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REVIEW

Changes in the occurrence range of hosts cause the expansion of the ornate dog tick *Dermacentor reticulatus* (Fabricius, 1794) in Poland

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Abstract
The turn of the twentieth and twenty-first centuries brought changes in the range of many pathogens and their vectors. An example is the *Dermacentor reticulatus* tick. So far, relatively not numerous, their range of occurrence was divided into two areas—western European and eastern. An increase in the number and spread of this tick has been observed since the 1990s. Possible causes may be changes in the average summer and winter temperature in Europe and changes in the structure and use of agricultural land and forest areas. Changes in the distribution and abundance of mammals which are the main hosts of adult ticks, such as elk *Alces alces*, red deer *Cervus elaphus,* raccoon dog *Nyctereutes procyonoides* and the red fox *Vulpes vulpes,* may be important factors as well. Increase in the size of the hosts populations correlates with the subsequent increase in numbers and the emergence of new tick populations. The food base of adult ornate dog ticks is a large herbivorous mammal population. Predatory mammals can support the expansion of the ticks. The expansion of the raccoon dog in the west correlates with the emergence of new *D. reticulatus* populations west to the previous border of the eastern range of their occurrence. The intrusion of foxes into inhabited areas may be a synanthropic factor that supports the rise of new tick populations in urban agglomerations.

Keywords Deer · *Dermacentor reticulatus* · Carnivores

Introduction

Ticks belong to the most dangerous blood-sucking arthropods targeting humans and pets. Their importance is emphasized by the fact that their harmfulness is not limited to the immediate consequence of blood feeding, but they are carriers of causative agents of several vector-borne diseases. Approximately 900 species of ticks are known worldwide, about 40 of which occur in Europe (Siuda 1993; Guglielmone et al. 2014; Estrada-Peña et al. 2017). As parasites directly dependent on environmental influences, ticks respond adequately to climate change with changes in their distribution and life cycles (Gray et al. 2009). The example among European species is the ornate dog tick *Dermacentor reticulatus* (Fabricius, 1794) (Bullová et al. 2009; Karbowiak and Kiewra 2010; Akimov and Nebogatkin 2011; Karbowiak 2014). The beginning of the expansion of this species occurred during the first decade of the twenty-first century, when an increase in the size of the existing populations and the emergence of new outbreaks in places previously free of these ticks were registered (Földvári et al. 2016).

Geographic range and environment of *Dermacentor reticulatus* until the end of the twentieth century

The ornate dog tick *D. reticulatus* inhabits open areas or areas slightly overgrown with trees and shrubs, moderately moist. It prefers natural deciduous forests with watercourses or large stagnant reservoirs. Therefore, these ticks are most abundant in riparian forests on the banks of rivers and lakes and in meadows at the edges of forests, at a relatively high level of groundwater, which prevents them from drying out (Siuda 1993; Földvári et al. 2016).

