

Chapter 7

The Changing Distribution Patterns of Ticks (Ixodida) in Europe in Relation to Emerging Tick-Borne Diseases

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Abstract Ixodid ticks are the most important vectors of human pathogens and are significant vectors of animal pathogens in Europe. Evidence is accumulating that several tick species have extended their distributions, related at least in part to climate and habitat changes. With increasing anthropogenic modification of the environment, these distributional modifications are likely to continue, with the likelihood that tick-borne diseases will spread to new areas. We discuss those factors which are involved in the changing distributions of ixodid ticks and provide a list of possible invading species given potential changes in tick habitat.

Keywords Climate change • Distribution • Invading species • Ixodidae • Vector-borne disease

7.1 Introduction

The ecological cycles of vector-borne zoonotic pathogens differ depending on the species and the hosts and host density, the species and density of arthropods which can act as vectors, and the transmission dynamics between the two. These parameters all influence the likelihood of transmission to humans. This ecology is naturally dynamic, not only between seasons, but also between years depending on changes in host and vector populations and environmental and climatic conditions (Randolph et al. 2002). Superimposed on these natural changes are major anthropogenic

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influences, such as land-use change, urbanization, human mobility, the introduction of invasive species, and global warming (Gilbert 2010; Reisen 2010). Unlike short-term natural variation, these changes are often long term and directional, such as the continuing trend to a warmer climate, or long-term and more or less abrupt, such as deforestation or reforestation (Foley et al. 2005; Rounsevell et al. 2006).

Studies on a wide variety of vector-borne disease systems have already established the likelihood that such dynamic environmental changes can have a strong influence on local and regional disease ecology (Patz et al. 2008). For example, malaria caused by *Plasmodium falciparum* is sensitive to rainfall and temperature changes, which can strongly influence the development and population dynamics of its mosquito vectors (Pascual et al. 2006). In addition, many mosquito species capable of transmitting malaria are highly sensitive to changes in land use (Yasuoka and Levins 2007; Imbahale et al. 2011), for example, deforestation in the northeast of Thailand has practically led to the eradication of malaria in this area (Petney et al. 2009).

Anthropogenic environmental changes are then an integral part of ecosystem change and, therefore, of changes in epidemiological cycles. Europe, for example, has been subject to the massive influence of humans on the environment from prehistoric times until now (Kalis et al. 2003; Schmidtchen and Bork 2003; Stoate et al. 2009). Intervention in the natural balance of the landscape started to increase from the end of the Stone Age owing to the growing density of the human population and incipient countrified landscape management (Jäger 1994; Rolle and Adroschko 1999; Ellenberg 2010). For instance, as early as 5500–1800 BC in the northern part and in the central and southern loess regions of Germany there were numerous peasants who cultivated the landscape, raised livestock, and let their cattle, pigs, sheep, and later also horses graze freely in the surrounding forests (Behre 2008; Ellenberg 2010). Such extensive grazing leads to the formation and maintenance of sites (e.g., neglected grassland) which serve as habitats for thermophilic species. During the seventh century AD, the first large-scale deforestation started, aimed at gaining arable farmland. A second phase of deforestation occurred because of the massive growth of the population in the thirteenth century (Heidel 2000). During the Neolithic the use of grassland and woodland led to the formation of heathlands, this formation reaching its maximum in the first half of the nineteenth century (Hallerbach 1994; Heidel 2000). The large open areas of heathland and farmland that developed by this means provide many native steppe inhabitants, such as the European brown hare (*Lepus europaeus*) and the wild rabbit (*Oryctolagus cuniculus*), with an optimal habitat, although today the subdivision of farmland into small lots has been widely replaced by large agricultural parcels (Schröpfer and Nyenhuis 1982; Pegel 1986; Kowarik 2010). The anthropogenic formation of such landscape is linked to a change in microclimatic factors, which can diverge strongly from the macroclimate and which create opportunities for microhabitat-specific arthropods to invade new environments (Ellenberg 2010).

In general, the emergence of a new disease in a certain area follows a set sequence involving introduction, establishment, and dispersal (Taraschewski 2006). In the case of vector-borne diseases, the requirements for each phase are

complex, depending on the presence or absence of suitable reservoir hosts and vectors. In some cases native species are capable of taking over the role of both of them. A recent review dealing with the introduction of West Nile virus into North America highlighted three important factors leading to the rapid success of this introduced pathogen: (1) the abundance of hosts and vectors in human-modified environments, (2) adaptation to local vectors, and (3) focused feeding leading to new and unexpected hosts (Kilpatrick 2011).

If the natural vector was introduced previously to or is introduced concurrently with the pathogen, the number of vector individuals introduced must be suitable for the establishment of a viable, reproducing population. The likelihood that such a population will develop in a new area is dependent on the conditions found in the off-host environment, on the presence of suitable hosts, on propagule pressure (the number of individuals introduced per introduction event and the number of such events), and on the source population of the vector. The habitat suitability in a specific area can change, for example, owing to global warming, in which case the natural dispersal of hosts and vectors into new habitats can occur (Fuente et al. 2004; Kowarik 2010).

Introduced plants can influence host species in complex ways, based not only on their suitability in terms of microclimatic conditions, but also on their acceptance by hosts. In Europe, mast production of the North American red oak (*Quercus rubra*) is greater than that of the native European oak (*Quercus robur*). As rodent populations are potentially regulated by such production (Ostfeld et al. 2006), the introduction of this species could have influenced the spread of rodent-associated viruses such as hantavirus (Tersago et al. 2008) and the populations of vector species such as ticks (Randolph 2001).

