Annals of Parasitology 2015, 61(4), 221–228
doi: 10.17420/ap6104.11

Review articles

The role of particular tick developmental stages in the circulation of tick-borne pathogens affecting humans in Central Europe. 1. The general pattern[1]

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ABSTRACT. Tick-borne pathogens are common in the natural environment, but their occurrence has a focal character. They occur in the natural environment in the form of the enzootic sources of infection. The general components include the animal reservoir, amplifiers and the efficient vector. However, the particular role of components can differ depending on the pathogen, the host range and possible transmission routes. Animal reservoir of pathogen are vertebrate animals, being the hosts of pathogens. In Europe these are small or medium-sized mammals and sometimes birds that feed on the ground. The competence of an animal reservoir is determined by the ability to communicate the infection; long-term persistence of the pathogen in the host; long-duration of infectivity of the animal for ticks; a sufficient number of animals in the endemic region. Amplifiers for ticks are artiodactyls. They are hosts for nymphs and adult ticks, thereby making it possible for ticks to propagate and maintain the proper size of their population. Efficient vector for pathogen are ticks. The first characteristic feature of efficient vectors is feeding duration exceeding 24 hours; the high density of the tick population. The conditions necessary to consider ticks as efficient vectors are met in Central Europe by the *Ixodes ricinus*, *Dermacentor reticulatus* and *D. marginatus* ticks. There are the general differences in biology between *Ixodes persulcatus* complex ticks and *Dermacentor* ticks, affecting their different role and ability in pathogens spreading – the range of hosts; the ability to inhabiting of various environments and resistance to unfavourable conditions; the duration of larvae and nymphs activity. The combination of tick's biology, pathogen ability to transmission, and mammal hosts' competence, determines the particular role of larvae, nymphs and adults in pathogen circulation in the natural environment, as well as transmission to new hosts.

Key words: ticks, tick-borne pathogens, zoonotic foci

Introduction

Ticks are second to mosquitoes as vectors of human vector-borne pathogens worldwide. Among 29 hard tick species occurring in western and central Europe, three have a great epidemiological significance – *Ixodes ricinus*, *Dermacentor reticulatus* and *D. marginatus*. These species are common in Central European countries and are able to transmit pathogens of transmission diseases from the natural reservoir to human and domestic animals. Many authors emphasize also the ability of the *Rhipicephalus* ticks to spread tick-borne pathogens. However, this genus, not being a permanent component of Central European fauna, is able to play a marginal role only and has a noticeable epidemiological significance in the Mediterranean region of Europe, below the northern

[1]Results of the following research projects were used in the paper: MNiSW N303 047 31/1487 and NCN 2011/01/B/NZ7/03574.

latitude of 45° [1,2]. Similarly, another tick species important from the epidemiological point of view is *Ixodes trianguliceps*, most common in Great Britain and the Atlantic Coast countries, and able to maintain the zoonotic foci of tick-borne diseases [3–5]. However, it is not often found in Central Europe. Fourth tick species, *Ixodes hexagonus*, fed on hedgehogs and carnivores mainly, on rodents and artiodactyls practically not [1]. Although is quite common in Central Europe and can be infected by *Borrelia burgdorferi* s.l., their participation in the maintenance of human transmission diseases foci has few significance.

These tick species common in Central Europe belong to the three-host group. It means that every active developmental stage looks for a host in environment, attacks it and feeds, and leaves it engorged. Successive active developmental stages have different hosts preferences. Principally, ticks in bigger stages prefer bigger hosts, but it is not general rule. Engorged larvae and nymphs leave the host and undergo metamorphosis in the environment, and attack further hosts as nymphs or adult ticks. In this way, ticks feed on three hosts during their lifespan, often on different species. The above mentioned species transmit over 20 different tick borne-pathogens affecting humans and domestic animals, most important of which include the tick-borne encephalitis virus (TBEV), human granulocytic anaplasmosis (HGE), *Rickettsia* spp., *Borrelia burgdorferi*, *Babesia microti*, *B. canis*, *B. divergens*. Moreover, newly described pathogens were added to this list in the last decade, such as *Borrelia miyamotoi* and *Candidatus* Neoehrlichia micurensis and *Babesia venatorum*. Epidemiological surveys have documented the presence of these pathogens throughout Europe.