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Ornate dog ticks occur throughout the temperate zone of Eurasia, from England and France to the Yenisei basin in Siberia. According to Immler (1973), the range of the tick's occurrence is determined by the area characterized by spring rainfall from 400 to 1000 mm and limited by an isotherm of 20–22 ℃ for the summer. Until the beginning of the twenty-first century, the northern boundary of the range ran at 56–57° N latitude, and the southern one at 50° N latitude (Siuda 1993, 1995). The area where the tick was found is characterized by a phenomenon that is unheard of in other European ticks and is inherently completely rare. It is divided into two parts—the so-called western European area and eastern area (Immler 1973; Siuda 1993, 1995; Siuda et al. 1997). The western part of the range covered populations from France (Upper Southern Jurassic, Rhone Valley, Northern French Alps, Ardennes) (Gilot et al. 1973; Panas et al. 1976; Martinod and Gilot 1991) to the eastern part of Germany (Taurus Mountains, Black Forest, Bavaria) (Mačička et al. 1956) and most east of Leipzig (Bauch 1990). The ornate dog tick was most numerous in the east wing of the eastern part of Poland, through Belarus and along the European part of Russia to Siberia. The northern boundary of the range in Russia runs through Moscow, Ivanovo, Ryazansky, Sverdlovsk, Tyumen, part of the Omsk region, the cities of Novosibirsk and Kanski to the Kemerovo region (Ravdonikas et al. 1968; Chigirik and Pleshivtseva-Eroshkina 1969). In the Asian part of Russia, numerous populations extend to the North Caucasus and Eastern Transcaucasia. The southern border of the eastern range included the mountains of Crimea, pre-Caucasus, eastern Kazakhstan and in Kyrgyzstan the mountains of western Altai (Mačička et al. 1956). In Belarus, *D. reticulatus* was common in Polesye (Savitsky and Kulnazarov 1988). The populations of Polesye are directly related to the populations of *D. reticulatus* in Podlasie in Poland and should be treated jointly. In Ukraine, this tick was detected in the central part of the country, including the Kiev region and the Transnistrian Lowland (Brovko 1966; Akimov and Nebogatkin 2002). Part of the eastern range also included populations found in the eastern part of Slovakia and Romania, where *D. reticulatus* was relatively common (Metianu 1951).

The area in Europe where *D. reticulatus* was absent was approximately triangular, with the northern edge running along the Baltic coast and arms extending from central Germany, from meridian 12–13° E to meridian 19° E in Poland. The southern arms of the triangle converged, reaching the southern border of Hungary (Karbowiak and Kiewra 2010).

Changes in the distribution of *Dermacentor reticulatus* in recent decades

The area of *D. reticulatus* occurrence described above did not change from the first descriptions of this tick species until the turn of the 1970s and 1980s.In the 1980s, there was a tendency for this species to expand to the mentioned areas and to occupy new localities. At the same time, the number of previously known populations has increased significantly. It was visible all over Europe (Földvári et al. 2016). Until the 1970s, this tick was a rare species in Germany (Immler 1973). In recent years, it has appeared in large numbers in Saxony, Saxony-Anhalt, Brandenburg, and the population in Hesse and Bavaria has increased (Dautel et al. 2006). The emergence of new populations of *D. reticulatus* in eastern Germany is accompanied by the emergence of new populations in western Poland. There have been new outbreaks in the Dolnośląskie and Lubuskie voivodeship (Nowak 2011; Kiewra and Czułowska 2013; Cuber et al. 2013; Ciebiera et al. 2021). New locations also appeared in Great Britain, north of the previously known towns (Wall 2012). The northern border of the eastern range of the tick reached Lithuania at the beginning of the twenty-first century. It has now been shifted north to Latvia, where new populations have been discovered in places where *D. reticulatus* had not been present before (Paulauskas et al. 2015).

At the western borders of the eastern range, *D. reticulatus* became more numerous. In Poland, it was observed in Podlasie and Masuria and in the Lublin region (Karbowiak and Kiewra 2010; Zając et al. 2020). It also appeared in recreational areas of large urban agglomerations, where it had not been observed previously. To the west of the compact range, new populations are also emerging. New populations appeared in central Poland, far west of the Vistula (Mierzejewska et al. 2016). In Hungary, the species has been continuously expanding for three decades. Currently, it occurs throughout the country and is much more numerous (Sréter et al. 2005; Földvári et al. 2016). Like in Hungary, the expansion of the tick has been observed in Ukraine, where new populations have emerged south of the current range limit (Akimov and Nebogatkin 2011).

In Slovakia and the Czech Republic, *D. reticulatus* was a rare species until the 1980s. It was registered along the Danube and Bodrog rivers and on the border with Ukraine (Daniel et al. 1986). Only in the last decade, new populations appeared at a rapid pace (Labuda et al. 1989; Bullová et al. 2009). Apart from changes in distribution, an increase in the number of ticks was observed in the villages where it had been found as a rare species (Široký et al. 2011).

