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## Zoonotic Peculiarities of *Borrelia burgdorferi* s.l.: Vectors Competence and Vertebrate Host Specificity

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### 1. Introduction

Tick-borne diseases are of increasing public health concern because of range expansions of both vectors and pathogens (Daniel et al., 2003). Lyme borreliosis is the most common arthropod-borne human disease in temperate regions of the northern hemisphere. The causative agents of Lyme borreliosis (and other tick-borne borrelioses) are spirochaetes belonging to the *Borrelia burgdorferi* sensu lato (s.l.) species complex. It is well known that *B. burgdorferi* are unique among the pathogenic spirochaetes by requiring obligate blood-feeding arthropods for their transmission and maintenance in vertebrate host populations. All known causative agents of borrelioses circulate between ticks (Arachnida, Acari, Ixodoidea) and wide variety of vertebrates species (mammals, birds and reptiles). Consequently, *Borrelia* populations are shaped by the dynamics and demographic processes of host and vector populations, host and vector immune responses and extrinsic abiotic factors (e.g. combination of temperature, humidity and types of climate and landscape) affecting host and vector populations (Margos et al., 2011).

The main goals of this chapter are to summarize the results of vector competence analyses and vertebrate hosts' specificity for Lyme disease agents, give a general description of *B. burgdorferi* (s.l.) – tick – vertebrate hosts relationships in natural foci.

### 2. *Borrelia burgdorferi* s.l. genospecies diversity and association with vectors and reservoirs

From the time of *B. burgdorferi* discovery a large number of *Borrelia* isolates has been obtained from various vertebrate species, including humans. Involvements of other species from the *B. burgdorferi* s.l. complex were recognized recently. *Borrelia* spirochaetes are transmitted to reservoirs (including humans) by all 3 developmental stages of ixodid ticks (Fig 1 A), but the nymphal stage appears to be the most important at least in the North America and West Europe (Anderson et al., 1990; Kurtenbach et al., 1998; Kurtenbach et al., 2006). Considering

<i>Borrelia</i> species	Vector	Reservoirs	Geographical distribution	Reference
1-st group				
<i>B. afzelii</i>	<i>Ixodes ricinus</i> , <i>Ixodes persulcatus</i>	Rodents	Asia, Europe	Canica et al. (1993)
<i>B. bavariensis</i>	<i>Ixodes ricinus</i>	Rodents	Europe	Margos et al. (2009)
<i>B. bissettii</i>	<i>Ixodes ricinus</i> , <i>Ixodes scapularis</i> , <i>Ixodes pacificus</i> , <i>Ixodes minor</i>	Rodents	Europe, United States	Postic et al. (1998)
<i>B. burgdorferi sensu stricto</i>	<i>Ixodes ricinus</i> , <i>Ixodes scapularis</i> , <i>Ixodes pacificus</i> , <i>Ixodes persulcatus</i>	Rodents, birds, lizards, big mammals	Europe, United States, Asia	Baranton et al. (1992); Alekseev et al. (2010)
<i>B. garinii</i>	<i>Ixodes ricinus</i> , <i>Ixodes persulcatus</i> , <i>Ixodes hexagonus</i> , <i>Ixodes nipponensis</i> , <i>Ixodes pavlovskyi</i> , <i>Ixodes trianguliceps</i>	Birds, lizards, rodents	Asia, Europe	Baranton et al. (1992); Gorelova et al. (1996); Korenberg et al. (2010)
<i>B. kurtenbachii</i>	<i>Ixodes scapularis</i>	Rodents	Europe, United States	Margos et al. (2010)
<i>B. lusitaniae</i>	<i>Ixodes ricinus</i> , <i>Ixodes persulcatus</i>	Rodents, lizards	Europe, North Africa	Le Fleche et al. (1997); Alekseev et al. (2010)
<i>B. spielmanii</i>	<i>Ixodes ricinus</i>	Rodents	Europe	Richter et al. (2004, 2006)
<i>B. valaisiana</i>	<i>Ixodes ricinus</i> , <i>Ixodes granulatus</i> , <i>Ixodes persulcatus</i>	Birds, lizards	Asia, Europe	Wang et al. (1997); Alekseev et al. (1998, 2010)
2-nd group				
<i>B. americana</i>	<i>Ixodes pacificus</i> , <i>Ixodes minor</i>	Birds	United States	Rudenko et al. (2009b)
<i>B. andersonii</i>	<i>Ixodes dentatus</i>	Cotton tail rabbit	United States	Marconi et al. (1995)
<i>B. californiensis</i>	<i>Ixodes pacificus</i> , <i>Ixodes jellisoni</i> , <i>Ixodes spinipalpis</i>	Kangaroo rat, mule deer	United States	Postic et al. (2007)

<i>Borrelia</i> species	Vector	Reservoirs	Geographical distribution	Reference
<i>B. carolinensis</i>	<i>Ixodes minor</i>	Rodents, birds	United States	Rudenko et al. (2009a)
<i>B. japonica</i>	<i>Ixodes ovatus</i>	Rodents	Japan	Kawabata et al. (1993)
<i>B. sinica</i>	<i>Ixodes ovatus</i>	Rodents	China	Masuzawa et al. (2001)
<i>B. tanukii</i>	<i>Ixodes tanuki</i>	Unknown (possibly dogs and cats)	Japan	Fukunaga et al. (1996)
<i>B. turdi</i>	<i>Ixodes turdus</i>	Birds	Japan	Fukunaga et al. (1996b)
<i>B. yangtze</i>	<i>Ixodes granulatus</i> , <i>Haemaphysalis longicornis</i>	Rodents	China	Chu et al. (2008)
3-rd group				
Genomospecies 2	<i>Ixodes pacificus</i>	Unknown	United States	Postic et al. (2007)

Table 1. Currently known species from the *Borrelia burgdorferi* sensu lato complex (Rudenko et al., 2011 with modifications)

the human sensitivity to *B. burgdorferi* s.l. and results of the newest publications, the complex of 18 *Borrelia* species (Table 1) can be divided into 3 major groups (Rudenko et al., 2011): the first and second groups contains 9 species with pathogenic potential and species that have not yet been reported in or isolated from humans, respectively, and the 3rd still not named group proposed as genomospecies 2 represented by two far-western US isolates.

### 3. Ticks–*Borreliae* interface

#### 3.1 Vectors ecological groups

There are two big ecological groups of tick species. Ticks seek hosts by an interesting behaviour called "questing." Questing ticks (=exophilic, polyxenous) crawl up the stems of grass or perch on the edges of leaves on the ground in a typical posture with the front legs extended, especially in response to a host passing by (Fig. 1 A). In contrast to questing ticks, nidicolous (=endophilic, mainly monoxenous) ticks live in secluded enclosures such as caves, burrows and nests of their hosts or harborages near these nests (Fig. 1 B, C) (Sonenshine, 1991).

#### 3.2 Vector competence for *Borrelia burgdorferi* s.l.

The primary vectors of Lyme borreliosis spirochaetes to humans in temperate regions of the northern hemisphere are closely taxonomically related tick species: *I. pacificus* in Western North America, *I. persulcatus* in Eurasia, *I. ricinus* in Europe and *I. scapularis* in eastern North

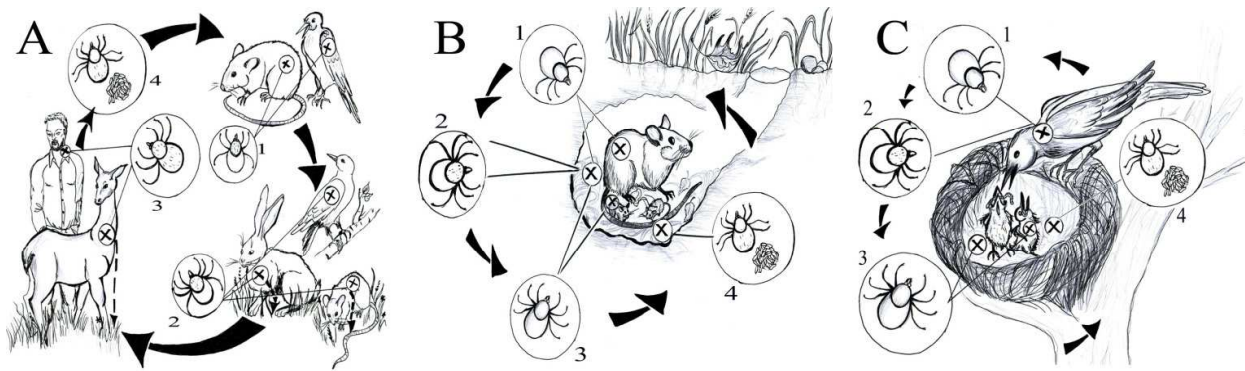


Fig. 1. The life circles of exophilic and endophilic ticks. A - exophilic tick life cycle, B - mammals-associated endophilic life cycle; C - bird-associated endophilic life cycle. 1 - Larvae, 2 - Nymph, 3 - Adult, 4 - Female with eggs

