



The role of wildlife in the epidemiology of tick-borne diseases in Slovakia

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ABSTRACT

Tick-borne diseases (TBD) represent an important challenge for human and veterinary medicine. In Slovakia, studies on the epidemiology of tick-borne pathogens (TBP) regarding reservoir hosts have focused on small mammals and to a lesser extent on birds or lizards, while knowledge of the role of the remaining vertebrate groups is limited. Generally, wild ungulates, hedgehogs, small- and medium-sized carnivores, or squirrels are important feeding hosts for ticks and serve as reservoirs for TBP. Importantly, because they carry infected ticks and/or are serologically positive, they can be used as sentinels to monitor the presence of ticks and TBP in the environment. With their increasing occurrence in urban and suburban habitats, wild ungulates, hedgehogs or foxes are becoming an important component in the developmental cycle of *Ixodes ricinus* and of TBP such as *Anaplasma phagocytophilum* or *Babesia* spp. On the other hand, it has been postulated that cervids may act as dilution hosts for *Borrelia burgdorferi* (*sensu lato*) and tick-borne encephalitis virus. In southwestern Slovakia, a high prevalence of infection with *Theileria* spp. (100%) was observed in some cervid populations, while *A. phagocytophilum* (prevalence of c.50%) was detected in cervids and wild boars. The following pathogens were detected in ticks feeding on free-ranging ungulates, birds, and hedgehogs: *A. phagocytophilum*, *Rickettsia* spp., *Coxiella burnetii*, *Neohelminthospora mikurensis*, *B. burgdorferi* (*s.l.*), and *Babesia* spp. The growing understanding of the role of wildlife as pathogen reservoirs and carriers of pathogen-infected ticks offers valuable insights into the epidemiology of TBP, providing a foundation for reducing the risk of TBD.

1. Introduction

Among arthropod vectors, ticks transmit the most diverse spectrum of disease agents. The occurrence of tick-borne diseases (TBD) is increasing globally, including in Slovakia, which represents a considerable threat to public health and veterinary medicine. During the course of evolution, ticks and tick-borne pathogens (TBP) have co-evolved with wildlife. Vertebrates serve as the obligate blood meal for ticks, and some species are also involved in the maintenance of endemic cycles as reservoir and/or amplifying hosts of TBP (Michelitsch et al., 2019; Pustijanac et al., 2024). Vertebrates possess the requisite characteristics to serve as sentinels for the monitoring of the occurrence of common and exotic tick species (Hubálek et al., 2020), as well as the risk of TBD in the corresponding environment (Springer et al., 2020; Pfeffer

et al., 2023). The distribution areas of wildlife, ticks and pathogens they carry are undergoing significant changes due to global climate change and other anthropogenic impacts such as urbanization, habitat fragmentation, changing land-use patterns, animal trade and travel. These changes are extending the seasonal activities of ticks (Nuttall, 2022). The increasing frequency of encounters between wildlife and domestic animals in green urban zones represents a potential risk of elevated contact rates between humans and infected ticks (Rizzoli et al., 2014). Furthermore, synanthropic, introduced and stray animals as well as companion and farm animals may become integral components of the developmental cycles of ticks and TBP. It is noteworthy that, together with humans, which represent incidental and dead-end hosts, they may be used as sentinel hosts for TBP. The epidemiology of TBD is highly complex and the emergence and spread of TBP depend on a number of

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factors, including climate, vegetation cover, the developmental cycle, host spectrum and vector competence of ticks, on the structure of the vertebrate host community, and on the reservoir competence and capacity of vertebrate hosts (Estrada-Peña and Fernández-Ruiz, 2023). Consequently, the identification of vector ticks, reservoir hosts and circulating pathogens, along with their interrelationships in natural and green urban environments is a prerequisite for TBD risk management.

The objective of this review is to provide a concise overview of the most important and emerging TBPs in Slovakia from a One Health perspective and to identify knowledge gaps regarding the involvement of wildlife in their endemic cycles.

2. Tick borne pathogens, vectors, reservoir hosts and knowledge gaps

The epidemiological knowledge of TBD in Slovakia is comparable to that of other Central European countries (Stanko et al., 2022). The generalist tick *Ixodes ricinus* infests many mammalian, avian and reptilian species and is the main vector of TBP such as tick-borne encephalitis virus (TBEV), *Borrelia burgdorferi* (s.l.), *Borrelia miyamotoi*, *Anaplasma phagocytophilum*, *Neorhlichia mikurensis*, *Rickettsia helvetica*, *Rickettsia monacensis*, *Babesia microti*, and *Babesia venatorum*. Other epidemiologically important tick species include *Dermacentor reticulatus*, *Dermacentor marginatus*, *Haemaphysalis concinna* and *Haemaphysalis inermis* (Stanko et al., 2022). In recent decades, considerable knowledge has been gained on the presence, prevalence, and genetic diversity of TBP in questing ticks in various habitat types, and a wide spectrum of common and emerging TBP have been detected in ticks from wildlife and domestic animals. However, research has focused mainly on the reservoir role of small rodents (mice, voles) and to a lesser extent on birds and lizards (see Table 1; Fig. 1). There is a paucity of knowledge regarding the reservoir role of other vertebrate groups, including free-ranging ungulates, hedgehogs, small- and medium-sized carnivores and squirrels. These animals frequently migrate to urban and suburban green areas, serve as important feeding hosts for ticks, and have been identified as reservoirs for diverse TBP (Rizzoli et al., 2014, Table 1).