Factors determining the *D. reticulatus* distribution and reasons for changing its occurrence range

The reasons for the division of the area of distribution of *D. reticulatus* into two separate areas so far are unknown. Possible explanations relate to natural conditions and climate change. Since there are no geographic barriers

between the natural forest and meadow ecosystems of the Palearctic in the area that extends along the strip between the 50th and 55th parallel from France to the Urals, there is no reason to believe that this was the natural case. It can be assumed that human activity resulted in the factors causing the disappearance of *D. reticulatus* populations in this area. Perhaps it is related to the intense melioration and liquidation of small watercourses and reservoirs, and the reduction of the host populations (Daniel et al. 1986). However, this assumption is not supported by any evidence. Intensive human activity took place throughout the entire distribution range of *D. reticulatus* without causing its extinction. As records of the presence of the tick date back to the mid-nineteenth century (Koch 1844), it is currently impossible to state when the withdrawal of *D. reticulatus* from western Germany, central Poland and Slovakia occurred in this process.

Natural causes may be related to Europe's climatic structure. Central Poland is a transition zone between the oceanic and continental climate, and in this area, humid air masses flowing out of the Atlantic Ocean collide with dry masses of continental origin (Błażejczyk 2006). This, in turn, affects vegetation and the animal world associated with it. In Poland, there is a transition zone between plant communities and fauna associated with deciduous forests typical of the oceanic climate, and communities associated with coniferous forests typical of the continental climate. For this reason, the range boundaries of many species of animals and plants run through the center of Poland. It is estimated that 52% of species occurring in Poland are of a transitional nature, i.e., they occur both to the east and west of borders of the country. Other species end or begin their occurrence in Poland (Matuszkiewicz 2006).

These reasons do not fully explain the gap in the presence of *D. reticulatus*, as its eastern range ends in Poland, and reappears farther west. The same does not apply to the distribution of the common tick *Ixodes ricinus* Linnaeus, 1758, the range of which is uninterrupted.

Climate change related to global warming is mentioned among the factors responsible for the spread of the ornate dog tick to new areas. Secondly, attention is paid to environmental changes caused by human activity—changes in the use of agricultural and forest land, and the import of ticks during travel and trade (Földvári et al. 2016). Ecological corridors play an important role in linking remote areas with the features of natural ecosystems. River valleys are the most common. They are an attractive habitat for *D. reticulatus*, but also represent migration routes for wild animals and their pathogens. Ecological corridors are important both on a national scale, allowing ticks to spread along with their hosts, and on a smaller scale, enabling the colonization of parks and green areas within cities (Supergan et al. 2008; Zając et al. 2021). Numerous observations suggest that the ornate dog tick and common tick are characterized by a certain plasticity and the ability to occupy environments changed by human activity. Széll et al. (2006) even considered *D. reticulatus* as anthropophilic. In urbanized areas, ticks mainly inhabit recreational areas characterized by trees and / or shrub vegetation. In city parks, these are most often areas made up of natural plant communities, with at least partially preserved original vegetation (Karbowiak and Siuda 2001; Supergan and Karbowiak 2009).

The role of hosts in changes in the geographic range of *D. reticulatus*

Changes in the number and distribution of adult tick hosts may also be important. The role of mammals in the spread of pathogens is not new; in Poland, it was demonstrated in large ruminants infected with internal parasites (Dróżdż et al. 2002; Karbowiak et al. 2014). Migratory birds are an important factor in the particular distribution of ticks (Hasle 2013). On the other hand, the potential role of the lack of suitable hosts in limiting the distribution range of ticks to particular regions was assumed by Daniel et al. (1986) even before the phenomenon of *D. reticulatus* extending its geographical range was noticed. The most important hosts of ornate dog ticks are the European bison *Bison bonasus* (Linnaeus, 1758), European elk *Alces alces* (Linnaeus, 1758), red deer *Cervus elaphus* Linnaeus, 1758, roe deer *Capreolus capreolus* (Linnaeus, 1758), wild boar *Sus scrofa* Linnaeus, 1758, red fox *Vulpes vulpes* (Linnaeus, 1758), and raccoon dog *Nyctereutes procyonoides* (Gray, 1834) (Nowak-Chmura 2013). The number and size of the population of these mammals in Poland have increased in recent decades due to the protection and restoration of natural habitats. However, it seems that four of them are involved in extending the geographical range of *D. reticulatus* – European elk, red deer, red fox, and raccoon dog. These mammals play an important role as hosts of adult ticks, their infestation is high, they are relatively common, and are able to migrate on long distances. The range of *D. reticulatus* hosts is of course wide, but the role of other hosts is limited due to low infestation with ornate dog ticks compared to those mentioned above, low mobility or small population size. In some cases, like for the wild boar, there host role is difficult to demonstrate due to the lack of relevant data on tick infestations.

