

Review articles

Epidemiological consequences of host specificity of ticks (Ixodida)

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ABSTRACT. Arthropod-borne diseases still pose a serious health problem worldwide. Epidemiological consequences result from various environmental connections and interaction between parasites and their host, including host specificity of parasites and transmitted pathogens. The ixodid ticks (Ixodida) occupy a prominent position within the group of parasites as being vectors on the northern hemisphere in temperate climate zone. They are blood-feeding ectoparasites with different host specificity and capacity to transmit various pathogens. Feeding on many mammals (including humans), birds, reptiles and amphibians they present a great medical problem. For example, *Ixodes ricinus* can infest several hundred species of animals. It is a vector of pathogenic viral, bacterial and protozoal organisms, including *Borrelia burgdorferi* sensu lato complex which is the etiological agent of Lyme borreliosis. The competent reservoir hosts of *Borrelia* include many common species of small and medium-sized rodents as well as several bird species. Epidemiological consequences are complicated by the fact that specific *Borrelia* genospecies are associated with particular reservoir hosts. Thus, detailed analysis of epidemiological consequences requires a comprehensive knowledge of the biology and ecology of vectors, pathogens and their reservoirs including host specificity of ticks. Spatial modelling tick-borne risk in time and space is made possible by the use of remote sensing and techniques of geographical information system (GIS).

Key words: tick specificity, tick-borne-disease, *Borrelia* genospecies, tick transmitted pathogens

Introduction

Parasitic infections affect persons living both in tropical and subtropical climates as well as in temperate climate. It makes parasitic diseases a serious health problem worldwide including the developed countries. The typical environmental studies concerning geographical spread and prevalence of parasites on their hosts as well as analysis of natural parasite life cycles are essential in the disease prophylaxis. Epidemiological consequences result from various environmental connections and interactions between parasites and their host, including parasite host specificity. According to the host specificity, two main groups of parasites can be recognized: stenoxenic parasites with a narrow range of host and euryxenic parasites

that use a broad range of hosts. Both groups contain many species of parasites that are of public health importance. Various host specificity is also characteristic for ticks (Ixodida). According to Siuda [1] slightly more than 10% of tick species are host nonspecific, many more are able to parasitize on hosts closely related to each other or on host from different species but closely ecologically related to tick habitat; only a few tick species attach and feed on single host species. Additionally, host specificity plays a significant role in vector-host-pathogen configuration, including tick-borne pathogens, in which the interactions concerning pathogen circulation should be additionally taken into account.

Of all parasitic diseases, malaria, which is transmitted by mosquitoes, is undoubtedly the most

important medical problem in the world. However, on the northern hemisphere in temperate climate zone, a prominent place in the group of vectors is taken by ixodid ticks, which are considered to be the most dangerous arthropods affecting humans. *Ixodes* ticks transmit pathogenic viral, bacterial and protozoal organisms, including spirochetes from *Borrelia burgdorferi* sensu lato complex and tick-borne encephalitis, as well as so-called emerging pathogens such like *Anaplasma phagocytophilum* and *Babesia* spp.

Ticks and their hosts

Broad specificity of many representatives of ticks Ixodida (containing about 900 species, i.e., almost 190 soft ticks from family Argasidae and over 700 hard ticks from family Ixodidae) presents a great veterinary-medicine problem [2]. Those worldwide blood-feeding ectoparasites with various host specificity feed on many mammals (including humans), birds, reptiles and amphibians [3]. Most ticks have preference for feeding on certain groups of animals and consequently the number of species pertinent to humans is limited [4]. Moreover, none of the known tick species is specifically associated with humans [1]. According to Estrada-Peña and Jongejan [5] approximately 12 argasid species (*Argas* and *Ornithodoros*) and over 20 ixodid tick species (4 *Amblyomma*, 7 *Dermacentor*, 3 *Haemaphysalis*, 2 *Hyalomma*, 6 *Ixodes*) are frequently attached to humans. In Poland, people are most often infested by *Ixodes ricinus*, which is able to infest several hundred species of animals and prefers to have a different host animal at each stage of their life. It is an important European vector of viral, rickettsial, bacterial and protozoan pathogens, including common spirochetes *B. burgdorferi* sensu lato and tick-borne encephalitis virus (TBEV). *I. ricinus* is associated with the moist and forested areas, living in mixed and deciduous forest but also in the urban parks and home surroundings (gardens), where they contact synanthropic animals [6]. However, *I. ricinus* is the most frequent in habitats where its hosts are plentiful. *I. ricinus* from vegetation can be collected using flagging or dragging method. Our results from over a decade (1998–2012) of environmental monitoring of ticks occurrence using flagging method shows *I. ricinus* common occurrence both in protected areas i.e., national and landscape parks as well as in forested and urban areas [7–11]. Colonization of suitable

