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Highly Variable Acquisition Rates of *Ixodes scapularis* (Acari: Ixodidae) by Birds on an Atlantic Barrier Island

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ABSTRACT Acquisition of ticks by bird hosts is a central process in the transmission cycles of many tick-borne zoonoses, but tick recruitment by birds has received little direct study. We documented acquisition of *Ixodes scapularis* Say on birds at Fire Island, NY, by removing ticks from mist-netted birds, and recording the number of ticks on birds recaptured within 4 d of release. Eight bird species acquired at least 0.8 ticks bird⁻¹ day⁻¹ during the seasonal peak for at least one age class of *I. scapularis*. Gray Catbirds, Eastern Towhees, Common Yellowthroats, and Northern Waterthrushes collectively accounted for 83% of all tick acquisitions; and six individuals apportioned among Black-billed Cuckoo, Gray Catbird, Eastern Towhee, and Common Yellowthroat were simultaneously infested with both larvae and nymphs. Bird species with the highest acquisition rates were generally ground foragers, whereas birds that did not acquire ticks in our samples generally foraged above the ground. Tick acquisition by birds did not differ between deciduous and coniferous forests. Among the 15 bird species with the highest recruitment rates, acquisition of nymphs was not correlated with acquisition of larvae. Tick acquisition rates by individual bird species were not correlated with the reservoir competence of those species for Lyme borreliae. However, birds with high tick acquisition rates can contribute large numbers of infected ticks, and thus help maintain the enzootic cycle, even if their levels of reservoir competence are relatively low.

KEY WORDS *Ixodes scapularis*, tick acquisition, bird hosts

Larvae and nymphs of *Ixodes scapularis*, the primary vector of *Borrelia burgdorferi* Johnson, Schmid, Hyde, Steigerwalt & Brenner (etiologic agent of Lyme disease), are known to infest a broad range of mammal and bird species (Anderson and Magnarelli 1984, Batty and Fish 1993). Nevertheless, despite numerous published surveys of tick body burdens across various vertebrate host species (Hoogstraal et al. 1963, Stafford et al. 1995, Hyland 2000), the process by which birds actually acquire ticks has received essentially no attention. This process has never been thoroughly quantified for *I. scapularis* at any North American site, and we are aware of just a single published estimate of acquisition rates for any tick, by any host, anywhere in the world: Scharf's (2004) report of 13 individual birds acquiring *I. scapularis* between captures in the Maryland piedmont.

Empirical estimates of actual acquisition rates, as opposed to simple body burdens, are necessary for understanding and quantifying the complex ecological interactions underlying the dynamics of tick-borne diseases at various spatial and temporal scales. Many authors have used simple body burdens, rather than actual acquisition rates, to assess the importance of various bird species as tick hosts, but this assumes that acquisition rates and detachment rates are in equilibrium at a given site. For highly vagile hosts such as birds, this assumption is likely to be violated because local body burdens reflect ticks acquired from multiple localities near and far, and because of seasonal trends in tick activity and bird behavior. Therefore, understanding of the roles of various bird species as hosts for immature *I. scapularis*, the relationships between bird behavioral ecology and tick recruitment, and the importance of various bird species in the transmission dynamics of *B. burgdorferi*, all require accurate estimates of the acquisition rates of larval and nymphal *I. scapularis* by local bird species.

In this study, we quantify acquisition of immature *I. scapularis* by birds at the Lighthouse Tract of Fire Island National Seashore, Suffolk County, NY; an area of high public use where *I. scapularis* exhibits high levels of *B. burgdorferi* infection (5–32% of nymphs and 15–50% of adults; Ginsberg 1992; H.S.G., unpublished). We then present the first preliminary analysis of the relationships between actual tick acquisition

