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POPULATION ECOLOGY

Woodland Type and Spatial Distribution of Nymphal
Ixodes scapularis (Acari: Ixodidae)

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ABSTRACT   Spatial distribution patterns of black-legged ticks, *Ixodes scapularis*, in deciduous and coniferous woodlands were studied by sampling ticks in different woodland types and at sites from which deer had been excluded and by quantifying movement patterns of tick host animals (mammals and birds) at the Lighthouse Tract, Fire Island, NY, from 1994 to 2000. Densities of nymphal ticks were greater in deciduous than coniferous woods in 3 of 7 yr. Only engorged ticks survived the winter, and overwintering survival of engorged larvae in experimental enclosures did not differ between deciduous and coniferous woods. Nymphs were not always most abundant in the same forest type as they had been as larvae, and the habitat shift between life stages differed in direction in different years. Therefore, forest type by itself did not account for tick distribution patterns. Nymphal densities were lower where deer had been excluded compared with areas with deer present for 3 yr after exclusion, suggesting that movement patterns of vertebrate hosts influenced tick distribution, but nymphal densities increased dramatically in one of the enclosures in the fourth year. Therefore, movements of ticks on animal hosts apparently contribute substantially to tick spatial distribution among woodland types, but the factor(s) that determine spatial distribution of nymphal *I. scapularis* shift from year to year.

KEY WORDS   *Ixodes scapularis*, spatial distribution, survival, habitat distribution

LYME DISEASE IS TRANSMITTED to humans by black-legged ticks, *Ixodes scapularis* Say (northern populations formerly called deer ticks, *I. dammini*; Spielman et al. 1979, Oliver et al. 1993), most commonly during the nymphal stage (Fish 1993). Nymphs dwell in leaf litter and ground level vegetation and are far more common in closed canopy woods than in open habitats or lawns (Ginsberg and Ewing 1989, Maupin et al. 1991, Siegel et al. 1991). This distributional pattern results, in part, from increased nymphal survival in the woods (Ginsberg and Zhioua 1996), presumably because of protection from desiccation in the moist leaf litter.

Nymphal abundance apparently also differs in different forest types, but results have been inconsistent, with some studies showing greater abundance in deciduous woods (Ginsberg and Zhioua 1996) and others showing greater abundance in coniferous forests (Lord et al. 1992, Lord 1995). Similarly, results of survival studies have been inconsistent, with differential nymphal survival in different habitats in some studies, but not others (Bertrand and Wilson 1996, 1997, Ginsberg and Zhioua 1996).

Two additional factors (other than nymphal survival) that might contribute to the observed habitat distribution patterns of nymphs are movement patterns of larvae between habitats on hosts (Ostfeld et al. 1995) and differential mortality of overwintering larvae in different habitats. The importance of these two phenomena in tick distribution is directly relevant to current hypotheses about tick population regulation. For example, the hypothesis that tick populations are regulated by deer population size (Spielman et al. 1985, Wilson et al. 1990, Deblinger et al. 1993) implies that deer distribution influences tick distribution. The hypothesis that tick populations increase after mast years in oak forests (Ostfeld 1997, Jones et al. 1998) depends on tick movement on hosts as a major determinant of tick distribution. Therefore, the factors that influence tick habitat distribution are central to an understanding of tick abundance patterns.

In this paper, we describe the distribution of nymphal ticks in different woodland types at the

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Lighthouse Tract of Fire Island, NY, and report the results of host movement and larval overwintering mortality studies that assess the contributions of these factors to tick distribution patterns.

Materials and Methods

Study Site. Fire Island is a 55-km-long barrier island off the south shore of Long Island, NY. The Lighthouse Tract is a natural area that includes meadows of beach grass (*Ammophila breviligulata* Fernald) and low beach plum (*Prunus maritima* Marshall), with thickets of bayberry (*Myrica pensylvanica* Mirbel) and poison ivy (*Toxicodendron radicans* L. Kuntze) that grade into maritime woodlands, consisting mostly of high-bush blueberry (*Vaccinium corymbosum* L.), choke-berry (*Aronia arbutifolia* L. Elliott), and American holly (*Ilex opaca* Aiton). These are interspersed with coniferous woods consisting largely of pitch pine (*Pinus rigida* Miller), with abundant poison ivy and catbrier (*Smilax rotundifolia* L.) beneath the canopy. The vegetation of Fire Island is described in detail by Art (1976), Stalter et al. (1986), and Dowhan and Rozsa (1989).

