

The Ecology of Lyme Borreliosis in Europe

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5.1 Introduction

The most common tick in Europe, the castor bean or sheep tick, *Ixodes ricinus* has been incriminated as a vector of the cause of the disease now referred to as Lyme borreliosis, ever since Dr. Arvid Afzelius in 1910 described, at the site of a tick bite on an elderly lady, the development of a skin lesion he referred to as erythema migrans. Since the etiology of this skin disorder was unknown, it was speculated that it might be a tick-associated toxin or infectious agent. The toxin hypothesis appeared unlikely because of the chronic nature of the disease. Lipschütz in 1923 suggested that the cause was associated with the tick bite and emphasized microscopic-bacteriologic investigations of the ticks' intestinal tract and salivary gland secretion. Similarly, Hellerström in 1950, referring to the demonstration of his colleague Carl Lennhoff of spirochete-like elements in skin sections of erythema migrans lesions, pointed to the possibility that this disease may be caused by tick-associated spirochetes.

Not only in erythema migrans, but also in other clinical manifestations now known to be related to Lyme borreliosis, ticks, particularly *I. ricinus*, have been implicated as the transmitting vectors. Thus, in 1922, Garin and Bujadoux described a case of tick paralysis in a patient bitten by *I. hexagonus*. The disorder was later recognized as lymphocytic meningoradiculitis or Bannwarth's syndrome (Bannwarth 1941) – a nervous system disorder commonly associated with the bite of *I. ricinus*. Similarly, numerous cases of acrodermatitis chronica atrophicans (ACA) and lymphadenosis benigna cutis were suspected to be associated with the bite(s) of *I. ricinus* even though many patients often no longer remembered having been bitten by ticks (Weber 1981; Rulli 1987).

The discovery in 1981 of a spirochete now known as *Borrelia burgdorferi* in the deer tick *I. dammini* in the United States (Burgdorfer et al. 1982), and in *I. ricinus* from Switzerland (Burgdorfer et al. 1982, 1983), which was found to be the agent of Lyme borreliosis, led to intensive epidemiological and ecological investigations on both sides of the Atlantic. This chapter is devoted to the natural history of *B. burgdorferi* in Europe and to the relationship(s) of this spirochete to its European tick vectors, primarily *I. ricinus*.

5.2 *Ixodes ricinus* – Principal Tick Vector of *B. burgdorferi* in Europe

5.2.1 Description and Geographic Distribution

The castor bean or sheep tick *I. ricinus* (Fig. 1, see color plate I after page 118) is the most common tick in Europe where it has long been recognized as an important vector of various human and/or animal pathogens, including the virus of tick-borne encephalitis, *Babesia*, rickettsiae, trypanosomes, and microfilariae (Aeschlimann et al. 1979).

The literature on the biology of this tick is voluminous and has been referred to by Aeschlimann (1972, 1981). *I. ricinus* belongs to the genus *Ixodes* in the large family of ixodid or hard-shelled ticks – a family characterized by the chitinous scutum that, in male ticks, covers the entire dorsum, but in female ticks, only the anterior portion of the dorsum (Fig. 2). *I. ricinus* is a three-host tick whose developmental stages, i.e., the larva, the nymph, and the adult, parasitize different hosts (Fig. 3). In doing so, the fast-ing ticks leave their hiding places and climb surrounding vegetation such as grasses

