland, Russia
<i>Otocolobus manul</i>	0/2	Russia	–	–
<i>Panthera leo</i> *	1/1	Spain	–	–
<i>Panthera pardus</i> *	1/1	Italy	–	–
<i>Phoca largha</i> *	1/1	South Korea	–	–
<i>Phoca vitulina</i> *	4/6	Portugal, South Korea	–	–
<i>Procyon lotor</i>	0/72	Spain	0/130	Poland, Spain
<i>Ursus arctos</i>	1/22	Greece, Romania, Slovakia	0/6	Romania, Slovakia
<i>Vormela peregusna</i>	0/1	Romania	–	–
<i>Vulpes corsac</i>	0/74	Kazakhstan, Uzbekistan	0/61	Uzbekistan
<i>Vulpes rueppellii</i>	2/5	Iran	–	–
<i>Vulpes vulpes</i> †	251/4231	Bosnia Herzegovina, Bulgaria, France, Hungary, Iran, Iraq, Italy, Kazakhstan, Portugal, Romania, Russia, Serbia, Slovakia, Spain, Ukraine, United Kingdom, Uzbekistan	140/2248	France, Germany, Italy, Macedonia, Poland, Romania, Russia, Serbia, Slovakia, Ukraine, Uzbekistan

*Including captive individuals.

†Number of positive individuals is not given in some cases.