Tick-borne encephalitis virus (TBEV) (genus *Orthoflavivirus*, family *Flaviviridae*) is the etiological agent of tick-borne encephalitis (TBE), a viral disease of the central nervous system. TBE is endemic in temperate regions of Europe and northeastern Asia and has become a growing public health challenge in Europe as the number of human TBE cases in endemic regions has increased and the risk areas have expanded northward and westward (Ruzek et al., 2019; Van Heuverswyn et al., 2023). Several longitudinal studies have intensively investigated foci of TBE in Slovakia, and identified small rodents as the main reservoirs of TBEV (Stanko et al., 2022). Cervids have been suggested as dilution hosts (Cagnacci et al., 2012) and serve as sentinels for the occurrence of TBE (Labuda et al., 2002). In addition to small rodents, presence of the virus has been detected in other vertebrates such as common buzzard, shrew, dormouse, hedgehog, and bat (Table 1). Antibodies against TBEV have been found in several wild animals (birds, small mammals, deer, mouflons) as well as in livestock (sheep, horses) (Table 1). The number of confirmed TBE cases in Slovakia has increased steadily over the last decade, with a considerable proportion of alimentary infections (EPIS, 2006; Kerlik, 2023). New foci of TBE have been identified, but comprehensive studies analysing the emergence and maintenance of foci of TBE in rural areas with agricultural farms are lacking.

Lyme borreliosis is a multisystemic disorder with a wide range of clinical manifestations. It is caused by spirochaetes of the *B. burgdorferi* (s.l.) complex and is the most significant TBD in Europe (Steinbrink et al., 2022) and in Slovakia, as evidenced by the country's national epidemiologic surveillance system (EPIS, 2006). The disease is distributed across all habitats where *I. ricinus* is present. The prevalence and diversity of species of the *B. burgdorferi* (s.l.) complex in questing ticks and their associations with different reservoir hosts are relatively well-documented (Stanko et al., 2022; Kazimírová et al., 2023). Small

wild rodents have been identified as reservoirs for *Borrelia afzelii* and *Borrelia bavariensis*, songbirds (mainly blackbirds and thrushes) as reservoirs for *Borrelia garinii* and *Borrelia valaisiana*, and lizards as reservoirs for *Borrelia lusitaniae*. However, reservoirs for the remaining species such as *Borrelia spielmanii*, *Borrelia burgdorferi* (sensu stricto) or *Borrelia kurtenbachii* need to be confirmed (Table 1). Serosurveys have demonstrated the presence of *Borrelia* antibodies in wild animals including pheasant, rock dove, small rodents, fallow deer, and mouflon, as well as domestic animals such as dogs and cattle. Additionally, *Borrelia*-infected ticks have been recovered from a diverse range of wildlife and domestic animals including lizards, birds, and mammals (Table 1). To date, there is only a single piece of evidence indicating the potential role of roe deer in the dilution of *Borrelia* spp. in a green urban area (Chvostáč et al., 2018).

Borrelia miyamotoi is a relapsing fever spirochete transmitted by *Ixodes* spp. It is an emerging TBP in the northern hemisphere and is the causative agent of *Borrelia miyamotoi* disease (Cleveland et al., 2023). The presence of *B. miyamotoi* disease in humans has not yet been confirmed in Slovakia. However, the pathogen may pose a potential risk to public health as its presence has been confirmed in questing *I. ricinus* and wild rodents from natural and green urban habitats (Hamsíková et al., 2017; Heglasová et al., 2020a). Small rodents are considered to play a role in the endemic cycle of *B. miyamotoi*, but involvement of other vertebrate groups in its circulation cannot be ruled out.

Tularemia is a disease with a complex epidemiology that remains poorly understood (Hestvik et al., 2015). *Francisella tularensis* (Gammaproteobacteria, Thiotrichales) is the causative agent and is widely distributed in the northern hemisphere. Transmission to humans occurs not only through ticks, but also through contact with infected animals, contaminated environments, and other ectoparasitic arthropods. In Slovakia, long-term monitoring of endemic foci of tularemia has been carried out in the past and small rodents and lagomorphs have been identified as the main reservoirs, but the bacterium has also been isolated, e.g. from shrews, hamsters, or mustelids (Guryčová and Letkovský, 1973; Guryčová et al., 1982; Kožuch et al., 1995; Stanko et al., 2022). In recent years, no outbreaks of tularemia have been registered in Slovakia (EPIS, 2006), and current information on the maintenance of its natural foci is scarce.

Rickettsioses caused by the spotted fever group (SFG) rickettsiae (gram-negative obligate intracellular bacteria of the genus *Rickettsia* in the order Rickettsiales), are transmitted by hard ticks and mites and pose a significant threat to public health worldwide (Zhang et al., 2023). Despite the low number of confirmed human cases in Slovakia, the disease remains a significant concern (Špitálská et al., 2022). Due to vertical transmission, ticks (*I. ricinus*, *D. reticulatus*, *D. marginatus*) are considered both vectors and reservoirs of SFG rickettsiae. The presence of rickettsial specific DNA has been identified in questing and host-feeding ticks as well as other ectoparasites (mites, fleas), and in the blood and tissues of several vertebrate species including small rodents, roe deer, and wild boars (Table 1). Antibodies against rickettsiae have been detected, e.g. in rodents, red deer, roe deer, wild boars, and hares (Table 1). However, the reservoir role for rickettsiae has not been reliably confirmed for any of these vertebrate species, although some of them may be temporarily involved in endemic cycles of the bacteria.

Coxiella burnetii (Coxiellaceae) is an obligate intracellular gram-negative bacterium and the etiologic agent of Q fever in humans and coxiellosis in animals (Celina and Černý, 2022). *Coxiella burnetii* has a wide and diverse host range and tick-to-host transmission is only one of the several potential routes of pathogen transmission. In recent decades, only a few cases of Q fever have been recorded in Slovakia (EPIS, 2006).

The presence of pathogenic species such as *Rickettsia helvetica*, *R. monacensis*, *R. raoultii*, and *C. burnetii* has been reported in ticks feeding on free-ranging ungulates and birds (Table 1), which serve as carriers of infected ticks and contribute to their dissemination and geographical spread.

Anaplasma phagocytophilum (Rickettsiales, Anaplasmataceae) is an

Table 1

Detection of tick-borne pathogens in animals and feeding ticks and of antibodies against tick-borne pathogens in Slovakia.

