Lyme Disease Spirochetes in Ticks Collected from Birds in Midwestern United States

THOMAS H. NICHOLLS[1] AND STEVEN M. CALLISTER[2]

J. Med. Entomol. 33(3): 379–384 (1996)

ABSTRACT In a tick–spirochete survey conducted from fall 1989 through fall 1992 in northwestern Wisconsin, 4,256 birds (composed of 91 species) were examined for ticks. Infestations were recorded for 400 birds (composed of 30 species). Of 1,184 ticks taken from 335 birds (composed of 26 species), 60 (5%) *Haemaphysalis leporispalustris* (Packard) from 8 species of birds were infected with the Lyme disease spirochete, *Borrelia burgdorferi* Johnson, Schmid, Hyde, Steigerwalt & Brenner. Similar surveys conducted in 1990 and 1991 in Minnesota and Michigan yielded 223 *H. leporispalustris* from 61 birds (composed of 23 species), all free of spirochetes. However, 1 *B. burgdorferi*-infected *Ixodes scapularis* (Say) was found on 1 bird species in Minnesota. Most ticks were collected in fall from ground-foraging birds such as thrushes and sparrows. These results confirm that tick-infested birds are important in disseminating Lyme disease spirochetes and may also play a role as sources for infecting ticks.

KEY WORDS *Borrelia burgdorferi, Haemaphysalis leporispalustris, Ixodes dammini, Ixodes scapularis,* migratory birds, Lyme disease

https://doi.org/10.1093/jmedent/33.3.379

LYME DISEASE IS the most common tick-associated disease of humans in the United States (Habicht et al. 1987, Steere 1989). Its causative agent, *Borrelia burgdorferi* Johnson, Schmid, Hyde, Steigerwalt & Brenner, is transmitted through the bite of an infected tick, primarily *Ixodes scapularis* (Say) (=*I. dammini* Spielman, Clifford, Piesman & Corwin) (Oliver et al. 1993) in the midwestern and eastern United States and *Ixodes pacificus* (Cooly & Kohls) in the western United States. The disease can affect the skin, joints, nervous system, and heart and can become serious if left untreated. Lyme disease has been found in at least 46 states, and its range is expanding (Cartter et al. 1991). In fact, it has become the most recognized tick-associated illness in the world.

Various vertebrates differ in their infectivity to ticks. Some, such as the white-footed mouse, *Peromyscus leucopus,* are quite proficient at infecting larval *I. scapularis* ticks, whereas others such as white-tailed deer, *Odocoileus virginianus,* are virtually incompetent as reservoirs (Mather et al. 1989a). Comparative studies have shown that mice exhibit the greatest potential as a reservoir for *B. burgdorferi* (Mather et al. 1989b). This spirochete is unique among *Borrelia* spp. in that it infects both mammals and birds that serve as hosts for *I. scapularis* ticks (Anderson et al. 1986).

Ticks have been found on many species of birds, and various species have been suggested as potential reservoirs. Although it is well established that birds provide a ready means for the dispersal of ticks, possibly even between continents (Weisbrod and Johnson 1989, Anderson 1990), we do not know whether certain species contribute to infecting ticks (Mather et al. 1989a, McLean et al. 1993). Our study provides new information on the rabbit tick, *Haemaphysalis leporispalustris* (Packard), as a host for *B. burgdorferi;* it identifies new bird species that host *B. burgdorferi*-infected ticks; and it suggests that birds may serve as sources for infecting *H. leporispalustris* ticks.

Materials and Methods

Birds were captured in Japanese mist nets (12 by 2.6 m, 36-mm mesh) placed in the town of Fifield, Price County, Wisconsin (S12, T39N, R1W), from 1989 through 1992. Up to 45 nets were placed along old logging roads in 5 forested and nonforested community types consisting of shrub swamp, upland deciduous, mixed deciduous–conifer, upland conifer, and lowland conifer. Nets were open from dawn to dusk, weather permitting, each spring (mid-April through May) and fall (mid-August through September) for totals of 30,924 and 27,992 net hours per season, respectively.