Ticks are the most important vectors of human and animal pathogens in the temperate Northern Hemisphere (Randolph 2001). In Europe, these pathogens include a wide variety of zoonotic viruses, bacteria, and protozoa which cause significant morbidity but only limited mortality (Süss et al. 2004; Süss and Schrader 2004). Although our database on changes in the density and distributions of tick populations is increasing continually, there is little predictive information on which species and diseases are likely to, or may, invade central European countries.

Our aims are (1) to consider the factors likely to influence the emergence of a new tick-borne disease in an area, (2) to consider what changes in the distribution patterns of ticks have been observed in central Europe over the last few decades, how these changes may be related to tick attributes and dynamic climatic and environmental factors, and how this may influence the emergence of tick-borne diseases, and (3) to speculate on potential future introductions into central Europe.

7.2 Tick Ecology

At a local level, the distribution of ticks and their hosts can be influenced by a variety of factors. Tick survival and rate of development are both dependent on temperature and humidity. Low and high temperatures and saturation deficits

preclude successful hatching. The microclimate is dependent on a variety of biotic and abiotic factors, such as the amount of vegetation present (shade and leaf litter provide lower temperatures but higher humidity) and the type of soil (water retention and potential interstitial refuges) (Merler et al. 1996; Schwarz et al. 2009). These factors are components of the habitat occupied by ticks. Hosts also have specific habitat preferences (see below), adding to the importance of habitat generally. Thus, each habitat must be considered separately in studies involving tick dynamics.

In one of the most comprehensive study on *Ixodes ricinus* to date, Estrada-Pena (2001) compared the abundance of ticks in 18 different habitats, defined by the vegetation present, over 3 years in Spain. He found that this species was absent from open, grassy habitats and hillsides as well as from young pine forest monocultures, and preferred sites with substantial secondary plant growth, in particular forests with oak species and fragmented forests with many ecotones. Estrada-Pena (2001) showed that 50% of the variation in tick abundance could be accounted for by temperature and vegetation characteristics of the habitat.

The dynamics of tick populations will follow the ecological changes occurring in a certain area depending on the habitat and host preferences of the different species. For the most important European vector species, *I. ricinus*, broadly assessed climatic conditions have a distinct influence on the activity patterns of all life history stages (Perret et al. 2004). For example, there has been a recent shift in the distribution of *I. ricinus* associated with higher average temperatures towards higher latitudes (Lindgren et al. 2000), as well as to higher altitudes (Daniel et al. 2003). Dautel et al. (2008) also suggested that the mild winter of 2006–2007 was responsible for the almost continuous yearly activity of *I. ricinus* in Berlin. Should such mild winters become more frequent, as predicted by climate models (Intergovernmental Panel on Climate Change data), the temporal window of exposure of the human population to tick-borne pathogens would increase. Not only *I. ricinus* is affected; *Dermacentor reticulatus* is not only increasing its area of distribution and population density, but is also moving out of its apparently preferred riparian habitats into drier, more forested areas (Dautel et al. 2006; Bullova et al. 2009).

Randolph (2001) suggested that the increases in both tick-borne encephalitis and Lyme borreliosis in central and northern Europe, as well as decreases in southern Europe, over the previous two decades may be due in part to changes in climate. She also pointed out that this problem has been increased by human-based land-use changes (e.g., habitat fragmentation), human behavior (e.g., outdoor recreation), and manipulation of host populations, which has allowed *I. ricinus* populations to increase in density. In addition, urban environments can differ from rural settings in the composition of the pathogen community in tick vectors. Fingerle et al. (2008), for example, showed unusually high prevalences of *Borrelia spielmanii* in the English Garden in Munich.

The predicted increases in temperature for Europe suggest that tick development will be accelerated during the coming decades if the predictions are correct. At the same time, tick survival is dependent on the humidity of the habitat occupied, with low humidity being unfavorable for survival and very high humidity potentially

conductive to fungal infections (Stafford and Allan 2010). Thus, climatic variation, either natural or with an anthropogenic origin, will influence how quickly the ticks develop, how long they survive, their activity period, and their transmission potential (Dautel et al 2008). To complicate this situation, the survivorship of ticks may depend on infection with a pathogen. *I. ricinus* infected with *Borrelia burgdorferi* sensu lato survived longer under various thermohygro-metric conditions than uninfected individuals (Herrmann and Gern 2010).

I. ricinus does not occupy a climatically homogeneous area. Estrada-Pena et al. (2006) showed that Europe contains nine groups of this species occupying climatically and ecologically significantly different areas. The differences in ecology are likely to play a major role in the dynamics of the host-tick pathogen system in these areas. During periods of glaciation, species would have been restricted to climatically suitable refuges and then would have moved to reoccupy their natural range as the climatic and host conditions became suitable again (Kowarik 2010).

Human-based land-use change has also undoubtedly influenced tick and tick-borne disease ecology from the earliest times. Deforestation to obtain agricultural land is likely to have reduced the population densities of *I. ricinus*, just as reforestation in the recent past will have increased the populations (Liebisch and Rahman 1976a, b). In the case of ticks, climate change has also been invoked as an agent causing expansion of the range of *I. ricinus* and *I. persulcatus* further to the north in Europe, in both cases accompanied by increasing prevalences of tick-borne encephalitis in the newly invaded areas (Gray et al. 2009; Tokarevich et al. 2011). Such change is consistent with the pattern found in many other species (Chen et al. 2011).

Habitat fragmentation, for example, via roads, may also be of significance, for example, by increasing host mortality or preventing or reducing the dispersal of non-avian hosts to new areas (Haemig et al. 2008; Petney et al. unpublished data). How this influences tick distribution is unknown, although preliminary data from the Hardtwald in northern Baden-Württemberg suggest that such fragmentation limits the dispersal of *D. reticulatus* (Petney et al. unpublished data).