European elk *Alces alces*

After World War II, the elk turned out to be sparse in Poland as free-living populations occurred along the Biebrza River in eastern Poland. In addition, it was kept in breeding in the Kampinos Forest. From the 1950s, its populations and area

of distribution began to gradually increase, mainly in the eastern part of the country. At the beginning of the 1970s, the presence of 4–6 thousand elks in Poland was estimated. European elk growth was possible thanks to its successful reintroduction in the Kampinos National Park in 1956 and the emigration of animals from beyond the eastern border (Pucek and Raczyński 1983; Zalewski et al. 2018). The upward trend was not stopped by the beginning of hunting in the mid-1970s. In 1981, the number of elks in Poland was estimated at 6.2 thousand individuals. In the 1990s, a temporary breakdown in the number of elks and changes in the distribution of the elk population in Poland were observed. In 1999, three provinces of north-eastern Poland remained a significant mainstay: Białystok, Łomża and Suwałki, and the Chełm Province, lying at some distance. At that time, each of them harbored of over 100 elk individuals.

The reconstruction of the elk population in Poland, initiated at the beginning of the twenty-first century, was possible mainly due to local decisions refraining from hunting. Elk numbers increased mainly in the eastern part of the country. This mainly concerned Podlasie, where the density in spring 2008 was estimated at about 2–5 elk individuals per 1000 ha of forest, and the Lublin region, where the density was estimated at 2–4 specimens / 1000 ha. Elk were also relatively numerous in most districts of Mazovia (1–3 individuals / 1000 ha), while retreatments of refuges in southern and western Poland were much slower (Kamieniarz and Panek 2008). The entire population of elk in Poland in 2008 was estimated at 6000, in 2011 at 8000, and in 2017 at 20,000 individuals. The largest number is found in hunting districts in the north-eastern part of the country, where the elk density reaches 10 or more individuals per 1000 ha of forests (Kamieniarz and Panek 2008; Budny et al. 2011; Zalewski et al. 2018).

Red deer *Cervus elaphus*

At the end of the 1980s, red deer were found in most forest complexes in Poland. However, the density of these animals varied greatly. Quite high numbers were recorded in northern, western and southern Poland, lower in the central regions and most voivodeships in the east of the country. A constant increase in the number and size of the red deer population has been observed in every region of Poland. In the early 1990s, the number of red deer in the entire country was estimated at 85,000–90,000, and in the spring of 2007, at 154,000 individuals, almost twice as many. The highest density was recorded in the west and south of the country. In turn, the lowest densities of red deer were found in the center of the country, which is characterized by low forest cover. In 2016, the number of red deer reached 220,000. The increasing density is accompanied by behavioral changes—with a large number of red deer, they began to occur even in agricultural areas with low forest cover (Zalewski et al. 2018).