Routine biological measurements were taken of each captured bird, after which they were banded and released unharmed. Because of the high interest in Lyme disease, we began to examine captured birds for ticks starting in the fall of 1989. Ticks were collected from birds in 1989–1991. In 1992, we did not remove or identify ticks, but their presence or absence was noted. We collected as many ticks as possible from each infested bird, but when ticks were too numerous to collect all of them, we collected a random sample. We found ticks by "combing" the feathers on the head and

[1] North Central Forest Experiment Station, USDA–FS, 1992 Folwell Ave., St. Paul, MN 55108.

[2] Microbiology Research Laboratory, Gundersen Medical Foundation, La Crosse, WI 54601.

Table 1. Number of birds found with ticks (1989–1992) and results of *B. burgdorferi* analysis of ticks collected from birds (1989–1991) in Price County, Wisconsin

Bird species	1989–1992			1989–1991			
				H. leporispalustris		*I. scapularis*	
	Total no. captured	No. infested with ticks	% with ticks	No. ticks analyzed	No. with *B. burgdorferi*	No. ticks analyzed	No. with *B. burgdorferi*
White-throated sparrow, *Zonotrichia albicollis*	380	92	24.2	273	16	2	0
Swainson's thrush, *Catharus ustulatus*	301	90	29.9	338	4	0	—
Hermit thrush, *Catharus guttatus*	279	89	31.9	326	31	7	0
Slate-colored junco, *Junco hyemalis*	273	45	16.5	49	0	0	—
Ovenbird, *Seiurus aurocapillus*	320	19	5.9	23	0	2	0
Gray-cheeked thrush, *Catharus minimus*	43	18	41.9	80	2	1	0
Lincoln's sparrow, *Melospiza lincolnii*	46	9	19.6	25	1	0	—
American robin, *Turdus migratorius*	37	6	16.2	14	2	0	—
Chipping sparrow, *Spizella passerina*	49	4	8.2	1	0	0	—
Fox sparrow, *Passerella iliaca*	10	4	40.0	14	0	0	—
Blackpoll warbler, *Dendroica striata*	61	2	3.3	3	2	0	—
Common grackle, *Quiscalus quiscula*	5	2	40.0	1	0	0	—
Yellow-rumped warbler, *Dendroica coronata*	267	2	0.7	2	0	0	—
Tennessee warbler, *Vermivora peregrina*	235	2	0.9	1	0	0	—
Black-capped chickadee, *Parus atricapillus*	267	1	0.4	1	0	0	—
Blue jay, *Cyanocitta cristata*	41	1	2.4	1	0	0	—
Brown creeper, *Certhia americana*	78	1	1.3	1	0	0	—
Brown thrasher, *Toxostoma rufum*	2	1	50.0	1	0	0	—
Northern waterthrush, *Seiurus noveboracensis*	10	1	10.0	2	0	0	—
Purple finch, *Carpodacus purpureus*	53	1	1.9	0	0	1	0
Rose-breasted grosbeak, *Pheucticus ludovicianus*	11	1	9.1	3	0	0	—
Savannah sparrow, *Passerculus sandwichensis*	2	1	50.0	1	0	0	—
Swamp sparrow, *Melospiza georgiana*	6	1	16.7	3	0	0	—
Veery, *Catharus fuscescens*	6	1	16.7	2	2	0	—
Gray jay, *Perisoreus canadensis*	8	1	12.5	5	0	0	—
Pine siskin, *Carduelis pinus*	241	1	0.4	1	0	0	—
Common yellowthroat, *Geothlypis trichas*	38	1	2.6	—	—	—	—
House wren, *Troglodytes aedon*	1	1	100.0	—	—	—	—
Magnolia warbler, *Dendroica magnolia*	126	1	0.8	—	—	—	—
White-crowned sparrow, *Zonotrichia leucophrys*	2	1	50.0	—	—	—	—
Totals (30 species)	3,198	400	12.5	1,171	60	13	0