isolated inner-city habitats, like for example urban parks or gardens, is possible by transportation of feeding ticks by hosts with birds being the primary candidates [12]. Thus, the ability of ticks to parasitize birds, especially migratory birds, make possible the spread of ticks to new areas, including isolated areas, where there are suitable biotic and abiotic conditions.

Of the remaining 18 tick species from the Polish tick fauna, people can be attacked by: *Argas polonicus* (generally ornithophilous tick found primarily on *Columba livia*), *A. reflexus* (generally ornithophilous), *Carios vespertilionis* (infesting bats), *Ixodes crenulatus* (mainly mammals, including insectivore, rodents and carnivores), *I. hexagonus* (mainly mammals, the main hosts are hedgehogs, mustelids, dogs and other canids), *Haemaphysalis punctata* (birds, mammals), *H. concinna* (birds, mammals), *Dermacentor reticulatus* (mammals, occasionally birds) and *I. persulcatus* belonging to the *I. ricinus* complex [13]. It is worth to mention that the last one belongs to the ticks of the highest medical importance in the world. Fortunately, in recent years it was not collected in Poland; however, it is distributed throughout Eastern Europe to the Far East.

Ticks can be divided into two groups according to their habitat: non-nidicolous ticks living in open habitats, and nidicolous ticks living in caves, burrows or nest of their host. The majority of the Polish fauna ticks is represented by nidicolous ticks, what makes them difficult to study. However, of greater medical significance are non-nidicolous ticks, to which belongs the mentioned above and the most important *I. ricinus*. Thus, humans are at risk of tick bites when they intrude tick-infested caves and burrows or when humans spent time outdoors visiting grassy, forested areas, and shrubs where ticks are waiting for the hosts on vegetation.

Tick range is limited by host's occurrence and their specificity. The argasid ticks generally occur in or close to the nests or resting places of their hosts [12]. For example, the pigeon tick *Argas reflexus*, a parasite of wild and domesticated pigeons and occasionally other birds, tends to inhabit attics, lofts, and building facades, i.e., pigeons' dwelling [14]. However, most tick species are less widely distributed than their principal hosts [15]. For the ticks infesting many animal species, the range of hosts can vary with geographic region, adapting to the local fauna. For example, until recently *Alces alces* was considered as a principal host of

D. reticulatus, due to the covering range of both species. However, the newest data shows the important role of deer as a host supportive of this tick species [16]. *D. reticulatus* occurs in the western Palearctic region. The recent study shows that this species has been extended substantially in new areas of many countries including Poland [17–21], Germany [22], Slovakia [23], and the Czech Republic [24]. According to own investigations, *D. reticulatus* can be ranked as a typical element of the fauna in Lower Silesia in South-western Poland suggesting the linkage between East and West populations of this species [25].

