

Temporal and Spatial Dynamics of *Ixodes scapularis* (Acari: Ixodidae) in a Rural Landscape

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ABSTRACT We studied seasonal, interannual, and both small- and large-scale spatial variation in the abundance of blacklegged ticks, *Ixodes scapularis* Say, in a semirural landscape in southeastern New York. Using transect drag sampling, we found that ticks were approximately twice as abundant in 1994 as in the preceding 2 yr. In 1994, larval ticks showed a strong peak in activity in late spring, coincident with the nymphal peak that year. All post-egg life stages were more abundant in forested than in shrubby or herbaceous habitat types, but peak abundance of larvae shifted from oak-dominated forest in 1992 to maple-dominated forest in 1993 and 1994. All life stages were highly clumped at small spatial scales, but larvae were the most aggregated. Within the forested habitat types, we observed an initial increase followed by a decrease in small-scale clumping during seasonal activity for each life stage. We discuss potential effects of the observed temporal and spatial variation on risk of Lyme disease. Because of pronounced variation in abundance and activity patterns among years and habitat types, we caution against generalizing from short-term or spatially limited studies.

KEY WORDS Lyme disease, tick ecology, tick population dynamics, tick seasonal activity, tick spatial distribution

THE PREVALENCE OF Lyme disease is closely related to the phenology of ixodid tick life cycles (Fish 1993). The enzootic cycle of Lyme disease is facilitated when larval ticks become active later in the season than do nymphs from the prior generation. Under these conditions, nymphal ticks have an opportunity to infect hosts such as small mammals before larvae become active. Thus, larval ticks are more likely to acquire the disease agent, *Borrelia burgdorferi*, and then infect other hosts during subsequent blood meals (Spielman et al. 1985, Lane et al. 1991, Barbour and Fish 1993, Ginsberg 1993).

In addition to seasonal dynamics, both long-term temporal and spatial dynamics of tick abundance and activity may be important in Lyme disease risk. The geographical spread of *I. scapularis* in the eastern United States has been accompanied by steady increases in tick density immediately after establishment (Ginsberg 1993). However, little attention has been paid to fluctuations in tick numbers over time within established Lyme disease endemic areas. Several researchers have documented variation in tick abundance among habitat types within different Lyme disease foci in the northeastern United States (Ginsberg and Ewing 1989, Adler et al. 1992, Stafford and Magnarelli 1993, Duffy et al. 1994, Ostfeld et al. 1995), but in most cases it is not known whether the distribution of

ticks among habitat types remains constant, or is variable among years.

We report on a 3-yr study of *I. scapularis* abundance and activity patterns in a rural landscape in Dutchess County, southeastern New York. Dense populations of *I. scapularis* were detected at our field site in 1984 (R. Winchcombe, unpublished data), and thus populations have been established for at least 1 decade. We focus on 2 scales of temporal variation in tick abundance: seasonal and multiannual; as well as 2 scales of spatial variation: large scale (≥ 1 ha) and small scale (tens of meters). We apply our results to further understanding temporal and spatial variability in Lyme disease risk.

Materials and Methods

Study Site. Tick sampling was performed at the Mary Flagler Cary Arboretum (MFCA) in Dutchess County, southeastern New York (41° 50' N, 73° 45' W). The MFCA consists of ≈ 325 ha of discontinuous patches of closed forest and ≈ 500 ha of various ages of successional oldfields and ornamental plots (Glitzenstein et al. 1990). We chose 5 habitat types to represent the most common, distinct plant community types in postagricultural landscapes of the northeastern United States. Two habitat types (maple and oak) are forested. The maple habitat type consists of young (60–80 yr old), relatively even-aged stands of sugar maple, *Acer saccharum* Marshall, which developed following abandonment of cultivated fields. The dominant canopy

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trees in the oak habitat type are 80 to 130-yr-old chestnut oaks, *Quercus prinus* L., and red oaks, *Q. rubra* L. The Dogwood habitat consists of dense thickets of grey dogwood, *Cornus racemosa* Lam., shrubs. The Bluestem habitat is dominated by little bluestem grass, *Schizachyrium scoparium* (Michaux), but at the time of the study, was being invaded by grey dogwood. Finally, the Hayfield habitat type consists of lowland fields dominated by the grasses *Bromus inermis* Leysser, *Phleum pratense* L., *Poa pratensis* L., and *Arrhenatherum elatius* (L.), and bedstraw, *Galium mollugo* L. More thorough descriptions of the habitat types are presented in Ostfeld et al. (1995).

