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The role of wild canids and felids in spreading parasites to dogs and cats in Europe.

Part I: Protozoa and tick-borne agents

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Highlights

► The resilience of ecosystems is being challenged by the thinning boundaries between domestic and wild animals.

The epidemiology of diseases caused by a number of infectious agents is undergoing profound readjustments.

Substantial risk exists for diseases of wildlife to spread to domestic carnivores and *vice versa*, and for zoonotic agents to emerge or re-emerge in human populations.

In the first part of this two-part article, we review the role wild canids and felids may play in the transmission of protozoa and arthropod-borne agents to dogs and cats in Europe.

Abstract

Over the last few decades, the world has witnessed radical changes in climate, landscape, and ecosystems. These events, associated to other factors such as increasing illegal wildlife trade and changing human behaviour towards wildlife, are resulting into thinning boundaries between wild canids and felids and their domestic counterparts. As a consequence, the epidemiology of diseases caused by a number of infectious agents is undergoing profound readjustments, as pathogens adapt to new hosts and environments. Therefore, there is a risk for diseases of wildlife to spread to domestic carnivores and *vice versa*, and for zoonotic agents to emerge or re-emerge in human populations. Hence, the identification of the hazards linked to the co-habitation of these species is critical in order to plan and develop adequate control strategies against these pathogens. In the first part of this

two-part article, we review the role that wild canids and felids may play in the transmission of protozoa and arthropod-borne agents to dogs and cats in Europe, and provide an account of how current and future progress in our understanding of the ecology and epidemiology of parasites, as well as of host-parasite interactions, can assist efforts aimed at controlling parasite transmission.

Key words: parasites; wildlife; Europe; wild canids; wild felids; dogs; cats; zoonoses; reservoirs.

1. From wildlife management to public health concerns

There is an increased awareness of the global effects of several aspects of human politics (e.g., industrialization, urbanization, fragmentation of the environment, land use, recycling in urban settings, lack of political will) on the ‘health’ of the planet, and on the alterations that humankind is causing on the precarious balances of the ecosystems. The resilience of ecosystems is being challenged by the thinning boundaries between domestic and wild animals, ultimately resulting in a redistribution of infective agents (Thompson et al., 2010; Colwell et al., 2011; Tompkins et al., 2015). These changing scenarios are not only of concern to animal and environmental conservation, but they are likely to become an issue of public health relevance, especially considering their effects on the epidemiology of some infectious diseases (**Figure 1**). For instance, parasites affecting both domestic and wild carnivores may circulate between and among sympatric populations of animals, thus facilitating potential spill-overs of the infections to humans (Polley, 2005). Indeed, wild and domestic carnivores are considered the first source of human infections with zoonotic agents, which include, in descending order, viruses, protozoa, bacteria, and fungi (Cleaveland et al., 2001). In particular, while until recently domestic animals were mostly blamed for the transmission of zoonoses to humans (e.g., livestock through consumption of meat and dairy products), the emergence or re-emergence of zoonotic infections have stimulated studies on the role that wild birds and mammals, including carnivores, may play

in their spreading (Polley, 2005). An increasing number of cases of infection or disease caused by parasites of wildlife origin may be a consequence of a plethora of factors, which may act alone or in concert (e.g., the introduction of a new parasite of wildlife origin or of new routes of transmission to humans), and a causality is usually hard to establish. Whether new cases can be attributed to the introduction of ‘new’ parasites of wildlife origin (i.e., emergence), or to a sudden peak after a period of reduced incidence (re-emergence) is difficult to assess, mainly as a result of incomplete and/or inaccessible epidemiological data for these pathogens (Thompson et al., 2009). Importantly, the flow of parasites from wildlife to domestic carnivores and *vice versa* mostly depends on the specific ecological variants which characterise each given area. For example, hunting practices (and therefore the presence of hunting dogs), as well as human encroachment in wildlife habitats (i.e., rural tourism facilities) may facilitate the spill-over of parasitic infections from domestic canids and felids to wild populations. Similarly, the establishment of wildlife reservoirs may determine a subsequent spill-back of the same parasites to populations of domestic animals, ultimately perpetuating the life cycles of parasites.

According to their behaviour and ecology, wild carnivores are free-ranging at low or high geographical scale (i.e., up to 800 km in wolves), their territories are characterised by no or limited boundaries and they are unlikely to be subjected to thorough veterinary inspections, except for specific national preventive programs, such as those promoted for the control of sylvatic rabies in foxes (Pastoret and Brochier, 1999). Therefore, data on parasitic diseases shared between domestic and wild carnivores is scant and limited to case reports or case series obtained under national programs for wildlife conservation (Table 1). In the first part of this two-part article, we review current knowledge of the role played by wild canids and felids in maintaining and spreading protozoal diseases, as well as other tick-borne infections, to domestic carnivores in Europe, with a particular focus on parasites of public health significance. We also discuss the relationships between wildlife infections and emergence (or re-emergence) of selected diseases caused by protozoa.

2. Wild felids and canids in Europe

Europe is the smallest continent of the world ($\cong 10.000.000$ square km), home to more than 700 millions inhabitants (at a density of ~ 70 per square km), with the vast majority of them clustered in towns. At the same time, ~ 75 and ~ 90 million dogs and cats, respectively, are estimated to inhabit the continent as household pets (FEDIAF, 2012), together with a few millions of stray dogs and cats, and wild carnivores (the red fox being the most abundant followed by the raccoon dog and wolf). The whole dynamic of infection disease transmission among wild and domestic carnivores is complex and driven by many host species that live in sympatry, and share susceptibility to the same parasite species, as well as dietary habits (which may include many intermediate and paratenic hosts). Each species occupies its own environmental niche (i.e., the spectrum of resources utilized by a species), which very often overlaps that of other species. For parasites, these scenarios represent opportunities to enlarge their own ecological niche. In this perspective, ecologically 'elastic' parasites are expected to expand their geographic distribution, abundance and host spectrum, while parasites living in very specialized ecological niches, as the Iberian lynx (*Lynx pardinus*) populations, are possibly directed towards extinction, thereby adding to further loss of biodiversity.

The resulting epidemiological landscape is complex, in that widely distributed, abundant domestic and wild species are sympatric with their domestic/wild hybrids, and often share the habitats with rare, endangered species. New species, harbouring specific parasites, are expanding their distribution range, thus adding complexity to the host/parasite relationship. Humans in particular occupy nearly all ecological niches inhabited by all other species, including parasites.

