

Influence of Deer Abundance on the Abundance of Questing Adult *Ixodes scapularis* (Acari: Ixodidae)

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ABSTRACT Nymphal and adult *Ixodes scapularis* Say were sampled by flagging at 2 sites on a barrier island, Fire Island, NY, and at 2 sites on the nearby mainland. Nymphal densities did not differ consistently between island and mainland sites, but adult densities were consistently lower on the island. We tested whether lower adult densities on the island resulted from greater nymphal mortality on the island than the mainland, or whether adult ticks on the island were poorly sampled by flagging because they had attached abundantly to deer, which were common on Fire Island. Differential nymphal mortality on islands versus mainland did not explain this difference in adult densities because survival of flat and engorged nymphs in enclosures was the same at island and mainland sites. Ticks were infected by parasitic wasps on the island and not the mainland, but the infection rate (4.3%) was too low to explain the difference in adult tick densities. In contrast, exclusion of deer by game fencing on Fire Island resulted in markedly increased numbers of adult ticks in flagging samples inside compared with samples taken outside the enclosures. Therefore, the scarcity of adult ticks in flagging samples on Fire Island resulted, at least in part, from the ticks being unavailable to flagging samples because they were on deer hosts. Differences in the densities of flagged ticks inside and outside the enclosures were used to estimate the percentage of questing adults on Fire Island that found deer hosts, excluding those that attached to other host species. Approximately 56% of these questing adult ticks found deer hosts in 1995 and 50% found deer hosts in 1996. Therefore, in areas where vertebrate hosts are highly abundant, large proportions of the questing tick population can find hosts. Moreover, comparisons of tick densities at different sites by flagging can be potentially biased by differences in host densities among sites.

KEY WORDS *Ixodes scapularis*, *Odocoileus virginianus*, *Ixodiphagus hookeri*, ticks, deer, sampling

TICKS ARE GENERALLY sampled either while questing or while attached to hosts. Host-seeking ticks are collected using flagging, dragging, or walking samples, or by using CO₂-baited tick traps (Clymer et al. 1970; Gray 1985; Falco and Fish 1989, 1992; Ginsberg and Ewing 1989b; Sonenshine 1993). Attached ticks are collected from captured host animals, animals in nest boxes designed to harvest ticks that drop off, or by hanging animal skins over water and collecting ticks as they drop (Sonenshine 1993, Wilson 1994).

Numerous studies have compared relative densities of ticks between sites by comparing the number of freeliving ticks collected per unit time, per unit distance, or per trap night (e.g., Mather et al. 1988, Ginsberg and Ewing 1989a, Maupin et al. 1991, Carroll et al. 1992, Li and Dunley 1998). Collections from hosts have also been used to compare tick densities by comparing the number of ticks per host animal (e.g., Wilson et al. 1988, Deblinger et al. 1993). However, the number of ticks per host animal is ambiguous because

it depends not just on tick density, but also on the density of the target host species, and on the density of alternative host species that can dilute tick numbers on the target host (Ginsberg 1992).

Tick densities estimated from flagging samples would presumably be less influenced by host densities than would estimates based on tick collections from hosts, because only a small proportion of questing ticks are believed to find suitable hosts (Sonenshine 1975, Haile and Mount 1987, Daniels et al. 1989). However, this belief has not been demonstrated for deer ticks, *Ixodes scapularis* Say, in the field. Therefore, it is plausible that host densities are sometimes high enough so that a large proportion of questing ticks find hosts. If a large enough proportion of ticks find hosts, the loss of freeliving ticks from the site can potentially influence density estimates obtained from flagging samples.

The current study was prompted by the observation that densities of adult *I. scapularis* from flagging samples at the Lighthouse Tract of Fire Island National Seashore, NY, were much lower than would have been expected based on the relatively high densities of larvae and nymphs at this site. Preliminary observations suggested that island sites, such as Fire Island,

Mice were maintained, handled, and used in this research according to protocols approved by the Institutional Animal Care and Use Committee (protocol number A9394–063) at the University of Rhode Island.