Recognition of main hosts is crucial in estimating the occurrence of tick-borne diseases. For example, the majority of *I. ricinus*, despite of a variety of potential hosts, feed on only a few mammalian species and tick infestation is frequently limited to only a part of the host population [26]. Expanded range of *I. ricinus* in Northern Sweden, for example, can be explained by the high availability of large numbers of important tick hosts, particularly roe deer *Capreolus capreolus*, and a warmer climate that permits greater survival and proliferation over a larger geographical area of both the tick itself and deer [27]. Also, in Denmark tick density was found to be influenced by roe deer abundance [28]. However many tick species lack their completed data on their distribution despite information about their hosts. *A. polonicus*, for example, is known only from a few sites in Poland, Czech Republic and Slovakia, nevertheless its range may be larger [29]. A comprehensive study of the prevalence of ticks requires extensive field studies taking into account behavior of the tick, i.e., a collections from vegetation, nests, burrows, and hosts. The recent data on the distribution of most important species of ticks, i.e., *Ixodes ricinus*, *Dermacentor marginatus*, *D. reticulatus*, *Haemaphysalis punctata*, *H. sulcata*, *Hyalomma marginatum*, *Hy. lusitanicum*, *Rhipicephalus annulatus*, *R. bursa*, and the *R. sanguineus* group in western Palearctic was published by Estrada-Peña et al. [30].

Tick parasites as vectors

Apart from direct result of parasitism (i.e., causing paralysis, toxicosis and allergic reaction) the roles of ticks as pathogen reservoir and pathogen vectors are even more important [3,4,31]. Approximately 10% of tick species act as vectors

for a broad range of pathogens [4]. The majority of tick-borne disease agents survive in nature by using animals as their vertebrates host and therefore they are called zoonoses [6]. Crucial in epidemiology, the transmission of disease agents, i.e., pathogenic viral, bacterial and protozoal organisms, take place during tick life span. It happens when the infectious agent replicates or develops in the vector until it could be transferred into a susceptible recipient host [31]. Vectors, so-called „bridge vectors”, capable of feeding on different group of vertebrates make possible the inclusion of additional vertebrates into the endemic cycle or transformation of a natural cycle into an urban cycle what makes them epidemiologically very important [31]. However, also ticks with narrower host specificity for example ornitophilus ticks parasiting migratory birds, even if they do not infest humans, they can play an important role in the ecology and pathogen circulation.

A wide range of hosts, including species that are competent reservoirs, significantly affect the prevalence of the various groups of pathogens in ticks. Thus, ticks with indiscriminate feeding behaviour are important vectors for a large number of zoonotic tick-borne diseases [4]. This is due to the fact that intermediate animal hosts (i.e., birds, rodents, game animals, foxes, cattle, sheep, goats, horses and dogs) often serve as reservoirs for the pathogens [6]. On the other hand, particularly in cases of lacking of systemic infections, simultaneous parasiting of infected and uninfected ticks on the same non-competent host allows the transfer of pathogens during feeding.

The most important role in transmission of pathogens responsible for vector-borne diseases is played by non-nidicolous ticks with three-host cycle (i.e., each life stage of the tick feeds on different vertebrate host) parasiting a wide range of hosts. The three-host cycle ticks are represented by genera *Ixodes*, *Dermacentor*, *Rhipicephalus*, and *Amblyomma* including species of the highest medical significance such as *I. ricinus*, *I. persulcatus*, *I. scapularis*, *I. pacificus*.

The spreading of tick-borne diseases is based on tick's presence and various interactions between the ticks, hosts and pathogens. In Sweden, for example, the geographical presence of Lyme borreliosis (LB) corresponds to the distribution of *I. ricinus* [27]. The increase of tick-borne diseases is related to exposure of humans to infected ticks. Tick species feeding on man are usually vectors of tick-borne

diseases. The distribution of ticks depends on extrinsic biotic (presence of hosts, and vegetation type) and abiotic factors (climate) which influence tick's presence in short and long term. Environmental elements which influence the presence, development, activity and longevity of pathogens, vectors, reservoirs and their interactions with humans, can be investigated by remote sensing and by using geographical information system (GIS) what enable modelling of tick-borne risk in space and time [32]. The combination of field data collection and GIS mapping increases the potential for interpretation of this information. For example, environmental tick monitoring data together with epidemiological data from medical interviews shown on one map allowed the presentation of the LB risk in Wroclaw, Poland [10].

