International Journal for Parasitology: Parasites and Wildlife 28 (2025) 101128

Contents lists available at ScienceDirect

International Journal for Parasitology: Parasites and Wildlife

journal homepage: www.elsevier.com/locate/ijppaw

Wild mammals as hosts of *Rickettsia*: a molecular evidence-based review

Agnieszka Perec-Matysiak [a,*], Katarzyna Buńkowska-Gawlik [a], Laura Tomassone [b], Joanna Hildebrand [a]

[a] Department of Parasitology, University of Wrocław, Poland
[b] Department of Veterinary Sciences, University of Turin, Italy

ARTICLE INFO

Keywords:
Rickettsia spp.
Reservoir hosts
Wildlife
DNA
Molecular tools

ABSTRACT

Rickettsia spp. are obligate intracellular bacteria that infect eukaryotic cells. These agents are transmitted primarily by hard ticks and other hematophagous arthropods, which are the vectors and primary reservoirs of several species. However, in the natural environment, *Rickettsia* spp. has been identified in wild and domestic mammals, as well as in ticks. This review comprehensively addresses the occurrence of rickettsiae in tissues of wild mammals on a global scale, considering different host groups across continents. *Rickettsia* DNA has been detected in bats, ungulates, carnivores, rodents and primates, thus underlining the broad spectrum of potential reservoirs. Extant evidence suggests that some may play role in endemic cycles of the bacteria. In Europe, a significant prevalence of *Rickettsia* DNA has been demonstrated in small rodents, indicating their potential as natural reservoir hosts. Research conducted in Asia and Africa has identified various *Rickettsia* species in rodents and insectivores, emphasizing their role in zoonotic transmission. The role of mammals as reservoirs of rickettsiae remains to be definitively established.

1. Background

The genus *Rickettsia* da Rocha-Lima, 1916, belonging to the order Rickettsiales and the family Rickettsiaceae, includes Gram-negative, non-motile, non-spore-forming, pleomorphic bacteria that may appear as cocci (0.1 μm in diameter), rods (0.3–0.5 μm × 0.8–2.0 μm), or thread-like (10 μm long), without flagella or pili. The type species of the genus is *Rickettsia prowazekii.* Representatives of the genus *Rickettsia* are obligate intracellular bacteria that infect eukaryotic cells (Guillemi et al., 2015). Rickettsiae enter the host cell by inducing phagocytosis, then escape from the phagosome to grow and reproduce within the cytoplasm of the host cell. They are transmitted mainly by hard ticks and other hematophagous arthropods (Merhej et al., 2014). Their reservoir in nature are wild and domestic animals and ticks themselves (Parola et al., 2013). Rickettsia is unable to survive in artificial nutrient environments and can only grow in tissue or embryo cultures. The genome of *Rickettsia* is small, between 1.1 and 1.6 Mb.

Some species of *Rickettsia* have varied pathogenicity for vertebrates and humans. In humans, *Rickettsia* spp. causes different diseases, i.e., the louse- and flea-transmitted typhus group rickettsiae cause epidemic and endemic typhus; the tick-transmitted spotted fever group rickettsiae (e.g., Mediterranean spotted fever - MSF, Lymphangitis-associated rickettsioses -LAR, Tick-borne lymphadenopathy - TIBOLA, Dermacentor-borne necrosis erythema lymphadenopathy - DEBONEL, and Scalp eschar and neck lymphadenopathy - SENLAT). Mites transmit the spotted fever rickettsia, causing rickettsial pox, and the scrub typhus rickettsia, causing tsutsugamushi fever (Oteo and Portillo, 2012). Although intensive research on rickettsiae has been conducted in recent years, it is interesting that almost 60 years ago, a study on the pathogenesis of *Rickettsia* infections was provided. In the experimental infection, researchers exposed monkeys to *R. rickettsii* via aerosol. The infected monkeys developed clinical signs and pathological changes characteristic of epidemic typhus infection in humans, including increases in leukocyte counts and typhus nodules in the brain (Saslaw and Carlisle, 1966).

Based on genomic studies of species belonging to *the Rickettsia* genus, Gillespie et al. (2008) proposed a modern version of the *Rickettsia* classification including four groups: the ancestral group (AG), typhus group (TG), transitional group (TRG), and spotted fever group (SFG). The ancestral group includes non-pathogenic endosymbiotic *R. bellii* and *R. canadensis*. The TG group consists of *R. prowazekii* and *R. typhi*, which cause typhus. The TGR group contains *R. felis* (murine typhus-like) and *R. akari* (rickettsial pox). The spotted fever group comprises the most species with different levels of pathogenicity, which are not always

* Corresponding author.
E-mail address: agnieszka.perec-matysiak@uwr.edu.pl (A. Perec-Matysiak).

https://doi.org/10.1016/j.ijppaw.2025.101128
Received 30 April 2025; Received in revised form 8 August 2025; Accepted 9 August 2025
Available online 10 August 2025
2213-2244/© 2025 The Authors. Published by Elsevier Ltd on behalf of Australian Society for Parasitology. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

confirmed. The recent phylogenetic analysis based on whole bacterial genomes divided the *Rickettsia* genus into five groups: I belli group (BG), II canadensis group (CG), III typhus group (TG), IV spotted fever group II (earlier TGR); and V spotted fever group I; additionally, *R. helvetica* was proposed as an independent clade (Rymaszewska and Piotrowski, 2024).

1.1. Wildlife–human interactions and the potential spillover of Rickettsia

Wildlife significantly influences the ecology of tick-borne pathogens (TBPs) by acting as hosts and reservoirs. Certain wild animals, including carnivores, provide essential blood meals that support tick development and reproduction. Additionally, wildlife can harbor pathogens without necessarily showing symptoms, maintaining the pathogens within the environment (Tsao et al., 2021).

Interactions between humans and wildlife can significantly influence the risk of zoonotic spillover of *Rickettsia* species. These interactions can increase spillover risks through several pathways. 1. *Habitat loss, fragmentation, and land-use changes*. Human activities such as deforestation, urban expansion, and agricultural development disrupt natural habitats, displacing wildlife and altering the distribution of host species. This displacement can force wildlife into closer proximity with human populations, increasing opportunities for direct contact and the potential transmission of pathogens (e.g., red foxes and raccoons). Additionally, changes in land use can affect vector breeding patterns, further influencing the dynamics of disease transmission. 2. *Disease transmission between humans, animals, and the environment.* Environments where humans and animals interact - such as markets, farms, and recreational areas - serve as interfaces that facilitate the transmission of zoonotic agents. These settings provide opportunities for pathogens to spill over from wildlife to humans, especially when biosecurity measures are inadequate or when animals are stressed due to captivity or transportation. Notably, such interfaces can also lead to "spill-back," where pathogens move from humans to domestic animals or wildlife, further complicating disease dynamics (Desvars-Larrive et al., 2024). 3. *Direct wildlife-human interactions.* Activities like hunting, wildlife trade, and outdoor recreational activities can bring humans into direct contact with wildlife, increasing the risk of exposure to zoonotic pathogens, including *Rickettsia* species. For example, the incidence of tick-borne rickettsial disease in the southeastern United States has been rising, and the range expansions of tick species and tick-borne infectious agents, new and old, have resulted in an unprecedented mix of vectors and pathogens. Three human-biting ticks, *Dermacentor variabilis*, *Amblyomma americanum*, and *A. maculatum,* are largely responsible for the spread of rickettsial pathogens such as *R. rickettsii, R. montanensis,* and *R. parkeri*, highlighting the role of direct interactions in disease transmission (Nadolny et al., 2014). 4. *Environmental modification and vector dynamics.* Human-induced environmental changes, such as altering water sources or modifying vegetation, can lead to changes in vector populations and their interactions with hosts, potentially increasing the risk of pathogen transmission. Understanding these dynamics is crucial, as evidenced by studies examining the eco-epidemiology of *R. amblyommatis* and *R. parkeri*, which are transmitted by ticks in various environments. Ecological factors, particularly those in deciduous and mixed forests as well as agricultural and livestock areas, play significant roles in the distribution of *Rickettsia* species. These environments influence the habitats of tick vectors, thereby affecting pathogens' prevalence (Gual-Gonzalez et al., 2024). Despite limited clinical evidence of *R. amblyommatis* pathogenicity, this SFGR species has the potential to play a regulatory role through a possible inhibitory interaction with *R. parkeri*. Ticks infected with *R. amblyommatis* appear less likely to harbor and transmit other SFGR pathogens, highlighting their potential role in public health. Given the widespread presence of *A. americanum* ticks and the relatively low incidence of *R. parkeri* infections, it is hypothesized that a higher prevalence of *R. amblyommatis*-infected *A. americanum* could lead to reduced transmission of SFGR among humans.

1.2. Environmental and ecological factors influencing Rickettsia occurrence in wildlife

In Central Europe, *Ixodes ricinus*, *Dermacentor reticulatus*, and *D. marginatus* are the primary tick species responsible for transmitting and hosting *Rickettsia* spp. (Karbowiak et al., 2016). These ticks are integral to the persistence and spread of *Rickettsia* spp., as they facilitate both vertical transmission (transovarial and transstadial) and horizontal transmission (from infected hosts to ticks and vice versa), as well as co-feeding (Eremeeva and Dasch, 2015). While ticks serve as vectors, acquiring *Rickettsia* during blood meals from infected vertebrates, the bacteria multiply within the vertebrate host's endothelial cells, facilitating transmission when the tick feeds again. This cycle underscores the critical role of vertebrate hosts in maintaining and spreading within ecosystems. Understanding the interactions between bacteria, hosts, and vectors is crucial, especially in light of environmental and socio-economic changes that are affecting tick habitats and contributing to an increase in human cases of tick-borne diseases. This is particularly important in the context of the emergence of new *Rickettsia* species (Kim, 2022).

Ixodes ricinus, recognized as one of the most significant vectors worldwide, is the most prevalent tick species parasitizing humans. Its geographical range is determined by environmental factors such as temperature and humidity, which influence its survival and spread (Medlock et al., 2012; Dyczko et al., 2024). Previous research suggests that climate change may expand the areas suitable for *I. ricinus*, potentially raising the risk of *Rickettsia* spp. Infections and other tick-borne diseases are spreading in regions that were previously unaffected. Some studies have demonstrated that variations in temperature, humidity, rainfall, and other climate factors can directly impact the life cycle and distribution of ticks, subsequently influencing the transmission patterns of *Rickettsia*. Warmer and wetter conditions typically support larger tick populations, which can lead to a higher incidence of tick-borne diseases, including those caused by *Rickettsia* spp. (Cunze et al., 2022). Conversely, extreme weather events such as heatwaves, cold spells, and flooding, likely linked to climate change, can disrupt tick populations and their activity, potentially decreasing *Rickettsia* prevalence in some areas (Gray et al., 2009; Ogden et al., 2021). Urbanization and habitat fragmentation, which result in changes to the availability and quality of forest habitats, have been identified as major factors influencing tick populations and the spread of tick-borne diseases (Hansford et al., 2023). Moreover, environmental changes such as deforestation and human-driven alterations to natural habitats can impact the distribution of tick populations and their pathogen load, ultimately affecting the epidemiology of tick-borne diseases (Medlock et al., 2012; Tack et al., 2013). Ultimately, the infection rates of *I. ricinus* with *Rickettsia* spp. are shaped by a range of factors, such as the presence of appropriate hosts, environmental conditions, and the genetic diversity of both the ticks and the pathogens (Takumi et al., 2019).

In North America, the proliferation of white-tailed deer (*Odocoileus virginianus*) has significantly influenced the populations of certain tick species that affect both humans and animals. These deer serve as primary hosts for the adult stages of the black-legged tick (*Ixodes scapularis*) and the lone star tick (*Amblyomma americanum*). As deer populations have expanded, there has been a corresponding increase in these tick species, leading to a higher incidence of tick-borne diseases. *Amblyomma americanum* is responsible for the transmission of Rocky Mountain spotted fever (*R. rickettsii*) (Tsao et al., 2021).

In Brazil, anthropogenic modifications in the state of São Paulo during the last three decades have favoured capybara's presence. This rodent is a recognized reservoir of *R. rickettsii*, and Brazilian Spotted Fever became endemic in the area (Luz et al., 2019).

1.3. Molecular tools for the detection of Rickettsia spp. in wildlife

Molecular assays (PCR and RT-PCR) are widely used for the

diagnosis of rickettsial infection, since they enable the rapid detection and identification of *Rickettsia* species with high sensitivity and specificity (Portillo et al., 2017). Blood is the main tissue analyzed in studies on wildlife and animals in general; however, the usefulness of PCR on blood for rickettsial detection is limited, due to low numbers of circulating rickettsiae (Walker and Ismail, 2008). Assays with high sensitivity (e.g., nested PCR) are thus recommended when testing blood specimens (Santibáñez et al., 2013). The molecular detection of *Rickettsia* spp. is more successful in other tissues, such as skin and organ biopsies (Portillo et al., 2017). However, such tissue samples are harder to obtain in live animals, although several studies have been performed on skin biopsies taken from anesthetized animals (e.g., rodent ear tissues). A wide number of studies have instead focused on the molecular detection of rickettsiae in arthropods collected on wild hosts; in this case, PCR positivity does not necessarily indicate the infection in the vertebrate, but only in the feeding vector. Raoult et al. (2005) suggest using five genes for the molecular characterization of rickettsiae: *rrs*, *gltA*, *ompA*, *ompB*, and *sca4*. The outer membrane proteins (OMPA, OMPB) and the surface cell antigens (SCA1 and SCA4) are particularly useful for the identification and phylogenetic analysis (Portillo et al., 2017). Finally, metagenomic approaches are getting increasingly popular also for the study of rickettsial diseases. However, due to the costs and technology required, they are still limited to reference/research diagnostic laboratories (Stewart and Stewart, 2021) and mostly used for surveillance purposes (Kipp et al., 2023).