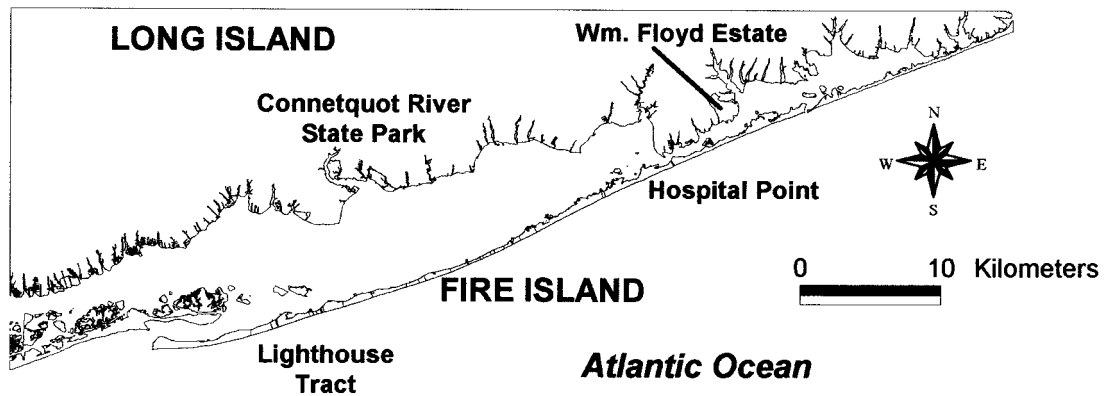


Fig. 1. Study area.

NY, had lower adult densities (relative to nymphal densities) than did mainland sites (e.g., at sample sites in southern Rhode Island), where adults seemed relatively common. The purpose of this study was to determine whether this observation was in fact correct, by comparing nymphal and adult populations from flagging samples at sites on Fire Island with sites on the nearby mainland Long Island, NY. Two major hypotheses were then tested that could explain lower adult tick numbers in flagging samples at island than at mainland sites: (1) nymphal mortality was greater on the island than at mainland sites (increased mortality could result from desiccating environmental conditions on the island caused by wind and salt spray, or from increased attack by parasitic wasps on the island), and (2) adult ticks were rare on vegetation on the island because they attached to deer before they could be collected in flagging samples.

Materials and Methods

Two sample sites were selected on Fire Island, and 2 on mainland Long Island, NY (Fig. 1). The Fire Island sites were at Hospital Point, near the eastern end, and at the Lighthouse Tract, near the western end of the barrier island. The mainland sites were at the William Floyd Estate and Connetquot River State Park. The study sites were all within closed-canopy deciduous woodlands with substantial shrub layers and accumulated leaf litter. Common canopy species included black cherry, *Prunus serotina* Ehrhart, at Hospital Point; highbush blueberry, *Vaccinium corymbosum* L.; and chokeberry, *Aronia arbutifolia* (L.), at the Lighthouse Tract; sassafras, *Sassafras albidum* Nuttall; and white oak, *Quercus alba* L., at the William Floyd Estate, and mixed oaks (*Quercus* spp.) at Connetquot River State Park.

Flagging Samples. Ticks were collected by flagging in the leaf litter at each site. The flags were made of white pin-wale corduroy, 1 by ½ m, and attached to wooden dowels. Samples were taken at each of the 4 sites during the nymphal activity period, from 2 June through 6 August 1996 (10 flagging samples, 1-min

each, taken on each of 5 sample days at each of the 4 sites; total of 200 samples). Samples were also taken during the period of adult activity, on 17–18 November 1996 (25 flagging samples, 1-min each, taken at each site; total of 100 samples).

Deer exclosures, consisting of game fencing (Gaucho Game Fence, Bekaert, Van Buren, AR) with 3 high-tension wires at the top to a height of 2.4 m, were built during the summer of 1995 surrounding 2 wooded sites as part of a mist-netting study of neotropical migratory birds at the Lighthouse Tract. The fence was mounted with large-size mesh at ground level (openings were 15 by 25.5 cm) narrowing toward the top (openings at the top were 8.5 by 15 cm). The large openings at the bottom allowed ready passage of small and medium-sized mammals, and even some fawns were observed passing through, but adult deer were excluded. Based on direct observation and on the absence of signs of deer (fresh pellets or hoof prints) deer were absent from the exclosures during this study, except for the occasional presence of fawns for brief periods. The eastern exclosure covered 1.1 ha, and included deciduous shrub-woodlands; primarily highbush blueberry; chokeberry; and bayberry, *Myrica pensylvanica* Mirbel. The western exclosure covered 0.9 ha of pitch pine, *Pinus rigida* Miller, woods. One deciduous and 1 coniferous control site were selected in the vicinity of each exclosure (total of 2 exclosures and 4 control sites). Tick samples were taken inside and outside of these exclosures to study the effects of deer exclusion on tick numbers. Flagging samples, 1-min each, of adult *I. scapularis* were taken at each of these 6 sites in 1994 (10–14 November) before the exclosures were built, and in 1995 (8–10 November) and 1996 (29 October–3 December) after the exclosures were completed. The number of samples at each of the 6 sites were 25 in 1994, 15 in 1995, and 20 in 1996 (total of 360 samples).