The general pattern of zoonotic foci structure

Tick-borne pathogens are common in the natural environment, but their occurrence has a focal character. Their holding depends on three etiological factors distinguished by Siński [6] as the structure pattern of the *Borrelia burgdorferi* zoonotic foci. They occur in the natural environment in the form of the so called enzootic sources of infection. The components include the animal reservoir, amplifiers and the efficient vector. This three-component pattern (disease agent, small mammal, big mammal) can be applied also to tick-borne infections other than *Borrelia burgdorferi*. However, the particular role of components can differ depending on the pathogen, the host range and possible transmission routes.

The animal reservoir (zoonotic reservoir, maintenance host)

This component of zoonotic foci consists in the first place in vertebrate animals, being the hosts of pathogens and the first source of infection for ticks, and thus named the competent reservoir. In Europe these are wild mammals, depending on the pathogen species either small (rodents, insectivores) or medium-sized mammals (hares, foxes), and sometimes even birds that feed on the ground [6–9]. The competence of an animal to act as a reservoir host for microorganisms is determined by several parameters: the ability to communicate the infection and survive the agent for some time; long-term persistence of the pathogen in the infected host; long-duration of infectivity of the animal for ticks; there must be a critical number of infectious agents and no resistance by the host to the tick feeding. The competence make possible the ability to amplify the infection in a focus by transmitting the agents to numerous vectors [10,11]. Another important factor is a sufficient number of animals in the endemic region as well as their even distribution [12,13]. Rodents are most significant as animal reservoirs. The fact that rodent populations commonly are numerous, dense and infested with large numbers of key vector species underlies this. Rodents serve as hosts for large numbers of immature ticks. Their activity enables the spread of disease agents and infected ticks to new areas. Ticks, due to their limited motility, are not able to travel distances over several meters [14]. The disadvantage of small mammals is their short lifespan in the natural environment, not longer than several months. Thus, *B. burgdorferi* s.l. and other tick-borne pathogens affecting small mammals survive winter in the tick vector rather than in the reservoir rodent.

Apart from the role as pathogen reservoir and source of infection for ticks, small mammals play the crucial role as hosts for ticks' larvae and nymphs, maintaining the tick population in the environment [15].

Some authors distinguish between different types of reservoirs. The first type is the true reservoir, comprising species able to maintain the infection alone; the second type is the accessory reservoir, comprising animals maintaining the infection secondary to the main reservoir; the third type is the opportunistic reservoir, comprising accidentally infected animals without serious consequences; the fourth type is the potential reservoir, comprising animals theoretically susceptible to infection but not identified as such in practice [16].

Amplifiers for ticks

The second element in the circulation of tick-borne pathogens are artiodactyls, such as deer or grazing livestock. They are hosts for nymphs and adult ticks, thereby making it possible for ticks to propagate and maintain the proper size of their population. For some pathogens, these animals are not competent hosts and are therefore considered to be "amplifier hosts" for ticks [6,9,17]. However, possible variation of pathogen prevalence in questing ticks in relation to the density of wild cervids has been observed according to pathogen species, increment or reduction [18,19]. Removal of such hosts can significantly reduce exophilic tick abundance [5,19].

Efficient vector for pathogen

The third group of animals, ticks, is considered to be efficient vectors. The first characteristic feature of efficient vectors is feeding duration exceeding 24 hours, which secures pathogen transmission to mammal hosts [20]. The second requirement is the high density of the tick population in a region many times exceeding the density of mammals and birds living in a biotope. This secures the prevalence of tick infestation of small rodents between 40 and 80% with at least several larvae or nymphs simultaneously. Moreover, rodents are infested with ticks for a long time, because their majority gets infested repeatedly.

This combined system ensures efficient circulation of pathogens among vectors and animal reservoirs and its resistance to seasonal and long-term changes in the number of its particular components [21]. Its stability is determined by the constancy of its microstructure, i.e. by the duration of topic and trophic relationships among pathogens, vectors and host animals. Large and relatively stable populations of wildlife maintain the presence and circulation of pathogens. A favourable factor is the diversity of wildlife species. Ticks collected from places inhabited by a range of rodent and ruminant species, for example ecotons, contain pathogens more frequently than ticks collected from stable but not so much differentiated habitats [22].