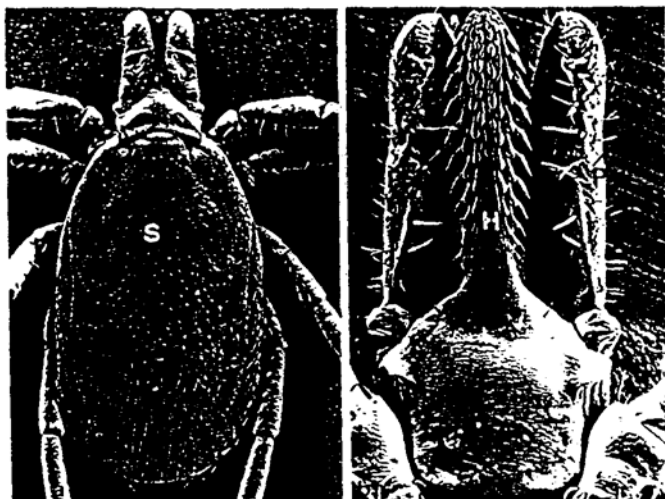


Fig. 2. a.b. *Ixodes ricinus*.
a Female, x 41.4 (S. scutum)
b Detail of a ventral view of the mouthpart, x 114.4 (P. pedi palps; H. hypostome)
Scanning electron photographs
(Courtesy of Tiago Cordas, Zoological Institute, Neuchâtel, Switzerland)

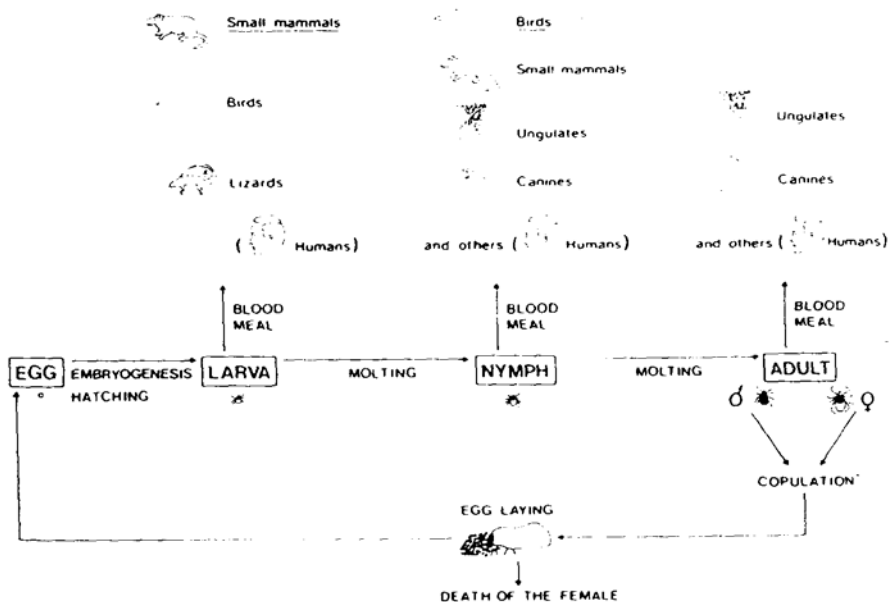


Fig. 3. Life cycle of *Ixodes ricinus* (modified from Aeschlimann et al 1990)

and bushes where they lie in wait for a passing host. *I. ricinus* is notorious for the wide range of vertebrates it feeds on. In its immature stages, it attacks primarily small and medium-sized vertebrates such as lizards, ground-frequenting birds, rodents, insectivores, carnivores, wild pigs, and humans (Fig. 3). The adults prefer larger animals such as deer, cattle, dogs, and occasionally also humans.

I. ricinus is widely distributed throughout Europe and occurs in wooded and pasture areas from Ireland, Britain, and southern Scandinavia to Spain, Portugal, Algeria, Tunisia, and Morocco, much of southern Europe, central Europe, and European Russia to the Caspian Sea and northern Iran. Within this large distributional area, successful infestation by *I. ricinus* depends on fulfilling at least three biological and microclimatic requirements: (a) availability of suitable hosts, (b) temperature fluctuations between minus 10°C and 35°C with extreme values lasting for short periods of time only, and (c) constant relative humidity of at least 80% in the air and of near saturation in the soil. The ideal biotope of this tick, therefore, is a deciduous forest with damp soil covered by a thick layer and a rich undergrowth.

