



Factors affecting the spread of parasites in populations of wild European terrestrial mammals

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Abstract

There are many different factors involved in parasitism. The general concept of “filters” proposed by Combes includes “encounter filters” (behavior, biodiversity) and “compatibility filters” (resources, defense) to explain mechanisms responsible for the formation of host–parasite coexistence. However, researches explaining the reasons for the spread and dynamics of parasites in populations of wild terrestrial mammals in Europe and the specific factors affecting prevalence and intensity of parasitosis are limited. Many factors, ecological, biological, and anthropogenic, form a complex network of interdependencies that shape this pattern. Here, I summarize the current state of knowledge on the factors affecting parasitic diseases in wild mammals inhabiting the European continent. It indicates the need to further development, not only for academic reasons, but also for the benefit of use in management of wild mammal species and disease control in nature.

Keywords Parasites · Wildlife · Mammals · Transmission · Zoonoses

Introduction

Parasite dynamics can be strongly affected by numerous (biological, ecological, and anthropogenic) factors. Combes (1991, 2001) proposed the concept of “filters” to describe the mechanisms responsible for formation of host–parasite coexistence. They are “encounter filters,” which determine the probability of contact between the parasite and potential host (e.g., behavior, biodiversity) and “compatibility filters,” which delimit the probability of the parasite and potential host living together (e.g., resource, defense). Combes’ concepts of encounter and compatibility as a sequence of filters allow a more complete understanding of the parasite–host relationship (Combes 2001); however, in this concept, there is no consideration of anthropogenic factors which also may play a very important role in host–parasite coexistence formation (e.g., Cunningham 1996; Murray et al. 2016; Vadlejch et al. 2016). Specific factors influencing host–parasite associations are, among others, climate conditions, behavioral traits, host

sociality, population density, diet, habitat, age, sex, host immunocompetence, supplementary feeding, and animal translocations (e.g., Cornell et al. 2008; Kołodziej-Sobocińska et al. 2014b, 2016a, 2018b; Solomon et al. 2015; Woolhouse 1998; Zuk and McKean 1996).

Parasitic infections that are present in wildlife may have important effects on individuals and populations (Møller 2005), which could be an especially critical issue in conservation of threatened species (Thompson et al. 2010). Parasites may cause deleterious effects on their hosts (Anderson and May 1979; Prado et al. 2009), and so both the host and parasite are forced to constantly adapt to one another (Schmid-Hempel 2011). This sometimes leads to a relatively stable relationship tending toward a parasite–host balance, as it is in the evolutionary interest of the parasite that its host survives (Rook 2007). Moreover, infected wild terrestrial mammals could have an important influence on human health, as they are reservoirs for many zoonotic diseases including echinococcosis (*Echinococcus* spp.), toxocarosis (*Toxocara* spp.), trichinellosis (*Trichinella* spp.), toxoplasmosis (*Toxoplasma* spp.), alariosis (*Alaria* spp.), and many others (Antolova et al. 2009, 2014; Duscher et al. 2017; Hurníková et al. 2016; Kern et al. 2003; Krucken et al. 2017; Lassen et al. 2016; Machnicka-Rowińska et al. 2002; Nahorski et al. 2013; Oksanen et al. 2016; Poepl et al. 2013; Suld et al. 2014; Sutor et al. 2014; Thompson 2013; Thompson et al. 2010).

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The complex processes and factors shaping the dynamics of parasitic diseases prompted me to review the current state of knowledge on this topic. I focus on parasites in populations of wild terrestrial mammals inhabiting the European continent because there is a particularly strong body of available research papers for European terrestrial mammals and their parasites; however, I noticed the lack of comprehensive literature review on factors affecting parasitosis in European wildlife. It can be assumed that comprehensive studies are only feasible through the combination of parasitological data with knowledge about the ecology and biology of mammalian hosts, their responses to infection, the history and range of non-native invasive species, or the methods of species management.

Difficulties in parasitological studies of mammals in the wild

One of the main problems concerning characterization and systematization of wild mammals' parasitofauna is the diversification of mammalian hosts. Further, for many species, it is difficult or even impossible to collect research material because of their protection status or rarity. In addition, there is scarce information on parasites and parasite gene sequences. Many studies on parasitic diseases of wild mammals involve determining the parasite species composition of particular wild hosts (Bień et al. 2010; Demiaszkiewicz et al. 2013; Drózd et al. 1998; Reiterová et al. 2006). Due to the limited availability of wild animal carcasses, especially of protected species, studies often rely on detection of parasite eggs in mammal feces (Górski et al. 2006; Szczesna et al. 2008; Turgeon et al. 2018). This method, however, has limitations, including the seasonality of parasite egg shedding and difficulty in their proper identification (Hines et al. 2007; Pyziel et al. 2011). Molecular methods for species identification are necessary to obtain reliable and accurate results (Haukisalmi et al. 2018; Kołodziej-Sobocińska et al. 2018c; Vichova et al. 2011; Walker et al. 2013) and these techniques should be further developed and implemented. Specifically, for many parasite species of mammals, there is a lack of reliable data entries to open-source repositories.

More generally, several difficulties arise in parasitological studies of wild mammals. First, advances in the methodology of parasite isolation and identification make comparisons of past and contemporary research difficult. In addition, inter-individual differences connected to coinfection with other pathogens (Viney and Graham 2013), food availability (Friesen et al. 2015), age (Woolhouse 1998), breeding status (Grear et al. 2009), etc., may significantly impede the interpretation of results and their comparison among wild animals of the same species from different populations, localizations, and habitats. Finally, rare and unique material from wild mammals is often used

not only for parasitological studies but also for other types of studies (e.g., diet analyses), which can distort parasitological analyses because some species of parasites inhabit mainly host stomachs (Kołodziej-Sobocińska et al. 2018a). The necessity of comprehensive studies taking into account these limitations is indispensable for understanding parasitic infections in wild populations. Many of them are discussed in the presented review, which should facilitate the planning of parasitological research of wild animals.