The subject of *Rickettsia* in wildlife is a broad one, and a significant number of review articles have been published in recent times, particularly with regard to the occurrence of *Rickettsia* in questing ticks or collected from animals. The number of molecular studies on *Rickettsia* in mammalian tissues is limited, and there is a lack of review articles on this topic as well. Therefore, the aim of this review was to compile and synthesise peer-reviewed articles reporting the presence of *Rickettsia* spp. DNA in tissue samples from wild mammals worldwide. Thus, the review provides a clear global overview of the prevalence of *Rickettsia* DNA across various mammalian groups and geographic regions, including tabular presentations of the data, thereby contributing to a better understanding of the potential role of these animals in the maintenance and transmission of rickettsiae in natural ecosystems.

2. Methods, literature search strategy

The present review is based on a comprehensive literature search. The search was primarily conducted using the PubMed (https://pubmed.ncbi.nlm.nih.gov/) and Google Scholar (https://scholar.google.com/), and Web of Science (https://www.webofscience.com/wos/woscc/basic-search). The following search terms and Boolean operators (AND, OR) were used: „*Rickettsia*", „PCR", „molecular study", „wild mammals", tailored to the targeted geographic regions (Europe, Africa, Asia, Australia, and the Americas). The references cited in the publications that we found also led to a snowball effect. We analyzed all peer-reviewed publications from 2008 to 2025 (the first quarter) which described the presence of *Rickettsia* only in tissues of wild mammals worldwide as determined by molecular techniques. Data were extracted from articles that met the inclusion criteria after appraisal. The following information was extracted and tabulated: region and country; host species; prevalence; species and genotypes of *Rickettsia*; type of tissue sample examined; detection technique; authors; year of publication.

3. Results and discussion

3.1. *Rickettsia spp. in wildlife - molecular data*

The presence of rickettsial-specific DNA has been identified in questing and host-feeding ticks, as well as other ectoparasites (mites and fleas), and in the blood and tissues of several vertebrate species, including small rodents, insectivores, bats, ungulates, game mammals, and carnivores. However, due to the low sensitivity of molecular analyses for the detection of *Rickettsia* spp. in blood, several studies failed in the detection (Yang et al., 2021). Conversely, the presence of antibodies against rickettsiae has been identified in several vertebrate species, including rodents, red deer, roe deer, wild boars, and hares. Evidence suggests that some may play a role in endemic cycles of the bacteria, nevertheless, the role of these species as reservoirs for rickettsiae has yet to be definitively confirmed (Kazimirova et al., 2024).

Tables 1–5 illustrate findings of *Rickettsia* DNA in wildlife around the world.

3.1.1. *Rodents and insectivores*

Wild rodents and insectivores can harbor various *Rickettsia* species, some of which have zoonotic potential. Understanding the role of rodents in the ecology and transmission of Rickettsia is crucial for assessing potential risks to human health.

Several studies have investigated the presence of rickettsial species in rodents and insectivores in Europe, highlighting their potential role as reservoirs and the involvement of ectoparasites in transmission. A study conducted in Saxony, Germany, showed *Rickettsia* DNA in 28.6 % of rodents, 3.9 % of fleas, and 41.6 % of ticks, by real-time PCR (Obiegala et al., 2016; 2017). Sequencing identified *R. helvetica* and *R. raoultii* in rodents, and *R. raoultii*, *R. monacensis*, and *R. helvetica* in ticks. Notably, this was the first detection of *R. raoultii* in *Myodes glareolus* and *R. helvetica* in *Apodemus agrarius* in Germany. The high prevalence of *R. helvetica* in small mammals suggests they may play a role in the transmission of the agent to feeding arthropods. Another study carried out by Galfsky et al. (2019) in Saxony, Germany investigated the prevalence of various tick-borne pathogens, including *Rickettsia* species, in small mammals and ticks in Saxony, Germany. The prevalence of *Rickettsia* spp. in rodents was found to be 29.1 %.

The study by Fischer et al. (2018) demonstrated screening of 3939 wild small mammals, including rodents and insectivores, for *Rickettsia* DNA. *Rickettsia helvetica* was the most prevalent species, detected in 90.9 % of positive samples. Other species identified included *R. felis* (7.8 %) and *R. raoultii* (1.3 %). The highest prevalence of *Rickettsia* DNA was found in rodents of the genus *Apodemus*, particularly the yellow-necked mouse (*A. flavicollis*). Additionally, older and male individuals of certain rodent species exhibited higher rates of *Rickettsia* DNA presence, and small mammals collected in forested habitats during summer and autumn had higher prevalence rates, suggesting that seasonal and habitat-related factors influence *Rickettsia* prevalence. The findings highlight the importance of considering ecological factors, such as host species, age, sex, and habitat, in understanding the dynamics of *Rickettsia* transmission.

In a study conducted by Minichová et al. (2017), the presence of *Rickettsia* spp. DNA was identified in 0.5 % (3/663) of rodent samples, comprising ear biopsies and/or spleen samples, from rodents (*A. flavicollis*) captured from Slovakia. The identified *Rickettsia* spp. were *R. helvetica* and *R. monacensis.* Concurrent studies in Slovakia have demonstrated the overall prevalence of *Rickettsia* spp. in examined small mammals (rodents and insectivores) as 11 %, with *R. helvetica* the most prevalent species and being confirmed in *A. agrarius, A. flavicollis, My. glareolus,* and *M. arvalis.* Furthermore, a *Rickettsia* species closely related to *R. felis* was identified in *A. flavicollis*, while *R. slovaca* was observed in *A. flavicollis* (Heglasová et al., 2018). The highest occurrence of rickettsiae-positive small mammals was recorded during the spring and autumn months, possibly related to the seasonal activity of tick vectors. The research by Špitalská et al. (2020) provides insights into the prevalence of *Rickettsia* species and rickettsial endosymbionts in small mammals and their ectoparasites, with *R. helvetica* identified with the highest frequency in *A. agrarius*.

A study conducted in south-western Poland identified the presence of *Rickettsia* DNA in the tissues of wild rodents, including species such as *A. agrarius* and *My. glareolus*. The prevalence of infection was

Table 1
Studies on molecular detection of *Rickettsia* spp. DNA from wild mammalian tissues in Europe.

Country	Group of hosts	Host species	No. of positive rickettsial DNA (no of positive/ examined/%)	Species/genotypes of *Rickettsia* and Rickettsia Candidatus sp. (frequency)	Type of tissue sample examined	Detection technique	Reference
France	carnivores	*Vulpes vulpes*	0/93/0 %	–	spleen	real-time PCR (qPCR) - *gltA*; PCR	Medkour et al. (2020)
Germany	rodents	*Rattus norvegicus*	3/368/0.8 %	*R. helvetica* (3)	ear	PCR - *ompB*	Heuser et al. (2017)
Germany	rodents	*Apodemus flavicollis*	130/925/14 %	*R. felis* (4), *R. helvetica* (30), *Rickettsia* sp. (96)	ear	real-time PCR (qPCR) - *gltA*; PCR - *ompB; ompA*	Fischer et al. (2018)
		Apodemus sylvaticus	17/105/16.2 %	*R. felis* (4), *R. helvetica* (30), *Rickettsia* sp. (96)			
		Arvicola amphibius	2/4/50 %	*R. felis* (1), *R. helvetica* (1)			
		Apodemus agrarius	4/43/9 %	*R. helvetica* (1), *Rickettsia* sp. (3)			
		Clethrionomys glareolus	119/1565/7.6 %	*R. helvetica* (19), *Rickettsia* sp. (100)			
		Micromys minutus	0/6/0 %	-			
		Microtus agrestis	9/207/4.3 %	*R. helvetica* (2), *Rickettsia* sp. (7)			
Germany	insectivores	*Sorex araneus*	15/519/2.9 %	*R. helvetica* (3), *Rickettsia* sp. (12)	ear	real-time PCR (qPCR) - *gltA;* PCR - *ompB; ompA*	Fischer et al. (2018)
		Sorex coronatus	4/101/4 %	*R. helvetica* (2), *Rickettsia* sp. (2)			
		Sorex minutus	0/72/0 %	-			
		Neomys fodiens	0/4/0 %	-			
		Crocidura russula	0/1/0 %	-			
Germany	carnivores	*Mustela nivalis*	0/2/0 %	-	ear	real-time PCR (qPCR) - *gltA;* PCR - *ompB; ompA*	Fischer et al. (2018)
Germany	rodents	*Clethrionomys glareolus*	32/104/30.8 %	*R. raoultii* (7), *R. helvetica* (7)	spleen	real-time PCR (qPCR) – *gltA;* PCR - *ompB*	Galfsky et al. (2019)
		Apodemus flavicollis	16/59/27 %				
		Apodemus terrestris	0/1/0 %	*R. helvetica* (2)			
		Myodes glareolus	0/1/0 %	-			
				-			
Germany	rodents	*Myodes glareolus*	10/42/23.8 %	*R. helvetica* (3), *R. raoultii* (2), *Rickettsia* spp. (5)	ear	real-time PCR - *gltA*; PCR - *ompB*	Obiegala et al., 2016
		Apodemus flavicollis	14/37/37.8 %	*R. helvetica* (7), *Rickettsia* spp. (7)			
		Apodemus agrarius	2/3/66.7 %	*R. helvetica* (2)			
		Arvicola terrestris	0/3/0 %	-			
Germany	insectivores	*Crocidura russula*	0/4/0 %	-	ear	real-time PCR - *gltA*; PCR - *ompB*	Obiegala et al., 2016
		Sorex araneus	0/1/0 %	-			
		Talpa europaea	0/1/0 %	-			
Germany	rodents	*Apodemus flavicollis*	50/214/23.4 %	*R. helvetica* (4), *R. felis* (1)	ear	real-time PCR – *gltA;* PCR - *ompB*	Obiegala et al., 2017
		Apodemus agrarius	0/7/0 %	-			
		Myodes glareolus	114/435/26.2 %	*R. raoultii* (5), *R. helvetica* (5)			
		Microtus arvalis	0/8/0 %	-			
Germany	carnivores	*Procyon lotor*	1/41/2.4 %	*R. helvetica*	ear	nested PCR – *gltA, ompB;*17 kDa	Hildebrand et al. (2022)
Germany	game	*Capreolus capreolus*	0/95/0 %	-	ear, spleen	PCR - *gltA*	Overzier et al. (2013)
Hungary	rodents	*Mus musculus*	1/5/20 %	*R. helvetica,*	skin, spleen,	real-time PCR	Szekeres et al. (2019)
		Sciurus vulgaris	1/5/20 %	*Rickettsia* sp.	liver, muscle,	(qPCR) - *gltA*	
			0/6/0 %	–	blood		
			0/6/0 %	–			
Hungary	insectivores	*Erinaceus roumanicus*	15/52/29 %	*R. helvetica,*	skin, spleen,	real-time PCR	Szekeres et al. (2019)
		Talpa europaea	19/52/37 %	*Rickettsia* sp.	liver, muscle,	(qPCR) - *gltA*	
		Crocidura suaveolens	0/15/0 %	-	blood		
			1/15/7 %	*Rickettsia* sp.			
			0/3/0 %	-			
			0/3/0 %	-			
Hungary	carnivores	*Martes foina*	1/2/50 %	*R. helvetica*	skin, spleen,	real-time PCR	Szekeres et al. (2019)
		Mustela nivalis	0/2/0 %	-	liver, muscle,	(qPCR) - *gltA*	
			0/4/0 %	-	blood		
			1/4/25 %	*Rickettsia* sp.			
Hungary	game	*Capreoulus capreolus*	0/3/0 %	-	skin, spleen,	real-time PCR	Szekeres et al. (2019)
			0/3/0 %	-	liver, muscle, blood	(qPCR) - *gltA*	
Hungary	carnivores	*Sus scrofa*	0/17/0 % blood	-	blood and	PCR - *R. helvetica* (*23S rRNA*); other rickettsiae – *gltA*	Hornok et al. (2018)
			0/79/0 % spleen	-	spleen		
Hungary	game	*Cervus elaphus*	0/48/0 % blood	-	blood and	PCR - *R. helvetica* (*23S rRNA*); other rickettsiae - *gltA*	Hornok et al. (2018)
		Dama dama	0/96/0 % spleen	-	spleen		
		Capreolus capreolus	0/33/0 % blood	-			
		Ovis orientalis musimon	1/85/1.2 % spleen	*R. helvetica*			

(*continued on next page*)

Table 1 (*continued*)