Vertebrate group/species	Pathogen	Detected	Confirmed reservoir	Positive serology	Positive ticks/ectoparasites	Reference
Reptiles						
<i>Lacerta viridis</i>	<i>Borrelia lusitaniae</i>	✓	✓		✓ (<i>I. ricinus</i>)	Majláthová et al. (2006)
<i>Lacerta agilis</i>	<i>Borrelia lusitaniae</i>	✓	✓		✓ (<i>I. ricinus</i>)	Majláthová et al. (2008)
<i>Lacerta viridis</i>	“ <i>Candidatus</i> Cryptoplasma”				✓ (<i>I. ricinus</i>)	Kočíková et al. (2018)
<i>Lacerta</i> spp.	<i>Anaplasma phagocytophilum</i> , <i>Borrelia lusitaniae</i> , <i>Rickettsia helvetica</i>				✓ (<i>I. ricinus</i>)	Václav et al. (2011)
<i>Lacerta viridis</i> , <i>Podacris muralis</i>	<i>Anaplasma phagocytophilum</i> , <i>Borrelia lusitaniae</i> , <i>Rickettsia</i> sp.				✓ (<i>I. ricinus</i>)	Didyk et al. (2024b)
Birds						
Anseriformes	TBEV			✓		Ernek et al. (1977)
<i>Buteo buteo</i>	TBEV	✓				Csank et al. (2016)
<i>Sylvia atricapilla</i>	TBEV			✓		Csank et al. (2019)
<i>Turdus merula</i> , <i>Sturnus vulgaris</i> , <i>Parus major</i>	Tribeč virus			✓		Peňaziová et al. (2022)
Birds	<i>Babesia</i> sp.				✓ (bird louse fly)	Čisovská Bazsalovicsová et al. (2023)
<i>Parus major</i>	<i>Coxiella burnetii</i> , <i>Rickettsia helvetica</i>	✓			✓ (<i>I. ricinus</i>)	Berthová et al. (2016)
<i>Erithacus rubecula</i>	<i>Rickettsia</i> spp.				✓ (<i>I. ricinus</i>)	Špitalská et al. (2006)
<i>Turdus philomelos</i>	Ehrlichia-like species “Schotti variant”				✓ (<i>I. ricinus</i>)	Špitalská et al. (2006)
Passeriformes, Turdidae	<i>Borrelia garinii</i>	✓	✓		✓	Taragelová et al. (2008)
Passeriformes	<i>Borrelia burgdorferi</i> (s.l.), <i>Rickettsia helvetica</i>				✓ (<i>I. ricinus</i>)	Chvostáč et al. (2018)
	“ <i>Candidatus</i> <i>Rickettsia vini</i> ”				✓ (<i>I. arboricola</i>)	Novakova et al. (2015)
	<i>Borrelia garinii</i>				✓ (<i>I. ricinus</i>)	Mtierová et al. (2020)
	<i>Borrelia garinii</i> , <i>B. valaisiana</i>	✓	✓		✓ (<i>I. ricinus</i>)	Hanincová et al. (2003)
	<i>Borrelia garinii</i> , <i>B. valaisiana</i>				✓ (<i>I. ricinus</i>)	Šujanová et al. (2023)
	<i>Borrelia garinii</i>	✓				Gronesova et al. (2008)
<i>Phalacrocorax carbo sinensis</i>	<i>Anaplasma phagocytophilum</i>	✓				Víchová et al. (2016b)
<i>Phasianus colchicus</i>	<i>Borrelia burgdorferi</i> (s.l.)			✓		Nadzamová et al. (2000)
<i>Columba livia</i>	<i>Borrelia burgdorferi</i> (s.l.)			✓		Nadzamová et al. (2000)
Mammals						
Small rodents (mice, voles)	TBEV	✓	✓		✓	Kožuch et al. (1967)
	TBEV	✓				Rosický and Bárdoš (1966)
	TBEV	✓		✓		Kožuch et al. (1990)
	TBEV	✓		✓		Kožuch et al. (1995)
	TBEV	✓				Cagnacci et al. (2012); Frey et al. (2014)
	<i>Anaplasma phagocytophilum</i> , <i>Borrelia burgdorferi</i> (s.l.)	✓		✓		Štefančíková et al. (2008a)
	<i>Borrelia burgdorferi</i> (s.l.)				✓	Štefančíková et al. (2008b)
	<i>Borrelia burgdorferi</i> (s.l.)				✓	Trávníček et al. (2003)
	<i>Borrelia afzelii</i>	✓	✓		✓ (<i>I. ricinus</i>)	Hanincová et al. (2003a)
	<i>Borrelia afzelii</i> , <i>B. myiamotoi</i>	✓	✓		✓ (<i>I. ricinus</i>)	Hamsíková et al. (2017)
	<i>Borrelia myiamotoi</i>	✓			✓ (<i>I. ricinus</i> , <i>H. inermis</i>)	Heglasová et al. (2020a)
	<i>Anaplasma phagocytophilum</i>	✓				Víchová et al. (2014)
	<i>Anaplasma phagocytophilum</i>	✓	✓		✓ (<i>I. trianguliceps</i>)	Blaňarová et al. (2014)
	<i>Anaplasma phagocytophilum</i>	✓			✓ (<i>I. ricinus</i>)	Svitálková et al. (2015)
	<i>Neohrlichia mikurensis</i>	✓	✓		✓ <i>I. ricinus</i>	Hamsíková Svitálková et al. (2016)
	<i>Neohrlichia mikurensis</i>	✓			✓ (<i>I. ricinus</i> , <i>I. trianguliceps</i>)	Blaňarová et al. (2016)
	<i>Coxiella burnetii</i> , <i>Rickettsia</i> spp.			✓		Řeháček et al. (1976)
	<i>Coxiella burnetii</i> , <i>Rickettsia</i> spp.	✓		✓		Špitalská et al. (2002)
	<i>Rickettsia helvetica</i> , <i>R. monacensis</i>				✓ (<i>I. ricinus</i>)	Minichová et al. (2017)
	<i>Rickettsia helvetica</i> , <i>Rickettsia slovacica</i> , <i>Rickettsia felis</i> -like	✓				Heglasová et al. (2018)
	<i>Rickettsia felis</i> , <i>R. helvetica</i> , <i>Rickettsia</i> sp.				✓ (fleas)	Heglasová et al. (2020b)
	<i>Rickettsia felis</i> , <i>R. helvetica</i> , <i>Rickettsia</i> sp., <i>Rickettsia</i> endosymbionts				✓ (fleas)	Špitalská et al. (2015)
	<i>Rickettsia helvetica</i> , <i>R. slovacica</i> , <i>Rickettsia</i> sp., <i>Rickettsia</i> endosymbionts	✓			✓ (<i>I. ricinus</i> , mites, fleas)	Špitalská et al. (2020)
	<i>Babesia</i> sp., <i>Hepatozoon</i> sp., <i>Rickettsia</i> spp.				✓ (fleas)	Špitalská et al. (2022)
	<i>Rickettsia helvetica</i>	✓				Nováková et al. (2022)
	<i>Francisella tularensis</i>	✓	✓			Guryčová and Letkovský (1973); Guryčová et al. (1982); Kožuch et al. (1995); Guryčová (1998)
	<i>Borrelia burgdorferi</i> (s.l.), <i>Francisella tularensis</i>	✓				Výrosteková et al. (2002)
	SFG rickettsiae			✓		Řeháček et al. (1972)
	<i>Babesia microti</i>	✓	✓		✓ (<i>I. ricinus</i> , <i>I. trianguliceps</i>)	Hamsíková et al. (2016a); Blaňarová et al. (2016)
	<i>Hepatozoon</i> spp.	✓	✓			Hamsíková et al. (2016b)