Factors affecting the spread of parasites in wildlife

Potential factors determining the transmission of parasites include environmental conditions that affect the viability and behavior of parasites (Rogers and Sommerville 1963) and feeding, movement, and defecation patterns of the host, which determine the parasites encountered (Lozano 1991; Price et al. 1988; Watve and Sukumar 1995). In addition, parasite species diversity and infection intensity can have a wide range of impacts on hosts, in terms of their (1) health (Johnson and Hoverman 2012; Tompkins et al. 2011); (2) behavior (Herbison et al. 2018; Milinski 1984; Moore 1984); (3) sexual selection (Auld et al. 2016; Penn and Potts 1998; Watve and Sukumar 1995); and (4) regulation of host populations (Dobson 1988; Kołodziej-Sobocińska et al. 2018a; Lefevre et al. 2009; Tompkins et al. 2011). Encounter (biodiversity, behavior) and compatibility (resource, defense) filters responsible for shaping host–parasite associations may be closed and/or open (Combes 1991, 2001). Thus, there are four possible combinations: (1) both filters are closed—the host–parasite association cannot exist; (2) the encounter filter is opened, but the compatibility filter is closed—the parasite–host association does not exist, but selective pressure on the parasite may allow some individuals of the parasite (e.g., selected mutants) to open the compatibility filter; (3) the encounter filter is closed, but the compatibility filter is open—the parasite–host association also does not exist, although a change in composition of the ecosystem or in host behavior may open the filter and result in association; (4) both the encounter and compatibility filters are open and the host–parasite association may exist (Combes 2001).

Worldwide, mammals are so diverse that it is impossible to discuss their interdependences with parasite communities in one paper. Thus, I decided to focus on selected terrestrial mammals of Europe, which are the closest to my interest and relatively little explored in this context. The choice of literature on factors affecting the spread of parasites in populations of wild European terrestrial mammals has been summarized in Table 1. The following sections address some of

Table 1 Review of factors affecting the spread of parasites in wild terrestrial mammals with examples of references

Type of factor	Factor name	References	
Ecological	Population ecology, population status, population density, population size	Anderson (1982); Anderson and May (1978); Beldomenico et al. (2008); Hoberg and Brooks (2015); Holmala and Kauhala (2006); Hudson et al. (2006a, b); Kelly et al. (2009); Lefevre et al. (2009); Lindenfors et al. (2007); Møller (2005); Peacock et al. (2018); Pedersen and Fenton (2007); Scott (1988); Smith et al. (2009); Stringer and Linklater (2015); Sugiura et al. (2018); Telfer et al. (2008, 2010); Tompkins et al. (2011); Torres et al. (2006); Wang et al. (2016); Watve and Sukumar (1995); Winternitz et al. (2012)	
	Migration, colonization	Altizer et al. (2011); Anisimova (2004); Brown and Hall (2018); Dobson (1988); Folstad et al. (1991); Kołodziej-Sobocińska et al. (2018a); Lindenfors et al. (2007); Mysterud et al. (2016); Peacock et al. (2018); Teitelbaum et al. (2018); Torres et al. (2006)	
	Competition, predation	Bohm et al. (2008); Bonsall and Hassell (1999); Kołodziej-Sobocińska et al. (2014b); Ostfeld and Holt (2004); Price et al. (1988); Raffel et al. (2010); Rohr et al. (2015); Telfer et al. (2010)	
	Climate, season	Altizer et al. (2006); Begon et al. (2009); Brooks et al. (2014); Cable et al. (2017); Cattadori et al. (2005); Cornell et al. (2008); Harvell et al. (2002); Hoberg and Brooks (2015); Holmes et al. (2018); Hudson et al. (2006a); Kołodziej-Sobocińska et al. (2016d); Kutz et al. (2014); Lafferty (2009); Martin et al. (2008); Mysterud et al. (2016); Pedersen and Fenton (2007); Pyziel et al. (2011); Studer et al. (2010); Turner and Getz (2010)	
	Food availability, diet	Bień et al. (2016); Brown and Hall (2018); Drózdź et al. (2003); Duscher et al. (2017); Friesen et al. (2015); Górski et al. (2006); Hart and Hart (2018); Kołodziej-Sobocińska et al. (2016c, d, 2018c); Lozano (1991); Pyziel et al. (2011); Rohr et al. (2015); Turner and Getz (2010)	
	Behavior, sociality	Bohm et al. (2008); Curtis (2014); Hart and Hart (2018); Herbison et al. (2018); Kavaliers and Choleris (2018); Kołodziej-Sobocińska et al. (2014b); Milinski (1984); Moore (1984); Sarabian et al. (2018); Weinstein et al. (2018a, 2018b)	
	Non-native invasive mammal species	Bonesi and Palazon (2007); Chaneton and Bonsall (2000); Colautti et al. (2004); Cybulska et al. (2018); Gendron et al. (2012); Humíková et al. (2016); Keogh et al. (2017); Kołodziej-Sobocińska et al. (2018a); Laurimaa et al. (2016); Lymbery et al. (2014); Poulin (2017); Prenter et al. (2004); Sherrard-Smith et al. (2015); Sugiura et al. (2018); Sutor et al. (2014); Torchin et al. (2003)	
	Non-native invasive parasite species	Daszak et al. (2000); Drózdź et al. (1998); Garbarino et al. (2017); Kanchev et al. (2012); Kołodziej-Sobocińska et al. (2016a); Lymbery et al. (2014); Price et al. (1986); Romeo et al. (2015); Taraschewski (2006); Vadlejch et al. (2016)	
	Biological	Sex, breeding status, sexual selection	Alexander and Stimson (1988); Auld et al. (2016); Folstad and Karter (1992); Friesen et al. (2015); Fuxjager et al. (2011); Grear et al. (2009); Kiffner et al. (2013); Klein (2004); Kołodziej-Sobocińska et al. (2016a, 2018a); Krishnan et al. (1996); Lloyd (1983); Penn and Potts (1998); Poulin (1996); Turner and Getz (2010); Watve and Sukumar (1995); Zuk and McKean (1996)
		Age	Bush et al. (2001); Cornell et al. (2008); Kethineni et al. (2006); Kołodziej-Sobocińska et al. (2016a, 2018a); Treboganova (2010); Turner and Getz (2010); Woolhouse (1998)
Body condition, health, immunocompetence		Beldomenico et al. (2008); Bize et al. (2008); Cornell et al. (2008); Davidson et al. (2015); Johnson and Hoverman (2012); Kołodziej-Sobocińska et al. (2014b, 2016b, 2018a); Lindenfors et al. (2007); Martin et al. (2003); Sánchez et al. (2018); Schulte-Hostedde and Elsasser (2011); Schulte-Hostedde et al. (2005); Stien et al. (2002); Tompkins et al. (2011); Turgeon et al. (2018); Wilder et al. (2016); Winternitz et al. (2012)	
Anthropogenic	Supplementary feeding	Kołodziej-Sobocińska et al. (2016a, d); Kozak et al. (1995); Loarie et al. (2009); Murray et al. (2016); Oja et al. (2017); Pyziel et al. (2011); Radwan et al. (2010); Sorensen et al. (2014); Suld et al. (2014)	
	Introduction, reintroduction, translocation, conservation	Cunningham (1996); Daszak et al. (2000); Dickens et al. (2010); Dobson (1988); Faria et al. (2010); Karbowski et al. (2014); Kołodziej-Sobocińska et al. (2018b, c); Mathews et al. (2006); Pedersen et al. (2007); Scott (1988); Stringer and Linklater (2015); Turgeon et al. (2018); Vadlejch et al. (2016); Viggers et al. (1993); Wakelin (1978)	
	Zoonotic diseases	Antolova et al. (2009, 2014); Bastien et al. (2018); Bień et al. (2016); Chen et al. (2018); Cybulska et al. (2018); Daszak et al. (2000); Duscher et al. (2017); Garbarino et al. (2017); Gazzonis et al. (2018); Górski et al. (2006); Humíková et al. (2016); Karamon et al. (2014); Karssin et al. (2017); Kołodziej-Sobocińska and Miniuk (2018); Kołodziej-Sobocińska et al. (2016c, 2018c); Krucken et al. (2017); Laurimaa et al. (2016); Mackenstedt et al. (2015); Polley (2005); Rentería-Solís et al. (2018a, b); Schweiger et al. (2007); Serrano-Moliner et al. (2018); Sutor et al. (2014); Thompson (2013); Weinstein et al. (2018b)	