Country	Group of hosts	Host species	No. of positive rickettsial DNA (no of positive/ examined/%)	Species/genotypes of *Rickettsia* and Rickettsia Candidatus sp. (frequency)	Type of tissue sample examined	Detection technique	Reference
			0/65/0 % blood 0/6/0 % spleen 1/16/6.25 % blood 0/4/0 % spleen	- - *R. helvetica*			
Hungary	bats	*Myotis* sp. *Pipistrellus* sp. *Nyctalus* sp. *Barbastella* sp. *Plecotus* sp. *Rhinolophus* sp. *Miniopterus* sp.	13/221/5.9 %	*R. helvetica* *Neorickettsia risticii* *Rickettsia* spp. *Rickettsia endosymbiont*	feaces	PCR - *R. helvetica - 23S rRNA;* other rickettsiae - *gltA*	Hornok et al. (2018)
Italy	carnivores	*Lutra lutra*	1/6/16.7 %	*R. conorii*	spleen	PCR - 17-kDa	Santoro et al. (2017)
Italy	rodents	*Apodemus* spp. *Myodes glareolus*	8/37/21.6 % 0/9/0 %	*R. slovaca*	ear	PCR – *ompA, gltA*	Martello et al. (2013)
Lithuania	rodents	*Apodemus flavicollis* *Micromys minutus* *Myodes glareolus* *Microtus oeconomus* *Microtus agrestis* *Microtus arvalis*	68/231/29.4 % 17/37/45.9 % 47/198/23.7 % 0/8/0 % 0/2/0 % 0/1/0 %	*R. helvetica*	spleen	nested PCR - *gltA* semi nested PCR - 17 kDa	Mardosaitė-Busaitienė et al. (2018)
Lithuania	insectivores	*Sorex araneus*	3/12/25 %	*R. helvetica*	spleen	nested PCR – *gltA;* semi-nested PCR -17 kDa	Mardosaitė-Busaitienė et al. (2018)
Netherlands	ungulates	*Capreolus capreolus*	15/461/3.3 %	*Rickettsia* sp.	blood	real-time PCR (qPCR) – *gltA*	Wijburg et al. (2022)
Netherlands	rodents	*Apodemus sylvaticus* *Myodes glareolus*	13/478/2.7 % 5/294/1.7 %	*R. helvetica*	ear	real-time PCR (qPCR) - *gltA*	Krawczyk et al. (2020)
Poland	carnivores	*Procyon lotor*	24/179/13.4 %	*gltA* *R. helvetica* (13) *R. monacensis* (1) *R. raoultii* (1) *Candidatus* R. kotlani (1) *ompB* *R. helvetica* (6), *R. monacensis* (1), *R. raoultii* (1) *Rickettsia endosymbionts* (6) 17 kDa *R. helvetica* (2) *Rickettsia endosymbionts* (1)	ear, spleen, liver	nested PCR - *gltA, ompB;*17 kDa	Hildebrand et al. (2022)
Poland	rodents	*Apodemus agrarius* *Apodemus flavicollis* *Myodes glareolus*	25/96/26 % blood 1/136/2.8 % spleen 5/25/20 % blood 0/31/0 % spleen 3/23/13 % blood 1/26/3.8 % spleen	*R. felis, R. helvetica*	blood spleen	real-time PCR (qPCR) – *gltA;* PCR - *gltA*	Gajda et al. (2017)
Romania	insectivores	*Erinaceus roumanicus*	1/8/12.5 %	*R. helvetica*	heart, liver, and skin, blood	PCR - *gltA*	Borşan et al., 2021
Romania	rodents	*Apodemus agrarius* *Apodemus sylvaticus* *Mus musculus*	3/14/21.4 % 1/3/33.3 % 1/1/100 %	*R. monacensis*	heart, liver, and skin, blood	PCR - *gltA*	Borşan et al., 2021
Romania	bats	*Nyctalus noctula* *Pipistrellus pipistrellus* *Myotis alcathoe* *Pipistrellus nathusii* *Pipistrellus pygmaeus* *Plecotus auritus* *Vespertilo murinus*	22/188/11.7 % 13/55/23.6 % 5/12/41.7 % 4/25/16 % 1/2/50 % 1/6/16.7 % 1/4/25 %	*R. monacensis* (12) *R. monacensis* (5)	heart	PCR - *gltA*	Matei et al. (2021)
Slovakia	rodents	*Apodemus flavicollis* *Apodemus sylvaticus* *Clethrionomys glareolus* *Microtus arvalis* *Microtus subterraneus* *Micromys minutus*	3/ 600/0.5% 0/63/0%	*R. helvetica, R. monacensis*	ear, blood, spleen	PCR - *gltA*	Minichová et al. (2017)
Slovakia	rodents	*Apodemus agrarius*	1/69/1.4 %	*R. helvetica* (1)	ear	PCR - *gltA*	Heglasová et al. (2018)

(*continued on next page*)

Table 1 (*continued*)

Country	Group of hosts	Host species	No. of positive rickettsial DNA (no of positive/ examined/%)	Species/genotypes of *Rickettsia* and Rickettsia Candidatus sp. (frequency)	Type of tissue sample examined	Detection technique	Reference
		Apodemus flavicollis	10/99/10.1 %	*R. helvetica* (1), *R.* sp. related to *R. felis* (3), *R. slovaca* (1)			
		Apodemus uralensis	1/1/100 %	ND			
		Clethrionomys glareolus	13/58/22.4 %	*R.helvetica* (4)			
		Micromys minutus	0/4/0 %	-			
		Micromys arvalis	1/10/10 %	*R. helvetica* (1)			
		Microtus subterraneus	0/1/0 %	-			
Slovakia	insectivores	*Crocidura leucodon*	1/3/33.3 %	ND	ear	PCR - *gltA*	Heglasová et al. (2018)
Slovakia	rodents	*Clethrionomys glareolus*	29/201/14.4 %	*R. helvetica* (6)	blood	PCR - 16S rRNA	Miťková et al. (2015)
		Apodemus flavicollis	14/247/5.7 %	*R. helvetica* (3)			
		Microtus arvalis	2/8/25 %	–			
		Apodemus sylvaticus	1/8/12.5 %	*R. helvetica* (1)			
		Microtus subterraneus	0/12/0 %	-			
Slovakia	rodents	*Apodemus agrarius*	20/340/5.9 %	*R. helvetica* (5), *R. endosymbionts* (4)	ear	PCR - *gltA*; TaqMan PCR - *23S rRNA* and *ompB*	Špitalská et al. (2020)
		Apodemus flavicollis	12/312/3.8 %	*R. helvetica* (3)			
		Clethrionomys glareolus	11/267/4.1 %	*R. helvetica* (3), *R. slovaca* (1), *R. endosymbionts* (2)			
		Microtus arvalis	1/14/7.1 %	*R. helvetica* (1)			
		Microtus subterraneus	0/7/0 %	-			
		Microtus minutus	0/3/0 %	-			
Slovakia	insectivores	*Crocidura suaveolens*	0/2/0 %	-	ear	PCR - *gltA*; TaqMan PCR - *23S rRNA* and *ompB*	Špitalská et al. (2020)
		Neomys fodiens	0/2/0 %	-			
		Sorex minutus	0/15/0 %	-			
		Sorex araneus	0/2/0 %	-			
Switzerland	rodents	*Clethrionomys glareolus*	0/19/0 %	-	blood	PCR - *23S-5S*	Burri et al. (2014)
		Apodemus flavicollis	0/45/0 %	-			
		Apodemus sylvaticus	0/35/0 %	-			
		Apodemsus spp.	0/9/0 %	-			
Spain	game	*Cervus elaphus*	2/262/0.7 %	*R. helvetica, R. slovaca*	spleen	nested PCR - *rOmpA* and *rOmpB*	Remesar et al., 2023
		Sus scrofa	0/83/0 %				
Turkey	game	*Sus scrofa*	1/30/3.3 %	*R. slovaca*	blood	PCR – *gltA*, *ompA*	Orkun and Çakmak, 2019
	lagomrophs	*Lepus europaeus*	0/30/0 %				
	carnivores	*Vulpes vulpes*	0/4/0 %				

ND = not determined.

approximately 17.6 %, with some samples specifically detecting the presence of *R. helvetica* and *Rickettsia felis*-like organisms (Gajda et al., 2017).

In the northern Appenines, Italy, *Rickettsia slovaca* was identified by PCR in ear biopsies in 8 *Apodemus* spp. (n = 37 examined), but not in *M. glareolus* (n = 9). Rodents were infested by *D. marginatus* larvae and nymphs. Prevalence of *R. slovaca* was greater in larvae feeding on PCR-positive *Apodemus* than in those feeding on negative mice, suggesting that heavily infested mice might play a role as amplifiers of the infection (Martello et al., 2013).

In Asia, examined tissues of rodents and insectivores are positive for various *Rickettsia* species, some of which are zoonotic and can infect humans. A study in Mudanjiang, Heilongjiang Province, detected *Candidatus* Rickettsia tarasevichiae in 1.29 % of 463 rodents, including *Rattus norvegicus* and *Clethrionomys rufocanus* (Yuan et al., 2020). This finding marked the first confirmation of this *Rickettsia* species in rodents in China. A nationwide survey identified *R. raoultii* in 2.9 % of 835 wild rodents. This was the first detection of *R. raoultii in S*outh Korean rodents and highlights the importance of continuous monitoring to mitigate public health risks (Kim et al., 2024). A comprehensive study in Taiwan documented the capture of 1285 small mammals, comprising 10 rodent species and one shrew species (Kuo et al., 2015). *Rattus losea* accounted for 54.6 % of rodent captures in a study conducted between 2006 and 2010 in Taiwan. High seropositivity rates were observed for *R. conorii* or *R. rickettsii* (94.6 %) and *R. typhi* (2.3 %). Additionally, DNA of spotted fever group (SFG) and typhus group (TG) *Rickettsia* species was detected in 41.1 % and 9.4 % of individuals, respectively. *Mus caroli*, representing 10.6 % of captures, showed seropositivity rates of 48.9 % for *R. conorii* or *R. rickettsii* and 5.9 % for *R. typhi*. SFG and TG Rickettsia DNA were found in 43.2 % and 6.8 % of individuals, respectively. *Bandicota indica* rodents exhibited seropositivity rates of 88.0 % for *R. conorii* or *R. rickettsii* and 0 % for *R. typhi*. SFG and TG *Rickettsia* DNA were detected in 41.2 % and 5.9 % of individuals, respectively. The high prevalence of *Rickettsia* infections in rodents across Taiwan indicates a significant potential for zoonotic transmission. Rodents, especially *Rattus* species, serve as primary reservoirs for these bacteria, with fleas acting as vectors. Infection with *Rickettsia* species can lead to murine typhus (*R. typhi*) and spotted fever group rickettsioses (*R. conorii* and *R. rickettsii*). Notably, *R. typhi* is transmitted by fleas found on rodents and can cause murine (endemic) typhus, characterized by fever, chills, and rash.

A study involving 95 wild rats (*R. diardii* and *R. norvegicus*) from Kuala Lumpur and Pulau Pinang in Malaysia detected *Rickettsia* DNA in 13.7 % of tissue samples (Tay et al., 2014). Sequence analysis revealed 98.6–100 % similarity with *R. honei, R. conorii,* and *R. raoultii*.

In the African continent, a study in the Democratic Republic of the Congo found that 13 % of rats (*R. rattus* and *R. norvegicus*) were positive for *R. typhi*, the causative agent of murine typhus (Laudisoit et al., 2014). Fleas (*Xenopsylla cheopis*) from these rodents also harbored *R. typhi* in 72 % of pools, highlighting the role of fleas in the transmission of this pathogen. Research across southern Africa and Namibia detected *Rickettsia* DNA in 15.5 % of 1616 ear-tissue samples from 23 small mammal species (rodents and insectivores) (Essbauer et al., 2018). Four human-pathogenic *Rickettsia* species were identified: *R. conorii*, *R. massiliae*, *R. felis*, and *R. helvetica*. Novel species such as *Candidatus* Rickettsia africaustralis, *Candidatus* Rickettsia rhabdomydis, and *Candidatus* Rickettsia muridii were also confirmed. The high prevalence of *Rickettsia* species in rodents and their fleas across Africa suggests

Table 2
Studies on molecular detection of *Rickettsia* spp. DNA from wild mammalian tissues in Asia.

Region	Group of hosts	Host species	No. of positive rickettsial DNA (no of positive/examined/%)	Species/genotypes of *Rickettsia* and Rickettsia Candidatus sp. (no of confirmed)	Type of tissue sample examined	Detection technique	Reference
China	rodents	*Mus musculus*	1/6/16.7 %	*R. felis* (1)	blood liver kidney spleen	FRET-PCR – *gltA* nested PCR - *gltA*	Zhang et al. (2014)
	insectivores	*Suncus murinus*	0/4/0 %				
China	rodents	*Apodemus agrarius*	0/211/0 %		spleen	PCR – *gltA, ompA*	Yuan et al. (2020)
		Apodemus peninsulae	0/35/0 %				
		Rattus norvegicus	2/58/3.5 %	*Candidatus* Rickettsia tarasevichiae (2)			
		Clethrionomys rufocanus	4/95/4.2 %	*Candidatus* Rickettsia tarasevichiae (4)			
		Clethrionomys rutilus	0/2/0 %				
		Microtus fortis	0/4/0 %				
		Cricetulus barabensis	0/5/0 %				
		Cricetulus triton	0/16/0 %				
		Tscherskia triton	0/14/0 %				
		Tamiops macclellandi	0/1/0 %				
	insectivores	*Sorex* spp.	0/17/0 %				
Japan	game/ ungulates	*Cervus nippon yesoensis*	8/112/7.1 %	*Rickettsia helvetica* (8)	blood	nested PCR - *gltA*, 17-kDa	Inokuma et al. (2008)
Kazakhstan	rodents	*Microtus arvalis*	3/87/3.4 %	*R. raoultii* (2)	ear lobes	RT PCR - *gltA* PCR - *ompAIV*, *23S–5S* interspacer region	Wagner et al. (2022)
		Clethrionomys glareolus	0/13/0 %				
		Microtus kirgisorum	0/49/0 %				
		Apodemus uralensis	5/259/1.9 %	*R. conorii* (1), *R. slovaca* (1), *R. raoultii* (1)			
		Mus musculus	9/128/7.0 %	*R. slovaca* (1), *R. raoultii* (5)			
		Rattus norvegicus	0/39/0 %				
		Meriones meridianus	0/2/0 %				
		Dryomys nitedula	0/15/0 %				
	insectivores	*Crocidura suaveolens*	0/28/0 %				
		Sorex spp.	0/4/0 %				
Korea	rodents	*Apodemus agrarius*	21/693/3.0 %	*R. raoultii* (21)		PCR – 16S rRNA	Kim et al. (2024)
		Apodemus peninsulae	0/5/0 %				
		Craseomys regulus	0/13/0 %				
		Craseomys rufocanus	0/1/0 %				
		Micromys minutus	0/25/0 %				
		Microtus fortis	0/4/0 %				
	insectivores	*Mogera robusta*	0/1/0 %				
		Crocidura lasiura dobson	0/1/0 %				
		Crocidura spp.	3/86/3.5 %	*R. raoultii* (3)			
Malaysia	rodents	*Rattus diardii*	9/58/15.5 %	*R. honei/R. conorii/R. raoultii* (12)	liver spleen heart kidney	nested PCR, PCR – *gltA, ompA, ompB*	Tay et al. (2014)
		Rattus norvegicus	4/37/10.8 %				
Malaysia	primates	*Macaca fascicularis*	12/50/24 %	*Rickettsia* sp. RF2125, *Candidatus* Rickettsia asemboensis, *Rickettsia* spp. clone 4G/JP102 and 11TP21, *R. felis*–type strain	blood	PCR – *gltA, ompB*	Tay et al. (2015)
Taiwan	rodents	*Apodemus agrarius*	SGF 7/11/63.6 % TG 1/11/9.1 %	*R. japonica* (1), *R. rickettsii* (2), *Rickettsia* sp. *IG-1* (5), *Rickettsia* sp. *TwKM01* (1), *R. typhi* (1)	liver spleen kidney	nested PCR - *gltA, ompB*	Kuo et al. (2015)
		Bandicota indica	SGF 7/17/41.2 % TG 1/17/5.9 %	*R. japonica* (4), *R. raoultii* (2), *R. rickettsii* (3), *Rickettsia* sp. *IG-1* (1), *R. typhi* (1)			
		Mus caroli	SGF 19/44/43.2 % TG 3/44/6.8 %	*R. conorii* (1), *R. felis* (1), *R. japonica* (7), *R. rickettsii* (10), *Rickettsia* sp. *IG-1* (2), *R. typhi* (3)			
		Mus musculus	SGF 6/6/100 % TG 0/6/0 %	*R. japonica* (4), *R. raoultii* (1), *R. rickettsii* (2), *Rickettsia* sp. *IG-1* (1), *Rickettsia* sp. *TwKM01* (1)			

