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Is the Small Mammal (*Clethrionomys glareolus*) or the Tick Vector (*Ixodes ricinus*) the Primary Overwintering Reservoir for the Lyme Borreliosis Spirochete in Sweden?

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ABSTRACT: We determined the capacity of bank voles (*Clethrionomys glareolus*) to infect feeding *Ixodes ricinus* ticks with *Borrelia burgdorferi sensu lato* (infectivity), during June to October 1991 and June to September 1992 in south-central Sweden. In both years, the infectivity of older voles to ticks was higher in August to September (48% to 59%) than in June to July (20% to 32%). We propose that the infectivity of bank vole populations in Sweden decreases during winter and spring due to death of highly infective voles and recruitment of uninfective young ones, and that the tick vector, rather than the mammalian host, is the primary overwintering reservoir of *B. burgdorferi*.

Key words: Lyme borreliosis, *Ixodes ricinus*, *Clethrionomys glareolus*, infectivity, winter.

The abundance of *Ixodes ricinus* ticks infected with *Borrelia burgdorferi sensu lato*, varies greatly during the tick season in Sweden (Mejlon and Jaenson, 1993). To understand why such variations occur, it is necessary to determine the seasonal patterns in the proportion of ticks that become infected with *B. burgdorferi* during feeding of important reservoir hosts, such as rodents and shrews (infectivity).

The bank vole (*Clethrionomys glareolus*) is an important reservoir host for *B. burgdorferi* in Sweden (Tälleklint and Jaenson, 1994). In our study area the *Borrelia* spp.-infectivity of young voles seemed to be lower than that of older voles (Tälleklint et al., 1993). Thus, young voles likely acquire *Borrelia* spp. from feeding ticks rather than from transplacental or oral transmission from the mother. Since host-seeking larval *I. ricinus* in Sweden only rarely harbor *B. burgdorferi* (Mejlon and Jaenson, 1993) and adult ticks are absent from rodents (Tälleklint and Jaenson, 1994), voles probably acquire *Borrelia*-infection primarily from nymphal *I. ricinus*. One infected nymphal tick can infect a rodent host. However, since the prevalence of *B. burgdorferi* in *I. ricinus* nymphs in Sweden is 10 to 20% (Mejlon and Jaenson, 1993), exposure to about 5 to 10 feeding nymphs usually will be required for transmission of spirochetes to take place.

European mice (*Apodemus* spp.) that harbor *B. burgdorferi* can remain infective for at least 14 mo (Gern et al., 1994). The mean life-span for bank voles is 3 to 5 mo in southern Sweden (Hansson, 1971). Hence, once infected, most voles presumably remain infective for life. However, Tälleklint et al. (1993) found evidence for seasonal variation in *Borrelia* spp.-infectivity of bank voles in central Sweden.

Our objective was to determine whether there were differences in the infectivity of bank voles for *Borrelia* spp. between the early and late parts of the tick season and to relate this to the overwintering success of *B. burgdorferi*.

The study was conducted from 11 June to 19 October 1991, and 24 June to 28 September 1992, at Bogesund (59°23′N, 18°20′E) in south-central Sweden. Bank voles were live-trapped for five successive days and nights each month during June to October 1991 and June to September 1992, using Ugglan special traps (Allan Ahlgren, Marieholm, Sweden) baited with sunflower seeds and apples. Trapped voles were brought into a field laboratory and kept in the traps over pans with water for about 5 days. All voles survived and subsequently were released at the place of capture. The infectivity of the voles for *Borrelia* spp. was defined as the proportion of molted nymphs, collected as engorged larvae detaching from the voles, that harbored *Borrelia* spp.-like spirochetes.

Nymphal ticks were examined for spirochetes by phase-contrast microscopy at 400× magnification. In addition, ticks originating from 26 voles were examined for *B. burgdorferi* s.l. by immunofluorescence assay using anti-OspB monoclonal antibodies (Mab H6831) or fluorescein-labeled polyclonal antiserum obtained from rabbits immunized with spirochetes isolated from Swedish *I. ricinus*, as reported by Tälleklint and Jaenson (1994).

Since Tälleklint et al. (1993) found differences in *Borrelia* spp.-infectivity between voles weighing 15 to 20 g, and >20 g, the voles in this study were divided into two groups, young (weighing 10 to 20 g) and older (weighing >20 g) voles.

Indices of infectivity were calculated as weighted mean percentages (Sokal and Rohlf, 1981) based on voles from which at least eight nymphs could be examined. Differences in mean infectivity and proportion of voles infested by nymphs were evaluated by a Chi-square test (Sokal and Rohlf, 1981). Differences in mean nymphal infestation were tested using a Mann-Whitney *U*-test corrected for sample sizes >20 (Sokal and Rohlf, 1981). Differences were considered significant when $P < 0.05$.

The infectivity for *Borrelia* spp. of older voles weighing 21 to 40g was significantly ($P < 0.001$ in all cases) greater than that of young voles weighing 10 to 20g during August to October 1991 (59% and 6%, respectively), June to July 1992 (32% and 1%, respectively) and August to September 1992 (48% and 5%, respectively) (Table 1). Only one young bank vole was caught between June and July 1991.