Tick borne diseases as result of their blood feeding

With regard to Siuda [3] three types of vector-borne diseases transmission are recognized: obligatory transmission (transmitted only by vector), optional obligatory transmission (transmitted mainly by vector) and optional transmission (transmitted by vector and without vector). For example, Lyme borreliosis (LB) can be transmitted only by ticks, whereas tick-borne encephalitis (TBE) can be transmitted mostly by ticks and rarely through non-pasteurized milk from infected goats, sheep and cows. LB is the most common arthropod-borne disease in temperate regions of the northern hemisphere. In Europe, it has a widespread distribution from southern Scandinavia to some parts of northern Mediterranean countries, with an incidence trending upward from west to east [33]. However, the most highly endemic regions are found in Central and Eastern Europe, where as many as 200,000 cases may occur annually [33]. Although it has been three decades since the discovery of *B. burgdorferi* (the discovery of a spirochete in *I. scapularis* was reported in 1982), LB is an expanding public health problem [34]. In Poland, in 2011 over nine thousand cases of LB were noted (24.0 cases LB per 100000 inhabitants), with the highest incidence in the Podlaskie province (www.pzh.gov.pl). However, LB occurs in all provinces in Poland. In Lower Silesia in 2011 were noticed over 660 incidence of LB (23.0/100000).

Apparently tick infection is necessary for

transmission via vector to the not susceptible hosts, including humans. The meta-analysis of literature on epidemiological studies of *I. ricinus* ticks infected with *B. burgdorferi* sensu lato showed that the overall mean infection rate was 13.6% and that the rate of infection of adult ticks was significantly higher (18.6%) than that of nymphs (10.1%). It was explained by the fact that host-seeking adult ticks had two blood meals on different hosts [35]. Our extensive studies of over 1350 *I. ricinus* ticks collected in five district of various LB incidences in Lower Silesia, Poland in 2011 shown that the average level of infection amounted for 18% (11% the minimal infection rate for nymphs and 37% for adults). Slightly lower was the infection rate for TBEV. It may attain from 0.5% to 3% in natural foci [36]. However, TBEV detection in ticks is not a sensitive indicator for a human risk assessment [37].

In Europe, confirmed competent reservoir hosts of *Borrelia* include many common species of small and medium-sized rodents as well as several bird species (especially passerines), reptiles and insectivores [38]. However, epidemiological consequences may be complicated by the fact that specific *Borrelia* genospecies (*B. burgdorferi* sensu lato complex currently contains at least 18 genospecies) are associated with particular reservoir hosts [38]. Many strains of *B. burgdorferi* s. l. are adapted to either mammalian or avian host, but not to both. It is due to different resistance of particular genospecies *B. burgdorferi* s. l. to the alternative pathway of complement from various vertebrate hosts [39]. For example, *B. afzelii* and *B. garinii*, the most common European circulating genospecies, are associated with rodents and birds, respectively. *B. bissetti* and *B. bavariensis* (previously *B. garinii* OspA serotype 4) are also associated with rodents, *B. valaisiana* and *B. burgdorferi* s. s. with birds, whereas *B. lusitaniae* infect lizards and *B. spielmanii* – dormice; *B. burgdorferi* s. s. appears to be more a generalist [34,38,40–45].

During the blood meal, ticks take up host complement and other host-derived proteins which are active in tick feeding and affect the selection of pathogen genospecies [39]. *B. afzelii*, for example, that encounters deer or avian complement, are killed in the midgut before they are transmitted to the host [39]. Genospecies of *B. burgdorferi* s. l. often circulate in the same habitats, involving many vertebrate host but mainly one tick species [39]. Ticks feeding on a host infected with a few *Borrelia* species or feeding simultaneously on host and

exchanging genospecies through co-feeding may get mixed infections [34]. Ixodid tick species with a wide range of hosts are the vectors of most *Borrelia* species and they can transmit all genospecies to their hosts. In Europe, *I. ricinus*, the main vector of *B. burgdorferi* s. l., feeds on extraordinarily broad array of hosts and can transmit to these hosts all *Borrelia* genospecies via infected saliva during the blood meal. Ticks having a narrower range of hosts can maintain circulation of not all *Borrelia* genospecies. Ornithophilous *I. uriae*, for example, feeding on seabirds, transmits *B. garinii* and maintains marine cycle involving seabirds. Other ornithophilous tick *I. lividus*, a nidicolous species restricted almost exclusively to sand martins and being unlikely to transmit infectious agents to humans, can play an important role in *B. garinii* and *B. burgdorferi* s. s. enzootic cycles [46].