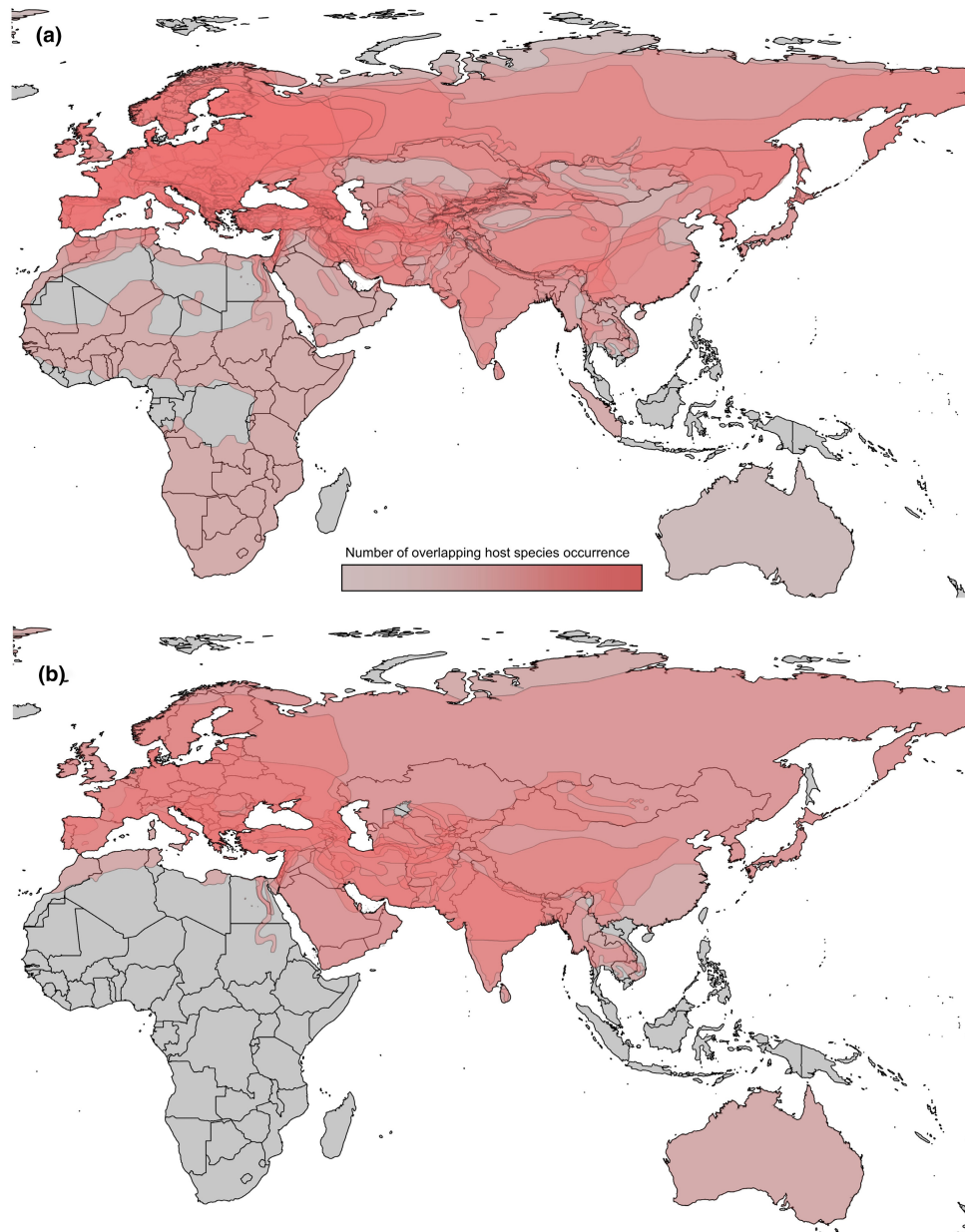


Fig. 2. Geographical distribution of *Dirofilaria immitis* (a) and *Dirofilaria repens* (b) hosts (Appendix S1). Distribution of potential or definitive *Dirofilaria immitis* hosts shows high overlapping in Europe and the Middle East (a), but little surveillance data is available from the latter geographical area. Distribution of several potential hosts overlaps in the Middle East and certain parts of South Asia (b) for *Dirofilaria repens*, where targeted surveillance is largely missing from potential carnivore host species.

suggested that red foxes might not be suitable reservoir hosts, due to the low prevalence of microfilaremia and the low presence of adult worms of both sexes in these hosts (Marconcini et al. 1996, Ionică et al. 2017), but some studies have shown a relatively high microfilaremia or infection by both adult sexes in these hosts at certain locations (Gortázar et al. 1998, Magi et al. 2008, Panayotova-Pencheva et al. 2016, Liulin et al. 2021). Hence, the

reservoir role of red foxes needs to be further investigated, as it has also been suggested by other authors (Otranto & Deplazes 2019), especially due to the low number of works that studied microfilaremia in the blood of these hosts. Nonetheless, red foxes are considered useful sentinel hosts (Veronesi et al. 2023). *Dirofilaria immitis* frequently infect red foxes in the Palearctic region as well as in Australia and North America (Hubert et al. 1980, Mulley

& Starr 1984). Additionally, red foxes show the widest geographical range as *Dirofilaria immitis* hosts, with infection having been detected in several countries in the Palearctic region (Table 1). In red foxes in the Palearctic region, *Dirofilaria immitis* has been found to reach a prevalence of 25% (Panayotova-Pencheva et al. 2016), while *Dirofilaria repens* has been found to reach a prevalence of 9% (Safarov et al. 2021). Red foxes should be of particular importance because they often exploit urbanised habitats, thus they could establish a transmission route between species in the wild and domesticated population of animals in the cities.

Grey wolves have been considered as important hosts of dirofilariosis, yet they show relatively low prevalence of infection, reaching 5% and 9% for *Dirofilaria immitis* and *Dirofilaria repens*, respectively (Georgeiva et al. 2001, Safarov et al. 2021). However, in certain areas, wolves can show *Dirofilaria immitis* infection prevalence as high as 13.6% (Moroni et al. 2020). In endemic areas, altitude and sympatric dog infection prevalence strongly shape infection patterns in grey wolves (Moroni et al. 2020).

Incidental hosts may show clinical signs of infection without providing a suitable environment for successful parasite development. During events, when a parasite can successfully colonise an incidental host, which may later result in an interspecies transmission, could play an important role in the evolution of host specificity (Boothroyd 2009, Leggett et al. 2013, Haelewaters et al. 2017). Humans are considered incidental hosts for both *Dirofilaria immitis* and *Dirofilaria repens* (Malik et al. 2016, Pupi c-Bakra c et al. 2021), but *Dirofilaria repens* microfilaremia has been identified in humans, suggesting that humans may serve as definitive hosts of this disease in very rare cases (Pupi c-Bakra c et al. 2021). Furthermore, we have limited understanding of which other species act as incidental, definitive or reservoir hosts to *Dirofilaria* species. In recent years a number of species have been newly described as hosts of *Dirofilaria immitis*, such as the European badger (*Meles meles*) (Ionic  et al. 2022) and the Eurasian otter (*Lutra lutra*) (Matsuda et al. 2003, Penezi c et al. 2018). These cases may reflect incidental infections, or that these species are suitable definitive hosts, but remain little studied. Since infection events likely go unnoticed in the wild, it is difficult to estimate their true scale and more research needs to be done to conclude the role of these species. Surveillance studies carried out in zoos and animal parks can help increase understanding of the spread of the parasite, especially from an epidemiological perspective, and facilitate the implementation of preventive measures. Furthermore, these approaches may reveal the potential host range of these parasites in the wild, as it has been shown in pinnipeds (Pinnipedia) (Alho et al. 2017), harbour seal (*Phoca vitulina*) (Kang et al. 2002), snow leopard (*Panthera*