The ways of pathogen transmission

The maintenance and circulation of pathogens in the natural environment requires their horizontal transfer between hosts and vectors, as well as within the vector and host populations. The infection of vertebrate hosts takes place during the feeding of the infected tick. Pathogens leave the organism of the tick with its saliva and are immediately injected into the subcutaneous tissue of the mammals. Unlike insects, ticks feed for a long time, generally about 2–3 days in the case of larvae, about week in the case of nymphs, and up to two weeks in the case of adult females. This fact determines the possibility of transfer and the range of transferred pathogens. In the case of viral, rickettsial and many bacterial pathogens, transfer of the infection to the host's blood during feeding within 24 hours is possible; in the case of pathogens that multiply slowly in ticks, or their multiplication is induced by feeding, the transfer occurs in the second phase of feeding. Females and males of *Ixodes* and *Dermacentor* tick species infected parenterally with TBEV at the adult or nymphal phase and containing the virus in their saliva are able to transmit the agent within minutes after biting a sensitive animal host [23].

Mammal infections may also occur orally. This has been documented in the case of *Babesia microti*, *B. canis* and viruses, which can infect new hosts when they swell infected blood. It is possible for example when males fight or in the case of cannibalism [24]. Another possibility consists in swallowing an infected tick, for example during fur grooming and combing.

Ticks may acquire pathogens in two ways – with the blood of infected hosts and through passage. Because the Ixodid ticks feed only once at each life stage, transmission within their population is a necessary component for their vectorial competence, because pathogens can be transmitted to another host only when the tick has progressed to its next developmental stage and feeds again. Transovarial transmission means a transfer of pathogens from adult female ticks to the next generation via the eggs.

Transstadial passage consists in the ability of pathogens to survive the moulting and metamorphosis of the larvae or nymphs to their next developmental stage. The transovarial and transstadial transmission within the population of ticks constitutes one of the most important factors determining pathogen circulation.

Apart from the above, there are other possible methods for circulation of tick-borne pathogens and infection with them. In many tick species, the sexual transmission from infected male to non-infected female ticks has been described; however, this process is unlikely to significantly propagate the infection in tick lineages; for example, sexually infected females do not appear to transmit rickettsiae transovarially [25]. The second method is cofeeding transmission. It occurs as several ticks feed in proximity on one host. Direct spread of bacteria from an infected tick to an uninfected one may occur during feeding at closely situated bite sites. The significance of this process is unknown, it depends on tick biology and the number of agents, get-away ticks. Tick biology limits this transfer to species feeding closely in one place, when many specimens make and use single haemorrhagic exudates in host skin. For example, such behaviour is observed in the *Rhipicephalus* ticks. In the case of Central European tick species, cofeeding of *Ixodes* and *Dermacentor* nymphs and adults is rarely observed. This behaviour is observed in the case of larvae; however, larvae attacking rodents come mostly from the same batch of eggs, and the probability of the cofeeding of larvae from an infected and an uninfected female is low. On the other hand, immature ticks prefer to attach to already damaged places on the skin (Karbowiak, unpublished), and interspecies transmission of infection is possible. Cofeeding infections among adult *I. ricinus* and *D. reticulatus* is still rarer. Although the range of their hosts largely coincides, the ticks often prefer different parts of mammal body to attach and feed [26,27].

The conditions necessary to consider ticks as efficient vectors are met in Central Europe by *I. ricinus*, *D. reticulatus* and *D. marginatus* ticks, while the role of *I. trianguliceps* and *I. hexagonus* ticks is less significant. Epidemiological papers usually define ticks as vectors with no analysis of the role of particular developmental stages in pathogen circulation. However, because of differences in habitat needs, hosts' preferences and life duration the roles can be quite different. The combination of tick's preferences, pathogen ability to transovarial and transstadial transmission, and mammal hosts' competence to infection, determine the particular role of larvae, nymphs and adults in pathogen circulation in the natural environment, as well as transmission to new hosts.