7.3 Emergence of Tick-Borne Disease

Ticks generally have a very limited radius of movement (Crooks and Randolph 2006), so dispersal across geographical barriers must be accomplished via some additional transport mechanism. Europe is largely buffered from the natural movement of ticks from sub-Saharan Africa by the Sahara, although there is some potential for introductions via migratory birds (Waldenström et al. 2007; Elfving et al. 2010) or stock or companion animals (Menn et al. 2010). However, North African ticks are largely of Palearctic origin, and movement from this area across the Mediterranean is probably much more likely (Arthur 1965). Similarly, natural movement from the New World is blocked by the North Atlantic Ocean. Movement from Asia, however, is not blocked by any large-scale geographical barriers, and European species are found both in East Asia and in the Middle East (Pomerantzev 1950).

The potential for a particular species of tick to exist within an area is dependent on the macroclimate, which influences vegetation and the presence of host species, on microhabitat conditions present in relation to the tick's physiological requirements, and on the suitability of potential host species (Oliver 1989; Petney et al. 2011). These requirements differ widely between different tick species, with some being highly habitat and host specific, whereas others can be found in a wide variety of habitats and in or on a wide variety of hosts (Petney et al. 2011, 2012).

With increasing globalization, the movement of ticks through human activity has become increasingly possible. For example, transport times, which are significant in relation to the attachment times of ticks, have been vastly reduced over the last two centuries (Beierkuhnlein 2007; Kowarik 2010). There are numerous publications on the introduction of ticks to new countries via host animals (Keirans and Durden 2001; Burridge 2011). The most common example in central and northern Europe is the introduction of the brown dog tick, *Rhipicephalus sanguineus*, which is relatively host specific for dogs (Walker et al. 1999), with this host. *R. sanguineus* is the most widely distributed tick today, occurring throughout the world in temperate and tropical countries (Walker et al. 1999). In warmer areas it lives within the general environment; however, in the colder areas of Europe it is restricted to kennels or houses where the dogs live. It is introduced with those hosts that picked up the ticks in areas where the dogs' owners were on vacation, for example, in countries around the Mediterranean. Although it is not usually a direct problem for humans, *R. sanguineus* can multiply within this environment and reach high population densities (Kimmig et al. 2010). It is also a potential transmitter of *Rickettsia conorii*, the pathogen causing Mediterranean spotted fever, to humans (Kimmig et al. 2010). Central Europe and Norway also saw the introduction of the North American winter tick, *Dermacentor albipictus*, via the transport of horses (Lillehaug et al. 2002; Liebisch et al. 2006).

The emergence of tick-borne diseases within an area is therefore dependent on the environment as well as the hosts, tick species, and pathogens involved. Assuming that the environment is appropriate, one needs to know if suitable hosts for both the tick species and the pathogen are present. This is critical as the successful introduction of vertebrate species to an area is vastly less common than the introduction of arthropods (Pimentel et al. 2005). In this case, ticks with high host specificity are in general less likely to be successfully introduced unless that host is very common, as in the case of *R. sanguineus* and dogs, and *Rhipicephalus (Boophilus) microplus* and cattle (Cutullé et al. 2009). It is also necessary for these hosts to be sufficiently common to allow infestation and transmission rates that are high enough to maintain a reasonably stable enzootic cycle (Smith 1983).

For the further expansion and establishment of tick populations over wider areas, the radius of host movement is of critical importance. If a migratory species or one which moves across large distances, such as many bird species, is involved, then the transport of ticks to new areas is likely (Elfving et al. 2010). At the tick level, for an invading species not only is host specificity of importance but so is the number of

hosts required in the life cycle (one-, two-, or three-host tick) as this determines the attachment (or contact) time with the host and therefore the likely distance over which it can be transported. Analogous with infectious disease ecology, the infective dose is important, as, in the case of ticks, is its life history stage. If a single gravid female is introduced, it would be capable of starting a population, whereas several nymphs or larvae would have to be introduced for nonparthenogenetic species or populations. In addition, the likelihood of a nymph or larva successfully becoming an adult and finding a mate would depend on the number introduced and the likelihood of finding a host and successfully engorging and molting (Hayes and Barry 2008).

At the level of the pathogen, host and vector specificity are also of importance; the rapid spread of West Nile virus throughout most of the USA was directly dependent on the presence of suitable avian reservoir hosts over winter and on the presence of native vector species (Kilpatrick 2011). Coupled with this are the usual factors defined by epidemiological models, such as how readily transmission occurs, how long the infection persists in the host or the tick, and if the host builds an immunity to the pathogen (Anderson and May 1991).

7.4 The Case of Central Europe

The most important central European tick species acting as vectors are listed in Table 7.1. Slovenia has been excluded from the central European list as it has a Mediterranean climate and coastline. Of the species present, *I. ricinus* and *D. reticulatus* are known to be extending their distributional limits (Gilbert 2010). Information on other species is too limited to provide significant evidence of range extension.