(continued on next page)

Table 1 (continued)

Vertebrate group/species	Pathogen	Detected	Confirmed reservoir	Positive serology	Positive ticks/ectoparasites	Reference
<i>Cricetus cricetus</i>	<i>Francisella tularensis</i>	✓	✓			Guryčová and Letkovský (1973)
<i>Sciurus vulgaris</i>	TBEV				✓	Kožuch et al. (1967)
Dormice	TBEV	✓				Kožuch et al. (1963); Nosek and Grulich (1967)
<i>Crocidura leucodon</i>	TBEV	✓				Nosek and Grulich (1967)
<i>Sorex</i> spp.	TBEV	✓	✓			Rosický and Bárdoš (1966); Nosek and Grulich (1967); Kožuch et al. (1990)
	<i>Francisella tularensis</i>	✓	✓			Guryčová and Letkovský (1973); Guryčová et al. (1982)
<i>Talpa europaea</i>	TBEV	✓	✓			Nosek and Grulich (1967)
<i>Talpa europaea</i> (nests)	TBEV				✓ (mites, fleas)	Kocianová and Kožuch (1988)
<i>Erinaceus roumanicus</i>	TBEV	✓	✓		✓	Kožuch et al. (1963, 1967)
<i>Erinaceus roumanicus</i>	<i>Anaplasma phagocytophilum</i> , <i>Babesia capreoli</i> , <i>B. venatorum</i> , <i>Borrelia afzelii</i> , <i>B. bavariensis</i> , <i>B. spielmanni</i> , <i>B. lusitaniae</i> , <i>B. myiamotoi</i> , <i>Rickettsia helvetica</i>				✓ (<i>I. ricinus</i>)	Didyk et al. (2024a)
<i>Lepus europaeus</i>	SFG rickettsiae			✓		Řeháček et al. (1972)
	<i>Francisella tularensis</i>	✓	✓			Guryčová and Letkovský (1973)
Chiroptera	TBEV	✓				Nosek et al. (1961)
<i>Meles meles</i>	<i>Babesia</i> sp. Badger	✓				Purgatová et al. (2023)
<i>Vulpes vulpes</i>	<i>Anaplasma phagocytophilum</i> , Hepatozoon <i>canis</i> , <i>Rickettsia</i> spp., <i>Theileria</i> sp.				✓ (<i>I. ricinus</i> , <i>I. hexagonus</i> , <i>H. concinna</i>)	Vířhová et al. (2018)
	<i>Hepatozoon canis</i>	✓				Majláthová et al. (2007); Miterpáková et al. (2017)
	<i>Babesia vulpes</i>	✓				Koneval et al. (2017)
<i>Ursus arctos</i>	<i>Anaplasma phagocytophilum</i>	✓				Vířhová et al. (2010)
Cervidae, <i>Sus scrofa</i> , <i>Ovis musimon</i>	TBEV			✓		Labuda et al. (2002)
<i>Capreolus capreolus</i> , <i>Cervus elaphus</i> , <i>Sus scrofa</i>	SFG rickettsiae			✓		Řeháček et al. (1972)
<i>Dama dama</i>	<i>Borrelia burgdorferi</i> (s.l.)			✓		Nadzamová et al. (2000)
<i>Ovis musimon</i>	<i>Borrelia burgdorferi</i> (s.l.)			✓		Nadzamová et al. (2000)
<i>Dama dama</i> , <i>Ovis aries musimon</i>	<i>Borrelia burgdorferi</i> (s.l.)			✓		Trávníček et al. (2003); Bhide et al. (2004)
<i>Capreolus capreolus</i> , <i>Cervus elaphus</i> , <i>Ovis musimon</i>	<i>Anaplasma phagocytophilum</i>	✓				Stefanidesova et al. (2008)
<i>Capreolus capreolus</i> , <i>Cervus elaphus</i> , <i>Sus scrofa</i>	<i>Anaplasma phagocytophilum</i>	✓				Smetanová et al. (2006); Štefanidesová et al. (2016)
<i>Capreolus capreolus</i>	<i>Anaplasma phagocytophilum</i>				✓ (deer ked <i>Lipoptena cervi</i>)	Vířhová et al. (2011)
<i>Capreolus capreolus</i> , <i>Cervus elaphus</i> , <i>Dama dama</i> , <i>Sus scrofa</i>	<i>Anaplasma phagocytophilum</i>	✓				Vířhová et al. (2014)
<i>Capreolus capreolus</i>	<i>Rickettsia helvetica</i>	✓				Stefanidesova et al. (2008)
<i>Sus scrofa</i>	<i>Anaplasma phagocytophilum</i>	✓				Štefanidesová et al. (2011)
<i>Sus scrofa</i>	<i>Anaplasma phagocytophilum</i>	✓				Reiterová et al. (2016)
<i>Sus scrofa</i>	<i>Rickettsia helvetica</i>	✓				Nováková et al. (2022)
<i>Ovis aries musimon</i> , <i>D. dama</i>	TBEV, <i>Borrelia</i> , <i>Francisella</i>			✓		Trávníček et al. (1999)
<i>Capreolus capreolus</i> , <i>Cervus elaphus</i>	<i>Anaplasma phagocytophilum</i>	✓				Štefanidesová et al. (2011)
<i>Capreolus capreolus</i> , <i>Cervus elaphus</i> , <i>Dama dama</i> , <i>Sus scrofa</i> , <i>Ovis aries musimon</i>	<i>Anaplasma phagocytophilum</i>	✓	✓		✓ (<i>I. ricinus</i> , <i>H. concinna</i>)	Kazimířová et al. (2018)
<i>Cervus elaphus</i>	<i>Theileria</i> sp.	✓				Černý (1958)
<i>Capreolus capreolus</i> , <i>Cervus elaphus</i> , <i>Dama dama</i>	<i>Theileria</i> spp.	✓	✓		✓ (<i>I. ricinus</i> , <i>H. concinna</i>)	Kazimířová et al. (2018)
<i>Capreolus capreolus</i> , <i>Cervus elaphus</i> , <i>Dama dama</i>	<i>Borrelia burgdorferi</i> (s.l.), <i>B. venatorum</i> , <i>Coxiella burnetii</i> , <i>Neoehrlichia mikurensis</i> , <i>Rickettsia helvetica</i> , <i>R. monacensis</i> , <i>Rickettsia</i> sp.				✓ (<i>I. ricinus</i>)	Kazimířová et al. (2018)
<i>Capreolus capreolus</i> , <i>Cervus elaphus</i> , <i>Dama dama</i>	<i>Babesia motasi</i> , <i>Babesia</i> spp.				✓ (<i>H. concinna</i>)	Kazimířová et al. (2018)
<i>Sus scrofa</i>	<i>Babesia crassa</i> , <i>Babesia</i> spp.				✓ (<i>H. concinna</i>)	Kazimířová et al. (2022)
<i>Rupicapra rupicapra</i>	<i>Anaplasma phagocytophilum</i>	✓				Vířhová et al. (2014)
Companion animals						
Dog, <i>Canis lupus familiaris</i>	<i>Borrelia burgdorferi</i> (s.l.)			✓		Čabanová et al. (2015); Bhide et al. (2004); Štefančířková et al. (2008b)
	<i>Babesia canis</i>	✓	✓			Chandoga et al. (2002); Řeháček et al. (2016)
	<i>Babesia canis</i>	✓			✓ (<i>D. reticulatus</i>)	Majláthová et al. (2011)
	<i>Babesia gibsoni</i>	✓				Vířhová et al. (2016a)
	<i>Hepatozoon canis</i>	✓				Miterpáková et al. (2017)