uncia) (Murata et al. 2003) and African lion (*Panthera leo*) (Ruiz de Yb n ez et al. 2006). Nevertheless, these data should be handled with caution as little information is available of the infection status of these hosts in their native range, and may not serve as hosts there.

Distinguishing definitive, reservoir and incidental hosts is challenging in nature. Generally, laboratory experiments are necessary to explore whether parasites can develop and reproduce successfully in a given host. In the case of dirofilariosis, showing the presence of adult nematodes in the pulmonary or the subcutaneous system provides an indication that the species may act as a definitive host, but demonstrate active reproduction (by examining the uterus of the female nematodes for uterine microfilariae and microfilariae in the blood) is more compelling, with some examples in wild carnivore species (Tolnai et al. 2014, Penezi c et al. 2018, Moroni et al. 2020). Reproductive ability in hosts under laboratory conditions can suggest that a certain species may be potential definitive host of these parasites, but host colonisation success should be examined in natural populations to reveal their true potential.

The distribution of sylvatic carnivore hosts can be considered as wide through the Palearctic region in the case of both parasite species (Fig. 2). However, the presence of *Dirofilaria immitis* or *Dirofilaria repens* has only been reported in a handful of countries, and surveillance data is missing in most areas where these hosts occur (Table 1). Based on host distribution, both *Dirofilaria* species may have a much wider range than is currently known.

Both *Dirofilaria* species are transmitted by several mosquito species (e.g. *Aedes* spp., *Culex* spp. and *Anopheles* spp.). Several of these vectors have a wide geographical range, which likely affects the range of these parasites. The impact of climate change is expected to further affect the range of both vectors and parasites, potentially leading to an increased occurrence of infections between and within species in the future.

THE EMERGENCE AND SPREAD OF DIROFILARIOSIS IN WILD CARNIVORES IN THE LAST 30 YEARS

Until the 1990s, *Dirofilaria immitis* and *Dirofilaria repens* were known to occur primarily in the Mediterranean region of Europe (Capelli et al. 2018). However, over the past few decades, these parasite species have increasingly been found in Central and Eastern Europe, and have become endemic in these areas, where they cause autochthonous infections in local dog populations (Capelli et al. 2018, Miterp kov  et al. 2018). Nevertheless, in wild carnivores, surveillance data from the past decades show a sharp decline in the number of reported tests since 2014, with an average of ~417 individuals being reported