Common mammals include whitetail deer (*Odocoileus virginianus* Zimmermann), Eastern cottontail rabbits (*Sylvilagus floridanus* Allen), white-footed mice (*Peromyscus leucopus* Rafinesque), meadow jumping mice (*Zapus hudsonius* Zimmermann), and meadow voles (*Microtus pennsylvanicus* Ord), and intermittently, small numbers of red fox (*Vulpes vulpes* L.) and raccoons (*Procyon lotor* L.). The most common resident birds are gray catbirds (*Dumetella carolinensis* L.) and Eastern towhees (*Pipilo erythrophthalmus* L.), with smaller numbers of song sparrows [*Melospiza melodia* (Wilson)], yellow warblers (*Dendroica petechia* L.), and common yellowthroats (*Geothlypis trichas* L.). In addition, large numbers of migratory birds pass through the area (some stopping over to feed before moving on) in spring and late summer/fall, numbering well over 100 species (P.A.B. and F.G.B., unpublished data).

As part of a mist netting study of neotropical migratory birds, two deer exclosures were built at the site in 1995. These mist netting lanes were surrounded by game fencing (Gaucho Game Fence; Bekaert, Van Buren, AR) with three high tension wires above the fence to a height of 2.4 m. The game fencing was erected with large mesh near the ground (see Ginsberg and Zhioua 1999) to allow easy passage of all animals except adult deer. The eastern exclosure (1.23 ha) included a deciduous thicket, whereas the western exclosure (0.95 ha) contained pitch pine woods. Unfenced coniferous and deciduous control sites were located outside and near to each exclosure site (total of six sample sites).

Tick Samples. Nymphal ticks were sampled from deciduous and coniferous woods using a 1 by 0.5-m white pinwale corduroy flag. Samples taken for yearly comparisons of habitat distribution included 15 flagging runs (1 min each) in each of the six sample sites (one site in each exclosure, plus a deciduous and

coniferous control site outside of each exclosure; total of 90 flagging runs for each yearly sample). The yearly samples were taken (by H.S.G.) during periods of peak nymphal activity, based on previous experience on Fire Island (Ginsberg and Ewing 1989, Ginsberg 1992) and on preliminary observations each year. Nymphs were sampled on 22–23 June 1994, 16–17 June 1995, 9–11 June 1996, 16 June–7 July 1997, 22–29 June 1998, 27–28 June 1999, and 3 July 2000 (in 2000, 10 samples/site for total of 60 samples). Additional details about the sampling methods are given by Ginsberg and Zhioua (1996). Nymphal densities were analyzed each year using a three-way analysis of variance (ANOVA) comparing forest type (deciduous versus coniferous) × presence of deer (inside versus outside enclosures) × location (east versus west) (SYSTAT, subprogram MGLH; Wilkinson et al. 1992). The data were transformed by $\ln(x + 1)$ to minimize trends in residuals.

To make sure that apparent differences in tick abundance in deciduous and coniferous woods did not result from different nymphal phenologies in the different habitats, nymphal phenology was studied in both forest types. Phenology samples were taken weekly (every other week during periods of low tick abundance) from 30 May to 30 August 1996 and 23 May to 23 September 1997. Ticks collected in these samples (taken by J.F.) were counted and released. Weekly samples during periods of high tick abundance in 1996 (4 June–17 July) and all samples in 1997 consisted of ten 1-min flagging runs, taken in each of the six sample sites (total of 60 flagging runs in each sample). The 30 May 1996 samples consisted of six flagging runs at each site (total of 36 runs), and the late-season 1996 samples (25 July–30 August) consisted of five flagging runs at each site (total of 30 runs for each sample).