Various *Borrelia* genospecies are associated with other clinical manifestation which reflects in epidemiological implications. Three genospecies that cause most human disease are *B. burgdorferi* s. s., *B. garinii*, and *B. afzelii*, although *B. spielmanii* have been detected in early skin disease, and *B. bissettii* and *B. valaisiana* in specimens from single Lyme borreliosis cases [33]. The pathogenicity of *B. lusitaniae* is uncertain [38]. All pathogenic genospecies may cause erythema migrans (EM) in humans but they differ in their organo-tropism. *B. afzelii* is most often associated with chronic skin condition acrodermatitis chronica atrophicans, *B. garinii* with neuroborreliosis, and *B. burgdorferi* s. s. with arthritis and neuroborreliosis [38].

Systemic infection is not necessary for successful transmission [47]. Many large wild and domesticated vertebrates are non-competent reservoirs for *Borrelia* and ticks may transmit *Borrelia* to each other when feeding very close together [38]. Thus, *B. burgdorferi* s. l. can be transmitted between ticks feeding on host with non-systemic infections. Also other pathogens like for example tick-borne encephalitis virus (TBEV), medically the most important arbovirus in Europe, can be transmitted from infected ticks to uninfected ticks during simultaneously feeding on non-viraemic host. This phenomenon is very important because TBEV is very short-lived in its principal rodent hosts [15]. This type of transmission between immature stages of ticks closely linked to tick seasonal dynamics, which influences simultaneous feeding of larvae and nymphs on rodent host, remarkably affects TBE [48]. Furthermore,

systemic infection can be negatively correlated with transmission potential [47]. Host with very high level of TBEV in their blood and internal organs suffer high mortality and they died before most of the ticks have been infected. On the other hand some free-living mammals do not support natural systemic infection and won't transmit the virus back to ticks [47]. The consequence of this type of pathogen transmission is tick-borne diseases distribution. TBE occurs only in discrete foci within the tick distribution in contrast to LB which occurs wherever competent tick species exist [48].

Tick saliva can play a critical role in promoting of pathogen transmission. For many pathogens, the salivary gland is the site of development and replication of pathogens [49]. In maintaining pathogen's circulation within tick population an important role plays the possibility of the infection of the subsequent stage via transstadial transmission or from female to larvae via transovarial transmission what enables the long-term maintenance of the pathogen. Transstadial and transovarial transmissions are taking place in case of TBEV.

Summary

As it was emphasized the spreading of tick-borne diseases is based on tick's presence and various interactions between the ticks, hosts and pathogens. Thus, detailed analysis of epidemiological consequences requires a thorough knowledge of the biology and ecology of vectors, pathogens and their reservoirs including host specificity of ticks. The distribution of ticks depends on extrinsic biotic (presence of hosts, vegetation type) and abiotic factors (climate), which influence tick's presence in short and long term. The host specificity of ticks effects tick spreading as well as their vector potential. Environmental elements, which influence the presence, development, activity and longevity of pathogens, vectors, reservoirs and their interactions with humans, can be investigated by remote sensing and by using geographical information system (GIS) what enable modelling of tick-borne risk in space and time.

References

- [1] Siuda K. 1991. Kleszcze (Acari: Ixodida) Polski. Część I. Zagadnienia ogólne. Monografie Parazytologiczne. PWN, Warszawa-Wrocław.