Common hard tick species vectoring tick-borne pathogens in Central Europe

Ixodes ricinus – this species belongs to the Ixodidae family, subfamily Ixodinae [28]. On the basis of occurrence, similar biology, host range and epidemiology it forms the *Ixodes persulcatus* species system with seven *Ixodes* species from Nearctic and Palaearctic zones [15]. This is the most ubiquitous tick in Europe, spread almost on the entire continent, excluding only its northern regions. In the east its range reaches Turkmenistan and northern Iran [28]. This tick occurs in a variety of habitats, including woodland, grassland, upland moor and heathland, where it acquires blood from a variety of hosts including rodents, birds, hares, livestock and deer. *I. ricinus* has a great variety of hosts – larvae and nymphs of this tick attack mainly small mammals – rodents and insectivores, while the nymphs attack also small carnivores like foxes, racoon-dogs and badgers, and adult ticks attack mainly medium-sized mammals, and less often ruminants, such as red deer, cattle and European bison. Only roe deer (*Capreolus capreolus*) is equally affected both by nymphs and adults [29]. Apart from these, small birds and lizards can be attacked, too. All developmental stages attack humans [27,28]. The preference of immature *I. ricinus* to *Apodemus* mice has been noted [30,31]. The prevalence and intensity of infestation differ depending on the host, season and habitat changes [31,32]. There are two activity peaks of adult *I. ricinus* – from March to the beginning of June and from September to October. Larvae and nymphs are active from March to October, with one activity peak in July–August. The activity duration is dependent on variations of weather conditions, and can shift in time [1,28,31,33]. The developmental cycle is normally completed during 3 years.

I. ricinus is the vector for tick-borne encephalitis virus, *Borrelia burgdorferi* s.l. spirochetes, *B. miyamotoi*, *Coxiella burnetii*, *Anaplasma phagocytophilum* variants, *Rickettsia slovaka*, *R. helvetica*, *Francisella tularensis* [11,20,34–38].

Dermacentor reticulatus – this species belongs to the Ixodidae family, subfamily Amblyomminae [28]. It is widespread in Europe and western Asia.

Table 1.The differences in the biology of European *Ixodes persulcatus* complex and *Dermacentor* ticks

	Ixodes persulcatus **complex ticks**	***Dermacentor*** **spp. ticks**
Hosts of adults	medium sized mammals (carnivores, hares), wild boar, cervids, cattle	medium sized mammals (carnivores, hares), wild boar, cervids, cattle
Hosts of nymphs	ground living and tree living rodents, walker birds, lizards, medium sized mammals (carnivores, hares), cervids	ground living rodents, hares
Hosts of larvae	ground living and tree living rodents, walker birds, lizards, medium sized mammals	ground living rodents
Habitat	open and wood areas	open areas
Duration of larvae and nymphs activity	practically whole growing season	two summer months
Resistance to unfavourable conditions	adults, nymphs, larvae – medium	adults – resistant to low temperatures, medium resistant to low humidity nymphs and larvae – susceptible

Its western distribution range covers the area of France, northern Spain, UK, Central Europe, and the areas of Eastern Europe reaching as far as the basin of the Yenisei River in Siberia to the east [28]. In recent years, the distribution range of this species has extended, following the increase of the epidemiological significance of this tick species [37–41]. This is the species typical for open areas. However, it prefers relatively wet localities – swampy mixed woods, shrub pastures, river and lake banks. Adults are active in the spring from the beginning of March to May, with the peak falling in April. In autumn activity duration ranges from August to November [28,42–44]. Larvae are active in July and August, and nymphs from July to the beginning of September [28,41,44,45]. The developmental cycle is completed during one year. Hosts of larvae and nymphs are insectivores and small rodents, mostly voles [28,31,46]. Adult ticks attack medium-sized mammals, such as carnivores, and ruminants, such as sheep, goats, deer, cattle and European bison [27,28,42]. In total, larvae and nymphs attack over 35 host species in Europe , and adults over 15, including domestic animals. Infrequently *D. reticulatus* has been found on human skin [47–49].

According to present knowledge, *D. reticulatus* is the vector for *Francisella tularensis*, *Rickettsia slovaca*, *Coxiella burnetii* and *Babesia canis* [35,49-51]. There also the single reports about the infection of this species with tick-borne encephalitis virus [48,50] and *Anaplasma phagocytophilum* [52,53].