Larvae were also sampled by flagging each year from 1994 to 1998. Samples were taken on 2–4 August 1994, 1–3 August 1995, 5–11 August 1996, 4–10 August 1997, and 5–9 August 1998. Larval samples consisted of 15 flagging samples, 1 min each, taken (by H.S.G.) with the 0.5-m^2 flag at each of the six sample sites (total = 90 samples). Larvae were collected and returned to the laboratory for identification. In samples with large numbers of larvae (one 1-min sample had over 900 larvae), the ticks were counted, and grab samples were collected for identification in the laboratory.

Larval Overwintering Survival. Free-living larvae were collected from the Fire Island Lighthouse Tract during August 1996 and returned to the laboratory at the University of Rhode Island, where they were re-refrigerated in vials with screened caps inside sealed plastic bags with moist paper toweling to maintain high humidity. A subset of the larvae was placed on laboratory-reared white footed mice, *Peromyscus leucopus*, allowed to engorge and drop off, and refrigerated as above. The larvae were placed in the toe ends of off-white stockings (No Nonsense, sheer-to-waist pantyhose, M58, Off White Sandalfoot; Kayser Roth, Burlington, NC), which were cut off at calf level, with the ends folded over and sealed with a clip. Stockings

were returned to Fire Island in a cooler with blue ice and were placed in the woods in pairs, one stocking with flat larvae and one with engorged larvae. Each pair was secured to the ground with a marking stake placed through holes in the clips, and the stockings were covered with leaf litter. Ten pairs were placed in deciduous and coniferous woods on 19 September, and eight pairs were placed on 26 September 1996.

Three sample sites with adjacent deciduous and coniferous woods were selected from the Lighthouse Tract. The entire area was surveyed for suitable sites (sites with adjacent patches of deciduous and coniferous woods), and one site each was selected at random from the eastern, central, and western portions of the Lighthouse Tract (total of three paired sites). Three sets of stockings (one with flat and one with engorged larvae) were placed in deciduous woods and three in coniferous woods at each site (total of 18 stockings with flat larvae in pairs with 18 stockings with engorged larvae). There were 10 larvae in each stocking (total of 180 flat larvae and 180 engorged larvae). The stockings were collected, and the larvae were examined for survival on 27 May 1997. Survival and percent molting were compared between deciduous and coniferous woods using Yates-corrected χ^2 tests (SYSTAT, subprogram tables; Wilkinson et al. 1992).

Mouse Samples. Small mammals were captured in Sherman collapsible traps (22.9 by 8.3 by 7.6 cm) that were placed in two trapping webs located in the eastern and western portions of the study area. Each trapping web consisted of 208 traps radiating from a central point, with 13 traps in each of 16 radial arms. Traps were placed 5.5 m apart, and the predominant vegetation type in the vicinity of each trap was recorded.

Traps were set at dusk with 5–10 g of bait along with polyester stuffing. The bait was a 6:2:1 mixture of peanut butter, quick oats, and paraffin wax. A trap night is defined as one trap set for 12 h that contained an animal or was unsprung. Traps that were sprung without a capture were not counted. Each captured animal was identified, sexed, and weighed, and ticks on the ears and muzzle were counted and removed. Mice were fitted with individually numbered metal ear tags (size 0) and released at the site of capture.

Bird Samples. Migrating and resident landbirds were sampled year-round from 1 August 1995 to 31 December 1998 in the two fenced, deer-proof exclosures. The western (coniferous) exclosure had three parallel N-S lanes supporting, respectively, 3, 6, and 4 12-m-long, four-shelf, 3-m high, 36-mm mesh nylon mistnets. The eastern (deciduous) exclosure was a single, long N-S lane of 16 nets. Whenever possible, both substations were run simultaneously from first light for 5 h every day of the year, weather permitting. If adequate staff was unavailable, operation of East and West was alternated daily.