the most relevant aspects and examples in detail. I provide examples referring to European terrestrial mammals, but in some cases, lack of research illustrating adequately a given problem forced me to use examples of terrestrial mammals

from other continents. To better illustrate the complexity of the reviewed topic, the network of host–parasite associations and factors influencing their coexistence are presented in Fig. 1.

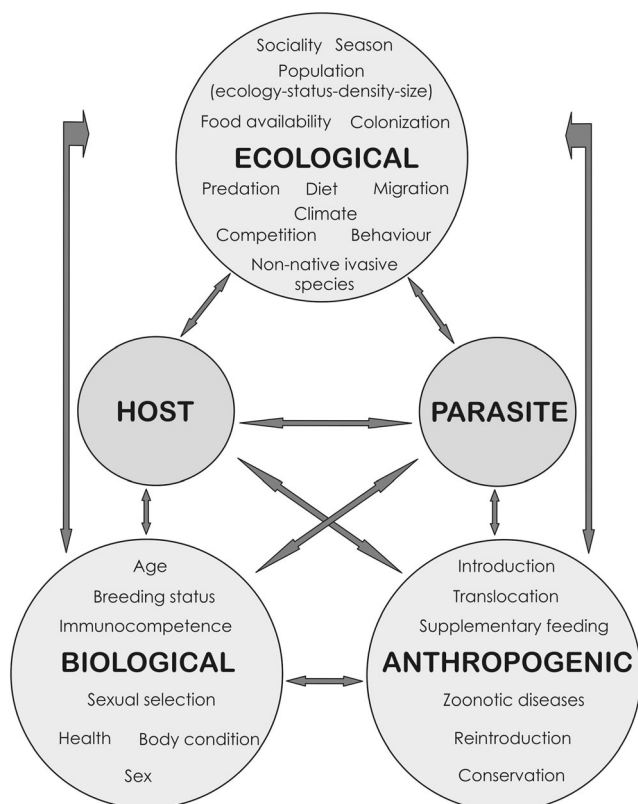


Fig. 1 The network of host–parasite associations with factors influencing their coexistence in wildlife

Ecological factors

Population ecology, status, density, and size

Host population size is important in the context of host–parasite interactions because the spread of parasites is able to persist only if the number of hosts is above critical threshold (Anderson and May 1979). Population size often depends on population health status; the size of the weakened population with higher mortality rates will be smaller, which should slow down pathogen transmission. On the other hand, such populations are more susceptible to infection, as lowered fitness, condition, and immune defense favor disease occurrence and spread. Also population density may strongly increase risk of disease transmission through close contact between mating pairs or group members (Sugiura et al. 2018). Contact rate between individuals may be also accelerated by host behavior and sociality. The pooled density of medium-sized carnivores showing high space use overlaps and increased potential contact rate may exceed the threshold density needed for disease spread (Holmala and Kauhala 2006). A novel approach is using contact networks to explore and understand the dynamics of disease transmission; for example, data on African lion (*Panthera leo*) behavior and movement provide sophisticated evidence that outbreaks of canine distemper virus are partly driven by interspecific interactions among lions, spotted

hyenas (*Crocuta crocuta*), and jackals (*Canis* spp.) (Craft et al. 2008; Tompkins et al. 2011). All these interdependencies work bidirectionally as pathogens have an impact on animal populations, but population status, size, and density influence the speed and efficiency of disease transmission and spread (Scott 1988; Tompkins et al. 2011).

Migration and colonization

Host migration affects parasite dynamics in many wildlife species (Peacock et al. 2018). Spatiotemporal changes in host density due to migration patterns have profound and diverse consequences for parasite–host interactions (Altizer et al. 2011). For example, seasonal migrations of ungulates, such as red deer (*Cervus elaphus*), have an impact on parasite species diversity, load, and epidemiology (Myserud et al. 2016). On the one hand, long-distance host migration enhances the spread of pathogens, including those of zoonotic potential, and facilitates cross-species transmission (Altizer et al. 2011); on the other, migratory hosts may escape parasitism. Such migratory escape has been proposed as a driver of post-calving migration in reindeer (*Rangifer tarandus tarandus*) in Norway (Folstad et al. 1991) and for non-native invasive American mink (*Neovison vison*) colonizing new territories in Poland (Kołodziej-Sobocińska et al. 2018a). Migratory demands can also reduce immune function, with consequences for host susceptibility and mortality (Altizer et al. 2011).