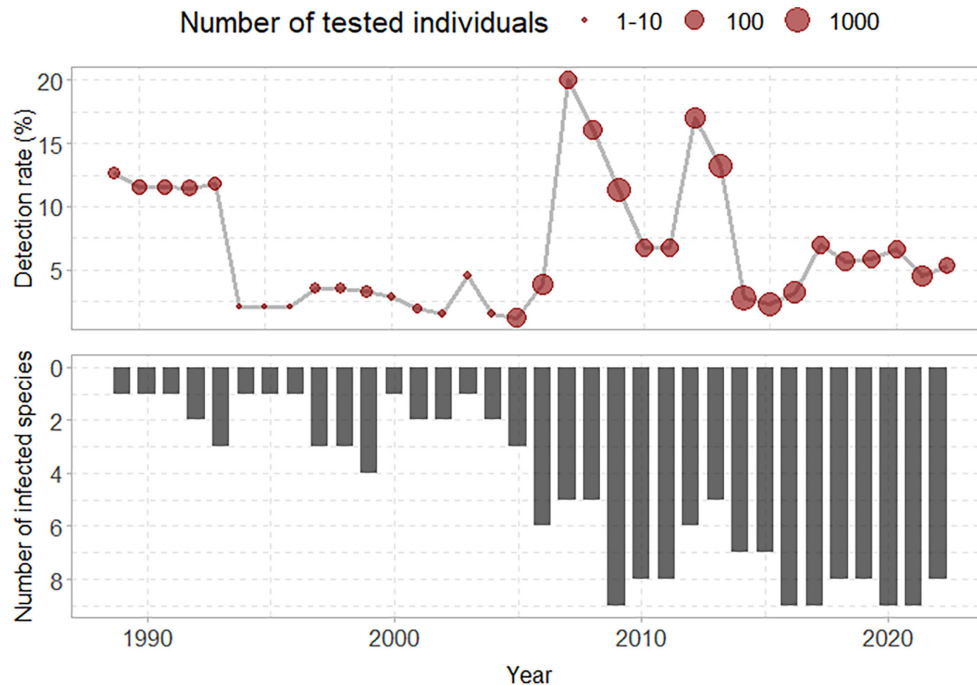


Fig. 3. *Dirofilaria* detection rate in infected species (upper panel) indicating the number of tested individuals (red circles), and number of infected species (lower panel) between 1989 and 2022.

as tested for *Dirofilaria* spp. in the past 6 years per year (Fig. 3). Therefore, even if dirofilariosis is currently considered an emerging disease in domestic dogs, we have lack of evidence for this phenomenon in sylvatic hosts.

Several factors can be considered as potential drivers in the increase of dirofilariosis in domestic animals, which likely affect sylvatic hosts, as well. First, climate change, which has extended warm weather periods in regions where these parasites were not previously endemic (Genchi et al. 2011). Climate and temperature strongly affect larval development, mosquito activity and survival, and the appearance of new potential vector species (Lahondère & Bonizzoni 2022), which is currently leading and will further shape the increased occurrence of new and emerging mosquito-borne diseases (Ludwig et al. 2019). Extreme weather events such as drought and hurricanes, which have increased in frequency under climate change, also influence mosquito density and the emergence of mosquito-borne diseases (Nosrat et al. 2021, Farooq et al. 2022).

Second, increased density of pets and stray dogs likely affects *Dirofilaria* occurrence (Anvari et al. 2019, Stoyanova et al. 2019, Potkonjak et al. 2020). In wild carnivore species, dirofilariosis may persist because of circulation within wildlife, or due to infected sympatric dogs (Weinmann & Garcia 1980, Aher et al. 2016, Moroni et al. 2020, Safarov et al. 2021).

Third, anthropization and urbanisation are tightly associated with the domestic dog populations and increase

domestic animal–wildlife interactions, with cities showing a higher dog density compared to rural areas (Acosta-Jamett et al. 2010), and urban and peri-urban areas appearing as important zone for wildlife and domestic dog co-occurrence and interactions (Mella-Méndez et al. 2019, Hernández et al. 2021). Population-level maintenance of *Dirofilaria* infection requires a sufficient number of infected and microfilaraemic mammalian host individuals and the presence of competent vectors with an appropriate abundance. Hence, anthropization and urbanisation may contribute to *Dirofilaria* occurrence and recent emergence (Čabanová et al. 2018, Worsley-Tonks et al. 2021). However, while urbanised mammals show a higher prevalence and diversity of some infectious pathogens (Albery et al. 2022), the opposite was found for some other parasites, including helminths (Werner & Nunn 2020). Therefore, the extent to which urban-adapted carnivores act as *Dirofilaria* hosts remains uncertain.

Fourth, pet travel is likely to affect *Dirofilaria* distribution (Genchi et al. 2005, Genchi & Kramer 2017). The emergence of native and newly introduced *Dirofilaria* species may result from pet travel (Sassnau & Genchi 2013, Anderson et al. 2019). In many European countries, such as those where echinococcosis or rabies are concerned, dirofilariosis in pets is not considered a condition that necessitates mandatory diagnosis and treatment prior to animal movement. Within the European Union, pet transport (Pet Travel Scheme in 2000) is logistically and

administratively simple (and not requiring a screening for parasites), easing the cross-border movement of potentially infected domestic animals from endemic countries to new areas (Trotz-Williams & Trees 2003). Transport of domesticated animals can contribute to the introduction and spillover of non-endemic diseases to local, naïve host populations (Fèvre et al. 2006). Nevertheless, parasite spillover from domestic animals to wildlife likely often remains undetected. Furthermore, wildlife trade and translocation may also contribute to *Dirofilaria* spread, however, we currently lack of data on this issue.