Nets were constantly checked for birds, and for every unbanded bird captured, data were taken on the substation, lane, net, side, shelf, time, species, sex, and age (when possible); birds were then removed from the nets and brought to a workshed for processing. There, species, age, and sex were determined or confirmed, and birds were weighed, coded for fat class, measured (normally only wing-chord and tail), and examined for ticks. Any ticks present were removed and placed in labeled, humidified vials for subsequent identification or laboratory use (previously banded birds had their band numbers recorded before removal from nets, and all were brought back to the workshed for band number reconfirmation). All birds were banded and released out the same window in each substation workshed after their numbers were recorded.

Movement of birds between enclosures was quantified by estimating the proportion of banded birds that were checked for ticks at one exclosure that moved to the other exclosure during the month of August (the peak of larval tick activity). We used a Peterson estimation method that was developed for geographically stratified data by Chapman and Junge (1956) and Darroch (1961) and expanded by Seber (1982). Maximum-likelihood estimates of the degree of movement between sites (Seber 1982, Ginsberg 1986) are given by the following: $b_{ij} = m_{ij}/(a_i P_j)$, where b_{ij} = probability that a bird marked at site i moves to site j; m_{ij} = number of birds marked at site i that were recaptured at site j; a_i = number of birds marked at site i; and P_j = probability of capturing a bird at site j if it is present there. Initial estimates of the individual P_j's were uninterpretable, so sites were combined (as suggested by Seber 1982), and an overall value of P_{LH} was estimated for the entire Lighthouse Tract by dividing the total number of recaptures in August by the total number marked (or released with a previous mark) during July and August: $P_{LH} = \Sigma m_{ij}/\Sigma a_k$.

Results

Densities of nymphal *I. scapularis* in deciduous and coniferous woods from 1994 to 2000 are given in Fig. 1A. Tick densities were higher in deciduous than in coniferous woods in 1994 ($F = 7.786$, df = 1,85, $P = 0.0065$), 1995 ($F = 19.194$, df = 1,85, $P = 0.00003$), and 2000 ($F = 6.043$, df = 1,55, $P = 0.017$), but not in other years ($P > 0.05$ in all cases). Phenologies of nymphal ticks are shown in Fig. 2. The peak of nymphal activity occurred at the same time in deciduous as in coniferous woods in both 1996 and 1997.

Overwintering survival of engorged larvae is given in Table 1. None of the flat larvae survived the winter. Survival of engorged larvae was the same in deciduous as in coniferous habitat, as was percent molting to the nymphal stage.

Habitat distribution of larval ticks in late summer is compared with the distribution of the same cohort of ticks as nymphs the following spring in Fig. 3. The habitat distribution shifted from larval to nymphal stages in different directions in different years. In some years, the net shift was toward deciduous habitats; in other years, the shift was toward coniferous habitats.
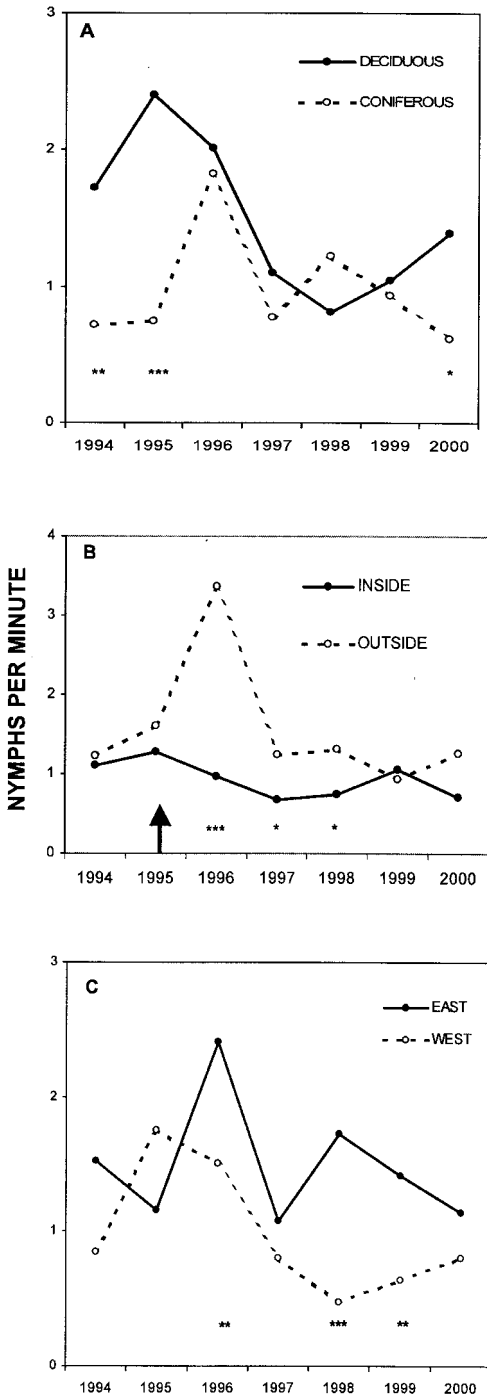
Fig. 1. Distribution of nymphal *I. scapularis* at the Fire Island Lighthouse Tract. Significant differences between categories are indicated for each year (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Arrow indicates year enclosures were built. (A) Distribution in deciduous and coniferous woods. (B) Distribution inside and outside of deer exclosures. (C) Distribution in eastern and western sample sites.

