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The role of wild canids and felids in spreading parasites to dogs and cats in Europe. Part II: Helminths and arthropods

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Highlights



Ecological factors, combined with everchanging landscapes contributed to modifications in the transmission of parasitic diseases from domestic to wildlife carnivores and *vice versa*.

In this second review article, we focus on parasitic diseases caused by helminth and arthropod parasites shared between domestic and wild canids and felids in Europe.

Advancements in current knowledge of transmission routes is crucial to provide policy-makers with clear indications on strategies to reduce the impact of these diseases on changing ecosystems.

Abstract

Over the last few decades, ecological factors, combined with everchanging landscapes mainly linked to human activities (e.g. encroachment and tourism) have contributed to modifications in the transmission of parasitic diseases from domestic to wildlife carnivores and *vice versa*. In the first of this two-part review article, we have provided an account of diseases caused by protozoan parasites characterised by a two-way transmission route between domestic and wild carnivore species. In this second and final part, we focus our attention on parasitic diseases caused by helminth and arthropod parasites shared between domestic and wild canids and felids in Europe. While a complete understanding of the biology, ecology and epidemiology of these parasites is particularly challenging to achieve, especially given the complexity of the environments in which these diseases

perpetuate, advancements in current knowledge of transmission routes is crucial to provide policy-makers with clear indications on strategies to reduce the impact of these diseases on changing ecosystems.

Key words: arthropods; wildlife; Europe; wild canids; wild felids; zoonoses; *Echinococcus multilocularis*; *Thelazia callipaeda*; *Dirofilaria*; *Onchocerca lupi*; *Toxocara canis*; *Aelurostrongylus abstrusus*; *Troglostrongylus brevior*; *Angiostrongylus vasorum*.

1. Helminths and arthropods of wild and domestic carnivores: a complex scenario

With a few exceptions in some areas, the knowledge of the ecology and epidemiology of helminths and arthropods shared by wild and domestic carnivores in Europe is limited. One of the exceptions examples is the tapeworm *Echinococcus multilocularis*, the causative agent of zoonotic alveolar echinococcosis, for which extensive data on its the ecology in rural and urban habitats is available for central Europe (Deplazes et al., 2004; Hegglin et al., 2015; Raoul et al., 2015). In addition, like protozoans, parasitic helminths and arthropods are also characterised by complex life cycles, often involving a range of intermediate (e.g., *Aelurostrongylus*, *Troglostrongylus*, *Angiostrongylus* and *Opisthorchis*) and paratenic hosts (i.e., *Toxocara*), which makes the identification of potential hazards of cross-transmission between wild and domestic carnivores and *vice versa* particularly challenging. This scenario is further complicated by the plague represented by the illegal trade of wildlife species into Europe (often carrying parasites) (Davidson et al., 2013) which, coupled with the ever-increasing human and pet travel, represents a serious obstacle to the implementation of control strategies aimed at preventing the cross-transmission of helminths and arthropods from wild to domestic carnivores (and humans). In the second part of this two-part article, we provide an overview of key diseases caused by parasitic helminths and arthropods shared by domestic and wild canids and felids (with a particular focus on those with potential public health implications) and discuss a potential way-forward

towards controlling the spread of these diseases (as well as those caused by protozoan parasites) *via* the combined efforts of veterinarians, physicians, microbiologists, biologists and health policy-makers.

2. Helminths infecting domestic and wild carnivores

2.1. Taeniids

Echinococcus granulosus complex

The taxonomy of *Echinococcus* spp. (Cestoda, Taeniidae), causing cystic echinococcosis (CE) in intermediate hosts (mainly wild and domestic large herbivores and omnivores) and humans, is still under revision (Lymbery et al., 2015; Romig et al., 2015). CE is an important zoonosis still persisting in Southern Europe and the Balcan and emerging in Eastern European countries and in the Baltic region (Marcinkutė et al., 2015), with severe clinical implications (Stojkovic et al., 2014). For Europe, *E. granulosus* sensu stricto (sheep strain, genotypes G1-3) represents the principal agent of zoonotic CE affecting humans (mainly in Southern and South-Eastern Europe) with a considerable burden of disease. *Echinococcus intermedius* (*E. granulosus* pig strain, G7) is the main human agent of human CE in countries of the Baltic region, Poland and parts of Eastern Europe (Marcinkutė et al., 2015), with sporadic cases recorded in other European areas (Sardinia, Spain, and Portugal). *Echinococcus canadensis* (cervide strain, G8 and G10) occurs in the circumpolar North, including Sweden, Finland and Estonia.

The life cycles of the CE species-complex in Europe rely on canids (mainly the domestic dog) as definitive hosts, and a range of large herbivorous and omnivorous species as intermediate hosts. Large wild canids are susceptible to *E. granulosus s.l.* and can contribute significantly to disease epidemiology and zoonotic transmission (e.g., the dingo in Australia; Jenkins et al., 2005). For *E. canadensis* possibly overlapping transmission cycles have been described: “the original wolf- wild cervid (reindeer or elk) -cycle; the semi-synanthropic cycle involving sled and hunting dogs

and wild cervids; and the synanthropic cycle involving herding dogs and semi-domesticated reindeer” (Oksanen and Lavikainen, 2015). In the intermediate hosts including humans (rare cases with low pathogenicity) cysts predominantly appear in the lungs. Actually, the wolf-cervid cycles sustain the parasite in Fennoscandia. However, feeding hunting and sled dogs raw meat or offal can sporadically cause patent infections with zoonotic potential.

Patent *E. granulosus* (s.l. or G1) infections have been detected in jackals (Takács et al., 2014; Breyer et al., 2004) and in wolves in Southern Europe (Italy, Guberti et al., 2004, Gori et al., 2015; Spain, Sobrino et al., 2006). A sylvatic cycle of *E. intermedius* involving wild boars and wolves was hypothesized to occur in a Portuguese national park (Guerra et al., 2013); in Spain, a wild boar infected with fertile *E. granulosus* (G1) cysts was detected in a region inhabited by wolves (Martín-Hernando et al., 2008). In addition, in Italy (Apennine region), a semi - domestic life cycle involving sheep and wolves has been proposed (Guberti et al., 2004). Spatial behaviour (large home ranges and long dispersion distances) of these large canids promotes the spread of this parasite throughout Europe. On the other hand, in Europe, infected foxes are only rarely detected (and usually with low burdens of *E. granulosus* s.l.) and are therefore considered of marginal importance in parasite transmission. Domestic and wild felids are not susceptible to intestinal infections with CE species occurring in Europe, but can suffer from CE, although very rarely (Armua et al., 2014).

In Europe, control of CE focuses on the domestic life cycles of the parasite, with veterinary public health measures including control of stray dogs and dog deworming campaigns (Craig and Larrieu, 2006). While continuous recommendations are made to refrain from feeding dogs offal of hunted or home slaughtered animals and to regularly administer deworming dog treatments, these are often neglected.

Echinococcus multilocularis

Echinococcus multilocularis (Cestoda, Taeniidae) are small tapeworms of carnivore definitive hosts whose cycle includes a range of rodent intermediate hosts (bearing the metacestode stage) and relies on a predator-prey relationship. The complex parasite ecology is intimately linked to the dynamics of the prey population and to the dietary needs of the predators (Raoul et al., 2015). Humans and a range of animals (e.g. pig, a variety of monkey species, dogs and others; Deplazes and Eckert, 2001) are accidental hosts. Alveolar echinococcosis (AE) is one of the most severe parasitic zoonoses in Europe and worldwide in the Northern Hemisphere, with very serious clinical implications and high burden of disease (Stojkovic et al., 2014; Torgerson et al., 2008). The range of occurrence of *E. multilocularis* is still expanding across Europe, and growing red fox populations (Figure 1) and colonisation of residential areas by these carnivores are major determinants of the progressive urbanisation of the parasite life cycle (Liccioli et al., 2015). This, in turn, contributes to a significant increase of the infection risk to dogs hunting infected voles and to human populations exposed to an *E. multilocularis*-contaminated environment (Deplazes et al., 2004). Several studies have reported an increase in human AE incidence in Austria, Switzerland, France, Poland and Lithuania (Gottstein et al., 2015; Marcinkutė et al., 2015). In Switzerland, an average twofold increase of the annual incidence was documented in 2001-2005 (10-15 years since a significant expansion of fox populations) when compared with that recorded in 1993-2000 (Schweiger et al., 2007). Besides known high endemic areas for AE (Southern Germany, Eastern France and Switzerland), cases of AE are increasingly being reported from Lithuania and parts of Poland, which are now considered 'new' highly endemic areas (Marcinkutė et al., 2015); therefore, the emergence of AE in areas previously considered 'disease-free' should not be underestimated (Gottstein et al., 2015).