The *Borrelia* spp.-infectivity of older voles was significantly ($P < 0.001$ in both cases) higher in the autumn periods of 1991 and 1992 (59% and 48%, respectively) than in the corresponding early summer periods of 1991 and 1992 (20 and 32%, respectively) (Table 1). Although the seasonal trend of infectivity for *Borrelia* spp. in young voles in 1992 resembled that of the older voles, the infectivity of young voles during August to September (5.0%) did not differ significantly ($P = 0.27$) from that of June to July (1.4%) (Table 1).

Although the 67 older voles had a greater mean (±SD) intensity of infestation by nymphal ticks than the 24 young voles during 1991 and 1992 (1.0 ± 2.1 and 0.2 ± 0.5 nymphs per vole, respectively), the difference was not significant ($P = 0.053$). However, the prevalence of infestation of older voles by nymphal ticks during 1991 and 1992 (37%) was greater ($P = 0.024$) than that of young ones (13%) for the same period.

That older rodents have higher values of *Borrelia* spp.-infectivity than young ones also has been reported from the Netherlands (De Boer et al., 1993) and France (Doby et al., 1991). We propose that this is because older rodents have been exposed to potentially infective ticks for a longer period of time than young rodents, and because older rodents are exposed to potentially infective nymphal ticks to a higher degree than the young ones (37% and 13% infested by nymphs, respectively, in our study), presumably as a result of higher activity levels of older voles.

In both years, the infectivity of older voles for *Borrelia* spp. was higher in autumn than in early summer. The same trend was found for the short-tailed vole (*Microtus agrestis*) in 1992, with mean infectivities of 79% in August to September and 56% in June to July (L. Tälleklint and T. G. T. Jaenson, unpubl.). Similarly, the proportions of shrews and rodents in Switzerland (Humair et al., 1993) and white-footed mice (*Peromyscus leucopus*) in the USA (Anderson et al., 1987) infective for *Borrelia* spp. were greater in autumn than in spring and early summer. We propose that decreases in infectivity of the vole population for *Borrelia* spp. during winter may occur because the mean life-span of bank voles in Sweden is shorter than the tick-free season. Low temperatures usually prevent most tick activity during November to mid-April in the study area (L. Tälleklint and T. G. T. Jaenson, unpubl.). Thus, loss of spirochetes from the vole population

TABLE 1. *Borrelia burgdorferi s.l.*-infectivity of 10 to 20 g (young) and 21 to 40 g (older) bank voles (*Clethrionomys glareolus*) at Bogesund, Sweden, during 1991 and 1992.

	June and July 1991[a]	August to October 1991[a]	June and July 1992	August and September 1992
10 to 20 g voles	0% (1/8)[b]	6.1 ± 8.4% (10/132)[c]	1.4 ± 3.2% (5/70)[c]	5.0 ± 9.6% (3/40)[c]
21 to 40 g voles	20 ± 26% (15/454)[d]	59 ± 38% (18/298)	32 ± 32% (15/213)[d]	48 ± 35% (14/197)

[a] Some of these data were reported in Tälleklint et al. (1993).
[b] Mean ± SD *Borrelia*-infectivity (number of voles examined/number of nymphal ticks dissected).
[c] Significant ($P < 0.001$) difference in mean infectivity between 10 to 20 g, and 21 to 40 g voles for the time span.
[d] Significant ($P < 0.001$) difference in mean infectivity between the two seasons for the year among 21 to 40 g voles.

during winter could have occurred because most highly infective voles present in the autumn died during the winter and because most overwintering and spring-born voles had been exposed to no or few potentially infective ticks. Furthermore, it also is possible that the infectivity of an individual host declines during long tick free periods. Thus, the *Borrelia*-infectivity to feeding larval *I. scapularis* of rice rats (*Oryzomus palustris*) infected by nymphal ticks decreased from 80% during the fourth week after infestation to 17% during the ninth week (Levin et al., 1995).

The relatively few infective shrews and rodents that survive the winter may not be sufficient to effectively maintain *B. burgdorferi* through the tick-free winter period in Sweden. Similarly, Wilson and Spielman (1985) suggested that white-footed mice are too short-lived to serve as effective winter reservoirs for *Babesia microti*. However, Tälleklint and Jaenson (1994) found that these short-lived small mammals accounted for more than 90% of all mammalian transmissions of *B. burgdorferi* to feeding *I. ricinus* larvae. We propose that diapausing ticks are the main winter reservoirs for *B. burgdorferi* and that *I. ricinus* effectively reintroduce the spirochete into the vole population during spring and early summer. The following increases in infectivity for *Borrelia* spp. during the summer and autumn most likely were due to accumulation of infected hosts as the transmission season progressed. Interestingly, based on drag-sampling, the abundance of host-seeking *Borrelia* spp.-infected nymphs in our study area in May was higher in 1992 than in 1991 (400 and 180 per hectare, respectively) (L. Tälleklint and T. G. T. Jaenson, unpubl.). The impact of infected nymphs on vole infectivity can be seen after about 1 mo (Tälleklint et al., 1993). Consequently, the infectivity of older voles for *Borrelia* spp. in June to July was higher in 1992 than in 1991 (32% and 20%, respectively).

Long-lived reservoirs such as lagomorphs could effectively maintain *B. burgdorferi* during the winter. However, transmission of *B. burgdorferi* from hares to shrews and rodents requires that larval ticks become infected during engorgement on hares and subsequently infest shrews and rodents in the nymphal stage. This transmission route seems not to be common in our study area since more larval ticks feed on shrews and rodents than on hares and many more nymphal ticks feed on hares than on shrews and rodents (Tälleklint and Jaenson, 1994).

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