Survival Experiments. Nymphal survival was studied at island and mainland sites by setting out flat and engorged ticks in enclosures in the field. Enclosures consisted of the foot-ends of off-white pantyhose (No nonsense, "Sheer to waist" pantyhose, M58, Off White

Sandfoot, Kayser-Roth, Burlington, NC) that were folded over at the calf-end and sealed with clips. Details of the technique were given by Ginsberg and Zhioua (1996). Nymphal ticks were collected at each site, placed on white-footed mice, *Peromyscus leucopus* (Rafinesque), in the laboratory at the University of Rhode Island, Kingston, RI, allowed to engorge and drop off, and then returned to the collection site and placed in the field in stocking enclosures. Flat ticks from each site were also placed in stocking enclosures at the site. Stockings with flat ticks were paired with stockings containing engorged ticks, placed at ground level, and buried under leaf litter.

The ticks were placed as follows: Hospital Point, 25 engorged ticks in 5 stockings and 28 flat ticks in 5 stockings; William Floyd Estate, 39 engorged ticks in 6 stockings and 29 flat ticks in 6 stockings; Connetquot River, 70 engorged ticks in 7 stockings and 69 flat ticks in 7 stockings; Lighthouse Tract, 42 engorged ticks in 5 stockings and 50 flat ticks in 5 stockings (totals of 176 engorged ticks and 176 flat ticks in this experiment). The experiment took place near the end of the seasonal nymph activity peak, with the stockings placed from 15 to 17 July, and collected on 6 August 1996, when numbers of live and dead ticks in each stocking were recorded. An additional survival study was performed in 1997, in which only engorged ticks were placed in the enclosures. Placement was as follows: Hospital Point, 3 ticks in 1 stocking; William Floyd Estate, 16 ticks in 3 stockings; Connetquot River, 16 ticks in 3 stockings; Lighthouse Tract, 11 ticks in 2 stockings (total of 46 engorged ticks). The 1997 enclosures were left out longer than in 1996, until adult emergence. The ticks were placed on 29 July and the stockings collected and survival recorded on 15 October 1997.

Infection with the parasitic wasp, *Ixodiphagus hookeri* Howard, is known to induce mortality in *I. scapularis* nymphs (Mather et al. 1987, Hu et al. 1993). Parasitism of nymphal ticks by these wasps was compared between sites by collecting nymphal ticks at the Lighthouse Tract on Fire Island, and in Connetquot River State Park on the mainland on 16 July 1998. The ticks were returned to the laboratory and dissected to determine whether they were infected with wasp eggs.

Statistics. Densities of nymphal *I. scapularis* were compared among sites by analysis of variance (ANOVA) using SYSTAT (Wilkinson et al. 1992), subprogram MGLH. Data were transformed by $\ln(x + 1)$ to stabilize variances that were heterogeneous according to $F_{\max}$ tests (Sokal and Rohlf 1981) and to eliminate trends in plots of residuals versus estimates. Transformations could not stabilize the variances of adult population samples, so they were compared using Kruskal-Wallis tests (SYSTAT, subprogram Npar). Survival of nymphal ticks at island versus mainland sites were compared using Fisher exact tests, two-tailed (SYSTAT, subprogram Stats).

Relative densities of adults inside and outside of deer exclosures at the Lighthouse Tract were compared, untransformed, using ANOVA (SYSTAT, sub-