Eight species of canids and felids are known to occur in Europe (Sillero-Zubiri, 2009; Sunquist and Sunquist, 2009), i.e. five canids (the wolf, *Canis lupus*; the golden jackal, *Canis aureus*; the raccoon dog, *Nyctereutes procyonoides*; the artic fox, *Alopex lagopus*, and the red fox, *Vulpes vulpes*), and three felids (the Iberian lynx, *Lynx pardinus*, the Eurasian lynx, *Lynx lynx*, and the wildcat, *Felis silvestris silvestris*). In addition, the raccoon

(*Procyon lotor*), an exotic species introduced to Europe over the past decades, may also be included, given its relative closeness to the family Canidae, its increased geographical distribution and the role played as epidemiological reservoir of zoonotic agents, including parasites.

Based on knowledge of their natural history, the species of canids and felids occurring in Europe can be ideally grouped into three main categories, namely with i) restricted, ii) wide or iii) very wide distribution. Among those with a restricted geographical distribution and reduced population size, the arctic fox conservation status is considered of “least concern” (IUCN, 2014). However, the European (Fennoscandian) population is very small (about 200 individuals) and distributed into four isolated sub-populations (Angerbjörn et al., 2011). These animals are unlikely to come into contact with domestic dogs and cats, as populations are highly constrained by the availability of suitable habitats and conflict with human settings. The demography of arctic foxes largely depends on lemming vole (*Alticola lemmings*) cycles and the availability of undisturbed areas for dens and cub care. The population dynamics of the arctic fox are also affected by the simultaneous presence of red foxes in their habitats. Indeed, red foxes have occupied most of the fennoscandian areas suitable to the arctic fox, thus resulting in the confinement of the latter to mountains which, in turn, represent a less suitable habitat. The Iberian lynx and the European population of the Eurasian lynx, also survive in very small populations. Amongst the large cats, the Iberian lynx is considered the closest to extinction (i.e., critically endangered, according to the IUCN list) with less than 200 individuals inhabiting two geographically separate areas of Spain (Von Arx and Breitenmoser-Wursten, 2008). The Eurasian lynx is considered ‘least endangered’ by the IUCN (IUCN, 2014), but the European population is divided into several small sub-populations (which include sub-species), of which most are critically endangered (Kaczensky et al., 2013).

For all these species, the limited availability of geographical corridors connecting small and isolated sub-populations leads to inbreeding which, in turn, results into a loss of genetic variability (Gaona et al., 1998; Schmidt et al., 2011). The attitude to dispersal of young individuals is limited, and thus the possibility to occupy new suitable habitats or territories is considerably reduced. It is well known that loss of genetic variability within the

host population limits its resilience to parasitic infections. Many eco-ethological barriers prevent cross breeding of these wild animals with domestic species. Therefore, the population sizes of the arctic fox, the Iberian lynx and the European populations of the lynx, respectively, are likely to be too small to allow the establishment of these species as epidemiologically important reservoirs of many or even host-specific parasites. In fact, these animals are more likely to be infected by parasites transmitted by abundant sympatric host species, such as the fox or the domestic cat (Ryser-Degiorgis et al., 2005).

Wolves and the wildcats are species with a wide geographical distribution range but with a limited population size. These species have recently expanded their distribution range and abundance, although their conservation status in Europe is still considered ‘under threat’ in most areas. Cross-breeding with domestic free ranging dogs and cats is considered disadvantageous, since it leads domestic genetic introgression (= movement of gene/s from one species to another, leading to “genetic pollution”) (Daniels et al., 2001; Verardi et al., 2006). However, it seems that cross breeding with the domestic equivalent species is common. In many areas, fertile hybrids (wolf x dog and wildcat x domestic cat) represent a conspicuous proportion of the wild populations. For example, a continuous “cline” between domestic cats and wildcats has been described in Scotland (Daniels et al., 2001) while in Italy the occurrence of dog x wolf hybrids has been reported in some wolf populations at the border of their historical geographical range (Ciucci et al., 2003) (**Figure 2**). Cross breeding may derive from the absence of consistent eco-ethological barriers between wild and domestic species (Biró et al., 2005), and from the capacity of wild species to undergo behavioural adaptation to fragmented habitat landscapes and to take advantages from human activities (including large populations of game, animal breeding and waste production). As a consequence of the taxonomic closeness between wild and domestic species, the use of common habitats and the presence of fertile hybrids, wolves, wildcats, hybrids and dogs and cats may be considered as a unique host population characterised by two distinct ecotypes: the genetically pure wild populations that

survive in remote wild areas, and the domestic dogs and cats living in overcrowded European towns. For the parasites, this translates into the availability of huge ecological niches encompassing both the wild and the anthropic environments.

Finally, amongst wild dogs and cats of Europe, the red fox is a unique example of a species with a very wide distribution range and with a huge population size, being the most common carnivore in Europe. Its local abundance benefits from the presence of humans. In urban areas, the availability of food and resting places, human tolerance and the absence of predators/competitors, make the red fox a very successful species. The red fox itself can be considered as a species connecting the wild and the anthropic environments. The geographical distribution of red foxes encompasses all ecological environments and habitats, and the population size enables the red fox to play the role of epidemiological reservoir for many parasites that infect all susceptible species sharing the same habitats, including humans. The golden jackal is a poorly studied species whose ecology (including punctual distribution, genetic variability and local abundance) is almost unknown (Arnold et al., 2012). In the late 1960's, the species range was restricted to the central Balkan area (Bulgaria, Romania, Serbia); nowadays, the geographical range of the species is expanding towards the West, such as in Italy and Austria that are inhabited by a few reproductive couples. Like the red fox, the golden jackal can be described as a generalist predator, due to the ability to establish successfully in any kind of environment. Thanks to its great colonising potential, the species is expected to further expand its geographical distribution range over the forthcoming years.

3. Protozoa infecting domestic and wild carnivores

Multiple routes of transmission of protozoan parasites from wild to domestic carnivores (and *vice versa*) are known, and they are characterised by complex webs within and among their ecosystems. These include transmission *via* food containing parasite stages (e.g., *Toxoplasma*) and water (e.g., *Giardia* and *Cryptosporidium*) as well as through one or more arthropod vectors (e.g., *Leishmania* and tick-borne protozoa); therefore,

determining the exact route of parasite transmission between or amongst wild and domestic host populations is challenging. However, knowledge of such transmission routes is pivotal to ensure that hazards are identified, thus leading to the determination of critical control options. In the following, we provide selected examples of diseases caused by protozoan and vector borne-bacterial infections circulating in wildlife and domestic carnivore populations, taking into account public health implications.