America. These ticks are basically forest dwellers, spending most of their time hiding in the leaf litter of the forest floor, where humidity is high and the risk of dehumidification is low. Ticks require three hosts, and their life cycle takes between 1-3 years to complete. The immature stages (larvae and nymphs) of the tick quest on low lying vegetation and tend to infest smaller hosts to obtain their blood meals, especially rodents, insectivores and birds. After feeding, they detach from their host and molt to the next development stage (larvae to nymph or nymph to adult tick) on the ground under leaves and other kind of the litter. The adult ticks have sexual dimorphism and only females take a big amount of blood meal, whereas males [at least *I. persulcatus* (Alekseev, 1992)] take a small amount of blood but nevertheless can transmit TBEV to human (for review see Alekseev et al., 2010). Both sexes tend to quest up on vegetations and generally infest different species of ungulates, carnivores and lagomorphs. After feeding, the female lay one batch of thousands of eggs and then die. Only one blood meal is taken during each of the three life stages.

In many ways, these ticks are ideally suited as vectors of zoonotic pathogens, since they feed on wide variety of animals but also include humans within the range of hosts they willing feed upon (Filippova, 1977; Xu et al., 2003).

To date, vector competence for *B. burgdorferi* s.l. has been experimentally confirmed for 12 tick species: *Ixodes affinis* Neumann, *Ixodes jellisoni* Cooley & Kohls, *Ixodes pacificus* Cooley & Kohls, *Ixodes persulcatus* Schulze, *Ixodes ricinus* (Linnaeus), *Ixodes scapularis* Say, *Ixodes angustus* Neumann, *Ixodes dentatus* Marx, *Ixodes hexagonus* Leach, *Ixodes minor* Neumann, *Ixodes muris* Bishopp & Smith and *Ixodes spinipalpis* Hadwen & Nuttall. Published vector competence studies have included only four *B. burgdorferi* s.l. genospecies (*B. burgdorferi* s.s., *B. afzelii*, *B. bissettii*, *B. garinii*) (Eisen & Lane, 2002).

The majority of the remaining confirmed vectors feed primary on rodents and/or lagomorphs (i.e. *I. dentatus*, *I. jellisoni*, *I. muris* and *I. spinipalpis* in North America and *I. minor* in North and South America), whereas *I. affinis* infests a wide variety of mammals in North and South America; *I. hexagonus* being a nidicolous arthropod is found on various medium sized mammals in Europe and north-western Africa (Jaenson et al., 1994). Their host preferences and *modus vivendi* render these tick species unlikely to act as vectors to humans.

In addition to the experimentally confirmed vectors, the presence of *Borrelia* in ticks and their primary hosts suggest vector competence for *B. burgdorferi* s.l. of several other *Ixodes*

spp. These includes the avian-associated nidicolous tick species such as *Ixodes uriae* White (Olsen et al., 1995), *Ixodes lividus* Koch (Movila et al., 2008), *Ixodes arboricola* Schulze & Schlottke (Špitalská et al., 2011), *Ixodes auritulus* Neumann (Morshed et al., 2005), *Ixodes turdus* Nakatsuji (Fukunaga et al., 1996a) and mammals-associated nidicolous ticks – *Ixodes trianguliceps* Birula (Gorelova et al., 1996) and *Ixodes neotomae* Cooley (Schwan et al., 1993).

Seven tick species evaluated for vector competence appear unable to transmit *B. burgdorferi* s.l.: *Amblyomma americanum* (Linnaeus), *Dermacentor andersoni* Stiles, *Dermacentor occidentalis* Marx, *Dermacentor variabilis* (Say), *Ixodes cookie* Packard, *Ixodes holocyclus* Neumann and *Ixodes ovatus* Neumann. In most cases these ticks acquired borreliae better feeding on infected hosts but transstadial passage was rare or absent, and there was no evidence of spirochaetes transmission during feeding (Eisen & Lane, 2002).

Taken all data together, there are 3 kinds of *Borrelia* species and vectors competence:

1. Those associated with a vector characterized by both a broad spectrum of hosts (*I. ricinus*, *I. persulcatus* or *I. scapularis*) and by a huge expansion area. These species have large populations of individuals and a variety of different vertebrate hosts which do not fully characterize the concerned *Borrelia* species. These species are genetically quite diverse and usually pathogenic or potentially pathogenic (*B. burgdorferi* s.s., *B. garinii*, *B. afzelii*, *B. valaisiana*, *B. lusitaniae*, etc.).
2. A second kind of species associated with either a unique reservoir or a unique specialized vector (*B. andersonii*, *B. turdi*, *B. tanukii*), or an unspecialized vector but still a unique reservoir (*B. spielmanii*).
3. Incompetence vector species. Mátlová et al. (1996) showed that unlike *I. ricinus*, *Dermacentor reticulatus* (Fabricius) reveals a gradual decline and the loss of Lyme borrelioses spirochaetes shortly after infection. This indicates a lack of this ixodid species to serve as a competent vector of *B. burgdorferi*.

Thus, the physiological mechanisms of vector competence in various tick species remain to be explained and require further studies.

### 3.3 Ticks behaviour and *Borrelia* transmission

Ticks can survive for years in their biotopes; however, they spend only a small part of their life in a parasitic phase. Most of the *Ixodes* spp. lifetime is spent outside of the hosts, either on the vegetation, ground or in the litter.

To find a host, *I. ricinus* climbs onto low vegetation and waits at the tip where they quest for a host for time-limited periods. During these periods of questing, ticks stay mainly immobile at the tip of the vegetation. When ticks are questing, they respond to mechanical and chemical stimuli produced by hosts, including humans. When hosts pass close enough, questing ticks grab their hosts but sometimes crawl in the direction of the possible prey. Such behaviour of *I. ricinus* is important since it implies that hosts, including humans, take some active part in the tick-host encounter. So, the successful transmission of pathogens to humans depends on the behaviour of the vectors.

Methods used to estimate tick behaviour vary and are generally directed to ascertain locomotor activity, which implies an orientation to physical parameters of the environment such as relative humidity, temperature, light and behaviour during questing for a host.

The predominant behaviour of *I. ricinus* is the tendency of the tick to ascend vegetation during the day and descent at night (Lees & Milne, 1951), while Okulova (1978) showed that *I. persulcatus* adults climbed up the aconite and fern stems to a maximum height of 80 cm (according to observations of Filippova (1977) some of *I. persulcatus* specimens in Primorye (Russian Far East) climb to a height of 2 m) when the temperature is 23.3° C. The maximum activity of *I. ricinus* larvae and adults was associated with the lightest part of the day, 1 p.m., when the air temperature was highest; the adults increased activity of females was observed between 1 p.m and 8 p.m. (Dubinina & Makrushina, 1997). Babenko (1985) suggested the crepuscular activity of ticks to be adaptive, coinciding with the activity of hosts they feed on.

Alekseev et al. (1998) reported that different *Borrelia* genospecies prevailed during different periods of the tick activity season. The author showed that *Borrelia*-infected nymphs and adults emerged within a day later than uninfected ticks and only after 11 a.m., when the temperature gradient exceeded 0.5° C. On the basis of these data Prof. Alekseev proposed a hypothesis that the response of *Borrelia*-infected *I. persulcatus* ticks to some external factors (plant and animal odors) was different from that of the uninfected ticks.

