Geographic Information Systems and Spatial Analysis of Adult *Ixodes scapularis* (Acari: Ixodidae) in the Middle Atlantic Region of the U.S.A.

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J. Med. Entomol. 40(4): 570–576 (2003)

ABSTRACT In the Middle Atlantic region of the U.S.A., the vector of Lyme disease, human granulocytic ehrlichiosis, babesiosis, and other human and veterinary pathogens is the black-legged tick, *Ixodes scapularis* Say. In 1997 and 1998, 663 adult *I. scapularis* ticks were collected from 320 transects spanning 66,400 km^2 in five states of the Middle Atlantic region. Tick abundance patterns were clustered, with relatively high numbers along the coastal plain of the Chesapeake Bay, decreasing to the west and south. There were significant associations between tick abundance and land cover, distance to water, distance to forest edge, elevation, and soil type.

KEY WORDS *Ixodes scapularis*, spatial correlation, GIS, environmental predictors, Poisson-normal model, soil

IN THE MIDDLE ATLANTIC REGION of the U.S.A., *Ixodes scapularis* Say, the blacklegged tick, transmits the etiologic agents of Lyme borreliosis, human granulocytic ehrlichiosis, babesiosis, and other human and veterinary pathogens. Previous studies demonstrated that soil type was correlated with abundance patterns for *Ixodes* spp. (Glass et al. 1994, De Mik et al. 1997, Jensen et al. 2000, Guerra et al. 2002). In an epidemiological study, Glass et al. (1995) found that positive risk factors for reported human Lyme disease cases included residing in forested areas and on particular soil types. To further characterize the quantifiable environmental attributes that influenced the geographic distribution of *I. scapularis* in the Middle Atlantic region, we undertook a study combining a number of analytical and surveillance techniques, with an emphasis on soils.

Remote sensing technology-based geographic information science (GIS) has a number of features that make it a valuable asset in linking environmental factors to epidemiological patterns (Vine et al. 1997). For example, cartographic display capabilities inherent in GIS have enabled production of risk maps that are accessible and understandable to nontechnical audiences as well as analytical researchers (Kitron 2000). Numerous researchers have made good use of GIS to interpret ecological aspects of vector-borne diseases (Kitron 1998), and of Lyme disease in particular (Glass et al. 1995, Nicholson and Mather 1996). The current study incorporates newly developed spatial statistical modeling as a means of overcoming the challenge of predicting tick abundance as an indicator of relative Lyme disease risk—estimations based on environmental factors that have proved problematic in the past (Randolph 2000). This approach can lead to more refined estimates of actual risk to humans of encountering potentially infected ticks, and therefore has a place in large-scale public health strategies, such as issuing alerts, targeting education campaigns, and providing scientific support to clinicians faced with questions about vaccinations.

Materials and Methods

Tick Collections. Adult *I. scapularis* were collected by the flagging method (Milne 1943) from late September to early December in 1997 and 1998 in Delaware, Maryland, New Jersey, Pennsylvania, and Virginia (Fig. 1). Collection sites (quadrats, or transects) were randomly selected within state parks, state forests, and other large, open areas. Sites that fell in open water, parking lots, or other obviously unsuitable habitats were discarded. One-meter square white corduroy flags were used in 15-min bouts. Ticks were kept alive in humid vials until processing for polymerase chain reaction (PCR). Latitudes and longitudes were recorded by a hand-held GPS device (Garmin GPS III, model #190-00128-00, Garmin Corp., Olathe, KS) and verified by cross-referencing selected points on USGS 7.5-min quadrangles.

PCR for *B. burgdorferi*. All PCRs were conducted and products stored in a room isolated from nucleic acid extraction to minimize potential contamination.