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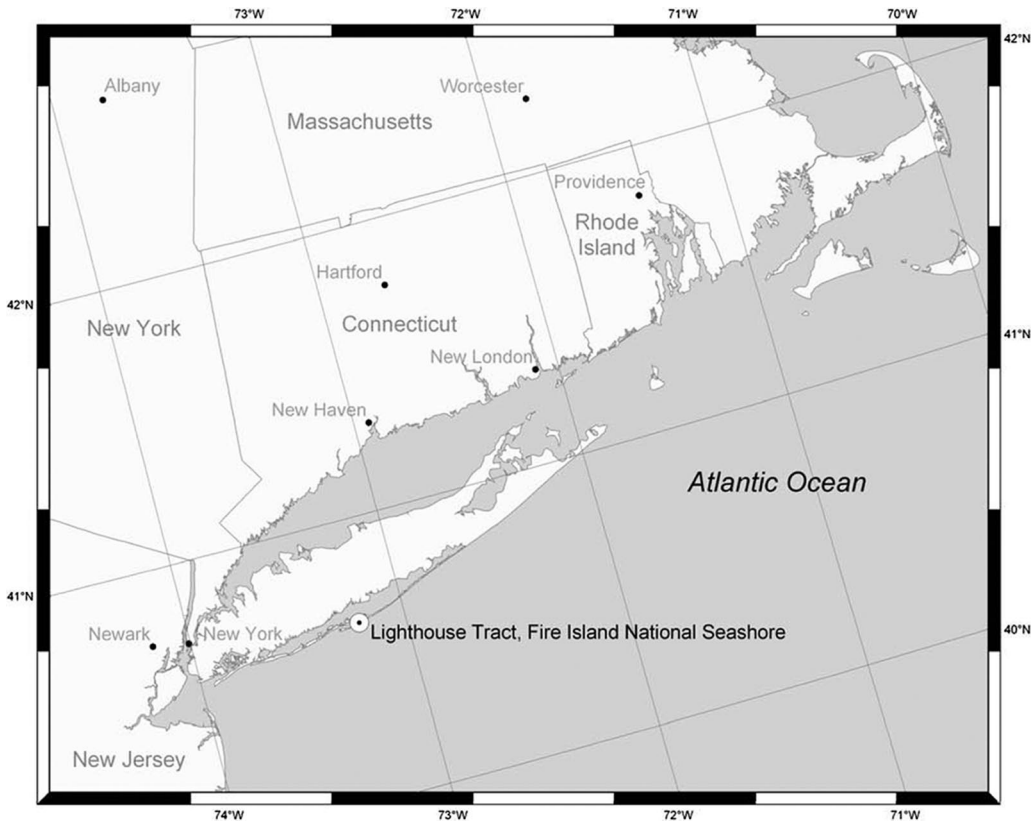


Fig. 1. Map of southeastern New York and southern New England, showing the location of the Lighthouse Tract of Fire Island National Seashore.

rates, habitat type, foraging behavior of different bird species, and their possible roles as reservoirs for *B. burgdorferi*.

Materials and Methods

Fire Island is a narrow, 53-km-long barrier island separating Great South Bay and the mainland of Long Island, NY, from the Atlantic Ocean (Fig. 1). At the extreme west end of Fire Island National Seashore (8 km east of Fire Island Inlet and 90 km east-northeast of New York City) is the area known as the Lighthouse Tract, a 65-ha section of natural vegetation where the 175-yr-old Fire Island Lighthouse stands. There, Fire Island narrows to ≈ 300 m from bay to ocean, with low (largely dune) vegetation seaward, and scattered native Pitch Pine (*Pinus rigida* Miller) groves alternating with mixed native deciduous shrub thickets (*Myrica-Rhus-Ilex*) bayward. Major plant species in the deciduous thickets included Bayberry (*Myrica pensylvanica* Mirbel), Low Beach Plum (*Prunus maritima* Marshall), Highbush Blueberry (*Vaccinium corymbosum* L.), Chokeberry (*Aronia arbutifolia* L. Elliott), American Holly (*Ilex opaca* Aiton), Poison Ivy (*Toxicodendron radicans* L. Kuntze), and Catbrier (*Smilax rotundifolia* L.). The Pitch Pine grove included some deciduous thickets, particularly around its periphery,

and abundant Poison Ivy and Catbrier beneath the canopy.

Within the Lighthouse Tract, two mist-netting sites 1 km apart were established. Owing to the presence of large numbers of White-tailed Deer (*Odocoileus virginianus* Zimmerman), whose unfettered movements would have precluded use of mist nets, a 0.9-ha deer-proof enclosure surrounding a Pitch Pine grove west of the lighthouse (termed coniferous) and a 1.2-ha deer-proof enclosure surrounding a section of maritime shrub thicket east of the lighthouse (termed deciduous) were constructed. Deer were driven from each enclosure before gates were secured in August 1995, and 8-foot (2.5-m)-high fencing precluded subsequent deer (and human) entry; all other vertebrates, including mammals as large as adult American Red Fox (*Vulpes vulpes* L.), were able to pass freely through the fencing.

In the pine grove, three parallel net lanes 30 m apart were oriented generally perpendicular to the long axis of Fire Island, hence also perpendicular to the route of travel of most migrating birds. Lanes were trimmed of close vegetation and mowed to preclude other than grasses/sedges from growing under nets. Up to 14 nylon mist nets, 12 m long, 3 m high, with four shelves and 36-mm mesh (general small-bird size), were placed on semipermanent poles in three par-

allel lanes. In the shrub thicket, a single bay-to-ocean net lane was similarly prepared, and up to 16 nets were placed parallel to those in the pine grove. All nets were within 50 m of enclosure fencing, and most were within ≈ 20 m.

Depending on weather, personnel, and intensity of migration, netting was conducted year round, involving ≤ 30 nets per day, for 5 h after first light. In general, the deciduous and coniferous sites were operated on alternate days. Acquisition assessment, which required consistent and frequent operation of both sites, was possible from March 1997 through August 1999. Data were taken on species, ages, and sexes; measurements and weights were recorded; and all birds were banded and released on site. Identical data were taken on all recaptures (captures on a subsequent day of individuals previously captured at the study site), repeats (captures later on the same day of individuals previously captured at the study site), and foreign retraps (initial captures at the study site of individuals banded elsewhere). Accounts were kept of the times of operation of nets, lanes, and sites.