Lefcort & Durden (1996) studied the behaviour of *I. scapularis* nymphs and adults, and compared specimens that were infected in the laboratory by *B. burgdorferi* s.s. to uninfected ticks. The authors showed a stimulating effect of *Borrelia* on the activity of tick nymphs.

However the work of Alekseev et al. (2000) may be the most interesting example of the behaviour of infected and naive *I. persulcatus* and *I. ricinus* ticks. The comparison of *I. persulcatus* and *I. ricinus* demonstrated that the entire locomotor activity of *I. persulcatus* nymphs was 4 times and that of adults approximately 2 times as great as that of *I. ricinus*. The activity of infected preimaginal and adults *I. ricinus* was less than that of uninfected ticks. These report support earliest opinion that the *I. persulcatus* ticks are more effective vectors of pathogens than *I. ricinus* (Alekseev & Dubinina, 1994; Kovalevskii & Korenberg, 1995). Interesting, the European *Borrelia* genospecies depressed the nymphal activity of *I. ricinus* and *I. persulcatus* ticks. The data of Alekseev et al. (2000) and Lefcort & Durden (1996) can explain the role of nymphs as major vector of Lyme disease in North America and adults - in Euro-Asia.

The group of prof. Alekseev A.N. (for review see Alekseev et al., 2010) demonstrated that adults having exoskeleton anomalies (Fig. 2) and *Borrelia* infection moved more actively than ticks with normal morphology and with infection. This anomalies ticks phenomenon appeared to be associated with the consequences of the anthropogenic pressure and with environmental pollution, which caused the development of tick population with changed morphology and metabolism. It is clear that the accumulation of these anomalies ticks in the vector population increased the risk of pathogen transmission.

The ability of anomalous and normal ticks to attack humans was tested by Alekseev & Dubinina (2006). During 25 minutes of the experiments, none of the normal females attached onto the human skin, while anomalous females started as earlier as 1 minute after the release and this process was painless. The attachment sites of the ticks were corresponded to the acupuncture points on the human body with the impedance  $172 \pm 3.2$  k $\Omega$  (Alekseev & Dubinina, 2006). The fact that ticks attach to different sites on the body of the same person perhaps reflects the temporal changes in impedance (Alekseev et al., 2010). The ticks with anomalous in exoskeleton contain heavy metals in their bodies (especially Cd) are more

sensitive in their impedance measurements. The attachment of the anomalous female may be an indicator of a higher aggressiveness exhibited by anomalous, even pathogen-free ticks to humans.

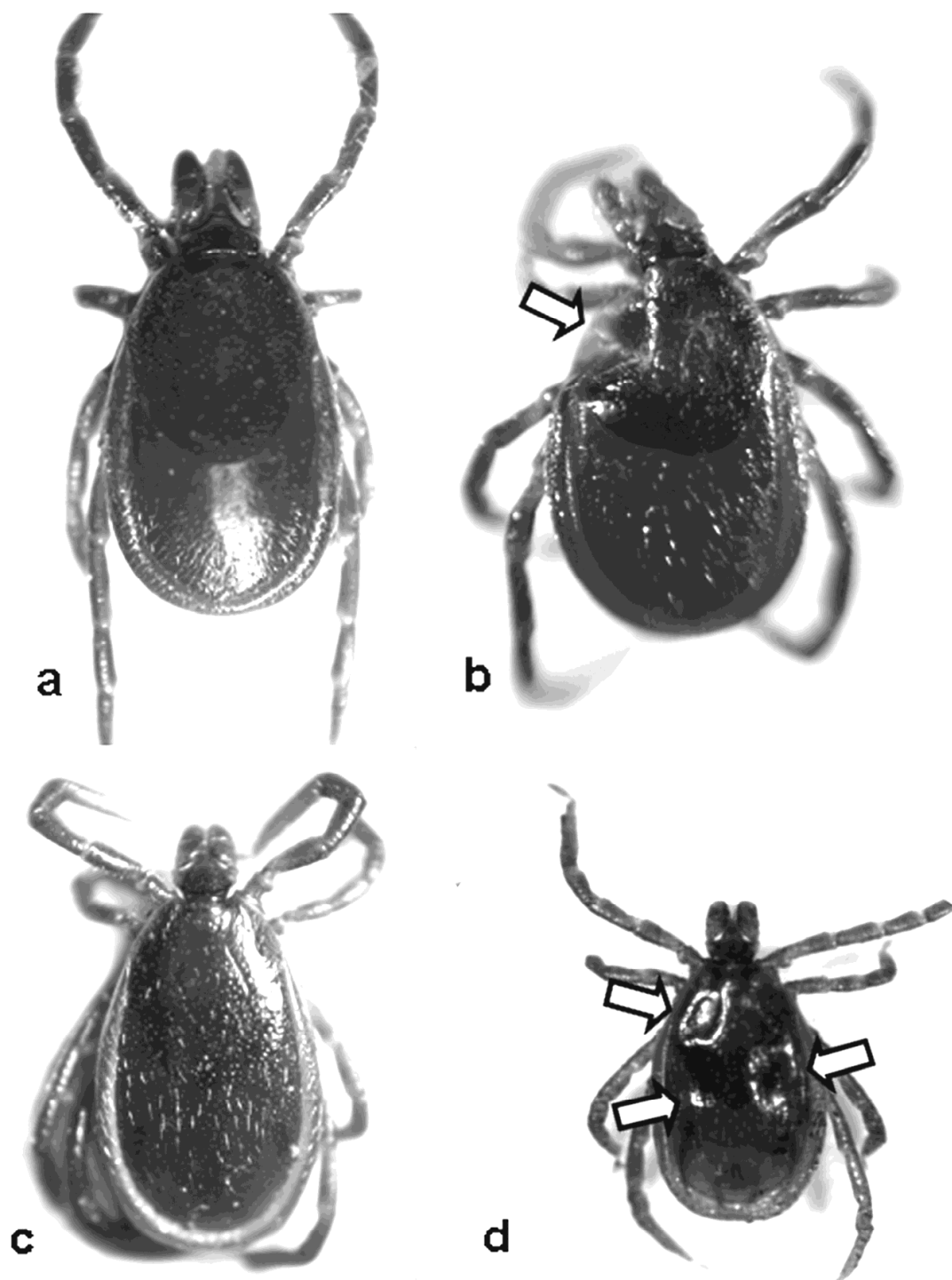


Fig. 2. Adult *Ixodes persulcatus* ticks, collected in vicinities of St. Petersburg (North-West Russia). Females: normal (a), anomalous (b); males: normal (c), anomalous (d). Arrows indicate prominent cuticular depressions symptomatic of exoskeleton pathologies in anomalous ticks (Original photos)



When unfed *I. ricinus* attaches to a vertebrate host, *Borrelia* transmission does not occur at the beginning of the blood uptake but later on, and transmission efficiency increases with the duration of the blood meal (Crippa et al., 2002; Kahl et al., 1998). The delay in transmission observed during the first hours of the blood meal might be due to this phenomenon, the migration of the spirochaetes from midgut to salivary glands. Crippa et al. (2002), comparing transmission dynamic of spirochaetes by *B. burgdorferi* s.s.- and *B. afzelii*-infected ticks, reported that this delay might also be influenced by the *Borrelia* species infecting the ticks. In fact, earlier transmission occurred when ticks were infected by *B. afzelii* rather than by *B. burgdorferi* s.s. These authors reported that during the first 48 h of attachment to the host, *B. burgdorferi* s.s.-infected ticks did not infect the 18 exposed mice, whereas *B. afzelii*-infected ticks transmitted infection to 33% of the mice. This study not only showed that *I. ricinus* transmits *B. afzelii* earlier than *B. burgdorferi* s.s., but also that *I. ricinus* is a more efficient vector for *B. afzelii* than for *B. burgdorferi* s.s. Unfortunately, nothing is known on the transmission delay for other pathogenic *Borrelia* species infecting *I. ricinus*, such as *B. garinii*, *B. valaisiana* and the recently described species *B. spielmanii*.