Leishmania

Leishmania (Kinetoplastida, Trypanosomatidae) are intracellular protozoa transmitted by sand flies to humans and animals (Schönian et al., 2010), currently distributed in at least 98 countries, and causing infections with a broad spectrum of symptoms and clinical signs, from asymptomatic to life threatening diseases (Alvar et al., 2012). The life cycle is complex and indirect, involving different morphological stages, in various vertebrate cell types and extraellularly in the insect hosts. The genus comprises many species, with the validity of some being still debated (Schönian et al., 2010). However, in Europe only three species are reported. *Leishmania infantum* is the predominant species causing canine leishmaniosis (CanL), as well as the visceral (VL) and cutaneous (CL) forms in humans (Faucher et al., 2011). The anthroponotic species *Leishmania tropica* and *Leishmania donovani* cause occasionally and focally human CL and VL in Greece and Cyprus, respectively (Mazeris et al., 2010). Less frequently, *L. infantum* may cause disease in cats (Pennisi et al., 2013), which may also eventually serve as a source of infection to sand fly vectors (Maroli et al., 2007).

Generally, the dog is regarded as the main reservoir of *L. infantum*, due to the high susceptibility to the infection/disease and to the great ability to transmit the parasite to the arthropod vector, mostly by individuals with overt clinical disease and, less often, subclinically infected dogs (Dantas-Torres et al., 2014). However, the recent occurrence of human outbreaks in Spain (Arce et al., 2013) that were not accompanied by an increase in

prevalence of leishmaniosis in dogs or cats (Miró et al., 2014), led to speculations that other animals, such as hares (*Lepus* spp.) and wild rabbits (*Oryctolagus cuniculus*) are able to transmit *Leishmania* to sand flies (Molina et al., 2012; Jiménez et al., 2014) eventually acting as reservoirs.

The role of wildlife in the epidemiology of leishmaniosis has been recently reviewed by Millán et al. (2014), who concluded that black rats (*Rattus rattus*) and hares could contribute to maintaining this parasite in a given area. The list of wild carnivores with confirmed cases of *Leishmania* infection in Europe includes red fox, wolf, polecat (*Mustela putorius*), stone marten (*Martes foina*), pine marten (*Martes martes*), European badger (*Meles meles*), European mink (*Mustela lutreola*), weasel (*Mustella* spp.), golden jackal (*Canis aureus*), Egyptian mongoose (*Herpestes ichneumon*), common genet (*Genetta genetta*), Iberian lynx and European wildcat, with red fox and wolf showing clinical signs of disease (see Millán et al., 2014). In most cases, infected wild carnivores were detected in areas where CanL is endemic, thus it is not known whether the control and prevention of the infection in dogs (Otranto and Dantas-Torres, 2013) could impact on the transmission of *L. infantum* to human disease in those areas, considering that wild carnivores could represent a permanent source of parasites to sand fly vectors. The advent of high-throughput molecular tools, such as next-generation sequencing, will contribute to a further understanding of the taxonomy of *Leishmania* and help answering questions surrounding the strains shared by and circulating amongst domestic and wild carnivores (Cantacessi et al., 2015).

For detailed information on drivers for the spreading of CanL in Europe see the article by Cardoso et al. (2015).

Giardia

Giardia (Diplomonadida, Hexamitidae) is a binucleated, flagellated protozoan with a worldwide distribution, affecting a wide range of hosts and causing mostly self-limiting diarrhea, less frequently, accompanied by chronic intestinal clinical signs (Ryan and Cacciò, 2013). The transmission is characterised by ingestion of *Giardia* cysts (Lloyd and Williams, 2014). After excystation, the trophozoites attach to the small intestinal wall with

the aid of a unique ventral adhesive disc (Thompson and Monis, 2011). The trophozoites remain extracellular, undergo multiple mitotic divisions, and encyst again. The taxonomy of *Giardia* is still under revision (Monis et al., 2009; Thompson and Monis, 2011). *Giardia duodenalis* (syn. *Giardia intestinalis*, *Giardia lamblia*) is a complex of genotypes infecting mammals and including at least eight distinct genetic groups or assemblages (from A to H) (Ryan and Cacciò, 2013). The host-specific assemblages C or D and F predominantly infect dogs and/or cats, respectively, and they are not considered to be zoonotic (Ryan and Cacciò, 2013). On the other hand, the human- and primate-specific assemblages A and B have been reported in dogs and cats, particularly under conditions of strict human-animal association in shared environments; humans have been indicated as the main source of animal infections (Ryan and Cacciò, 2013; Thompson, 2013). *Giardia duodenalis* is a common parasite of dogs and cats (Bowman and Lucio-Forster, 2010), being reported as the most prevalent pathogen in dog populations (Batchelor et al., 2008; Claerebout et al., 2009; Bryan et al., 2011).

While *Giardia* occur in wildlife, especially in wild rodents and cervids, the majority of the infections are caused by human- or domestic animal-specific assemblages, rather than by wildlife-specific genotypes (Thompson, 2013). This suggests that wildlife can act as amplifiers of *Giardia* assemblages specific to other hosts, as it has been documented in beavers (reviewed in Thompson, 2004). In Europe *Giardia* has been reported in 20-46% of wolves from Poland (Bajer, 2008), in 4.6% of red foxes, 10% of wolves and 12.5% of golden jackals from Croatia (Beck et al., 2011), in 4.8% of red foxes in Norway (Hamnes et al., 2007), in 5-15.7% of red foxes from Bosnia and Herzegovina (Hodžić et al., 2014). Only the canid genotypes C and D have been detected in wolves (Beck et al., 2011); however, given the small number of cysts recovered from faeces, a passive ingestion of cysts from a contaminated source could not be excluded. To the best of our knowledge, no information on *Giardia* infection in wild felids is currently available.

Cryptosporidium

Cryptosporidium (Eucoccidiorida, Cryptosporidiidae) share several epidemiological features with *Giardia*, being a waterborne pathogen causing self-limiting intestinal infection distributed worldwide; it infects a wide range of animals including humans, and is characterised by a direct transmission, with an environmentally resistant oocyst (infectious when shed by the host). Following ingestion, the oocyst releases four sporozoites that invade enterocytes in the small intestine, develop to merozoites and finally gametocytes resulting in oocysts formation (Lendner and Dauschies, 2014). The taxonomy of *Cryptosporidium* has been controversial; based on biological and genetic features, ~30 species are currently recognized as valid, of which at least 14 are potentially zoonotic (Šlapeta, 2013).