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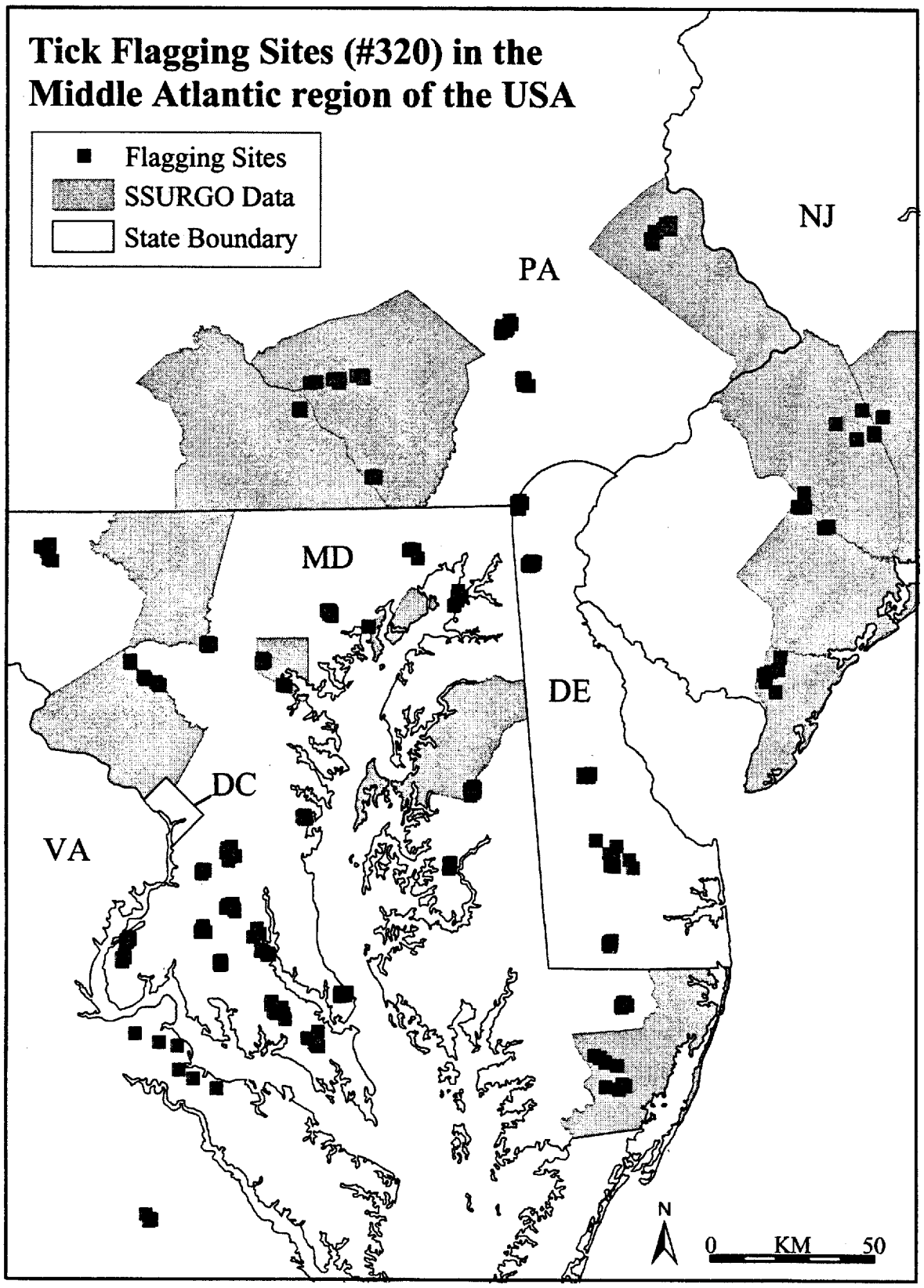

Fig. 1. Tick flagging sites in the Middle Atlantic region of the U.S.A. Gray areas show regions with digital SSURGO soils data used for the analysis of the subset of 75 sites.

PCRs were prepared in 50 μl total reaction volumes containing 200 nM of each primer in PCR buffer included with ELONGase thermostable DNA polymerase (1 U per reaction), 5 μl of DNA template, and 2.0 mM final Mg^{2+}. Oligonucleotide primers BAE-1 and BAE-2 were used to amplify a 126 basepair region of the *Borrelia burgdorferi* Johnson, Schmid, Hyde, Steigerwalt, and Brenner OspA gene (Hofmeister et al. 1992). Reaction conditions were as follows: semihot start, denaturing at 94°C for 30 s, annealing at 61°C for 30 s, and extension at 72°C for 30 s, repeated for 40 cycles. After electrophoresis, ethidium bromide-stained PCR products were visualized under UV transillumination with an EagleEye gel documentation system (Stratagene, LaJolla, CA) in 0.9% agarose gels. Identity of products was verified using an ABI 373 XL automated DNA sequencer (PE Biosystem, Foster City, CA). Each reaction contained positive control DNA, a water blank, and DNA from a known negative control (uninfected) tick. Positive control *B. burgdorferi* DNA was obtained from a commercial source (Kirkegaard & Perry, Gaithersburg, MD). Potential false negative results were ruled out using a separate internal control PCR, conducted for each tick to amplify a region of tick mitochondrial 16S rDNA (Black and Piesman 1994).