- [2] Barker S. C., Murrell A. 2008. Systematics and evolution of ticks with a list of valid genus and species names. In: *Ticks. Biology, Disease and Control*. (Eds. A. S. Bowman, P. Nuttall). Cambridge University Press: 1-39.
- [3] Siuda K. 1998. Arthropods as disease vectors. *Wiadomości Parazytologiczne* 44: 21-35.
- [4] Jongejan F., Uilenberg G. 2004. The global importance of ticks. *Parasitology* 129 S1: S3-S14.
- [5] Estrada-Peña 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.
- [6] Lonc E., Kiewra D., Rydzanicz K., Król N. 2011. The risk of arthropod vector configuration in Europe. *Wiadomości Parazytologiczne* 57: 223-232.
- [7] Lonc E., Buczek A., Kiewra D., Ciosek K. 2001. Występowanie kleszczy *Ixodes ricinus* (L.) na Śląży (Dolny Śląsk). In: *Stawonogi. Pasożyty i nosiciele*. (Eds. A. Buczek, C. Błaszak). KGM Lublin: 87-92.
- [8] Kiewra D., Lonc E., Głuszkowski M., Malinowska A. 2002. Geoklimatyczne uwarunkowania prevalencji kleszczy pospolitych – *Ixodes ricinus* (L.). In: *Stawonogi w medycynie*. (Eds. A. Buczek, C. Błaszak). LIBER, Lublin: 115-126.
- [9] Kiewra D., Rydzanicz K., Lonc E. 2006. Prevalence of *Borrelia burgdorferi* s. l. in *Ixodes ricinus* collected from five wooded areas in Lower Silesia (Poland). In: *Stawonogi. Znaczenie epidemiologiczne*. (Eds. A. Buczek A., C. Błaszak). Koliber, Lublin: 183-187.
- [10] Kiewra D., Lonc E. 2010. Mapping Lyme borreliosis risk in the Wrocław area (Lower Silesia, Poland). In: *Stawonogi. Ekologiczne i patologiczne aspekty układu pasożyt-żywiciel*. (Eds. A. Buczek, C. Błaszak). Akapit, Lublin: 199-206.
- [11] Kiewra D., Zaleśny G., Czułowska A. 2012. *Ixodes ricinus* ticks as vectors of *Borrelia burgdorferi* sensu lato in the Milicz County, Lower Silesia. In: *Stawonogi. Znaczenie medyczne i gospodarcze*. (Eds. A. Buczek, C. Błaszak). Akapit, Lublin: 155-162.
- [12] Dautel H., Kahl O. 1999. Ticks (Acari: Ixodoidea) and their medical importance in the urban environment. In: *Proceedings of the Third International Conference on Urban Pests: 19–22 July 1999, Czech Republic*: 73-82.
- [13] Siuda K. 1995. Fauna kleszczy (Acari: Ixodida) w Polsce. *Wiadomości Parazytologiczne* 41: 277-288.
- [14] Buczek A., Bartosik K. 2011. Occurrence of *Argas reflexus* (Fabricius, 1794) (Ixodida, Argasidea) in urban habitat of south-eastern Poland. *Wiadomości Parazytologiczne* 57: 277-279.
