

Influence of Meso- and Microscale Habitat Structure on Focal Distribution of Sympatric *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae)

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ABSTRACT We compared the distribution of sympatric *Ixodes scapularis* Say and *Amblyomma americanum* (L.) within several suitable forested habitats at different spatial scales and characterized differences in microhabitat features accounting for the observed distribution of questing ticks. We used automatic data loggers placed in the shrub and litter layers to contrast mesoclimate and microclimate conditions experienced by questing ticks. Larger numbers of *I. scapularis* were collected at sites where the forest canopy was more fragmented and where the canopy contained more hardwood species than pitch pine, *Pinus rigida* Mill. Dominance of pine in the canopy affected the character of the shrub layer vegetation and composition of the litter layer, which concomitantly affected the microclimate conditions experienced by questing ticks. Pitch pine-dominated habitats were drier and hotter than those under a broad-leaved canopy, and questing ticks experienced increased saturation deficit in the later spring and summer in pine forest sites. The shrub layer vegetation seemed to have a moderating effect on the microclimate experienced by questing ticks and subtle differences in vegetation structure resulted in substantially different conditions as encountered by questing ticks over the space of a few meters. In contrast to questing *I. scapularis*, all three stages of questing *A. americanum* exhibited poor relationships with microclimate variables recorded in the litter and shrub layers. Further research is required to determine which environmental conditions and which habitats are most likely to support this species.

KEY WORDS *Ixodes scapularis*, *Amblyomma americanum*, microclimate, habitat, Lyme disease

THE TICK *Ixodes scapularis* Say is the principal vector of *Borrelia burgdorferi* in the northeast (Lane 1994) and the role of *Amblyomma americanum* (L.) as a vector of zoonotic pathogens to humans may increase in the coming years (Childs and Paddock 2003). An understanding of the factors that affect the distribution of vector tick populations is important in evaluating risk factors for disease transmission and the development of targeted control programs (Schulze and Jordan 1996).

In particular, both *I. scapularis* and *A. americanum* exhibit nonrandom distributions within suitable forested habitats (Semtner et al. 1971; Patrick and Hair 1978; Koch 1984; Ginsberg and Ewing 1989; Adler et al. 1992; Stafford and Magnarelli 1993; Duffy et al. 1994; Schulze and Jordan 1996, 2003; Schulze et al. 2001b). Vegetative cover in different forest habitats has profound effects on the environmental conditions below the forest canopy (Havens 1979) and influences the

microclimate necessary for the development and survival of questing ticks (Daniel and Dusbábek 1994).

The apparent abundance of questing *I. scapularis* in different forested and oldfield habitats has been found to vary widely from year to year and between seasons, suggesting that broad habitat descriptions provide only a gross mechanism for projecting tick populations in a given area (Schulze and Jordan 1996, Schulze et al. 1998). The environment of free-living exophilic ticks is the lower part of the vegetation, the leaf litter, and the upper layers of the soil column (duff layer) (Sonenshine 1993). However, the factors causing one microsite to be more favored than another have yet to be fully elucidated. Sonenshine (1993) and Daniel and Dusbábek (1994) differentiate between the mesoclimate (atmospheric conditions within the vegetation and below the forest canopy) and microclimate (conditions at the soil and soil-vegetation interface), the latter being where ticks live while undergoing development and shelter between questing events, as well as restoring body water lost during questing. Previous studies have shown that questing activity of both species were chiefly mediated by diurnal changes in temperature and relative humidity in these microenvironments (Schulze et al. 2001a; Schulze and Jordan 2003). These microclimate gradients varied between habi-

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tats, where differences in litter and shrub layer composition and structure modified the ambient microclimate in subtle ways (Schulze et al. 2002).

We conducted a study to compare the distribution of sympatric *I. scapularis* and *A. americanum* within several suitable forested habitats at different spatial scales and to characterize any differences in microhabitat features that might account for the observed distribution of questing ticks. Measurements in the tick habitats (mesoclimate), but above the environment experienced by ticks (microclimate), can only be used to describe large differences between abiotic conditions of the habitat types and the general climate (Daniel and Dusbábek 1994). We attempted to describe the microenvironment in the leaf litter by using automatic data loggers. To our knowledge, this is the first study that attempted to contrast mesoclimate and microclimate conditions experienced by questing ticks. Although data loggers do not represent the actual ecological conditions experienced by ticks, they can elucidate how conditions vary between shrub and litter layers and how these differences may modify activity of questing ticks. The implications of these findings on monitoring tick populations and assessing disease transmission risk also are discussed.

Materials and Methods

Study Area. Naval Weapons Station Earle (NWS Earle) is a 41-km² secured naval installation located in Colts Neck, NJ, where tick surveillance since 1981 has shown *I. scapularis* and *A. americanum* to be consistently abundant (Schulze et al. 1986, Schulze and Jordan 1996). Although the forest habitats varied across the base, the 10- to 15-m canopy was classified into three major forest types: mixed hardwood forests (MH) (70% or more of the dominant and codominant tree crowns were hardwood species), pine forests (PF) (70% or more of the dominant and codominant tree crowns were pine species), and mixed hardwood/pine forests (HP) (hardwoods and pines each comprising ≈50% of dominant and codominant trees). Forest type descriptions follow Burns and Honkala (1990). Wetlands (bogs and freshwater swamps) were present at NWS Earle, but excluded from the study as unsuitable habitats for *I. scapularis* and *A. americanum*.