Dermacentor marginatus – this species belongs to the Amblyomminae family, subfamily Rhipicephalinae [28]. It occurs in Europe and western Asia. In Europe it has been noted in France, Switzerland, southern Germany, Czech, Slovakia, Hungary, Romania, southern Ukraine, and to the south up to the Mediterranean Sea, to the east in the lowland zone and alpine steppes, as well as southern semidesert areas from northern Kazakhstan, Kirghizia and Iran, up to the Altai Mountains [28,46]. It inhabits open areas but prefers relatively dry biotopes, such as pasture, forest steppe and margins of forests [42]. Adult specimens are active from middle March to the beginning of May, with the peak occurring in April. The second peak falls in September and October [41,53]. The activity season of the larvae begins in June and continues up to the second decade of July, and of the nymphs from the first decade of June to the end of August [42,54,55]. The developmental cycle is completed during one, rarely two years.

Adult ticks attack cattle, goat, sheep, deer, horses, dogs, foxes and nymphs attack the *Microtus arvalis* voles. Other rodents, such as *M. glareolus*, *A. agrarius* and *Citellus suslica*, are also hosts, but the levels of infestation observed were lower [54,55]. Apart from these, nymphs can be found on goats, dogs, foxes, hares and deer. Adult ticks can attack humans [46].

D. marginatus is known as vector for the TBE virus, *Rickettsia slovaca*, *Coxiella burnetii, Francisella tularensis* and piroplasms from the *Babesia* genus [28,35].

Apart the particular features, there are the general differences in biology between *Ixodes persulcatus* complex ticks and *Dermacentor* ticks, affecting their different role and ability in pathogens spreading. These are: the range of hosts, higher in *Ixodes* larvae and nymphs; the ability to inhabiting of various environments and resistance to unfavourable conditions, both higher in *Ixodes* larvae and nymphs; the duration of larvae and nymphs activity, all the growing season in the case of *Ixodes* and two months only in *Dermacentor*. These features are gathered in the Table 1.

References

[1] Siuda K. 1991. Kleszcze (Acari: Ixodida) Polski. PWN, Warszawa - Wrocław.

[2] Estrada-Peña A., Bouattour A., Camicas J.L., Walker A.R. 2004. Ticks of domestic animals in Mediterranean region: a guide to identification of species. University of Zaragoza, Zaragoza.

[3] Toutoungi L.N., Gern L. 1993. Ability of transovarially and subsequent transstadially infected *Ixodes hexagonus* ticks to maintain and transmit *Borrelia burgdorferi* in the laboratory. *Experimental and Applied Acarology* 17: 581-586.

[4] Bown K.J., Begon M., Bennett M., Woldehiwet Z., Ogden N.H. 2003. Seasonal dynamics of *Anaplasma phagocytophila* in a rodent-tick (*Ixodes trianguliceps*) system, United Kingdom. *Emerging Infectious Diseases* 9: 63-70.

[5] Bown K.J., Begon M., Bennett M., Birtles R.J., Burthe S., Lambin X., Telfer S., Woldehiwet Z., Ogden N.H. 2006. Sympatric *Ixodes trianguliceps* and *Ixodes ricinus* ticks feeding on field voles (*Microtus agrestis*): potential for increased risk of *Anaplasma phagocytophilum* in the United Kingdom? *Vector-Borne and Zoonotic Diseases* 6: 404-410.

[6] Siński E. 1999. Enzootyczne źródła nowych infekcji przenoszonych przez kleszcze *Ixodes ricinus*. *Wiadomości Parazytologiczne* 45: 135-142.

[7] Matuschka F.R., Fischer P., Heiler M., Richter D., Spielman A. 1992. Capacity of european animals as reservoir hosts for the Lyme disease spirochete. *Journal of Infectious Diseases* 165: 479-483.

[8] Tälleklint L., Jaenson T.G.T. 1993. Maintenance by hares of european *Borrelia burgdorferi* in ecosystems without rodents. *Journal of Medical Entomology* 30: 273-276.