(continued on next page)

Table 1 (continued)

Vertebrate group/species	Pathogen	Detected	Confirmed reservoir	Positive serology	Positive ticks/ectoparasites	Reference
Livestock Sheep	<i>Anaplasma phagocytophilum</i>	✓				Majláthová et al. (2011); Víchová et al. (2014)
	<i>Anaplasma phagocytophilum</i>			✓		Cabanová et al. (2015)
	TBEV			✓		Hubálek et al. (1985)
	<i>Borrelia burgdorferi</i> (s.l.)			✓		Štefančíková et al. (2008b)
	<i>Anaplasma phagocytophilum</i>			✓		Čobádiová et al. (2013)
Sheep, goats	<i>Anaplasma phagocytophilum</i>	✓				Víchová et al. (2014)
	<i>Anaplasma phagocytophilum</i>	✓			✓ (<i>I. ricinus</i>)	Derdáková et al. (2011)
	TBEV			✓		Ministry of Agriculture and Rural Development of the Slovak Republic (2020)
Goats	<i>Anaplasma ovis</i>	✓				Derdáková et al. (2011)
	<i>Anaplasma ovis</i>	✓				Víchová et al. (2014)
	<i>Borrelia burgdorferi</i> (s.l.)			✓		Štefančíková et al. (2008b)
Cattle, goats	TBEV			✓		Ernek et al. (1967)
Cattle	<i>Borrelia burgdorferi</i> (s.l.)			✓		Štefančíková et al. (2002, 2008b)
Horses	TBEV			✓		Csank et al. (2018)
	<i>Borrelia burgdorferi</i> (s.l.)			✓		Štefančíková et al. (2008b)
	<i>Anaplasma phagocytophilum</i>	✓				Slivinska et al. (2016)
	<i>Anaplasma phagocytophilum</i>			✓		Drážovská et al. (2021)
	<i>Coxiella burnetii</i>			✓		Drážovská et al. (2022)

Notes: Information for TBEV, rickettsiae, *F. tularensis* and *C. burnetii* is not exhaustive, as not all sources from the 1960s–1980s, monographs, conference proceedings, and publications in Slovak language are available in public databases. ✓ indicates detected, confirmed.