Dominant species in the canopy of the MH forest habitat type included white oak, *Quercus alba* L., and red oak, *Quercus rubra* L., with associated species including red maple, *Acer rubrum* L.; black cherry, *Prunus serotina* Ehrh.; yellow poplar, *Liriodendron tulipifera* L.; American beech, *Fagus grandifolia* Ehrh.; black gum, *Nyssa sylvatica* Marsh.; and sweetgum, *Liquidambar styraciflua* L. The understory and shrub layer was comprised of saplings and seedlings of the dominant tree species, highbush blueberry, *Vaccinium corymbosum* L.; lowbush blueberry, *V. angustifolium* Ait.; huckleberries, *Gaylussacia* spp.; sweet pepperbush, *Clethra alnifolia* L.; spicebush, *Lindera benzoin* (L.) Blume; laurels, *Kalmia* spp.; and the vine catbriar, *Smilax glauca* Walt. PF habitats were dominated by pitch pine, *Pinus rigida* Mill. In addition to bayberry,

Myrica pensylvanica Loisel, the understory and shrub layer consisted of many of the species found in the MH sites. The HP forest type was dominated by oaks and pitch pine. The understory and shrub layer were similar to those described above.

The study was conducted in three phases designed to characterize tick distribution at different spatial scales. The first phase, which examined mesoscale distributions, was initiated in 1997 and used 57 study sites established for long-term monitoring of both tick species. Sites were uniformly distributed across the accessible portions of the facility (i.e., those areas not subject to security closure) and in numbers representative of the proportions of the habitats across the base (Schulze and Jordan 1996). Sites were a minimum of 300 m apart. Results of this study (mesoscale effects) suggested a second phase begun in 1998 to compare tick numbers between different habitat types that examined differences in both the habitat structure and microclimate experienced by both tick species. This second phase study (between-habitats effects) used 36 sites representing the three major upland forest types at NWS Earle, MH ($n = 8$), PF ($n = 14$), and HP ($n = 14$), and incorporated one 100-m² plot established within each of the 36 forest sites, placed at least 30 m from any habitat edge (including roads, fire trails, or canopy gaps) to minimize ecotonal effects. Finally, results from the between-habitats study led us to design a fine-scale examination of microhabitat effects on tick numbers within a single major forest type at NWS Earle. This within-habitat study was conducted in a 15-ha HP stand, the dominant habitat type at the facility, and incorporated 20 100-m² plots.

Tick Collections. Estimates of the numbers of questing *I. scapularis* and *A. americanum* on each plot were obtained by a combination of drag sampling and walking surveys (Ginsberg and Ewing 1989, Schulze et al. 1997). Sampling for adults was conducted in April of each year, when adults of both species are active (Schulze et al. 1986). Nymphs and larvae were collected in late May–early June and August, respectively. Plots were sampled three times each for each active life stage in all years. All sampling was performed between 1000 and 1400 hours by working 1-m² drags back and forth across the entire 100 m² of each of the study plots, maintaining contact between the drag and shrub vegetation (for adult collections) or litter surface (for subadults). To avoid investigator sampling biases, dragging was performed by the same individuals throughout the study (Schulze et al. 1997). Ticks found on the drags and investigators' clothing were removed at 20-m intervals, identified, and returned to the plot. No sampling was performed when vegetation was wet or when winds exceeded 10 km/h.

Mesoscale Effects. We measured an array of environmental variables at 57 study sites established for long-term monitoring of both species. At each site, we estimated numbers of questing adult ticks during spring the activity period in 1997. We also measured distance between the sampling plots and roadways, field edges, and large canopy gaps to determine whether there was a habitat edge within 30 m in each

of four cardinal directions (as a measure of habitat fragmentation). We estimated canopy coverage by using a spherical densiometer (Forestry Suppliers, Jackson, MS) (Lemmon 1956) and characterized canopy composition on an ordinal scale: PF, MH, and HP sites ranked 1, 2, and 3, respectively. Shrub cover was characterized as percentage of cover by using cover boards placed at the four cardinal directions from plot centers (Hays et al. 1981). Shrub height was classified on an ordinal scale as tall (shrubs >2 m in height over >50% of the plot), medium (shrubs 1–2 m height over >50% of the plot), or low (shrubs <1 m height over >50% of the plot), ranked 1, 2, and 3, respectively. Finally, depth of leaf litter was measured using a 1-m length of narrow-gauge wire, which was driven into the litter layer until the soil surface was encountered. Depth of litter was then read from a metric scale. Litter depth was recorded at five randomly chosen locations within each plot. In addition, we established elevation, slope, and aspect of all sampling plots from U.S. Geological Survey topographic maps by using TopoScout software (MapTech, Greenland, NH).