Whereas *B. burgdorferi* transmission to the host usually does not occur during the first 40 h of the blood meal in the North American vector ticks *I. scapularis* and *I. pacificus* (Peavey & Lane, 1995; Piesman et al., 1987, 1991), while *I. ricinus* nymphs were shown to be capable of transmitting *B. burgdorferi* s.l. to mongolian gerbils as early as within the first 24 h of feeding (Kahl et al., 1998). There is a method that allows assessment of the duration of tick feeding as a basis for determining the individual risk of *B. burgdorferi* transmission to the person bitten by a tick. Piesman & Spielman (1980) were the first to establish the so-called scutal index as a quick and simple measure of engorgement and feeding time in partially fed *I. scapularis* nymphs. The scutal index is the ratio between length of the tick alloscutum (a) and width of scutum (b) (Fig. 3). Falco et al. (1996) reported that the scutal index of *I. scapularis* nymphs detached from humans was on average equality to 34.7 h post-attachment. Yeh et al. (1995) reported that only 10% and 41% of people had found and removed *I. scapularis* nymphs by 24 h and 36 h of attachment, respectively. The situation is probably similar in Europe, but there is one important difference: whereas North American tick bite victims have a very good chance to avoid *Borrelia* infection after a tick bite lasting approximately 36 h, many *I. ricinus* nymphs might already have transmitted borreliae to their host after this feeding time.

Meiners et al. (2006) reported that a scutal index of 1.1 as a cutoff allows a clear distinction between high-risk versus low-risk group ticks. The large majority of *I. ricinus* nymphs with a scutal index <1.1 may have fed for <24 h, and the resulting risk of *B. burgdorferi* transmission and host infection might be low, even in the case of a *B. burgdorferi*-infected tick. The risk of host infection might be distinctly higher when a *B. burgdorferi*-infected *I. ricinus* nymph has a scutal index 1.1-1.5 (corresponding to ~24 - ~40 h feeding duration). Infection risk might be very high, if the detached tick has a scutal index >1.5 indicating that it might have fed for >36 h. Sood et al. (1997) identified a long feeding duration in *I. scapularis* ticks as a major risk indicator of *B. burgdorferi* host infection. Influence of borreliae on the salivary gland genome results the appearance of proteins, which suppress vertebrate immune system and properties of *Borrelia*.

Among vast family of proteins derived from tick salivary glands as a result of its genome activity the most interesting multifunctional one is presented by so called salp15 (14.7 kDa).

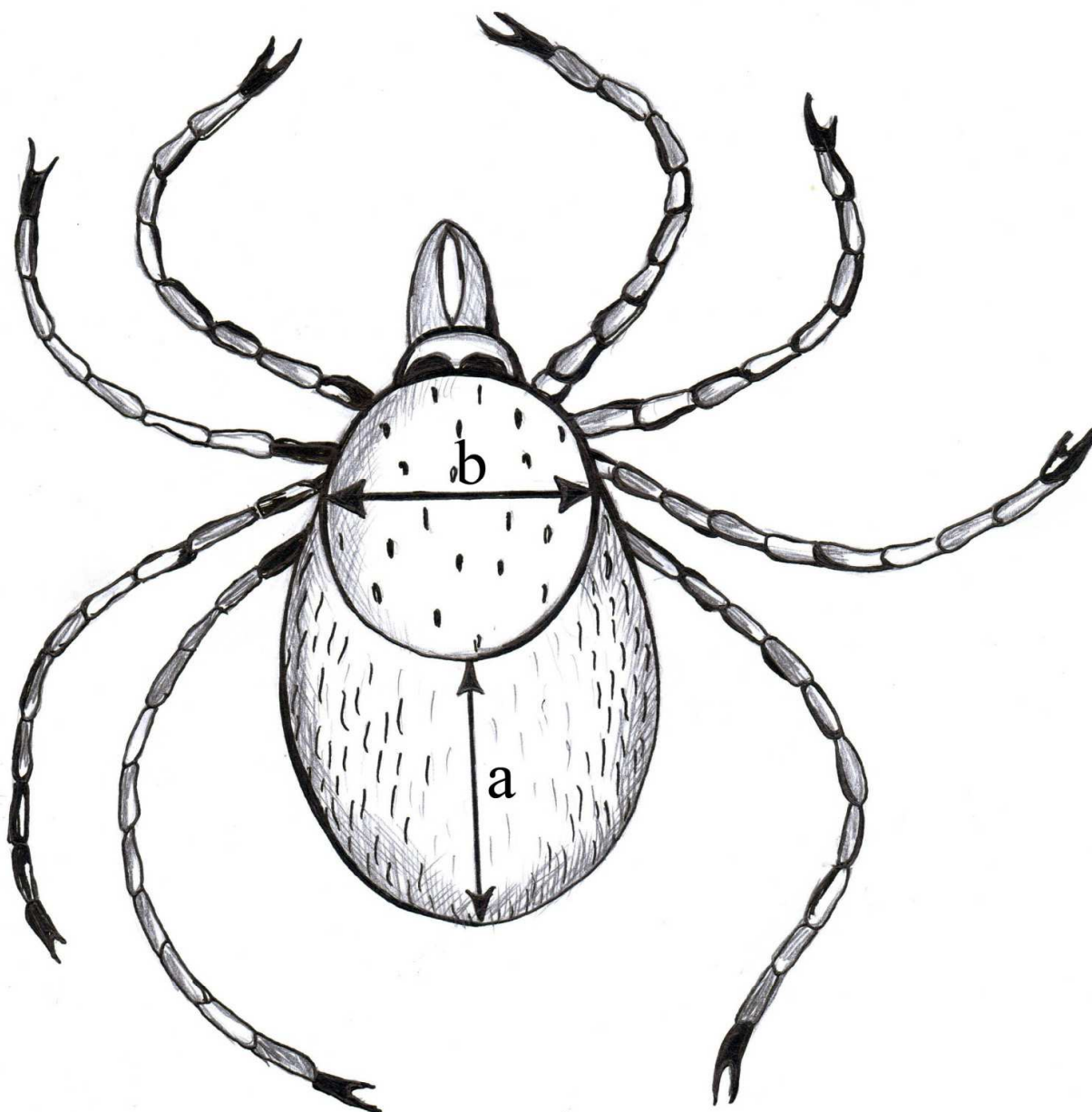


Fig. 3. Scutual index ( $= a/b$ ) of *Ixodes ricinus* nymphs (Meiners et al., 2006)

Actions of this protein have two directions: the first one channeled on vertebrate immune system suppression, the second one directed on infection enlighten of both pathogenic for human microorganism hosts. The first one is working independently of the presents of pathogenic for human microorganisms. The second one is working in dependence of infection. For example *I. scapularis* salp15 inhibits CD4<sup>+</sup> T-cell activation (Anguita et al., 2002) by binding to the CD4 receptor (Garg et al., 2006). Hovius and his colleagues (Hovius et al., 2008) found that salp15 from the same species of tick is able to bind the C-type lectin DC-SIGN on human dendritic cells. Such binding inhibits cytokine expression by impairing both nucleosome remodeling and mRNA stabilizations. All these mechanisms are functioning without borreliae action.

It is known now that the presence of OspC facilitates *B. burgdorferi* invasion of *I. scapularis* salivary glands. Pal et al. (2004), Rudenko et al. (2005) affirmed that in the beginning of infected (OspA) vertebrate' blood consuming borreliae enhanced salp15 production, which lightens tick infection. Just the opposite action, in which salp15 is also included, consist in prevention of *B. burgdorferi* infected (OspC) tick saliva from killing by anti-OspC antibodies in the tick just after beginning of attachment and feeding (Ramamoorthi et al., 2005). Rosa (2005) naming his article "Lyme disease agent borrows a practical coat" meaning that coat helped spirochaetes "to change into a new suit" and transfer themselves into the vertebrate host.