(*continued on next page*)

Table 2 (*continued*)

Region	Group of hosts	Host species	No. of positive rickettsial DNA (no of positive/examined/%)	Species/genotypes of *Rickettsia* and Rickettsia Candidatus sp. (no of confirmed)	Type of tissue sample examined	Detection technique	Reference
		Niviventer coxingi	SGF 1/2/50 % TG 0/6/0 %	*R. conorii* (1)			
		Rattus exulans	SGF 3/6/50 % TG 1/6/16.7 %	*R. japonica* (2), *Rickettsia* sp. *IG-1* (1), *Rickettsia* sp. *TwKM01* (1), *R. typhi* (1)			
		Rattus losea	SGF73/181/40.3 % TG 18/181/9.9 %	*R. conorii* (33), *R. felis* (8), *R. japonica* (14), *R. rickettsii* (21), *Rickettsia* sp. *IG-1* (5), *Rickettsia* sp. *TwKM02* (3), *R. typhi* (18)			
		Rattus norvegicus	SGF 3/6/50 % TG 1/6/16.7 %	*R. japonica* (2), *Rickettsia* sp. *IG-1* (1), *Rickettsia* sp. *TwKM01* (1) *TwKM02* (1), *R. typhi* (1)			
	insectivores	*Suncus murinus*	SGF 8/36/22.2 % TG 4/36/11.1 %	*R. japonica* (4), *R. rickettsii* (5), *Rickettsia* sp. *TwKM01* (1), *R. typhi* (4)			
Thailand Bangkok	rodents	*Ratttus exulans*	0/12/0 %		spleen	nested PCR - *gltA*	Rungrojn et al.,
		R. norvegicus	0/2/0 %				
		R. rattus-complex	4/162/2.5 %	*R. typhi* (3), *R. felis* (1)			
	insectivores	*Tupaia belangeri*	0/19/0 %				
		Suncus murinus	0/3/0 %				

Table 3
Studies on molecular detection of *Rickettsia* spp. DNA from wild mammalian tissues in Australia.

Region	Group of hosts	Host species	No. of positive rickettsial DNA (no of positive/examined/%)	Species/genotypes of *Rickettsia* and Rickettsia Candidatus sp. (no of confirmed)	Type of tissue sample examined	Detection technique	Reference
Australia	rodents	*Rattus rattus*	0/33/0 %	-	blood	metatranscriptomics followed by *gltA* qPCR and PCR - *gltA, ompB*	Gofton et al., 2021
		Rattus fuscipes	0/11/0 %	-			
	marsupials	*Perameles nasuta*	0/19/0 %	-			
		Trichosurus vulpecula	0/6/0 %	-			

significant public health risks. Rodents and fleas act as reservoirs and vectors, respectively, facilitating the transmission of these pathogens to humans. Infection can lead to diseases such as murine typhus, characterized by fever, chills, and rash. While often mild, severe cases can result in complications affecting organs like the liver, heart, and lungs. The detection of diverse *Rickettsia* species in rodents and insectivores and their ectoparasites across various African regions underscores the importance of monitoring these populations. Enhanced surveillance and control measures targeting rodents and fleas are essential to mitigate the risk of *Rickettsia* transmission to humans.

Rickettsia rickettsii is the main etiological agent of severe spotted fever, named with different names across north, central and south America (e.g. Rocky Mountain spotted fever, Brazilian spotted fever), and different tick species are responsible of its transmission to humans. Studies in Latin America show that ticks are rarely infected by *R. rickettsii* in nature, possibly due to the pathogenic effect of the rickettsia for ticks. Thus, transovarial transmission is not sufficient to maintain it in nature, and amplifier vertebrate hosts are needed to infected new tick lines through horizontal transmission (Labruna, 2009). In Brazil, *Amblyomma sculptum* and *A. aureolatum* ticks are the main vectors of *R. rickettsii* to humans and xenodiagnostic experiments have demonstrated that capybaras (*Hydrochoerus hydrochaeris*) and opossums (*Didelphis aurita*) act as amplifier host (Horta et al., 2009; Souza et al., 2009; Ramírez-Hernández et al., 2020a; 2020b). In other studies in South America, a wide variety of rodent species were examined, but *Rickettsia* spp. was found in a very low percentage and only in a few rodent species in Mexico, including *R. parkeri* identified in *Mus musculus* (Arroyo-Ramírez et al., 2023; López-Pérez et al., 2022a,b, Table 4).

3.1.2. Bats

Molecular studies have demonstrated the presence of *Rickettsia* sp. in European bats. In a study conducted in Hungary, 13 out of 221 (5.9 %) bat faecal samples were found to contain rickettsia DNA. These included sequences of a rickettsial insect endosymbiont, a novel *Rickettsia* genotype, and *R. helvetica* (Hornok et al., 2018a,b). Furthermore, a study conducted in Romania revealed a high prevalence of *R. monacensis* in two species of insectivorous bats, *Nyctalus noctula* and *Pipistrellus pipistrellus* (Matei et al., 2021). The study utilised PCR detection techniques, confirming the presence of *Rickettsia* DNA in 14.6 % of the bat samples. Furthermore, the presence of *Rickettsia* spp. DNA has been confirmed in bats in Africa. A study conducted across South Africa and Swaziland found diverse *Rickettsia* spp. in both insectivorous and frugivorous bats, as well as their blood-feeding ectoparasites. Subsequent analysis of the partial *glt*A sequence data has enabled the identification of bat-associated *Rickettsia* spp. that are closely related to *R. conorii* (Dietrich et al., 2016).

3.1.3. Game animals/ungulates

Only a few studies report the occurrence of *Rickettsia* DNA in tissues of wild living ungulates. Much more work concerns the ticks collected from these animals. In Europe, among game animals, cervids were particularly investigated since they are major hosts for *I. ricinus*, the most important tick vector in this region. *Rickettsia* spp. was reported in *Dama dama* and *Capreolus capreolus*, with a prevalence between 1.2 % and 3.3 % in Hungary and the Netherlands, respectively (Hornok et al., 2018a,b; Wijburg et al., 2022). The higher level of *R. helvetica* infections (6.3 %) was in the blood of Hungarian mouflons (Hornok et al., 2018a, b).

The interesting results were recorded in Kenya, where in topi (*Damaliscus lunatus jimela*), *Rickettsia* DNA was detected in 30 % of blood isolates, whereas in other ungulates the prevalence was an order of magnitude lower, or no DNA of the tested bacterium was detected (Ndeereh et al., 2017).

Wild boars are also suspected as having a role in rickettsial cycle. In

Table 4
Studies on molecular detection of *Rickettsia* spp. DNA from wild mammalian tissues in the Americas.

Country	Group of hosts	Host species	No. of positive rickettsial DNA (no of positive/examined/ %)	Species/genotypes of *Rickettsia* and Rickettsia Candidatus sp. (frequency)	Type of tissue sample examined	Detection technique	Reference
Brazil	carnivores	*Cerdocyon thous*	0/1/0 %	-	blood	PCR -*gltA, OmpA*	de Oliveira et al. (2020)
	carnivores	*Cerdocyon thous*	1/78/1.28 %	ND	blood	qPCR - *ompA*,17-kDa, *56-kD;* PCR -*gltA, OmpA, OmpB*,17 kDa	De Sousa et al. (2018)
		Nasua nasua	0/31/0 %	-			
		Leopardus pardalis	0/7/0 %	-			
	rodents	*Hydrochoerus hydrochaeris*	0/17/0 %	-	blood	Real-time PCR -*gltA*, PCR - *gltA, ompA*	Neves et al. (2023)
	rodents		0/21/0 %	-	blood	PCR -*gltA*	Yang et al. (2021)
			0/57/0 %	-	blood	PCR -*gltA, OmpA*	Quadros et al. (2021)
		Thrichomys laurentius	0/40/0 %	-	blood	PCR -*gltA, OmpA*	de Oliveira et al. (2020)
		Rhipidomys cariri	0/3/0 %	-			
		Calomys *expulsus*	0/2/0 %	-			
		Wiedomys pyrrhorhinos	0/2/0 %	–			
		Galea spixii	0/1/0 %	–			
		Kerodon rupestris	0/1/0 %	–			
		Rattus rattus	0/2/0 %	–			
		Thrichomys fosteri	0/77/0 %	–	blood	qPCR - *ompA*,17-kDa,56-*kDa*; PCR - *gltA, OmpA, OmpB*,17 kDa	De Sousa et al. (2018)
		Oecomys mamorae	0/25/0 %	-			
		Clyomys laticeps	0/8/0 %	-			
	marsupials	Monodelphis domestica	0/9/0 %	-	blood	PCR - *gltA, OmpA*	de Oliveira et al. (2020)
		Didelphis al biventris	0/7/0 %	-			
		Gracilinanus agilis	0/2/0 %	-			
		Thylamys macrurus	0/14/0 %	-	blood	qPCR - *ompA*,17-kDa,56-kDa; PCR - *gltA, OmpA, OmpB*,17 kDa	De Sousa et al. (2018)
		Gracilinanus agilis	0/11/0 %	-			
		Monodelphis domestica	0/4/0 %	-			
		Didelphis albiventris	0/1/0 %	-			
Mexico	rodents	*Mus musculus*	9/32/28.1 %	*R. parkeri* (1)	spleen	semi-nested PCR - *sca5* after propagation of *Rickettsia* on Vero cells	Arroyo-Ramírez et al. (2023)
		Peromyscus yucatanicus	1/3/33.3 %	ND			
		Ototylomys phyllotis	0/1/0 %	–			
	rodents	*Neotoma albigula*	0/4/0 %	–	ear tissue	PCR - *gltA, ompB*	López-Pérez et al. (2022)
		Neotoma lepida	0/7/0 %	–			
		Onychomys sp.	0/1/0 %	–			López-Pérez et al. (2022)
		Peromyscus boylii	6/103/5.8 %	ND			
		Peromyscus crinitus	0/29/0 %	–			
		Peromyscus eremicus	0/46/0 %	–			
		Peromyscus fraterculus	0/3/0 %	–			
		Peromyscus maniculatus	1/26/3.8 %	ND			
		Chaetodipus baileyi	0/12/0 %	–			
		Chaetodipus fallax	0/6/0 %	–			
		Chaetodipus formosus	0/5/0 %	–			
		Chaetodipus penicillatus	0/50/0 %	–			
		Chaetodipus spinatus	0/3/0 %	–			
		Dipodomys merriami	1/41/2.4 %	ND			
		Dipodomys simulans	0/24/0 %	–			
		Mus musculus	2/15/13.3 %	*R. typhi* (2)			
		Rattus rattus	1/2/50 %	*R. typhi* (1)			
		Neotamias merriami	0/5/0 %	–			
		Otospermophilus beecheyi	0/3/0 %	–			
		Spermophilus tereticaudus	0/3/0 %	–			
	carnivores	*Canis latrans*	1/6/16.7 %	*R. rickettsii* (1)	blood		
		Urocyon cinereoargenteus	0/3/0 %	–			
		Lynx rufus	0/4/0 %	–			
		Procyon lotor	0/3/0 %	–			

(*continued on next page*)

Table 4 (*continued*)

Country	Group of hosts	Host species	No. of positive rickettsial DNA (no of positive/examined/ %)	Species/genotypes of *Rickettsia* and Rickettsia Candidatus sp. (frequency)	Type of tissue sample examined	Detection technique	Reference
		Mephitis mephitis	0/4/0 %	–			
Peru	rodents	*Rattus rattus*	0/66/0 %	–	spleen	qPCR - *htrA*	Ferradas et al. (2025)
Trinidad, West Indies	rodents	*Dasyprocta leporina*	0/22/0 %	–	blood	qPCR- *gltA*	
	game	*Cuniculus paca*	0/1/0 %	–	blood	qPCR- ITS2	Sant et al. (2022)
Chile	marsupials	*Mazama americana*	0/1/0 %	–			Cabello et al. (2013)
	eutherians	*Didelphis*	0/15/0 %	–			
	game	*marsupialis*	0/2/0 %	–			
	carnivores	*insularis*	0/2/0 %	–			
		Dasypus novemcinctus *Tayassu tajacu* *Lycalopex fulvipes*	1/30/3.3 %	*Rickettsia* related to *R. felis*			
USA	game	*Odocoileus virginianus*	0/245/0 %	–	blood	TickPath layerplex qPCR test	Yu et al. (2020)
	carnivores	*Canis latrans*	0/122/0 %	–			
	carnivores	*Canis latrans*	4/138/2.9 %	*R. rickettsii* (4)	skin		Green et al. (2020)

ND = not determined.

Europe, *R. slovaca* was found in a wild boar skin biopsy in Tuscany, where SENLAT cases occur (Selmi et al., 2009). However, whether wild boars are able to develop a sufficient rickettsemia to infect feeding ticks or simply act as hosts for infected vectors remains unclear. A recent study showed that wild boars do not act as competent amplifying hosts of *R. rickettsii* for *A. sculptum* ticks in Brazil. Experimental infection of four wild boars through *R. rickettsii* – infected *A. sculptum* did not led to detectable rickettsemia (Neves er al., 2025). A moderate seroconversion was detected, as already shown in other serological studies (Sousa et al., 2024). However, wild boars are deemed important for to the dissemination of infected *A. sculptum*, especially in areas where competent hosts for *R. rickettsii* are present (Neves et al., 2023).