On the basis of the criterion that a successful introduction is likely to be a non-nest-dwelling generalist species with relatively wide environmental tolerance or a more specialized species with avian or domestic animals as hosts, a list of the most likely candidates for invading ixodid tick species can be constructed (Table 7.2). In most cases, such introductions will become more likely with warmer, drier climates such as those in southern European and North Africa, although species which currently live where there are continental climatic conditions may also benefit. Eleven species (57.9%) occupy arid, semiarid, or steppe environments, whereas *Haemaphysalis inermis*, *Haemaphysalis parva*, *Hyalomma lusitanicum*, *Hyalomma marginatum*, *Ixodes gibbosus*, *Ixodes redikorzevi*, *Rhipicephalus turanicus*, and *Rhipicephalus (Boophilus) annulatus* are all found in less harsh Mediterranean climates. With the exception of *I. redikorzevi*, which has been most commonly reported from rodents and other small mammals, and *R. (B.) annulatus*, which is predominantly a cattle tick, all of these species have a wide host range which frequently includes stock and companion animals (Table 7.2). Of particular importance are those species associated with such hosts as well as those which infest

Table 7.1 Common central European ixodid tick species known to transmit pathogens to humans and animals

Species	Range	Pathogens	Range expansion	Range contraction	Direction	Higher altitude
<i>Dermacentor marginatus</i>	Europe	OHFV, spotted fever group rickettsiae (e.g., <i>Rickettsia slovaca</i> , <i>R. raoultii</i>), <i>Francisella tularensis</i> , <i>Borrelia burgdorferi</i> s.l. (e.g., <i>B. lusitanae</i>)	–	–	–	–
<i>Dermacentor reticulatus</i>	Central and eastern Europe	OHFV, spotted fever group rickettsiae (e.g., <i>R. slovaca</i> , <i>R. raoultii</i> , <i>R. helvetica</i>), <i>Coxiella burnetii</i> , <i>F. tularensis</i> , <i>Anaplasma phagocytophilum</i> , <i>Babesia canis</i>	Yes	No	East	
<i>Haemaphysalis concinna</i>	Europe	TBEV (<i>B. burgdorferi</i> s.l.), spotted fever group rickettsiae (e.g., <i>R. hulinii</i>), <i>F. tularensis</i>	–	–	–	–
<i>Haemaphysalis inermis</i> ^a	Eastern and southern Europe	High vector capacity for <i>R. helvetica</i> in Hungary				
<i>Haemaphysalis punctata</i>	Central and eastern Europe	TBEV, CCHFV	–	–	–	–
<i>Ixodes ricinus</i>	Europe	TBEV, <i>B. burgdorferi</i> s.l. and <i>Borrelia miyamotoi</i> , <i>A. phagocytophilum</i> , <i>Ehrlichia</i> spp. (e.g., <i>Ehrlichia canis</i>), <i>Bartonella</i> spp., spotted fever group rickettsiae (e.g., <i>R. helvetica</i> , <i>R. massiliae</i> , <i>R. monacensis</i>), <i>C. burnetii</i> , <i>F. tularensis</i> , <i>Babesia</i> spp. (e.g., <i>B. divergens</i> , <i>B. microti</i>)	Yes	No	North	Yes
<i>Rhipicephalus sanguineus</i>	Europe (introduced to central Europe)	<i>Ehrlichia</i> spp. (e.g., <i>E. canis</i>) spotted fever group rickettsiae (e.g., <i>R. conorii</i> , <i>R. siberica</i> , <i>R. rickettsi</i> , <i>R. massiliae</i>), <i>Babesia</i> spp. (e.g., <i>B. canis</i> , <i>B. gibsoni</i>)	No	No	–	No

Modified after Estrada-Pena and Jongejan (1999) and Petney et al. (2012)
OHFV Omsk hemorrhagic fever virus, TBEV tick-borne encephalitis virus, CCHFV Crimean-Congo hemorrhagic fever virus
^aSee Table 7.2, where *H. inermis* is also considered as it does not occur in the northern or western parts of central Europe

Table 7.2 Ixodid tick species with a significant vector capacity not currently occurring in central Europe (Germany) but with the potential to be transported to Germany

Species	Hosts required	Area of origin	Habitat	Generalist/ specialist (at least one life history stage)	Bird hosts	Stock animals	Dogs/cats	Humans	Major diseases isolated from, associated with, or known to be transmitted by
<i>Haemaphysalis inermis</i> (central European but not in Germany)	3	EE, SE	Deciduous forests at various altitudes	G	Yes	Yes	Yes	No	Paralysis in roe deer by heavy infestations, spotted fever group rickettsiae (e.g., <i>R. helvetica</i> , <i>R. aeschlimannii</i>)
<i>Haemaphysalis parva</i>	3	EE, SE	Steppe and lower montane forests; urban environments	G	No	Yes	Yes	Yes	<i>F. tularensis</i> , <i>Babesia ovis</i>
<i>Haemaphysalis sulcata</i>	3	EE, NA, SE	Lowland and montane semideserts and steppes	G	Yes	Yes	Yes	No	Bhanja virus, <i>Ehrlichia canis</i> , <i>Rickettsia</i> spp., <i>Anaplasma</i> spp., <i>Babesia</i> spp., and <i>Theileria</i> spp.
<i>Hyalomma anatolicum</i>	2/3	NA, SE	Semidesert, steppe and savanna stock grazing areas	S	No	Yes	No	Yes	CCHFV, Thogoto virus, <i>Theileria annulata</i> , <i>T. mutans</i> , <i>Babesia equi</i> , <i>B. caballi</i>
<i>Hyalomma asiaticum</i>	3	EE	Desert areas	G	Yes	Yes	Yes	No	CCHFV, <i>C. burnetii</i> , spotted fever group rickettsiae (e.g., <i>R. sibirica mongolitimonae</i> , <i>Theileria</i> spp., <i>Anaplasma</i> spp.)
<i>Hyalomma excavatum</i>	3	NA, SE	Semidesert, steppe and savanna nonagricultural habitats	S	Yes	Yes	Yes	Yes	CCHFV, <i>C. burnetii</i> , spotted fever group rickettsiae (e.g., <i>R. sibirica</i>), <i>Theileria</i> spp. (e.g., <i>T. annulata</i> ,

(continued)

Table 7.2 (continued)