Movement of *P. leucopus* between habitat types was assessed in two ways. First, mouse abundance in each habitat type was recorded as the number of mice captured per trap night in each habitat. If mice are more abundant in a given habitat type, they would return to that habitat after foraging trips, presumably carrying ticks into their nesting habitat. The numbers of mice collected per trap night in deciduous versus coniferous woods are shown in Table 2. Mouse numbers were comparable in the two wooded habitats. Certainly, mice were not consistently more abundant in deciduous woods. Mice were also marked with ear tags and recaptured, and the habitats of the release and recapture trap sites were recorded. Movement patterns of mice (Table 3) showed most moves occurred between traps in the same habitat. Moves between habitats showed no consistent directionality favoring one forest type over the other.

The possible role of deer in tick movements can be assessed by examining trends in tick densities in the mist netting areas from which the deer had been excluded (Fig. 1B). Nymphal densities were the same in the mist netting areas as in the control sites before the fences were installed. However, after deer were excluded (fences were built during the summer of 1995), nymphal densities declined inside the enclosures relative to the outside control sites. In 1999, 3 yr after deer exclusion, nymphal densities did not differ significantly between sites with and without deer, primarily because of a dramatic increase in tick densities in the eastern (deciduous) exclosure. The number of nymphs per 1-min sample differed significantly among sites in 1999 ($F = 7.928$, df $= 5,84$, $P = 0.000004$), with highest numbers in the deciduous exclosure (back-transformed means, 2.660 nymphs/min). Back-transformed means at the other sites were 0.149 nymphs/min in the coniferous exclosure, 0.644 and 0.676 nymphs/min in the deciduous sites with deer, and 1.340 and 1.149 nymphs/min in the coniferous sites with deer.