Competition and predation

Competition and predation can influence rates of parasite infection by altering population densities of hosts and vectors (Raffel et al. 2010). These traits increase the contact rate between individuals of the same or multiple species and therefore increase the likelihood of being infected. This pattern has been shown in studies of sarcoptic mange in carnivore communities inhabiting Białowieża Primeval Forest (BPF), Poland (Kołodziej-Sobocińska et al. 2014b). Intra-guild predation observed among wolves (*Canis lupus*) and lynxes (*Lynx lynx*) preying upon medium-sized carnivores like the red foxes (*Vulpes vulpes*) or raccoon dogs (*Nyctereutes procyonoides*) was one of the behavioral traits affecting sarcoptic mange occurrence (Kołodziej-Sobocińska et al. 2014b). Alternately, predators compete for and kill their prey; therefore, they consume both parasites and their hosts, and limit the number and density of infected individuals (Rohr et al. 2015). Lower host density may either decrease density-dependent transmission or increase per capita exposure, when the source of infection is at least temporarily independent of host density (Ostfeld and Holt 2004; Raffel et al. 2010). Additionally, predators often induce changes in behavioral traits of prey, which can modulate parasite transmission by

altering the rate of encounter described as the Combes' encounter filter (Combes 2001; Raffel et al. 2010).

Climate and season

Host–parasite dynamics can be strongly affected by both climate and season (Altizer et al. 2006; Brooks et al. 2014; Cattadori et al. 2005; Cornell et al. 2008; Hudson et al. 2006a). Long dry seasons or very low temperatures limit development and survival of parasites in the environment and, as a result, host contact and parasite transmission. In addition, during the dry season, hosts shed far fewer parasite propagules into the environment than during the wet season (Holmes et al. 2018; Kutz et al. 2014; Turner and Getz 2010). Climate change affects hosts, vectors, parasites, vegetation, abiotic elements of the ecosystem, and many of the associations among these that affect the parasite web and parasite flow (Cable et al. 2017). Identification of all components of an ecosystem potentially susceptible to climate change is difficult, but perhaps easier than predicting the impacts of change. Among them, temperature, precipitation, and atmospheric CO₂ have been studied, but interactions between them and consequent effects on parasite transmission are complex and very difficult to trace (Harvell et al. 2002). This is because these climate components may counteract each other, such that the overall rate of parasite transmission remains unchanged. For example, a higher temperature increases parasite growth and infectivity; however, if too high, it may also increase parasite mortality (Lafferty 2009; Studer et al. 2010).

Food availability and diet

Source of food is an important factor for parasite transmission, because predators and scavengers consume prey along with their parasites. Some prey may be a source of infection, such as when a predator or scavenger is a viable host for a particular parasite species, e.g., *Trichinella* spp., *Toxocara* spp., or *Echinococcus* spp. (Bień et al. 2016; Duscher et al. 2017; Górski et al. 2006; Kołodziej-Sobocińska et al. 2018c); this can cause disease spread and transmission. Otherwise, when the predator is not and cannot be a host (Combes' compatibility filters are closed), infection does not occur and the consumed parasite will die. This is the case for some gastrointestinal parasites of herbivorous mammals, where disease transmission occurs only through the excretion of eggs/oocysts in feces and contamination of the environment (Drózdź et al. 2003; Kołodziej-Sobocińska et al. 2016a, d; Pyziel et al. 2011; Turner and Getz 2010). In this situation, predation is not the cause of spread; parasite transmission occurs because animals are more densely aggregated in a particular place due to human activity, such as supplementary feeding or utilization of the same pastures as livestock (Barger et al. 1994; Kołodziej-Sobocińska et al. 2016a, d). The seasonal

availability of food is also an important aspect. One American mink study revealed significantly lower *Aonchotheca putorii* nematode abundance in the non-breeding season (September–January) than in the breeding season (February–May) (Kołodziej-Sobocińska et al. 2018a). The increased abundance of this nematode in mink gastrointestinal tracts between February and May possibly resulted from the availability of earthworms, which are intermediate hosts for *A. putorii*. In Canada, infection intensity of *A. putorii* in the raccoon (*Procyon lotor*) was also the highest during spring and lowest during winter (Butterworth and Beverleyburton 1981).

Behavior and sociality

Wild animals are subject to strong selection from parasites and other infectious agents. This results in behavioral adaptations that help potential hosts avoid falling prey to parasites (Sarabian et al. 2018). This phenomenon is known as the “landscape of disgust” (Weinstein et al. 2018a) and is similar to the “landscape of fear” theory of predator avoidance in that parasite avoidance behavior can also affect ecology and evolution (Kuijper et al. 2013; Schmidt and Kuijper 2015; Weinstein et al. 2018a). Parasite and predator avoidance strategies sometimes have mutual effects, e.g., avoiding predator feces protects prey against both predators and their parasites (Weinstein et al. 2018b). In much the same way as predator avoidance, parasite avoidance has strong effects on foraging, movement, and social interactions (Curtis 2014). Several strategies have evolved that enable wild mammals to deal with parasites. These include eliminating infectious agents from sleeping/resting areas, having an array of grooming techniques, consuming medicinal plant-based compounds, and others (Hart and Hart 2018). These strategies are species-specific and reflect particular environments that animals inhabit. Sarcoptic mange is an example of a disease whose spread depends on host sociality and behavior. It is a highly contagious mite infection responsible for epizootic skin disease in populations of wild and domestic mammals worldwide (Arlan 1989; Pence and Ueckermann 2002; Sugiura et al. 2018). Social carnivores are more susceptible to mange than solitary ones (Kołodziej-Sobocińska et al. 2014b; Sugiura et al. 2018) due to a high overlap of space, habitat use, and denning behavior, including the shared use of den sites (Kowalczyk et al. 2008). In contrast to social mammals, the rate of encounters between individuals of solitary species was much lower and often limited to a few specific periods such as the mating season (Arlan 1989; Schmidt et al. 1997).