In the interface of field collected *I. ricinus* infected by different quantity of representatives of 4 species *Borrelia* determined by real time PCR and RLB a very interesting fact was discovered: the better surviving of adult ticks infected by mean doses of pathogens (Herrmann & Gern, 2010). This phenomenon was a brilliant confirmation of prof. Alekseev (1984) theory that among other criteria of interface specificity in the couple "vector–pathogen" the existence of optimum pathogen doses (mean ones) do exist not only in the pairs "*Leishmania – sand flies*", plague agent and fleas (Alekseev, 1984), "Tick-borne encephalitis (TBE) virus – *Ixodes persulcatus*" (Alekseev & Kondrashova, 1985), but in the couple "*Borrelia – Ixodes ticks*" (Herrmann & Gern, 2010).

### 3.4 *Borrelia* circulation in tick population

Ticks may acquire various *Borrelia* species through their successive blood meals on various hosts, and maintain the infection to the subsequent stage via transstadial transmission: larvae – nymph – adult.

Transovarial transmission of infection agents, which is an important factor of maintaining the disease foci, depends not only on the female obtaining the infection agents at the previous developmental stage, but also on the female contacting the infected male. The success of these contacts, and thus the probability of transmission, is based on the details of the sexual behaviour of the vectors. According to available data, which are scarce and often insufficiently representative, the frequency of *Borrelia* transovarial transmission in Lyme disease main vectors (*I. ricinus*, *I. persulcatus* and *I. scapularis*) may vary but never was estimated as frequent phenomenon (Du et al., 1990; Dubinina, 2000; Lane & Burgdorfer, 1987; Nakao & Miyamoto, 1992; Nefedova et al., 2004). On the basis of published data, probably, this transmission pathway apparently plays no significant role in the maintenance of *Borrelia* circulation and the dynamics of parameters of infection in adult ticks of the next generation. Nevertheless, transovarially transmitted spirochaetes may also contribute to mixed infections in ticks (Gern, 2009). However, *Borrelia miyamotoi* (a relapsing fever spirochete) is transmitted transovarially in *Ixodes* ticks and occurs sympatrically with *B. burgdorferi* spirochaetes (Piesman, 2002).

Thus, mixed infection with more than one species in ticks can be observed in some European endemic areas. These multiple infections may result from the tick species feeding on a host infected by more than one *Borrelia* species or from infected ticks feeding simultaneously with uninfected ticks on a host and exchanging the *Borrelia* species through co-feeding transmission from infected to uninfected ticks (Fig. 4). Different combinations of mixed infections with 2 or 3 species have been detected in *I. ricinus*. *Borrelia garinii* and

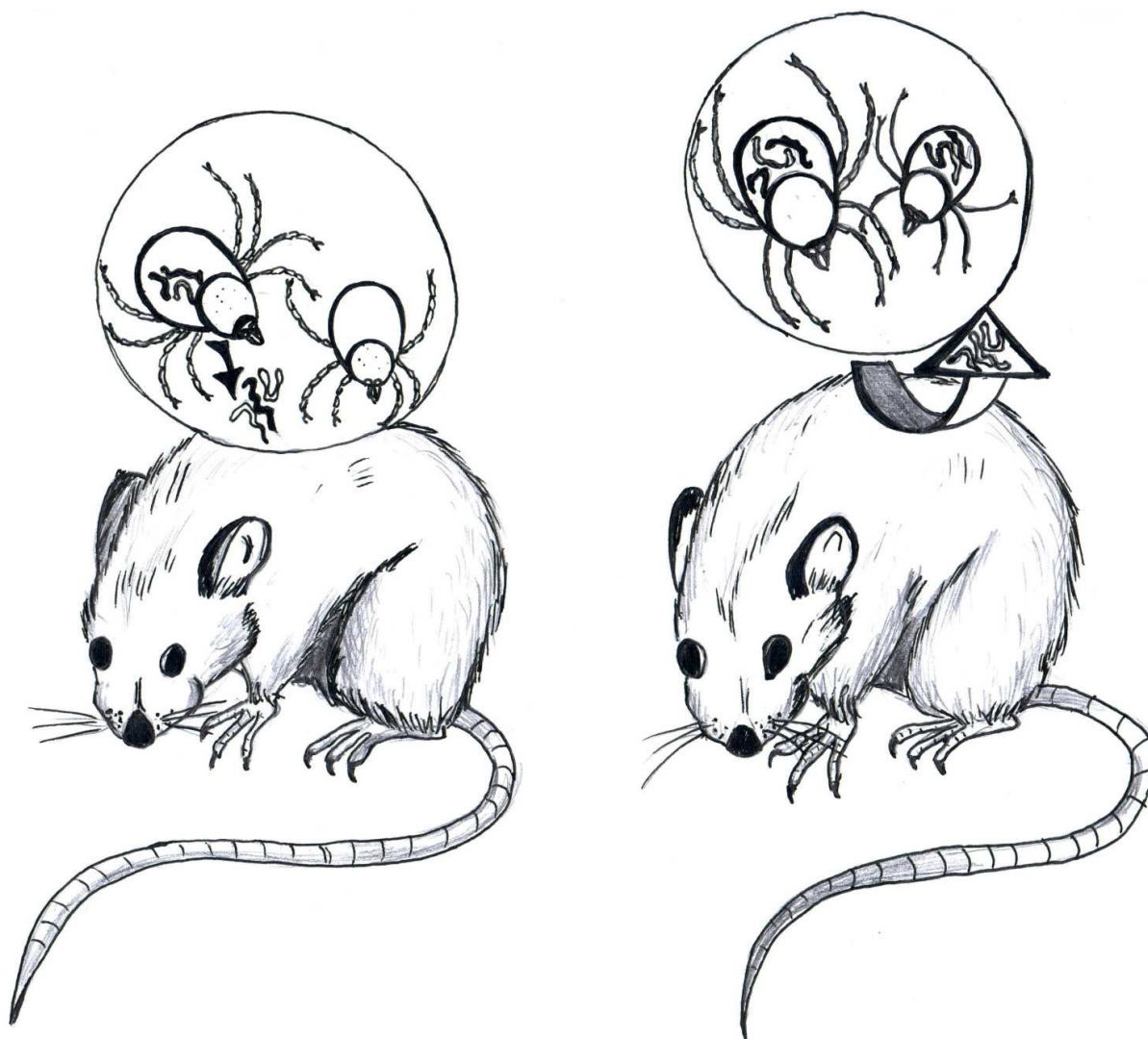


Fig. 4. *Borrelia* spp. co-feeding transmission

*B. valaisiana* constitute the majority of mixed infections, followed by mixed infections with *B. garinii* and *B. afzelii*. Such mixed infections are reported less frequently than single infections, and are often detected by PCR.

Ticks also can get *Borrelia* during copulation. Sexual transmission of microbial pathogens is a well-known phenomenon in arthropods. It was first described in soft ticks (Ornithodorinae) for relapsing fever *Borrelia* (Gaber et al., 1982, 1984; Wagner-Jevseenko, 1958). Chunikhin et al. (1983) studied the sexual transmission of the (TBE) virus in *I. persulcatus*. The virus was transmitted from the infected male tick to the female tick and was present in spermatocytes and spermatids of male ticks (Stefutkina, 1989). TBE virus was subsequently detected in the ovaries of 10% of the infected female ticks. Alekseev et al. (1999) have demonstrated that *B. garinii* (but not *B. afzelii*) spirochaetes can be transmitted from male to female in *I. persulcatus* ticks during copulation. Transmission of *B. garinii* to the female tick was observed more often when the male tick carried high numbers of spirochaetes. This observation is in accordance with the fact that ticks which carry high numbers of spirochaetes in the gut show systemic infection (i.e. outside the gut lumen) more often than ticks which contain low

numbers of spirochaetes (Moskvitina et al., 1995). Thus, infection of the generative apparatus of male *I. persulcatus* by *B. garinii* may depend on the presence of high numbers of spirochaetes in the tick gut. The preferred transmission of *B. garinii* among tick partners offers an explanation for the predominance of *B. garinii* over *B. afzelii* in field-collected *I. persulcatus* ticks (Alekseev et al., 2010; Korenberg et al., 1997).