Canid species (particularly the red fox) are the most important definitive hosts of *E. multilocularis*. Small numbers (< 50) of mostly non-gravid worms have occasionally been detected in wild felids and in domestic cats (Deplazes et al., 2011; Deplazes, 2015). Furthermore, the reduced capacity of domestic cats to excrete parasite eggs has been documented under experimental conditions (Kapel et al., 2006). Therefore, even if wild

or domestic felids often predate on infected intermediate hosts, they are not considered to play a major role in the maintenance of the parasite life cycle and are of minor zoonotic relevance. Unlike cats, experimental studies have revealed that red foxes, domestic dogs and raccoon dogs excrete comparable large numbers of *E. multilocularis* eggs (Kapel et al., 2006).

Even if the prevalence of *E. multilocularis* infection is usually lower in dogs (0.3-1% in average, up to 7% in animals with free access to rodents), they can contribute substantially to environmental contamination by parasite eggs, also given their high population density particularly in urbanised areas (Hegglin and Deplazes, 2013). Furthermore, given the close human-dog relationship, the frequent contamination of dogs' coats by taeniid eggs and the frequent dog habit to roll in fox faeces, canine fur may represent an important source of infection (Deplazes et al., 2011). An even more prominent role of the domestic dog in the zoonotic transmission of this parasite has been described in Asia (Craig and Larrieu, 2006; Raoul et al., 2015).

The raccoon dog is highly susceptible to most dog parasites; however, its contribution to the epidemiology of *E. multilocularis* is poorly understood. Studies performed in endemic areas for this parasite revealed that the prevalence of infection in raccoon dogs is much lower than in foxes (Bružinskaitė-Schmidhalter et al., 2012). Based on characteristic behavioural traits, such as the habit to defecate in latrines, their reduced activity on meadows and pastures (major vole habitats) and in cold winters, this species is unlikely to play a key role in maintaining the life cycle of *E. multilocularis* (Hegglin et al., 2015). Large canids are highly susceptible to patent *E. multilocularis* infections. In Europe, wolves (Martínek et al., 2001; Bagrade et al., 2009) and jackals (Széll et al., 2013) with patent *E. multilocularis* infection have been recorded. However, their contribution to parasite transmissions is rather limited, especially considering their generally low population densities; however, the extended spatial behaviour of wolves (Figure 2) and jackals could contribute to the introduction of the parasite in new areas.

Intervention strategies to minimise the risk of AE to humans must consider the complex ecology of the wild host, the possible involvement of domestic dogs, and foresee effects of planned human-wildlife interactions such as increased hunting pressure (Hegglin et al., 2015). Fox deworming campaigns with praziquantel containing baits have shown some promise (reviewed by Hegglin and Deplazes, 2013). This strategy was implemented in defined rural and urban areas, and within 1-2 years, a significant reduction of the egg contamination was recorded in the environment. However, on a larger scale and over extended periods, this strategy is expensive and, given the long incubation time of the disease in humans, a tangible benefit could realistically take ~20 years (Hegglin and Deplazes, 2013). The effect of controlling AE by means of monthly deworming treatments of domestic dogs has not been investigated in detail, but is recommended by the European Scientific Counsel on Companion Animal Parasites (ESCCAP) (http://www.esccap.org/uploads/docs/nkzqxmxn_esccapgl1endoguidelines.pdf).

Taenia spp.

A variety of *Taenia* spp. has been described in wild felids. In Eurasian lynx from Estonia the predominant species were *T. pisiformis* and *T. laticollis* (both with mountain hares as intermediate hosts), *T. hydatigena* (probably with the roe deer as principal intermediate host) and *T. taeniaeformis* (with rodents as intermediate host) (Valdmann et al., 2004). The Iberian lynx has been described as the definitive host of *T. polyacantha* and, in single cases, of *T. pisiformis* (Millán and Casanova, 2009). *Taenia taeniaeformis*, *T. crassiceps* and *T. martis* have been described from wild European cats (Krone et al., 2008). The epidemiological role of wild felids in the transmission of *Taenia* spp. is not well understood, and they are hypothesized to play only a minor role in the transmission to domestic cats or dogs. Domestic cats (stray or free roaming cats) play a dominant role in the transmission of *T. taeniaeformis* to rodents as intermediate hosts, based on their high population density especially in residential areas.

Wild canids are definitive hosts of a large range of *Taenia* spp., with rodents or large mammals serving as intermediate hosts. Foxes and raccoon dogs are predominately infected with *Taenia* spp. transmitted *via* rodents (e.g. *T. polyacantha*, *T. crassiceps*) (Bružinskaitė-Schmidhalter et al., 2012) and, in some areas, foxes can be infected with *T. pisiformis* through predation of rabbits/hares (Vergles Rataj et al., 2013). Dogs with free access to rodents or hunting dogs (fed with offal of hunted hares/rabbits) can develop patent infections and contribute to the transmission of the parasite. In jackals, *T. pisiformis*, *T. hydatigena* and *T. crassiceps* have been described (Takács et al., 2014). The wolf is a known definitive host for *T. taeniaeformis*, *T. polyacantha* and *T. crassiceps* (rodents are intermediate hosts), *T. serialis* (hares/rabbits), *T. krabbei* (wild cervids), and *T. hydatigena*, *T. multiceps* and *T. ovis* (sheep and goats) (Guberti et al., 1993; Craig and Craig, 2005). However, the role of this species in spreading the parasites to domestic cats and dogs is likely marginal, and probably limited to populations ‘at risk’, such as hunting dogs and shepherd dogs. Nevertheless, similarly to *Echinococcus* spp., the extended spatial behaviour of wolves likely translates into spread of parasite infections to domestic canids.

2.2. Trematodes

Opisthorchis felineus

Opisthorchis felineus (Trematoda, Opisthorchiidae) is a liver fluke affecting the biliary tract of domestic and wild mammals, and humans. The life cycle is complex and indirect; immediately following excretion of embryonated eggs with the faeces of the definitive host in a freshwater environment, they infect and hatch within *Bithynia* snails, the first intermediate hosts (Kaewkes, 2003). Following a phase of asexual reproduction in the snail, free-living cercariae are released into the environment and ingested by a fish of the family Cyprinidae (the second intermediate hosts), where they develop into metacercariae (Kaewkes, 2003). The final hosts (e.g., humans, dogs and cats) acquire the infection *via* ingestion of raw or

poorly cooked infected fish. Infection by *O. felineus* is of public health concern in Asia and Eastern Europe, and it is considered re-emerging in Italy, where eight outbreaks have been documented from 2003 to 2011 (De Liberato et al., 2011; Pozio et al., 2013). In Western and Central Europe, the parasite has been detected in domestic (cats and dogs) and wild mammals (red foxes, polecats), with prevalence ranging from 16 to 73% (reviewed by Pozio et al., 2013).

Both fish-eating domestic and wild mammals contribute to maintaining the parasite life cycle, especially when defecating in the proximities of freshwater bodies, that are the habitat of snails as intermediate hosts. Large carnivores characterised by a wider home-range (e.g., foxes and stray dogs), may also contribute to spreading *O. felineus* in other environments. However, this occurrence is considered limited (Filatov et al., 1989), especially when compared with the capacity of mankind to spread infections *via* travel and trade of infected fish. The prevention of infection in humans and pets is theoretically achievable through adequate alimentary education, and by freezing fish for raw consumption. This may contribute to reducing the prevalence of infection also in wildlife sharing the same environment with domestic animals. However, *O. felineus* can be propagated by fish-eating wildlife only, which thus represent a source of infection or re-infection especially for feral cats and stray dogs.

2.3. Nematodes

Spirocerca lupi

Spirocerca lupi (Spirurida, Thelaziidae) is a nematode of worldwide distribution, most common in tropical and subtropical areas (Bailey, 1972). Dogs and other wild carnivorous are the natural hosts of this parasite (Anderson, 2000); adult *S. lupi* live embedded in gastric and oesophageal nodules and intermediate as well as paratenic hosts are involved in their transmission (Anderson, 2000). Embryonated eggs are shed in the faeces of the infected host and develop to infective L3 within the intermediate hosts (i.e., coprophagous beetles) within two months (reviewed in van der

Merwe et al., 2007). Final hosts may become infected by ingesting either infected intermediate or paratenic hosts, which include poultry, wild birds, lizards, rodents, hedgehogs and rabbits (Anderson 2000). In the final host, larvae are liberated in the gastric lumen and migrate through the thoracic aortic wall to the caudal oesophagus within 90 to 109 days, where they mature to adults and embed in nodules (Bailey 1972; van der Merwe et al., 2007).