Fifth, the increase in new potential vectors could contribute to the emergence of vector-borne diseases in humans and local fauna (Schaffner et al. 2013, Ganassi et al. 2022). Invasive mosquito species typically find their way into new regions through the transportation of goods, such as used car tyres and lucky bamboo (Ibáñez-Justicia 2020). They can also be inadvertently carried by aircraft and ferry transport, allowing mosquito eggs, larvae or adults to persist. Furthermore, their natural dispersal plays a significant role in their spread to non-native areas (Ibáñez-Justicia 2020). Invasive *Aedes aegypti*, *Aedes albopictus*, *Aedes japonicus* and *Aedes koreicus* have been shown to act as *Dirofilaria* vectors either under laboratory or natural conditions (Cancrini et al. 2007, Montarsi et al. 2015, Silaghi et al. 2017), and they are intensively spread in the temperate zone (Wilke et al. 2020, Perrin et al. 2022). Furthermore, these mosquito species can be often characterised by wide host spectra, like *Aedes albopictus* and *Aedes japonicus* (Cebrián-Camisón et al. 2020), and with *Dirofilaria* vectorial capacity is likely important in interspecies transmission.

Lastly, the emergence of non-native mammals in the Palearctic region may drive parasite introduction to local, naïve hosts (Chinchio et al. 2020). Introduced mammals may also become new reservoirs of local parasites and pathogens (Schatz & Park 2021), and are especially likely to act as reservoirs for parasites that already infect phylogenetically close native hosts (Schatz & Park 2021).

FUTURE PERSPECTIVES: THE NEED FOR TARGETED AND LONG-TERM SURVEILLANCE, AND IMPROVING SAMPLING BIAS

About 82 carnivora species currently occur in the Palearctic region (including introduced species). From the available literature, we identified seven species that underwent *Dirofilaria* testing, revealing no infection. These species include the grey seal (*Halichoerus grypus*), examined through PCR and the Knott test; the Eurasian lynx (*Lynx lynx*), tested via PCR and necropsy; the

European pine marten (*Martes martes*), assessed through PCR and necropsy; the stoat (*Mustela erminea*), analysed by PCR and necropsy; the steppe polecat (*Mustela erminea*), evaluated through necropsy; the European mink (*Mustela lutreola*), subjected to PCR and necropsy; and the marbled polecat (*Vormela peregusna*), investigated through necropsy. However, relatively few individuals were tested, thus these species cannot be excluded as potential hosts. Generally, such negative results likely remain unpublished. A strong sampling bias is present when considering the number of tested individuals/numbers of infected hosts, indicating the lack of surveillance in most wild carnivore species (Table 1).

Sampling bias is also present geographically, as most infection data are from the Western Palearctic, and comparably few observations have been made in the Middle East and the Eastern Palearctic. As parts of these regions are climatically suitable environments for the vector species, where the annual number of *Dirofilaria* generations may be high due to high average temperatures (Genchi et al. 2009), *Dirofilaria* populations may be common in these geographical areas.

Suspected *Dirofilaria* spp. hosts (e.g. species that have similar ecologies to known reservoir species) should be monitored to establish their reservoir or definitive host potential. Carnivore species with wide geographical ranges should also be monitoring targets (e.g. red foxes and golden jackals), to determine intraspecific variance of *Dirofilaria* occurrence on a greater geographical scale, which could help determine environmental factors that play a role in infection dynamic. As prevalence and infection intensity might differ geographically, seasonally and depending on host species, it is difficult to determine the minimum study effort to certainly detect *Dirofilaria* spp. occurrence in their hosts. Our understanding of geographical differences in infection patterns between host species is also limited, and main sylvatic hosts, such as red foxes and golden jackals would be suitable target species in future studies to explore these questions. Nonetheless, it is essential to employ conventional monitoring techniques to compare results across studies, due to the varying levels of detectability associated with different diagnostic methods, coupled with the sensitivity of available samples (such as the potential degradation of parasites in frozen animal samples for necroscopy), necessitate a standardised approach. Additionally, future efforts should explore *Dirofilaria* spp. occurrence, diversity and host spectra in geographically underrepresented areas.