Between- and within-Habitat Effects. Canopy cover over each plot was estimated directly using a spherical densiometer. In addition, all trees (woody vegetation ≥ 10 cm diameter at breast height [dbh]) in each 100-m² plot were recorded by species and measured for dbh by using a metal diameter tape. From these measurements density (stems per hectare) and basal area (square meters per hectare) for each species in each plot and each habitat was calculated. Two 25-m² quadrats were established within each of the 100-m² plots. Within each quadrat, all shrubs and small saplings (stems <4 cm and ≥ 1.4 cm dbh at 1.4 m above the ground) were counted by species and measured for height. In addition, we recorded total number of stems and quadrat coverage of shrubs. Because most shrub species occurred as single stems and clonal connections could not be determined, each stem was considered a separate individual for the purposes of this study. Herbaceous and seedling cover (<1.0 m in height) was estimated in each of four 1-m² subquadrats established at the corners of each 100-m² plot. Percentage of herbaceous cover was recorded by visual estimate (Daubenmire 1959). Litter depth was recorded within each sampling plot as described previously.

Temperature and relative humidity were measured in the litter and shrub layer by using StowAway data loggers launched using Boxcar Pro software (Onset Computer Corp., Pocasset, MA). Data loggers were positioned just below the litter surface and ≈ 0.5 m above ground level to measure conditions in the litter and shrub layers, respectively. Data loggers were allowed to equilibrate for 20 min after placement before tick collections. Three pairs of data loggers (one each in the shrub and litter layers) were allowed to operate simultaneously with tick collections. Mean temperature and relative humidity were calculated for each data logger over each collection period. These measurements do not attempt to accurately depict conditions actually experienced by questing ticks, but

Table 1. Spearman correlation coefficients comparing mean numbers of ticks collected with habitat variables recorded at forested study plots at NWS Earle, Colts Neck, NJ

Variable	Tick species	
	<i>I. scapularis</i>	<i>A. americanum</i>
Site elevation (m)	-0.11	0.33
Prevailing slope (%)	-0.16	0.27
Prevailing aspect (degrees azimuth)	-0.14	-0.21
Distance to nearest habitat edge (m)	-0.32*	-0.50*
Number of adjacent habitat edges ^a	0.80*	-0.13
Canopy cover (% of area)	-0.45*	-0.03
Canopy species composition ^b	0.27*	-0.26
Shrub layer cover (% of area)	0.35*	0.02
Mean shrub height (m)	0.57*	0.00
Mean litter depth (mm)	0.28*	-0.22

Coefficients followed by an asterisk (*) indicate are significant ($P < 0.05$).

^a Number of adjacent habitat edges: a habitat edge within 30 m of one, two, three, or four cardinal directions.

^b Canopy species composition represented as pine (1), oak (2), or mixed pine-oak (3).

rather they are an index of plotwide conditions. Insolation measurements (estimated as percentage of ambient below the forest canopy) were made using a Luna-Pro light meter (Gossen, Nuremberg, Germany). Saturation deficit (SD), which provides a measure of the drying power of the atmosphere, was calculated from temperature (T) and relative humidity (RH) by using the following formula (Randolph and Storey 1999): $SD = (1 - RH/100)4.9463e^{0.0621T}$. Saturation deficit increases with increasing temperature and decreasing humidity.

Statistical Analysis. Variables were transformed where necessary to more closely approximate assumptions of normality (Sokal and Rohlf 1981). Analysis of variance (ANOVA) for repeated measures, or non-parametric equivalent, was used to determine the effects of sampling date and plot on numbers of questing ticks. Relationships between tick numbers and environmental parameters were explored using Spearman correlation coefficients and linear regression (Sokal and Rohlf 1981). We used multiple linear regressions to examine relationships between environmental variables. A tolerance value of 0.1 (as an indicator of multicollinearity) was set, a priori, for acceptance of independent variables into regression models. All statistical tests were performed using Statistica analysis packages (StatSoft, Tulsa, OK).

Results

Mesoscale Effects. Numbers of questing *I. scapularis* adults were correlated with several of the habitat parameters measured at long-term monitoring plots (Table 1). Tick numbers were greater at sites adjacent to ecotonal edges and at sites characterized by greater habitat fragmentation. More ticks were collected at sites with less canopy cover and at sites with greater hardwood species dominance in the canopy. Finally, more ticks were collected from plots with more well developed shrub layers and deeper litter cover. There was significant correlation between fragmentation

Table 2. Comparison of habitat structural variables between three forest types at NWS Earle

Variable	Forest canopy type			Kruskal-Wallis test
	Hardwood(<i>n</i> = 8)	Mixed(<i>n</i> = 14)	Pine(<i>n</i> = 14)	
Canopy density (stems/ha)	13.3 ± 1.7	13.7 ± 0.7	15.6 ± 1.1	H _(2,36) = 2.96; <i>P</i> = 0.23
Canopy basal area (m ² /ha)	4.4 ± 0.6a	3.4 ± 0.6a	0.9 ± 0.2b	H _(2,36) = 33.02; <i>P</i> < 0.01
Percent pine in canopy	13.0 ± 2.6a	51.3 ± 3.1b	87.3 ± 1.9c	H _(2,36) = 52.20; <i>P</i> < 0.01
Shrub cover (%)	64.2 ± 10.6a	31.8 ± 3.3b	25.5 ± 1.4b	H _(2,36) = 14.69; <i>P</i> < 0.01
Shrub height (m)	0.48 ± 0.04a	0.67 ± 0.07b	0.46 ± 0.03a	H _(2,36) = 9.07; <i>P</i> < 0.05
Herbaceous cover (%)	8.5 ± 1.1a	6.7 ± 1.7a	32.8 ± 6.6b	H _(2,36) = 3.42; <i>P</i> = 0.05
Litter depth (mm)	5.2 ± 0.2a	5.7 ± 0.2a	4.6 ± 0.3b	H _(2,36) = 8.35; <i>P</i> = 0.02