Transect Drag Sampling. We used transect drag sampling to estimate the relative abundance of host-seeking ticks (Falco and Fish 1992). We sampled in 3 replicate sites of each habitat type. Replicates of any given habitat type were separated by 100–2,500 m. At each site we established a set of parallel line transects totaling 400 m. Transects were 10 m apart, and varied from 40 to 100 m in length.

We used a 1-m² piece of white corduroy cloth sewn at one end to a wooden dowel for support, and weighted at the opposite, free end by small lead weights sewn into the cloth. In 1993 and 1994 the drag cloth was examined every 20 m along transects. Ticks also were removed from the investigator's clothing. In the 1st yr of the study (1992), all ticks collected were removed with fine forceps and preserved in 70% ethanol for later identification. Because >99% of ticks collected were *I. scapularis*, we removed but did not preserve ticks in 1993 or 1994.

We sampled tick abundance at regular intervals from summer 1992 through autumn 1994. We conducted 5, 7, and 14 sampling periods in 1992, 1993, and 1994, respectively. For each sampling period, all transects were dragged within a 10-d period. Because of the weather, 1 sampling period lasted 15 d. All drag sampling was performed between 1000 and 1600 hours and was not performed on rainy days, or when vegetation was wet.

Statistical Analysis. We analyzed variation in tick abundance seasonally, among years, within transects, and among habitat types. We used chi-square analysis to determine whether annual peak densities of ticks within a habitat type varied among years. To test whether tick densities varied among habitat types, we used repeated measures analysis of variance (ANOVA) with tick density as the dependent variable and habitat type and time as the independent variables. Tests were performed for each year separately. To test whether ticks were distributed uniformly, randomly, or in aggregations, we calculated an index of dispersion (variance/mean ratio) based on tick counts for each 20-m length of the drag transects. We then tested whether observed distributions differed significantly from the expectation of a random distribution using chi-square goodness of fit tests. These

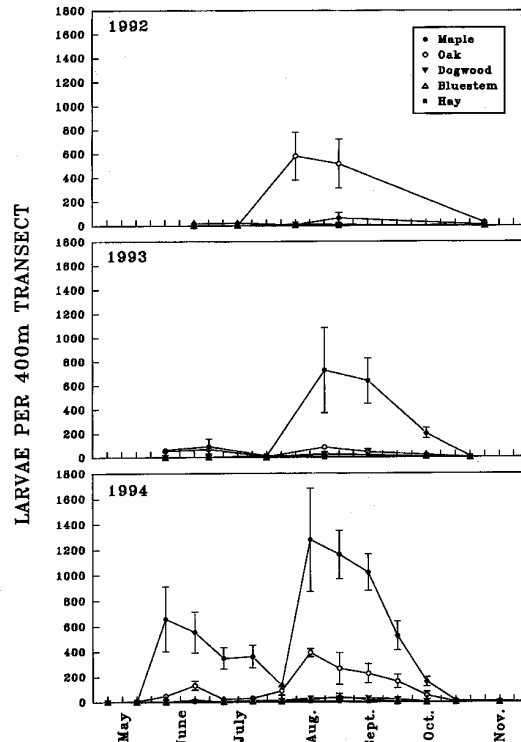


Fig. 1. Densities of questing larval *I. scapularis* in 5 habitat types at the Institute of Ecosystem Studies in Dutchess County, southeastern New York. Symbols show means (± 1 SE) of 3 replicate sites for each habitat type.

tests are inherently conservative because of low power to detect aggregations at a scale <20 m.