Raccoon dog *Nyctereutes procyonoides*

The raccoon dog breed comes from the forests of Northeast Asia. In 1928–1957, raccoon dogs were introduced as fur animals to the European part of the former Soviet Union. Raccoon dogs were intentionally released in Estonia, the St. Petersburg region and the Kola Peninsula. In some areas, raccoon dogs may have escaped from livestock farms and these individuals have created new populations (Heltai et al. 2000). Escaped and released animals began to colonize new areas to the north and west. Wild raccoon dogs soon appeared in Finland in 1935. In the 1950s, the first raccoon dogs appeared in Poland and Romania, in the 1960s in Germany, Czechoslovakia, Hungary and Austria, in the late 1970s in France, in 2001 in the Netherlands (Nowak and Pielowski 1964; Kauhala 1996; Kauhala and Kowalczyk 2011; Mulder 2012). By 1984, raccoon dogs had colonized an area of over 1,400,000 km^2. The European range of raccoon dogs is systematically growing, at a rate of 40 to 120 km per year (Kauhala 1996; Kauhala and Kowalczyk 2011). The current range of raccoon dogs in Europe includes the European part of Russia, Finland (except Lapland), Belarus, the Baltic States, Poland, most of Germany, Romania, Moldova, Ukraine, part of Bulgaria and Hungary. Single populations are also found in Sweden, Norway, the Netherlands, France, Switzerland, Austria (Kauhala 1996).

Raccoon dogs have been a component of the fauna of Poland since 1955. The population of this predator was spreading very quickly, in 1963 the raccoon dog was observed in at least 106 forest districts all over Poland, in 1971 in at least 238. In 1983 it occupied the entire north eastern and eastern Poland. Currently, it is found in large numbers throughout the country, with the exception of high altitudes in the mountains. Along with the increase in the range, the number of this species, despite intensive hunting, was constantly growing (Pucek and Raczyński 1983).

A possible cause of the described expansion of the raccoon dog is the decrease in mortality due to rabies, which these animals previously suffered from quite often. In the 1980s, the raccoon dog took second place—after the fox, on the list of animals with this disease. From the mid-1990s, the epidemiological threat began to decline due to the spread of oral vaccines designed to immunize the fox against rabies. This way, the role of one of the important mortality factors in the populations of raccoon dogs was limited (Kamieniarz and Panek 2008). The same trend in spread and similar habitat preferences of the raccoon dog and *D. reticulatus* ticks suggest an association of these phenomena. Raccoon dogs inhabit open or not very compact areas, moist deciduous and mixed forests, river valleys, lake shores and wetlands (Kauhala and Kowalczyk 2011). Ornate dog ticks occur in the same habitats, except in dense forests. Another biological feature associated with the expansion of both species is the

tendency of raccoon dogs to take long walks in new areas. During migration, animals carry ticks attached to their skin. Annually, the raccoon can move from 150 to almost 500 km (Kauhala and Kowalczyk 2011; Mulder 2012). Moreover, the fact of raccoon dog hibernation has been documented, which creates favorable wintering conditions for attached meadow ticks, and the ability to hibernate on their hosts has been documented (Karbowiak et al. 2003).

Red fox *Vulpes vulpes*

The territorial range of this species is one of the largest among all wild predatory mammals. According to hunting reports, the number of foxes in Poland in the 1970s and 1980s was estimated at 50,000 individuals and did not change significantly until the early 1990s. From around the middle of that decade, a noticeable increase in their population began, which continued until at least 2006, with an estimated number of about 204,000 individuals. In 2007–2008, the estimates of the number of these predators gave a slightly lower result, interpreted as stabilization of the population at a high level (Kamieniarz and Panek 2008; Zalewski et al. 2018). It is assumed that the most important reason for the increase in the population of this species is the introduction of anti-rabies vaccination. Apart from changes in the number and size of the population, changes in the biology of foxes are also observed (Goszczyński et al. 2008). Their preferred habitat type is and has always been a mosaic of forests and fields. However, there is an increasing occurrence and reproduction of foxes in the agricultural landscape, near human settlements, and even in urban areas. The second change concerns food resources. At the end of the 1990s, the diet of foxes was significantly more complex than before, and was composed of a certain proportion of domestic animals, mainly carcasses and carcass remains. This type of food replaced the once important prey, mainly hares, but also black grouse, which became less accessible to foxes due to a significant decline in their numbers in the 1990s. (Goszczyński et al. 2008; Panek and Budny 2017).

The positive effect of vaccination against rabies on the increase in the fox population was observed not only in Poland—a similar trend was reported in Germany (Vos 1995).