Tick examinations were limited to the feather tracts of the head and the margins of the gape, orbital rings, and auricular openings, because capture volumes and animal welfare precluded the lengthy handling times required for full-body examinations. Ticks were collected and saved for identification as to age and species. To estimate total body burdens from tick examinations, selected birds from which ticks had been removed at capture were transported to a nearby field laboratory, where they were maintained in $38 \times 38 \times 48$ -cm wire cages over trays of water until all ticks had dropped off. Temperature in the field laboratory was maintained between 22.7 and 27.7°C, and relative humidity was between 37 and 68%. Birds were maintained on a diet of locally collected blueberries, a seed mix, waxworms, and mealworms. Bird species included American Robin, *Turdus migratorius* L., Gray Catbird, *Dumetella carolinensis* L., Eastern Towhee, *Pipilo erythrophthalmus* L., Song Sparrow, *Melospiza melodia* (A. Wilson), Northern Cardinal, *Cardinalis cardinalis* L., and Brown Thrasher, *Toxostoma rufum* L. Methodological details are given by Ginsberg et al. (2005).

In the present context, acquisition refers to the numbers of parasites acquired $\text{host}^{-1} \text{day}^{-1}$ (Sonenshine 1993). In the current study, acquisition rates were calculated when a given bird was recaptured between 1 and 4 d after removal of all visible ticks. This protocol insured that ticks removed on recapture had been acquired locally, and that most ticks acquired since the previous capture were recorded (engorged larval *Ixodes* at Fire Island detach 60–96 h after placement on captive birds: Balmforth 2002). We refer to these paired captures—and the single 4-d interval between them, during which the individual bird was free to acquire ticks in the natural environment—as acquisition events or simply as events, regardless of whether any ticks were actually acquired; events in which one or more *I. scapularis* were acquired are referred to as positive events. Acquisition rates were

calculated from the full sample of acquisition events by dividing the number of ticks acquired during each event by the duration of that event, rounded to the nearest whole day. Thus, all acquisition rates reported in this work are given in units of ticks $\text{bird}^{-1} \text{day}^{-1}$. Because of the strikingly different seasonal activity of *I. scapularis* larvae versus nymphs in southeastern New York State (Fish 1993), the data were divided into nymphal (May–July) and larval periods (July–August) for some analyses.

Basic statistical analyses, including descriptive statistics, *t* tests, correlations, linear regressions, and goodness-of-fit (*G*) tests, were performed using Systat 5.2.1 (1992, Systat, Chicago, IL), Statview 5.0 (1998, SAS Institute, Cary, NC), and BIOMstat 3.3 (1999, Exeter Software, Setauket, NY).

Results

In total, 371 paired captures of individual birds within 4 d were recorded (of a total of 14,405 captures of 12,270 individuals representing 115 species), the dates of re-examination ranging from 18 March to 22 November (1997–1999 pooled). At least one immature *I. scapularis* was acquired during 88 (24%) of these events, the dates ranging from 19 April to 26 September. We recorded all recaptures after 1–4 d, including repeated captures of the same individuals. The frequency of acquisition events varied seasonally, with a primary peak in May and a secondary peak in August–October, in both the overall sample and in the subsample in which ticks were actually acquired. The seasonal distributions of events recorded in the deciduous and coniferous habitat types were very similar (Fig. 2).

Gray Catbird alone accounted for 168 acquisition events (45%), including 46 positive events (52%). Three others, Common Yellowthroat, Northern Waterthrush, and Eastern Towhee, accounted for an additional 38 events (27 positive). Together, these four species were responsible for 56% of all events and 83% of positive events recorded. The remaining 165 events were divided among 39 other species (Tables 1 and 2). Several species contributed relatively large numbers of events, but all negative. Most extreme in this regard were Myrtle (=Yellow-rumped) Warbler ($n = 43$), Slate-colored (=Dark-eyed) Junco ($n = 10$), and Brown Creeper ($n = 9$), all of which occur on Fire Island primarily from late fall through early spring, outside the primary periods of tick activity. Twenty-five additional species for which paired captures of individual birds within 4 d were recorded between March and November, but during which no ticks were actually acquired, are listed in Table 2.