Non-native invasive mammal species

One of the largest pillars of invasion ecology is understanding what happens to parasite faunas when host species become

established in a new region (Keogh et al. 2017; Kołodziej-Sobocińska et al. 2018a; Laurimaa et al. 2016; Poulin 2017; Stricker et al. 2016). Commonly debated questions include: Which parasites are prevalent in native ranges but absent in new territories, and vice versa? Do some parasites pose a particular threat to local fauna and to human health in invasive ranges? In Europe, invasive non-native species (INNS) such as raccoon dogs, raccoons, and American mink are known to be important vectors of multiple zoonotic agents, of which some (e.g., *Echinococcus multilocularis*, *Toxocara* spp., *Trichinella* spp., and *Alaria* spp.) are highly pathogenic for humans (Bagrade et al. 2016; Cybulska et al. 2018; Hurníková et al. 2016; Laurimaa et al. 2016; Machnicka-Rowińska et al. 2002). Carnivores often act as definitive hosts that carry reproductive adults and shed eggs into the environment. Humans become intermediate, paratenic, or “dead end” host for these parasites because larval stages settled in human organs and tissues cause severe pathological changes and serious health consequences (Antolova et al. 2014; Chen et al. 2018; Kern et al. 2003; Nahorski et al. 2013). The Enemy Release Hypothesis (ERH) is one of the most important hypotheses explaining successful introduction and rapid spread of INNS (Dobson 1988; Elton 1958). Many studies have confirmed the possibility of escape from parasites, having shown that parasite species richness or prevalence is lower in host populations inhabiting invaded ranges compared to those in native ranges (Colautti et al. 2004; Torchin and Mitchell 2004). Yet the question remains: for how long? A recent study revealed that following American mink introduction to an invaded range, parasite abundance in the invasive mammal increased significantly for only 20 years (Kołodziej-Sobocińska et al. 2018a). This suggests that INNS escape from parasite pressure for a shorter duration than expected (Gendron et al. 2012). INNS that escape their native range may benefit not only from reduced parasite pressure at the beginning of the invasion, but also from relaxed selection for costly immune response, which promotes reallocation of available resources toward growth, reproduction, and survival. As a result, invasive hosts may be less infected but—on the other hand—more susceptible to infection due to the weakening of defense mechanisms (Keogh et al. 2017).

Non-native invasive parasite species

According to Lymbery et al. (2014), alien parasites can be divided into two groups: coinroduced parasites which have been transported with an alien host to a new territory and coinvading parasites which have been coinroduced and then spread to new, native hosts. Coinroductions of parasites with alien hosts occur over a wide range of parasite and host taxa; however, most examples came from non-mammalian hosts (Britton et al. 2011; Ewen et al. 2012; Gaither et al. 2013; Lymbery et al. 2014; Poulin et al. 2011). Nearly 80% of

coinroduced alien parasites switch to coinvaders. “Pathogen pollution” occurs when coinvading parasites that have been successfully transmitted from alien hosts colonizing new territories to native hosts lead to emergence of new disease in the native species (Daszak et al. 2000; Taraschewski 2006). Alien host populations may benefit from this. If those parasites subsequently infect and cause population declines in native species, the alien host population may be more likely to establish and spread as a result. This idea was discussed by Price et al. (1986) and is known as the Novel Weapon Hypothesis. There are many documented examples of alien parasite introduction to native European terrestrial mammals. Parasitic alien terrestrial arthropods occur in small mammals inhabiting Bulgaria (Kanchev et al. 2012). In Italy, native red squirrels coinhabiting with gray squirrels are more likely to be infected by gastrointestinal helminths, including the alien North American nematode *Strongyloides robustus* (Romeo et al. 2015). The introduction of Asian sika deer (*Cervus nippon*) has led to rapid spread of the alien invasive blood-sucking nematode *Ashworthius sidemi* in European bison (*Bison bonasus*) populations in Poland (Drózdź et al. 1998; Kołodziej-Sobocińska et al. 2016a). Finally, *Trichinella spiralis* was introduced in Italy, probably from Eastern Europe by hunters, hunting dogs, or immigrants who illegally carried infected meat in their personal baggage (Garbarino et al. 2017).

Biological factors

Sex, breeding status, and sexual selection

Sex differences in parasite prevalence or intensity are commonly observed (Poulin 1996). Sex-biased parasitism may be due to ecological, behavioral, or physiological differences between males and females (Zuk and McKean 1996). Male-biased parasitism is a common phenomenon in vertebrate-parasite systems (Grear et al. 2009; Poulin 1996), but is not universal (Fuxjager et al. 2011; Kiffner et al. 2013). Male contact with parasites is often more likely than in females (Klein 2004); for example, American mink males are larger, consume more diverse food, and disperse over longer distances (Oliver et al. 2016; Zalewski and Bartoszewicz 2012). Male-biased infection has alternatively been explained by the Immunocompetence Handicap Hypothesis, which suggests an immunosuppressive effect of testosterone that increases susceptibility to infection (Folstad and Karter 1992; Klein 2004). The elevated testosterone level during the breeding season reduces the immune response and accelerates an increase in infection intensity (Grear et al. 2009). However, the lower *A. sidemi* infection intensity observed in European bison bulls (Kołodziej-Sobocińska et al. 2016a) stands in opposition to the widely observed patterns

of the higher susceptibility of males to parasitosis (Alexander and Stimson 1988; Klein 2004; Zuk and McKean 1996). It has been suggested that behavioral traits may be responsible for the lower parasitic load in European bison bulls, as European bison males live solitarily or in small groups, in contrast to subadults and females with calves (Krasińska and Krasiński 1995; Krasińska et al. 2000). In addition, pregnant and lactating females are immunosuppressed and therefore more susceptible to infection (Krishnan et al. 1996; Lloyd 1983). Apart from reproductive status, host immunity may also vary seasonally in relation to stress, food availability, photoperiod, etc. (Martin et al. 2008). Time of the mammal host parturition may also influence parasite spread and transmission dynamics. Synchrony in parturition concentrates young at times of resource abundance (Sinclair et al. 2000), adding a seasonal pulse of susceptible, immunologically naive hosts for parasites in the population (Altizer et al. 2006).