neck with a crochet hook. Ticks were removed carefully with forceps, placed in petri dishes (47 mm diameter) with moistened filter paper, and sealed with parafilm. The ticks were kept alive and refrigerated until identified and tested for *B. burgdorferi* at the University of Minnesota Microbiology Department in Minneapolis, MN (1989 samples), or at the Gundersen Medical Foundation in La Crosse, WI (1990 and 1991 samples). Tick midguts were examined for *B. burgdorferi* with an indirect fluorescent antibody test (Barbour et al. 1983) and species-specific monoclonal antibody H5332 (Alan Barbour, University of Texas, San Antonio). Similar methods were used to collect, identify, and analyze ticks from birds banded by cooperators in Anoka, Crow Wing, and Washington counties, Minnesota, and Crawford, Ogemaw, and Oscoda counties, Michigan, in 1990 and 1991. Permits and protocol for trapping, banding, handling, and releasing birds are on file in the laboratory of the senior author.

Results

Wisconsin. From fall 1989 through fall 1992, we trapped and examined 4,256 individual birds of 91 species. Ticks were observed on 400 birds of 30 species. In total, 1,380 ticks were collected from 335 birds of 26 species. Of these, 1,184 were identified and examined for *B. burgdorferi* (Table 1). On average, 3.5 ticks (range, 1–40; median, 2) were removed from birds, mostly from the neck and head, especially around the ears. We identified 940 larvae and 231 nymphs of *H. leporispalustris* from 26 bird species (98% of all ticks collected). Thirteen *I. scapularis* ticks (2 larvae and 11 nymphs) were recovered from 5 bird species.

Ticks positive for *B. burgdorferi* were observed on birds captured in all 5 vegetative community types. However, we were unable to determine whether ticks were picked up from those areas because most birds were passing through during migration and could have picked them up elsewhere. Swainson's thrush, *Catharus ustulatus*, hermit thrush, *Catharus guttatus*, white-throated sparrow, *Zonotrichia albicollis*, and slate-colored junco, *Junco hyemalis*, accounted for nearly 80% of the tick-infested birds. Most of the infested birds (94.5%) were observed during fall migration.

Twenty-five (83.3%) of the 30 tick-infested bird species were neotropical migrants (birds that winter in Mexico, the Caribbean, and Central and

Table 2. *B. burgdorferi* in ticks collected from birds in Minnesota, 1990 and 1991

Bird species	No. birds	No. ticks		Tick species			No. ticks with *B. burgdorferi*
		Collected	Analyzed	Hl	Is	Dv	
American robin, *Turdus migratorius*	1	1	0	—	—	—	. .
Blue jay, *Cyanocitta cristata*	1	1	2	0	1	1	0
Brown thrasher, *Toxostoma rufum*	3	37	18	18	0	0	0
Gray catbird, *Dumetella carolinensis*	5	26	23	23	0	0	0
Hermit thrush, *Catharus guttatus*	2	2	2	2	0	0	0
House wren, *Troglodytes aedon*	1	1	1	0	1	0	0
Indigo bunting, *Passerina cyanea*	1	1	0	—	—	—	. .
Lincoln's sparrow, *Melospiza lincolnii*	1	8	8	8	0	0	0
Mourning warbler, *Oporornis philadelphia*	1	2	2	2	0	0	0
Nashville warbler, *Vermivora ruficapilla*	3	6	6	6	0	0	0
Northern waterthrush, *Seiurus noveboracensis*	1	1	1	1	0	0	0
Orange-crowned warbler, *Vermivora celata*	2	3	3	3	0	0	0
Ovenbird, *Seiurus aurocapillus*	3	3	1	1	0	0	0
Rose-breasted grosbeak, *Pheucticus ludovicianus*	1	7	7	7	0	0	0
Red-winged blackbird, *Agelaius phoeniceus*	1	1	1	0	1	0	1
Slate-colored junco, *Junco hyemalis*	5	14	14	14	0	0	0
Song sparrow, *Melospiza melodia*	8	16	16	15	1	0	0
Swamp sparrow, *Melospiza georgiana*	2	10	10	10	0	0	0
Swainson's thrush, *Catharus ustulatus*	1	6	6	6	0	0	0
Veery, *Catharus fuscescens*	2	3	3	3	0	0	0
White-throated sparrow, *Zonotrichia albicollis*	8	23	23	23	0	0	0
Totals (21 species)	53	172	147	142	4	1	1

Hl, *H. leporispalustris;* Is, *I. scapularis;* Dv, *D. variabilis.*

South America). The rest were resident species (10.0%) and short-distance migrants (6.7%). Twenty-one (70%) of the 30 tick-infested bird species were primarily ground foragers.