Moreover, Alekseev et al. (1999) showed that tick females never transmit *Borrelia* to the *I. persulcatus* males during copulation act. In *I. ricinus* ticks males transmit to the females mostly *B. afzelii*, but the ticks that are more heavily infected by *B. afzelii* do not copulate at all (Alekseev et al., 2010). Dubinina (2000) studied the copulation peculiarities of *Borrelia*-infected/uninfected *I. ricinus* and *I. persulcatus* ticks in laboratory condition. The author reported that *I. ricinus* tick usually copulates on horizontal surfaces, while *I. persulcatus*, on vertical ones. The copulation period of uninfected *I. persulcatus* ticks is 1.3–1.5 times shorter to compare to *I. ricinus*, while borreliae-infection of one or both sexual partners increases the copulation time of *I. persulcatus*.

The *Borrelia*-positive ticks were 35.9% in forest biotopes, 23% in agrarian biocenoses and 36.7% in urbanocenoses. The author found that quite a number of Lyme borreliosis foci in Moldova have been situated in recreation areas where the contact between ticks and humans can be expected to be high (Movila et al., 2006). Similar data exist for other countries (Daniels et al., 1997; Juntala et al., 1999).

#### 4. Vertebrates species specificity

The efficient persistence of the borreliae in endemic areas requires the involvement of reservoir hosts. Potential hosts for ticks are numerous, and more than 300 vertebrate species have been identified as hosts for *I. ricinus*, including small mammals, birds, larger mammals and reptiles. Among these hosts, some act as blood meal sources and as reservoir hosts for pathogens, others as blood meal sources only. Important, that natural host does not seem to develop clinical manifestations of Lyme disease and it is difficult to evaluate the impact of *Borrelia* infection on their health. Minor clinical manifestations may escape medical attention (Gern, 2009).

Halos et al. (2010) reported that the *B. burgdorferi* s.l. infection prevalence was higher on pastures that had a high percentage of shrubs on the perimeter. This result is consistent with the fact that *B. burgdorferi* s.l. reservoir hosts, i.e., rodents and birds, are particularly concentrated in the shrubby vegetation around pastures (Boyard et al., 2008; Vourc'h et al., 2008). The *B. burgdorferi* s.l. infection prevalence also increased in pastures surrounded by forests with low perimeter length/surface area ratios. The lowest theoretical ratio corresponds to a circle; conversely, a high ratio indicated an indented shape with more edge compared to the surface area, which, again, should favor the small vertebrate abundance. This effect was thus in contrast to what we observed on woodland sites, where the prevalence tended to be associated with fragmented forest (Movila, 2008; Movila et al., 2006). Infected ticks found in pastures could have become infected by feeding on infected reservoir hosts located in the pasture itself or by feeding on infected woodland hosts that then imported the ticks into the pasture (Boyard et al., 2007). Halos et al. (2010) hypothesized that a decreased flow of tick hosts between woodlands and pastures could occur when the forest surrounding the pasture has a high perimeter length/surface area

ratio, a characteristic which would consequently hinder the infection prevalence in pasture ticks. This mechanism could be mediated by factors that we have not taken into consideration in this study, such as the pasture isolation from woodlands and the lack of connectivity between woodlands and pastures.

#### 4.1 Mammals as reservoirs for *Borrelia* spp.

Only a few mammal species have been identified as reservoirs for *B. burgdorferi* s.l. in Europe. Globally, little information is available on the real significance of most animal hosts as sources for infecting ticks with *B. burgdorferi* s.l. At present, several species of mice, voles, rats and shrews are recognized as reservoirs of *B. burgdorferi* s.l. in Europe (Gern & Humair, 2002). In particular, it was evidenced that the mice *Sylvaemus flavicollis* (Melchior), *Sylvaemus sylvaticus* (Linnaeus), *Apodemus agrarius* (Pallas) and the vole, *Myodes* (= *Clethrionomys*) *glareolus* (Schreber), play key roles in the ecology of Lyme borreliosis as reservoirs for *B. burgdorferi* s.l. in many European countries. Once infected by an infectious tick bite, some reservoir hosts, like *Sylvaemus* mice, have been shown to persistently remain infectious for ticks. Small rodents are frequently parasitized by larval and nymphal *I. ricinus*, and this also contributes to their importance as reservoirs. Less information has been obtained on the roles of other small mammal species in the maintenance cycles of *Borrelia* in nature. Nevertheless, another species of vole *Microtus agrestis* (Linnaeus) in Sweden, and black rats *Rattus rattus* (Linnaeus) and Norway rats *Rattus norvegicus* (Berkenhout) in urbanized environments in Germany and in Madeira, may serve as sources of infection for *I. ricinus* ticks. Similarly, only few data have been collected on *B. burgdorferi* s.l. in shrews (*Sorex minutus* Linnaeus and *Sorex araneus* Linnaeus and *Neomys fodiens* (Pennant) or in ticks attached on them. Observations in endemic areas of Germany and France showed that edible dormice *Glis glis* (Linnaeus) and garden dormice *Eliomys quercinus* (Linnaeus) are reservoir hosts for *Borrelia*. Other rodent species, like grey squirrels (*Sciurus carolinensis* Gmelin) in the UK and red squirrels *Sciurus vulgaris* (Linnaeus) in Switzerland also contribute to the amplification of *Borrelia* in the tick population. Interestingly, red and grey squirrels are usually very heavily infested with ticks.

In other investigations in Ireland, Germany and Switzerland, it was reported that the European hedgehog (*Erinaceus europaeus* Linnaeus) also perpetuates *B. burgdorferi* s.l. (Rauter & Hartung, 2005). An enzootic transmission cycle of *B. burgdorferi* s.l. involving hedgehogs and another tick vector, *I. hexagonus*, has been observed in an urban environment. This shows that gardens can also represent zones at risk of Lyme borreliosis as further discussed below. Examination of the role of lagomorphs *Lepus europaeus* (Pallas), *Lepus timidus* (Linnaeus) and *Oryctolagus cuniculus* (Linnaeus) in the support of the enzootic cycle of *B. burgdorferi* s.l. has also elucidated their roles as reservoirs (Gern & Humair, 2002).

Assessment of the reservoir competency of large mammals is clearly a difficult task. It necessitates, if xenodiagnosis is applied, capture of the animals and maintenance in a laboratory structure. The consequence of this is that the role of medium-sized and large mammalian species has been studied less and is not yet clearly understood. Red foxes seem to be implicated in the maintenance of borreliae in nature, as described in Germany. However, these animals do not appear to be very potent reservoirs, since spirochaetes were poorly transmitted to ticks feeding on them. According to various reports, ruminants appear to act primarily as sources of blood for ticks. Controversy long surrounded the exact role of

large animals, particularly cervids, in the maintenance cycle of *Borrelia* in endemic areas. Currently, most studies seem to indicate that they do not play a role as reservoirs. In fact, studies undertaken in Sweden and in the UK on roe deer *Capreolus capreolus* (Linnaeus), moose *Alces alces* (Linnaeus), red deer *Cervus elaphus* (Linnaeus) and fallow deer *Dama dama* (Linnaeus) suggested that these species do not infect feeding ticks with *B. burgdorferi* s.l. However, according to some recent developments, the possibility exists that they may act as supports for co-feeding transmission of borreliae between infected and uninfected ticks, and therefore may represent amplifying hosts (for review see Gern, 2009).

To date, it was shown that different *Borrelia* genospecies are associated with different vertebrate host. Our data and data of other authors showed that small rodents of the genus *Apodemus* and of the genus *Myodes* as well as red (*S. vulgaris*) and grey squirrels *Sciurus carolinensis* (Gmelin) were usually infected by *B. afzelii* and less frequently by *B. burgdorferi* s.s. and that they transmitted these 2 *Borrelia* species to ticks feeding on them (Gern, 2009; Movila, 2008). As far as less common *Borrelia* species are concerned, like *B. lusitaniae*. Thus, Dsouli et al. (2006) demonstrated the reservoir role of the lizard *Psammmodromus algirus* (Linnaeus) for *B. lusitaniae* in Tunisia, Richter & Matuschka (2006) the roles of the common wall lizard *Podarcis muralis* (Laurenti) and sand lizard *Lacerta agilis* Linnaeus in Germany and Amore et al. (2007) reported that *P. muralis* was a reservoir for this *Borrelia* species in Italy.