The role of the hosts in the expansion of *D. reticulatus*

Until the end of the twentieth century, the European elk (*A. alces*) was considered by many authors the most important host of the adult *D. reticulatus* ticks, due to the high infestation and overlapping range of both species (Dróżdż 1963; Kadulski 1989; Siuda 1993). It was confirmed by the large number of ticks collected from elk, similar habitat preferences and the overlapping of the elk area with the location of the most numerous populations of *D. reticulatus* (Dróżdż 1963, 1964; Szymański 1986; Kadulski 1989; Siuda 1993). Unfortunately, apart from the reports on the high prevalence and intensity of *D. reticulatus* infestation, none of the authors published detailed data. Only Bogdaszewska (2004, 2005), on the basis of the available individual animals, reported the prevalence from 75 to 100%. Due to the lack of systematic observations, it is difficult to say whether the spread of elk by the end of the 1980s in the northern and western parts of Poland could have contributed to the emergence of *D. reticulatus* populations. Ornate dog ticks were observed in the Kampinos Forest and West Pomeranian Voivodeship in the late 1990s (Szczurek 2001), i.e. before the assumed beginning of expansion, as well as in the Pomeranian Voivodeship at the beginning of its expansion, from the west to the border of the area of occurrence (Kadulski and Izdebska 2009). An undoubted relationship is the rapid, twofold increase in the number of elk in the first decade of the twenty-first century and the spread to previously rare areas, with the simultaneous increase in the population of ornate dog ticks and the emergence of their new habitats in the Masurian Lake District (Kamieniarz and Panek 2008; Kadulski and Izdebska 2009; Karbowiak 2014; Mierzejewska et al. 2016; Kubiak et al. 2018).

Red deer have always been numerous in Poland, but as hosts of adult *D. reticulatus*, they were recognized in the last decade of twentieth century, after intensive research on this species (Kadulski 1989; Dróżdż and Bogdaszewska 1997; Bogdaszewska 2005). These animals were common throughout the country, but the most numerous populations were found in the north-eastern regions, and strong tick populations were found at the same sites. Their role as hosts of *D. reticulatus* is indicated by the fact that numerous populations of ornate dog ticks survived in Poland in the post-war period, when elk practically did not occur. Recognition of the elk as the main host is also problematic due to the presence of *D. reticulatus* in western Germany and France, where this species of mammal has not been present in the wild for many decades. Specific data on the prevalence and the intensity of cervid infestation by *D. reticulatus* are rare but known. The increase in the number of these animals in recent decades may have contributed to the expansion of *D. reticulatus*, providing them with a food base. The aforementioned increase in the number of red deer in south-western Poland may be related to the emergence of new *D. reticulatus* outbreaks in this part of the country in 2000 and 2010 (Nowak 2011; Kiewra and Czułowska 2013). In the Lublin region, the infestation of red deer with *D. reticulatus* ticks in 2000 was 31.2% to 36.4% and was higher in bulls—36.9%—than in the case of females—15.4%. The authors noted that the infestation level differs depending on the region; it was

higher in the northern and eastern parts of the region, which was consistent with the reported range of the tick (Biaduń and Najda 2007).

The role of predatory mammals as hosts of *D. reticulatus* was appreciated in the latest decades only (Kočišová et al. 2006; Karbowiak et al. 2020). Carnivores are important hosts for immature as well as adult stages of ticks. Most studies report a mixed fauna of ticks on these animals. The common tick *I. ricinus* is the most common, followed by *Ixodes canisuga* Johnston, 1849 (also known as *I. crenulatus* Koch, 1844), *Ixodes hexagonus* Leach, 1815, *D. reticulatus*, and *Haemaphysalis concinna* Koch, 1844 in the south to the Carpathians. The infestation of foxes with *D. reticulatus* is the most variable. In Slovakia it reached 17.9% (Kočišová et al. 2006), in Poland 60.0% (Karbowiak et al. 2016, 2020), in Hungary 27% (Sréter et al. 2003). Until now, this tick has been considered rare in Germany, even in Berlin this tick was not found on foxes (Schöffel et al. 1991). The last time when a low level of infestation of foxes was recorded, was in Thuringia, Germany, where the incidence of these ticks was 0.29% (Meyer-Kayser et al. 2012).