3.1.4. Primates

Studies on natural infection of *Rickettsia* in wild living primates are rare, but interesting. In Africa, in South Luangwa National Park, Zambia, spleen samples derived from 88 free-ranging non-human primates, comprising yellow baboons and vervet monkeys, were studied. Rickettsia DNA was detected in almost 40 % of isolates (Nakayima et al., 2014). Sequencing of selected positive samples revealed 99 % identity with *R. africae*, a known causative agent of African tick-bite fever. The other study from Central Africa analyzed over 1000 fecal samples from wild chimpanzees, gorillas, and bonobos. Using real-time PCR targeting the *gltA* gene, *Rickettsia* DNA was detected in 11 % of samples, with gorillas showing the highest positivity rate at 17.2 %. The sequences matched *R. felis*, a flea-borne pathogen known to infect humans (Keita et al., 2013). It is worth considering whether it is possible that the DNA was ingested or encountered through environmental contact (e.g., grooming behavior or eating contaminated food). The study conducted in Asia, in Malaysia, examined blood samples from 50 cynomolgus monkeys captured in residential areas. The *Rickettsia* DNA was confirmed in 24 % of blood samples, indicating that these monkeys were naturally infected.

These finding highlights the potential role of primates in the transmission cycles of *Rickettsia* species, which may have additional significance in the case of monkeys living near humans (e.g., urban or peridomestic macaques) that could be part of a zoonotic cycle of pathogens.

Research provided in Australia and South America has shown that marsupials do not play a role in the circulation and maintenance of *Rickettsia* spp. in the environment (de Sousa et al., 2018; de Oliveira et al., 2020; Gofton et al., 2021, Tables 3 and 4).

3.1.5. Carnivores

There is a broad consensus that wild and domestic carnivores constitute a substantial reservoir for tick-borne zoonotic agents transmitted to humans. The dynamics of tick-borne pathogen transmission are contingent upon the presence of diverse species of vertebrates in proximity, and, in such instances, the convergence of ecological niches among species engenders opportunities for parasites to expand their geographic distribution, abundance, and host range. Consequently, numerous newly discovered arthropod-borne pathogens that originated in wildlife have emerged or reemerged (Otranto et al., 2015; André, 2018).

The extant literature on the subject is inconclusive and limited in scope, with a paucity of studies examining the role of the red fox in the epidemiology of rickettsiosis. However, a recent study by Liu et al. (2021) has identified the presence of *R. raoultii* in the organs of three red foxes, *Candidatus* Rickettsia barbariae in the organs of a red fox, *R. sibirica* in the liver of a red fox, and *R. raoultii* in two tick species (*Ixodes canisuga* and *D. marginatus*) from foxes in China. Conversely, no foxes were found to be positive for *Rickettsia* spp. in Italy (Torina et al., 2013). In the same study, the flea pool that contained the two *Ctenocephalides felis* specimens also tested positive for *R. felis.*

Furthermore, the presence of *R. raoultii* DNA has been identified in feeding *I. ricinus* ticks removed from wolves in northwestern Spain (Del Cerro et al., 2022) and in *Dermacentor reticulatus* ticks removed from a migrating golden jackal (*C. aureus*) in Denmark (Klitgaard et al., 2017). Conversely, a study by Wymazał et al. (2024) revealed the absence of rickettsial DNA in the blood and tissue (muscle) samples of wolves from an expanding population in Eastern Europe (Poland). A similar finding was reported for the North American canid, the red wolf (*Canis rufus*), which was found to be devoid of *Rickettsia* DNA in its blood samples (Tyrrell et al., 2020).

On the other hand, a variety of rickettsiae are in circulation among wild canids in South America. Between the years 2005 and 2012, a survey was conducted on maned wolves (*C. brachyurus*) residing within the Serra da Canastra National Park (SCNP), a Cerrado preservation area located in the south-eastern region of Brazil (Arrais et al., 2021). Despite the absence of PCR-positive blood samples for *Rickettsia*, serological reactions were identified through the indirect immunofluorescence assay, which tested the serum samples from these wolves against the antigens of *R. parkeri, R. rickettsii, R. amblyommatis, R. rhipicephali,* and *R. bellii.* Of the wolves that were tested, 95 % (74/78) exhibited a positive reaction to at least one Rickettsia species, with *R. parkeri* producing the highest endpoint titers. Furthermore, some maned wolves that were recaptured during the study demonstrated a seroconversion to *R. parkeri.* Furthermore, molecular analyses conducted on ticks extracted from the aforementioned subjects revealed the presence of *Candidatus* Rickettsia andeanae and *R. parkeri* in adult *A. tigrinum* ticks (Arrais

Table 5
Studies on molecular detection of *Rickettsia* spp. DNA from wild mammalian tissues in Africa.

Country	Group of hosts	Host species	No. of positive rickettsial DNA (no of positive/examined/%)	Species/genotypes of *Rickettsia* and Rickettsia Candidatus sp. (frequency)	Type of tissue sample examined	Detection technique	Reference
southern Africa	rodents	*Rhabdomys* spp.	192/1223/15.7 %	*R. conorii* (4), *R. felis* (5), *R. helvetica* (3) *R. massiliae* (7), *Candidatus* R. africaustralis (11), *Candidatus* R. rhabdomydis (6), *Candidatus* R. muridii, Genotype R. hogsbackensis (1), Genotype R. stutterheimensis (1), Genotype R. kaalplaasensis (1)	Ear tissues	for initial screening rtPCR - partial *gltA;* for MLST - *ompB*, *ompA, 23S-5S, 16S, sca4, gltA*	Essbauer et al. (2018)
		Micaelamys namaquensis	17/99/17 %	*R. helvetica* (1)			
		Mastomys coucha	6/64/9 %	*Candidatus* R. africaustralis (3)			
		Mus musculus	3/61/5 %	*Candidatus* R. africaustralis (1), Genotype R. hofmannii (1)			
		Otomys irroratus	5/33/15 %	Candidatus R. rhabdomydis (1), Genotype R. stutterheimensis (1)			
		Myotomys unisulcatus	7/21/33 %	–			
		Lemniscomys rosalia	9/15/60 %	*R. massiliae* (1), Candidatus R. africaustralis (1), Candidatus R. rhabdomydis (1), Candidatus R. muridii (2)			
		Mastomys natalensis	0/12/0 %	–			
		Mus minutoides	0/11/0 %	–			
		Saccostomus campestris	0/11/0 %	–			
		Steatomys pratensis	0/11/0 %	–			
		Aethomys chrysophilus	4/9/44 %	Candidatus R. africaustralis (3), Candidatus R. rhabdomydis (1)			
		Rattus rattus	1/6/17 %	ND			
		Desmodillus auricularis	1/5/20 %	ND			
		Gerbillurus paeba	0/1/0 %				
	insectivores	*Crocidura mariquensis*	2/10/20 %	*R. helvetica* (1), Candidatus R. africaustralis (2)			
		Crocidura flavescens	0/9/0 %	–			
		Myosorex varius	1/6/17 %	ND			
		Macroscelides proboscideus	1/3/33 %	ND			
		Crocidura cyanea	1/2/50 %	*R. helvetica* (1)			
		Myosorex cafer	1/2/50 %	*R. helvetica* (1)			
		Elephantulus rupestris	0/1/0 %	–			
		Crocidura bicolor	0/1/0 %	–			
Democratic Republic of the Congo	rodents	*Rattus norvegicus*	12/106/11.3 %	*R. typhi*	spleen, heart, liver and kidney	real-time qPCR - *gltA* (for all spotted fever group rickettsiae (SFGR) and by *R. typhi*-specific qPCR - RTB9991CWPP_01310 gene	Laudisoit et al. (2014)
		Rattus rattus	4/20/20 %	*R. typhi*			
northeastern Algeria	wild animals	*Chiroptera* spp., *Sus scrofa algira,* cattle, sheep, boars and jackals, dogs, hedgehogs	0/16/0 %	-	spleen	qPCR - *gltA*	Leulmi et al., 2016
Namibia and Tanzania	carnivores (hyenas)	*Parahyaena brunnea*	1/17/5.9 %	*R. raoultii*	blood	PCR - *gltA*	Krücken et al. (2021)
		Crocuta crocuta	3/19/15.8 %	*R. raoultii*			
		Crocuta crocuta	0/25/0 %	-			
Zambia	primates	*Papio cynocephalus*	16/48/33.3 %	*R. africae*	spleen	PCR - *gltA*	Nakayima et al., 2014
		Chlorocebus pygerythrus	19/40/47.5 %	*R. africae*			
central Africa (Cameroon)	primates	*Pan troglodytes troglodytes*	39/313/12.5 %	*R. felis, R. felis*-like	Fecal samples	qPCR - *gltA, bioB*; PCR - *gltA, ompA*	Keita et al., 2013
		Gorilla gorilla gorilla	74/430/17.2 %	*R. felis, R. felis*-like			
The Democratic Republic of Congo	primates	*Pan paniscus*	8/285/2.8 %	*R. felis, R. felis*-like			
Kenya	ungulates	*Damaliscus lunatus* ssp. *jimela*	3/10/30 %	*R. sibirica*	blood	PCR - *rpmE*-tRNA^{fMet}, *gltA*	Ndeereh et al., 2017
		Kobus ellipsiprymnus ssp. *ellipsiprymnus*	0/2/0 %	-			
		Equus burchellii	1/39/2.6 %	ND			

(*continued on next page*)

Table 5 (*continued*)

Country	Group of hosts	Host species	No. of positive rickettsial DNA (no of positive/ examined/%)	Species/genotypes of *Rickettsia* and Rickettsia Candidatus sp. (frequency)	Type of tissue sample examined	Detection technique	Reference
		Connochaetes taurinus	1/35/2.9 %	ND			
		Syncerus caffer	1/31/3.2 %	ND			
		Alcelaphus buselaphus	0/5/0 %	-			
		Nanger granti	0/7/0 %	-			
South Africa and Swaziland	bats	*Miniopterus natalensis* *Nycteris thebaica* *Epomophorus wahlbergi* *Scotophilus dinganii* *Glauconycteris variegata*	5/384/1.3 %	*Rickettsia* sp.	blood	PCR - *gltA*	Dietrich et al. (2016)

et al., 2021).

A comparable pattern was identified in the case of the foxes examined. A total of 78 *C. thous* foxes from the Pantanal region of Brazil were sampled between 2013 and 2015 and subjected to serological and molecular testing. The results demonstrated that 75.6 % (59/78) of the animals exhibited seroreactivity to at least one *Rickettsia* species (*R. rickettsii, R. parkeri, R. amblyommatis*) in all subjects. Additionally, one crab-eating fox was also PCR-positive for SFG *Rickettsia*. Of the 1582 ticks removed from the tested foxes, predominantly of the *Amblyomma* spp. variety, 23.5 % were found to be PCR positive for SFG *Rickettsia*. Furthermore, 30 samples yielded evidence of *Candidatus* Rickettsia andeanae (de Sousa et al., 2018). Additionally, the Pampas fox (*Chrysocyon brachyurus*) and South American grey fox (*Lycalopex gymnocercus*) from the Brazilian Pampa were examined. It was found that 62.5 % (20/32) of the animals were seropositive for *R. parkeri.* Furthermore, 7.5 % (22/292) of the ticks collected from the aforementioned foxes were found to contain *R. parkeri* DNA. However, the pathogenicity of *R. parkeri* for domestic and wild canids remains unknown (Dall'Agnol et al., 2018). Additionally, DNA of rickettsiae was found in two desert kit foxes in California (Shultz et al., 2023).

In the study by Santoro et al. (2017), the authors presented evidence of *Rickettsia* pathogen infection in the Eurasian otter (*Lutra lutra*) from the southern Italian population for the first time. Despite the limited number of carcasses examined, the researchers employed molecular methods to demonstrate that Eurasian otters can be naturally infected by *Rickettsia* sp. A molecular test was employed to detect *Rickettsia*-specific for *R. conorii* and *R. rickettsii*, yet the test was unable to distinguish between the two species.

It has been hypothesized that coyotes residing in the USA may be involved in the dissemination of *R. rickettsii*. A study was conducted on coyotes from Arizona, USA, and the results revealed the presence of *R. rickettsii* antigen. Furthermore, polymerase chain reaction (PCR) analyses of skin samples from the same animals demonstrated evidence of *Rickettsia* spp. in 2.9 % (4/138) of samples, despite the inability to identify the specific rickettsial species (Green et al., 2020). Recently, *R. rickettsii* has been identified in the blood of a coyote from the US–Mexico transboundary region, confirming the susceptibility of this wild canid to the infection (López-Pérez et al., 2022a,b).

Research has demonstrated that wild hyenas, encompassing both spotted and brown varieties, have also been found to carry *Rickettsia* species. A study conducted in Namibia and Tanzania identified *R. raoultii* DNA in hyena (*Parahyaena brunnea* and *Crocuta crocuta*) blood samples (Krücken et al., 2021).

Furthermore, Szekeres et al. (2019) reported the detection of *Rickettsia* DNA in the muscle tissues of the European lesser weasel (*Mustela nivalis*) and *R. helvetica* in the stone marten (*Martes foina*). Additionally, procyonids have been shown to play a significant role in the epidemiology of rickettsial agents. For instance, serological evidence of exposure to *R. rickettsii, R. montana, R. parkeri*, and *R. bellii* (369-C strain) has been documented in raccoons in the USA (Castellaw et al., 2011; Rainwater et al., 2017; Tufts et al., 2020). Furthermore, molecular identification of other *Rickettsia* species has been documented in skin fragments from introduced raccoons in Germany and Poland (Hildebrand et al., 2022). These included R. *monacensis, R. raoultii, Candidatus* Rickettsia kotlanii-like, *R. helvetica*, and *Rickettsia* sp. endosymbionts, which were also identified in spleen tissue. Samples from feral raccoons introduced into Japan yielded the following *Rickettsia* species: *R. japonica, R. felis, R. heliongjiangensis/R. japonica, R. amblyommi, R. helvetica*, and *Rickettsia* sp. strain Hj126 (Sashika et al., 2010; Baba et al., 2012). In Brazil, *Rickettsia amblyommatis* and *R. bellii* were identified in *Amblyomma coelebs* and *A. ovale*, respectively, obtained from coatis in Iguaçu National Park (Paraná state) (Magalhães-Matos et al., 2021).