Dogs and cats are infected by the host-specific species *Cryptosporidium canis* and *Cryptosporidium felis*, respectively, which can occasionally infect humans and are considered of minor and moderate public health significance (Lucio-Forster et al., 2010; Šlapeta, 2013). The reported prevalence of *Cryptosporidium* spp. in dogs in Europe has been 7.4% in Spain (Causapé et al., 1996), 1.1-3.3% in Italy (Rinaldi et al., 2008; Zanzani et al., 2014), 13% in kennel dogs of Poland (Bajer et al., 2011), 2.8% in shepherd and hunting dogs in Greece (Papazahariadou et al., 2007), 8.7% in owned dogs of The Netherlands (Overgaaauw et al., 2009), and 2% in dogs in rural areas of the Czech Republic (Dubná et al., 2007). If one repeats faecal sampling of dogs during the first year of age, the prevalence of infection can rise to up to 44.1% (Hamnes et al., 2007). The recorded prevalence in cats is more variable: 0% in colony cats (Spada et al., 2013) and in owned and free-roaming cats of Italy (Paoletti et al., 2011), 4.6% in household cats of The Netherlands (Overgaaauw et al., 2009), 8.1% and 17.2% in the UK (Scorza et al., 2014). In affected cats, the prevalence can rise to up to 24.4% (UK; Paris et al., 2014). Studies on the occurrence of *Cryptosporidium* spp. in wild carnivores in Europe are scant, with high prevalence (38.7%) registered in red foxes from Slovakia (Ravaszova et al., 2012) and in wolves in Poland (37.5-55%) (Kloch et al., 2005; Paziewska et al., 2007). In the latter country, up to five genotypes were recorded to infect rodents (Paziewska et al., 2007). In Ireland, 5% of

American minks (*Mustela vison*) were infected with *Cryptosporidium andersoni* (infecting cattle); both mink genotype (Stuart et al., 2013) and *Cryptosporidium parvum* were also detected in red foxes (Nagano et al., 2007). There is currently no evidence of wild carnivores infected by *C. canis* or *C. felis*.

Toxoplasma

Toxoplasma gondii (Eucoccidiorida, Sarcocystidae) is one of the most successful protozoan parasites, virtually infecting all cell types and an enormous range of mammals (including cetaceans and humans) and birds, and occupying a great variety, if not all, of habitats (Dubey, 2004; Smith, 2009; Schlüter et al., 2014). This zoonotic agent has been estimated to affect one-third of the human population (Tenter et al., 2000). *T. gondii* is characterised by an indirect, complex life cycle involving cats and other felids as definitive hosts (sexual reproduction); warm-blooded animals act as intermediate hosts (asexual reproduction), as can cats (see White et al., 2014 for details). Cats shed non-sporulated resistant oocysts *via* the faeces, which contaminate water and feedstuffs. Following the ingestion of the sporulated oocysts by an intermediate host, the sporozoites transform to tachyzoites, which and undergo asexual reproduction. This pathogenic process is terminating with the formation of a tissue cyst containing bradyzoites which can persist lifelong in the intermediate host. Warm-blooded animals can acquire *Toxoplasma* by ingesting sporulated oocysts in the environment, or tissue cysts (*via* predation), or from an infected mother (congenital or lactogenic transmission). *T. gondii* is a unique species comprising three main clonal lineages known as types I, II and III. In Europe, type II predominates and is transmitted mainly by the domestic cat to wild and domestic mammals and birds (Sibley et al., 2009).

Although less than 1% of cats is estimated to shed oocysts worldwide (Hartmann et al., 2013), environmental contamination is ensured by the extreme resistance of the oocysts, which can remain viable for at least 1 year in soil at cold temperatures and from 2 to 4.5 years in marine and fresh

water (VanWormer, 2013). This characteristic, coupled with the small infectious dose (even 1 oocyst is able to infect a mouse (Smith, 2009), the persistence over years in intermediate hosts and the multiple routes of transmission explain the enormous burden of *Toxoplasma* infection and toxoplasmosis in humans and animals worldwide.

In Europe, exposure to or infection with *Toxoplasma* has been detected in almost all the wild species of carnivores, i.e. wild cat (Millán et al., 2009a; Hermann et al., 2013), Eurasian and Iberian lynx (Millán et al., 2009b; Jokelainen et al., 2013), red fox (Jakubek et al., 2012; Herrmann et al., 2013; Verin et al., 2013), wolf (Akerstedt et al., 2010; Lopes et al., 2011) and mustelids (Burrells et al., 2013; Chadwick et al., 2013), even at very high percentages (see also Sobrino et al., 2007; De Craeye et al., 2011; Dubey et al., 2014).

The contribution of European wild felids to environmental contamination with oocysts and, in turn, to cat and dog (and other animals) infections is likely minimal, given their low density compared with that of owned or colony cats (with the exception of confined small populations, as the case of the wild cat in Majorca island, Spain, whose prevalence of infection was up to 85%) (Millán and Casanova, 2009). Other wildlife, including wild canids, contribute to maintaining *Toxoplasma* in the environment *via* tissue cysts, which represent a source of infection for predators and scavenger animals, and of transmission to the offspring. Many wild small animals, particularly rodents and birds, can also act as sources of infection for domestic cats and hunting dogs. While *Toxoplasma* infection in wildlife is mostly subclinical (Thompson, 2013), the spill-over of virulent strains from domestic to wild cats could threaten endangered species, such as the Iberian lynx in Spain.

4. *Tick-borne diseases*

Piroplams

Piroplasms (Apicomplexa, Piroplasmida) are intra-erythrocytic protozoan parasites comprising several genera, of which *Babesia*, *Theileria* and *Cytauxzoon* affect wild and domestic carnivores.

Babesia spp. have been traditionally divided into large and small *Babesia* based on the morphology of the parasite in the erythrocytes (Solano-Gallego and Baneth, 2011). Three species of so-called ‘large’ *Babesia* are known as dog pathogens: *B. rossi*, transmitted by *Haemaphysalis elliptica*, *B. vogeli*, transmitted by *Rhipicephalus sanguineus* sensu lato (the brown dog tick), and *B. canis*, transmitted by *Dermacentor* spp. ticks, with the latter two occurring in Europe (Irwin, 2009). *Babesia vogeli* is distributed (almost) worldwide and, in Europe, has been reported from areas where the brown dog tick is present, i.e. mainly in the countries bordering the Mediterranean sea (reviewed in Solano-Gallego et al., 2011). Because *B. canis* is transmitted by *Dermacentor* spp., mostly *D. reticulatus*, this parasite causes the most widespread canine babesiosis in Europe (Solano-Gallego and Baneth, 2011). The parasite merozoites within the infected erythrocytes are ingested by ticks during blood feeding. In the tick gut, the parasites undergo sexual development, followed by sporogony. The parasites then travel to the tick salivary glands, from which the infectious sporozoites are transmitted to a susceptible canine host. Infection by *B. vogeli* is usually characterised by milder clinical signs; however, *B. canis* infections are frequently associated with haemolytic anemia, fever, lethargy, jaundice and vomiting, splenomegaly, and hematuria. Disease severity ranges from mild clinical infections to peracute hemolytic crises, which can result in shock and death. Chronically infected dogs act as carriers, even in the presence of high specific antibody concentrations and represent sources of infection for ticks. *Babesia vogeli* has not been reported in wild carnivores but *B. canis* was found in one fox in Portugal (Cardoso et al., 2013) and in two fatal cases of captive wolves in Hungary (Erdélyi et al., 2014), indicating a negligible role of these animals as reservoirs of “large” *Babesia* for dogs.