Targeted surveillance of potential, or understudied species can improve our understanding of parasite host ranges. Ideally, potential hosts could be predicted by using, among other traits, host and parasite ecological traits. Towards

this direction, a great amount of infection data is needed in a wide variety of hosts, and more information about their ecological and life-history traits, that can affect host range, host switch and distribution, to apply machine learning methods and to reliably predict potential host range of these parasites. Machine learning has been used to successfully predict viral zoonotic hosts among small mammals and bats (Han et al. 2015, 2016), which can also be useful in this context given that the required monitoring data are available. The vectorial potential of zoonotic pathogens can also be explored using data-driven machine learning predictions, as has been done in ticks and mosquitoes (Evans et al. 2017, Martin et al. 2022). This method could be especially useful for identifying host species of rarely detected infections, such as *Dirofilaria repens*, which is particularly difficult to monitor as infections are often asymptomatic. Nevertheless, more occurrence data are needed (i.e. presence-absence of *Dirofilaria* spp. in a wide variety of hosts) to successfully apply this approach.

Xenomonitoring (disease surveillance using hematophagous insects) of mosquitoes is frequently used to understand *Dirofilaria* spp. presence at a large geographic scale, where host surveillance is operationally difficult (Masny et al. 2016, Pilotte et al. 2016). However, such a monitoring approach may not detect *Dirofilaria* spp. when infection levels are low (Masny et al. 2016). Moreover, detection rates may depend on the mosquito species tested, and their vectorial capacity (Latrofa et al. 2012). Xenosurveillance should focus on mosquito species, which are known as *Dirofilaria* spp. vectors, such as *Culex pipiens*, *Culex theileri*, *Aedes albopictus*, *Aedes koreicus* and *Aedes vexans* (Cancrini et al. 2003, 2007, Morchón et al. 2012, Montarsi et al. 2015). Overall, while xenomonitoring is a useful tool, it cannot replace the surveillance and monitoring of carnivore hosts, but a standardised sampling and molecular screening methodology is needed to make inter-study comparisons possible in the long term.

Dirofilariosis should also be explored further as a potential conservation threat to species that may get naturally infected in the wild either as incidental hosts or as definitive hosts (e.g. in Iberian lynx (*Lynx pardinus*) (Endangered) and Eurasian otter (Near Threatened)) (Penezić et al. 2018, Acosta et al. 2019). Additionally, there is no data on *Dirofilaria* spp. in several threatened carnivores, likely due to lack of testing. Xenomonitoring or the testing of naturally deceased hosts would prove especially beneficial here. Future surveillance efforts should consider dirofilariosis as a potential conservation risk in vulnerable carnivore species.

Lastly, as *Dirofilaria* detection is not subject to mandatory reporting in wildlife, it would be essential for governmental and academic institutions to work together to prevent potential underdetection. Given that infections of

both *Dirofilaria immitis* and *Dirofilaria repens* typically exhibit no symptoms in wildlife, relying on passive surveillance of deceased animals is essential for gaining insights into infection rates, parasite intensity and the reproductive capacity of *Dirofilaria* in various wild hosts.

CONCLUDING REMARKS

The occurrence of dirofilariosis shows an alarming increase worldwide in domestic dogs. Currently, data is limited, and therefore we lack evidence that dirofilariosis is increasing in wild carnivore populations. Long-term *Dirofilaria* monitoring and surveillance is currently largely inefficient and would be necessary both in mosquito vectors and in wild carnivore hosts to understand the infection patterns, geographic distributions and host spectra of these parasites. This work highlights the potential importance of wild carnivore species in the maintenance and interspecific transmission of *Dirofilaria* spp., with relevance to conservation, public health and veterinary research. Unfortunately, the currently limited scientific knowledge undermines the application of mitigation strategies in practice. Specifically, the full host spectrum of *Dirofilaria* spp. across wildlife is currently unknown, while several species are potentially able to host and act as reservoirs for these parasites in nature. The pathogenicity of the disease caused by these pathogens is poorly described in nature, thus the morbidity and mortality aspects of infections need to be further explored. Additionally, understanding the drivers of *Dirofilaria* spp. spread in this multi-host system can further contribute to the prevention, prediction and diagnosis of this disease in wildlife species. Increasing levels of dirofilariosis are expected due to climate change, increasing invasive vector occurrence and urbanisation. Therefore, exploring environmental factors and eco-evolutionary host traits that can drive the occurrence and spread of this disease is urgently needed and should be a priority in eco-epidemiological research.

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DATA AVAILABILITY STATEMENT

Data supporting the conclusions of this work can be found in Appendix S1.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Occurrence of *Dirofilaria immitis* and *Dirofilaria repens* in Carnivore species across the Palearctic region.