[9] Humair P.F., Rais O., Gern L. 1999. Transmission of *Borrelia afzelii* from *Apodemus* mice and *Clethrionomys* voles to *Ixodes ricinus* ticks: differential transmission pattern and overwintering maintenance. *Parasitology* 118: 33-42.

[10] Gern L., Siegenthaler M., Hu C.M., Leuba-Garcia S., Humair P.F., Moret J. 1994. *Borrelia burgdorferi* in rodents (*Apodemus flavicollis* and *A. sylvaticus*): duration and enhancement of infectivity for *Ixodes ricinus* ticks. *European Journal of Epidemiology* 10: 75-80.

[11] Stuen S., Granquist E.G., Silaghi C. 2013. *Anaplasma phagocytophilum* – a widespread multi-host pathogen with highly adaptive strategies. *Frontiers in Cellular and Infection Microbiology* 3: 31.

[12] Mather T.N., Nicholson M.C., Hu R., Miller N.J. 1996. Entomological correlates of *Babesia microti* in an area where *Ixodes scapularis* (Acari: Ixodidae) is endemic. *Journal of Medical Entomology* 33: 866-870.

[13] Peavey C.A., Lane R.S., Kleinjan J.E. 1997. Role of small mammals in the ecology of *Borrelia burgdorferi* in a peri-urban park in north coastal California. *Experimental and Applied Acarology* 21: 569-584.

[14] Arumova E.A. 1979. O peredvizheniakh kleshchey *Ixodes persulcatus* s momenta nasyshchenia nimf do aktivatsii golodnykh imago. *Meditsinskaya Parazitlogiia i Parazitarnyie Bolezni* 48: 34-37.

[15] Gray J.S. 1998. The ecology of ticks transmitting Lyme borreliosis. *Experimental and Applied Acarology* 22: 249-258.

[16] Martin C., Pastoret P.P., Brochier B., Humblet M.F., Saegerman C. 2011. A survey of the transmission of infectious diseases/infections between wild and domestic ungulates in Europe. *Veterinary Research* 42: 70.

[17] Kurtenbach K., Kampen H., Dizij A., Arndt S., Seitz H.M., Schaible U.E., Simon M.M. 1995. Infestation of rodents with larval *Ixodes ricinus* (Acari: Ixodidae) is an important factor in the transmission cycle of *Borrelia burgdorferi* s.l. in German Woodlands. *Journal of Medical Entomology* 32: 807-817.

[18] Rosef O., Paulauskas A., Radzijevskaja J. 2009. Prevalence of *Borrelia burgdorferi* sensu lato and *Anaplasma phagocytophilum* in questing *Ixodes ricinus* ticks in relation to the density of wild cervids. *Acta Veterinaria Scandinavica* 51: 47.

[19] Cagnacci F., Bolzoni L., Rosà R., Carpi G., Hauffe H. C., Valent M., Tagliapietra V., Kazimirova M., Koci J., Stanko M., Lukan M., Henttonen H., Rizzoli A. 2012. Effects of deer density on tick infestation of rodents and the hazard of tick-borne encephalitis. I: Empirical assessment. *International Journal of Parasitology* 42: 365-372.

[20] Burgdorfer W., Barbour A.G., Hayes S.F., Péter O., Aeschlimann A. 1983. *Erythema chronicum migrans* – a tick-borne spirochetosis. *Acta Tropica* 40: 79-83.

[21] Balashov Yu.S. 1996. Mesto iksodovykh kleshchei (Ixodidae) v lesnykh ekosistemakh. *Parazitologiya* 30: 193-204.

[22] Nosek J., Kožuch O., Grulich I. 1970. The structure of tick-borne encephalitis (TBE) foci in Central Europe. *Oecologia* 5: 61-73.

[23] Alekseev A.N., Chunikin S.P. 1990. The experimental transmission of the tick-borne encephalitis virus by ixodid ticks (the mechanisms, time periods, species and sex differences). *Parazitologiia* 24: 177-185.

[24] Jefferies R., Ryan U.M., Jardine J., Broughton D.K., Robertson I.D., Irwin P.J. 2007. Blood, bull terriers and babesiosis: further evidence for direct transmission of *Babesia gibsoni* in dogs. *Australian Veterinary Journal* 85: 459-463.