Sixty *H. leporispalustris* (58 larvae and 2 nymphs) (5.0%) from 8 bird species tested positive for *B. burgdorferi* (Table 1). The bird hosts included the white-throated sparrow, hermit thrush, Swainson's thrush, gray-cheeked thrush, *Catharus minimus,* American robin, *Turdus migratorius,* Lincoln's sparrow, *Melospiza lincolnii,* blackpoll warbler, *Dendroica striata,* and veery, *Catharus fuscescens.* All of the *B. burgdorferi*-infected ticks were found on birds during August and September, suggesting a southward movement of infected ticks carried by migratory birds.

Minnesota. Minnesota bird banders collected 172 ticks from 53 birds of 21 bird species during the months of May through September 1990 and 1991 and October 1991 (Table 2). Of these, 147 (86%) ticks were analyzed; 142 (97%) were *H. leporispalustris,* 4 were *I. scapularis,* and 1 was *Dermacentor variabilis* (Say). Only one tick, an *I. scapularis* collected from a red-winged blackbird, *Agelaius phoeniceus,* in Anoka County, was positive.

Michigan. During a banding study of the endangered Kirtland's warbler, *Dendroica kirtlandii,* in August 1990 and July 1991, 91 ticks from 8 birds of 4 species were collected (Table 3). Of these, 76 (84%) ticks were analyzed. Seventy (92%) of these were *H. leporispalustris,* 3 were *I. scapularis,* 2 were *D. variabilis,* and 1 was an unknown *Ixodes* spp. Of these, 2 were collected from the endangered Kirtland's warbler, 1 tick was lost, and the other was identified as *I. scapularis. B. burgdorferi* was not detected in any of the Michigan ticks we analyzed.

Discussion

Our results confirm and extend other reports of the potential importance of tick-infested birds disseminating the Lyme disease spirochete (Anderson

Table 3. *B. burgdorferi* in ticks collected from birds in Michigan, 1990 and 1991

Bird species	No. birds	No. ticks		Tick species				No. ticks with *B. burgdorferi*
		Collected	Analyzed	Hl	Is	Dv	I	
Black and white warbler, *Mniotilta varia*	1	1	0	—	—	—	—	—
Hermit thrush, *Catharus guttatus*	5	75	62	57	2	2	1	0
Kirtland's warbler, *Dendroica kirtlandii*	1	2	1	0	1	0	0	0
Ovenbird, *Seiurus aurocapillus*	1	13	13	13	0	0	0	0
Totals (4 species)	8	91	76	70	3	2	1	0

Hl, *H. leporispalustris;* Is, *I. scapularis;* Dv, *D. variabilis;* I, *Ixodes* spp.

Table 4. Comparison of results from 5 bird–tick–Lyme disease vector studies

Study and location	No. bird species with ticks (total no. bird species)	No. individual birds with ticks (total no. birds examined)	No. ticks and species	No., % Lyme-positive ticks (no. ticks tested)
Anderson et al. 1986				
Connecticut	8 (18)	44 (62)	169 *I. dammini*[a]	37, 22% (169)
Battaly et al. 1987				
New York	19 (41)	88 (310)	117 *I. dammini*[a]	6, 17% (36)
			110 *I. dentatus*	0, 0% (5)
			3 *H. leporispalustris*	–
			1 *D. variabilis*	–
Weisbrod and Johnson 1989				
Wisconsin	15 (99)	58 (9,200)	250 *I. dammini*[a]	56, 22% (250)
Levine et al. 1991				
Virginia	8 (8)	10 (10)	43 *I. dentatus*	5, 12% (43)
			5 *H. leporispalustris*	2, 40% (5)
Current study				
Wisconsin	30 (91)	400 (4,256)	1,171 *H. leporispalustris*	60, 5% (1,171)
			13 *I. scapularis*	0, 0% (13)