4. Conclusions and limitations

Despite significant progress in molecular biology, there are still significant gaps in our knowledge of *Rickettsia* infections in wild mammals, which hinders a comprehensive theoretical and practical understanding of these pathogens. The eco-epidemiological aspect of *Rickettsia* research is still far from completed for several reasons.

Limited knowledge of geography and taxonomy: The geographical and taxonomic coverage of research is limited, resulting in a fragmented understanding of *Rickettsia* species distribution. Research on *Rickettsia* frequently concentrates on certain regions or species, resulting in an incomplete representation of the global distribution and diversity of *Rickettsia* species (Kim, 2022). The restriction in scope and range of investigation results in findings that are not widely applicable.

In recent years, a significant diversity within rickettsiae has been revealed, and the number of rickettsiosis cases and cases of Rickettsia species transmission has increased significantly. This is reflected, among other things, in subsequent changes in the systematic position of individual taxa or epidemiological groups (Rymaszewska and Piotrowski, 2024). Furthermore, Rickettsiaceae includes both pathogenic and symbiotic organisms. However, recent molecular studies raise questions about the nature of strains classified as symbiotic that have been isolated from vertebrate tissues.

Emerging and novel species: The identification of novel *Rickettsia* species continues to exceed the capacity of our understanding of their epidemiology and pathogenic potential (Guccione et al., 2023). Emerging species may possess distinct transmission dynamics and host ranges, which hinder efforts to predict and manage outbreaks.

Detection sensitivity: The sensitivity of detection is a crucial consideration, as it can influence the accuracy and reliability of research

findings. While molecular techniques boast a high level of sensitivity, their inability to penetrate the intracellular nature of *Rickettsia* may hinder their capacity to identify low-level infections. This can result in underreporting and an incomplete understanding of infection prevalence (Guccione et al., 2023). Thus, there are difficulties in determining the competent definitive and reservoir hosts for individual Rickettsia species.

Despite the development of molecular methods used in the diagnosis of pathogens and parasites, it is still not possible to find fully satisfactory solutions for some of them. In the case of *Rickettsia* DNA detection from tissue isolates, a fragment of the *gltA* gene has been used for years (proposed by Roux et al., in 1997), and is still used. Its advantage is that, in comparison to other markers, it seems to be the most sensitive, however, the sensitivity is related to the use of a short fragment of the gene, but a short fragment does not allow for determining taxonomic distinctiveness. Fournier et al., in 2003 proposed multilocus sequence typing (MLST) using housekeeping genes as a tool for the effective classification of these bacteria, i.e., using 16S rRNA and *gltA* genes in the first step, and *ompA*, *ompB*, and the *D gene* in the second step. However, the analysis of the conducted studies (also those included in this review) shows that the proposed standard is difficult to implement, especially with the use of tissues. However, the analysis of the conducted studies (including those included in this review) shows that the proposed standard is difficult to implement, especially on tissue originating from wild mammals, and the *gltA* gene is still the most often used marker, not only in the screening step. Thus, the new proposition using a whole-genome sequence WGS for a new classification of rickettsial isolates (Diop et al., 2020) may encounter difficulties with bacteria obtained from natural sources.

Complex host-pathogen interactions: The interactions between *Rickettsia* and their mammalian hosts are complex and not yet fully understood (Kim, 2022). Further investigation is required to elucidate the mechanisms by which *Rickettsia* evade the immune responses of their mammalian hosts and establish themselves as infections.

Vector dynamics: The role of arthropod vectors, such as ticks, in the transmission of *Rickettsia* to wild mammals is well-documented; however, the dynamics of these interactions are not yet fully understood (Guccione et al., 2023). Further study is required on factors influencing the competence of vectors, seasonal variations in transmission dynamics, and environmental influences on vector populations.

In order to address these knowledge gaps, a multidisciplinary approach is essential, combining field studies, advanced molecular techniques, and collaborative efforts across regions and disciplines. Enhanced surveillance and improved diagnostic methods are essential for the advancement of our knowledge of *Rickettsia* in wild mammals. A deeper understanding of host-pathogen-vector interactions is also necessary for this purpose.

CRediT authorship contribution statement

Agnieszka Perec-Matysiak: Writing – review & editing, Writing – original draft, Supervision, Data curation, Conceptualization. **Katarzyna Buńkowska-Gawlik:** Writing – review & editing, Writing – original draft, Data curation, Conceptualization. **Laura Tomassone:** Writing – review & editing, Writing – original draft, Data curation. **Joanna Hildebrand:** Writing – review & editing, Writing – original draft, Data curation, Conceptualization.

Declaration of competing interests

The authors declare that they have no conflict of interest regarding the publication of this manuscript.

References

André, M.R., 2018. Diversity of *Anaplasma* and *ehrlichia/neoehrlichia* agents in terrestrial wild carnivores worldwide: implications for human and domestic animal health and wildlife conservation. Front. Vet. Sci. 23 (5), 293. https://doi.org/10.3389/fvets.2018.00293.

Arrais, R.C., Paula, R.C., Martins, T.F., Nieri-Bastos, F.A., Marcili, A., Labruna, M.B., 2021. Survey of ticks and tick-borne agents in maned wolves (*Chrysocyon brachyurus*) from a natural landscape in Brazil. Ticks tick. Borne Dis 12, 101639. https://doi.org/10.1016/j.ttbdis.2020.101639.

Arroyo-Ramírez, A., Lugo-Caballero, C., Panti-May, J.A., Reyes-Novelo, E., Rodríguez-Vivas, R.I., Noh-Pech, H., Suárez-Galaz, A., Osorio-Primo, T., Puerto, F.I., Dzul-Rosado, K., Torres-Castro, M., 2023. An unusual identification of *Rickettsia parkeri* in synanthropic rodents and domiciliated dogs of a rural community from Yucatán, Mexico. Zoon. Pub. Health 70, 594–603. https://doi.org/10.1111/zph.13068.

Baba, K., Kaneda, T., Nishimura, H., Sato, H., 2012. Molecular detection of spotted fever group rickettsia in feral raccoons (*Procyon lotor*) in the western part of Japan. J. Vet. Med. Sci. 75, 195–197. https://doi.org/10.1292/jvms.12-0143.

Borşan, S.D., Ionică, A.M., Galon, C., Toma-Naic, A., Peştean, C., Sándor, A.D., Moutailler, S., Mihalca, A.D., 2021. High diversity, prevalence, and co-infection rates of tick-borne pathogens in ticks and wildlife hosts in an urban area in Romania. Front. Microbiol. 12, 645002. https://doi.org/10.3389/fmicb.2021.645002.

Burri, C., Schumann, O., Schumann, C., Gern, L., 2014. Are *Apodemus* spp. mice and *Myodes glareolus* reservoirs for *Borrelia miyamotoi, Candidatus* Neoehrlichia mikurensis, *Rickettsia helvetica, R. monacensis* and *Anaplasma phagocytophilum*? Ticks Tick Borne Dis. 5, 245–251. https://doi.org/10.1016/j.ttbdis.2013.11.007.

Cabello, J., Altet, L., Napolitano, C., Sastre, N., Hidalgo, E., Dávila, J.A., Millán, J., 2013. Survey of infectious agents in the endangered Darwin's fox (*Lycalopex fulvipes*): high prevalence and diversity of hemotrophic mycoplasmas. Vet. Microbiol. 167, 448–454. https://doi.org/10.1016/j.vetmic.2013.09.034.

Castellaw, A.H., Chenney, E.F., Varela-Stokes, A.S., 2011. Tick-borne disease agents in various wildlife from Mississippi. Vector Borne Zoonotic Dis. 11, 439–442. https://doi.org/10.1089/vbz.2009.0221.

Cunze, S., Glock, G., Kochmann, J., Klimpel, S., 2022. Ticks on the move – climate change induced range shifts of three tick species in Europe: current and future habitat suitability for *Ixodes ricinus* in comparison with *Dermacentor reticulatus* and *Dermacentor marginatus*. Parasitol. Res. 121, 2241–2252.

Dall'Agnol, B., Souza, U.A., Weck, B., Trigo, T.C., Jardim, M.M.A., Costa, F.B., Labruna, M.B., Peters, F.B., Favarini, M.O., Mazim, F.D., et al., 2018. *Rickettsia parkeri* in free-ranging wild canids from Brazilian Pampa. Transbound. Emerg. Dis. 65, e224–e230.

Del Cerro, A., Oleaga, A., Somoano, A., Barandika, J.F., García-Pérez, A.L., Espí, A., 2022. Molecular identification of tick-borne pathogens (*Rickettsia* spp., *Anaplasma phagocytophilum, Borrelia burgdorferi* sensu lato, *Coxiella burnetii* and piroplasms) in questing and feeding hard ticks from North-Western Spain. Ticks Tick Borne Dis. 13, 101961.

de Sousa, K.C.M., Herrera, H.M., Rocha, F.L., Costa, F.B., Martins, T.F., Labruna, M.B., Machado, R.Z., André, M.R., 2018. *Rickettsia* spp. among wild mammals and their respective ectoparasites in Pantanal wetland, Brazil. Ticks Tick Borne Dis. 9, 10–17. https://doi.org/10.1016/j.ttbdis.2017.10.015.

de Oliveira, G.M.B., da Silva, I.W.G., da Cruz Ferreira Evaristo, A.M., de Azevedo Serpa, M.C., Silva Campos, A.N., Dutra, V., Nakazato, L., de Aguiar, D.M., Bahia Labruna, M., Horta, M.C., 2020. Tick-borne pathogens in dogs, wild small mammals and their ectoparasites in the semi-arid Caatinga biome, northeastern Brazil. Ticks Tick Borne Dis. 11, 101409. https://doi.org/10.1016/j.ttbdis.2020.101409.

Desvars-Larrive, A., Vogl, A.E., Puspitarani, G.A., Yang, L., Joachim, A., Käsbohrer, A., 2024. A one Health framework for exploring zoonotic interactions demonstrated through a case study. Nat. Commun. 15, 5650. https://doi.org/10.1038/s41467-024-49967-7.

Dietrich, M., Tjale, M.A., Weyer, J., Kearney, T., Seamark, E.C., Nel, L.H., Monadjem, A., Markotter, W., 2016. Diversity of *Bartonella* and *Rickettsia* spp. in bats and their blood-feeding ectoparasites from South Africa and Swaziland. PLoS One 21 (11), e0152077. https://doi.org/10.1371/journal.pone.0152077.

Eremeeva, M.E., Dasch, G.A., 2015. Challenges posed by tick-borne rickettsiae: Eco-epidemiology and public health implications. Front. Public Health 21 (3), 55. https://doi.org/10.3389/fpubh.2015.00055.

Essbauer, S., Hofmann, M., Kleinemeier, C., Wölfel, S., Matthee, S., 2018. *Rickettsia* diversity in southern Africa: a small mammal perspective. Ticks Tick Borne Dis. 9, 288–301. https://doi.org/10.1016/j.ttbdis.2017.11.002.

Ferradas, C., Salvatierra, G., Payahuanca, D., Contreras, W., López-Pérez, A.M., Hangawatte, T.A., León, D., Ghersi, B.M., Gamboa, R., Villanueva, K.M., Pinedo-Cancino, V., Pesapane, R., Salmón-Mulanovich, G., Lescano, A.G., Foley, J., 2025. Spotted fever group rickettsiae in black rats, pets, and humans in Zungarococha community, A rural area in the surroundings of Iquitos, Peru. Ticks Tick Borne Dis. 16, 102436. https://doi.org/10.1016/j.ttbdis.2024.102436.

Fischer, S., Spierling, N.G., Heuser, E., Kling, C., Schmidt, S., Rosenfeld, U.M., Reil, D., Imholt, C., Jacob, J., Ulrich, R.G., Essbauer, S., 2018. High prevalence of Rickettsia helvetica in wild small mammal populations in Germany. Ticks Tick Borne Dis. 9, 500–505. https://doi.org/10.1016/j.ttbdis.2018.01.009.

Gajda, E., Hildebrand, J., Sprong, H., Buńkowska-Gawlik, K., Perec-Matysiak, A., Coipan, E.C., 2017. Spotted fever rickettsiae in wild-living rodents from south-western Poland. Parasites Vectors 6 (10), 413. https://doi.org/10.1186/s13071-017-2356-5.

Galfsky, D., Król, N., Pfeffer, M., Obiegala, A., 2019. Long-term trends of tick-borne pathogens in regard to small mammal and tick populations from Saxony, Germany. Parasites Vectors 26 (12), 131. https://doi.org/10.1186/s13071-019-3382-2.

Gray, J.S., Dautel, H., Estrada-Pena, A., Kahl, O., Lindgren, E., 2009. Effects of climate change on ticks and tick-borne diseases in Europe. Interdiscip. Perspect. Infect. Dis., 593232 https://doi.org/10.1155/2009/593232.

Green, E.N., Porter, W.T., Howard, A.L., Yaglom, H., Benford, R., Busch, J.D., Nieto, N.C., 2020. Coyotes (*Canis latrans*) in Arizona, USA, exhibit immune and genetic evidence of rickettsial infections. J. Wildl. Dis. 56, 261–269.

Gual-Gonzalez, L., Self, S.C.W., Zellars, K., Meyer, M., Dye-Braumuller, K.C., Evans, C.L., Cantillo-Barraza, O., Torres, M.W., Nolan, M.S., 2024. Eco-epidemiology of *Rickettsia amblyommatis* and *Rickettsia parkeri* in naturally infected ticks (Acari: Ixodida) from South Carolina. Parasites Vectors 17, 33. https://doi.org/10.1186/s13071-023-06099-z.