The host's competence, biology and spread to new areas allow the raccoon dog to be included in the set of factors favoring the development of *D. reticulatus* ticks. Research conducted on raccoon dogs in the Augustów Primeval Forest in north-eastern Poland showed the presence of *D. reticulatus* infestation in above 39.3% of the animals, with an intensity of up to 20 ticks per individual. At the same time, there was a strong competition from the common tick *I. ricinus* (frequency 44.7%, intensity up to 40 individuals) (Karbowiak et al. 2016). Ticks attack these animals practically throughout the growing season. In earlier, single observations, more than 50 ornate dog ticks were found on a single raccoon dog, with no competition from other ticks. Therefore, it was confirmed that the raccoon dog is a competent host for the ornate dog tick (Karbowiak, unpbl.). Other species of ticks—the dog tick *I. crenulatus* and the hedgehog tick *I. hexagonus,* were found to infest a lower percentage of these animals (Karbowiak et al. 2016, 2020).

The role of red foxes and raccoon dogs as hosts for ticks does not differ significantly, it can be concluded that their infestation depends more on the presence of ticks in the environment than on the preferences of the host. Both species of mammals are characterized by a similar high mobility, ability to walk and the fact of a huge increase in the population size, which coincided with the increase in the number and expansion of *D. reticulatus*.

The direction of the spread of the raccoon dog is consistent with the expansion of the *D. reticulatus* tick in Poland. The first individuals of this predator appeared in Podlasie and Roztocze (Kauhala and Kowalczyk 2011), i.e. in the primary outbreak areas of this tick in Poland (Dróżdż 1963; Siuda 1993). At the same time, Dróżdż (1964) observed the fall of foxes and raccoon dogs in the spring, which he associated on the base of clinical symptoms with the appearance of *D. reticulatus* ticks and the piroplasms they transmit – unfortunately, he did not confirm the diagnosis by laboratory tests. The rate of expansion of the raccoon dog, of course, is well ahead of the expansion rate of the tick as the latter is dependent on the former. On the other hand, it takes at least many years for a new species of mammals to become a significant host for the parasite and, above all, to create a sufficiently large population (Fig. 1).

Overall, the increase in the host population contributed to an increase in the pre-expansion tick population density. Eastern Poland is a good example. In the 1960s, there were few ornate dog ticks in the vicinity of Lublin (Dutkiewicz and Siuda 1969), now it is the most common tick species (Zając et al. 2020). The same explanation may also be applied to the population growth of *D. reticulatus* in the Masurian Lake District (Kubiak et al. 2018). Biaduń and Najda (2007) noted the appearance of ornate dog ticks on red deer in 2007 near Piotrków Trybunalski, east of the San River, considered to be the western border of this tick in Poland. A similar result was obtained in Germany, also in the 2000s—*D. reticulatus* ticks were found on the heads of red deer obtained from towns in Brandenburg, Saxony-Anhalt,