In central Europe, the tick's seasonal activity begins in March and ends in November. It is characterized by a bimodal pattern because of decreased activity during the hot summer months. At the end of November, the ticks disappear from hosts and vegetation to spend the winter months in the protective superficial layer of the soil. All developmental stages are active almost simultaneously, although nymphal and adult activity may occur 3–4 weeks before that of the larvae. Copulation of *I. ricinus* takes place during waiting periods on vegetation as well as on the host. Male ticks do attach, but ingest small quantities of blood only; they never engorge.

After 7–10 days of feeding, mated females drop to the ground where, after 8–30 days, they oviposit up to 3000 eggs, which develop after 4–8 weeks into the six-legged larval stage. Larval and nymphal *I. ricinus* that engorge in early summer molt to nymphs and adults, respectively, the same year. Engorged ticks or eggs oviposited during the fall period of activity go into a diapause, hibernate, and molt in early spring of the following year.

Although all stages of *I. ricinus* parasitize a large variety of animal hosts including humans, field studies in several European countries have shown that the larvae prefer small rodents, particularly the long-tailed and yellow-necked field mice (*Apodemus sylvaticus* and *A. flavicollis*, respectively) and the bank vole (*Clethrionomys glareolus*). Nymphs, on the other hand, are apparently more frequently found on ground-frequenting birds and on larger animals, whereas adult *I. ricinus* parasitize roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*).

5.2.2 The Role of *Ixodes ricinus* as Vectors of *Borrelia burgdorferi* in Europe

The detection in *I. ricinus* from Switzerland of spirochetes identical with or similar to the causative agent of Lyme borreliosis in the United States has led to tick spirochete surveys in many countries including Austria, Germany, Switzerland, France, Czechoslovakia, the Scandinavian countries, the United Kingdom, and Ireland. According to the results summarized in Table 1, as many as 66% of the ticks examined were found to be infected with spirochetes, suggesting throughout large areas of Europe the existence of natural foci in which *B. burgdorferi* occurs in cycles between its tick vectors and animal hosts.

Recent tick/spirochete surveys in Germany and near Leningrad, Russia, revealed spirochetes also in other species of ticks such as *I. hexagonus* and *I. persulcatus* (see Table 1). The former parasitizes primarily hedgehogs and mustelidae, but is known to

Table 1. Prevalence of ticks infected with *Borrelia burgdorferi* in Europe

Country	Reference	Species	Ticks examined n	Developmental stage	n	Infection rate %	Range (%) *
Austria	Radda et al. 1986	<i>I. ricinus</i>	1207 ^a	adults and nymphs	27/90 ^b	20	2-40
Germany	Wilske et al. 1987	<i>I. ricinus</i>	1052	adults	220	21	11-34
			984	nymphs	104	11	3-26
			367	larvae	4	1	0-4
	Pelz et al. 1989	<i>I. ricinus</i>	129	adults	37	29	
			45	nymphs	3	7	
	Kahl et al. 1989	<i>I. ricinus</i>	173 ^a	adults	12/73 ^b	16	
			1365 ^a	nymphs	34/280 ^b	12	
			124	adults	10	8	
			49	nymphs	0		
Czechoslovakia	Kmeny et al. 1986	<i>I. ricinus</i>	550	adults	45	8	3-20
Sweden	Stenstedt 1985	<i>I. ricinus</i>	332	adults	20	14	
			159	adults	30	19	
	Mejlon et al. 1990	<i>I. ricinus</i>	1032	nymphs	119	12	7-12
			388	larvae	0		
	Bergstrom et al. 1990	<i>I. ricinus</i>	88	adults	9	10	
Switzerland	Bugdorfer et al. 1983	<i>I. ricinus</i>	381	adults	112	29	
			2500	nymphs		20	5-34
	Aeschlimann et al. 1986	<i>I. ricinus</i>	2500	nymphs			