[a] Oliver et al. (1993) have indicated that *I. dammini* is synonymous with *I. scapularis*.

et al. 1986, Battaly et al. 1987, Weisbrod and Johnson 1989, Levine et al. 1991). This dissemination may occur locally or during migration when birds fly hundreds of miles in a short period of time while carrying infected ticks that drop off their bodies during routine activities. For example, the Swainson's thrush, gray-checked thrush, Lincoln's sparrow, and veery, which were found carrying infected ticks in our study, had the potential to transport them during migration to Central or South America where these birds winter. Thus, bird dispersal of infected ticks may be responsible for establishing new tick–spirochete foci. Resident birds likely contribute to local spread of the pathogen and short-distance migrants may contribute to regional spread. Dispersal of *B. burgdorferi* by birds could help explain the dissemination of *B. burgdorferi* throughout the United States.

In addition to our study, Anderson et al. (1986), Battaly et al. (1987), Weisbrod and Johnson (1989), and Levine et al. (1991) have demonstrated the importance of birds in the dissemination of *B. burgdorferi*-infected ticks (Table 4). These 4 studies showed a total of 99 *B. burgdorferi*-positive *I. scapularis* among 460 ticks tested. Anderson et al. (1990) showed that *B. burgdorferi* can be transferred between rodents and birds by subadult *I. scapularis,* suggesting that ticks found on birds could transmit infectious spirochetes to humans and other mammalian hosts.

Collectively, and in sharp contrast to our study, these investigators found only 8 rabbit ticks on birds. Of the 5 tested for *B. burgdorferi,* 2 were positive (Levine et al. 1991), 1 from a brown thrasher, *Toxostoma rufum,* and 1 from a white-throated sparrow. In our investigation, we confirmed and extended their findings by removing infected rabbit ticks not only from the white-throated sparrow but from 7 additional migratory bird species. In addition, the SDS-PAGE profile of a *B. burgdorferi* organism isolated from *H. leporispalustris* was almost identical to SDS-PAGE profiles of *B. burgdorferi* B-31, the original Shelter Island isolate, and a *B. burgdorferi* isolate from an erythema migrans lesion of a human patient from Wisconsin (data not shown). These results pose an important question about the role of rabbit ticks in the epidemiology of Lyme disease.

The rabbit tick is one of the most common and widely distributed species of ticks in North America, ranging from Alaska and the southern Canadian provinces southward into Mexico (Bishopp and Trembley 1945); it has frequently been found in high numbers on birds (Joyce and Eddy 1943, Snetsinger et al. 1970, Sonenshine and Stout 1970). Rabbit ticks prefer to feed on rabbits, but they are opportunistic and readily feed on ground foraging birds as well (Joyce and Eddy 1943, Camin and Drenner 1978). Rabbit tick larvae and nymphs reach their peak of abundance in late summer and fall (Bishop and Trembley 1945), explaining the high percentage (94.5%) of these ticks we collected during that period. Camin and Drenner (1978) found that rabbit ticks climb up to a position on low vegetation where they can encounter a host and that this strato-orientation restricts the tick's host spectrum to ground-dwelling animals. This explains why most of the tick-infested birds we found in our study were on ground-foraging species.

The detection and isolation of *B. burgdorferi* from rabbit ticks add to the list of important human pathogens hosted by this tick species. Unlike *I. scapularis, H. leporispalustris* does not attach itself to humans readily (Joyce and Eddy 1943), so it is unlikely to transmit *B. burgdorferi* to humans. However, rabbit ticks are capable of transmitting tularemia and Rocky Mountain spotted fever from animal to animal (Parker 1923, Parker et al. 1924, Rivers and Horsfall 1959), and they could possibly transmit *B. burgdorferi* as well. Consequently, the rabbit tick may serve as an important "pass-through agent," especially when other ticks, capable of attaching and transmitting pathogens to humans or other animals, also feed on the same host as do rabbit ticks.