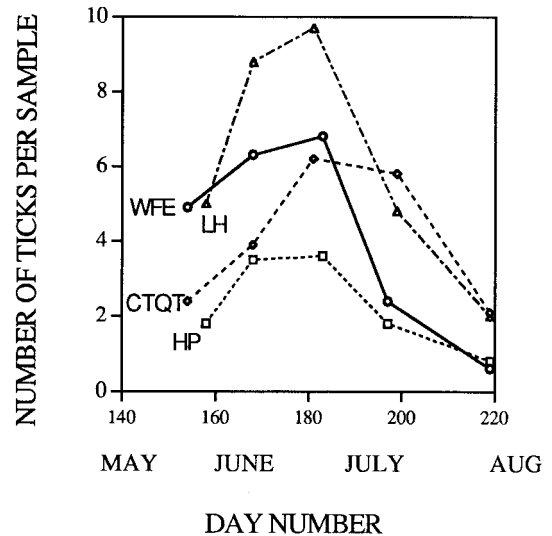


Fig. 2. Number of nymphal *I. scapularis* per minute in flagging samples at island and mainland sites, 1996. WFE, William Floyd Estate; LH, Lighthouse Tract; CTQT, Connetquot River State Park; HP, Hospital Point.

program MGLH). Data were not transformed because variances were homogeneous (by $F_{\max}$) in 1994 and 1996. Variances were heterogeneous in 1995, but transformation did not stabilize the variances that year so untransformed data were used for consistency with other years.

The game fencing used to exclude deer was designed to allow all other vertebrate species to pass freely. Therefore, the lower densities of questing adult ticks outside the exclosures were due entirely to removal of ticks from the vegetation on deer. Thus, if adult ticks on other host species are removed from consideration (cottontail rabbits were the only other common host for adult *I. scapularis* at the Lighthouse Tract), we could estimate the overall proportion of adult ticks that had found deer hosts in 1995 and 1996. The proportion of adults that were on deer during our samples (P_d) was estimated using the following relationship: $P_d = 1 - n_o/n_i$, where n_o = number of adults collected per minute outside the deer exclosures, and n_i = number of adults collected per minute inside the deer exclosures.

Results

Relative populations of nymphal *I. scapularis* at the 4 study sites in 1996 are shown in Fig. 2. Relative nymph densities differed significantly among sites ($F = 11.679$; $df = 3, 180$; $P < 0.0001$), but these differences were not consistent between Fire Island and mainland sites. The sites with the highest and lowest tick densities were on Fire Island, with mainland sites intermediate, so there was no overall difference between Fire Island and the mainland ($F = 0.967$; $df = 1, 196$; $P = 0.327$). Densities of adults (Fig. 3) also

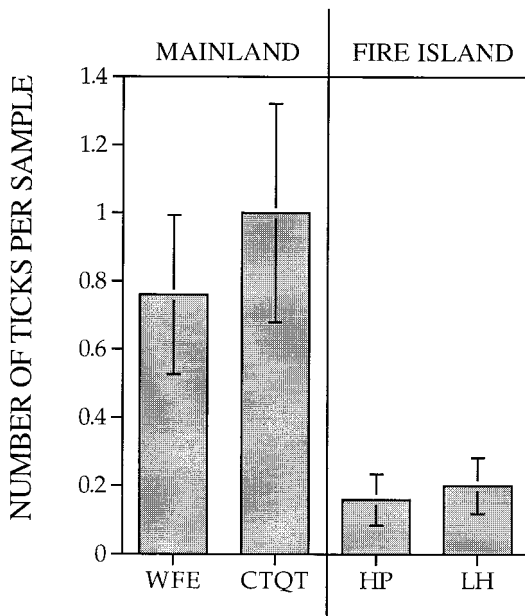


Fig. 3. Number of adult *I. scapularis* per minute in flagging samples at island and mainland sites, 1996. Error bars are $\pm$ SE. Abbreviations as in Fig. 2.

differed significantly among sites (Kruskal-Wallis test statistic = 0.114, $df = 3$, $P = 0.0097$). However, in contrast to nymphs, adult densities overall were significantly lower on Fire Island than they were on the mainland (Kruskal-Wallis test, $U = 1640.5$, $P = 0.001$). Thus, adults were consistently less common in flagging samples on Fire Island than on the mainland, whereas nymphs were not.

This finding is strengthened by comparing the number of nymphs collected per minute during peak nymphal densities with the number of adults collected per minute at each site. The ratio of nymphal density to adult density in flagging samples was 8.9 at the Wm. Floyd Estate, 6.2 at Connetquot River State Park, 22.5 at Hospital Point, and 48.5 at the Lighthouse Tract. Thus, the ratio of nymphs to adults flagged was higher at the Fire Island sites than on the mainland.