The “small” forms of *Babesia* in dogs, considered for long time as *B. gibsoni*, have been sporadically reported in Europe (Solano-Gallego and Baneth, 2011; Yisaschar-Mekuzas et al., 2012), because the main tick vector (i.e., *Haemaphysalis longicornis*) is present only in Russia. However,

the increasing use of molecular tools suggested that a higher number of "small" species of *Babesia* could circulate in dog populations. These protozoa are closely related to members of the genus *Theileria* (Beck et al., 2009) and have been named *B. microti*-like piroplasms, also known as "Spanish dog isolate". This species was later named as *Theileria annae* and has been reported in dogs of Spain, Croatia and Portugal (Farkas et al., 2015), causing a severe disease. In wild carnivores *T. annae* is increasingly reported in red foxes, i.e. in 69.2% of foxes in Portugal (Cardoso et al., 2013), 50% in Austria (Duscher et al., 2014), 46.4% in Germany (Najm et al., 2014a), 20% in Hungary (Farkas et al., 2015) and 0.98% in Italy (Zanet et al., 2014). These findings suggest that foxes could act as wild reservoirs of the protozoan.

Babesiosis is less common in domestic cats and is due mainly to *B. felis*, which cause anemia and icterus in South Africa. In Europe other *Babesia* spp. are found in cats and *B. vogeli* is considered the most common agent circulating among cats in Portugal (Maia et al., 2014). In addition, *B. canis* and *T. annae* infections have been sporadically reported in cats from Spain and Portugal (Solano-Gallego and Baneth, 2011). The information on the occurrence of piroplasms in wild felids is even more scarce and only an intraerythrocytic small piroplasm was reported in the wild Iberian lynx of Spain (Luaces et al., 2005).

Cytauxzoonosis of felids is a tick-borne disease caused by *Cytauxzoon felis* (Theileriidae), which recognizes in the vertebrate host an intra-erythrocytic phase and schizonts in macrophages or monocytes (Millán et al, 2007). *Cytauxzoon felis* causes a severe and fatal disease of cats in the USA and the bobcat (*Lynx rufus*) is considered the natural host since it shows a persistent, subclinical infection (Millán et al, 2007). Recently, other species of *Cytauxzoon* infecting wild and domestic felids have been sporadically described. In Europe, a cat was found to be co-infected by *Cytauxzoon* sp. (0.8%) and *H. canis* in France (Criado-Fornelio et al., 2009). An endemic focus of cytauxzoonosis was for the first time described in

Italy, with a prevalence of 23% in colony and owned cats (Carli et al., 2012). A *Cytauxzoon*-like piroplasm has also been described in the Iberian Lynx from Spain (Luaces et al., 2005; Millán et al., 2007, 2009b).

Anaplasma

Anaplasma spp. (Rickettsiales, Anaplasmataceae) are Gram-negative, obligate intracellular bacteria; two species infect dogs, namely *Anaplasma phagocytophilum*, the causative agent of granulocytic anaplasmosis, and *A. platys*, causing thrombocytic anaplasmosis. The latter has a worldwide distribution, with reports of infection from South and North America, Australia, Asia and Africa. Within Europe, the geographical distribution of *A. platys* is associated to that of *R. sanguineus* s.l., although the vectorial role of this tick species has never been ascertained (Dantas-Torres et al., 2013). *A. phagocytophilum* occurs in the northern hemisphere, and it is transmitted by hard ticks of the *Ixodes ricinus* complex. The main vector of this pathogen is the taiga tick *I. persulcatus* in Asia, the sheep tick *I. ricinus* in Europe, the deer tick (*Ix. pacificus*) in eastern North America, and the Western black-legged tick (*Ix. scapularis*) in western North America. Besides these major vector tick species, *A. phagocytophilum* has been detected in a range of other *Ixodes* species, as well as some *Dermacentor* and *Haemaphysalis* species; however, the latter two genera are not considered of epidemiological importance (reviewed in Stuenkel et al., 2013). *Anaplasma phagocytophilum* has been detected in a range of European countries, with varying prevalence in ticks, ranging from zero to over 20% (23.6% in Denmark; Skarphedinsson et al., 2007; 24.4 % in Italy; Cinco et al., 1997; and 20.5 % in Spain; Ruiz-Fons et al., 2012), and up to 33% in Bulgaria (Christová et al., 2001). Infection rates in dog samples were recently reviewed (Stuenkel et al., 2013), and prevalence ranged between 0.5% in Poland (408 animals; Zygner et al., 2009) to 7.5 % in Italy (50 dogs; Alberti et al., 2005). Seroprevalence rates in dogs are generally higher, i.e. 8.76% in central Italy (Ebani et al., 2008), 9% in a mixed dog cohort from Spain, Portugal and Italy (René-Martellet et al., 2015), 10.6% in Romania and Hungary (Hamel et al., 2012), 13.5% in Portugal (Alves et al.,

2009), 14.8% in Italy (Ebani et al., 2013), and up to 40% in Albania (Hamel et al., 2009). Little information is available on natural infections of dogs with *A. platys*, probably as a consequence of the subclinical form of disease despite the detectable haematological changes and in serum enzyme activities (Warner and Harrus, 2013). Acute clinical forms may present with fever, weight loss and pale mucous membranes, and petechiae or echymoses that coincide with severe thrombocytopenia. Studies on the genetic heterogeneity of strains of *A. phagocytophilum* led to the identification of four distinct clusters, three of which are only found in ungulates (two only in wild ungulates) and one cluster including *A. phagocytophilum* sequences from dogs, cats, humans, horses, as well as ungulates; this finding provided evidence for (i) a diverse ecology and (ii) a range of virulence and host association of different *A. phagocytophilum* strains (Scharf et al., 2011; Stuenkel et al., 2013).