- [15] Randolph S. 2008. The impact of tick ecology on pathogen transmission dynamics. In: *Ticks. Biology, Disease and Control*. (Eds. A. S. Bowman, P. Nuttall). Cambridge University Press: 40-72.
- [16] Karbowski G. 2009. Kleszcz łąkowy *Dermacentor reticulatus* – występowanie, biologia i rola wektorowa chorób odkleszczowych. Rozprawa habilitacyjna. Wydawca Agencja Reklamowo-Wydawnicza A. Grzegorzcyk, Warszawa.
- [17] Kadulski S., Izdebska J. N. 2009. New data on distribution of *Dermacentor reticulatus* (Fabr.) (Acari, Ixodidae) in Poland. In: *Stawonogi. Inwazje i ich ograniczanie*. (Eds. A. Buczek, C. Błaszak). Akapit, Lublin: 53-58.
- [18] Karbowski 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.
- [19] Nowak M. 2010. Discovery of *Dermacentor reticulatus* (Acari: Amblyomidae) populations in the Lubuskie Province (Western Poland). *Experimental and Applied Acarology* 54: 191-197. doi:10.1007/s10493-010-9422-4.
- [20] Kiewra D., Lonc E., Król N. 2011. Ryzyko chorób odkleszczowych na Dolnym Śląsku. Materiały Konferencji Naukowej „Środowiskowe zagrożenia zdrowia ludzi i zwierząt”. Szczecin, 18 listopada 2011: 14.
- [21] Kiewra D., Lonc E. 2012. Epidemiologiczne konsekwencje żywicielskiej specyficzności kleszczy (Ixodida). Materiały XX Wrocławskiej Konferencji Parazytologicznej „Specyficzność pasożytów a środowisko”. Wrocław-Karpacz, 21-23 czerwca 2012: 11.
- [22] 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. *International Journal of Medical Microbiology* 296 Suppl 40: 149-156.
- [23] Bullová E., Lukáš 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.
- [24] Široký P., Kubelová M., Bednář M., Modrý D., Hubálek Z., Tkadlec E. 2011. The distribution and spreading pattern of *Dermacentor reticulatus* over its threshold area in the Czech Republic – How much is range of this vector expanding? *Veterinary Parasitology* 183: 130-135.
- [25] Kiewra D., Czułowska A. 2012. Evidence for an increased distribution range of *Dermacentor reticulatus* (Fabricius, 1794) in south-west Poland. *Experimental and Applied Acarology*. DOI 10.1007/s10493-012-9612-3
- [26] Labuda M., Nuttall P. A. 2008. Viruses transmitted by ticks. In: *Ticks. Biology, Disease and Control*. (Eds. A. S. Bowman, P. Nuttall). Cambridge University Press: 253-280.
- [27] Jaenson T. G., Jaenson D. G., Eisen L., Petersson E., Lindgren E. 2012. Changes in the geographical distribution and abundance of the tick *Ixodes ricinus* during the past 30 years in Sweden. *Parasites and Vectors* 10: 5-8.
- [28] Jensen P. M., Hansen H., Frandsen F. 2000. Spatial