All species that acquired large numbers of ticks forage routinely on the ground (Table 1), whereas many of those that did not acquire ticks in our sample forage primarily in trees and shrubs (Table 2). The foraging microhabitats in Tables 1 and 2 were based on observations of these species at the study site. Acquisition of nymphs averaged $0.17 \text{ bird}^{-1} \text{ day}^{-1}$ overall ($SD = 0.69$, $n = 371$); $0.32 \text{ bird}^{-1} \text{ day}^{-1}$ during the

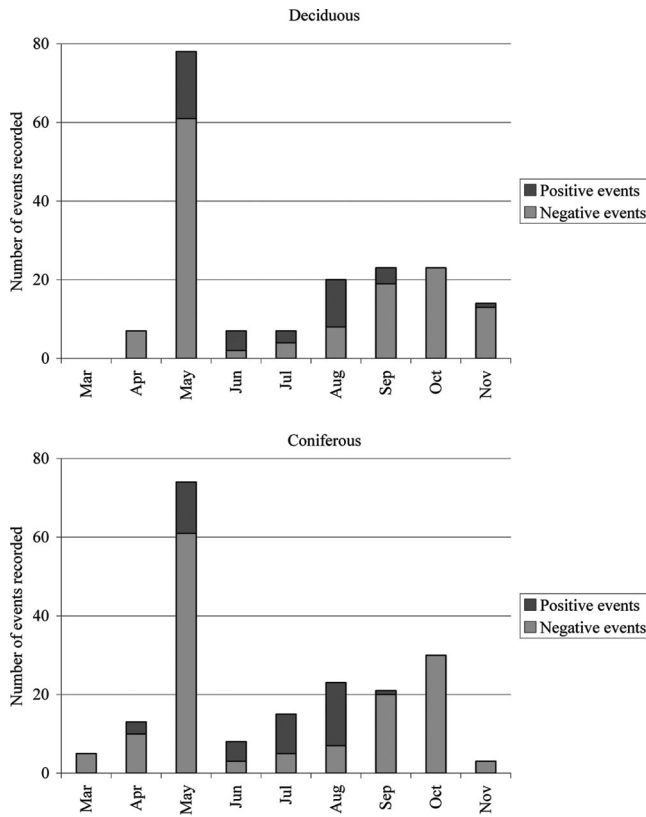


Fig. 2. Seasonal distribution of events in which individual birds were captured and recaptured over intervals of 1–4 d ($n = 371$), in two habitats (deciduous and coniferous) on Fire Island, Long Island, NY, 1995–1999.

period of high nymphal activity, May–July ($SD = 0.93$, $n = 189$); and $1.58 \text{ bird}^{-1} \text{ day}^{-1}$ during June, the peak month ($SD = 2.29$, $n = 15$). The greatest single example of nymphal acquisition involved an adult Gray Catbird that acquired eight nymphs 24–25 June 1998.

Acquisition of larvae averaged $0.16 \text{ bird}^{-1} \text{ day}^{-1}$ overall ($SD = 0.85$, $n = 371$); $0.88 \text{ bird}^{-1} \text{ day}^{-1}$ during the period of high larval activity, July–August ($SD = 1.86$, $n = 65$); and $1.13 \text{ bird}^{-1} \text{ day}^{-1}$ during July, the peak month ($SD = 2.62$, $n = 22$); cf. Table 3. The greatest

Table 1. Birds of 15 species that acquired larval or nymphal (or both) deer ticks in the Lighthouse Tract between March and November 1995–1999

Species	Percent acquiring ticks	Events	Larvae acquired	Nymphs acquired	Primary foraging microhabitats
Gray Catbird	14	329	75	64	Understory/litter
Eastern Towhee	37	27	35	17	Understory/litter
Northern Waterthrush	44	18	20	5	Understory/litter
Common Yellowthroat	35	26	11	16	Understory/litter
Hermit Thrush	0.4	5	6	0	Understory/litter
Black-billed Cuckoo	0.3	3	4	1	Foliage
American Robin	0.5	2	2	0	Diverse
Song Sparrow	0.1	8	2	0	Understory/litter
Carolina Wren	0.5	8	1	12	Understory/litter
Black-capped Chickadee	0.3	4	1	0	Tree trunks, twigs
Brown Thrasher	0.2	6	1	0	Understory/litter
American Redstart	0.05	19	1	0	Foliage
Palm Warbler ^a	100	1	0	0	Open ground
Red-breasted Nuthatch	12	17	0	4	Tree trunks, twigs
Swamp Sparrow	11	9	0	1	Understory/litter
Totals		482	159	120	

Events refer to birds recaptured and checked again for ticks 1–4 d following complete tick removal; species sorted by number of larvae acquired. Primary foraging microhabitats taken from species accounts in *Birds of North America* and local observations.

^a Two ticks were collected from this individual, but were damaged or lost prior to analysis.