	Péter 1990	<i>I. ricinus</i>	508	adults	159	31	4-52
			119	nymphs	51	43	0-66
	Zhioua et al. 1988	<i>I. ricinus</i>	55	adults	8	15	
			258	nymphs	33	12	
			652	larvae	20	3	
	Miserez et al. 1990	<i>I. ricinus</i>	88	adults	22	25	
			94	nymphs	34	36	
			216	larvae	7	3	
United Kingdom	Muhlemann and Wright 1987	<i>I. ricinus</i>	130	adults	10	8	
			191	nymphs	15	8	
Germany	Liebisch et al. 1989	<i>I. hexagonus</i>	111	adults	13	12	
			178	nymphs	0		
			14	larvae	0		
	Liebisch and Olbrich 1990	<i>I. hexagonus</i>	610	larvae, nymphs and adults	52 ^{a)}	8	
Estonia	Barotov and Jõgiste 1990	<i>I. persulcatus</i>	**	adults		12	≤35
		<i>I. ricinus</i>	**	adults		8	≤15
Russia	Korenberg (personal communication)	<i>I. persulcatus</i>					≤60
							≤30

*depending on the areas

a) tested in pools

b) infection rate of pools

^{a)} 2 larvae, 32 nymphs and 18 adults^{b)} A total of 2638 *I. ricinus* and *I. persulcatus* were examined

The Lyme borreliosis spirochete exhibits, in its tick vectors, a behavior characteristically different from that of the hitherto investigated tick-borne spirochetes (Burgdorfer 1976) in that it causes a persistent infection in the ticks' midgut, from where it may penetrate during and after the ticks' engorgement to invade other tissues (Fig. 5). Of 112 infected adult *I. ricinus*, for example, only six had a generalized or systemic infection; all others had spirochetes in their midgut only (Burgdorfer et al. 1983).

Gut penetration and systemic infection by *B. burgdorferi* in American and European tick vectors have been the subjects of several investigations using conventional as well as electron microscopy (Benach et al. 1987; Ribeiro et al. 1987; Zung et al. 1989; Gem et al. 1990). Findings available so far suggest that *B. burgdorferi* persists in the midgut, where it aggregates between epithelial cells and becomes closely associated with the gut's basement membrane (Fig. 6). Penetration of the gut epithelium and dissemination into other tissues appears to take place during early and mid-feeding, i.e., 1–3 and 5–7 days after attachment, respectively. In *I. ricinus*, this phenomenon is said to take place as early as 3 days after tick attachment (Gem et al. 1990). Tick tissues other than the midgut are usually only mildly infected.

The presence and development of spirochetes in ovarian tissues has been demonstrated in all principal vectors of the Lyme borreliosis spirochete, and there is convincing evidence that transovarial transmission also occurs. This phenomenon, however, is

Fig. 5. Internal anatomy of *Ixodes ricinus*.

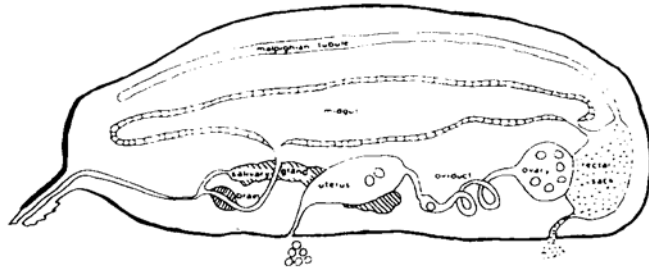


Fig. 6. *Borrelia burgdorferi* colonizing the basal lamina (BL) of *Ixodes ricinus* midgut. Spirochetes perturb the space of a gut wall muscle cell. Arrows denote colonization site at the base of a degenerating digestive cell. Transmission electron micrograph (Bar. 0.5 μ m). Provided by one of us (W.B.) and S.F. Hayes, Rocky Mountain Laboratories, Hamilton, Montana, USA



not considered a major ecological factor for infecting *I. ricinus* with *B. burgdorferi* because filial infection rates established so far do not exceed 3% (Wilske et al. 1987; Zhioua et al. 1988). Oviposition of spirochete-infected eggs has been recorded for two *I. ricinus* from Switzerland (Burgdorfer et al. 1983). One produced 100% infected eggs, the other only 60%. The F₁ larvae were unfortunately not examined.