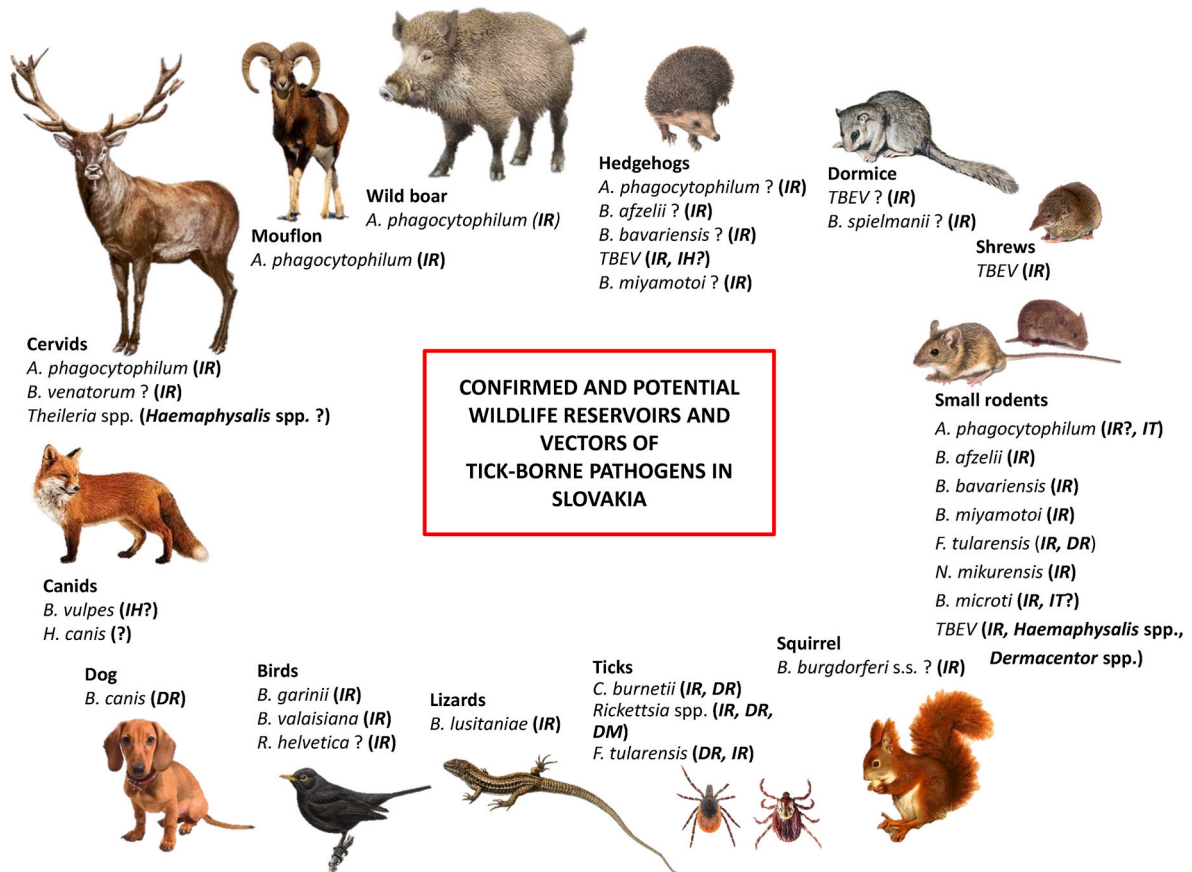


Fig. 1. Confirmed and potential wildlife reservoirs and vectors of tick-borne pathogens in Slovakia. Abbreviations: IR, *Ixodes ricinus*; IH, *Ixodes hexagonus*; IT, *Ixodes trianguliceps*; HC, *Haemaphysalis concinna*; DR, *Derma-centor reticulatus*; DM, *Derma-centor marginatus*; TBEV, tick-borne encephalitis virus; *B. burgdorferi* (s.s.), *Borrelia burgdorferi* (sensu stricto); *B. afzelii*, *Borrelia afzelii*; *B. bavariensis*, *Borrelia bavariensis*; *B. lusitaniae*, *Borrelia lusitaniae*; *B. spielmanii*, *Borrelia spielmanii*; *B. garinii*, *Borrelia garinii*; *B. valaisiana*, *Borrelia valaisiana*; *B. miyamotoi*, *Borrelia miyamotoi*; *A. phagocytophilum*, *Anaplasma phagocytophilum*; *N. mikurensis*, *Neoehrlichia mikurensis*; *R. helvetica*, *Rickettsia helvetica*; *C. burnetii*, *Coxiella burnetii*; *F. tularensis*, *Francisella tularensis*; *B. venatorum*, *Babesia venatorum*; *B. microti*, *Babesia microti*; *B. vulpes*, *Babesia vulpes*; *B. canis*, *Babesia canis*; *H. canis*, *Hepatozoon canis*; ?, potential reservoir or vector.