Table 2. Birds meeting acquisition criteria for immature deer ticks (recaptured and checked again for ticks 1–4 d following complete tick removal) between March and November 1997–1999, but that nonetheless failed to acquire any ticks

Species	No. events (no. May–Aug.)	Primary foraging microhabitats
Myrtle Warbler	43 (5)	Diverse ^a
Slate-colored Junco	10 (0)	Open ground
Brown Creeper	9 (0)	Bark
Ovenbird	5 (0)	Understory/litter
White-eyed Vireo	4 (1)	Foliage
Blue-headed Vireo	3 (3)	Foliage
Red-eyed Vireo	3 (1)	Foliage
Golden-crowned Kinglet	3 (0)	Foliage, bark
Black-throated Blue Warbler	3 (1)	Foliage
Blackpoll Warbler	3 (2)	Foliage
White-throated Sparrow	3 (1)	Understory/litter
Baltimore Oriole	3 (3)	Flowers, fruit
Ruby-crowned Kinglet	2 (1)	Foliage, bark
Northern Parula	2 (2)	Foliage
Magnolia Warbler	2 (2)	Foliage
Pine Warbler	2 (0)	Foliage, bark
Black-and-white Warbler	2 (2)	Bark
Canada Warbler	2 (0)	Foliage
Yellow-bellied Sapsucker	1 (0)	Bark
Yellow-bellied Flycatcher	1 (0)	Sallying insectivore
Traill's Flycatcher ^a	1 (1)	Sallying insectivore
Eastern Phoebe	1 (0)	Sallying insectivore
Yellow Warbler	1 (0)	Foliage
Wilson's Warbler	1 (0)	Foliage
Hooded Warbler	1 (0)	Foliage
Indigo Bunting	1 (1)	Open ground
Orchard Oriole	1 (1)	Flowers, fruit
Brown-headed Cowbird	1 (1)	Open ground

The numbers of events during primary immature tick questing season (May–August) are in parentheses. Primary foraging microhabitats taken from local observations and from species accounts in *Birds of North America*.

^a Foraging behavior strikingly different on barrier beach than elsewhere, frequently on short grass.

single example of larval acquisition involved a juvenile Gray Catbird that acquired 34 larvae 20–23 July 1999 (11.33 d⁻¹). Seasonal variation in acquisition of nymphs and larvae is summarized in Fig. 3. Although

the magnitude of acquisition rates varied widely among host species, patterns of seasonal variation in acquisition rates were qualitatively similar among the most important avian host species (Fig. 4). Acquisition rates of larvae by the 15 bird species in Table 1 were not correlated with acquisition rates of nymphs by these species ($r = 0.331, P = 0.228$).

Pooled acquisition rates did not differ significantly between deciduous and coniferous habitats: 0.35 and 0.33 total *Ixodes* bird⁻¹ day⁻¹, respectively ($t = 0.17, df = 325, P = 0.86$). Similarly, acquisition of nymphs May–July did not differ between habitats (0.35 deciduous versus 0.30 coniferous, $t = 0.36, df = 157, P = 0.72$), nor did acquisition of larvae July–August (1.02 deciduous versus 0.77 coniferous, $t = 0.49, df = 41, P = 0.63$).

Pooling host species and comparing the peak activity periods for each age class of *Ixodes* (May–July for nymphs and July–August for larvae), larvae acquisition exceeded nymph acquisition: 0.88 ± 1.86 larvae bird⁻¹ day⁻¹ versus 0.32 ± 0.93 nymphs bird⁻¹ day⁻¹ ($t = 2.31, P = 0.01, df = 75$). Simultaneous local acquisition of both larvae and nymphs by a single bird was observed in six individuals of four species, once during May and five times during July (Table 4).

Overall, tick body burdens on birds were well predicted by the number of ticks removed from the birds' heads ($r^2 = 0.840, n = 34, P < 0.001$). Of birds recaptured on the day of release, only nine of 883 (1%) were found to have one or more ticks when recaptured (some possibly newly acquired), whereas 24% of birds recaptured 1–4 d after initial inspection and removal were found to have acquired ticks. Therefore, the proportion of ticks on birds' heads that were missed during routine inspections was extremely small. In any case, because the same field crew inspected birds that were later held over water, this factor would not affect the accuracy of the regression analysis. The regression equation was as follows: total body burden = 1.1699

Table 3. Acquisition of immature *Ixodes scapularis* (ticks bird⁻¹ day⁻¹) by 15 species of birds at Fire Island, Long Island, New York, 1995–1999

Species	May–July					July–Aug.				
	Nymphs	SD	<i>n</i>	Min birds	Min ticks	Larvae	SD	<i>n</i>	Min birds	Min ticks
Gray Catbird ^a	0.33	1.03	122	309	102.0	0.81	1.97	39	170	137.7
Northern Waterthrush ^a	0.33	0.24	4	21	6.9	3.08	4.30	3	47	144.8
Common Yellowthroat ^a	0.87	0.85	9	68	59.2	0.98	0.55	4	51	50.0
Eastern Towhee	0.75	1.56	8	28	21.0	3.15	2.45	5	21	66.2
American Robin	0.00	0.00		15	0.0	1.00	0.00	1	13	13.0
Palm Warbler	0.00	0.00		3	0.0	0.00	0.00	0	0	0.0
Hermit Thrush	0.00	0.00	1	2	0.0	0.00	0.00	0	0	0.0
Song Sparrow	0.00	0.00	1	18	0.0	0.50	0.71	2	28	14.0
Carolina Wren	1.78	0.19	3	6	10.7	0.25	0.00	1	6	1.5
Black-billed Cuckoo ^a	1.00	0.00	1	2	2.0	4.00	0.00	1	1	4.0
Red-breasted Nuthatch	0.44	0.72	4	3	1.3	0.00	0.00	2	4	0.0
Swamp Sparrow	0.17	0.29	3	5	0.9	0.00	0.00		0	0.0
American Redstart ^a	0.00	0.00	5	36	0.0	0.25	0.00	1	38	9.5
Brown Thrasher ^a	0.00	0.00	2	11	0.0	0.33	0.00	1	3	1.0
Black-capped Chickadee	0.00	0.00	1	2	0.0	1.00	0.00	1	2	2.0
Totals/Means	0.34	0.95	164	529	179.9	1.05	2.03	61	384	403.2