Common clinical signs associated with spirocercosis are associated with the presence of oesophageal nodules and include regurgitation, emesis and weight loss, and other non-specific signs such as pyrexia (van der Merwe et al., 2007). Beside the typical oesophageal nodules, the parasite may also induce other lesions that include aortic scarring (with or without osseous metaplasia and/or dystrophic calcification) as well as aneurysm formation, and caudal thoracic vertebral spondylitis (van der Merwe et al., 2007).

Infections by *S. lupi* have been reported in wildlife species across Europe, such as foxes in Serbia (Pavlović et al. 1997), Belarus (Shimalov and Shimalov, 2003), Spain (Segovia et al., 2004), Greece (Diakou et al., 2012), Denmark (Al-Sabi et al., 2014b) and Italy (Magi et al., 2014) and in wolves and raccoons in Poland (Szafrńska et al., 2010; Popiołek et al., 2011). *Spirocerca lupi* has been extensively described in dogs from Europe (i.e, in southern Italy; Giannelli et al., 2014). In a survey carried out in 260 privately owned dogs from Greece, the prevalence of *S. lupi* infection was 10% (Mylonakis et al., 2001), with a higher prevalence in trace hunting dogs (21%), than in scent hunting dogs (5%) or household animals (0%), thus lending credit to the association between *S. lupi* and hunting dogs. Interestingly, *S. lupi* isolates from Denmark are genetically distinct from other isolates from Europe, Asia and Africa, thus raising questions on the occurrence of cryptic species within isolates from Europe, Asia and Africa (Al-Sabi et al., 2014a). To date, this parasite is considered non-zoonotic.

Thelazia callipaeda

Thelazia callipaeda (Spirurida, Thelaziidae) has been traditionally known as the “oriental eyeworm”, because it infests primarily dogs in the Far Eastern countries (i.e., Indonesia, Thailand, China, Korea, Myanmar, India, and Japan) (see Anderson, 2000). However, over the last 15 years, this parasite has been recognised as a ‘new’ agent of ocular disease in several areas of Europe (Otranto et al., 2013a), having been described in dogs in Northern Italy (Rossi and Bertaglia, 1989) and, soon after, in cats and foxes from Northern and Southern Italy, with a prevalence of up to 60.1% in dogs from some municipalities of the Basilicata region (Otranto et al., 2003). From these first studies, and within only a few years, infections by *T. callipaeda* have been reported in France (Dorchies et al., 2007), Switzerland (Malacrida et al., 2008), Spain (Miró et al., 2011), Portugal (Rodrigues et al., 2012) and in Bosnia and Herzegovina and Croatia (Hodžić et al., 2014). Due to the ocular disease this parasite causes in animals (e.g., conjunctivitis, epiphora, and ocular discharge, keratitis, and corneal ulcers) (Otranto and Traversa, 2005), infection by *T. callipaeda* adults is easily differentiated from that of other ocular nematodes (e.g., *Dirofilaria* spp.). Therefore, the increased number of cases of *T. callipaeda* infection in Europe reported in the literature may be partly explained by the growing awareness of veterinarians and parasitologists, but may also indicate that canine thelaziosis is emerging in some European areas. Importantly, where the infection in dogs is prevalent, it has also been reported in other host species such as cats (Maia et al., 2014) and foxes (Malacrida et al., 2008; Hodžić et al., 2014; Sargo et al., 2014).

The widespread distribution of this nematode in Europe is probably related to the presence of suitable vectors and hosts in different European countries. For example, its vector, *Phortica variegata* (Drosophilidae, Steganinae), is distributed throughout Europe (Máca and Otranto, 2014). Studies conducted on the ecology of this lachrymophagous drosophilid identified large areas of Europe as suitable habitats for *P. variegata* and, therefore, for the expansion of thelaziosis (Otranto et al., 2006a). Although the role of hunting dogs travelling throughout Europe has been hypothesized as a possible factor of the introduction of *T. callipaeda* in some areas (Miró et al., 2011), clear evidence on this is still lacking. In addition to the ubiquitous distribution of the vector, the availability of several competent wild hosts may also facilitate the spreading of *T.*

callipaeda into new areas. Indeed, wild canids (i.e., foxes, wolves), mustelids (i.e., beech martens) and felids (i.e., wild cats) are suitable hosts for this parasite (Otranto et al., 2009), and live in forested and meadow areas where *P. variegata* perpetuates. The importance of wild canids (e.g., foxes) and the existence of a natural, wild cycle *T. callipaeda*, regardless the presence of dogs, is confirmed by the high prevalence of infection (e.g., 27.7%) recorded in foxes in areas where dog infection has yet to be described (Hodžić et al., 2014). Prevalence in foxes may reach 49.3% (Otranto et al., 2009) in highly endemic areas, where the infection is well-established in populations of dogs and cats. Although other wildlife species act as hosts for *T. callipaeda* (Table 1), foxes are likely to represent the primary hosts due to their habits, which may favour their contact with the vector. Indeed, the seasonality and the crepuscular activity of *P. variegata* (Otranto et al., 2006b) coincide with the activity patterns of foxes, during dawn and dusk (Fedriani et al., 1999). The role of red foxes in spreading thelaziosis *via* their movements within their own territories (which vary between 10 and 30 km) (Niewold, 1980; Doncaster et al., 1991) should be further studied, along with that of wolves, which occupy vast territories (>800 km) (Mech, 1970). Finally, in highly endemic areas for canine thelaziosis (e.g., China), human infection is prevalent (Shen et al., 2006); therefore, the recent cases of human infections diagnosed in areas of Italy, France and Spain are unsurprising (Otranto and Dutto 2008; Fuentes et al., 2012).

Ascarids

Ascarioses (Ascaridida, Ascarididae) are worldwide-diffused geohelminthiasis of medical and veterinary significance caused by large (usually 10-15 cm in length) roundworms found in the intestine of their vertebrate hosts (O'Lorcain and Holland, 2000). Ascarioses of wild and domestic carnivores include those caused by *Baylisascaris procyonis* (in racoons and dogs), *Toxocara canis* (in dogs) and *T. cati* (in cats) (Crompton, 2001). The ascarid life cycle is direct, with thick-shelled eggs being passed in the faeces of the infected host; under suitable environmental conditions (i.e.,

28-33 °C), third-stage larva (L3) develop within 2-6 weeks. After ingestion of embryonated eggs, the L3 invade the intestinal wall and migrate to the liver and lungs ('hepato-pulmonary migration'), reach the trachea and are swallowed and develop to adult males and females within 21-29 days in the small intestine. Upon entering the systemic circulation, some *T. canis* larvae will become arrested in somatic tissues (reviewed by Crompton, 2001; Schnieder et al., 2011), to then re-activate in the bitches during the last trimester of pregnancy when they are transmitted to the litter *in utero* (Fülleborn, 1921). Conversely, infection of female cats with *T. cati* during pregnancy results in transmammary transmission of infective larvae to the kittens (Coati et al., 2004). Infective larvae also occurs in a range of paratenic hosts (including rodents) (reviewed by Sprent, 1958) that further complicate the epidemiology of ascarid infections, and particularly that of species infecting predatory wildlife such as *B. procyonis*, the raccoon roundworm. This species has been reported as a potentially zoonotic, albeit all *Baylisascaris* (including *B. transfuga* of bears) are considered as potential zoonotic agents (cf. Sato et al., 2004; Gavin et al., 2005).

Raccoons are the primary hosts of *B. procyonis*; however, infection can also reach patency in dogs and causes *larva migrans* in humans. Experimental evidence in mice and jirds (*Meriones unguiculatus*) supports the hypothesis that *B. transfuga* (infecting bears) may also be responsible for cases of neural *larva migrans* (Sato et al., 2004), with severe (fatal) neurological or ocular outcomes (Otranto and Eberhard, 2011). In raccoons, the infection occurs *via* the ingestion of larvated eggs around the animals' burrows; raccoons' defecation sites are therefore important areas of contamination for domestic carnivores as well as humans (Page et al., 1999). Raccoons have firstly been imported to western Russia, Estonia and Ukraine from North America in the first half of the 20th century (Nowak, 1984; Helle and Kauhala, 1991) and have become established in Eastern and Northeastern Europe since the 1970s (Bauer, 2013). Nowadays, raccoons are an integral part of the wildlife fauna of several European areas (Singer et al., 2009), where they can cause serious problems in the implementation of rabies control and eradication programs (Singer et al., 2009).

The illegal importation of raccoons may also represent a major threat for the spread of ascarids to domestic dogs and humans. For example, *B. procyonis*, *Toxocara* and *Toxascaris* sp. have been recently recovered from the intestine of raccoons illegally imported to Norway (Davidson et al., 2013). The extreme resistance of ascarid eggs in the environment (i.e., up to 5 years under favourable environmental conditions) further enhances the risk of transmission of these parasites from wild to domestic animals and *vice versa*, and therefore the risk of zoonotic infections. For instance, a case of human neurological *larva migrans* by *B. procyonis* has been described in Germany (Sorvillo et al., 2002).