Guccione, C., Colomba, C., Iaria, C., Cascio, A., 2023. Rickettsiales in the WHO European Region: an update from a one Health perspective. Parasites Vectors 30 (16), 41. https://doi.org/10.1186/s13071-022-05646-4.

Guillemi, E.C., Tomassone, L., Farber, M.D., 2015. Tick-borne rickettsiales: molecular tools for the study of an emergent group of pathogens. J. Microbiol. Methods 119, 87–97. https://doi.org/10.1016/j.mimet.2015.10.009.

Hansford, K.M., Gillingham, E.L., Vaux, A.G.C., Cull, B., McGinley, L., Catton, M., et al., 2023. Impact of green space connectivity on urban tick presence, density, and *Borrelia*-infected ticks in different habitats and seasons in three cities in southern England. Ticks Tick Borne Dis. 14, 102103. https://doi.org/10.1016/j.ttbdis.2022.102103.

Heglasová, I., Víchová, B., Kraljik, J., Mošanský, L., Miklisová, D., Stanko, M., 2018. Molecular evidence and diversity of the spotted-fever group *Rickettsia* spp. in small mammals from natural, suburban and urban areas of Eastern Slovakia. Ticks Tick Borne Dis. 9, 1400–1406. https://doi.org/10.1016/j.ttbdis.2018.06.011.

Heuser, E., Fischer, S., Ryll, R., Mayer-Scholl, A., Hoffmann, D., Spahr, C., Imholt, C., Alfa, D.M., FrƱhlich, A., Lıschow, D., Johne, R., Ehlers, B., Essbauer, S., Nцckler, K., Ulrich, R.G., 2017. Survey for zoonotic pathogens in Norway rat populations from Europe. Pest Manag. Sci. 73, 341–348. https://doi.org/10.1002/ps.4339. Epub 2016 Jul 29. PMID: 27299665.

Hildebrand, J., Perec-Matysiak, A., Popiołek, M., Merta, D., Myśliwy, I., Buńkowska-Gawlik, K., 2022. A molecular survey of spotted fever group rickettsiae in introduced raccoons (*Procyon lotor*). Parasites Vectors 7 (15), 162. https://doi.org/10.1186/s13071-022-05280-0.

Hornok, S., Sugár, L., Fernández de Mera, I.G., de la Fuente, J., Horváth, G., Kovács, T., Micsutka, A., Gönczi, E., Flaisz, B., Takács, N., Farkas, R., Meli, M.L., Hofmann-Lehmann, R., 2018a. Tick- and fly-borne bacteria in ungulates: the prevalence of *Anaplasma phagocytophilum*, haemoplasmas and rickettsiae in water buffalo and deer species in Central Europe, Hungary. BMC Vet. Res. 14, 98. https://doi.org/10.1186/s12917-018-1403-6.

Hornok, S., Szőke, K., Estók, P., Krawczyk, A., Haarsma, A.J., Kováts, D., Boldogh, S.A., Morandini, P., Szekeres, S., Takács, N., Kontschán, J., Meli, M.L., Fernández de Mera, I.G., de la Fuente, J., Gyuranecz, M., Sulyok, K.M., Weibel, B., Gönczi, E., de Bruin, A., Sprong, H., Hofmann-Lehmann, R., 2018b. Assessing bat droppings and predatory bird pellets for vector-borne bacteria: molecular evidence of bat-associated *Neorickettsia* sp. in Europe. Antonie Leeuwenhoek 111, 1707–1717. https://doi.org/10.1007/s10482-018-1043-7.

Horta, M.C., Moraes-Filho, J., Casagrande, R.A., Saito, T.B., Rosa, S.C., Ogrzewalska, M., Matushima, E.R., Labruna, M.B., 2009. Experimental infection of opossums *Didelphis aurita* by *Rickettsia rickettsii* and evaluation of the transmission of the infection to ticks *Amblyomma cajennense*. Vector Borne Zoonotic Dis 9. https://doi.org/10.1089/vbz.2008.0114, 109–18.

Inokuma, H., Seino, N., Suzuki, M., Kaji, K., Takahashi, H., Igota, H., Inoue, S., 2008. Detection of *Rickettsia helvetica* DNA from peripheral blood of Sika deer (*Cervus nippon yesoensis*) in Japan. J. Wildl. Dis. 44, 164–167. https://doi.org/10.7589/0090-3558-44.1.164.

Karbowiak, G., Biernat, B., Stańczak, J., Szewczyk, T., Werszko, J., 2016. The role of particular tick developmental stages in the circulation of tick-borne pathogens affecting humans in Central Europe. 3. Rickettsiae. Ann. Parasitol. 62, 89–100. https://doi.org/10.17420/ap6202.38.

Kazimirova, M., Chvostáč, M., Didyk, Y., Alba, P., Anabela, M., Purgatová, S., Selyemova, D., Tarageľová, V., Schnittger, L., 2024. The role of wildlife in the epidemiology of tick-borne diseases in Slovakia. Curr. Res. Parasitol V 6, 100195. https://doi.org/10.1016/j.crpvbd.2024.100195.

Kim, H.K., 2022. *Rickettsia*-host-tick interactions: knowledge advances and gaps. Infect. Immun. 15 (90), e0062121. https://doi.org/10.1128/iai.00621-21.

Kim, B., Lee, Y.-J., Kwak, D., Seo, M.-G., 2024. Nationwide survey of vector-borne diseases in rodents and mites in Korea: *anaplasma, Ehrlichia*, and *Rickettsia*. Animals 14, 2950. https://doi.org/10.3390/ani14202950.

Kipp, E.J., Lindsey, L.L., Khoo, B., et al., 2023. Metagenomic surveillance for bacterial tick-borne pathogens using nanopore adaptive sampling. Sci. Rep. 13, 10991. https://doi.org/10.1038/s41598-023-37134-9.

Klitgaard, K., Chriél, M., Isbrand, A., Jensen, T.K., Bødker, R., 2017. Identification of *Dermacentor reticulatus* ticks carrying *Rickettsia raoultii* on migrating jackal, Denmark. Emerg. Infect. Dis. 23, 2072–2074.

Krawczyk, A.I., van Duijvendijk, G.L.A., Swart, A., Heylen, D., Jaarsma, R.I., Jacobs, F.H.H., Fonville, M., Sprong, H., Takken, W., 2020. Effect of rodent density on tick and tick-borne pathogen populations: consequences for infectious disease risk. Parasites Vectors 13, 34. https://doi.org/10.1186/s13071-020-3902-0. PMID: 31959217; PMCID: PMC6971888.

Krücken, J., Czirják, G.Á., Ramünke, S., Serocki, M., Heinrich, S.K., Melzheimer, J., Costa, M.C., Hofer, H., Aschenborn, O.H.K., Barker, N.A., Capodanno, S., de Carvalho, L.M., von Samson-Himmelstjerna, G., East, M.L., Wachter, B., 2021. Genetic diversity of vector-borne pathogens in spotted and brown hyenas from Namibia and Tanzania relates to ecological conditions rather than host taxonomy. Parasites Vectors 16 (14), 328. https://doi.org/10.1186/s13071-021-04835-x.

Kuo, C.C., Shu, P.Y., Mu, J.J., Wang, H.C., 2015. High prevalence of *Rickettsia* spp. infections in small mammals in Taiwan. Vector Borne Zoonotic Dis. 15, 13–20. https://doi.org/10.1089/vbz.2014.1584.

Laudisoit, A., Falay, D., Amundala, N., Akaibe, D., de Bellocq, J.G., Van Houtte, N., Breno, M., Verheyen, E., Wilschut, L., Parola, P., Raoult, D., Socolovschi, C., 2014. High prevalence of *Rickettsia typhi* and *Bartonella species* in rats and fleas, Kisangani, Democratic Republic of the Congo. Am. J. Trop. Med. Hyg. 90, 463–468. https://doi.org/10.4269/ajtmh.13-0216.

Liu, G., Zhao, S., Tan, W., Hornok, S., Yuan, W., Mi, L., Wang, S., Liu, Z., Zhang, Y., Hazihan, W., Gu, X., Wang, Y., 2021. Rickettsiae in red fox (*Vulpes vulpes*), marbled polecat (*Vormela peregusna*) and their ticks in northwestern China. Parasites Vectors 19 (14), 204. https://doi.org/10.1186/s13071-021-04718-1.

López-Pérez, A.M., Sánchez-Montes, S., Maya-Badillo, B.A., Orta-Pineda, G., Reveles-Félix, S., Becker, I., Bárcenas-Barreto, K., Torres-Monroy, A., Ojeda-Flores, R., Sánchez-Betancourt, J.I., 2022a. Molecular detection of *Rickettsia amblyommatis* and *Rickettsia parkeri* in ticks collected from wild pigs in Campeche, Mexico. Ticks Tick Borne Dis. 13, 101844. https://doi.org/10.1016/j.ttbdis.2021.101844.

López-Pérez, A.M., Chaves, A., Sánchez-Montes, S., Foley, P., Uhart, M., Barrón-Rodríguez, J., Becker, I., Suzán, G., Foley, J., 2022b. Diversity of rickettsiae in domestic, synanthropic, and sylvatic mammals and their ectoparasites in a spotted fever-epidemic region at the western US-Mexico border. Transbound. Emerg. Dis. 69, 609–622. https://doi.org/10.1111/tbed.14027.

Magalhães-Matos, P.C., Araújom, I.M., Valim, J.R.A., Ogrzewalska, M., Guterres, A., Cordeiro, M.D., Cepeda, M.B., Fonseca, A.H.D., 2021. Detection of *Rickettsia* spp. in ring-tailed coatis (*Nasua nasua*) and ticks of the Iguaçu National Park, Brazilian Atlantic Rainforest. Ticks Tick Borne Dis. 13, 101891. https://doi.org/10.1016/j.ttbdis.2021.101891.

Mardosaitė-Busaitienė, D., Radzijevskaja, J., Balčiauskas, L., Paulauskas, A., 2018. First detection of *Rickettsia helvetica* in small mammals in Lithuania. New Microbes New Infect 22, 19–23. https://doi.org/10.1016/j.nmni.2017.12.012. PMID: 29556404; PMCID: PMC5857161.

Martello, E., Selmi, M., Ragagli, C., Ambrogi, C., Stella, M.C., Mannelli, A., Tomassone, L., 2013. *Rickettsia slovaca* in immature *Dermacentor marginatus* and tissues from *Apodemus* spp. in the Northern Apennines, Italy. Ticks Tick Borne Dis. 4, 518–521. https://doi.org/10.1016/j.ttbdis.2013.07.002.

Matei, I.A., Corduneanu, A., Sándor, A.D., Ionică, A.M., Panait, L., Kalmár, Z., Ivan, T., Papuc, I., Bouari, C., Fit, N., Mihalca, A.D., 2021. *Rickettsia* spp. in bats of Romania: high prevalence of *Rickettsia monacensis* in two insectivorous bat species. Parasites Vectors 10 (14), 107. https://doi.org/10.1186/s13071-021-04592-x. Erratum in: Parasit. Vectors. 6, 14:187. doi: 10.1186/s13071-021-04702-9. PMID: 33568213; PMCID: PMC7873661.

Medkour, H., Laidoudi, Y., Mariť, J.L., Fenollar, F., Davoust, B., Mediannikov, O., 2020. Molecular investigation of vector-borne pathogens in red foxes (*Vulpes vulpes*) from southern France. J. Wildl. Dis. 56, 837–850. https://doi.org/10.7589/2019-09-234. PMID: 32402231.

Medlock, J.M., Shuttleworth, H., Copley, V., Hansford, K.M., Leach, S., 2012. Woodland biodiversity management as a tool for reducing human exposure to *Ixodes ricinus* ticks: a preliminary study in an English woodland. J. Vector Ecol. 37, 307–315.

Minichová, L., Hamšíková, Z., Mahríková, L., Slovák, M., Kocianová, E., Kazimírová, M., Škultéty, L., Štefanidesová, K., Špitalská, E., 2017. Molecular evidence of *Rickettsia* spp. in ixodid ticks and rodents in suburban, natural and rural habitats in Slovakia. Parasites Vectors 24 (10), 158. https://doi.org/10.1186/s13071-017-2094-8.

Miťková, K., Berthová, L., Kalúz, S., Kazimírová, M., Burdová, L., Kocianová, E., 2015. First detection of Rickettsia helvetica and R. monacensis in ectoparasitic mites (Laelapidae and Trombiculidae) infesting rodents in south-western Slovakia. Parasitol. Res. 114, 2465–2472.

Nadolny, R.M., Wright, C.L., Sonenshine, D.E., Hynes, W.L., Gaff, H.D., 2014. Ticks and spotted fever group rickettsiae of southeastern Virginia. Ticks Tick Borne Dis. 5, 53–57. https://doi.org/10.1016/j.ttbdis.2013.09.001.

Neves, L.C., Paula, W.V.F., de Paula, L.G.F., da Silva, B.B.F., Dias, S.A., Pereira, B.G., Silva, B.S.A., Sevá, A.D.P., Dantas-Torres, F., Labruna, M.B., Krawczak, F.D.S., 2023. Detection of *Rickettsia* spp. in animals and ticks in Midwestern Brazil, where human cases of rickettsiosis were reported. Animals (Basel) 13, 1288. https://doi.org/10.3390/ani13081288.

Obiegala, A., Oltersdorf, C., Silaghi, C., Kiefer, D., Kiefer, M., Woll, D., Pfeffer, M., 2016. *Rickettsia* spp. in small mammals and their parasitizing ectoparasites from Saxony, Germany. Vet. Parasitol. Reg Stud. Reports. 5, 19–24. https://doi.org/10.1016/j.vprsr.2016.08.008.

Obiegala, A., Król, N., Oltersdorf, C., Nader, J., Pfeffer, M., 2017. The enzootic life-cycle of *Borrelia burgdorferi* (sensu lato) and tick-borne rickettsiae: an epidemiological study on wild-living small mammals and their ticks from Saxony, Germany. Parasites Vectors 13 (10), 115. https://doi.org/10.1186/s13071-017-2053-4.

Ogden, N.H., Beard, C.B., Ginsberg, H.S., Tsao, J.I., 2021. Possible effects of climate change on ixodid ticks and the pathogens they transmit: predictions and observations. J. Med. Entomol. 58, 1536–1545. https://doi.org/10.1093/jme/tjaa220.