GIS and Spatial Statistics. The spatial attributes included in the analysis were soil type, land cover, elevation (DEM), and distance to bodies of water. Soil data were obtained from the State Soil Geographic (STATSGO) Data Base which is at a scale of 1:250,000 (United States Department of Agriculture, Natural Resources Conservation Service, National Soil Survey Center). Digital elevation models (DEM) provided

Table 1. Classification of environmental covariates as quartiles about the median

Variable	Minimum (m)	Maximum (m)	Median (m)	Category	Range (m)
Elevation	0	529	23	DEM_1	0–9
				DEM_2	9–23
				DEM_3	23–57.75
				DEM_4	57.75–529
Distance to deciduous forest	0	495	30	Deci_1	0.0–0.0
				Deci_2	0.0–30
				Deci_3	30.5–60
				Deci_4	60–495
Distance to evergreen forest	0	1243	95	Ever_1	0–33.5
				Ever_2	34–95
				Ever_3	95–190
				Ever_4	190–1243
Distance to mixed forest	0	797	67	Mix_1	0–30
				Mix_2	30.5–60
				Mix_3	60–117
				Mix_4	117–797
Distance to water	0	3208	443	Wat_1	0–240.5
				Wat_2	240.5–452
				Wat_3	452–856
				Wat_4	856–3208

All units in meters.

topographic data at a scale of 1:24,000 (U.S. Geological Survey, Reston, VA). Landcover, as well as derived forest and water distance, attribute sets were obtained from Multiresolution Landscape Characterization (MRLC) Landsat TM source data (U.S. Geological Survey, Earth Resources Observation Systems, Sioux Falls, SD) at a 30-m spatial resolution. Idrisi 2.0 (Clark University, Worcester, MA) and ArcView 3.2 (ESRI Inc., Redlands, CA) GIS packages were used for raster- and vector-based data formats, respectively. For Poisson regression, environmental variables with scalar measures were classified by taking quartiles around the median (Table 1). Soil types were combined into nine groups with the following distinguishing and similar features: (1) siliceous, fine-loamy, (2) micaceous, (3) skeletal, siliceous, fine-loamy, (4) fine-silty, fine-loamy, (5) clayey, acidic, (6) loamy, siliceous, (7) fine-loamy, (8) loamy-skeletal, and (9) sandy, loamy, siliceous. S-Plus (version 2000, MathSoft Inc., Seattle, WA), as well as SAS (version 6.12, SAS Institute, Carey, NC) software were used to explore and analyze the data, using ordinary Poisson and mixed Poisson-Log Normal regression models, the latter incorporating spatial correlation and over-dispersion (Das et al. 2002).

Soil Data at Higher Resolution. All sites with digital county soil data were analyzed further to refine the soil associations observed based on coarser resolution STATSGO data, and to generate hypotheses relating these characteristics to the tick's biology. The source of these data were the Soil Survey Geographic (SSURGO) Data Base (United States Department of Agriculture, Natural Resources Conservation Service, National Soil Survey Center, Lincoln, NE) which is typically at a scale of 1:24,000, corresponding to individual soil series. Statistical analysis for this subset was limited to ordinary Poisson regression, since the relatively small size of the data precluded the expression of enough spatial structure or replication to have enabled fitting a sophisticated spatial model (Das et al. 2002) that incorporates separate parameters for spatial correlation and over-dispersion.

Results

In 1997, 125 sites were sampled, while in 1998 195 sites were sampled for a total of 320 transects. Of these, 24 sampled in 1997 were resampled in 1998. The mean length of the transects, representing 15 min flagging bouts at each site, was 163 m.

Tick Abundance/Density. Ticks (n = 663) were collected from 68 of 125 (54%) transects (sites) in 1997 and from 129 of 195 (66%) sites in 1998. The number of ticks flagged per transect ranged from 0 to 26, with a mean of two ticks per transect. Standardized by time, the overall flagging effort resulted in capture of 0.14 (663/4,800) ticks per min.

***B. burgdorferi* Infection Prevalence.** The crude prevalence of *B. burgdorferi* infection in adult *I. scapularis* was 23/233 (9.9%) in 1997, and 94/430 (21.9%) in 1998. The overall crude prevalence of *B. burgdorferi* in adult *I. scapularis* was 117/663 (17.6%).