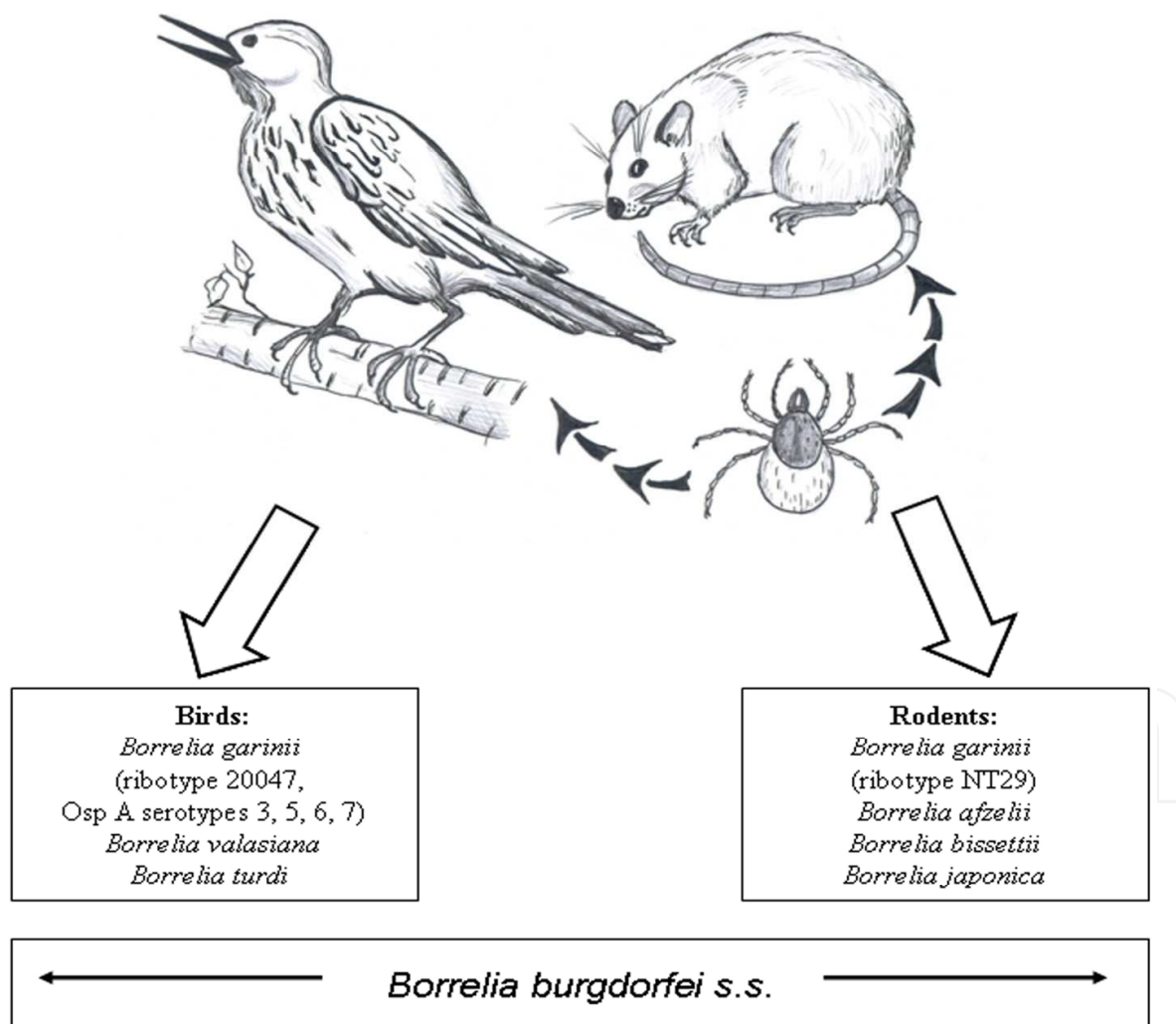
#### 4.2 Birds as reservoirs for *Borrelia* spp.

When attention was first directed at the role of birds in the ecology of Lyme borreliosis, their role was minimized (Gern, 2009). However, at the beginning of the 1990s, the reservoir role of birds was clarified in Europe, and now it is commonly accepted that some bird species are reservoirs for *B. burgdorferi* s.l. In 1998, 2 studies clearly defined the reservoir role of birds, one on a passerine bird, the blackbird *Turdus merula* (Linnaeus), the other one on a gallinaceous bird species, the pheasant *Phasianus colchicus* (Linnaeus) (Gern & Humair, 2002). Both studies examined the reservoir role of these bird species using xenodiagnosis. Tick xenodiagnosis consists of infecting uninfected ticks - usually larvae - during feeding on the animal suspected to be reservoir host. The fact that some of the same species of *Borrelia* exist both in the northern and in the southern hemisphere is further evidence that birds participate in the natural circulation of *Borrelia* spirochaetes (Poupon et al., 2006). These results and others have evidenced the contribution of birds to the circulation of *Borrelia* in endemic areas. A transmission cycle of *B. burgdorferi* s.l. was discovered in environmental settings other than the biotopes where *I. ricinus* usually live. In fact, it was demonstrated, on a Swedish island, that *B. burgdorferi* spirochaetes could be maintained in seabird colonies among razorbills *Alca torda* (Linnaeus) by an associated tick species, *I. uriae*. The involvement of seabirds and *I. uriae* (in the marine environment) in the transport of infected *Borrelia garinii* between the northern and the southern hemispheres was described. (Comstedt et al., 2009; Gern et al., 1998; Kurtenbach et al., 2006). In this context, it is interesting to mention that in a laboratory study, reactivation of latent *Borrelia*-infection could be induced in passerines experimentally submitted to stressful conditions simulating migration. This implies that during their migration, birds can infect ticks all along their migration route. Bird migration also allows the transfer and establishment of particular *Borrelia* species, as described for *B. lusitaniae*. In fact, birds migrating between south-west Europe/North Africa to north-western Europe have been suggested to be responsible for the transfer of *B. lusitaniae* from

North Africa and south-west Europe, where this *Borrelia* species clearly dominates, to north-west Europe where it is much less frequent (Poupon et al., 2006).

The most commonly parasitized birds are blackbirds and song thrushes, both ground-dwelling birds, which most likely come into contact with *I. ricinus* subadults. Overall, nymphs were more commonly found on birds than were larvae. This result contrasts with those of previous studies involving rodents, in which nymphs feeding on rodents were less abundant than larvae (Hanincová et al., 2003; Movila et al., 2008; Špitalská et al., 2006).

According to classical theory of Kurtenbach et al. (2002) (Fig. 5), *B. afzelii*, *B. garinii* (NT29 ribotype, OspA type 4\*), *B. japonica* and *B. bissettii* are resistant to the rodent complement, that makes rodents appropriate reservoir hosts for these genospecies. *B. garinii* (except the abovementioned strains), *B. valaisiana* and *B. turdi* are resistant to the bird complement. *B. burgdorferi* s.s. has an intermediate resistance to both bird and rodent complement and often seem to be infectious to birds and rodents.



\* Margos et al. (2008) proposed a new species *B. bavariensis* as separate from *B. garinii* OspA serotype 4 based on genetic distance and ecological differences.

Fig. 5. Schematic diagram of host specificity of *Borrelia burgdorferi* s.l. (Kurtenbach et al., 2002, with modifications).