Results

Temporal Dynamics. Our data generally confirmed previous observations of activity peaks in midsummer for larvae, late spring to early summer for nymphs, and autumn and spring for adults (Figs. 1–3; Main et al. 1982, compare Fish 1993). However, there were several notable exceptions to this general pattern. First, larval *I. scapularis* showed a bimodal activity peak in 1994 that was much more extreme than in the other sampling years. Density of questing larval ticks reached 1.65 m^{-2} (± 0.64 [SE]) in late May 1994, quite similar in magnitude to the more typical midsummer peaks observed in 1992 and 1993 (Fig. 1). Second, although in all 3 yr nymphs reached peaks in late June to early July, they remained abundant ≈ 1 mo longer in 1994 (through September) than in 1992 or 1993 (Fig. 2). Third, adult ticks were undetectable in June and July of 1992, but showed considerable activity in spring through early summer of both 1993 and 1994 (Fig. 3).

Throughout the landscape, ticks were more abundant in 1994 than in the other 2 yr. Larvae

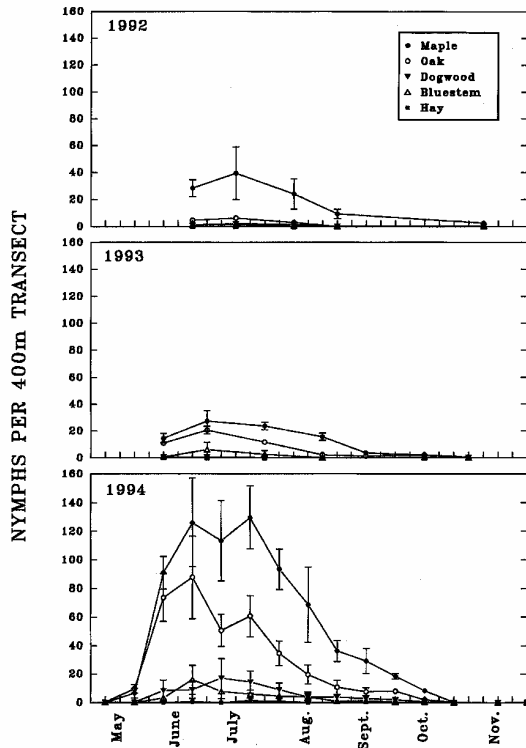


Fig. 2. Densities of questing nymphal *I. scapularis* in 5 habitat types at the Institute of Ecosystem Studies in Dutchess County, southeastern New York. Symbols show means (± 1 SE) of 3 replicate sites for each habitat type.

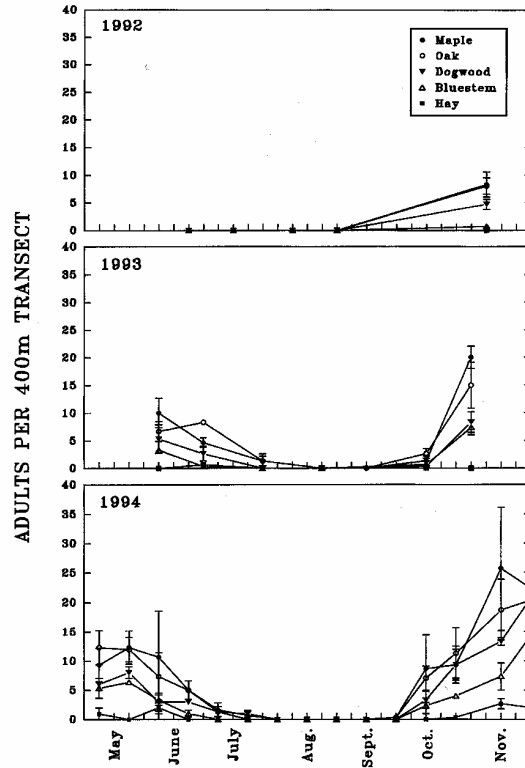


Fig. 3. Densities of questing adult *I. scapularis* in 5 habitat types at the Institute of Ecosystem Studies in Dutchess County, southeastern New York. Symbols show means (± 1 SE) of 3 replicate sites for each habitat type.