The number of birds captured per 100 net h was slightly greater in the eastern (deciduous) site than in the western (coniferous) site (Table 4). However, more larval ticks were collected from birds in the western than in the eastern exclosure (1996; eastern exclosure = 10.56 ticks per 100 net h, western exclosure = 60.92 ticks per 100 net h). Directional movement of recaptured birds is shown in Table 5. The values of P_{LH} are undoubtedly underestimates of the probabilities of capture for resident birds, because they include data from several species that were not residents and were just passing through. However, this bias is the same at both eastern and western exclosures, and therefore, does not influence the relative magnitudes of the estimates of b_{ij}. The birds showed a strong directional bias in movement between exclosures, with a higher proportion of birds moving from the western to the eastern exclosure than vice versa in 1996, 1997, and 1998. Nymphal tick abundance in eastern versus western sample sites showed a corresponding skew (Fig. 1C), with significantly higher densities in eastern than western sites in 1998 ($F = 29.226$, df $=$
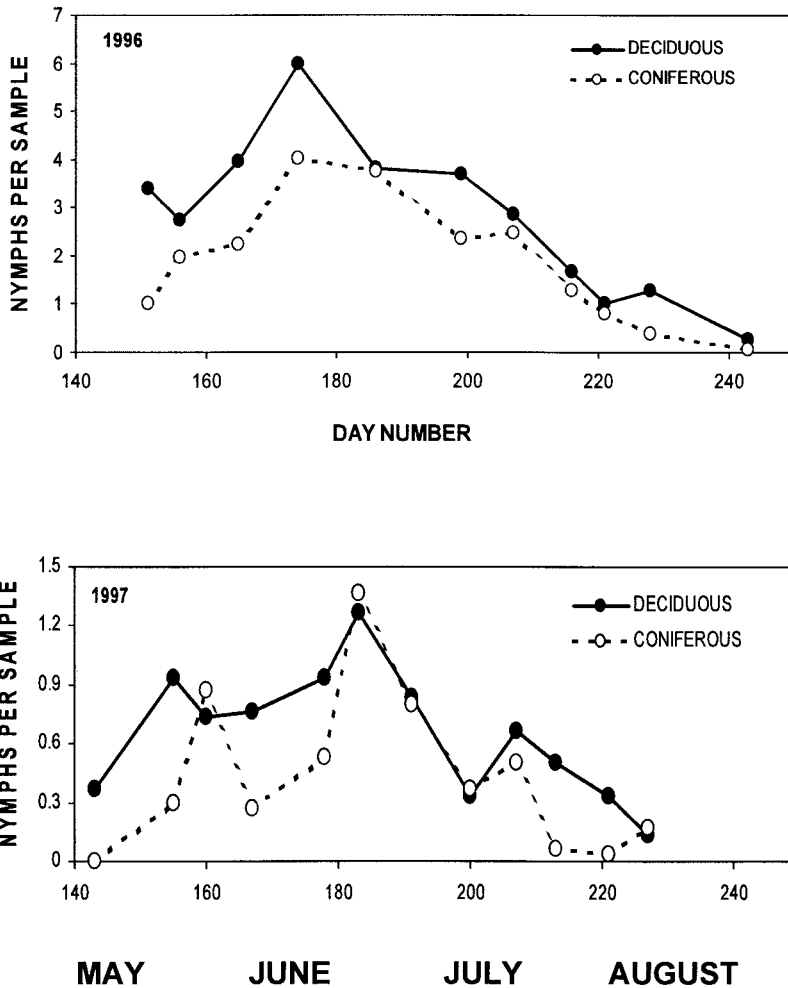
Fig. 2. Phenology of nymphal *I. scapularis* in deciduous and coniferous habitats, Fire Island Lighthouse Tract.

1,85, $P = 0.00000058$) and 1999 ($F = 8.122$, df $= 1,86$, $P = 0.005$).

Discussion

Several factors can potentially influence tick spatial distribution, including patterns of tick natality and mortality at different sites and movement patterns of ticks or of their vertebrate hosts (Fish 1993, Ostfeld et al. 1995). Survival experiments indicate that the

Table 1. Overwintering survival of engorged *I. scapularis* larvae in deciduous and coniferous woods, Fire Island Lighthouse Tract, 1996–1997

	Deciduous	Coniferous	χ^{2a}	P
Percent surviving (N)	31.1 (90)	26.7 (90)	0.243	0.622
Percent molting (N)	70.0 (60)	73.8 (61)	0.0671	0.796

[a] Yates-corrected χ^2, df = 1.

greater abundance of *I. scapularis* nymphs in closed canopy woodlands compared with open habitats results, at least in part, from higher mortality in the unprotected open habitats than in the woods (Ginsberg and Zhioua 1996). However, survival in different woodland types did not differ consistently in different trials.