Age

The level of infection is associated with a host's age (Bush et al. 2001; Cornell et al. 2008), and examination of how parasitism changes with host age can provide insight into the existence of host-acquired immunity and age-dependent variation in host exposure to parasites (Woolhouse 1998). Thomas et al. (1995) argued that older individuals are less heavily infected because they may cease to acquire parasites as a consequence of changes in feeding or behavioral patterns, habitat utilization, or immunity acquisition. In most systems, however, young and subadult animals with immature immune systems are most susceptible to infection and disease and spread a higher number of infective eggs into the environment through their feces (e.g., Cornell et al. 2008; Kethineni et al. 2006; Treboganova 2010; Woolhouse 1998). The study by Cornell et al. (2008) revealed that in Scottish populations of European rabbit (*Oryctolagus cuniculus*) the effectiveness of hosts' immune response to the gastrointestinal nematode *Trichostrongylus retortaeformis* possibly acts, among others, through a maternal effect dependent on the European rabbit's month of birth. Cohorts of rabbits born in different months show the characteristic humpbacked relationship between parasite intensity and host age with the lowest parasite intensity in the youngest individuals. This could be a result of short exposure time of the host to the parasite as well as availability of maternal antibodies, which provide immunological protection (Hurley and Theil 2011; Jackson and Nazar 2006). Breastfed, young mammals should be better protected against diseases because they get maternal antibodies with milk. This is not always true, because some parasites, e.g., *Toxocara* spp., can be transmitted to puppies and kittens with the mother's milk, and during pregnancy through the placenta (Coati et al. 2004; Lee et al. 1976). By adulthood, animals have usually

developed a stronger immunity and harbor lower infection levels (Kethineni et al. 2006). However, this pattern is not always confirmed. In *Arvicola terrestris*, an intermediate host for *E. multilocularis*, infections accumulate with increasing age in single vole generations and prevalence increases (Burlet et al. 2011). Similar to *E. multilocularis*, *Taenia taeniaeformis* causes lifelong infections in intermediate hosts and is more prevalent in older animals (Theis and Schwab 1992). This pattern is probably true also for other intermediate hosts, when larval stages accumulate in organs and tissue throughout the host life.

Body condition, health, and immunocompetence

Body condition metrics are often used to assess costs of parasitic infections in wildlife (Sánchez et al. 2018). However, the relationship between infection intensity and body condition is not well understood. It has been suggested that individuals in poor condition could be a "bad choice" for parasites due to the lack of available resources (Bize et al. 2008; Schulte-Hostedde and Elsasser 2011). However, parasites may negatively influence the body condition of their hosts (Turgeon et al. 2018; Winternitz et al. 2012), e.g., mink body condition has been negatively associated with nematode abundances in the gastrointestinal tract (Kołodziej-Sobocińska et al. 2018a). The deterioration of the body condition may be accelerated because individuals in poor condition are unable to control parasitic infection by mounting sufficient immune defenses (Martin et al. 2003). Body condition has been empirically linked with survival probability and reproductive success in many taxa, including carnivores (Schulte-Hostedde et al. 2005). In some studies of parasite–wildlife interactions, experimental manipulations are needed to confirm directional relationships and point to underlying mechanisms (Sánchez et al. 2018). For example, treating wild reindeer with anthelmintics increased their body condition, revealing negative relationships between parasitic load and body mass, fat deposition, and fecundity (Stien et al. 2002).

Anthropogenic factors

Supplementary feeding

In large herbivore management, supplementary feeding is mainly intended to reduce herbivore impact on agriculture, to enhance body condition and reproductive performance, or to supply endangered animals with food or water in crucial periods of their annual life cycle (Kozak et al. 1995; Loarie et al. 2009). However, it is known that supplementary feeding may have negative long-term effects on wildlife populations (Murray et al. 2016), including increasing parasite transmission in wild boar (*Sus scrofa*) (Oja et al. 2017), European

bison (Kołodziej-Sobocińska et al. 2016a, d; Pyziel et al. 2011; Radwan et al. 2010), and other wild mammals (Sorensen et al. 2014). Oja et al. (2017) showed that the effects of supplementary feeding on gastrointestinal parasite infections in wild boar depend on the life cycle of the parasite species, as well as on environmental factors that affect survival and accumulation of oocysts and eggs at feeding sites. An additional effect of supplementary feeding was increased density of wild boar, which promotes the transmission of parasites with a direct life cycle (Oja et al. 2017). An annual survey of parasite eggs and oocyst excretion from European bison dung showed an increase in their prevalence and abundance during winter months, when supplementary feeding is provided (Kołodziej-Sobocińska et al. 2016d; Pyziel et al. 2011). This indicates a strong need to modify management practices in order to scatter herds, increase animal ranges, lower animal densities, and consequently reduce parasite transmission.

Introduction, reintroduction, translocation, and conservation programs

Risk factors for disease emergence in introduction, reintroduction, and conservation programs are complex and often neglected (Cunningham 1996; Scott 1988; Viggers et al. 1993). The translocation of wildlife for conservation, agriculture, and hunting occurs on a global scale, with an inherent risk of wildlife species exposure to exotic infectious agents (Daszak et al. 2000). Diseases are often a real threat to rare and endangered species; thus, the importance of diseases and their impact on reintroduced animals should be taken into account (Viggers et al. 1993). Reduced exposure to natural antigens and loss of immunogenetic variation during captive breeding may impair the survival probability of released animals (Cunningham 1996; Mathews et al. 2006; Viggers et al. 1993). Another issue is the potential transfer of pathogens into previously unexposed wild populations in often sensitive, protected areas (Barrio et al. 2012; Daszak et al. 2000; Kołodziej-Sobocińska et al. 2018b; Vadlejch et al. 2016). For example, the successful introduction of wild alpine marmot (*Marmota marmota*) in the Pyrenees, Iberian Peninsula, Spain, is associated with various threats from this introduced species (Barrio et al. 2012). Alpine marmots are likely to impact Pyrenean grasslands (grazing, burrowing), alter Pyrenean food webs, and act as vectors of parasites and diseases (Barrio et al. 2012). Preliminary studies revealed that the introduced alpine marmots have fewer parasites in the Pyrenees than they have in their native range; however, some of the alpine marmot parasite species were new to the Pyrenees, e.g., *Calodium hepaticum*, *Ctaenotenia marmotae*, *Eimeria marmotae*, and *E. arctomyxi* (Gortázar et al. 1996; Riba and Tena 1999). Thus, the potential transmission of parasites introduced with alpine marmots to other species in the Pyrenees should be considered. Parasites can be also