[25] Parola P., Paddock C.D., Raoult D. 2005. Tick-borne rickettsioses around the world: emerging diseases challenging old concepts. *Clinical Microbiology Review* 18: 119-156.

[26] Izdebska J.N., Cydzik K. 2010. Analysis of the reasons for differences in topical specificity among various species of tick (Acari, Ixodidae) infesting European bison. *European Bison Conservation Newsletter* 3: 75-84.

[27] Karbowiak G., Demiaszkiewicz A.W., Pyziel A.M., Wita I., Moskwa B., Werszko J., Bień J., Goździk K., Lachowicz J., Cabaj W. 2014. The parasitic fauna of the European bison (*Bison bonasus*) (Linnaeus, 1758) and their impact on the conservation. Part 1. The summarising list of parasites noted. *Acta Parasitologica* 59: 363-371.

[28] Siuda K. 1993. Ticks of Poland (Acari: Ixodida). Polish Parasitological Society, Warszawa.

[29] Vor T., Kiffner C., Hagedorn P., Niedrig M., Rühe F. 2010. Tick burden on European roe deer (*Capreolus capreolus*). *Experimental and Applied Acarology* 51: 405-417.

[30] Matuschka F.R., Lange R., Spielman A., Richter D., Fischer P. 1990. Subadult *Ixodes ricinus* (Acari: Ixodidae) on rodents in Berlin, West Germany. *Journal of Medical Entomology* 27: 385-390.

[31] Karbowiak G. 2000. The role of *Apodemus flavicollis* and *Clethrionomys glareolus* as hosts of *Ixodes ricinus* and *Dermacentor reticulatus* in northern Poland. In: *Proceedings of the 3rd International Conference "Ticks and tick-borne pathogens: into the 21st century*". (Eds. M. Kazimírová, M. Labuda, P.A. Nuttall). High Tatra Mountains, Slovakia, 30 August–3 September 1999. Institute of Zoology SAS, Bratislava: 181-183.

[32] Paziewska A., Zwolińska L., Harris P.D., Bajer A., Siński E. 2010. Utilisation of rodent species by larvae and nymphs of hard ticks (Ixodidae) in two habitats in NE Poland. *Experimental and Applied Acarology* 50: 79-91.

[33] Schulz M., Mahling M., Pfister K.J. 2014. Abundance and seasonal activity of questing *Ixodes ricinus* ticks in their natural habitats in southern Germany in 2011. *Journal of Vector Ecology* 39: 56-65.

[34] Homer M.J., Aguilar-Delfin I., Telford III S.R., Krause P.J., Persing D.H. 2000. Babesiosis. *Clinical Microbiology Review* 13: 451-469.

[35] Süss J., Fingerle V., Hunfeld K.P., Schrader C., Wilske B. 2004. Durch Zecken übertragene humanpathogene und bisher als apathogen geltende Mikroorganismen in Europa. Teil II: Bakterien, Parasiten und Mischinfektionen. *Bundesgesundheitsblatt - Gesundheitsforschung - Gesundheitsschutz* 47: 470-486.

[36] Biernat B., Stańczak J., Michalik J., Sikora B., Wierzbicka A. 2015. Prevalence of infection with *Rickettsia helvetica* in *Ixodes ricinus* ticks feeding on non-rickettsiemic rodent hosts in sylvatic habitats of west-central Poland. *Ticks* and *Tick-borne Diseases*, http://dx.doi.org/10.1016/j.ttbdis.2015.10.001

[37] Woldehiwet Z. 2010. The natural history of *Anaplasma phagocytophilum*. *Veterinary Parasitology* 167: 108-122.

[38] Kiewra D., Stańczak J., Richter M. 2014. *Ixodes ricinus* ticks (Acari, Ixodidae) as a vector of *Borrelia burgdorferi* sensu lato and *Borrelia miyamotoi* in Lower Silesia, Poland – preliminary study. *Ticks and Tick-borne Diseases* 5: 892-897.

[39] Bullová E., Lukáň M., Stanko M., Pet'ko B. 2009. Spatial distribution of *Dermacentor reticulatus* tick in Slovakia in the beginning of the 21st century. *Veterinary Parasitology* 165: 357-360.