GIS and Statistical Analysis. Poisson log-normal regression, used to control for spatial autocorrelation, revealed statistically significant correlations between tick abundance and distance to deciduous forests and water bodies, as well as elevation, land cover and soil type (Table 2). The data were analyzed separately for each year to exclude potential variability introduced by factors that mask the spatial effects of interest, and because some of the same sites were sampled in both years. Exponential and Gaussian correlation models were selected for 1997 and 1998, respectively, based on the best fit when the empirical (observed/sample) variograms for each year's data were compared with a number of theoretical models.

Based on the consolidation of the original 38 STATSGO soil types into the nine categories used in

Table 2. GLMM analysis using exponential (1997) and Gaussian (1998) correlation (variables used as reference categories not shown)

Predictor variables	Coefficient	SEM	*P*-value
	1997		
DEM_1	1.4873	0.4514	0.0013
DEM_2	0.7840	0.5056	0.1240
DEM_3	−0.0418	0.5348	0.9379
Wat_1	0.4911	0.5000	0.3282
Wat_2	0.6564	0.4581	0.1549
Wat_3	0.0735	0.4274	0.8639
Deci_1	0.1169	0.4316	0.7871
Deci_2	1.0857	0.5609	0.0556
Ever_1	−0.3189	0.3872	0.4121
Ever_2	−0.2200	0.3540	0.5355
Ever_3	0.7281	0.3991	0.0709
Extreme drainage	−0.6752	0.4427	0.1303
Siliceous, fine-loamy soil	−3.4969	0.5670	0.0001
Micaceous soil	−1.7417	0.4983	0.0007
Skeletal, siliceous, fine-loamy	−2.0911	0.7851	0.0090
Fine-silty, fine-loamy soil	−1.0637	0.4745	0.0271
Loamy, siliceous soil	−0.8426	0.8068	0.2987
Fine-loamy soil	−2.4643	0.5941	0.0001
Loamy-skeletal soil	−1.5824	0.7209	0.0304
	1998		
No annual flooding	−0.5140	0.3618	0.1572
Elevation (m)	−0.0090	0.0038	0.0184
Distance to water (m)	−0.0005	0.0002	0.0158
Emergent vegetation	−0.3259	0.5084	0.5223
Row crops	0.1116	0.3557	0.7540
Low density residential	0.5145	0.4358	0.2394
Woody wetland	−1.1258	0.4733	0.0185
Pasture/hay	−0.5595	0.3786	0.1413
Evergreen forest	−0.9752	0.3632	0.0080
Mixed (decid./evergr.) forest	−0.3617	0.2904	0.2147
Distance to mixed forest (m)	−0.0031	0.0017	0.0517
Distance to deciduous (m)	0.0046	0.0016	0.0033
Siliceous, fine-loamy soil	0.5065	0.3843	0.1893
Micaceous soil	2.2480	0.6742	0.0010
Skeletal, siliceous, fine-loamy	0.4051	0.4330	0.3507
Fine-silty, fine-loamy soil	0.7520	0.4057	0.0555
Loamy, siliceous soil	0.6829	0.3936	0.0845
Fine-loamy soil	2.1030	0.4958	0.0001
Sandy soil	1.9890	0.4372	0.0001

See Table 1 for quartile-based categories.

Table 3. Poisson regression results for the 75 site subset for which soil series data (SSURGO) was available (variables used as reference categories not shown)

Predictor variables	*n*	Coefficient	SEM	*P*-value
Particle size				
Fine-silty	6	−0.6700	0.8634	0.4378
Fine-loamy	18	−0.4085	0.6902	0.5539
Loamy	8	−0.2282	0.8336	0.7842
Coarse-loamy	19	1.3799	0.6009	0.0217
Sandy, sandy-skeletal	8	−0.0747	0.6021	0.9013
Surface textural class				
Peat, muck, silty clay loam	4	0.5340	0.9670	0.5808
Loam, silt loam	19	0.6475	0.5128	0.2067
Loamy sand, sandy loam	14	0.4484	0.7822	0.5665
Sandy soil	15	1.9720	0.8187	0.0160
Channery soil, gravel	11	2.2010	0.7262	0.0024
Soil great group				
Fragiaqualfs	8	−1.5411	0.4469	0.0006
Endoaquults	2	−16.3831	490.431	0.9734
Soil subgroup				
Ultic	4	0.8314	0.4975	0.0947
Aeric	6	−0.2336	0.3289	0.4775
Aquic	9	1.8382	0.3029	0.0000
Haplaquodic	7	2.0895	0.7321	0.0043
Oxyaquic	3	1.6793	0.8067	0.0374
AWC				
0.102–0.267	15	7.8260	40.7454	0.8477
0.267–0.406	16	1.1071	0.4104	0.0070
0.406–0.508	25	−1.3376	0.3794	0.0004
Annual flooding	12	−1.5034	0.6167	0.0148
Drainage				
Very poor	7	−4.5725	40.7657	0.9107
Poor	7	−14.3642	57.6252	0.8032
Somewhat poor	7	0.9255	1.0792	0.3912
Moderately well	15	0.0545	0.7291	0.9404
Well drained	32	−2.3652	0.8690	0.0065