In an investigation on tick-borne pathogens in foxes in Palermo and Ragusa provinces of Sicily, Italy, none of the 13 foxes molecularly tested were positive for *A. platys* (Torina et al., 2013). To our knowledge, no further information is available on *A. platys* infection in wild canids. This might be a consequence of the limited clinical relevance of this pathogen in European dogs, or of the fact that most studies investigating the prevalence of a panel of tick-borne diseases simply ignore this bacterium. Conversely, studies are available on the natural reservoir hosts for *A. phagocytophilum* (e.g., Víchová et al., 2014; Zele et al., 2012). The fact that transovarial transmission has never been demonstrated in any of the major *Ixodes* vectors is conducive to the existence of a vertebrate host reservoir. Several mammals are likely to act as host and reservoir (e.g., Keesing et al., 2012). Beside domestic ruminants (cattle, sheep, goats), horse and man, *A. phagocytophilum* has been detected in several small mammal species and nine species of wild ruminants in Europe alone (reviewed in Stuenkel et al., 2013). Foxes harbour *A. phagocytophilum* with prevalences of 16.6% in Italy (Ebani et al., 2011), 4% in the Czech Republic (Hulínká et al., 2004), 2.7% in Poland (Karbowski et al., 2009), 2.8% in Switzerland (Pusterla et al., 1999) were recorded, with no infected red foxes found in Slovakia (Víchová et al., 2014). A single report of acute granulocytic anaplasmosis was described in a captive wolf from Austria (Leschnik et al., 2012). As prevalence rates in cats (even stray cats) are rarely exceeding 0.5% (Hamel et al.,

2012; Morgenthal et al., 2012), studies on wild felids are sparse. However, antibodies against *A. phagocytophilum* were detected in 4 out of 106 Eurasian lynx from Sweden (Ryser-Degiorgis et al., 2005).

Ehrlichia

Ehrlichia canis (Rickettsiales, Anaplasmataceae) is the aetiological agent of canine monocytic ehrlichiosis (CME). *Ehrlichia canis* is transmitted by the brown dog tick *R. sanguineus* s.l., whose geographical distribution in the Neotropics overlaps that of the pathogen. In Switzerland, almost 1,000 dogs were tested for antibodies against *E. canis*, and 2.2% were found positive; all of these came from south of the Alps or had travelled further south (Pusterla et al., 1998). In the same study, the authors failed to detect any positive red fox (out of 1,500 tested), thus lending support to the hypothesis that dog infections by *E. canis* had not been acquired in the same region (Pusterla et al., 1999). Like all members of the Rickettsiales, *E. canis* is an obligatory intracellular pathogen targeting blood monocytes and tissue macrophages. Prevalence of 2.9%, 8%, and 9.7% were detected in dogs from northern, central, and southern Italy, respectively (Solano-Gallego et al., 2006b), and 11% and 26% of dogs from Italy, Spain and Portugal (René-Martellet et al., 2015) by PCR and serology, respectively. Likewise, 17% of dogs were positive to *E. canis* by PCR, and 50% by serology (Hamel et al., 2009). *Ehrlichia canis* was found by PCR in 31% of 13 foxes in Sicily, Italy (Torina et al., 2013), but none of 150 red foxes from central Italy and of 1,550 foxes from Switzerland (see above) scored molecularly positive for *E. canis* (Pusterla et al., 1998; Ebani et al., 2011).

Ehrlichia canis has been detected in *Ixodes canisuga* larvae collected from red foxes in Hungary, suggesting a possible role of this wild carnivore in the epidemiology of CME (Hornok et al., 2013b).

Besides CME, *E. canis* has been imputed as an agent of infection in cats. Following the initial description of a disease in a cat serologically positive in France (Charpentier and Groulade, 1986), reports of feline infections have originated in Southern Europe supported mainly by seroreactivity

(Vita et al. 2005; Solano-Gallego et al., 2006a; Ayllón et al., 2012; Vilhena et al., 2013) and confirmed by PCR and sequencing in Portugal (Maia et al., 2014). However, since the agent has not been yet isolated from cats, the molecular evidence supporting *E. canis*-like infection must be interpreted with caution (Breitschwerdt et al., 2002).

Hepatozoon

Hepatozoon protozoa (Eucoccidiorida, Hepatozoidae) are apicomplexan parasites; three species are known to cause disease in dogs and cats (i.e., *Hepatozoon canis*, *Hepatozoon americanum*, and *Hepatozoon felis*) (Baneth, 2013; Baneth et al., 2013). *H. canis* is responsible for a variety of manifestations, ranging from subclinical infection to mild and moderate disease, characterised by weight loss, lethargy, anaemia and elevated temperature and, in severe cases, life-threatening cachexia. Clinical severity is directly associated with levels of parasitaemia in blood neutrophils (Krargenc et al., 2006; Marchetti et al., 2009; Sakuma et al., 2009). Sexual development and sporogony of *Hepatozoon* species occur in the tick host, while formation of merozoites (merogony) and gametes (gametogenesis) occurs in the intermediate vertebrate host. The tick vectors of *H. felis* are currently unknown, whereas *H. canis* is transmitted by *R. sanguineus* s.l.. Consequently, the geographic distribution of *H. canis* overlaps that of *R. sanguineus* s.l.; however, reports of canine hepatozoonosis in non-endemic areas for this tick species (e.g. north of the Alps and the Balkans), indicate that other ixodid species may transmit *H. canis* (Dezdek et al., 2010; Farkas et al., 2014; Najm et al., 2014b). However, the detection of *H. canis* DNA in *Dermacentor marginatus*, *D. reticulatus* and *Haemaphysalis concinna* removed from dogs (Hornok et al., 2013a) needs confirmatory evidence. Indeed, experimentally infected *I. ricinus* were incapable of transmitting *H. canis* (Giannelli et al., 2013a). Despite the fact that *Hepatozoon* spp. are transmitted by haematophagous ectoparasites, transmission does not occur during the blood meal, since transmission relies on the ingestion of infected ticks (both adults or nymphs) by the vertebrate host (Giannelli et al., 2013b). Then, sporozoites are released from the

sporocysts in the intestine during the digestion process; they penetrate the gut and invade mononuclear cells, which subsequently disseminate *Hepatozoon* spp. via the blood stream to various organs, where merogony takes place. The diagnosis of hepatozoonosis relies on the detection of gamonts within the infected mononuclear cells by cytology or PCR on whole blood, bone marrow or buffy coat smears (Otranto et al., 2011; De Tommasi et al., 2014).

Studies on the prevalence of *H. canis* infection in dogs from various countries in the Mediterranean area have been reviewed elsewhere (Baneth, 2011). More recent reports are available from Albania (Hamel et al., 2009), France (Criado-Fornelio et al., 2009), Romania (Andersson et al., 2013), Hungary (Hamel et al., 2012) and Poland (Bajer et al., 2014). Conversely, for *H. felis*, reports are only available from field studies in Spain (Ortuño et al., 2008; Tabar et al., 2008) and Portugal (Vilhena et al., 2013; Maia et al., 2014). In Europe, *H. canis* has been reported in 23% of red foxes from Croatia (Dezdek et al., 2010), 13.4% from Italy (Gabrielli et al., 2010), 45.2% from Germany (Najm et al., 2014b), 40.6% and 75.6% from Portugal (Abranches et al., 1982; Cardoso et al., 2014), 8% from Hungary (Farkas et al., 2014), 58.3% from Austria (Duscher et al., 2014), and 28% from Spain (Gimenez et al., 2009). In addition, *H. canis* has been detected in one road kill golden jackal in Austria (Duscher et al., 2013) and in 60% of 15 shot golden jackals from Hungary (Farkas et al., 2014).