obligate intracellular alpha-proteobacterium with several genetic variants (ecotypes) occurring in Europe. These variants are associated with a diversity of reservoir hosts and exhibit varying pathogenicity to domestic animals and humans (Stuenkel et al., 2013). In Slovakia, a variety of genetic variants of *A. phagocytophilum* has been identified in wildlife species, including rodents, roe deer, fallow deer, red deer, wild boars, mouflons, chamois, brown bears, and ticks (mainly *I. ricinus*) feeding on lizards, birds, small mammals, hedgehogs, and free-ranging ungulates. Additionally, infections with the pathogen have been confirmed in dogs, sheep, and horses (Table 1). Serosurveys have revealed the presence of antibodies against *A. phagocytophilum* antigens in small rodents, dogs, goats, and horses (Table 1). A distinct *A. phagocytophilum* variant has been found to circulate between the endophilic *Ixodes trianguliceps* tick and small rodents (Blařarová et al., 2014). *Ixodes ricinus* is the vector for most of the genetic variants of the bacterium. In certain regions of Slovakia, more than 50% of cervids and wild boars have been found to be infected with *A. phagocytophilum* (Kazimířová et al., 2018, 2022; Purgatová et al., 2024). The variant associated with roe deer is unlikely to be pathogenic to humans and domestic animals. In contrast, red deer are thought to be a reservoir for variants pathogenic to domestic ruminants and horses. Hamšířková et al. (2019) found that the presence of roe deer at a site affected the diversity of *A. phagocytophilum* variants in questing *I. ricinus*, with a shift to the non-pathogenic variant associated with roe deer. Notably, the 16S rRNA and *groEL* gene sequences of the variant isolated from wild boar showed identity with the causative agent of human granulocytic anaplasmosis (HGA) (Kazimířová et al., 2018). However, to date only three clinical cases of HGA have been confirmed in Slovakia (Spitalská et al., 2022).

Anaplasma ovis (Rickettsiales, Anaplasmataceae) is the etiological agent of ovine anaplasmosis. It has been identified in sheep and goats, but the vector(s) in Slovakia remain unconfirmed (Table 1). Furthermore, data on the endemic cycle and zoonotic potential are lacking.

Neoehrlichia mikurensis is an obligate intracellular gram-negative bacterium that belongs to the family Anaplasmataceae and is considered an emerging pathogen (Portillo et al., 2018). It causes febrile illness, mainly in immunocompromised patients. In Slovakia, its presence has been demonstrated in questing *I. ricinus* and small rodent tissues as well as in ticks feeding on several wild hosts (Table 1). Rodents are postulated to serve as reservoirs for the bacterium. No human cases have been documented in Slovakia and further research is required to elucidate the endemic cycle of the pathogen.

Babesia spp. and *Theileria* spp. (order Piroplasmida) are hemoprotozoan parasites transmitted by ticks which infect a wide range of mammalian and some bird species. *Babesia* spp. are known to cause babesiosis in humans and animals (Schnittger et al., 2012; Yabsley and Shock, 2013). In general, the knowledge base on zoonotic *Babesia* spp. in Europe including Slovakia is limited (Bajer et al., 2022). Infections of *I. ricinus* and various wild rodent species with the zoonotic Jena/-Germany genotype of *Babesia microti* and the occurrence of *Babesia venatorum*, *Babesia capreoli* and *Babesia* cf. *odocoilei* in questing *I. ricinus* have been recorded, while the presence of *Babesia divergens* in ticks or wildlife has not yet been confirmed. Additionally, *Babesia motasi* and the potentially human-pathogenic *Babesia crassa*, known to infect small ruminants in the Middle East, were detected in *H. concinna* ticks attached to roe deer and wild boar, respectively (Kazimířová et al., 2018, 2022). Genotypes of *Babesia* spp. reported from Far Eastern Russia and China (*Babesia* sp. Irk-Ip525, *Babesia* sp. hc-hlj212, *Babesia* sp. Kh-Hc222) were detected in questing and host-feeding *H. concinna* (Hamšířková et al., 2016a; Kazimířová et al., 2022). The reservoirs and the zoonotic potential of *Babesia* spp. found in *Haemaphysalis* spp. remain unknown. It remains uncertain if these *Babesia* spp. are endemic in Slovakia, or have been introduced, for example by migratory birds.

Babesia vulpes and *Babesia* sp. Badger have been detected in the red fox (Koneval et al., 2017) and European badger (Purgatová et al., 2023), respectively, but their vectors have not been identified. Red fox is the suspected reservoir for *B. vulpes*, yet the extent to which local dog

populations are affected remains unclear.

Roe deer, fallow deer and red deer in south-western Slovakia have been found to be heavily infected with *Theileria* spp. (prevalence up to 100%), but the infection with these hemoparasites is considered asymptomatic and the parasites are unlikely to be of public health significance. Candidate vectors for transmission are *Haemaphysalis* spp., but confirmation is necessary. Comparative molecular phylogeny of the 18S rRNA gene of *Theileria* spp. isolated from infected cervid species suggests that parasite-host co-speciation has occurred. The provisional designation *Theileria* sp. Elaphus has been suggested for the novel taxon isolated from red deer and fallow deer, while the species isolated from roe deer does not segregate into a single well-defined clade and further genetic analysis is required (Schnittger et al., 2022b).

In contrast to the paucity of knowledge regarding the aforementioned piroplasmid species, there is a wealth of information on the epidemiology of canine babesiosis (Schnittger et al., 2022a), that currently represents a significant veterinary concern in Slovakia. *Dermacentor reticulatus* is the main vector of the causative agent, *Babesia canis* (Table 1). *Babesia gibsoni* is another species that has been found to cause disease in dogs. To date, only two cases have been reported with an unclear origin of infection (Víchová et al., 2016a).

In red foxes and dogs, natural infections with *Hepatozoon canis* have been identified (Miterpáková et al., 2017). In contrast to *Babesia* spp., animals become infected by ingestion of *Hepatozoon*-infected ticks. The brown dog tick *Rhipicephalus sanguineus* is the primary vector of the parasite. However, it is unclear whether the animals were infected by ticks introduced either by dogs or migrating golden jackals or foxes or via another route. Furthermore, *Hepatozoon*-specific DNA was also detected in questing *I. ricinus* adults (Hamšířková et al., 2016b), but their vector competence for *H. canis* has not yet been confirmed. The infection of wild rodents (bank voles and mice) with *Hepatozoon* spp. has been shown (Hamšířková et al., 2016b), but these hemoparasites do not represent any risk for humans or domestic animals and fleas have been identified as their vectors.