(number of ecotonal edges adjacent to the study plot) and both canopy cover ($r = 0.50$, $P < 0.05$) and shrub cover ($r = 0.46$, $P < 0.05$). In contrast, with the exception of habitat edge (more ticks being collected nearer to ecotonal edges), numbers of questing *A. americanum* was not correlated with any of the measured mesoscale habitat variables.

Between-Habitats Effects. Habitat Variables. Habitat structural variables are summarized in Table 2. PF stands were characterized by lower tree basal area (fewer large-diameter trees) than either MH or HP sites. Shrub cover was greatest in MH sites, tending to be a low, dense cover of ericaceous species, whereas shrub cover in PF sites was notably patchier. In contrast, herbaceous layers in MH and HP sites were depauperate, whereas PF sites supported often dense carpets of false heather, *Hudsonia ericoides* L.; mosses, *Pyxidanthera Polytrichum* spp.; and lichens, *Cladonia* spp. Litter depth was not as well developed in PF sites as in either MH or HP sites. Table 3 summarizes seasonal differences in litter and shrub layer microclimate across habitats. April conditions in both the shrub and litter layers did not differ significantly between the three forest types. Ambient temperatures remained cool during the period, but lack of canopy cover in the MH and HP sites, relatively higher insolation reaching the understory and forest floor, coupled with lack of rainfall, kept SD high at all sites during the period. By the peak of nymphal activity in June, SD in both litter and shrub layers at PF sites had remained high but had fallen significantly in MH and HP sites as higher humidity and lower temperatures prevailed below a developing broad-leaved canopy. These trends continued into the August larval activity peak, because higher humidity in the MH and HP sites kept SD significantly lower than at PF sites.

Correlations between the vegetation and microclimate variables are presented in Table 4. The primary determinant of forest structure was the relative dominance of pitch pine (relative to hardwoods, PCP) in the forest canopy. Poorly developed shrub and litter layers and denser herbaceous cover characterized pine-dominated forest plots and PF sites. Dominance of pitch pine in the forest canopy also seemed to have significant effects on microclimate, and PF sites tended to have higher SD in both the shrub and litter layer. Conditions were generally drier below pine canopies.

Effects on Questing Ticks. Significantly more questing *I. scapularis* of all active stages were collected at MH and HP sites than at PF sites (Table 5). Numbers of all three stages of questing *I. scapularis* were negatively correlated with both shrub and litter layer SD and with dominance of pitch pine in the forest canopy (Table 6). As SD decreased, more *I. scapularis* were collected at all sites. In contrast, numbers of questing *A. americanum* did not differ significantly between habitat types (Table 5). All stages of *A. americanum* were poorly related to the microclimate variables recorded in both litter and shrub layers and to forest structure (Table 6).

Within-Habitat Effects. Habitat Variables. Vegetation variables within the HP stand did not differ between the three tick activity periods, whereas microclimate conditions varied significantly between all three seasons (Table 7). Litter layer SD did not differ between April and June but increased significantly in August as temperatures increased. Similar trends were observed in shrub layer SD. Litter layer SD was consistently less than shrub layer SD in all seasons. The difference between litter and shrub layer SD also

Table 3. Seasonal differences in litter layer and shrub layer SD (mmHg) in three forest types at NWS Earle

	Forest canopy type			Kruskal-Wallis test
	Hardwood(<i>n</i> = 8)	Mixed(<i>n</i> = 14)	Pine(<i>n</i> = 14)	
April				
Litter layer SD	12.5 ± 1.5	10.2 ± 1.5	9.8 ± 0.9	H _(2,36) = 1.65; <i>P</i> = 0.44
Shrub layer SD	16.9 ± 1.7	17.1 ± 3.8	16.2 ± 1.1	H _(2,36) = 0.11; <i>P</i> = 0.94
June				
Litter layer SD	8.3 ± 1.2a	6.1 ± 1.1a	12.7 ± 0.3b	H _(2,36) = 12.84; <i>P</i> < 0.01
Shrub layer SD	10.7 ± 0.9a	8.9 ± 0.9a	15.4 ± 0.6b	H _(2,36) = 13.30; <i>P</i> < 0.01
Aug.				
Litter layer SD	4.5 ± 0.7a	5.1 ± 0.9a	13.9 ± 0.9b	H _(2,36) = 14.39; <i>P</i> < 0.01
Shrub layer SD	6.4 ± 0.8a	6.9 ± 0.9a	15.9 ± 1.4b	H _(2,36) = 14.32; <i>P</i> < 0.01

Values (mean ± SE) in the same row followed by the same letter are not significantly different (Dunn's multiple comparisons test).