Despite the high prevalence of *H. canis* based on detection of the DNA of this pathogen, no *Hepatozoon*-like parasites have thus far been detected in foxes or jackals north of the Alps, in areas where no dog infections have been described over the last decade. This observation raises the question of whether the molecular identification of *H. canis* (based on one gene marker only) might be yielding false positive results. Indeed, a longer sequence of the 18s rRNA amplified from a parasite recovered from a jackal in Hungary clustered separately from the *H. canis* group (Farkas et al., 2014); however, in a Portuguese study, the parasite was detected in 23.4% out of 47 fox bone marrow samples by histopathology and 83.0% by PCR (Cardoso et al., 2014).

Rickettsia

Rickettsia spp. (Rickettsiales, Rickettsiaceae) consist of a growing number of Gram-negative, small, obligate intracellular alpha-proteobacteria, generally classified into three large groups. The spotted-fever group consists of more than 30 different species most of which are tick-borne, with some also transmitted by fleas or mites. The typhus group consists of two species (*R. prowazekii*, *R. typhi*), like the so-called ancestral group (*R. canadensis* and *R. bellii*). *Rickettsia* spp. have a worldwide distribution, with the geographical range of each pathogen overlapping that of their specific tick vector(s) (Parola et al., 2013). Thus far, a total of 16 *Rickettsia* spp. have been described in Europe, with six further species awaiting confirmation. While *R. felis* is the only rickettsia in the spotted-fever group molecularly found in a range of flea and tick species, most rickettsiae rely on a unique tick genus for transmission to vertebrate hosts (Fournier, 2013). In Europe, the most important rickettsia species are *R. conorii* (two of the four subspecies) transmitted by *R. sanguineus* s.l., *R. massiliae* also transmitted by *R. Sanguineus* s.l., *R. raoultii* and *R. slovaca* transmitted by *Dermacentor* spp., *R. helvetica* and *R. monacensis* transmitted by *I. ricinus*, *R. felis* primarily transmitted by the cat flea, and *R. sibirica* subsp. *mongolotimonae*, transmitted by *Hyalomma* spp. Upon inoculation by the tick, rickettsiae invade endothelial cells for a first round of replication, which is followed by release of progeny bacteria, rickettsiemia and dissemination of the infection to new endothelial cells. As a result, an eschar forms at the site of tick bite, followed by disseminated vasculitis, which leads to a variety of symptoms, including fever. Although *R. conorii* and the Mediterranean spotted fever have been known for over 100 years, the role of dogs in the epidemiology of the disease has been investigated only recently. Seroprevalence in dogs around the Mediterranean ranges from 81% in rural areas in Israel where human cases occur (Harrus et al., 2007), to 56.4% (Solano-Gallego et al., 2006a) and 31%-53% in dogs from Spain (Ortuño et al., 2009), and 38.5% in dogs from southern Portugal (Alexandre et al., 2011). Some reports describe a seasonality of antibody titers, indicating a short lived immune response in dogs as the cause of frequent reinfections (Espejo et al., 1993); based on this observation, seroprevalence in dogs has been used as an epidemiological marker of *R.*

conorii infections (Ortuño et al., 2009). Seroprevalence of *R. typhi* in dogs from north-eastern Spain was 9.7%, and 51.1% for *R. felis* (Nogueras et al., 2009). However serological results must be carefully interpreted since cross-reactivity among different *Rickettsia* species is well documented (Wächter et al., 2015). Only one report described three acutely ill, febrile dogs from Sicily, Italy (Solano-Gallego et al., 2012). Nevertheless, even under experimental conditions, dogs do not generally display clinical signs; dogs, however, are competent reservoir hosts for *R. conorii* (Levin et al., 2011). *R. sanguineus* s.l. also acts as a reservoir for this pathogen, as transovarial transmission occurs in 100% of naturally infected ticks (Socolovschi et al., 2012). Only a few attempts to detect *Rickettsia* spp. other than *R. conorii* in dogs have been made (Hamel et al., 2009). *R. raoultii*, *R. helvetica*, and *R. monacensis* were detected in ticks removed from dogs in Kiev, Ukraine (Hamel et al., 2013), while 16.2% of cats were seropositive for *Rickettsia* spp. in Portugal (Alves et al., 2009).

Thus far, no *Rickettsia* has been detected in wild carnivores in Europe. Thirty-six foxes from the north-eastern part of Austria were negative for *Rickettsia* spp. (Duscher et al., 2014). However, since some *Rickettsia* spp. are transmitted by *Ixodes* species (which also feed on carnivores), the prevalence of these pathogens in wildlife is likely underestimated.

5. Conclusions

The combined experience of microbiologists, parasitologists, veterinarians, physicians, biologists and epidemiologists is the key for a better understanding of the ecology of diseases caused by protozoan parasites that wild carnivores may share with dogs and cats and, in some instances, with humans. Nonetheless, the flow of infection from wildlife to domestic animals or humans may vary according to the specific transmission dynamics of each agent. In addition, the sudden emergence of ‘new’ parasites in wildlife may greatly impact on their population dynamics and on conservation of endangered species (Thompson et al., 2010). Nonetheless, an increasing number of reports is becoming available on the

transmission of protozoan pathogens from humans to animals outside Europe (reviewed by Messenger et al., 2014), e.g. *Giardia* and *Cryptosporidium*. Despite the increasing interest for the everchanging relationships between animals and humans, and between domestic and wildlife species (Messenger et al., 2014), the flow of human and domestic animal protozoan parasites to wild carnivores has long been neglected. The integration of novel molecular and bioinformatics technologies is likely to aid our understanding of the transmission routes of protozoan parasites (e.g. *Hepatozoon* spp.), as well as the role that animals and humans play as reservoirs (Viana et al., 2014).

Clearly, defining the structures of protozoan parasite populations in domestic and wild hosts has important implications for studies of the pathogen transmission, immunogenicity and disease pathogenesis (Sibley et al., 2009). Further research is needed to investigate the genetic diversity of protozoans (and, for ectoparasites, their associated pathogens) that may be shared with wild and domestic felids and canids. These studies could provide information on the dynamics of parasite infections among wild and domestic populations and enable the development of more effective control strategies, which represent the core of conservation, veterinary and public health legislations.

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Figure legend

Figure 1 General potential drivers and interactions among wild, domestic carnivores and humans which might affect parasite circulation among host populations in different environments.