AWC = maximum available water capacity (cm water per cm soil).

the statistical model, significant positive correlations were found with sandy, micaceous, and fine-loamy soils. Distance from mixed (deciduous–evergreen) forests was also marginally associated with tick abundance. None of the environmental factors included in the model were associated with *B. burgdorferi* infection of the ticks when logistic regression for that binomial dependent variable was examined.

To validate the fitted regression model, we used cross validation by obtaining 90% prediction intervals of tick counts for each location, based on data from every other location, and finding the proportion of these prediction intervals that actually included the observed counts (Stone 1974). If the fitted model was sensible, this should have been close to 90%, the nominal level of coverage. Accordingly, we predicted tick counts for each of the 320 sampled locations, based on data from the remaining 319 locations. The 90% prediction intervals included the observed values at these locations in over 86% (276 out of 320) of the cases, thus satisfactorily validating the model in this study region.

Higher Resolution Soil Data. Higher resolution, and more comprehensive, soil data were available for 75 sites in counties that have registered their soil series data digitally (SSURGO). The number of ticks collected per transect from this subset of sites ranged from 0 to 16, with a mean number of two ticks per transect. In roughly one-third (31) of the sites no ticks were collected, one or two ticks were collected in another third (24 sites), and in the remaining third (20 sites) three or more ticks were collected. Six soil orders were represented in this data subset: Aflisols, Entisols, Inceptisols, Histosols, Spodosols, and Ultisols. Significant positive correlations were found between tick abundance and the following soil characteristics: coarse-loamy particle size, other soils of coarse texture (sandy, gravelly, channery [thin and flat limestone, sandstone, or schist fragments]), acidic soils, and a narrow range of low available water capacity (Table 3). Tick abundances increased significantly with increasing particle size (textural class), up to a cut-off point. The significant Great group correlation was negative for Fragiaqualfs, characterized by a loamy, brittle subsurface, silty soil, and very fine sand. An observable, albeit nonstatistically significant trend in the data were that older, fertile soils tended to be associated with low tick abundances, while younger, less-developed soil orders tended to be associated with higher tick abundances.

Discussion

As ectoparasites, the distribution of ticks is largely determined by their vertebrate hosts. However, the relative success of a tick population once established in a certain area is a function of the suitability of the local environment and microclimate. In this study, a number of environmental covariates were associated with adult *I. scapularis* density patterns. The factors that proved useful in estimating relative tick abundances at locations in the Middle Atlantic region of the U.S.A. may be considered surrogates for the risk to humans in acquiring Lyme disease or another *I. scapularis*-transmitted disease, assuming disease risk is an increasing function of tick abundance. Moreover, the current study identified soil factors that may provide insight into the biological mechanisms for observed statistical correlation between ticks and these environmental parameters.

The generalized linear mixed models revealed significant statistical correlations between tick abundance and environmental factors (Table 2). The implications of these statistical models are that sites with sandy soils, at lower elevations, and of moderate distance to forest and water are positive risk factors for tick encounter. Conversely, the following "protective" covariates characterize sites that were negatively correlated with high tick abundance: wetlands, increasing distance to water, higher elevations, siliceous soils, and skeletal and fine-loamy soil types. Surprisingly, the drainage attribute (STATSGO) was not found to be a significant predictor. The lack of statistical significance of drainage in this analysis may be a result of an interaction whereby poorly drained sites with shallow water tables or well-drained sites with deep water tables are conducive to tick development. Other investigators have noted that pedologic microclimate extremes favor tick survival (Bertrand and Wilson 1996). For instance, flooding per se does not favor tick survival, but periodic saturation does appear to exert an important positive effect.