Species	Hosts required	Area of origin	Habitat	Generalist/ specialist (at least one life history stage)	Bird hosts	Stock animals	Dogs/ cats	Humans	Major diseases isolated from, associated with, or known to be transmitted by
<i>Hyalomma impeltatum</i>	3	NA	Semidesert, steppe and savanna environments	G	Yes	Yes	No	Rarely	<i>T. parva</i> , <i>Babesia</i> spp. (e.g., <i>B. equi</i> , <i>B. ovis</i>) CCHFV, Dugbe virus, Wanowrie virus
<i>Hyalomma lusitanicum</i>	3	NA, SE	Forested areas with natural grass patches	G	No	Yes	Yes	Yes	Spotted fever group rickettsiae (e.g., <i>Rickettsia conorii</i>), <i>T. annulata</i> , <i>T. equi</i>
<i>Hyalomma marginatum</i>	2	EE, NA, SE	Mediterranean environments	G	Yes	Yes	Yes	Yes	CCHFV, OHFV, Astrakhan virus, Dhori and other arboviruses, spotted fever group rickettsiae (e.g., <i>R. aeschlimanni</i> , <i>R. conorii</i>), <i>F. tularensis</i> , <i>C. burnetii</i> , <i>Babesia</i> spp. (e.g., <i>B. equi</i> , <i>B. caballi</i>), <i>T. annulata</i>
<i>Hyalomma rufipes</i>	2	SE, NA	Savanna environments	G	Yes	Yes	Yes	Yes	CCHFV, Tete, Dugbe, Jos, and Bhanja viruses, <i>R. conorii</i>
<i>Hyalomma scupense</i>	1	EE, NA, SE	Areas with high moisture levels in arid areas	S	No	Yes	No	No	CCHFV, <i>C. burnetii</i> , <i>Theileria</i> spp. (e.g., <i>T. annulata</i>)
<i>Ixodes gibbosus</i>	3	SE	Deciduous forests and their ecotones with fields and grazing areas	G	Yes	Yes	No	No	Unknown

<i>Ixodes redikorzevi</i>	3	EE	Mediterranean environments; urban environments	S	Yes	No	Yes	Yes	Tick toxicosis, <i>A. phagocytophilum</i>
<i>Rhipicephalus bursa</i>	2	EE, NA, SE	Grassy areas, as well as arid shrub, steppe, and forest biomes	S	No	Yes	Yes	Yes	CCHFV, spotted fever group rickettsiae (e.g., <i>R. massiliae</i>), <i>A. marginale</i> , <i>A. ovis</i> , <i>Babesia</i> spp. (e.g., <i>B. bigemina</i> , <i>B. bovis</i> , <i>B. caballi</i> , <i>B. equi</i> , <i>B. motasi</i> , <i>B. ovis</i> , <i>Theileria</i> spp. (e.g., <i>T. ovis</i>))
<i>Rhipicephalus pumilio</i>	3	EE	Wide ranging from desert to humid habitats	G	No	Yes	Yes	Yes	CCHFV, spotted fever group rickettsiae (e.g., <i>R. conorii</i> <i>caspiensis</i>), <i>F. tularensis</i> , <i>C. burnetii</i>
<i>Rhipicephalus pusillus</i>	3	SE	Nest-dwelling; semiarid land and shrubland	S	No	No	Yes	No	Spotted fever group rickettsiae (e.g., <i>R. conorii</i> , <i>R. slovaca</i>)
<i>Rhipicephalus rossicus</i>	3	EE	Steppe and mountain steppe	G	No	Yes	Yes	Yes	CCHFV, <i>F. tularensis</i> , <i>C. burnetii</i>
<i>Rhipicephalus turanicus</i> ^a	3	NA, SE	Widely differing habitats; urban environments	G	Yes	Yes	Yes	Yes	Spotted fever group rickettsiae (e.g., <i>Rickettsia massiliae</i>), <i>C. burnetii</i> , <i>Babesia</i> spp. (e.g., <i>B. canis</i> , <i>B. traubmanii</i>)
<i>Rhipicephalus (Boophilus) annulatus</i>	1	EE, NA, SE	Mediterranean environments	S	No	Yes	Rarely	No	CCHFV, <i>Babesia bigemina</i>

Distribution and host information from Pomerantzev (1950), Balashov (1997), Manilla (1998), Walker et al. (1999), Wilamowski et al. (1999), Földvári et al. (2007), Kolonin (2009), and Guglielmo et al. (2010)

EE eastern Europe, NA North Africa, SE southern Europe (including Mediterranean Asia), G generalist, S specialist

^aThere is some taxonomic confusion in the *R. sanguineus/R. turanicus* species groups and these are currently undergoing systematic molecular analysis

birds, particularly migratory species, as these hosts provide a likely method of cross-border movement.

Taking all 19 species into account, 17 (89.5%) are found on stock (cattle, sheep, goats), 14 (73.7%) on companion animals, 10 (42.6%) on birds, and 11 (57.9%) have been reported from humans. *H. marginatum* and *Hyalomma rufipes* are known to reach central Europe irregularly, most likely via migratory birds (Siuda and Dutkiewicz 1979). The species belonging to the genera *Hyalomma* and *Rhipicephalus* are particularly significant vectors of both veterinary and medically important diseases. *H. marginatum*, for example, has been implicated in the introduction of Crimean-Congo hemorrhagic fever into Turkey in the late 1990s, with the first clinical cases being reported in 2002 (Estrada-Pena et al. 2010). Interestingly, neither single climate nor single vegetation variables could account for the spread of the disease; however, high levels of habitat fragmentation and connectivity were strongly associated with disease prevalence (Estrada-Pena et al. 2010).