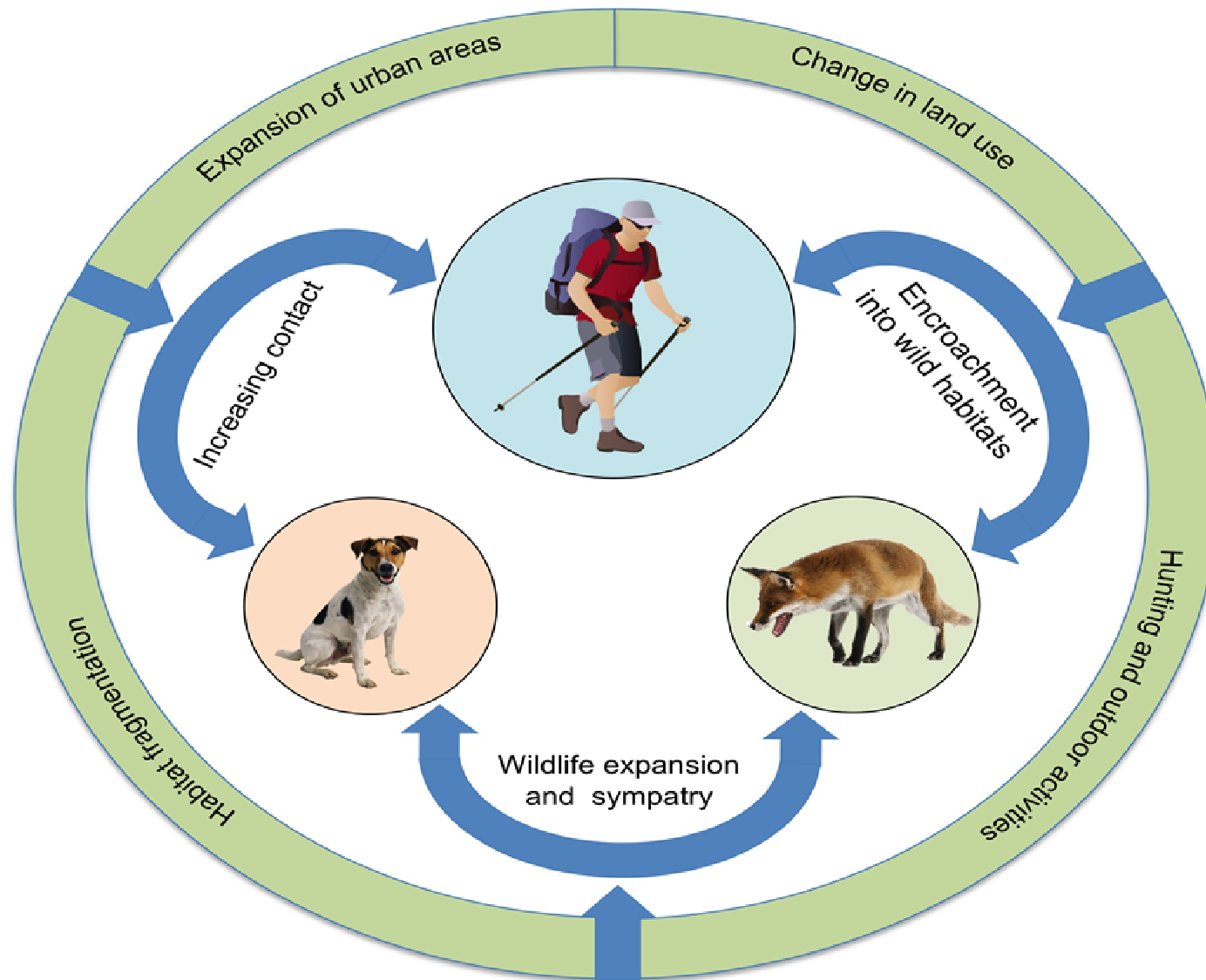
Figure 2

A wolf (*Canis lupus*) on the left followed by three wolf-dog hybrid cubs in the Maremma Regional Park, a mixed mediterranean forest located on the Thyrrhenian coast of central Italy (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>Leishmania infantum</i>	Red fox (<i>Vulpes vulpes</i>), wolf (<i>Canis lupus</i>), golden jackal (<i>Canis aureus</i>) Iberian lynx (<i>Linx pardinus</i>), wild cat (<i>Felis silvestris silvestris</i>), and mustelids	Portugal, Spain, Italy, France, Croatia, Greece, Cyprus	Visceral, cutaneous and rarely mucocutaneous leishmaniosis
<i>Giardia duodenalis</i> complex	Wolf (<i>Canis lupus</i>), red fox (<i>Vulpes vulpes</i>), golden jackal (<i>Canis aureus</i>)	Poland, Croatia, Norway, Bosnia and Erzegovina	Gastrointestinal infection
<i>Cryptosporidium</i> spp.	Wolf (<i>Canis lupus</i>), red fox (<i>Vulpes vulpes</i>), american mink (<i>Mustela vison</i>)	Slovak Republic, Poland, Ireland	Gastrointestinal infection
<i>Toxoplasma gondii</i>	Wild cat (<i>Felis s. silvestris</i>), Eurasian lynx (<i>Lynx lynx</i>), Iberian lynx (<i>Lynx pardinus</i>), red fox (<i>Vulpes vulpes</i>), wolf (<i>Canis lupus</i>) and mustelids	All over Europe	Accidental hosts: acute infection (influenza-like) and congenital infection

			(abortion and fetal damages, ocular problems later on).
<i>Babesia canis</i>	Red fox (<i>Vulpes vulpes</i>), captive Wolf (<i>Canis lupus</i>)	Portugal, Hungary	Not reported
<i>B. microti-like/Theileria annae</i>	Red fox (<i>Vulpes vulpes</i>)	Portugal, Italy, Austria, Germany, Hungary	Rare human cases (<i>B. microti-like</i> organisms)
<i>Cytauxzoon spp.</i>	Iberian Lynx (<i>Lynx pardinus</i>)	Spain	Not reported
<i>Anaplasma phagocytophilum</i>	Red fox (<i>Vulpes vulpes</i>), Eurasian lynx (<i>Lynx lynx</i>)	Italy, Czech Republic, Poland, Switzerland, Sweden	HGA (Human granulocytic anaplasmosis)
<i>Ehrlichia canis</i>	Red fox (<i>Vulpes vulpes</i>)	Italy	Not reported
<i>Hepatozoon canis</i>	Red fox (<i>Vulpes vulpes</i>), golden jackal (<i>Canis aureus</i>)	Croatia, Germany, Portugal, Hungary, Austria, Spain	Not reported



Figure_1 .



Figure_2 .