In addition to the rabbit tick's likely ability to transmit organisms to host animals, its blood-sucking habit alone may weaken or even kill birds (Banks 1915, Green et al. 1938). This poses an important question as to the effect ticks and tick-associated diseases have on migratory birds, some of which are already declining in numbers from unknown causes (Robbins et al. 1989). Twenty-five (83.3%) of the 30 bird species found to be tick-infested in Wisconsin were neotropical migrants, which are of special concern to the International Migratory Bird Conservation Program. A few of these birds were heavily infested with ticks and appeared to be in a weakened condition. Two of the birds eventually died. The effect of ticks and tick-associated diseases on threatened or endangered bird species could be much more important than their effect on bird species that are more numerous. In Michigan, for example, ticks were found on the endangered Kirtland's warbler, whose population comprises only a few hundred individuals.

It was beyond the scope of our study to determine whether larval *H. leporispalustris* ticks were infected through transovarial transmission before they attached to birds or whether they became infected while feeding on infected birds. There is evidence that some bird species are competent *Borrelia* reservoirs capable of infecting *I. scapularis* ticks that feed on them (Anderson et al. 1986, Weisbrod and Johnson 1989, Anderson 1990, Anderson et al. 1990, Battaly and Fish 1993), but similar evidence is lacking for *H. leporispalustris*. We feel that work is needed to determine the reservoir competence of *H. leporispalustris*.

We conclude that more research is needed to determine the effect of ticks and tick-associated diseases on birds, especially on those classified as endangered, threatened, or sensitive. We also feel work is needed to clarify the role of birds as dispersers of infected ticks and as sources for infecting ticks with pathogens capable of causing animal and human diseases.

Acknowledgments

We thank the following for their help with this study: Leanne Egeland, Joan Elias, Peg Robertsen, and Jane Wiedenhoeft (USDA–FS, North Central Forest Experiment Station); Ron Refsnider and Wes Jones (retired) (USDI–Fish and Wildlife Service); Dean Granholm (USDA–FS, Chequamegon National Forest); Richard Weisbrod (USDI, National Biological Service); Russell Johnson and James Gill (University of Minnesota Microbiology Department); Anne Hendel-Selness, Justin Boge, and Paul Molling (Gundersen Medical Foundation); and Minnesota bird banders. We also thank Robert Haack and Lucy Burde (USDA–FS, North Central Forest Experiment Station) and Ronald Schell (University of Wisconsin, Department of Medical Microbiology and Immunology) for their critical review and improvement of the manuscript.

References Cited

Anderson, J. F. 1990. Mammalian and avian reservoirs for *Borrelia burgdorferi*. Ann. N.Y. Acad. Sci. 539: 180–191.

Anderson, J. F., R. C. Johnson, L. A. Magnarelli, and F. W. Hyde. 1986. Involvement of birds in the epidemiology of the Lyme disease agent *Borrelia burgdorferi*. Infect. Immunol. 51: 394–396.

Anderson, J. F., L. Magnarelli, and K. Stafford III. 1990. Bird-feeding ticks transstadially transmit *Borrelia burgdorferi* that infect Syrian hamsters. J. Wildl. Dis. 26: 1–10.

Banks, N. A. 1915. The Acarina or mites. U.S. Dep. Agric. Bur. Entomol. Tech. Ser. Bull. 22.

Barbour, A. G., W. Burgdorfer, S. F. Hayes, O. Peter, and A. Aeschlimann. 1983. Isolation of a cultivable spirochete from *Ixodes ricinus* ticks in Switzerland. Curr. Microbiol. 8: 123–126.

Battaly, G. R., and D. Fish. 1993. Relative importance of bird species as hosts for immature *Ixodes dammini* (Acari: Ixodidae) in a suburban residential landscape of southern New York state. J. Med. Entomol. 30: 740–747.

Battaly, G. R., F. Durland, and R. C. Dowler. 1987. The seasonal occurrence of *Ixodes scapularis* and *Ixodes dentatus* (Acari: Ixodidae) on birds in a Lyme disease endemic area of southeastern New York State. J. N.Y. Entomol. Soc. 95: 461–468.