One substantial problem in recognizing such emerging infectious diseases involves the continual advances being made in diagnostic medicine, as well as in our knowledge of the pathogens present in ticks, which may or may not have had a continual presence but have been unrecognized in the past, as is likely to be the case with tick-borne encephalitis (Süss 2008) or with several *Rickettsia* species (Walker et al. 2008; Dobler and Wölfel 2009). Another problem with tick studies is the lack of taxonomic expertise in several central European countries, including Germany, making the rapid and accurate identification of invading species difficult (Petney et al. 2012).

References

- Anderson RM, May RM (1991) Infectious diseases of humans: dynamics and control. Oxford University Press, Oxford
- Arthur DR (1965) Ticks of the genus *Ixodes* in Africa. Athlone, London
- Balashov YS (1997) Distribution of ixodid ticks (Acarina, Ixodidae) over landscapes within their ranges. *Entomol Rev* 77:625–637
- Behre KE (2008) Landschaftsgeschichte Norddeutschlands: Umwelt und Siedlung von der Steinzeit bis zur Gegenwart. Wachholtz, Neumünster
- Beierkuhnlein C (2007) Biogeographie: Die räumliche Organisation des Lebens in einer sich verändernden Welt. Ulmer, Stuttgart
- Bullova E, Lukan M, Satnko M, Petko B (2009) Spatial distribution of *Dermacentor reticulatus* tick in Slovakia in the beginning of the 21st century. *Vet Parasitol* 165:357–360
- Burridge MJ (2011) Non-native and invasive ticks: threats to human and animal health in the United States. Florida University Press, Gainesville
- Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026
- Crooks E, Randolph SE (2006) Walking by *Ixodes ricinus* ticks: intrinsic and extrinsic factors determine the attraction of moisture or host odour. *J Exp Biol* 209:2083–2142
- Cutullé C, Jonsson NN, Seddon J (2009) Population structure of Australian isolates of the cattle tick *Rhipicephalus (Boophilus) microplus*. *Vet Parasitol* 161:283–291

- Daniel M, Danielova V, Kriz B, Nozicka J (2003) Shift of the tick *Ixodes ricinus* and tick-borne encephalitis to higher altitudes in Central Europe. *Eur J Clin Microbiol Infect Dis* 22:327–328
- Dautel H, Dippel C, Oehme R, Hartelt K, Schettler E (2006) Evidence for an increased geographical distribution of *Dermacentor reticulatus* in Germany and detection of *Rickettsia* sp. RpA4. *Int J Med Microbiol* 296:149–156
- Dautel H, Dippel C, Kämmer D, Werkhausen A, Kahl O (2008) Winter activity of *Ixodes ricinus* in a Berlin forest. *Int J Med Microbiol* 298:50–54
- Dobler G, Wölfel R (2009) Fleckfieber und andere Rickettsiosen. Alte und neu auftretende Infektionen in Deutschland. *Deutsches Ärzteblatt* 106:348–354
- Elfving K, Olsen B, Bergström S, Waldenström J, Lundkvist A, Sjöstedt A, Mejlön H, Nilsson K (2010) Dissemination of spotted fever rickettsia agents in Europe by migrating birds. *PLoS One* 5:e8572
- Ellenberg H (2010) Vegetation Mitteleuropas mit den Alpen: In ökologischer, dynamischer und historischer Sicht. UTB, Stuttgart
- Estrada-Pena A (2001) Distribution, abundance, and habitat preferences of *Ixodes ricinus* (Acari: Ixodidae) in northern Spain. *J Med Entomol* 38:361–370
- Estrada-Pena A, Jongejans F (1999) Ticks feeding on humans: a review of records on human-biting Ixodoidea with special reference to pathogen transmission. *Exp Appl Acarol* 23:685–715
- Estrada-Pena A, Venzal JM, Sanchez Acedo C (2006) The tick *Ixodes ricinus*: distribution and climate preferences in the western Palaearctic. *Med Vet Entomol* 20:189–197
- Estrada-Pena A, Vatansever Z, Gargili A, Ergönül Ö (2010) The trend towards habitat fragmentation is the key factor driving the spread of Crimean-Congo haemorrhagic fever. *Epidemiol Infect* 138:1194–1203
- Fingerle V, Schulte-Spechtel UC, Ruzic-Sabljic E, Leonhard S, Hofmann H, Weber K, Pfister K, Strle F, Wilske B (2008) Epidemiological aspects and molecular characterization of *Borrelia burgdorferi* s.l. from southern Germany with special respect to the new species *Borrelia spielmanii* sp. nov. *Int J Med Microbiol* 298:279–290
- Földvári G, Márialigeti M, Solymosi N, Lukács Z, Majoros G, Kósa JP, Farkas R (2007) Hard ticks infesting dogs in Hungary and their infection with *Babesia* and *Borrelia* species. *Parasitol Res* 101:S25–S34
- Foley JA, Defries R, Asner GP et al (2005) Global consequences of land use. *Science* 309:570–574
- Fuente J, Naranjo V, Ruiz-Fons F, Vicente J, Estrada-Pena A, Almazán C, Kocan KM, Martín MP, Gortázar C (2004) Prevalence of tick-borne pathogens in ixodid ticks (Acari: Ixodidae) collected from European wild boar (*Sus scrofa*) and Iberian red deer (*Cervus elaphus hispanicus*) in central Spain. *Eur J Wildl Res* 50:187–196
- Gilbert L (2010) Altitudinal patterns of tick and host abundance: a potential role for climate change in regulating tick-borne diseases? *Oecologia* 162:217–225
- Gray JS, 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*. doi:[10.1155/2009/593232](https://doi.org/10.1155/2009/593232)
- Guglielmone AA, Robbins RG, Apanaskevich DA, Petney TN, Estrada-Pena A, Horak IG, Shao R, Barker SC (2010) The Argasidae, Ixodidae and Nuttalliellidae (Acari: Ixodida) of the world: a list of valid species names. *Zootaxa* 2528:1–28
- Haemig PD, Wladenström J, Olsen B (2008) Roadside ecology and epidemiology of tick-borne diseases. *Scand J Inf Dis* 40:853–858
- Hallerbach J (ed) 1994 Die Wahner Heide. Landschafts- und Nutzungsgeschichte. Naturschutz. Studie im Auftrag Bündnis 90/Die Grünen, Köln
- Hayes KR, Barry SC (2008) Are there any consistent predictors of invasion success? *Biol Invasions* 10:483–506
- Heidel A (2000) Der mittelalterliche Mittelgebirgsraum-Waldwirtschaft und Landschaftshaushalt. GRIN, München
- Herrmann C, Gern L (2010) Survival of *Ixodes ricinus* (Acari: Ixodidae) under challenging conditions of temperature and humidity is influenced by *Borrelia burgdorferi* sensu lato infection. *J Med Entomol* 47:1196–1204