were approximately twice as abundant during the 1994 midsummer peak ($3.20 \text{ m}^{-2} [\pm 1.02]$ in maple habitat) than during the 1992 or 1993 peaks ($1.45 \text{ m}^{-2} [\pm 0.50]$ in oak and $1.82 \text{ m}^{-2} [\pm 0.89]$ in maple habitat, respectively) (Fig. 1). Nymphs were ≈ 3 -fold more abundant during the peak of 1994 than in either of the previous 2 yr (totals for maple, 1994: $0.32 \text{ m}^{-2} [\pm 0.08]$; 1993: $0.07 \text{ m}^{-2} [\pm 0.02]$; 1992: $0.10 \text{ m}^{-2} \pm 0.05$; Fig. 2). Chi-square analysis of larvae and nymphs demonstrated significant variation among years in peak juvenile

tick abundance both in maple ($\chi^2 = 141.5$, $df = 2$, $P < 0.0001$) and in oak ($\chi^2 = 81.04$, $df = 2$, $P < 0.0001$) habitat types. Adults could not be similarly analyzed due to the truncation of our sampling effort in autumn.

Spatial Dynamics. In all years and for all post-egg life stages, variation among habitat types in tick abundance was statistically significant (Table 1). All 3 life stages of ticks were more abundant in forested than in nonforested habitat types in all 3 yr

Table 1. Results of repeated measures ANOVA for tick abundance across the 5 different habitat types

Year	Life stage	F	P	Rank order of abundance
1992	Larvae	9.78	0.002	Oak ¹ > Maple ² = Dogwood ² = Bluestem ² = Hayfield ²
	Nymphs	29.41	0.000	Maple ¹ > Oak ² = Dogwood ² = Bluestem ² = Hayfield ²
	Adults	8.91	0.003	Maple ¹ = Oak ¹ = Dogwood ^{1,2} = Bluestem ^{2,3} = Hayfield ^{2,3}
1993	Larvae	5.64	0.012	Maple ¹ > Oak ² = Bluestem ² = Dogwood ² = Hayfield ²
	Nymphs	22.21	0.000	Maple ¹ > Oak ² > Bluestem ³ = Dogwood ³ = Hayfield ³
	Adults	33.22	0.000	Maple ¹ = Oak ¹ > Dogwood ² = Bluestem ² > Hayfield ³
1994	Larvae	236.57	0.000	Maple ¹ > Oak ² > Dogwood ³ = Bluestem ³ = Hayfield ³
	Nymphs	15.21	0.000	Maple ¹ > Oak ² > Dogwood ³ = Bluestem ³ = Hayfield ³
	Adults	45.59	0.000	Maple ¹ = Oak ¹ > Dogwood ² > Bluestem ³ > Hayfield ⁴

Analyses were performed separately for each of the 3 yr of study. F and P values are shown for the independent variable habitat type ($df = 4$). Student-Newman-Keuls tests were used for a posteriori pairwise comparisons, where superscript numbers unite values that are not significantly different at the 0.05 level.