3. The role of wildlife in the increase of abundance and geographical expansion of ticks and tick-borne pathogens

Wild ungulates play a pivotal role in the life-cycle of ticks serving as a blood source for all three active life stages of *I. ricinus* and *Haemaphysalis* spp., as well as for *Dermacentor* spp. adults. The populations of wild ungulate species including the wild boar, fallow deer, and red deer are experiencing a notable increase in Slovakia (Herz, 2022). Roe deer, wild boars and fallow deer are commonly observed in urban parks and peri-urban forests of Slovakia, and thus support the maintenance of tick populations in these areas. As reservoirs of TBP, wild ungulates facilitate the circulation of *A. phagocytophilum*, *B. venatorum*, and *Theileria* spp. and support the dispersal of infected ticks to urban green areas (Rizzoli et al., 2014). The implementation of an examination of hunted wildlife for the presence of ectoparasites throughout the year can provide valuable insights into the seasonal occurrence and winter activity of ticks (Chvořtác et al., 2024; Mangová et al., 2024). This approach may also facilitate the identification of introduction pathways and overwintering sites for exotic tick species.

Hedgehogs are known to inhabit urban parks and gardens and are considered reservoirs of TBP and carriers of infected ticks and other ectoparasites (Benkacimi et al., 2023). Due to the proximity of hedgehogs to human dwellings, humans and domestic animals may be exposed to various zoonotic TBP. Despite the growing knowledge on hedgehogs in the epidemiology of TBD, and the increasing attention being paid to these animals in this context, hedgehogs have only recently begun to attract attention in Slovakia (Didyk et al., 2024a). Ticks removed from hedgehogs residing in green areas in Bratislava were found to be infected with several TBP including *Borrelia afzelii*, *B. bavariensis*, *B. spielmanni*, *B. lusitaniae*, *B. myiamotoi*, *R. helvetica*, *A. phagocytophilum*, *Babesia capreoli*, and *B. venatorum*. Further studies in hedgehogs are

therefore warranted.

Birds were found to harbor ticks infected with a wide range of pathogenic microorganisms (Table 1). Tick larvae and nymphs feed on avian hosts and are involved in the transmission of pathogens such as *B. garinii* and *B. valaisiana* (Hanincová et al., 2003a, 2003b; Taragel'ová et al., 2008). Birds disperse pathogen-infected ticks to urban parks and gardens (Rizzoli et al., 2014; Chvostáč et al., 2018). Additionally, through avian migration, birds facilitate the long-distance transport of ticks and pathogens. Some non-native tick species, including *Hyalomma marginatum* and *Ixodes frontalis*, have been transported by migratory birds to Central Europe (Capek et al., 2014; Stanko et al., 2022). Birds may also play a role in the introduction of *Babesia* spp. found in *H. concinna* (see Section 2).

The introduction of non-native ticks can occur via several pathways, including transport by travel or trade, or the geographical spread by invasive species. Buczek and Buczek (2020) have highlighted that species of the *Rhipicephalus sanguineus* (s.l.) complex have been frequently imported by companion animals to Central Europe. Recently, the occurrence and reproduction of the brown dog tick has been confirmed in two flats in southwestern Slovakia, despite the owners having not travelled with their dogs abroad (Didyk et al., 2022). It has been suggested that these dogs had acquired this tick species through contacts with infested dogs with a travel history. The migration of golden jackals may represent another potential route of introduction of the brown dog tick and its associated pathogens (e.g. *H. canis*) to Slovakia (see above). The introduction of exotic ticks and invasive vertebrate species poses a risk of the emergence or re-emergence of pathogens of medical and veterinary relevance, such as Mediterranean SFG rickettsiae, *B. divergens* or *B. motasi*.

4. Future directions

To characterize and effectively manage TBD in humans and animals, comprehensive knowledge of the pathogens, their vectors, reservoirs, their endemic cycles, abiotic and biotic factors, land use, agricultural practices, and human behavior that determine the circulation, emergence and re-emergence of TBP in new areas is needed.

In this respect, many pieces of the “puzzle” of TBD in Slovakia are missing. Future research activities should be conducted to obtain a more complete picture of TBD, which will facilitate an efficient management of their control. The following areas should be included in these research activities.

- The seasonal activity of ticks, their geographical spread and pathogen burden in the era of global changes should be updated by involving citizen science and other monitoring systems such as tick gardens, regular examination of hunted game, livestock, companion animals, and humans for attached ticks.
- In addition to the traditionally explored territories in southwestern and eastern Slovakia, research on TBP should be extended to other parts of the country.
- Additional studies are required to elucidate endemic cycles of *B. miyamotoi*, emerging species of the *B. burgdorferi* (s.l.) complex, *N. mikurensis*, SFG rickettsiae, *Babesia* spp. and of genetic variants of *A. phagocytophilum* of medical and veterinary importance. Furthermore, the identification of their wildlife reservoir and amplifying hosts is necessary.
- Increasing attention should be paid to the role of migrating birds as carriers of exotic tick species and to the risk of their introduction.
- Long-term and comprehensive surveillance of wildlife, livestock, companion animals, ticks and TBD should be carried out using highly sensitive and specific tests and diagnostic methods. In addition, the expertise of parasitologists, wildlife biologists, ecologists, entomologists, epidemiologists, medical doctors, and veterinarians should be integrated.

- Finally, actions should be taken to increase community knowledge about TBD and tick bite prevention.

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Ethical approval

Not applicable.

CRediT authorship contribution statement

Mária Kazimírová: Conceptualization, Writing – original draft, Writing – review & editing. **Barbara Mangová:** Writing – review & editing, Visualization. **Michal Chvostáč:** Writing – review & editing. **Yuliya M. Didyk:** Writing – review & editing. **Paloma de Alba:** Writing – review & editing. **Anabela Mira:** Writing – review & editing. **Slávka Purgatová:** Writing – review & editing. **Diana Selyemová:** Writing – review & editing. **Veronika Rusnáková Taragel'ová:** Writing – review & editing. **Leonhard Schnitger:** Writing – original draft, Writing – review & editing.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

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

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