In this study, relative tick abundance in different woodland types did not differ consistently from year to year for either larvae or nymphs (Figs. 1A and 3). Furthermore, our field experiment showed no difference in larval overwintering survival between deciduous and coniferous woods on Fire Island (Table 1). Thus, although habitat physiognomy clearly influences tick survival, woodland type did not consistently affect tick distribution. When densities differed significantly between woodland types, nymphs were always more abundant in deciduous woods, but proportional abundance in deciduous woods sometimes declined from the larval to nymphal stages. Thus, the
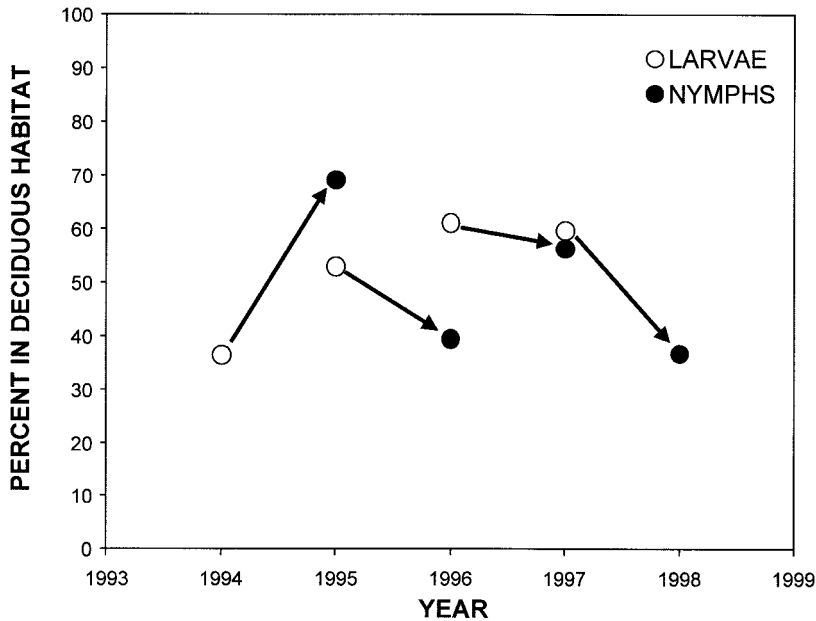
Fig. 3. Shifts in habitat distribution of *I. scapularis* from the larval to the nymphal stage.

effect of woodland type on tick distribution varied from year to year.

Nymphal densities differed significantly between deciduous and coniferous woods in some years and not others (Fig. 1A). These results are similar to those of Schulze et al. (2001), who found that tick densities differed in different woodland types, but that the differences were inconsistent from year to year and from site to site. Similarly, abundances differed significantly between sites with deer and sites from which deer had been excluded and between eastern and western sites on the Lighthouse Tract in some years and not others (Fig. 1B and C). Finally, changes in the habitat distribution of ticks between the larval and nymphal stages differed in direction in different years, with ticks shifting from coniferous to deciduous habitats in some years and in the other direction or not at all in other years (Fig. 3). Therefore, the factors that determine spatial distribution of nymphal ticks change from year to year. This could result either from different factors determining tick distribution in different years or from a single factor or suite of factors determining tick distribution, which themselves change from year to year. Woodland type does not change on a yearly basis, so deciduousness or coniferousness per se is not the primary factor influencing spatial distribution of nymphal *I. scapularis* in wood-

lands on Fire Island. In contrast, movement patterns of host animals, in aggregate, can shift from year to year. For example, in 1997, *P. leucopus* populations were far lower than usual (J.F., unpublished data), so a higher than normal proportion of larval ticks was on other mammals and on birds that year. The different movement patterns of these other vertebrate species relative to *P. leucopus* could have influenced nymphal distribution.