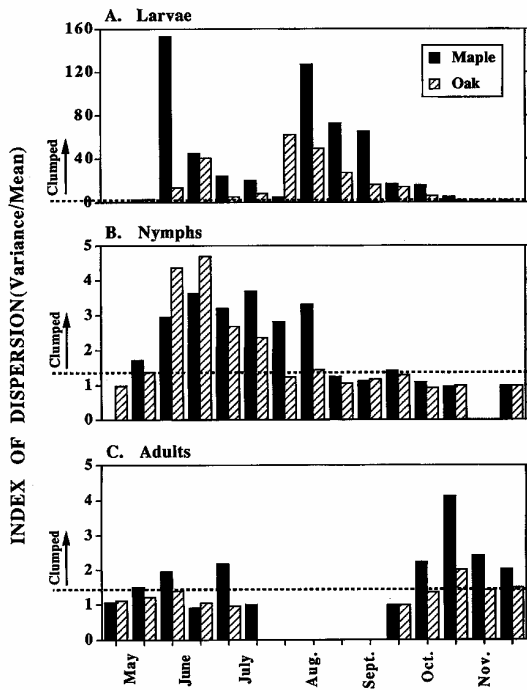


Fig. 4. Index of dispersion (variance/mean ratio) for the 3 post-egg life stages of *I. scapularis* in 1994. Bars represent means for each of the 2 habitat types of greatest tick abundance. Values above the dashed lines indicate distributions of ticks that were significantly aggregated (chi-square tests against the expectation of random distribution).

(Figs. 1–3). However, for larvae, annual peak density shifted from oak habitat in 1992 to maple patches in 1993 and 1994. Densities of nymphs were highest in maple in all 3 yr, although in 1993, peak density of nymphs was nearly as high in oak ($0.05 \text{ m}^{-2} [+0.01]$) as in maple ($0.07 \text{ m}^{-2} [\pm 0.02]$).

Both juvenile and adult ticks tended to be spatially clumped (Fig. 4). The degree of aggregation was most extreme for larvae, and was statistically significant in 13 of 14 sampling sessions during which larvae were active. For nymphs and adults, aggregation was statistically significant in about half of the sampling sessions (Fig. 4). For each life stage, seasonal peaks in activity were accompanied by increasing, then gradually decreasing degrees of aggregation (Fig. 4). All 3 life stages tended to be substantially more aggregated in maple than in oak habitat types (Fig. 4).

Discussion

Seasonal Dynamics. Our results indicate that seasonal dynamics of activity for *I. scapularis* may vary substantially among years. In 1993, we observed a modest, early (late May–early June) activ-

ity peak for larval ticks, similar to that observed in several localities in the northeastern United States (Main et al. 1982, Spielman 1986, Fish and Dowler 1989, Fish and Daniels 1990). Typically, this early peak reaches a level only about 10% of the main larval activity peak of midsummer (Fish 1993, Sonenshine 1993). In 1994, however, May–June larval density was $\approx 50\%$ of that during the midsummer peak, and May density was roughly equivalent to the annual peaks for the prior 2 yr. The origin of this large, early cohort of larval ticks is somewhat obscure, but it appears likely that it corresponds to an early spring peak in oviposition by adults that fed early the prior autumn. Controversy regarding whether *I. scapularis* shows a unimodal or bimodal activity peak (Sonenshine 1993) may be explained by interannual differences in tick phenology.

The early activity peak for larvae in 1994 resulted in substantial larval activity both preceding and during nymphal activity. We postulate that this unusual temporal pattern reduced the probability of the early cohort of larval ticks obtaining Lyme disease spirochetes. The principal reservoir for *B. burgdorferi* in the northeastern United States is the white-footed mouse, *Peromyscus leucopus* (Rafinesque) (Piesman and Spielman 1979; Donahue et al. 1987; Mather et al. 1989, 1990; Mather 1993). Because *P. leucopus* typically do not become infective to feeding ticks until ≈ 10 d after themselves becoming infected (Donahue et al. 1987), it is likely that a relatively low percentage of hosts parasitized by larval ticks in May and early June were infected with *B. burgdorferi*. Therefore, whatever the cause of the early activity peak, its effect may be to partially disrupt the enzootic cycle of spirochete transmission between vector and host. We hasten to add, however, that although the early activity peak in 1994 may have reduced the proportion of nymphs infected with *B. burgdorferi*, it may not have reduced the risk of Lyme disease, because of the high total number of nymphs that year.