Wild and domestic canids (dogs and foxes) and felids are natural hosts for *T. canis* and *T. cati*, respectively. *T. canis* roundworms are common in red foxes in Denmark (estimated prevalence: 49%) (Saeed et al., 2006), Switzerland (44%) (Reperant et al., 2007), Italy (9%) (Magi et al., 2009), Ireland (20%) (Stuart et al., 2013) and Poland (11%) (Borecka et al., 2013). Similarly, *T. canis* has been isolated from golden jackals in Hungary (20%) (Takács et al., 2014) and from wolves in Italy (Guberti et al., 1993) and Poland (7%) (Borecka et al., 2013). Environmental contamination by *T. canis* eggs is mainly linked to eggs passed in faeces of infected domestic and wild canids; however, given the importance of transplacental transmission in puppies, these should be dewormed immediately after birth (Overgaauw, 1997). While domestic dogs are likely to receive regular deworming treatments, thus limiting the spread of the infection to populations of wild carnivores, uncontrolled populations of feral dogs play a crucial role in the contamination of the environment by *Toxocara* eggs, thus effectively acting as a “bridge” between domestic and wild host populations (Deplazes et al., 2011). In addition, given the predatory nature of wildlife host species of *T. canis*, paratenic hosts (including rodents, birds and invertebrates) play a crucial role in the spreading of this parasite, thus further complicating the epidemiological scenario (reviewed by Reperant et al., 2007). Prevalence data in wildlife species lead to speculations that foxes play a major role in the maintenance of the wildlife cycle of *T. canis*; notably, since the mid-1980s, a steady increase in populations of urbanised foxes had been reported throughout Europe (Scott et al., 2014); foxes are known predators, and feed predominantly on small mammals, birds and invertebrates (reviewed by Reperant et al., 2007). This

behaviour is likely to impact on the epidemiology of *T. canis*, thus strengthening the link between wild and domestic canid populations (Morgan et al., 2013). Conversely, wildlife hosts for *T. cati* include feral cats in England (35%; Nichol et al., 1981), feral cats and Iberian lynxes in Spain (35%; prevalence in feral cats; Millán and Casanova, 2009), Eurasian lynx in Finland (98%; Deksne et al., 2013) and pine martens in Poland (13%; Borecka et al., 2013).

Both *B. procyonis* and *T. canis* can cause ocular or visceral *larva migrans*, or covert toxocarosis, in humans (reviewed by Lee et al., 2014; Deplazes et al., 2011). Compared with *T. canis*, visceral *larva migrans* caused by *B. procyonis* can be particularly severe, as a consequence of the fact that the larvae grow larger as they migrate (reviewed by Kazacos, 2001). Rare cases of human infections have been reported in Europe (Küchle et al., 1993); notably, a case of unilateral neuroretinitis syndrome was reported in a patient who had purchased a raccoon from a local zoo (Küchle et al., 1993). While the zoonotic role of *T. cati* is controversial (Macpherson, 2013; Sturbe et al., 2013), the presence of large populations of feral cats in several European countries, together with the intrinsic challenges associated with anthelmintic treatments of these populations, contribute to the maintenance of parasite pressure to domestic felids (Rendón-Franco et al., 2013).

Hookworms (*Ancylostoma*, *Uncinaria*)

Ancylostoma caninum and *Uncinaria stenocephala* (Strongylida, Ancylostomatidae) are cosmopolitan hookworms of the intestine of dogs and other canids (Anderson, 2000). The life cycle of these parasitic nematodes is direct, with female hookworms excreting morphologically similar thin-shelled eggs, which are passed in the faeces of the host. Under suitable environmental conditions (i.e., 23-33 °C), the ‘rhabditiform’ L1s hatch from the eggs. The L1s feed on bacteria and, within 2 days, moult to L2s and subsequently to the L3s within 4-5 days. This latter stage retains the cuticle of the L2 (i.e., sheath) and is referred as to ‘filariform’ larva (Anderson, 2000). The infection occurs when the infective L3s are ingested by (*U.*

stenocephala) or penetrate the skin of (*A. caninum*) the vertebrate host (Anderson, 2000); while larvae of *U. stenocephala* mature to adult males and females in the small intestine of the vertebrate hosts, larvae of *A. caninum* enter the subcutaneous tissues and migrate via the circulatory system to the heart and lungs, where they moult to fourth-stage larvae (L4s). From the lungs, the larvae migrate (via the trachea and pharynx) to the small intestine, where they develop to adult males and females within 2-7 weeks depending on species (reviewed by Beveridge, 2002). The adult stages attach by their buccal capsule to the intestinal mucosa, rupture capillaries and feed on blood (Anderson, 2000). L3s of *Ancylostoma* spp. can undergo developmental arrest (= hypobiosis) in the somatic tissues of the vertebrate host and, following activation during pregnancy, undergo transmammary transmission to the offspring (Arasu and Kwak, 1999). The pathogenesis of hookworm disease is mainly a consequence of the blood loss, which is caused by tissue damage and direct ingestion of red cells by the adult worm (reviewed by Gasser et al., 2008).

Epidemiological surveys of wild carnivore populations in Europe have highlighted a role of red foxes as reservoirs of *U. stenocephala* infections in Denmark (prevalence: 86%; Willingham et al., 1996), Spain (58%; Criado-Fornelio et al., 2000), Switzerland (78%; Reperant et al., 2007), Ireland (38%; Stuart et al., 2013), and Poland (combined prevalence of *A. caninum* and *U. stenocephala* infections 9%; Borecka et al., 2013). However, a significant prevalence of hookworm infections has been detected in golden jackals in Hungary (*A. caninum* 45% and *U. stenocephala* 40%; Takács et al., 2014), in wolves in Italy (Guberti et al., 1993) and Poland (combined prevalence of *A. caninum* and *U. stenocephala* 6%; Borecka et al., 2013).

Occasionally, the migration of *A. caninum* larvae through the skin of human hosts may result in cutaneous *larva migrans* (CLM), also known as 'creeping eruptions' (Bowman et al., 2010); the role of *U. stenocephala* in CLM remains unclear (Bowman et al., 2010). Therefore, clearly, the presence of these parasites in wildlife populations represents a significant threat to populations of domestic dogs in Europe and, in turn, to the occurrence of cases of CLM in humans. For instance, cases of CLM have been reported from several European countries over the last decade,

including the UK, Germany, Italy and Serbia (reviewed by Bowman et al., 2010); in the UK, the infection was attributed to *U. stenocephala* due to the absence of autochthonous *A. caninum* infections (Beattie and Fleming, 2002). Four cases of CLM attributed to canine hookworms have been described in Germany (reviewed by Bowman et al., 2010). Interestingly, one of the CLM cases detected in Germany was reported to occur following the flooding of the river Elbe, which had forced the patient to spend considerable time in a shelter together with domestic and wild animals (reviewed by Bowman et al., 2010). The other three cases were described in patients who had visited lakesides and riverbanks around urban areas (Klose et al., 1996); although the original source of infection was not conclusively determined (Klose et al., 1996), it is plausible that wildlife species acting as hosts for these parasites may have contributed to the contamination of such environments. The same areas represent frequent destinations of dog-walkers, thus encouraging transmission of hookworms among wildlife, dogs and humans (cf. Smith et al., 2014). It is however important to point out that such transmission should not be considered unilateral, in that undisposed of dog faeces may act as a source of infection for wildlife (Smith et al., 2014).

Trichuris vulpis

Trichuris vulpis (Enoplida, Thichuridae) are common whipworms of the large intestine of domestic and wild canids. The life cycle is direct; the cephalic end of adult worms (= stichosome) is embedded in the mucosa of the large intestine of the vertebrate host, while the caudal end is free in the lumen. Eggs laid by adult females are excreted with the hosts' faeces and develop into larvated, infective eggs over a period of 3 to 8 weeks depending on environmental conditions (reviewed by Traversa, 2011). Following the ingestion of infective eggs by a suitable host, larvae hatch and develop within the intestinal mucosa before returning to the lumen to develop to adult worms (reviewed by Traversa, 2011). Importantly, infective eggs are particularly resilient in the environment; this feature, together with the inability of the host to mount a protective immunity against

successive infections, contribute to the build-up of high parasite burdens in the canine hosts and, in turn, make control of the infection particularly challenging (reviewed by Traversa, 2011).