Survival of ticks in stocking enclosures during the last portion of nymphal activity (July–early August 1996) on Fire Island and on the mainland are shown in Fig. 4. Survival was high in all trials, with no significant difference between Fire Island and the mainland for either flat ticks (Fisher exact test, $n = 145$, $P = 0.145$) or engorged ticks (Fisher exact test, $n = 163$, $P = 1.000$). The 1997 experiment, in which engorged nymphs were left out in stocking enclosures from July until adult emergence in October, also showed no difference in tick survival between Fire Island and mainland sites (Fisher exact test, $n = 40$, $P = 1.000$), with 71.4% survival at Fire Island sites and 73.1% survival on the mainland.

Nymphal ticks collected at the Lighthouse Tract on Fire Island and in Connetquot River State Park on the

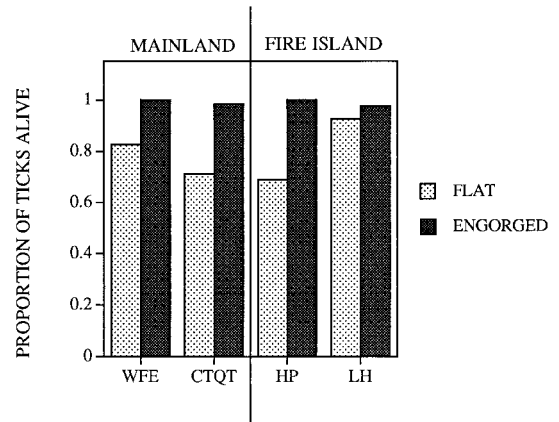


Fig. 4. Survival of nymphal *I. scapularis* at island and mainland sites, 1996. Abbreviations as in Fig. 2.

mainland were dissected to determine if they were infected by parasitoid wasps. Infection with *I. hookeri* was 4.3% on Fire Island (2 infected of 47 ticks dissected) and 0% on the mainland (86 ticks dissected).

Relative densities of questing adult *I. scapularis* from flagging samples inside and outside the deer exclosures are shown in Fig. 5. In 1994, before the exclosures were erected, there was no significant difference in adult tick densities in exclosure versus control sites ($F = 0.683$; $df = 1, 148$; $P = 0.410$). After the exclosure fences were built, however, questing tick densities were higher inside the exclosures in both 1995 ($F = 3.956$; $df = 1, 88$; $P = 0.0498$) and 1996 ($F = 5.788$; $df = 1, 118$; $P = 0.0177$). Based on the differences in the number of ticks collected per flagging sample inside and outside the deer exclosures, the percentage of adult ticks that were on deer at the Lighthouse Tract was 55.9% in 1995 and 50.0% in 1996.

Discussion

Our results corroborate the perception of scarcity of adult ticks on Fire Island. Adults were consistently less common in flagging samples from Fire Island than

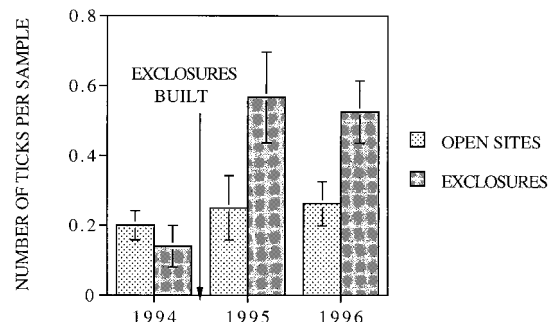


Fig. 5. Number of adult *I. scapularis* collected per minute flagging at open sites and at sites within deer exclosures at the Fire Island Lighthouse Tract, 1994–1996. Error bars are $\pm$ SE.

on the mainland, whereas nymphs were not (Figs. 2 and 3). The relative rarity of free-living adults on the barrier island raises the question of whether adults were, in fact, less common on the island or just less available for collection.

Survival experiments including both flat and engorged nymphs showed no differences in survival between island and mainland sites (Fig. 4). Nymphal mortality from the desiccating effects of wind and salt spray apparently does not explain the paucity of adult ticks on the island. Parasitism by the encyrtid wasp *I. hookeri* was detected on Fire Island and not on the mainland, so this parasite might contribute to the differences in adult densities. However, the parasitism rate (4.3%) was too low to account, by itself, for the striking difference in adult densities between the Fire Island and mainland sites (Fig. 3). Unfortunately, we were unable to assess the possible effect of vertebrate predation of nymphs (e.g., by shrews or ground-foraging birds) on adult tick densities.