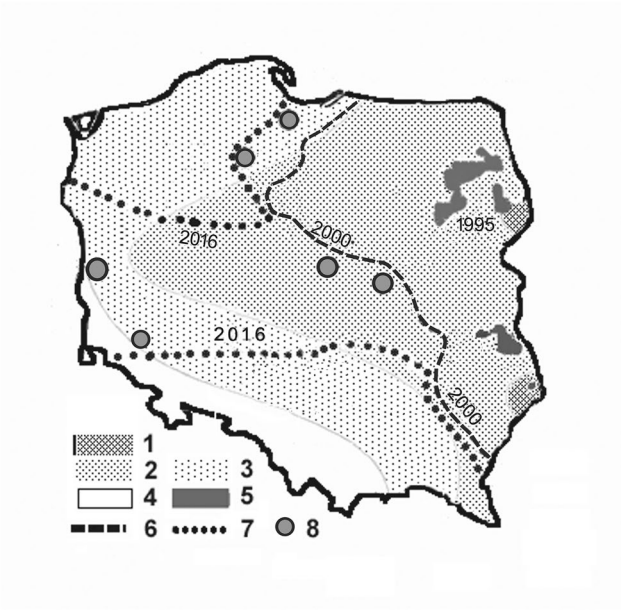

Fig. 1 The expansion of *Nyctereutes procyonoides* and *Dermacentor reticulatus* in Poland. 1 – the expansion range of raccoon dog in 1955; 2 – the expansion range of raccoon dog in 1955–1960; 3 – the expansion range of raccoon dog in 1960–1965; 4 – the expansion range of raccoon dog after 1965 (according to Kamieniarz and Panek 2008; Kauhala and Kowalczyk 2011); 5 – the known localities of *D. reticulatus* before 1995; 6 – the known range of *D. reticulatus* until 2000; 7 – the known range of *D. reticulatus* until 2016; 8 – the new records between 2000–2021

Hesse and Bavaria, where the tick had not been found before (Dautel et al. 2006).

The latest reports confirmed the existence of large mammals as carriers, as well as a tool supporting the development of the newly emerging population of the ornate dog tick in the Lubuskie voivodeship, where the prevalence of infestation of red deer and wild boars with these ticks was almost 100% (Ciebiera et al. 2021).

Due to the growing number of individuals, all the abovementioned species of mammals are looking for new habitats. As a result, they enter inhabited and developed areas, including recreational areas of cities (Bateman and Fleming 2012; Krauze-Gryz et al. 2016, 2020). The invasion of foxes into cities may be a factor that probably explains the emergence of new *D. reticulatus* outbreaks in large urban agglomerations. The emergence of new populations within the city limits, where ticks were previously absent, has been documented in Warsaw (Supergan and Karbowiak 2009; Karbowiak 2014). However, the role of large herbivores in cities in the reproduction of ticks is limited. They stay mainly on the outskirts of cities, in places directly related to suburban forests, and periodically visit city parks. A limited number of ticks can only be brought into cities with these hosts. The fox and the raccoon dog, thanks to their smaller size and greater behavioral plasticity, are able to permanently inhabit areas transformed by humans. In addition, they are able to overcome architectural barriers such as roads and fences. Therefore, they become an important factor in the survival of *D. reticulatus* populations in urban areas. A beneficial factor, seemingly not intricately related to the above, is the creation of ecological corridors for animals through landscape areas. Ecological corridors favor the expansion of many animal species, including predators, wild boars and external parasites carried on their bodies. This happens in many cities with rivers flowing. The strands of trees, as well as vast parks with varied vegetation, serve as a migration route for many species of wild animals through the city, with which the migrating ticks attach to their bodies. Dense downtown clusters of trees and shrubs create a local microclimate with lower temperatures and higher humidity than built-up areas (Szumacher 2005). This allows some animal species to live permanently in cities, and the engorged female ticks can lay eggs and develop larvae. The larvae are the beginning of new tick populations in human-inhabited areas.

The role of hosts in the expansion of *D. reticulatus* described above mainly concerns the territory of Poland, as a result of the analysis of Polish literature sources. In neighboring countries, hosts also must play an important role, but this may vary due to local differences in their numbers, and the simultaneous influence of other factors, such as local natural, climatic and geographical conditions (Karbowiak 2014; Földvári et al. 2016; Mierzejewska et al. 2016). To sum up, both elk and raccoon dog can play a big role in the countries north-east of Poland, where they are still numerous, but they do not have any role in Western Europe and south of the Carpathian Mountains, because they simply are rare or absent there (Schönfeld 2009; Bragina et al. 2018).

Declarations Not applicable.

Ethical approval The studies described were in compliance with all ethical principles.

Informed consent Not applicable.

Conflict of Interest As the corresponding author I state that there is no conflict of interest.

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