Infections by *T. vulpis* have been widely reported in a range of wildlife species across Europe; these include golden jackals in Hungary (prevalence: 10%) (Takács et al., 2014), wolves in Italy (Guberti et al., 1993), wolves and pine martens in Poland (*T. vulpis* 13% and *Trichuris* spp. 40%, respectively) (Borecka et al., 2013) and foxes in Ireland (4%), Denmark (0.5%) and Poland (65%) (Saeed et al., 2006; Borecka et al., 2013; Stuart et al., 2013). In particular, a survey conducted in the latter country revealed infections by *T. vulpis* to be rather intense in foxes and martens, with an average of 132.2 and 84.7 eggs per gram, respectively, being detected in these two species (Borecka et al., 2013). Based on these observations, the authors speculated that these species, and particularly foxes, act as the main reservoirs of infections for dogs in those geographical areas, linked to the presence of these (and other) parasites in national parks (Borecka et al., 2013), although the zoonotic potential of *T. vulpis* is yet to be ascertained. Similarly to *T. canis*, the steady increase in urbanised populations of foxes (reviewed by Deplazes et al., 2004; Scott et al., 2014; Liccioli et al., 2015), together with knowledge that infective eggs of *T. vulpis* are highly resistant in the environment (years under harsh environmental conditions), makes public parks of metropolitan areas important sources of *T. vulpis* contamination for domestic dogs (Zanzani et al., 2014). While *T. vulpis* is generally considered non-zoonotic, a few cases of presumptive human cases of visceral *larva migrans* caused by this parasite have been reported over the past few years; however, the true identity of the worms detected in such cases remains blurry (reviewed by Traversa, 2011). Nevertheless, clearly, infections by *T. vulpis* are particularly common in wild carnivores in Europe and, given the resilience of *T. vulpis* eggs, as well extended spatial behaviour of wild carnivore species are likely to impact on the circulation of whipworms.

Dirofilaria immitis and *Dirofilaria repens*

Dirofilarioses are mosquito-borne parasitic infections caused by nematodes of the superfamily Filarioidea. Although several species are included within the genus *Dirofilaria* (Spirurida, Onchocercidae), *D. immitis* and *D. repens* are the most important members, being common parasite of domestic carnivores, such as dogs and cats, but also of other hosts such as wild carnivores and humans (McCall et al., 2008; Penezić et al., 2014). *D. immitis* has a worldwide distribution and it is endemic in many countries in Europe, Asia, Africa and the Americas. *D. repens* is endemic in the Old World but has not been found in the Americas thus far.

Adult *D. immitis* worms occur in the pulmonary arteries and right heart chambers, causing a severe condition known as canine and feline heartworm (HW) disease, while *D. repens* is found mainly in subcutaneous tissues, causing subcutaneous dirofilariosis (McCall et al., 2008). Aberrant migrations with ectopic localizations (e.g. body cavities, central nervous system, eye) have been described for both *Dirofilaria* species (Dantas-Torres et al., 2009; Favole et al., 2013).

The life cycle of both parasites consists of five larval stages developing both within an intermediate mosquito host (from embryo to infective L₃), that also acts as vector, and in a definitive vertebrate host (from L₃ to the adult stage). The prepatent period is 120-180 days for *D. immitis* and 189-259 days for *D. repens*, respectively (McCall et al., 2008). The adult females of both species release embryos (microfilariae) into the blood of the mammalian host. Mosquitoes become infected when taking a blood meal from a microfilaraemic host (McCall et al., 2008). *Dirofilaria* infective larvae are transmitted by several mosquito genera, including *Culex*, *Aedes*, *Ochlerotatus*, *Anopheles*, *Armigeres* and *Mansonia*; however *Aedes vexans*, *Culex pipiens* complex and *Aedes albopictus* are implicated as the main natural vectors of these worms (Cancrini et al., 2007; Capelli et al., 2013).

Until a few years ago, interest in dirofilariosis was focused primarily on *D. immitis* because of its pathogenicity in companion animals. However, the increasing spread of *Dirofilaria* infections, particularly of *D. repens* towards Eastern and Northern European countries, has translated into an

increase of veterinary awareness and perception (Genchi et al., 2014). Furthermore, both *Dirofilaria* species are zoonotic, and human cases of infection by *D. repens* are dramatically increasing in Europe (Genchi et al., 2011; Simón et al., 2012; Salamatin et al., 2013).

Further to the abundance of susceptible mosquitoes and a suitable climate to permit development of the parasites in the intermediate host, transmission of *Dirofilaria* spp. is dependent upon the presence of a sufficient number of microfilaraemic hosts.

The domestic dog and some wild canids are the definitive hosts for both *Dirofilaria* species, where the parasites are able to develop to adult stages, producing abundant and persistent microfilaremia in the blood stream, and thus serve as the main reservoirs of the infection. Cats and wild felids are considered ‘aberrant’ hosts, where seldom the parasites develop to the adult stage, although a low-level, transient microfilaremia probably plays a role as a source of infection for mosquitoes during these short periods (McCall et al., 2008).

D. immitis infections have been reported in wild felids, such as the wild cat, ocelot (*Leopardus pardalis*), mountain lion (*Felis concolor*), clouded leopard (*Neofelis nebulosa*), snow leopard (*Uncia uncia*), Bengal tiger (*Panthera tigris*) and lion (*Panthera leo*) in their natural habitats or while held in captivity in urban zoos or free ranging in ‘safari’ parks located in endemic areas of canine infection (for references until 2007 see McCall et al., 2008; further data is available in Penezić et al., 2014). In most cases, the infection was an accidental finding at necropsy and circulating microfilariae were never detected. However, microfilariae were recently recovered from a leopard (*Panthera pardus pardus*) in a highly endemic area of northern Italy (Mazzariol et al., 2010). In Serbia, one wild cat was found infected in 2009 in Serbia (Penezić et al., 2014), but no data of microfilaremia was reported.

More consistent is the role of wild canids as reservoir hosts of *Dirofilaria*, e.g. coyotes (*Canis latrans*) in the USA (Wang et al., 2014). In this host, microfilaremia ranges from 16% to 35% (Miller et al., 2009; Paras et al., 2012). This species can also serve as source of infection for mosquitoes. In Europe, *D. immitis* prevalence in jackals was 9.6% in Bulgaria (Kirkova et al., 2011), 7.4% in Hungary (Tolnai et al., 2014), and it ranged from 2%

to 12.7% in repeated surveys (2009-2013) in Serbia (Penezić et al., 2014), albeit no data on microfilaremia in these animals is available. Infection was detected in wolves in Spain (~2%; Segovia et al., 2001), Italy (Pascucci et al., 2007), Bulgaria (Georgieva et al., 2001), Serbia (1.4%; Penezić et al., 2014) and reported from Belorussia (Shimalov and Pen'kevich, 2012). Data of microfilaremia in wolves is unavailable; however, 37 adult worms were recovered from a single individual (Penezić et al., 2014), this suggesting that microfilaremia is likely to occur in this species.

Only limited data is available on microfilaremia in foxes. For instance, 6.8% out of 132 foxes from an area endemic for canine *Dirofilaria* in Italy were infected, and *D. immitis* and/or *D. repens* microfilariae were found in 2.3% of the examined animals (Magi et al., 2008). No additional information is available on the prevalence of microfilaremia in this host species, although several surveys had shown that foxes can serve as hosts for *Dirofilaria*. For instance, prevalence of infection by *D. immitis* was 1-3% in Bulgaria and Serbia (Kirkova et al., 2011; Penezić et al., 2014), and 3.7% in Hungary with a worm burden ranging from 1 to 5 in infected animals (Tolnai et al., 2014). Prevalences seem to be associated by the climatic conditions of the areas under investigation; for instance, in the Ebro Valley (Spain), prevalence of *D. immitis* ranges from 1.7% to 32.3% in foxes from semiarid and irrigated habitats, respectively (Gortázar et al., 1998).

Until now, data on the occurrence of *D. repens* in wild carnivores is very scant. Recently, Ćirović et al. (2014) recovered one single worm from 71 examined wolves and one from 48 foxes in Central Balkan.

Therefore, reports of *Dirofilaria* infection in wild felids are anecdotal, and most originate from animals held in captivity in HW heavy endemic areas. Wild felids are likely to represent “innocent victims” of HW infections (Genchi et al., 2008) rather than possible reservoirs of infection for domestic cats and dogs, and the contribution of this wildlife to the spreading of disease is marginal. Even though little information is available on the microfilaremia in wild canids, these hosts are more likely to actively contribute to the spreading of the disease. In some areas of Eastern Europe, *D. immitis* prevalence is relatively high and the finding of adult male and female worms suggests that microfilariae may occur in the blood stream.