Min birds, average number of individuals captured season⁻¹; Min ticks, product of the acquisition rate and Min birds shown. Species are listed in order of March to November Min ticks.

^a Neotropical migrants.

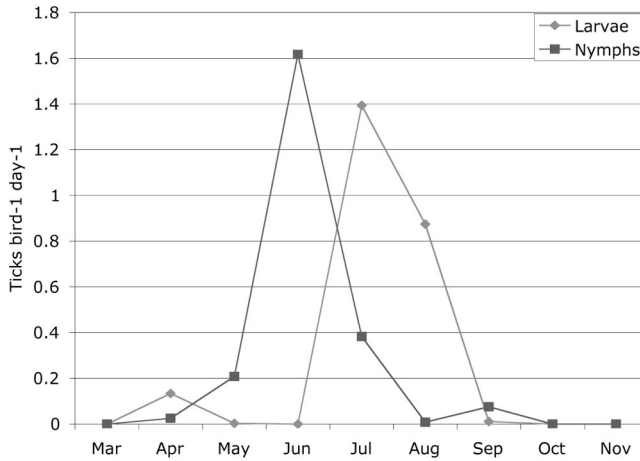


Fig. 3. Seasonal variation in acquisition of deer tick larvae and nymphs by birds at Fire Island, Long Island, NY, 1995-1999 ($n = 371$).

(number of ticks removed from head) + 2.5191. The proportion of the total number of ticks on the bird that was found on the bird's head averaged 58.8% for all birds, but differed among bird species ($G = 46.717$, $df = 4$, $P < 0.001$), ranging from 21.4% for Northern Cardinals and Brown Thrashers (combined) to 81.5% for Eastern Towhees. Correlations between the number of ticks found on the birds' heads and the total body burdens are given in Table 5. The number found on the birds' heads was significantly correlated with total body burden in all cases. Thus, the acquisition rates based solely on ticks removed from birds' heads can be revised by using the above equation to estimate the total numbers of ticks acquired. In this manner, total body acquisition is estimated as 4.37 nymphs bird⁻¹ day⁻¹ during the peak month of June, and 3.84 larvae bird⁻¹ day⁻¹ during the peak month of July.

Discussion

Our results provide strong support for the importance of foraging microhabitat to tick acquisition by birds (Tables 1 and 2). Other authors have suggested, based on tick body burdens, that ground-foraging birds acquire more ticks than birds that forage above the ground (Weisbrod and Johnson 1989, Stafford et al. 1995). We directly quantified actual acquisition rates, and found that ground-foraging birds generally acquired more ticks than birds that forage in trees or shrubs, with some notable exceptions possibly related to particular local factors. Furthermore, this trend was consistent across species that varied tremendously in relative abundance, as estimated from mist-net captures. Although caution must be used in estimating relative abundance using this (or any other) technique, mist nets probably offer the best means of

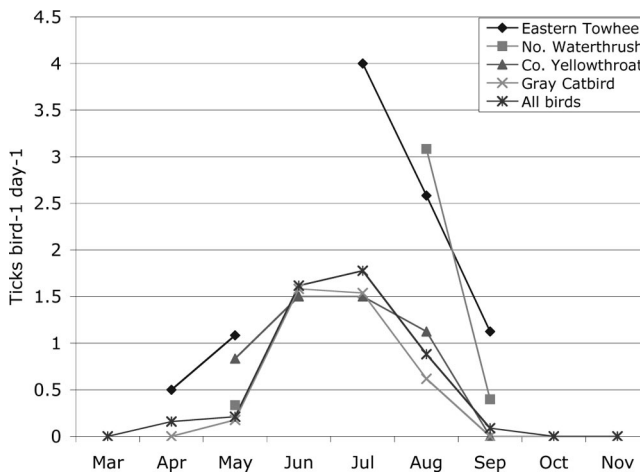


Fig. 4. Seasonal variation in acquisition rates of immature deer ticks by four important avian host species at Fire Island, Long Island, NY, 1995-1999.