- risk assessment for Lyme borreliosis in Denmark. *Scandinavian Journal of Infectious Diseases* 32: 545-550.
- [29] Siuda K. 1993. Kleszcze Polski (Acari: Ixodida). II. Systematyka i rozmieszczenie. Monografie Parazytologiczne. Polskie Towarzystwo Parazytologiczne, Warszawa.
- [30] Estrada-Peña A., Farkas R., Jaenson T. G., Koenen F., Madder M., Pascucci I., Salman M., Tarrés-Call J., Jongejan F. 2012. Association of environmental traits with the geographic ranges of ticks (Acari: Ixodidae) of medical and veterinary importance in the western Palearctic. A digital data set. *Experimental and Applied Acarology*. DOI 10.1007/s10493-012-9600-7.
- [31] Hubalek Z., Rudolf I. 2011. Microbial zoonoses and sapronoses. Springer Science+Business Media B. V. DOI 10.1007/978-90-481-9657-9_6.
- [32] Daniel M., Kolar J., Zeman P. 2004. GIS tools for tick and tick-borne disease occurrence. *Parasitology* 129: 329-352.
- [33] Heymann W. R., Ellis D. L. 2012. *Borrelia burgdorferi* infections in the United States. *The Journal of Clinical and Aesthetic Dermatology* 5: 18-28.
- [34] Piesman J., Gern L. 2008. Lyme borreliosis in Europe and North America. In: *Ticks. Biology, Disease and Control*. (Eds. A. S. Bowman, P. Nuttall). Cambridge University Press: 220-252.
- [35] Rauter C., Hartung T. 2005. Prevalence of *Borrelia burgdorferi* sensu lato genospecies in *Ixodes ricinus* ticks in Europe: a metaanalysis. *Applied and Environmental Microbiology* 71: 7203-7216.
- [36] Hubalek Z., Rudolf I. 2012. Tick-borne viruses in Europe. *Parasitology Research* 111: 9-36.
- [37] Stefanoff P., Pfeffer M., Hellenbrand W., Rogalska J., Rühle F., Makówka A., Michalik J., Wodecka B., Rymaszewska A., Kiewra D., Baumann-Popczyk A., Dobler G. 2012. Virus detection in questing ticks is not a sensitive indicator for risk assessment of tick-borne encephalitis in humans. *Zoonoses and Public Health*. doi: 10.1111/j. 1863-2378.2012.01517. x.
- [38] Rizzoli A., Hauffe H. C., Carpi G., Vourc'h G. I., Neteler M., Rosa R. 2011. Lyme borreliosis in Europe. *Euro Surveillance* 16 (27). pii: 19906.
- [39] Kurtenbach K., De Michelis S., Etti S., Schäfer S. M., Sewell H. S., Brade V., Kraiczy P. 2002. Host association of *Borrelia burgdorferi* sensu lato – the key role of host complement. *Trends in Microbiology* 10: 74-79.
- [40] Hanincová K., Schäfer S. M., Etti S., Sewell H. S., Taragelová V., Ziak D., Labuda M., Kurtenbach K. 2003. Association of *Borrelia afzelii* with rodents in Europe. *Parasitology* 126 (Pt 1): 11-20.
- [41] Hanincová K., Taragelová V., Koci J., Schäfer S. M., Hails R., Ullmann A. J., Piesman J., Labuda M., Kurtenbach K. 2003. Association of *Borrelia garinii* and *B. valaisiana* with songbirds in Slovakia. *Applied and Environmental Microbiology* 69: 2825-2830.
- [42] Majlathova V., Majlath I., Hromada M., Tryjanowski P., Bona M., Antczak M., Vichova B., Dzimko S., Mihalca A., Petko B. 2008. The role of the sand lizard (*Lacerta agilis*) in the transmission cycle of *Borrelia burgdorferi* sensu lato. *International Journal of Medical Microbiology* 298 S1: 161-167.
- [43] Michalik J., Wodecka B., Skoracki M., Sikora B., Stańczak J. 2008. Prevalence of avian-associated *Borrelia burgdorferi* s. l. genospecies in *Ixodes ricinus* ticks collected from blackbirds (*Turdus merula*) and song thrushes (*T. philomelos*). *International Journal of Medical Microbiology* 298 S1: 129-138.
- [44] Richter D., Schlee D. B., Matuschka F. R. 2011. Reservoir competence of various rodents for the Lyme disease Spirochete *Borrelia spielmanii*. *Applied and Environmental Microbiology* 77: 3565-3570.
- [45] Wodecka B. 2012. Biology of *Borrelia* genus. In: *Stawonogi. Znaczenie medyczne i gospodarcze*. (Eds. A. Buczek, C. Błaszak). Akapit, Lublin: 213-220.
- [46] Movila A., Gatewood A., Toderas I., Duca M., Papeiro M., Uspenskaia I., Conovalov J., Fish D. 2008. Prevalence of *Borrelia burgdorferi* sensu lato in *Ixodes ricinus* and *I. lividus* ticks collected from wild birds in the Republic of Moldova. *International Journal of Medical Microbiology* 298 S1: 149-153.
- [47] Randolph S. 2011. Transmission of tick-borne pathogens between co-feeding ticks: Milan Labuda's enduring paradigm. *Ticks and Tick-borne Diseases* 2: 179-182.
- [48] Capri G., Cagnacci F., Neteler M., Rizzoli A. 2008. Tick infestation on roe deer in relation to geographic and remotely sensed climatic variables in a tick-borne encephalitis endemic area. *Epidemiology and Infection* 136: 1416-1424.
- [49] Bowman A. S., Ball A., Sauer J. R. 2008. Tick salivary glands. In: *Ticks. Biology, Disease and Control*. (Eds. A. S. Bowman, P. Nuttall). Cambridge University Press: 73-91.

Received 5 November 2012

Accepted 2 December 2012