- Imbahale SS, Paaijmans KP, Mukabana WR, Van Lammeren R, Githeko AK, Takken W (2011) A longitudinal study on *Anopheles* mosquito larval abundance in distinct geographical and environmental settings in western Kenya. *Malar J* 10:81
- Jäger H (1994) Einführung in die Umweltgeschichte. Wissenschaftliche Buchgesellschaft, Darmstadt
- Kalis AJ, Merkt J, Wunderlich J (2003) Environmental changes during the Holocene climatic optimum in Central Europe – human impact and natural causes. *Q Sci Rev* 22:33–79
- Keirans JE, Durden LA (2001) Invasion: exotic ticks (Acari: Argasidae, Ixodidae) imported into the United States. A review and new records. *J Med Entomol* 38:850–861
- Kilpatrick AM (2011) Globalization, land use, and the invasion of West Nile virus. *Science* 334:323–327
- Kimmig P, Pluta S, Naucke T (2010) Infektionsgefahr aus dem Süden. Globale Erwärmung. *Biol Unserer Zeit* 40:21–28
- Kolonin GV (2009) Fauna of ixodid ticks of the world. <http://www.kolonin.org/1.html>. Assessed 15 Nov 2011
- Kowarik I (2010) Biologische Invasionen: Neophyten und Neozoen in Mitteleuropa. Ulmer, Stuttgart
- Liebisch A, Rahman MS (1976a) Zum Vorkommen und zur vektoriellen Bedeutung der Zecken *Dermacentor marginatus* (Sulzer, 1776) und *Dermacentor reticulatus* (Fabricius, 1794) in Deutschland. *Tropenmed Parasitol* 27:393–404
- Liebisch A, Rahman MS (1976b) Zum Vorkommen und zur Ökologie einiger human- und veterinärmedizinisch wichtiger Zeckenarten (Ixodidae) in Deutschland. *Z Angew Entomol* 82:29–37
- Liebisch G, Paufler S, Liebisch A (2006) Ein aktueller Fallbericht über die Gefahr der Verbreitung von Zecken durch die Aktivitäten des Menschen: Import der Zeckenart *Dermacentor albipictus* aus den USA mit einem Pferd nach Deutschland. *Prakt Tierarzt* 87:874–882
- Lillehaug A, Mehl R, Gjerde B (2002) Importation of *Dermacentor albipictus* into Europe. *Vet Rec* 151:94–95
- Lindgren E, Tälleklint L, Polfeldt T (2000) Impact of climatic change on the northern latitude limit and population density of the disease-transmitting European tick *Ixodes ricinus*. *Environ Health Perspect* 108:119–123
- Manilla G (1998) Fauna d'Italia 36: Acari-Ixodida. Calderini, Bologna
- Merler S, Furlanello C, Chemini C, Nicolini G (1996) Classification tree methods for analysis of mesoscale distribution of *ixodes ricinus* (Acari: Ixodidae) in Trentino, Italian Alps. *J Med Entomol* 33:888–893
- Menn B, Lorentz S, Naucke TJ (2010) Imported and travelling dogs as carriers of canine vector-borne pathogens in Germany. *Parasit Vectors* 3:34
- Oliver JH Jr (1989) Biology and systematics of ticks (Acari: Ixodidae). *Annu Rev Ecol Syst* 20:397–430
- Ostfeld RS, Canham CD, Oggenfuss K, Winchcombe RJ, Keesing F (2006) Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. *PLoS Biol* 4:1058–1068
- Pascual M, Ahumada JA, Chaves LF, Rodó X, Bouma M (2006) Malaria resurgence in East African highlands: temperature trends revisited. *Proc Natl Acad Sci USA* 103:5829–5834
- Patz JA, Olson SH, Uejio CK, Gibbs HK (2008) Disease emergence from global climate and land use change. *Med Clin North Am* 92:1473–1491
- Pegel M (1986) Der Feldhase (*Lepus europaeus* Pallas) im Beziehungsgefüge seiner Um- und Mitweltfaktoren. Schriftenreihe des Arbeitskreis Wildbiologie und Jagdwissenschaft an der Justus-Liebig-Universität Gießen, vol 16. F. Enke, Stuttgart
- Perret J-L, Rais O, Gern L (2004) Influence of climate on the proportion of *Ixodes ricinus* nymphs and adults in a tick population. *J Med Entomol* 41:361–365
- Petney TN, Sithithaworn P, Satrawaha R, Grundy-Warr C, Andrews RH, Wang YC, Feng CC (2009) Potential for the re-emergence of malaria in northeast Thailand. *Emerg Inf Dis* 15:1330–1331