Table 4. Simultaneous local acquisition of *Ixodes scapularis* larvae and nymphs by birds at Fire Island Lighthouse, 1995–1999

Species	Dates	Nymphs	Larvae	Habitat
Eastern Towhee	20–22 May 1997	9	1	Coniferous
Common Yellowthroat	6–9 July 1998	4	2	Deciduous
Black-billed Cuckoo	28–29 July 1999	1	4	Coniferous
Gray Catbird	20–22 July 1998	2	1	Coniferous
Gray Catbird	13–15 July 1998	2	1	Coniferous
Gray Catbird	20–23 July 1999	1	34	Deciduous

detecting birds that forage on the ground under dense vegetation (i.e., those most likely to acquire ticks at Fire Island and other similar sites). Furthermore, the abundance of secretive migrants, such as Northern Waterthrush, would likely be grossly underestimated by any other technique, as illustrated by the contrast between direct counts (maximum for southbound migrants in New York State = 55: Eaton 1998), versus the capture rates we observed (maximum single-day capture total = 85, on 5 September 1997). Thus, there is little reason to doubt that Gray Catbird, Common Yellowthroat, Northern Waterthrush, and Eastern Towhee acquire very large numbers of larvae on Fire Island—not only because of their foraging behavior, but also because of their relatively high population densities at appropriate times of year.

Interestingly, the birds that acquired the most ticks, Gray Catbirds and Eastern Towhees, generally display low to moderate levels of reservoir competence (Mather et al. 1989, Ginsberg et al. 2005), so one might assume that they contribute less than highly reservoir-competent species such as American Robins (Richter et al. 2000) to Lyme spirochete transmission at this site. However, the larger numbers of larvae acquired by these species (resulting from higher local populations as well as ground-foraging behavior) can result in substantial contributions of infected ticks from species with relatively low levels of reservoir competence. For example, 5.4% of uninfected *I. scapularis* larvae placed on Gray Catbirds at this site were infected after molting to the nymphal stage, and 16.1% of larvae placed on American Robins were infected as nymphs (Ginsberg et al. 2005). Therefore, Gray Catbirds would contribute more infected ticks (4.1 of the 75 acquired) than American Robins (0.3 of the two acquired) at this site. Therefore, birds with relatively low levels of reservoir competence, such as Eastern Towhees and Gray Catbirds, can nevertheless contribute substantially to maintenance of the enzootic cycle of *B. burgdorferi*.

The 15 species for which acquisition of *I. scapularis* was observed at Fire Island form an ecologically dis-

parate group. Their collective abundance during the peak periods of nymphal and larval activity implies that they acquire biologically significant numbers of *I. scapularis* nymphs and larvae on Fire Island. In particular, Gray Catbird, Northern Waterthrush, Common Yellowthroat, and Eastern Towhee appear to play quantitatively important roles in the ecology of *I. scapularis* at this site. The variable, but generally exceptionally high vagility of these bird species not only guarantees that locally acquired *I. scapularis* will be dispersed to distant sites, but it also seriously constrains the spatial and temporal scales at which acquisition and drop-off rates can be assumed to remain in equilibrium, compromising the reliability of body-burden data as a proxy for local acquisition rates.

All four of the most important avian host species on Fire Island are highly migratory and spend much time foraging on the ground under dense, woody vegetation. Northern Waterthrush, the only nonbreeder among the top four, is an abundant passage migrant at Fire Island and has the longest migration route of the four. Like this species, Gray Catbird and Common Yellowthroat are Neotropical migrants—species whose temperate North American breeding populations winter largely in tropical habitats of the West Indies and Central and South America—but both of these (and also the medium-distance migrant Eastern Towhee) are also abundant local breeders in the Lighthouse Tract. This duality underscores the complex nature of the local host community, which consists of varying proportions of conspecific residents and passage migrants present together simultaneously at various times of year.

Among the other 11 species for which positive events were documented, American Robin, Song Sparrow, and Brown Thrasher are common to abundant local breeders, are migratory, and forage on the ground under dense woody vegetation. Only Carolina Wren is essentially sedentary, but it resembles those just mentioned in that it breeds locally and forages low in thickets. Black-billed Cuckoo and American Redstart are Neotropical migrants. The absence of positive events for such well-sampled species as Myrtle Warbler, Slate-colored Junco, and Brown Creeper can be attributed to their migratory phenology, which brings them through Fire Island earlier in the spring and later in the fall than the May–August period when immature *Ixodes* are most active there, and possibly also to their foraging behavior and other factors.

The exclusion of White-tailed Deer from the immediate vicinity of our nets did reduce numbers of questing nymphs in these very limited areas, at least

Table 5. Correlations between numbers of *Ixodes scapularis* larvae on birds' heads and their whole body burdens

Bird species	No. birds	<i>r</i>	<i>P</i>
All species	34	0.916	<0.001
American Robin	7	0.933	0.002
Gray Catbird	10	0.642	0.046
Eastern Towhee	6	0.996	<0.001
Song Sparrow	8	0.927	0.001

temporarily (Ginsberg et al. 2004). This effect presumably arose because excluding deer (the preferred host of adult *I. scapularis*) reduced the number of adult female ticks able to feed, detach, and lay eggs within the enclosures. Even so, any depression of larval acquisition among birds captured within the enclosures is likely to have been small, given the small size of the enclosures (≈ 1 ha) and the proximity of the nets to the fences (< 50 m in almost all cases). Bird movement was generally broad relative to the size of the enclosures, with estimates of bird movement between the enclosures (> 800 m apart) ranging up to 50% (Ginsberg et al. 2004).