introduced with translocated captive mammals. Recently, the invasive nematode *A. sidemi* was introduced to the Czech Republic with European bison translocated there from BPF, NE Poland (Vadlejch et al. 2016). In such situations, an effective procedure for animal deworming is necessary to avoid parasite transmission into new territories. On the other hand, treatment of animals prior to release may not be beneficial because it may reduce their levels of immunity to disease (Faria et al. 2010; Viggers et al. 1993). This is especially important if such pathogens are present in wild populations, e.g., regularly dewormed captive mammals may have no chance of acquiring immunity against parasites that they come into contact with upon release. It has been proposed that when there are parasites present in wild populations to which captive animals have not been exposed, it may be advisable to provide low-level exposure in captivity to develop some immunity (Viggers et al. 1993). Moreover, releasing captive-bred animals into the wild can increase their levels of stress, which could make them more susceptible to infection (Dickens et al. 2010). Thus, the pathological effects of infectious agents further debilitate released animals (Viggers et al. 1993; Wakelin 1978).

Zoonoses

Wildlife is now recognized as an important source of emerging human pathogens, including parasites (Daszak et al. 2000; Jones et al. 2008). Among emerging and reemerging infectious agents that people can acquire from wildlife, viruses and bacteria are the subject of intensive study. Unfortunately, much less attention is paid to parasitic diseases (Polley 2005), possibly because their effects are less dramatic, with fewer sudden outbreaks involving substantial human mortality. However, numerous wildlife-derived parasitic diseases of zoonotic potential have recently been of particular interest in Europe, e.g., *Baylisascaris procyonis*, *Echinococcus multilocularis*, *Alaria* spp., *Toxocara* spp., and *Toxoplasma gondii* (see details in Table 2). Among wild hosts for zoonotic parasites, carnivores are identified as the most likely source of human infection (43% of pathogens), with ungulates (39%), rodents (23%), and non-human primates (13%) next in order (Polley 2005). The most common zoonoses transmitted from animals to humans are diseases caused by viruses (Polley 2005). However, among all groups of pathogens (viruses, bacteria, fungi, parasites, etc.), parasitic protozoa are second after viruses in being the primary cause of zoonotic diseases, with helminths also playing a lesser but still formidable role in disease transmission (Polley 2005). The ways in which humans acquire zoonotic parasites are complex. Definitive hosts for parasites such as *Echinococcus multilocularis* shed parasite eggs into the environment; this further leads to a persistent source of infection not only for intermediate hosts like rodents, but also for humans as incidental hosts (Bastien et al.

Table 2 Selected wildlife-derived zoonotic parasitic diseases occurring in Europe with the examples of recent study (since 2000)

Parasite	Wild mammalian host	Localization	References	
Protozoa				
<i>Babesia</i> spp.	Red fox	Austria	Duscher et al. (2017)	
	Brown hare	Italy	Rocchigiani et al. (2018)	
	Red fox	Romania	Daskalaki et al. (2018)	
<i>Toxoplasma gondii</i>	Red fox	Spain	Checa et al. (2018)	
	Red fox	France	Bastien et al. (2018)	
	Wild boar, small rodents	Germany	Beltrán-Beck et al. (2012); Krucken et al. (2017)	
	Wild boar	Italy	Gazzonis et al. (2018)	
	Red fox	Poland	Karbowiak et al. (2010)	
Helminths				
Nematoda				
<i>Baylisascaris procyonis</i>	Raccoon	Austria	Duscher et al. (2017)	
	Raccoon	Germany	Beltrán-Beck et al. (2012); Rentería-Solís et al. (2018a)	
	Raccoon	Poland	Popiolek et al. (2011)	
<i>Dirofilaria</i> spp.	Red fox	Austria	Duscher et al. (2017)	
	Brown bear	Greece	Papadopoulos et al. (2017)	
	Golden jackal, red fox, wildcat, wolf, least weasel	Romania	Ionica et al. (2017)	
	River otter, golden jackal, red fox, wolf, wildcat	Serbia	Penezić et al. (2014, 2018)	
<i>Toxocara</i> spp.	Red fox	Austria	Duscher et al. (2017)	
	Red fox, raccoon dog, wolf	Belarus	Chen et al. (2018); Shimalov and Shimalov (2000, 2002a, 2003)	
	Red fox, raccoon dog	Denmark	Al-Sabi et al. (2014); Chen et al. (2018)	
	Raccoon dog, small rodents	Germany	Krucken et al. (2017); Sutor et al. (2014)	
	Red fox	Great Britain	Chen et al. (2018); Smith et al. (2003)	
	Red fox	Ireland	Chen et al. (2018); Stuart et al. (2013)	
	Red fox, wildcat	Italy	Chen et al. (2018); Magi et al. (2009); Napoli et al. (2016)	
	Raccoon dog	Lithuania	Bružinskaitė-Schmidhalter et al. (2011); Sutor et al. (2014)	
	Lynx, red fox, wolf, pine marten	Poland	Górski et al. (2006); Karamon et al. (2018); Kołodziej-Sobocińska et al. (2018c)	
	Red fox, Iberian wolf	Portugal	Figueiredo et al. (2016)	
	Red fox	Slovenia	Chen et al. (2018); Vergles Rataj et al. (2013)	
	Red fox	Switzerland	Chen et al. (2018); Reperant et al. (2007)	
	<i>Trichinella</i> spp.	Red fox, wild boar	Austria	Duscher et al. (2017)
		Raccoon dog, red fox, stoat, least weasel, river otter, wolf, polecat, American mink	Belarus	Pozio (2000); Shimalov et al. (2000); Shimalov and Shimalov (2000, 2001a, b, 2002a, b, 2003); Sutor et al. (2014)
		Red fox, raccoon dog	Estonia	Karssin et al. (2017)
Raccoon dog		Finland	Oivanen et al. (2002); Sutor et al. (2014)	
Raccoon dog		Germany	Pannwitz et al. (2010); Sutor et al. (2014)	
Wild boar		Italy	Garbarino et al. (2017)	
Red fox, raccoon dog		Lithuania	Bružinskaitė-Schmidhalter et al. (2011)	
Raccoon, wolf, American mink, wild boar, lynx		Poland	Bień et al. (2016); Bilska-Zajac et al. (2017); Humíková et al. (2016); Cybulska et al. (2018); Kołodziej-Sobocińska et al. (2018c)	
Raccoon dog		Russia	Pozio (2000); Sutor et al. (2014)	
Red fox, golden jackal		Serbia	Dmitric et al. (2017)	