Orkun, Ö., Çakmak, A., 2019. Molecular identification of tick-borne bacteria in wild animals and their ticks in Central Anatolia, Turkey. Comp. Immunol. Microbiol. Infect. Dis. 63, 58–65. https://doi.org/10.1016/j.cimid.2018.12.007.

Oteo, J.A., Portillo, A., 2012. Tick-borne rickettsioses in Europe. Ticks Tick. Borne Dis. 3, 271–278. https://doi.org/10.1016/j.ttbdis.2012.10.035.

Otranto, D., Cantacessi, C., Pfeffer, M., Dantas-Torres, F., Brianti, E., Deplazes, P., Genchi, C., Guberti, V., Capelli, G., 2015. The role of wild canids and felids in spreading parasites to dogs and cats in Europe. Part I: protozoa and tick-borne

agents. Vet. Parasitol. 30 (213), 12–23. https://doi.org/10.1016/j.vetpar.2015.04.022.
Overzier, E., Pfister, K., Herb, I., Mahling, M., Bųck Jr., G., Silaghi, C., 2013. Detection of tick-borne pathogens in roe deer (*Capreolus capreolus*), in questing ticks (*Ixodes ricinus*), and in ticks infesting roe deer in southern Germany. Ticks Tick Borne Dis. 4, 320–328. https://doi.org/10.1016/j.ttbdis.2013.01.004. Epub 2013 Apr 6. PMID: 23571115.
Portillo, A., de Sousa, R., Santibáñez, S., Duarte, A., Edouard, S., Fonseca, I.P., Marques, C., Novakova, M., Palomar, A.M., Santos, M., Silaghi, C., Tomassone, L., Zúquete, S., Oteo, J.A., 2017. Guidelines for the detection of *Rickettsia* spp. Vector Borne Zoonotic Dis. 17, 23–32. https://doi.org/10.1089/vbz.2016.1966.
Quadros, A.P.N., Rêgo, G.M.S.D., Silva, T.F.D., Carvalho, A.M., Martins, T.F., Binder, L. C., Castro, M.B., Mattos, P.S.R., Labruna, M.B., Paludo, G.R., 2021. Capybara (*Hydrochoerus hydrochaeris*) exposure to *Rickettsia* in the Federal District of Brazil, a non-endemic area for Brazilian spotted fever. Rev. Bras. Parasitol. Vet. 30, e028720. https://doi.org/10.1590/S1984-29612021035.
Rainwater, K.L., Marchese, K., Slavinski, S., Humberg, L.A., Dubovi, E.J., Jarvis, J.A., McAloose, D., Calle, P.P., 2017. Health survey of free-ranging raccoons (*Procyon lotor*) in Central Park, New York, New York, USA: implications for human and domestic animal health. J. Wildl. Dis. 53, 272–284. https://doi.org/10.7589/2016-05-096.
Ramírez-Hernández, A., Uchoa, F., Serpa, A.M.C., Binder, L.C., Rodrigues, A.C., Szabó, M.P.J., Fogaça, A., Souza, C.E., Labruna, M.B., 2020a. Clinical and serological evaluation of capybaras *(Hydrochoerus hydrochaeris*) successively exposed to an *Amblyomma sculptum*-derived strain of *Rickettsia rickettsii*. Sci. Rep. 10. https://doi.org/10.1038/s41598-020-57607-5.
Ramírez-Hernandez, A., Uchoa, F., Serpa, M.C.A., Binder, L.C., Souza, C.E., Labruna, M. B., 2020b. Capybaras (*Hydrochoerus hydrochaeris*) as amplifying hosts of *Rickettsia rickettsii* to *Amblyomma sculptum* ticks: evaluation during primary and subsequent exposures to *R. rickettsii* infection. Ticks Tick-Borne Dis 11, 101463. https://doi.org/10.1016/j.ttbdis.2020.101463.
Raoult, D., Fournier, P.E., Eremeeva, M., Graves, S., et al., 2005. Naming of Rickettsiae and rickettsial diseases. Ann. N. Y. Acad. Sci. 1063, 1–12.
Rungrojn, A., Chaisiri, K., Paladsing, Y., Morand, S., Junjhon, J., Blacksell, S.D., Ekchariyawat, P., Prevalence and molecular characterization of *Rickettsia* spp. from wild small mammals in public parks and urban areas of Bangkok metropolitan, Thailand. Trop. Med. Infect. Dis. 6:199. doi: 10.3390/tropicalmed6040199.
Rymaszewska, A., Piotrowski, M., 2024. *Rickettsia* species: genetic variability, vectors, and rickettsiosis – a review. Pathogens 13, 661. https://doi.org/10.3390/pathogens13080661.
Sant, C., Seunarine, D., Holder, N., et al., 2022. Tick-borne pathogens in neotropical animals in Trinidad, West Indies. Parasites Vectors 15, 62. https://doi.org/10.1186/s13071-022-05184-z.
Santibáñez, S., Portillo, A., Santibáñez, P., Palomar, A.M., et al., 2013. Usefulness of rickettsial PCR assays for the molecular diagnosis of human rickettsioses. Enferm. Infecc. Microbiol. Clín. 31, 283–288.
Santoro, M., D'Alessio, N., Cerrone, A., Lucibelli, M.G., Borriello, G., Aloise, G., Auriemma, C., Riccone, N., Galiero, G., 2017. The Eurasian otter (*Lutra lutra*) as a potential host for rickettsial pathogens in southern Italy. PLoS One 7 (12), e0173556. https://doi.org/10.1371/journal.pone.0173556.
Sashika, M., Abe, G., Matsumoto, K., Inokuma, H., 2010. Molecular survey of rickettsial agents in feral raccoons (*Procyon lotor*) in Hokkaido, Japan. Jpn. J. Infect. Dis. 63, 353–354.
Saslaw, S., Carlisle, H.N., 1966. Aerosol infection of monkeys with *Rickettsia rickettsii*. Bacteriol. Rev. 30, 636–645. https://doi.org/10.1128/br.30.3.
Selmi, M., Martello, E., Bertolotti, L., Bisanzio, D., Tomassone, L., 2009. *Rickettsia slovaca* and *Rickettsia raoultii* in *Dermacentor marginatus* ticks collected on wild boars (*Sus scrofa*) in Tuscany, Italy. J. Med. Entomol. 46, 1490–1493. https://doi.org/10.1603/033.046.0636.
Shultz, L., López-Pérez, A.M., Jasuja, R., Helman, S., Prager, K., Tokuyama, A., Quinn, N., Bucklin, D., Rudd, J., Clifford, D., Brown, J., Riley, S., Foley, J., 2023. Vector-borne disease in wild mammals impacted by urban expansion and climate change. EcoHealth 20, 286–299. https://doi.org/10.1007/s10393-023-01650-x.
Sousa, A.C.P., Suzin, A., da Silva Rodrigues, V., Rezende, L.M., da Costa Maia, R., Vieira, R.B.K., Szabó, M.P.J., 2024. Ticks (Acari: ixodidae) and rickettsiae associated with wild boars in a rural area of Minas Gerais, Brazil. Vet. Parasitol. Reg. Stud. Rep. 50, 101016. https://doi.org/10.1016/j.vprsr.2024.101016.
Souza, C.E., Moraes-Filho, J., Ogrzewalska, M., Uchoa, F.C., Horta, M.C., Souza, S.S., Borba, R.C., Labruna, M.B., 2009. Experimental infection of capybaras *Hydrochoerus hydrochaeris* by *Rickettsia rickettsii* and evaluation of the transmission of the infection to ticks *Amblyomma cajennense*. Vet Parasitol 161. https://doi.org/10.1016/j.vetpar.2008.12.010, 116–21.
Špitalská, E., Kraljik, J., Miklisová, D., Boldišová, E., Sparagano, O.A.E., Stanko, M., 2020. Circulation of *Rickettsia* species and rickettsial endosymbionts among small mammals and their ectoparasites in Eastern Slovakia. Parasitol. Res. 119, 2047–2057. https://doi.org/10.1007/s00436-020-06701-8.
Stewart, A.G., Stewart, A.G.A., 2021. An update on the laboratory diagnosis of *Rickettsia* spp. infection. Pathogens 10, 1319. https://doi.org/10.3390/pathogens10101319.
Szekeres, S., Docters van Leeuwen, A., Tóth, E., Majoros, G., Sprong, H., Földvári, G., 2019. Road-killed mammals provide insight into tick-borne bacterial pathogen communities within urban habitats. Transbound. Emerg. Dis. 66, 277–286. https://doi.org/10.1111/tbed.13019.
Tack, W., Madder, M., Baeten, L., Vanhellemont, M., Verheyen, K., 2013. Shrub clearing adversely affects the abundance of Ixodes ricinus ticks. Exp. Appl. Acarol. 60, 411–420. https://doi.org/10.1007/s10493-013-9655-0.
Takumi, K., Sprong, H., Hofmeester, T.R., 2019. Impact of vertebrate communities on *Ixodes ricinus*-borne disease risk in forest areas. Parasites Vectors 12, 434.
Tay, S.T., Koh, F.X., Kho, K.L., Sitam, F.T., 2015. Rickettsial infections in monkeys, Malaysia. Emerg. Infect. Dis. 21, 545.
Tay, S.T., Mokhtar, A.S., Low, K.C., Mohd Zain, S.N., Jeffery, J., Abdul Aziz, N., Kho, K. L., 2014. Identification of Rickettsiae from wild rats and cat fleas in Malaysia. Med. Vet. Entomol. 28, 104–108.
Torina, A., Blanda, V., Antoci, F., Scimeca, S., D'Agostino, R., Scariano, E., et al., 2013. A molecular survey of *Anaplasma* spp., *Rickettsia* spp., *Ehrlichia canis* and *Babesia microti* in foxes and fleas from Sicily. Transbound. Emerg. Dis. 60, 125–130. https://doi.org/10.1111/tbed.12137.
Tsao, J.I., Hamer, S.A., Han, S., Sidge, J.L., Hickling, G.J., 2021. The contribution of wildlife hosts to the rise of ticks and tick-borne diseases in North America. J. Med. Entomol. 16 (58), 1565–1587. https://doi.org/10.1093/jme/tjab047.
Tufts, D.M., Goodman, L.B., Benedict, M.C., Davis, A.D., VanAcker, M.C., Diuk-Wasser, M., 2020. Association of the invasive *Haemaphysalis longicornis* tick with vertebrate hosts, other native tick vectors, and tick-borne pathogens in New York City, USA. Int. J. Parasitol. 51, 149–157. https://doi.org/10.1016/j.ijpara.2020.08.008.
Tyrrell, J.D., Qurollo, B.A., Mowat, F.M., Kennedy-Stoskopf, S., 2020. Molecular prevalence of selected vector-borne organisms in captive red wolves (*Canis rufus*). J. Zoo Wildl. Med. 51, 663–667. https://doi.org/10.1638/2019-0162.
Wagner, E., Tukhanova, N., Shin, A., et al., 2022. Incidence of tick-borne spotted fever group *Rickettsia* species in rodents in two regions in Kazakhstan. Sci. Rep. 12, 14872. https://doi.org/10.1038/s41598-022-19145-0.
Walker, D.H., Ismail, N., 2008. Emerging and re-emerging rickettsioses: endothelial cell infection and early disease events. Nat. Rev. Microbiol. 6, 375–386.
Wijburg, S.R., Fonville, M., de Bruin, A., van Rijn, P.A., Montizaan, M.G.E., van den Broek, J., Sprong, H., Rijks, J.M., 2022. Prevalence and predictors of vector-borne pathogens in Dutch roe deer. Parasites Vectors 15, 76. https://doi.org/10.1186/s13071-022-05195-w. PMID: 35248157.
Wymazał, A., Nowak, S., Mysłajek, R.W., Bajer, A., Welc-Falęciak, R., Szewczyk, M., Kwiatkowska, I., Stępniak, K.M., Figura, M., Kloch, A., 2024. Tick-borne infections in wolves from an expanding population in Eastern Europe. Ticks Tick Borne Dis. 15, 102272. https://doi.org/10.1016/j.ttbdis.2023.102272.
Yang, W.H., Hsu, M.S., Shu, P.Y., Tsai, K.H., Fang, C.T., 2021. Neglected human *Rickettsia felis* infection in Taiwan: a retrospective seroepidemiological survey of patients with suspected rickettsioses. PLoS Neglected Trop. Dis. 15, e0009355. https://doi.org/10.1371/journal.pntd.0009355.
Yang, S.G.N.D.S., Souza, D.D.S.E., Santiago, A.C.D.S., Silva, R.B.S., Melo, M.A., Souza, E. A.R., Labruna, M.B., Horta, M.C., Oliveira, J.B., 2021. Rickettsial infection in free-ranging capybaras (*Hydrochoerus hydrochaeris*) and their ticks (Acari, Ixodidae) in the Caatinga and Atlantic forest biomes, Northeastern Brazil. Vet. Parasitol Reg. Stud. Rep. 26, 100649. https://doi.org/10.1016/j.vprsr.2021.100649.
Yu, S., Modarelli, J., Tomeček, J.M., French, J.T., Hilton, C., Esteve-Gasent, M.D., 2020. Prevalence of common tick-borne pathogens in white-tailed deer and coyotes in south Texas. Int. J. Parasitol. Parasites Wildl. 11, 129–135. https://doi.org/10.1016/j.ijppaw.2020.01.005.
Yuan, T.T., Ma, L., Jiang, B.G., Fu, W.M., Sun, Y., Jia, N., Jiang, J.F., 2020. First confirmed infection of *Candidatus* Rickettsia tarasevichiae in rodents collected from Northeastern China. Vector Borne Zoonotic Dis. 20, 88–92. https://doi.org/10.1089/vbz.2019.2443.
Zhang, J., Lu, G., Kelly, P., Zhang, Z., Wei, L., Yu, D., Kayizha, S., Wang, C., 2014. First report of *Rickettsia felis* in China. BMC Infect. Dis. 16, 682. https://doi.org/10.1186/s12879-014-0682-1.