- Petney TN, Robbins RG, Guglielmone AA, Apanaskevich DA, Estrada-Peña A, Horak IG, Shao R (2011) A look at the world of ticks. *Parasitol Res Monogr* 2:283–296
- Petney TN, Pfäffle M, Skuballa J (2012) An annotated checklist of the ticks of Germany. *Syst Appl Acarol* (May)
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol Econ* 52:273–288
- Pomerantzev BI (1950) Fauna of the USSR, Arachnida, vol. IV, no. 2. Academy of Sciences USSR, Moscow
- Randolph SE (2001) The shifting landscape of tick-borne zoonoses: tick-borne encephalitis and Lyme borreliosis in Europe. *Philos Trans R Soc Lond B* 356:1045–1056
- Randolph SE, Green RM, Hoodless AN, Peacey MF (2002) An empirical quantitative framework for the seasonal population dynamics of the tick *Ixodes ricinus*. *Int J Parasitol* 32:979–989
- Reisen WK (2010) Landscape epidemiology of vector-borne diseases. *Annu Rev Entomol* 55:461–483
- Rolle R, Adroschko FM (1999) Frühe Nutzung pflanzlicher Ressourcen. LIT, Berlin
- Rounsevell MDA, Reginster I, Araújo MB et al (2006) A coherent set of future land use change scenarios for Europe. *Agric Ecosyst Environ* 114:57–68
- Schmidtchen G, Bork HR (2003) Changing human impact during the period of agriculture in Central Europe: the case study Biesdorfer Kehlen, Brandenburg, Germany. In: Lang A, Hennrich K, Dikau R (eds) *Lecture notes in earth sciences*, vol 101. pp 183–200. Springer, Heidelberg
- Schröpfer R, Nyenhuis H (1982) Die Bedeutung der Landschaftsstruktur für die Populationsdichte des Feldhasen (*Lepus europaeus* Pallas 1778). *Z Jagdwissenschaft* 28:213–231
- Schwarz A, Maier WA, Kistemann T, Kampen H (2009) Analysis of the distribution of the tick *Ixodes ricinus* L. (Acari: Ixodidae) in a nature reserve of western Germany using Geographic Information Systems. *Int J Hyg Environ Health* 212:87–96
- Siuda K, Dutkiewicz J (1979) *Hyalomma marginatum* Koch, 1844 (Acarina: Ixodidae) in Poland – an example of transport of southern tick by migratory birds. *Wiad Parazytol* 25:333–338
- Smith RD (1983) *Babesia bovis*: computer simulation of the relationship between the tick vector, parasite, and bovine host. *Exp Parasitol* 56:27–40
- Stafford KC, Allan SA (2010) Field applications of entomopathogenic fungi *Beauveria bassiana* and *Metarhizium anisopliae* F52 (Hypocreales: Clavicipitaceae) for the control of *Ixodes scapularis* (Acari: Ixodidae). *J Med Entomol* 47:1107–1115
- Stoate C, Baldi A, Beja P, Boatman ND, Herzon I, Van Doorn A, De Snoo GR, Rakosy L, Ramwell C (2009) Ecological impacts of early 21st century agricultural change in Europe – a review. *J Environ Manag* 91:22–46
- Süss J (2008) Tick-borne encephalitis in Europe and beyond—the epidemiological situation as of 2007. *Euro surveillance: bulletin européen sur les maladies transmissibles. Eur Commun Dis Bull* 13:270–277
- Süss J, Schrader C (2004) Durch Zecken übertragene humanpathogene und bisher als apathogen geltende Mikroorganismen in Europa. Teil 1: Zecken und Viren. *Bundesgesundheitsbl Gesundheitsforsch Gesundheitsschutz* 47:392–404
- Süss J, Fingerle V, Hunfeld KP, Schrader C, Wilske B (2004) Durch Zecken übertragene humanpathogene und bisher als apathogen geltende Mikroorganismen in Europa. Teil 2: Bakterien, Parasiten und Mischinfektionen. *Bundesgesundheitsbl Gesundheitsforsch Gesundheitsschutz* 47:470–486
- Taraschewski H (2006) Host and parasites as aliens. *J Helminthol* 80:99–192
- Tersago R, Verhagen A, Servais P, Heyman P, Ducoffre G, Leirs H (2008) Hantavirus disease (nephropathia epidemica) in Belgium: effects of tree seed production and climate. *Epidemiol Infect* 137:250–256
- Tokarevich NK, Tronin AA, Blinova OV, Buzinov RV, Boltenkov VP, Yurasova ED, Nurse J (2011) The impact of climate change on the expansion of *Ixodes persulcatus* habitat and the

- incidence of tick-borne encephalitis in the north of European Russia. Glob Health Action. doi:[10.3402/gha.v4i0.8448](https://doi.org/10.3402/gha.v4i0.8448)
- Waldenström J, Lundkvist A, Falk KI, Garpmo U, Bergström S, Lindegren G, Sjöstedt A, Mejlon H, Fransson T, Haemig PD (2007) Migrating birds and tickborne encephalitis virus. *Emerg Infect Dis* 13:1215–1218
- Walker JB, Keirans JE, Horak IG (1999) The genus *Rhipicephalus* (Acari, Ixodidae). A guide to the brown ticks of the world. Cambridge University Press, Cambridge
- Walker DH, Paddock CD, Dumler JS (2008) Emerging and re-emerging tick-transmitted rickettsial and ehrlichial infections. *Med Clin North Am* 92:1345–1361
- Wilamowski A, Bromley-Schnur HJ, Ioffe-Uspensky I, Uspensky I (1999) Ticks (Ixodoidea) in Israeli towns. In: *Proceedings of the 3rd international conference on urban pests*, Czech University of Agriculture, Prague, pp 477–483
- Yasuoka J, Levins R (2007) Impact of deforestation and agricultural development on anopheline ecology and malaria epidemiology. *Am J Trop Med Hyg* 76:450–460