Table 2 (continued)

Parasite	Wild mammalian host	Localization	References
Trematoda			
<i>Alaria</i> spp.	Wild boar, red fox	Austria	Duscher et al. (2017)
	Raccoon dog, red fox, stoat, least weasel, river otter, wolf, striped field mouse, polecat, American mink, European mole, water shrew	Belarus	Sutor et al. (2014); Shimalov (2002, 2017); Shimalov and Shimalov (2000, 2001a, 2001b, 2001c, 2002a, 2002b, 2003); Shimalov et al. (2000)
	Raccoon, raccoon dog	Germany	Rentería-Solís et al. (2013); Sutor et al. (2014)
	Wild boar	Italy	Gazzonis et al. (2018)
	Red fox, raccoon dog	Lithuania	Bružinskaitė-Schmidhalter et al. (2011)
	Wild boar, badger, red fox, river otter, wolf, American mink, lynx	Poland	Górski et al. (2006); Karamon et al. (2018); Rentería-Solís et al. (2018b); Szczęśna et al. (2008)
	European mink	Romania	Tăbăran et al. (2013)
Cestoda			
<i>Echinococcus multilocularis</i>	Red fox, rodents	Austria	Duscher et al. (2017)
	Red fox	Belarus	Shimalov and Shimalov (2003)
	Red fox	France	Bastien et al. (2018)
	Raccoon dog	Germany	Sutor et al. (2014)
	Red fox, raccoon dog	Latvia	Bagrade et al. (2016); Sutor et al. (2014)
	Red fox, raccoon dog	Lithuania	Bružinskaitė-Schmidhalter et al. (2011)
	Red fox, raccoon dog	Poland	Karamon et al. (2014); Nahorski et al. (2013); Machnicka-Rowińska et al. (2002)
	Red fox, wolf	Slovakia	Antolova et al. (2009, 2014); Martínek et al. (2001)
Red fox	Switzerland	Reperant et al. (2007)	
<i>Spirometra</i> sp.	European mink, American mink, river otter, raccoon dog, stoat, least weasel, red fox, wolf, polecat, European mole	Belarus	Anisimova (2004); Shimalov and Shimalov (2000, 2001a, 2001b, 2001c, 2002a, 2002b, 2003); Shimalov et al. (2000)
	European hedgehog, stone marten, polecat, brown rat	Italy	Pampiglione et al. (2003)
	Badger, wild boar, lynx	Poland	Kołodziej-Sobocińska et al. (2014a, 2016c, 2018c); Szczęśna et al. (2008)

Latin names of mammal species used in alphabetical order: American mink (*Neovison vison*), badger (*Meles meles*), brown bear (*Ursus arctos*), brown hare (*Lepus europeus*), brown rat (*Mus decumanus*), European hedgehog (*Erinaceus europeus*), European mink (*Mustela lutreola*), European mole (*Talpa europaea*), golden jackal (*Canis aureus*), Iberian wolf (*Canis lupus signatus*), least weasel (*Mustela nivalis*), lynx (*Lynx lynx*), pine marten (*Martes martes*), polecat (*Mustela putorius*), raccoon (*Procyon lotor*), raccoon dog (*Nyctereutes procyonoides*), red fox (*Vulpes vulpes*), river otter (*Lutra lutra*), stoat (*Mustela erminea*), stone marten (*Martes foina*), striped field mouse (*Apodemus agrarius*), water shrew (*Neomys fodiens spennant*), wild boar (*Sus scrofa*), wildcat (*Felis silvestris*), wolf (*Canis lupus*)

2018; Karamon et al. 2014; Lempp et al. 2017). Some parasites settle in the muscle tissue of hosts, e.g., *Alaria* spp., *Trichinella* spp., *Spirometra* sp., and *Toxoplasma* spp.; thus, they can be ingested by humans eating raw or inadequately cooked meat (Dmitric et al. 2018; Gazzonis et al. 2018; Kołodziej-Sobocińska et al. 2016c). It is important to carry out parasitological monitoring of wild animals, especially those that are hunted or live near human settlements, and therefore have the potential to become a threat to humans. For parasites acquired from food obtained from wild animals, the ability to accurately predict risk of infection is also influenced by cultural traditions for food preparation that may affect parasite viability (Polley 2005). Unfortunately, there is an absence of adequately detailed data on key aspects of the ecology of many zoonotic parasites in wildlife; therefore, only

general predictions of risk of human infection are possible. The importance of public education for prevention and control of human infections is neglected, which often leads to new outbreaks of zoonotic parasitic diseases acquired from wildlife, especially in poorly developed countries.

Human activity may be important for opening both encounter and compatibility filters by many ways: changing ecosystems (climate change, urbanization), providing additional resources (supplementary feeding, pastures), changing host behavior (destruction of habitats, translocations), changing the level of host defense (stress, emerging diseases), and others. Not only “natural” factors shape the host–parasite associations in wildlife. Human impact plays an important, and often negative, role in wild populations also through opening “natural filters” that normally control parasite transmission in natural conditions.

Conclusions

Herein, I have summarized the current state of knowledge about factors that affect dynamics and spread of parasites in populations of wild terrestrial mammals in Europe. These factors form a complex network of interdependencies that influence host–parasite coexistence (see Fig. 1). It should be emphasized that human activity and natural factors are very important. I hope that this review paper allowed for a better understanding of parasitic disease persistence in wildlife and indicates the need to further develop knowledge on this topic, not only for academic reasons, but also for the benefit of use in the management of wild mammal species and disease control in nature.

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