Bishopp, F., and H. Trembley. 1945. Distribution and hosts of certain North American ticks. J. Parasitol. 31: 1–54.

Camin, J. H., and R. Drenner. 1978. Climbing behavior and host-finding of larval rabbit ticks (*Haemaphysalis leporispalustris*). J. Parasitol. 64: 905–909.

Cartter, M. L., J. L. Hadler, J. D. Smith, J. A. Wilber, M. G. Stobierski, K. R. Wilcox, H. D. Donnell, C. Genese, K. C. Spitainy, J. J. Kazmierczak, and J. P. Davis. 1991. Lyme disease surveillance—United States, 1989–1990. Morb. Mortal. Wkly. Rep. 40: 417–421.

Green, R. G., J. F. Bell, and C. A. Evans. 1938. Rabbit tick populations on the Lake Alexander area, 1931–1938. Report of Minnesota Wildlife Disease Investigation 4: 80–86.

Habicht, G. S., G. Beck, and J. L. Benach. 1987. Lyme disease. Sci. Am. 257: 78–83.

Joyce, C. R., and G. Eddy. 1943. Hosts and seasonal notes on the rabbit tick, *Haemaphysalis leporis-palustris*. Iowa State Coll. J. Sci. 17: 205–212.

Levine, J. F., D. E. Sonenshine, W. L. Nicholson, and R. T. Turner. 1991. *Borrelia burgdorferi* (Acari: Ixodidae) from coastal Virginia. J. Med. Entomol. 28: 668–674.

Mather, T. N., S. R. Telford III, A. B. MacLachlan, and A. Spielman. 1989a. Incompetence of catbirds as reservoirs for the Lyme disease spirochete (*Borrelia burgdorferi*). J. Parasitol. 75: 66–69.

Mather, T. N., M. L. Wilson, S. I. Moore, J.M.C. Ribeiro, and A. Spielman. 1989b. Comparing the relative potential of rodents as reservoirs of the Lyme disease spirochete (*Borrelia burgdorferi*). J. Epidemiol. 130: 143–150.

McLean, R. G., S. R. Ubico, C. A. Norton Hughes, S. M. Engstrom, and R. C. Johnson. 1993. Isolation and characterization of *Borrelia burgdorferi* from blood of a bird captured in the Saint Croix River Valley. J. Clin. Microbiol. 31: 2038–2043.

Oliver, J. H., M. R. Owsley, H. J. Hutcheson, A. M. James, C. Chen, W. S. Irby, E. M. Dotson, and D. K. McLain. 1993. Conspecificity of the ticks *Ixodes scapularis* and *I. dammini* (Acari: Ixodidae). J. Med. Entomol. 30: 54–63.

Parker, R. R. 1923. Transmission of Rocky Mountain spotted fever by the rabbit tick, *Haemaphysalis leporis-palustris* Packard. Am. J. Trop. Med. 3: 39–45.

Parker, R. R., R. Spenser, and E. Francis. 1924. Tularemia infection in wood ticks of the species *Dermacentor andersoni* Stiles. Public Health Rep. 41: 1403–1407.

Rivers, T. M., and F. L. Horsfall. 1959. Viral and rickettsial infections of man. Lippincott, Philadelphia.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the neotropics. Proc. Natl. Acad. Sci. U.S.A. 86: 7658–7662.

Snetsinger, R., D. Bordner, and J. Luke. 1970. Ixodid populations on fall migrating birds at Island Beach State Park, New Jersey. Melsheimer Entomol. Ser. 6: 1–4.

Sonenshine, D. E., and I. J. Stout. 1970. A contribution to the ecology of ticks infesting wild birds and rabbits in the Virginia–North Carolina Piedmont (Acarina: Ixodidae). J. Med. Entomol. 7: 645–654.

Steere, A. C. 1989. Lyme disease. New Engl. J. Med. 321: 586–596.

Weisbrod, A. R., and R. Johnson. 1989. Lyme Disease and migrating birds in the Saint Croix River Valley. Appl. Environ. Microbiol. 55: 1921–1924.

Received for publication 24 February 1995; accepted 27 November 1995.