Table 4. Spearman correlation coefficients comparing microclimate and vegetation variables recorded at forested study plots at NWS Earle, Colts Neck, NJ

	Variable									
	LSD	SSD	INSO	LTYP	LDEP	CDEN	PCP	SCOV	SHT	HCOV
Litter layer saturation deficit (LSD)										
Shrub layer saturation deficit (SSD)	0.82*									
Insolation (INSO)	0.16	-0.25								
Litter type (LTYP)	-0.08	-0.04	0.08							
Litter depth (LDEP)	0.05	0.10	-0.18	-0.26						
Canopy stem density (CDEN)	0.07	0.10	-0.07	0.09	-0.08					
Canopy percent pine (PCP)	0.38*	0.37*	0.13	-0.60*	-0.21*	0.09				
Shrub cover (SCOV)	-0.19	-0.14	-0.14	0.20	0.08	-0.45*	-0.49*			
Shrub height (SHT)	-0.19	-0.15	-0.15	-0.27*	0.51*	-0.33*	-0.10	0.40*		
Herbaceous cover (HCOV)	0.18	0.10	0.11	-0.28*	-0.47*	-0.24	0.48*	-0.18	-0.24	

An asterisk (*) indicates significance ($P < 0.05$).

varied between the seasons, being greatest in the nymphal season in June.

There were only poor correlations between the physical structure of the plots and the microenvironment recorded by the data loggers (Table 8). Litter layer SD was negatively correlated with litter layer depth and positively correlated with ambient insolation, whereas litter SD was negatively correlated with shrub cover and shrub height. Also, shrub layer SD was negatively correlated with shrub cover. Plots with more substantial shrub cover tended to have cooler litter layers, whereas plots with sparser shrub cover and thus more ground level insolation tended to have warmer litter. This suggests that there is some insulating effect of the shrub layer vegetation on the litter surface. Denser shrub cover and greater litter depth resulted in lower litter SD.

Effects on Questing Ticks. Numbers of questing *I. scapularis* adults were positively related to litter depth, but they were not significantly related to litter microclimate (Table 9). Greater numbers of adults were collected in plots with lower shrub layer cover and SD. Numbers of *I. scapularis* nymphs were significantly related to microclimate in the shrub layer. More nymphs were collected in plots with deeper leaf litter layers, with higher shrub cover, and where shrub layer humidity was high. There was no relationship between questing nymphs and litter layer SD. The difference between litter and shrub layer SD was greatest in June, when nymphs were questing (Table 7). Numbers of questing nymphs were negatively related to this dif-

ference ($r = -0.52, P < 0.05$): The greater the differences between litter and shrub SD, the fewer nymphs were collected. Thus, when conditions in the shrub layer were moister and cooler, larger numbers of nymphs were collected.

Numbers of questing *I. scapularis* larvae were poorly related to the microclimate and habitat variables recorded in both the shrub and litter layers (Table 9). Litter conditions were moister and cooler than shrub layer conditions in August. Numbers of larvae were positively correlated with the difference in the SD between litter and shrub layers ($r = 0.38, P < 0.05$). As litter layers became moister than shrub layers (or as SD above the litter exceeded that within the litter layer), more questing larvae were collected.

Numbers of both adult and nymphal *A. americanum* were positively related to litter depth (Table 10). Numbers of *A. americanum* were not significantly related to litter microclimate; however, greater numbers of both adults and nymphs were encountered when shrub layer SD increased (i.e., numbers increased as shrub layer humidity declined and shrub layer temperature increased). No significant relationships between environmental variables and questing *A. americanum* larvae were detected.

Discussion

Results from mesoscale measurements recorded in three forest types showed that larger numbers of *I. scapularis* were collected at sites where the forest

Table 5. Results of Kruskal-Wallis one-way tests comparing mean number of ticks collected (\pm SE) in three forest types, NWS Earle, Colts Neck, NJ

Species	Forest type			Kruskal-Wallis test
	Hardwood (n = 8)	Mixed Canopy (n = 14)	Pine (n = 14)	
<i>I. Scapularis</i>				
Adults (spring)	4.3 \pm 1.1a	4.7 \pm 1.8a	2.1 \pm 0.5b	$H_{(2, 36)} = 3.69; P < 0.05$
Nymphs	7.7 \pm 2.5a	8.3 \pm 4.3a	3.6 \pm 1.3b	$H_{(2, 36)} = 4.84; P < 0.05$
Larvae	133.4 \pm 32.1a	150.0 \pm 93.8a	73.0 \pm 29.5b	$H_{(2, 36)} = 3.81; P < 0.05$
<i>A. americanum</i>				
Adults	4.6 \pm 1.9	3.3 \pm 2.3	4.1 \pm 1.0	$H_{(2, 36)} = 1.03; P = 0.59$
Nymphs	25.5 \pm 9.4	40.3 \pm 26.2	14.6 \pm 4.2	$H_{(2, 36)} = 2.56; P = 0.27$
Larvae	170.4 \pm 30.1	428.4 \pm 151.0	311.9 \pm 59.7	$H_{(2, 36)} = 1.72; P = 0.42$

Numbers in the same row followed by the same letter denote nonsignificant Dunn's test.