Undoubtedly, the detection of *D. immitis* in the pulmonary arteries and in heart right chambers is less challenging than searching for *D. repens* in the subcutaneous tissue. Nevertheless, given that, in Eastern European countries, *D. repens* is more prevalent than *D. immitis* in dogs and it is a frequent cause of human infection (Genchi et al., 2011; Simón et al., 2012; Sałamatin et al., 2013; Tasić-Otašević et al., 2015), surveys on this parasite in wild carnivores are necessary. Whichever the *Dirofilaria* species, the assessment of the presence of microfilariae in the peripheral blood of these animals is critical to clearly elucidate the role of wild carnivores as reservoirs of infections in Europe.

Onchocerca lupi

Onchocerca lupi (Spirurida, Onchocercidae) is a little known filarioid, which primarily infects dogs in some areas of Europe (i.e., Hungary, Greece, Germany and Portugal; reviewed in Otranto et al., 2013a) and USA (i.e., California, Nevada, Colorado and Utah; Labelle et al., 2011; Labelle et al., 2013). Recently, the zoonotic potential of this parasite has been recognised, therefore spurring the interest of the scientific community on this nematode (Otranto et al., 2011). *O. lupi* has been reported for the first time in a Caucasian wolf from Gruziya (Georgia, former USSR; Rodonaja, 1967), but information on the occurrence of this nematode in wild canids such as wolves and foxes is lacking. The lack of knowledge of the epidemiology of this parasite in wild animals is mostly associated to the difficulties in achieving a reliable diagnosis and, subsequently, in monitoring the infection in animal populations. Indeed, while in the acute phase of the infection, canine onchocercosis is characterised by conjunctivitis, chemosis, lacrymation, periorbital swelling (Komnenou et al., 2002; Sréter and Széll, 2008), the definitive diagnosis of infection is achieved through the detection of nematodes in nodules followed by their identification, *via* morphological and/or molecular examination. However, in cases of parasitic granulomas involving the retrobulbar space of the eye, dogs may remain subclinically infected (Otranto et al., 2013b) and, in these animals, the detection of *O. lupi* microfilariae in skin sediments remains the only option for diagnosis. Indeed, a prevalence of the infection of

8.4% was registered in apparently healthy dogs sampled in areas of Greece and Portugal, where clinical cases had previously been reported in dogs (Otranto et al., 2013b). The detection of viable *O. lupi* microfilariae in wild canids or felids, which are usually examined at necropsy, seems complicate and studies of the epidemiology of the infection in these animals are very difficult to perform. Moreover, studies of the distribution of the parasite based on that of the vector, which remains unknown, are currently missing. However, the occurrence of human cases of zoonotic infections by *O. lupi* in Turkey, Tunisia and Iraq deserves attention, especially in areas where dog infection is endemic, and raises a flag on the importance of conducting studies of the biology and epidemiology of this filarioid (as well as the identification of its insect vector) in domestic and wild carnivore species.

Metastrongyloids

Metastrongyloids are bursate nematodes whose adults infect the lungs *Aelurostrongylus abstrusus* (Strongylida, Angiostrongylidae) and *Troglostrongylus brevior* (Strongylida, Crenosomatidae) or the heart and pulmonary arteries, *Angiostrongylus vasorum* and *Angiostrongylus chabaudi* (Strongylida, Angiostrongylidae) of wild and domestic carnivores (Anderson, 2000). Dogs and wild canids (e.g., foxes, wolves, coyotes and jackals) are definitive hosts for *A. vasorum*; the infection is considered endemic in several areas of Europe (Morgan and Shaw 2010; Elsheikha et al., 2014). Conversely, domestic and wild cats are natural hosts of *A. abstrusus* and *T. brevior*, while infection by *A. chabaudi* is confined to wild cat populations (Biocca, 1957), with a single case of infection recently reported in a domestic cat in Italy (Varcasia et al., 2014).

Metastrongyloids are characterised by an indirect life cycle, with gastropod molluscs serving as intermediate hosts; in these hosts, the nematode first-stage larvae (L1) (excreted with the faeces of infected hosts), develop into the infective, third-stage larvae (L3). Different species of snails and slugs may serve as competent intermediate hosts, and parasite development to its infective form varies according to the species of snail, as well as

environmental and climatic conditions. Interestingly, the terrestrial gastropod *Helix aspersa* has been shown to permit simultaneous development of both *A. abstrusus* and *T. brevior*, thus potentially representing a source of multiple infections in the definitive host (Giannelli et al., 2014b). Paratenic hosts such as small mammals, birds, lizards and frogs may act as amplifiers of the infection (Bolt et al., 1994; Morgan et al., 2005). In addition, recent observations of infections by *T. brevior* in suckling kittens have shed some light on alternative routes of transmission, such as direct transmission from the queen to the offspring (Brianti et al., 2013).

Infections by metastrongyloids may be subclinical or induce a wide spectrum of clinical presentations. When symptomatic, respiratory signs are the most common clinical manifestations, accompanied by disorders in blood circulation and coagulation, which may complicate the clinical scenario, e.g. in cases of canine angiostrongylosis (reviewed in Schnyder et al., 2010). Fatal cases of disease caused by *A. abstrusus* and *T. brevior* have also been recorded, although the latter species is suspected to hold a greater pathogenetic potential (Brianti et al., 2012; 2014).

The best known wildlife reservoir of infection by *A. vasorum* is represented by the red fox; in Europe, prevalence of infection in this animal (from 5 to 56%) is higher than that in dogs (from 0.3 to 9.8%) from the same geographical area (Koch and Willeesen, 2009), thus prompting the hypothesis that foxes are mainly responsible for the transmission of infection to dogs (Morgan et al., 2005; Elsheikha et al., 2014). This hypothesis is supported by experimental evidence showing a lack of genetic separation between *A. vasorum* isolates from dogs and foxes (Jefferies et al., 2009). The increase in fox density, along with climate change and increased pet movements, have been incriminated as driving factors of the spread of cases of canine angiostrongylosis (Elsheikha et al., 2014). Other wild canids may play minor roles in the epidemiology of angiostrongylosis (Elsheikha et al., 2014). Thus far, only two cases, namely in northwestern Spain (Segovia et al., 2001) and central Italy (Eleni et al., 2014), have been described in wolves from areas where canine and fox angiostrongylosis is endemic (Traversa et al., 2010). Angiostrongylosis has been recently reported also in golden jackals in Hungary (Takács et al., 2014), while other wild hosts, such as Eurasian badger and otter (*Lutra lutra*), have been identified as

putative reservoirs of the infection, although their role in transmitting the infection to dogs remains uncertain (Torres et al., 2001; Millán et al., 2004). Much remains to be investigated about the dynamics of infection in wild populations and factors underpinning the spill-over to dogs (Morgan and Shaw 2010; Elsheikha et al. 2014).

European wild cats have been hypothesized to act as reservoirs and spreaders of *T. brevior* infection to domestic cats. Indeed, while troglostrongylosis has occasionally been reported in domestic cats, infection by this lungworm is frequent (up to 71.4% prevalence) in wild cat populations (Falsone et al., 2014). However, the occurrence of feline troglostrongylosis may have been missed over the past few years (Otranto et al., 2013c; Brianti et al., 2014), which may explain the paucity of previous reports. Unlike *T. brevior*, *A. abstrusus* is mainly reported in domestic cats, with only a small number of cases reported in wild felids (West et al., 1977; Szczesna et al., 2006; González et al., 2007). Indeed, the increased awareness of this parasite amongst clinicians and parasitologists has been accompanied by a rise of reports in domestic cats (Brianti et al., 2014), which may be misinterpreted as an apparent increase in the number of cases of infection. It may also happen that there is currently an increased incidence of troglostrongylosis in cats in Europe, but the absence of previous data prevents us to draw any reliable picture about the current epidemiological situation of the disease at both regional and local level.

A recent report of infection by *A. chabaudi* in a cat in Sardinia (Italy) has spurred the hypothesis that the domestic cat may be also act as a suitable host for metastrongyloids that localise to pulmonary vessels and heart (Varcasia et al., 2014). *A. chabaudi* was first described from wild cats by Biocca (1957), who considered these animals as the primary host for the parasite; indeed, prevalence of infection was 85% in wild cats from central Italy, while no positive samples were detected from stray cats and dogs, or in other wildlife species (i.e., *M. meles* and *V. vulpes*), from the same area. However, since data on the distribution and impact of *A. chabaudi* in wild and domestic cats is limited, any definitive conclusion is unwarranted.