Deer, however, clearly contributed to the phenomenon of adult tick scarcity at the Lighthouse Tract. Before deer exclusion, adult ticks were roughly equally abundant inside and outside the enclosure areas. When the enclosures were built, the number of adults flagged increased dramatically inside, but not outside the enclosures (Fig. 5). Therefore, at least part of the reason adult ticks were rare in flagging samples at the Lighthouse Tract was that many of these ticks were on deer and therefore were no longer available for flagging samples.

This effect should be distinguished from the influence of fencing on overall tick populations. Tick populations eventually decline when important hosts are excluded by fencing (Daniels et al. 1993, Stafford 1993). The samples taken for this study were all within 2 yr of deer exclusion, which is not enough time to lower the underlying population of adult ticks, because of the 2-yr life cycle of *I. scapularis* in this area.

We have enclosure data from the Lighthouse Tract only, but data on deer densities are available from all of our sample sites. A study performed for the National Park Service (Underwood et al. 1998) used a distance sampling technique to estimate deer densities at several sites coincident with or near to our sample sites. The Lighthouse Tract apparently does not have a resident deer herd, although deer frequently use the area, and adult females and juveniles sometimes set up temporary residence for 3–4 mo at the site. During October and November, however, large numbers of deer enter the Lighthouse Tract from the adjacent communities of Kismet to Lonelyville on Fire Island. This is the breeding season for the deer population, which coincides with the time of adult tick activity when we conducted our flagging samples. Deer densities in these neighboring areas were estimated by Underwood et al. (1998) to range from 77.6 to 90.0 deer per square kilometer during the fall of 1996. Contrast this to deer density estimates of 26.0/km² (coefficient of variation [CV] = 19.8) at the William Floyd Estate (in September 1996) and 15.5/km² (CV = 21.6) in the Wilderness Area, which includes

Hospital Point (in April 1997). Deer density estimates taken using the same distance-estimation technique at Connetquot River State Park in September 1996 (H. B. Underwood, F. D. Verret, and J. P. Fischer, USGS Patuxent Wildlife Research Center, SUNY CESF, Syracuse, NY, personal communication) gave an estimate of 33 deer per square kilometer.

Thus, available deer density estimates in and near our study areas are compatible with the hypothesis that during our adult tick sampling period, deer densities were higher at the Lighthouse Tract than at our other sample sites, corroborating the hypothesis that high deer densities resulted in low numbers of questing adult ticks at the Lighthouse Tract. The low deer density at Hospital Point is consistent with the low populations of both nymphal and adult ticks at that site. However, Hospital Point had a higher ratio of flagged nymphs to adults than the 2 mainland sites, suggesting that some other factor in addition to deer density contributed to the paucity of adults on Fire Island. Perhaps parasitism by wasps is one such contributing factor.

The enclosure experiment allows us to estimate the proportion of questing ticks that were on deer outside of the enclosure areas. The deer fencing did not influence ticks on other host species (which could easily pass through the fences), and these ticks are excluded from the analysis. By the time of sampling, an estimated 55.9% of the questing adult ticks had found deer hosts in 1995 and 50.0% in 1996. This result stands in dramatic contrast to the popular supposition, based on indirect evidence, that only ~10% of questing ticks typically find hosts (Sonenshine 1975, Haile and Mount 1987, Daniels et al. 1989). Apparently, when hosts are superabundant, as is the case for deer on parts of Fire Island, a large proportion of the questing tick population can find hosts.

This finding suggests an additional hypothesis for a phenomenon that has thus far been difficult to explain: the difficulty of flagging immature *I. scapularis* in the southeastern United States. Larvae and nymphs are readily collected by flagging in northern states, but not in the south. This could result from differences in questing behavior in southern populations, but the role of deer abundance in the rarity of adult ticks on Fire Island suggests an alternative hypothesis. Perhaps immature *I. scapularis* are difficult to collect in the southeast because hosts for immature ticks are far more abundant there than in the north. For example, the importance of lizards as hosts for this species in the south is well documented, but the ranges of these lizard species do not extend into the northern states. Questing immature *I. scapularis* might be hard to find in southern states because most of them find hosts more quickly than in the north.

Our results also sound a cautionary note about the use of flagging samples to get relative estimates of tick population size (Ginsberg and Ewing 1989b, Solberg et al. 1992, Li and Dunley 1998). Flagging can give valuable estimates of relative densities of questing ticks, but the proportion of the tick population quest-

ing can vary dramatically between sites that differ in the abundance of vertebrate tick hosts.

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