[40] Karbowiak G., Kiewra D. 2010. New locations of *Dermacentor reticulatus* ticks in Western Poland: the first evidence of the merge in *D. reticulatus* occurrence areas? *Wiadomości Parazytologiczne* 56: 333-340.

[41] Karbowiak G. 2014. The occurrence of the *Dermacentor reticulatus* tick – its expansion to new areas and possible causes. *Annals of Parasitology* 60: 37-47.

[42] Nosek J. 1972. The ecology, bionomics, behaviour and public health importance of *Dermacentor marginatus* and *D.reticulatus* ticks. *Wiadomości Parazytologiczne* 18: 721-725.

[43] Szymański S. 1987. Seasonal activity of *Dermacentor reticulatus* (Fabricius, 1794) (Acarina, Ixodidae) in Poland. I. Adults. *Acta Parasitologica Polonica* 31: 247-255.

[44] Bogdaszewska Z., Karbowiak G., Siuda K. 2006. Występowanie i biologia kleszcza łąkowego *Dermacentor reticulatus* (Fabricius, 1794) w północno-wschodniej Polsce. In: *Stawonogi: znaczenie epidemiologiczne*. (Eds. A. Buczek, C. Błaszak). Koliber, Lublin: 75-79.

[45] Szymański S. 1987. Seasonal activity of *Dermacentor reticula*tus (Fabricius, 1794) (Ixodidae) in Poland. III. Larvae and nymphs. *Acta Parasitologica Polonica* 32: 265-280.

[46] Nosek J. 1972. The ecology and public health importance of *Dermacentor marginatus* and *D.*

reticulatus ticks in Central Europe. *Folia Parasitologica* 19: 93-102.

[47] Bartosik K., Sitarz M., Szymańska J., Buczek A. 2011. Tick bites on humans in the agricultural and recreational areas in south-eastern Poland. *Annals of Agricultural and Environmental Medicine* 18: 151-157.

[48] Biernat B., Karbowiak G., Werszko J., Stańczak J. 2014. Prevalence of tick-borne encephalitis virus (TBEV) RNA in *Dermacentor reticulatus* ticks from natural and urban environment, Poland. *Experimental and Applied Acarology* 64: 543-551.

[49] Estrada-Peńa A., Jongejan F. 1999. Ticks feeding on humans: a review of records on human biting Ixodoidea with special reference to pathogen transmission. *Experimental and Applied Acarology* 23: 685-715.

[50] Wójcik-Fatla A., Cisak E., Zając V., Zwoliński J., Dutkiewicz J. 2011. Prevalence of tick-borne encephalitis virus in *Ixodes ricinus* and *Dermacentor reticulatus* ticks collected from the Lublin region (eastern Poland). *Ticks and Tick-borne Diseases* 2: 16-19.

[51] Duh D., Slovák M., Saksida A., Strašek K., Petrovec M., Avšič-Županc T. 2006. Molecular detection of *Babesia canis* in *Dermacentor reticulatus* ticks collected in Slovakia. *Biologia* 61: 231-233.

[52] Karbowiak G., Víchová B., Slivinska K., Werszko J., Didyk J., Peťko B., Stanko M., Akimov I. 2014. The infection of questing *Dermacentor reticulatus* ticks with *Babesia canis* and *Anaplasma phagocytophilum* in the Chernobyl exclusion zone. *Veterinary Parasitology* 204: 372-375.

[53] Wirtgen M., Nahayo A., Linden A., Garigliany M., Desmechtl D. 2011. Detection of *Anaplasma phagocytophilum* in *Dermacentor reticulatus* ticks. *Veterinary Record* 168: 195.

[54] Pokrovskaia E.I. 1951. K ekologii lichinok i nimf kleshcha *Dermacentor marginatus* Sulz. v usloviiakh Voronezhskoi Oblasti. *Zoologicheskij Zhurnal* 30: 224-228.

[55] Pokrovskaia E.I. 1953. K ekologii kleshcha *Dermacentor marginatus* v usloviiakh Voronezhskoi Oblasti. *Zoologicheskij Zhurnal* 32: 435-440.

Received 3 October 2015
Accepted 25 November 2015