Table 6. Spearman correlation coefficients comparing mean numbers of ticks collected with microclimate and vegetation variables recorded at forested study plots at NWS Earle, Colts Neck, NJ

Variable	Tick species					
	<i>I. scapularis</i>			<i>A. americanum</i>		
	Adults	Nymphs	Larvae	Adults	Nymphs	Larvae
Litter layer saturation deficit (LDF)	-0.45*	-0.42*	-0.49*	0.13	-0.14	0.15
Shrub layer saturation deficit (SDF)	-0.29*	-0.47*	-0.27*	0.17	-0.15	0.19
Canopy percent pine (PCP)	-0.48*	-0.36*	-0.45*	-0.16	-0.30	0.27

Coefficients followed by an asterisk (*) indicate are significant ($P < 0.05$).

canopy was more fragmented and where the canopy contained more hardwood species than pitch pine. Both habitat fragmentation and canopy composition were related to shrub cover. However, shrub cover did not differ significantly between the seasons because the shrub layer in the study plots was dominated by ericaceous species (*Vaccinium* and *Gaylussacia* spp.), which are semievergreen in the coastal plain forests typical of NWS Earle (Collins and Anderson 1994), so that there was no "leafing out" as the growing season progressed. Thus, the structure of the physical environment in the study plots did not differ for questing adults, nymphs, and larvae of either species.

Rather, between-habitat comparisons suggested that forested sites at NWS Earle were largely shaped by the presence of pitch pine in the canopy. Pitch pine overstories affected the character of the shrub layer vegetation and the composition of the litter layer, and concomitantly affected the microclimate conditions experienced by questing ticks (Havens 1979). Pitch pine-dominated habitats were drier and hotter than those under a broad-leaved canopy and questing ticks experienced increased SD in the later spring and summer in PF sites. We have previously shown that *I. scapularis* is not tolerant of these drier conditions (Schulze et al. 2001a, Schulze and Jordan 2003) and tends to be less abundant in pitch pine-dominated forests (Schulze and Jordan 1996, Schulze et al. 2002).

I. scapularis in eastern North America is largely associated with deciduous forest with substantial leaf litter layers (reviewed by Piesman 2002). However, Apperson et al. (1993) described *I. scapularis* habitat in the southeastern United States as pine (*P. palustris* and *P. taeda*) and oak forest with very similar structure to the PF sites at NWS Earle. Higher humidity and greater rainfall during the spring and summer in the southeast, compared with that experienced in pine

forests farther north (Christensen 1988), may generate conditions in southern forests that are more hospitable for ticks. Mediterranean climates with cool, wet winters and warm, dry summers allow *Ixodes pacificus* (Cooley & Kohls) to exploit an array of otherwise dry habitats, including open grassland and chaparral in California (Li et al. 2000). Olson et al. (1992) found *I. pacificus* at high elevations (>2,000 m) in the otherwise arid Mojave Desert in Arizona where sky-islands of oak capture snowmelt and where leaf litter provides high-humidity microenvironments. Similarly, the American dog tick, *Dermacentor variabilis* Say, at the northern limit of its range, is most abundant in moist meadow and meadow/forest ecotones (Sonenshine 1993), whereas in the mid-Atlantic (where seasonal temperatures are higher and rainfall is lower) it is found more abundantly in the ecotone than in either meadow or forest (Smart and Caccamise 1988). Thus, these ixodid species are able to exploit seemingly hostile environments where vegetation or topography modifies the local climatic conditions to provide favorable microsites.

The shrub layer vegetation at NWS Earle seemed to have a moderating effect on the microclimate experienced by questing ticks. Denser shrub cover helped to maintain lower temperatures, probably by intercepting and reducing the intensity of the ambient insolation that penetrated the tree canopy, while trapping moisture (whether rainfall or dew) and reducing evaporation within the shrub understory and at the shrub-litter interface. This moderating effect of the shrub cover also seemed to help keep litter layer temperatures cooler. Thus, in what were apparently uniform forest stands, the subtle differences in vegetation structure, resulting from the patchy nature of the shrub cover, created substantially different conditions as encountered by questing ticks over the

Table 7. Results of ANOVA comparing microclimate variables between sampling periods (April, adults; June, nymphs; and August, larvae) in hardwood-pine forest plots at NWS Earle, Colts Neck, NJ

Variable	Month			F	P > F
	April	June	Aug.		
Litter humidity (%)	28.1 ± 12.5a	62.8 ± 9.6b	44.5 ± 19.8c	28.21	<0.01
Shrub humidity (%)	21.4 ± 5.5a	35.5 ± 5.6b	50.2 ± 12.9c	54.06	<0.01
Litter temp (°C)	19.9 ± 0.6a	22.9 ± 3.0b	26.1 ± 3.5c	47.26	<0.01
Shrub temp (°C)	20.8 ± 2.4a	23.5 ± 3.0b	31.8 ± 0.9c	126.81	<0.01
Litter saturation deficit	10.9 ± 2.1a	7.7 ± 2.5a	14.7 ± 6.7b	13.33	<0.01
Shrub saturation deficit	14.4 ± 2.6a	13.9 ± 2.5a	17.8 ± 4.7b	7.89	<0.01

Values in the same row followed by different letters are significantly different (Tukey's honestly significant difference test).