The barrier beach habitats where this study was conducted are extremely variable and dynamic (Art 1976). The similarity we report regarding avian acquisition of *I. scapularis* in Pitch Pine forest and deciduous shrub thickets—two of the most disparate woody habitats on the barrier beach—was undoubtedly due in part to the heterogeneous, mosaic distribution of these habitats and the likelihood that many or most individual birds spent time in both habitat types. To the extent that this was true, the rates of acquisition we observed were unlikely to have been artifacts of some unique feature of the particular sites in which we worked. Several investigators have reported larger numbers of *I. scapularis* immatures in deciduous than in coniferous woodlands (Guerra et al. 2002), whereas others have reported the reverse (Lord 1995). Clearly, physical factors relevant to tick survival can differ in deciduous versus coniferous forests, but the similar acquisition rates in both forest types in our study support the conclusion that factors other than deciduousness or coniferousness can strongly influence tick abundance (Ginsberg et al. 2004).

Several tick species in addition to *I. scapularis* occur on Fire Island (Ginsberg 1992), including *Amblyomma americanum*, *Dermacentor variabilis*, and *Haemaphysalis leporis-palustris*. All *Ixodes* identified from birds were *I. scapularis*, although not all ticks were identified because many were processed for associated studies. Aside from *A. americanum*, ticks associated with birds and other potential hosts were not commonly collected at the study site. Indeed, seven Eastern cottontails (*Sylvilagus floridanus*) captured in the study area had few ticks. Immature *A. americanum* were common on birds, but not in the head region where *I. scapularis* was collected. Of 15 birds of six species sampled in 1997, the total body burdens averaged 15.47 *A. americanum* ticks per bird (range: 0–82 on individual birds), but none were collected from the birds' heads. Therefore, although some of the ticks recorded in this study might have included some other *Ixodes* species, these were rare and had little effect on the estimates reported, or on the conclusions of the study.

The peak period of larval acquisition was in July, which also featured the highest rates of coacquisition of nymphs and larvae by individual birds. Coacquisition is potentially important to the local ecology of Lyme disease because it can facilitate the transfer of *Borrelia* from infected nymphs to uninfected larvae on

individual hosts that are poor reservoirs for *Borrelia* (Stafford et al. 1995, Ogden et al. 1997)—but also in competent reservoirs whose infectivity (e.g., to uninfected larvae) diminishes over time after the host's last exposure to infected nymphs (Donohue et al. 1987, Richter et al. 2000). Importantly, at least three locally abundant bird species on Fire Island are now known to be variably competent reservoirs for *B. burgdorferi*: American Robin, competent; Northern Cardinal, moderately competent; and Gray Catbird, low to moderately competent (Mather et al. 1989, Richter et al. 2000, Balmforth 2002, Ginsberg et al. 2005). The high rates of nymphal acquisition we observed June–July (≈ 1 bird⁻¹ day⁻¹), combined with the local infection rate of nymphs (between 15 and 32% at various sites on Fire Island), imply that virtually all breeding individuals of several species of birds were repeatedly exposed to *Borrelia* immediately before, and coincident with, the peak period of larval infestation (Ginsberg 1992). Thus, the reservoir competence observed among some of these species is likely to be exploited by *Borrelia* and to influence local infection rates of immature *Ixodes*.

Ostfeld and Keesing (2000) reported an inverse relationship between small mammal diversity and the incidence of Lyme disease across sites in northeastern and midwestern North America. They attribute this dilution effect to the influence of numerous non- or quasi-competent hosts, which, although heavily infested with ticks, fail to infect those ticks with *Borrelia*. These authors also report a positive association between Lyme disease and bird diversity. The situation at Fire Island, where a high infection rate among *Ixodes* nymphs is associated with a low diversity of small mammals (Ginsberg 1992) and a seasonally high diversity of birds, is consistent with either pattern. In a sense, however, this dual consistency weakens the explanatory power of either hypothesis. The quantitative importance of birds as hosts for ticks at Fire Island favors consideration of bird species as potential dilutors. Viewed this way, Fire Island's vertebrate host community would be regarded as highly diverse, and its high *Borrelia* infection rates would not be explained well by the dilution effect hypothesis. We suggest that the generality of various explanations for the spatial and temporal distribution of Lyme disease could be strengthened if they included more detailed data acknowledging the complexity—and variability—of the host ecology of *Ixodes* at various sites. At a minimum, such data should include measures of tick acquisition rates at sites whose host communities feature large numbers and many species of highly migratory birds, some of which might be underrecognized reservoirs.

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