A review analysis by Humair (2002) indicated that in Eurasia, *B. garinii* is strongly associated with grounddwelling and sea birds. In Europe, also *B. valaisiana* and *B. burgdorferi* s.s are associated with birds (Derdáková & Lenčáková, 2005). At the same time, Comstedt et al. (2006) demonstrated the presence of five *Borrelia* genospecies (*B. garinii*, *B. valaisiana*, *B. afzelii*, *B. burgdorferi* s.s. and *B. miyamotoi*) in migratory birds in northern Europe. Poupon et al. (2006) found that in Switzerland, *B. valaisiana*, *B. garinii*, and *B. lusitaniae* were the most frequently found species in ticks collected from migratory birds, with *B. lusitaniae* found in a surprisingly high abundance. In the western Mediterranean Basin, however, a high prevalence of *B. lusitaniae* has been observed in some localities, suggesting that this genospecies has a narrow spectrum of reservoir hosts, restricting its geographical range (de Michelis et al., 2000). *B. lusitaniae* appears to be infrequent in *I. ricinus* in most areas of Europe (Gern et al., 1999), but it has been described as the dominant *Borrelia* species in *I. ricinus* in south-western Europe (de Michelis et al., 2000) and in North Africa (Younsi et al., 2001). Moreover, *B. lusitaniae* was the most frequently detected species after *B. valaisiana* in Moldavian questing *I. ricinus* ticks collected in the “Codri” forest reserve (Movila, 2008). A question for further investigation is whether the dominant *Borrelia* species in birds has shifted from *B. burgdorferi* s.s. to *B. valaisiana* and *B. lusitaniae* during last decades in that area (Movila et al., 2008).

Interestingly, *B. afzelii* was detected in bird-feeding ticks (Comstedt et al., 2006; Kipp et al., 2006; Taragelova et al., 2008), even in engorged larvae (Dubska et al., 2009; Olsen et al., 1995; Poupon et al., 2006), but in relation to other species, the rate was unusually high. Stern et al. (2006) detected *B. afzelii* in only 3 out of 806 bird-feeding ticks from the Greifswalder Oie, using reverse line blot as identification method. The study of Stern et al. (2006) included no robins, accounting for 5 out of 11 *B. afzelii* infections in the present investigation. Dubska et al. (2009) found *B. afzelii* in 13 bird-feeding nymphs and 2 larvae. Although they detected other species more frequently, they suggested that birds may be able to transmit *B. afzelii*.

In Europe, *B. afzelii* occurs in bird-feeding ticks even more frequently than *B. burgdorferi* s.s. (Comstedt et al., 2006; Dubska et al., 2009; Kipp et al., 2006), whereas in North America birds are reservoirs for *B. burgdorferi* s.s. (Jordan et al., 2009; Wright et al., 2006). However, *B. burgdorferi* s.s. seems to be generally rare in many European regions (Burri et al., 2007; Hanincová et al., 2003; Kipp et al., 2006; Smetanova et al., 2007), and consequently this is not necessarily due to a reservoir incompetence of birds for this species in Europe.

There are only a few xenodiagnostic studies on the reservoir competence of birds for certain *Borrelia* species available. Kurtenbach et al. (2002) came to the conclusion that pheasants, a non-passerine species have *B. valaisiana* and *B. garinii* species reservoir competence and no for *B. afzelii*. Another investigation by Ginsberg et al. (2005) states that certain North American passerines, infected with *B. burgdorferi*, show temporal variability in infectiousness to larval ticks, which may be an explanation for different prevalence rates of European genospecies in the literature. This could indicate that the birds may be infected with *B. afzelii*, but transovarial transmission of *B. afzelii* and co-feeding with *B. afzelii*-carrying nymphs may also explain these findings.

There are 3 mechanisms of the birds' role in spreading *Borrelia*-infected ticks:

1. Passive transport of previously infected nymphs and transovarially infected larvae may occur.

2. Infected migratory birds may infect the ticks, which are then dropped off in a new location. In support of this mechanism, Gylfe et al. (2000) found a reactivation of *B. garinii* infection in experimentally infected *Turdus iliacus* Linnaeus during migratory restlessness, indicating an increased risk of transmitting *Borrelia* sp. to the tick vector during migration. If the migratory birds are chronic carriers of tick-borne diseases, then they may continue to transfer them to ticks that parasitize them after arrival. Sampling of blood or tissue from the birds would provide more information of this issue.
3. The tick vectors may transfer *Borrelia* species between each other through co-feeding while being transported (Randolph et al., 1998; Dubinina & Alekseev, 2003).

## 5. Conclusion

The description of the various *Borrelia* species in ticks has opened an entire new field of research in the ecology of Lyme borreliosis. It seems prudent to review the importance of the different types of associations between *Borrelia* species, tick vectors, and vertebrate hosts in various geographic areas.

Host specialization is an important factor in vector-borne disease, and different pathogens show varying levels and patterns of host specialization, which may impact the spread of pathogens. Lyme borreliosis group of spirochaetes, *B. garinii* and *B. valaisiana* are transmitted by avian species while *B. afzelii* is associated with rodents and certain insectivore species. *B. burgdorferi* s.s. is a generalist species, known to infect both rodent and avian species, as well as other hosts. The diversity in host specialisms in the Lyme borreliosis group of spirochaetes makes this an ideal system to examine the interplay between the ecology of the host and the epidemiology of the bacteria. As ticks do not move over large distances independently, the spread of *Borrelia* spp. spirochaetes is likely to be linked to the migration of their hosts. Species that are maintained by rodents are therefore predicted to show more limited migration than those associated with birds. In addition to being of public health importance, the delineation and monitoring of the geographic ranges of the different Lyme borreliosis species also provides an opportunity to examine in more general terms the role of host ecology in the epidemiology of vectored zoonoses.

Clearly, additional field studies are needed of *Borrelia* host specificities, keeping in mind particularly the newly described *Borrelia* species and the great subtype diversity hidden in most *Borrelia* species, as well as the geographic diversity of local ecosystems. Future studies in Lyme borreliosis ecology seeking to identify the *Borrelia* spirochaetes in both ticks and reservoir hosts in various endemic areas are strongly encouraged. Those studies are extremely important for the determination of the complete spectrum of *Borrelia* species involved in human Lyme disease worldwide with its unknown, rare, and unusual clinical manifestation.

## 6. Acknowledgment

We indebted to Mr. Igor Babic (InTech Open Access Publisher) and Mr. Alexandr Morozov (Institute of Zoology, Moldova) for rendered assistance in this chapter preparation. We acknowledge the perfect original images of Mrs. Anna Movila. The authors thank Moldova Academy of Science for financial support.

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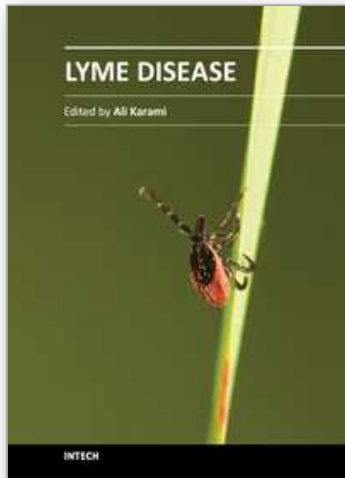
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## **Lyme Disease**

Edited by Dr. Ali Karami

ISBN 978-953-51-0057-7

Hard cover, 160 pages

**Publisher** InTech

**Published online** 17, February, 2012

**Published in print edition** February, 2012

Lyme disease, or Lyme borreliosis, is an emerging infectious disease caused by bacteria belonging to the genus *Borrelia*. *Borrelia burgdorferi*, in the strict sense. This book deals mostly with the molecular biology of the Lyme disease agent *Borrelia burgdorferi*. It has been written by experts in the relevant field and is tailored to the need of researchers, advanced students of biology, molecular biology, molecular genetics of microorganism. It will also be of use to infectious disease experts and people in other disciplines needing to know more about Lyme borreliosis. The book contains chapters on the molecular biology of the Lyme disease agent, zoonotic peculiarities of Bb, advancement in Bb antibody testing, the serology diagnostic schemes in Bb, discovering Lyme disease in ticks and dogs, adaptation to glucosamine starvation in Bb, and porins in the genus *Borrelia*.

### **How to reference**

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Alexandru Movila, Ion Toderas, Helen V. Dubinina, Inga Uspenskaia and Andrey N. Alekseev (2012). Zoonotic Peculiarities of *Borrelia burgdorferi* s.l.: Vectors Competence and Vertebrate Host Specificity, Lyme Disease, Dr. Ali Karami (Ed.), ISBN: 978-953-51-0057-7, InTech, Available from:

<http://www.intechopen.com/books/lyme-disease/zoonotic-peculiarities-of-borrelia-burgdorferi-s-l-vectors-competence-and-vertebrate-host-specificit>

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