Investigations into the development of *B. burgdorferi* in the American tick vector *I. dammini* have also shown that massive spirochetal development in oögonia and oocytes may have an adverse effect on egg development (Burgdorfer et al. 1988; Burgdorfer and Hayes 1989). Spirochetes between the vitelline and oocyte membranes were invariably found to denude the oögonial surface and to interfere with the formation of the egg shell. Ticks with heavy systemic infections rarely produced viable eggs.

5.2.5 Transmission of *Borrelia burgdorferi* by *Ixodes ricinus*

Successful transmission of *B. burgdorferi* by ticks with spirochetal infections limited to the midgut led to the hypothesis that transmission may occur by regurgitation of gut material rather than by saliva (Burgdorfer 1984). This hypothesis, however, was questioned by the demonstration (Ribeiro et al. 1987) of spirochetes in experimentally obtained saliva as early as 3 days after tick attachment. Increasing numbers of spirochetes thereafter also suggested invasion by *B. burgdorferi* that had penetrated the gut epithelium during early feeding (see discussion above). Thus, if effective transmission via saliva does occur, it must take place during late feeding, i.e., from 3–8 days after tick attachment. Whether regurgitation of spirochete-containing gut material represents an additional mode of transmission awaits the results of ongoing investigations with *I. dammini* and *I. ricinus*.

5.3 Concluding Remarks

To understand the natural history of Lyme borreliosis in Europe, it is necessary to establish the parameters of interactions between the causative spirochete *B. burgdorferi*, its primary vector *I. ricinus*, and its animal hosts. Although valuable information has been obtained since the discovery of the spirochete 10 years ago, our understanding of how this agent interacts with the ecological components of its natural history is far from complete and appears to be more complex than initially assumed. *I. ricinus*, for instance, was considered the only tick vector until tick/spirochete surveys in Germany revealed *B. burgdorferi*-like spirochetes in the hedgehog tick *I. hexagonus*. If shown to serve as a competent vector of *B. burgdorferi* (see: Gem et al. 1991), this tick and possibly other species such as *I. trianguliceps* may contribute to the establishment of enzootic foci of Lyme borreliosis in areas where *I. ricinus* is rare or absent. Similarly, the finding (Staneck and Simeoni 1989) in Southern Tirol (Italy) of *B. burgdorferi* in the argasid tick *Argas persicus*, which is associated with pigeons, deserves our attention and suggests that certain species of birds may play a role in the ecology of this organism.

The question of species unity or plurality for the Lyme borreliosis spirochete has led to extensive efforts to recover spirochetes from patients, ticks, and tick hosts, for identification and comparison with isolates from the United States. Recent deoxyribonucleic acid (DNA)/DNA hybridization and ribosomal ribonucleic acid (rRNA) gene restriction studies have identified two genomic species in *B. burgdorferi* (Postic et al. 1990). Whether either species is associated with certain ecological factors or specific

clinical manifestations remains to be determined. Species plurality should be considered, and encounter, in other vertebrate and invertebrate hosts, of other species, such as *B. theileri*, the causative agent of bovine borreliosis, and of hitherto undescribed spirochetal agents should not be ruled out. Finally, according to Stanek (personal communication), the incidence of Lyme borreliosis in Europe, which has now been reported from at least 19 countries, will increase. Therefore, good surveillance of natural hosts and of the vector(s) of *B. burgdorferi* are essential in defining the boundaries of natural foci and the risk of human infection.

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