The best direct evidence we have of the role of host animal movements in tick distribution comes from our deer exclosure data. When deer were excluded, tick numbers declined for 3 yr relative to control sites where deer were still present (Fig. 1B). These results corroborate the role of deer in tick distribution surmised from similarities in microgeographic distribution by Wilson et al. (1990). However, tick populations increased in the deciduous exclosure and did not differ inside from outside of the enclosures in 1999. Again, this result suggests that deer abundance alone does not determine nymphal distribution (although it seems to contribute) and that determining factors for tick spatial distribution differ in different years. Of course, the relatively small size of the deer exclosures (≈1 ha each) might have allowed abundant movement of immature ticks into the exclosures on small animals, thus obscuring the effects of deer movements (which

Table 2. Number of mice collected per trap night in different habitats

Year	Deciduous woods	Coniferous woods	Open habitats
1996	0.04	0.043	0.018
1997	0.049	0.071	0.044

Table 3. Number of mice recaptured moving among habitat types

Year	Within same habitat	Deciduous to coniferous	Coniferous to deciduous
1996	18	1	3
1997	41	13	11

Table 4. Distribution of mist-netted birds (birds per 100 net h) in August at the Fire Island Lighthouse Tract

Year	Deciduous exclosure	Coniferous exclosure
1996	70.37	43.13
1997	56.41	35.11

might have had a more consistent effect in a larger area). Nevertheless, similar fluctuations in nymphal tick numbers were observed in a long-term deer reduction study at the Crane Reservation in Massachusetts (Deblinger et al. 1993).

The importance of deer in tick distribution was also posited by Ostfeld (1997) and Jones et al. (1998), who proposed that acorn abundance during oak mast years attracted deer into oak forests, resulting in increased densities of larval ticks in the year after an oak mast year and increased nymphal densities the next year (Ostfeld et al. 2001). Our results support this scenario in that they support the hypothesis that deer distribution influences tick distribution. However, larval and nymphal distributions shifted between deciduous and coniferous woods in our study despite the fact that neither were oak forests (the nearest oak forest was several kilometers away, across Great South Bay), so factors other than oak mast regulate tick distribution and abundance on Fire Island (Ginsberg et al. 1998). Furthermore, increased nymphal densities in the deciduous exclosure in 1999 suggests that the effect of deer density is inconsistent, as was found by Schulze et al. (2001). Thus deer distribution is a major determinant of nymphal tick distribution in some, but not all years.

The data on bird movements supply indirect evidence for the possible role of birds in tick distribution, because after abundant movement of resident birds from the western to the eastern sample sites in August 1997 (the month of greatest larval abundance), nymphal densities were far higher in the eastern sites in 1998, regardless of habitat type (Fig. 1A and C). Furthermore, the 1999 increase in nymphal abundance in the deer exclosures was in the eastern (deciduous) exclosure, again possibly resulting from the predominant movement of resident birds from the western to the eastern exclosure during August 1998. Nymphal densities did not differ significantly between deciduous and coniferous woods in either 1998 or 1999 (Fig. 1A). Thus, woodland type was not the most

Table 5. Movement of birds between eastern and western exclosures during August at the Fire Island Lighthouse Tract, 1996–1998

Year	No. marked	No. recaptured	P_{LH}	β_{EW}	β_{WE}
1996	104	15	0.1442	0.1691	0.4403
1997	208	73	0.3510	0.3930	0.4945
1998	298	117	0.3926	0.2374	0.5326

P_{LH}, estimate of probability of capturing a bird if it is present; β_{ij}, estimate of probability that a marked bird at site i moves to site j.

important variable underlying tick abundance in those years, but bird movements might well have played a role.

In summary, microgeographic distribution of *I. scapularis* on Fire Island results from both physical and biotic factors. Greater abundance in woods than in open habitats results largely from greater survival in the moist leaf litter of woodlands protected by the tree canopy than in open habitats (Ginsberg and Ewing 1989, Ginsberg and Zhioua 1996). Distribution in different habitats with similar physiognomy (such as different woodland types) results from factors that shift from year to year. On balance, the weight of evidence supports the hypothesis that the local distribution of nymphal *I. scapularis* in woodlands on Fire Island resulted predominantly from movements of ticks on animal hosts. Apparently, the distinction between deciduous and coniferous woods influences tick distribution primarily because of the influence of habitat type on the movements of tick host animals and not because of differences in the physical environments of the different forest types.

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