Interannual Patch Dynamics. Although forested habitat types supported greater densities of ticks than did nonforested habitat types in all 3 yr (Figs. 1–3, Ostfeld et al. 1995), considerable variation existed between the oak and maple habitats. In 1992, larval ticks were most abundant in oak, but in 1993 and 1994, maple supported the highest larval densities. This observation indicates that abiotic conditions in forests per se cannot explain variation in tick density among patch types. Elsewhere (Ostfeld et al. 1995), we have postulated that the spatial pattern of larval abundance in summer is caused by activity patterns of white-tailed deer, *Odocoileus virginianus* (Boddaert), the prior autumn (Wilson et al. 1985). Deer are the principal host for adult *I. scapularis* and the site of mating and fertilization (Anderson and Magnarelli 1980, Spielman et al. 1985, Wilson et al. 1985). Thus, the locations of oviposition, and thus of larval ag-

gregations, will be determined by the activity patterns of deer the prior autumn. White-tailed deer concentrate activity in oak-dominated forest stands when acorns are available (McShea and Schwede 1993), which occurs only every several years because of masting behavior (Janzen 1971, Silvertown 1980, Sork et al. 1993). In years of poor acorn production, deer use nonoak habitat types more intensively than in mast years. We believe that the heavy acorn production observed at our study site in 1991 (Ostfeld et al. 1995) caused the irruption of larval ticks in oak sites in 1992. We postulate that poor acorn production in 1992 and 1993 caused the relatively low densities of larval ticks in oak sites in 1993 and 1994.

Nevertheless, although the relative abundance of ticks in different habitat patches may be determined by acorn abundance the prior year, the absolute abundance of ticks in the landscape is not. Ticks were significantly more abundant, and active for longer periods, in nearly all habitat types in 1994 than 1992 or 1993. We suspect that abiotic conditions supported higher survivorship in 1994, but we cannot identify the conditions that resulted in higher density across the landscape.

One possible explanation for high abundance of questing ticks in 1994 is the unusually low abundance of white footed mice, *Peromyscus leucopus*, we observed that year at our study site (Ostfeld et al. 1996b). Low density of white-footed mice in 1994 may have resulted in a high proportion of ticks that had not found hosts, and which consequently were collected during our drag sampling. However, the following evidence suggests that low mouse density had only a modest effect on abundance of questing ticks. First, abundances of both larvae and nymphs were higher in 1994 than in other years, but nymphal *I. scapularis* are much less frequent on mice (Main et al. 1982), and probably less dependent on mouse density, than are larvae. Second, although the total proportion of ticks successfully attaching to white-footed mice increases with increasing mouse density, per capita tick burdens are higher at low mouse density (Ostfeld et al. 1996a). Thus, the tick population partially compensates for low mouse density by parasitizing mice in greater numbers per mouse.

Small-Scale Spatial Dynamics. We found that all 3 post-egg stages were spatially clumped at the level of resolution of 20-m segments of transect. We also found that the degree of aggregation increased early in the activity season to a peak at peak density, and then declined gradually throughout the remainder of the activity season. Previous studies of the distribution of larval *I. scapularis* showed clumping was extreme early in the activity season, and then declined through time (Daniels and Fish 1990, Stafford 1992). Daniels and Fish (1990) argued that the high variance/mean ratio observed early in the activity season resulted from newly hatched larvae remaining near the egg mass, and that the declining degree of aggregation was

caused by gradual disappearance and dispersal of larvae. The increasing degree of aggregation we observed early in the season may have resulted from an extended season of hatching and consequent gradual appearance of larvae in clusters. The cause(s) of the greater degree of clumping in maple than in oak habitat is unknown.

We expected that, due to host dispersal of juvenile ticks, distributions of nymphs and adults would be random rather than clumped. We postulate that the clumped distribution of nymphs and adults was caused by either synchronous detachment of fed ticks from hosts, resulting in clusters of newly molted individuals, or to orientation by ticks to limited, favorable microsites for seeking hosts.

In conclusion, substantial variation in abundance and activity of *I. scapularis* occurred at several different spatial and temporal scales at our study site in southeastern New York. These results challenge conclusions drawn from studies limited to a single year or habitat type, and suggest that risk of Lyme disease cannot be predicted accurately without more extensive data sets. Unfortunately, in some cases we were unable to determine the cause of the observed variation in space or time. We believe that a combination of long-term monitoring of tick populations and field experiments will lead to a predictive understanding of tick dynamics and Lyme disease risk.

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