Capillaria aerophila

Capillaria aerophila (syn. *Eucoleus aerophilus*) (Enoplida, Capillaridae) is a small lungworm whose adult stages infect the lungs of domestic and wild carnivores and, seldom, human beings (Anderson 2000). The adults live beneath the epithelium of the bronchi and trachea (Conboy 2009), where females lay eggs that are coughed up, swallowed and excreted *via* the faeces into the environment, where larvae mature inside the eggs and become infective within 40-60 days (Conboy, 2009). Vertebrate hosts acquire the infection through the ingestion of larvated eggs; these hatch in the intestine and larvae migrate *via* the bloodstream and/or the lymphatics to the lungs, where they invade the mucosa and mature to adult worms within ~6 weeks. Although *C. aerophila* is characterised by a direct cycle, facultative or transport hosts, such as earthworms, are involved in the transmission and diffusion of the parasite (Anderson 2000).

Animals harbouring *C. aerophila* may be either subclinically infected or show respiratory distress ranging from a mild disease to a severe and potentially fatal pneumonia. Adult parasites damage the lung parenchyma and cause bronchovesicular breath sounds, sneezing, wheezing, and chronic dry or moist and productive cough, especially when accompanied by bacterial secondary infections (Barrs et al., 2000; Bowman et al., 2002).

The parasite is common in wild carnivorous, and it is also being increasingly reported in dogs and cats from Europe (Traversa and Di Cesare, 2014). Prevalence in wild carnivores is usually high; in populations of European red foxes, prevalence reaches 88% in Norway (Davidson et al., 2006), 74.1% in Denmark (Saeed et al., 2006), 66% in Hungary (Sréter et al., 2003), 46.8% in the Netherlands (Borgsteede, 1984) and 41.8% in Italy (Magi et al., 2014). *Capillaria aerophila* has been also reported in European wild cat, wolf, jackal, beech marten (*Martes foina*) and raccoon dog with prevalence rates ranging from 5% (jackals) to 33.3% (wild cats) (Thiess et al., 2001; Szafrńska et al., 2010; Takács et al., 2014; Di Cesare et al., 2014; Falsone et al., 2014). Distinct genetic populations of *C. aerophila* in foxes, beech marten, cats and dogs from Europe have recently been

identified, thus supporting the existence of common patterns of transmission between wildlife and domestic carnivores (Di Cesare et al., 2014). These findings suggest that wild carnivores act as reservoirs hosts for *C. aerophila* and thus sympatry with dogs and cats may enhance the risk of capillariosis for domestic animals.

In humans, infections by *C. aerophila* can mimic the clinical and radiographic findings of pulmonary neoplasias, with cough, mucoid sputum, haemoptysis, fever, dyspnoea, and eosinophilia (Lalošević et al., 2008). Cases of human infection have been described in Ukraine, Russia, Morocco, Iran and France (reviewed in Di Cesare et al., 2012) as well as, recently, Serbia, where the prevalence of infection in foxes is particularly high (Lalošević et al., 2008; 2013).

3. Artropods

Wild canids and felids can harbour several arthropod species, which may be shared with domestic dogs and cats. These include ticks (order Ixodida), fleas (order Siphonaptera), lice (order Phthiraptera) and mites (orders Sarcoptiformes and Trombidiformes). While some of these ectoparasites are primarily associated with wild canids and felids, and only seldom detected on their domestic counterparts, some of these are commonly observed on domestic cats and dogs, particularly those living in rural areas (e.g., wooded areas). This is the case of some tick (e.g., *I. ricinus*, *Dermacentor reticulatus*, and *Rhipicephalus turanicus*) and flea species (e.g., *Ctenocephalides felis* and *Pulex irritans*), commonly retrieved from both wild and domestic canids and felids in Europe (Gabrielli et al., 2010; Lorusso et al., 2011; Meyer-Kayser et al., 2012). Dogs and cats may also share mange-causing mites with their wild counterparts (Nimmervoll et al., 2013; Oleaga et al., 2013; Al-Sabi et al., 2014b), although little information is available on whether some of these mites (e.g., *Sarcoptes scabiei*) may indeed belong to distinct populations or even species.

In addition to irritation, blood depletion and skin lesions, ectoparasites of wild canids and felids may transmit a range of pathogens to domestic dogs and cats. A number of studies have reported the finding of DNA fragments from different pathogens in wild canids and felids and their associated ectoparasites (Gabrielli et al., 2010; Marié et al., 2012; Jahfari et al., 2014; Najm et al., 2014). These pathogens (e.g., *Hepatozoon canis* and *Ehrlichia canis*) have been frequently associated to diseases in domestic dogs and cats, and some of them (e.g., *Anaplasma phagocytophilum* and *Rickettsia massiliae*) may be also transmitted to humans.

Foxes are habitual hosts of some ectoparasite species that may infest domestic dogs, particularly ticks (Gabrielli et al., 2010; Lorusso et al., 2011; Meyer-Kayser et al., 2012). In a study conducted in Germany, out of a total of 1286 foxes examined, 989 (76.9%) were infested with ticks belonging to four species: *I. ricinus*, *Ixodes canisuga*, *Ixodes hexagonus*, and *D. reticulatus*. Some of these ticks harboured DNA of *H. canis*, a widespread pathogen of dogs in some European countries. Interestingly, *H. canis* 18S rRNA gene sequences obtained from foxes, *I. ricinus* and *D. reticulatus* were identical among each other and 99% similar to sequences detected in a dog and in a fox from Austria and in a jackal in Croatia (Najm et al., 2014). On the other hand, three different sequences were detected in *I. canisuga* and *I. hexagonus*, one of which was identical to the one found in foxes and in *I. ricinus* and *D. reticulatus*. Another sequence was identical to sequences from a dog in Japan, from a fox in Spain and from a Falkland Island wolf and a fox in Brazil. The third sequence type shared an identity of 99 % to *Hepatozoon* sp. sequence generated from Japanese martens. The aforementioned study suggests that different *H. canis* variants may be circulating among different hosts and tick species. It also raises questions on the role of foxes and their associated ticks in the transmission of this protozoon, thus far thought to be restricted to its main vector tick species, *Rhipicephalus sanguineus* sensu lato.

The cat flea *C. felis*, the dog flea *Ctenocephalides canis*, and the human flea *P. irritans*, are commonly found in a wide range of wild and domestic canids and felids (Farkas et al., 2009; Capári et al., 2013; Gracia et al., 2013). Other fleas, including *Xenopsylla cheopis*, may also be found in both

wild and domestic felids and canids (Koutinas et al., 1995; Torina et al., 2013). A recent, comprehensive study carried out in Albania reported the finding of the flea *Leptopsylla segnis* on domestic cats (Knaus et al., 2014). This rodent-associated flea species has been found infected by *Rickettsia typhi*, the causative agent of murine typhus, in Cyprus (Christou et al., 2010). The rickettsia has recently been detected in naturally infected cats and in *C. felis* fleas in Spain (Nogueras et al., 2013). Interestingly, DNA of both *R. typhi* and *R. felis* could be detected in some flea specimens.

Finally, a *Cytauxzoon* species, distinct from *Cytauxzoon felis* but closely related to *C. manul*, has been found in wild and domestic cats in Europe (Carli et al., 2012), suggesting that the range of ectoparasites and associated pathogens shared by wild and domestic canids and felids is probably larger than currently hypothesized.

4. Conclusions

The study of the ecology of wildlife parasites in Europe requires a holistic approach, being an ever-fluctuating science due to the fact that ecosystems are often open and inter-related at small or large scales. This is not only caused by the continued incursions of humans into ever-changing environments, but also a reduced resilience of the environments to such changes. A major constraint of these studies is the limited access to samples, especially from remote areas. From this perspective, ecologists and biologists involved in population conservation programs represent key partners for parasitologists working in the field.

Another important issue is the distribution range and abundance of some exotic species that are still expanding, as a consequence of their demographic elasticity and the absence of natural constraints. This is the case, for instance, of the raccoon dog and the raccoon that have been introduced into Europe only over the last few decades (Kauhala, 1996; Kauhala and Kowalczyk, 2011; García et al., 2012). Accordingly, there is a

tangible risk of further spread of “exotic parasites”, i.e. the natural parasitofauna of these two species. Despite the wealth of scientific data highlighting the effect of diseases on population dynamics of wildlife (De Castro and Bolker 2005; Lafferty et al., 2008; Smith et al., 2009), diseases are rarely included into international or national legislation concerning the conservation of biodiversity. In some instances, the protection level of a rare host species can be lowered to facilitate disease control/eradication (92/43/EEC), *via* a ‘population control’ approach that, as a final step, might even include host depopulation.