Table 8. Spearman correlation coefficients comparing microclimate and vegetation variables recorded at the HP forested sampling plots at NWS Earle, Colts Neck, NJ

	LSD	SSD	SCOV	SHT	LDEP	INSOL
Litter layer saturation deficit (LSD)						
Shrub layer saturation deficit (SSD)	0.19					
Shrub cover (SCOV)	-0.36*	-0.67*				
Shrub height (SHT)	-0.28*	-0.47*	0.71*			
Litter depth (LDEP)	-0.26*	-0.19	-0.19	-0.06		
Insolation (INSOL)	0.63*	-0.34*	0.11	0.04	-0.24	

Coefficients followed by an asterisk (*) indicate are significant ($P < 0.05$).

space of a few meters. We have previously demonstrated that subtle changes in topography and edaphic conditions, and resultant small-scale differences in humidity and temperature, may determine habitat suitability that differs for the two sympatric tick species (Schulze et al. 2002).

Differences in environmental conditions, including temperature, humidity, and solar radiation, play important roles in influencing the distribution of many species of exophilic ticks, but the degree of influence and the relative importance of different environmental factors vary from species to species (reviewed in Daniel and Dusbábek 1994). In general, questing ticks are most active in microhabitats with the lowest temperature fluctuation and the highest ambient humidity (Sonenshine 1993). Subadult *I. scapularis* (Yoder and Spielman 1992, Stafford 1994) and *I. ricinus* (L.) (Randolph and Storey 1999) require high relative humidity to survive in the summer. The distribution of *D. variabilis* seems to be tied to conditions of high ambient humidity and soil moisture content (Sonenshine 1993). Numbers of questing *I. scapularis* at NWS Earle were significantly related to microclimate conditions in both the litter and shrub layers across forest type. More questing adults and nymphs were encountered in plots characterized by denser shrub layers, and, consequently, less drying conditions in the litter and

shrub layers (lower SD). Also, numbers of questing nymphs increased when the difference in temperature between the litter and shrub layers decreased (i.e., when questing above the litter surface would not expose ticks to drying conditions).

It is not clear why we encountered larger numbers of larvae despite a negative difference in SD between litter and shrub layers. Under such circumstances, we would expect more larvae to remain within the litter to avoid drying conditions above. It may be that moisture in the litter is trapped at the interface and that larvae are pulled along to the surface as the SD difference draws moisture from the litter column. Unfortunately, the data loggers used here did not allow us to record microenvironmental conditions at a scale experienced by larval ticks. Alekseev and Dubinina (2000) showed that *I. persulcatus* (Schulze) activity was closely tied to temperature gradients between the soil layer and ambient conditions. We have shown that numbers of questing *I. scapularis* and *A. americanum* adults (Schulze et al. 2001a) and nymphs (Schulze and Jordan 2003) are consistently more abundant during particular times of the day and that these differences seemed to be substantially explained by gradients between ambient temperature and humidity and conditions recorded in the leaf litter. Similar relationships may also influence questing by larvae.

Table 9. Numbers of *I. scapularis* regressed against shrub and litter layer variables recorded in the HP forest sampling plots at NWS Earle, Colts Neck, NJ

Predictor variable	Coefficient		Tolerance	<i>t</i>	<i>P</i> > <i>t</i>
	Beta	SE			
Adults^a					
Litter depth	0.686	0.257	0.614	2.67	0.02
Shrub cover	0.299	0.233	0.748	1.28	0.04
Litter saturation deficit	0.110	0.275	0.537	0.40	0.69
Shrub saturation deficit	-1.546	0.814	0.061	1.91	0.04
Nymphs^b					
Litter depth	0.427	0.211	0.873	2.51	0.02
Shrub cover	0.457	0.286	0.478	1.59	0.03
Litter saturation deficit	-0.051	0.214	0.846	0.24	0.81
Shrub saturation deficit	-0.796	0.291	0.462	2.73	0.02
Larvae^c					
Litter depth	0.103	0.267	0.816	0.38	0.71
Shrub cover	0.38	0.280	0.743	0.14	0.89
Litter saturation deficit	0.361	0.398	0.368	0.91	0.38
Shrub saturation deficit	-0.006	0.395	0.374	0.01	0.98

^aAdjusted $R^2 = 0.278$; $F_{(4, 15)} = 2.13$; $P < 0.05$

^bAdjusted $R^2 = 0.256$; $F_{(4, 15)} = 2.64$; $P < 0.05$

^cAdjusted $R^2 = 0.123$; $F_{(4, 15)} = 0.53$; $P = 0.71$.