The main international legislation dealing with wildlife disease aims at protecting human health (i.e., rabies in foxes) or meeting the requirements of international trade of live animals or animal-derived products (i.e. classical and African swine fever in wild boars). The World Organization for Animal Health (OIE) includes wildlife diseases in its international reporting system for animal health (World Animal Health Information Database–WHAIS, available at: <http://www.oie.int/animal-health-in-the-world/the-world-animal-health-information-system/the-oie-data-system/>); however, no strict indications on the development of a robust surveillance system are contemplated. In all of the EU Member States, wildlife management and conservation authorities are not directly responsible for animal health, since the National Veterinary Services usually oversee these activities, for both economic and historical reasons (mainly linked to domestic animal health and food safety). As a result, the impact of diseases on wildlife population dynamics is mainly assessed through research projects or local surveys. The scientific debate on a possible approach to monitor wildlife health, and its feasibility and sustainability is still open (Ciliberti et al., 2015; Guberti et al., 2014). An improved knowledge of the complex wildlife-domestic animals-humans-parasites relationships would certainly result in a better management of these diseases, in line with the ‘One Health’ approach to scientific research in these areas. Finally, given the impact of both micro and macroparasites on the population dynamics of several endangered species, a robust health risk assessment (including mitigating actions) should be a pillar of any Action Plan to restore/reintroduce animal populations. Health risk assessments should integrate data on host population size, geographical distribution, presence of

sympatric wild and domestic species and data on macro and microparasites that (might) affect the conservation status of the species under consideration.

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Figure legends

Figure 1 The red fox (*Vulpes vulpes*) is the most abundant and widespread canid of Europe (courtesy of Adriano de Faveri).

Figure 2 A wolf-dog hybrid crossing the road which connects the village with the sea beach in central Italy (Maremma Regional Park). These animals can live - almost unobserved - even in a very crowded environment (courtesy of Lorenzo Rigacci).

Table 1 Parasites infecting wild canids and felids in Europe and risk for humans (references in the text).

Parasites	Carnivore wildlife host	Occurrence in Europe	Zoonotic aspects
<i>Echinococcus canadensis</i> (cervide strain, G8 and G10)	Wolf (<i>Canis lupus</i>)	Fennoscandia	Accidental host developping cystic echinococcosis (CE) in the lungs. Restricted to the circumpolar North, including Sweden, Finland, and Estonia
<i>Echinococcus granulosus</i> sensu stricto(G1)	Golden jackal (<i>Canis aureus</i>), wolf (<i>Canis lupus</i>)	Hungary, Italy, Spain	Accidental host developping cysts mainly in the liver and the lungs. The main CE agent in Southern and South-eastern Europe
<i>Echinococcus intermedius</i> (G7)	Wolf (<i>Canis lupus</i>)	Portugal, Spain	Accidental host developping cysts mainly

			<p>in the liver and the lungs.</p> <p>The main CE agent in countries of the Baltic region, Poland and parts of Eastern Europe</p>
<i>Echinococcus multilocularis</i>	<p>Red fox (<i>Vulpes vulpes</i>), wolf (<i>Canis lupus</i>), wild cat (<i>Felis s. silvestris</i>), golden jackal (<i>Canis aureus</i>), arctic fox (<i>Alopex lagopus</i>), raccoon dog (<i>Nyctereutes procyonoides</i>)</p>	<p>Germany, France, Belgium, The Netherlands, Switzerland, Austria, northern Italy, Eastern Central Europe from the Baltic to Rumania and Slovenia, Sweden, Denmark, Russia, Svalbard archipelago</p>	<p>Accidental host developping cysts especially in the liver.</p> <p>Alveolar echinococcosis is a severe zoonosis in Europe and worldwide in the Northern Hemisphere</p>
<i>Taenia</i> spp. (e.g. <i>T.</i>	<p>Iberian lynx (<i>Linx pardinus</i>), wild cat (<i>Felis s. silvestris</i>), red fox (<i>Vulpes</i></p>	<p>All over Europe</p>	<p>Sporadic cysticercosis</p>

<i>crassiceps</i> , <i>T. martis</i>)	<i>vulpes</i>), raccoon dog (<i>Nyctereutes procyonoides</i>), wolf (<i>Canis lupus</i>), artic fox (<i>Alopex lagopus</i>), mustellids		
<i>Opisthorchis felineus</i>	Red fox (<i>Vulpes vulpes</i>), polecat (<i>Mustela putorius</i>), European otter (<i>Lutra lutra</i>)	Belarus, Russia, Ukraine, Lithuania, Siberia, Netherlands, Scandinavia, Romania, Hungary, Austria, Germany, Poland, Italy, France, Portugal Spain	Liver infection, definitive host shedding viable eggs
<i>Spirocerca lupi</i>	Red fox (<i>Vulpes vulpes</i>), wolf (<i>Canis lupus</i>), four raccoons (<i>Procyon lotor</i>)	Belarus, Denmark, Greece, Italy, Poland, Serbia, Spain	Not reported
<i>Thelazia callipaeda</i>	Red fox (<i>Vulpes vulpes</i>), wolf (<i>Canis lupus</i>), beech marten (<i>Martes foina</i>), brown hare (<i>Lepus europaeus</i>), Eurasian badger (<i>Meles meles</i>), wild cat (<i>Felis s. silvestris</i>)	France, Switzerland, Spain, Portugal, Bosnia and	Ocular infection

		Herzegovina, Italy, Croatia	
<i>Toxocara canis</i>	Red fox (<i>Vulpes vulpes</i>), golden jackal (<i>Canis aureus</i>), wolf (<i>Canis lupus</i>), raccoon dog (<i>Nyctereutes procyonoides</i>)	all over Europe	Ocular or visceral <i>larva migrans</i> , toxocariasis
<i>Toxocara cati</i>	Feral cat (<i>Felis catus</i>), Iberian lynx (<i>Lynx pardinus</i>), Eurasian lynx (<i>Lynx lynx</i>), pine marten (<i>Martes americana</i>)	all over Europe	Debated (<i>visceral larva migrans</i> ?)
<i>Baylisascaris procyonis</i>	Raccoon dog (<i>Nyctereutes procyonoides</i>), four raccoons (<i>Procyon lotor</i>)	Germany, Norway	Visceral <i>larva migrans</i>
<i>Ancylostoma caninum</i> and <i>Uncinaria stenocephala</i>	Red fox (<i>Vulpes vulpes</i>), golden jackal (<i>Canis aureus</i>), wolf (<i>Canis lupus</i>)	all over europe	Cutaneous <i>larva migrans</i>
<i>Dirofilaria immitis</i> and <i>D. repens</i>	Red fox (<i>Vulpes vulpes</i>), wolf (<i>Canis lupus</i>), golden jackal (<i>Canis aureus</i>)	Italy, Spain, Bulgaria, Hungary, Italy, Serbia, Spain,	Subconjunctival and ocular localizations, subcutaneous and pulmonar nodules
<i>Trichuris vulpis</i>	Red fox (<i>Vulpes vulpes</i>), golden jackals (<i>Canis aureus</i>), wolf (<i>Canis lupus</i>), pine marten (<i>Martes americana</i>)	all over europe	Of minor significance

<i>Dirofilaria immitis</i>	Golden jackal (<i>Canis aureus</i>), wolf (<i>Canis lupus</i>), red fox (<i>Vulpes vulpes</i>)	Bulgaria, Hungary, Serbia, Spain, Italy, Bulgaria, Serbia	Accidental host. Subcutaneous nodules
<i>Dirofilaria repens</i>	Red fox (<i>Vulpes vulpes</i>), wolf (<i>Canis lupus</i>)	Central Balkan	Accidental host. Subcutaneous and pulmonary nodules
<i>Onchocerca lupi</i>	Wolf (<i>Canis lupus</i>)	Hungary, Greece, Germany, Portugal	Ocular infection
<i>Angiostrongylus vasorum</i>	Red fox (<i>Vulpes vulpes</i>), wolf (<i>Canis lupus</i>), golden jackal (<i>Canis aureus</i>), Eurasian badger (<i>Meles meles</i>), otter (<i>Lutra lutra</i>)	Denmark, England, Hungary, Italy, Poland, Spain	Not reported
<i>Angiostrongylus chabaudi</i>	European wild cat (<i>Felis s. silvestris</i>)	Germany, Italy	Not reported
<i>Aelurostrongylus abstrusus</i>	Eurasian lynx (<i>Lynx lynx</i>)	Poland, Russian federation	Not reported
<i>Troglostrongylus brevior</i>	European wild cats (<i>Felis s. silvestris</i>)	Italy	Not reported
<i>Capillaria</i>	Red fox (<i>Vulpes vulpes</i>), wolf (<i>Canis lupus</i>), golden jackal (<i>Canis aureus</i>),	Denmark, England,	Pulmonary infection

<i>aerophila</i>	raccoon dog (<i>Nyctereutes procyonoides</i>), European wild cat (<i>Felis s. silvestris</i>), beech marten (<i>Martes foina</i>)	Germany, Hungary, Italy, Norway, the Netherland, Poland, Serbia	
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Figure_1 .



Figure_1 .



Figure_2 .