Table 10. Numbers of *A. americanum* regressed against shrub and litter layer variables recorded in the HP forest sampling plots at NWS Earle, Colts Neck, NJ

Predictor variable	Coefficient		Tolerance	<i>t</i>	<i>P</i> > <i>t</i>
	Beta	SE			
Adults^a					
Litter depth	0.458	0.218	0.916	2.10	0.05
Shrub cover	-0.264	0.249	0.697	1.06	0.31
Litter saturation deficit	-0.505	0.489	0.182	1.03	0.32
Shrub saturation deficit	0.865	0.494	0.178	1.75	0.10
Nymphs^b					
Litter depth	0.679	0.176	0.892	3.86	0.002
Shrub cover	0.593	0.238	0.920	2.49	0.02
Litter saturation deficit	-0.005	0.178	0.721	0.03	0.97
Shrub saturation deficit	0.797	0.242	0.731	3.29	0.005
Larvae^c					
Litter depth	-0.115	0.297	0.708	0.38	0.71
Shrub cover	0.105	0.279	0.801	0.37	0.71
Litter saturation deficit	0.101	0.327	0.585	0.31	0.76
Shrub saturation deficit	0.014	0.293	0.731	0.05	0.96

^aAdjusted $R^2 = 0.348$; $F_{(4, 15)} = 2.00$, $P < 0.15$

^bAdjusted $R^2 = 0.594$; $F_{(4, 15)} = 5.48$, $P < 0.01$

^cAdjusted $R^2 = 0.062$; $F_{(4, 15)} = 0.25$, $P < 0.91$.

Although *I. scapularis* tended to be collected with greater frequency in deciduous forest habitats with well-developed shrub layers, it remains unclear whether the data reflect actual tick abundance or simply provide a measurement of differences in the number of ticks within a local population that quest in response to a more favorable microclimate (higher humidity, lower temperature) (Daniel and Dusbábek 1994, Belozerov and Naumov 2002). It may be that ticks are more uniformly distributed across habitats than these data suggest but that conditions favorable to questing may occur less frequently in marginal habitats, such as the pitch pine-dominated forests with sparse shrub layers that were sampled in this study. If true, sampling these habitats will generally yield fewer ticks and lead to the assumption that such habitats are of low risk for tick encounters and disease transmission. Cool, moist microclimates increase the ability of questing ticks to extend their periods of activity, resulting in a better chance of finding a host (Sonenshine 1993) and also of being collected. As conditions more favorable to questing arise, such as a decline in the SD after significant rainfall, these generally marginal habitats may demonstrate increased risk as a greater proportion of the tick population is now able to quest. Tick response to specific meteorological events requires further study.

Habitat also includes conditions that enhance the survival and development of hosts. When climate conditions are favorable and host use is heavy, suboptimal tick habitats can support large numbers of *A. americanum* (Sonenshine 1993). In periods where ambient climate produced more desiccating conditions, the habitat did not sustain large numbers of ticks. Similarly, Lindsay et al. (1999b) recorded mesoclimate conditions in four habitats and showed *I. scapularis* abundance to be linked to seasonal variation in climate conditions. Hot and dry habitats supported low numbers of questing ticks because of higher mortality of fed and unfed ticks (Lindsay et al. 1999a). However, greater than expected numbers of ticks observed in suboptimal habitats seemed to reflect higher use by white-tailed deer, *Odocoileus virginianus* Zimmerman, and introduction of larger numbers of replete females. Thus, high host use of marginal tick habitats can maintain tick populations at levels similar to more conducive habitats. Previous work at NWS Earle (Schulze et al. 2001b) showed that white-tailed deer activity did not differ between the three forest types studied here and that tick distribution patterns were influenced by factors other than host activity.

In contrast to *I. scapularis*, all three stages of questing *A. americanum* seemed to be successful in all of the habitats studied here and were active under conditions that were both drier and warmer than those tolerated by sympatric *I. scapularis*. Previous laboratory (Stafford 1994) and field studies (Schulze et al. 2001a, Schulze and Jordan 2003) have suggested that *A. americanum* may be more tolerant of drying conditions than sympatric *I. scapularis*. It may be that *A. americanum* is better able to meet the metabolic demands of desiccating conditions than the smaller *I.*

scapularis (Clark 1995). The role of *A. americanum* in the transmission of various pathogens remains poorly understood, but it is expected to expand as more is learned about the role of this tick species in existing zoonoses (Schulze and Bosler 1996, Childs and Paddock 2003) and more people come in contact with this aggressive vector (Armstrong et al. 2001). Further research is required to determine which environmental conditions and which habitats are most likely to support this species at the northern extent of its range.

Environmental conditions across different spatial scales influence the activity of questing *I. scapularis* and *A. americanum*. Thus, the apparent abundance of one or both species may seem to vary from year to year or season to season, even within apparently uniform forested habitats, as questing ticks respond to differing microclimate conditions (Schulze and Jordan 1996). Effective monitoring of microenvironmental conditions at a scale that captures this within-habitat variability in questing abundance is both expensive and labor-intensive. Yet, apparently suitable habitats may not support large numbers of ticks or may only yield large numbers of ticks in certain years or under certain conditions (e.g., before or after weather fronts). This argues for monitoring actual tick populations before any planned intervention. However, it may be that microclimate conditions vary so widely at such small scales that a gross appreciation of habitat type (e.g., dominance of pitch pine in the forest canopy) (Schulze et al. 1991) provides just as effective a means of assessing transmission risk as more intensive sampling of the microenvironment.

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