Some variables that were negatively correlated with tick abundance in 1997 were positively associated in 1998 (e.g., micaceous soil). While possibly artifactual, it may reflect the limitation of using soil texture alone to predict tick abundance. It appears that there is interaction between soil textural properties and moisture regimes. The same type of micaceous soil might be flooded more or less often in one location than in another based on climate, slope, aspect, and vegetation cover, for example. Intriguingly, the Middle Atlantic region was both wetter in winter and drier in summer in 1998 as compared with 1997 (National Climate Data Center, Asheville, NC; data not shown). Interactions between these two environmental covariates are being examined in greater detail (see below).

The distance to forest edge term implies that as compared with being inside the forest, being relatively close to the forest edge favors tick abundance. This phenomenon may reflect the suitability of ticks to ecotones (Sonenshine 1993). It is important to note complexities in interpreting results based on this covariate. Deciduous, evergreen, and mixed (deciduous–evergreen) forests were discernable by the MRLC. Sites that fell in forested areas were classified as one of those types, but distance to particular forest type was calculated for all sites, regardless of whether they occurred in another forest type. In fact, 27 of the 59 (45.7%) sites in 1998 with distance to deciduous forest >60 m were in another forest type (22 evergreen, five mixed). Similarly, the majority of the 80 sites in the highest quartile distance to evergreen forest (190–1243 m) were located in deciduous forests (48/80, 60.0%). That the correlative effects were different for the various forest types implies that there are actual differences in tick suitability depending on forest type, with evergreen forests apparently relatively less likely to be associated with high tick abundances.

The overall infection prevalence for *B. burgdorferi* in adult *I. scapularis* for this region of 17.6% compares with 8.5% measured in Maryland one decade ago (Amerasinghe et al. 1992) and 14.3% in Connecticut from 1989 to 1996 (Stafford III et al. 1998). In contrast to the significant associations identified between certain environmental factors and tick abundance, no such correlations emerged when those same themes were tested for association with *B. burgdorferi*-infection in adult *I. scapularis*. These analyses were only performed using the 1998 data because ticks collected in 1997 were assayed for *B. burgdorferi* in pools, and we could not assign them to specific transects. The results from 1998 imply that so long as environmental conditions are suitable for the local establishment of *I. scapularis*, then *B. burgdorferi* can be maintained and there is little evidence for a tick population threshold needed for bacterial persistence. *B. burgdorferi*-infected ticks were collected at 130 of the 195 (67%) sites sampled that had *I. scapularis*. Of those 130 sites, only 45 (35%) were characterized by having more than one *B. burgdorferi*-infected tick.

The sampling method of flagging introduces potential bias (Ginsberg and Ewing 1989). Many more ticks may be collected from hunter-killed deer than by flagging in an equal amount of time. However, analyses of tick abundance collected from deer also have many difficulties. Most significantly, deer have sufficiently wide geographic ranges so that at our spatial scale there is uncertainty in assigning environmental attributes to the numbers of ticks collected where the deer were reported killed. Another potential confounding factor is fluctuations in environmental variables that change on a short time scale (Clark 1995). For example, temperature, wind speed and relative humidity affect sampling success. The distances between flagging locations and the large number of sites sampled made it logistically impossible to record these environmental variables at a local scale. The overall average flagging efficiency of 0.14 ticks per min compares favorably with 0.16 *I. ricinus* per min in a Danish study (Jensen et al. 2000), suggesting the results observed here are comparable to other studies.

Because larvae and nymphs probably fed on mice or other small mammals with relatively restricted geo-

graphic ranges, most of the questing adult ticks collected in this study were likely collected not far from where the eggs had been deposited by the previous generation's gravid females. Therefore, the interpretations of the environmental influences on tick distribution patterns reflect differential egg deposition or survival. There are several possible links between soil type and tick distribution: (1) *Indirect:* soil type influences the plant communities that determine the suitability of supporting small mammal and deer populations, natural hosts for *I. scapularis;* (2) *Direct:* (a) water-holding capacity of soil is an important regulator of larval, nymphal and adult ticks' need to resist desiccation, but not become so moist that fungi have the opportunity to colonize the ticks, and (b) soil type determines differential egg hatch success rates. The latter association may be because the ticks deposit a profusion of eggs more or less randomly, and those that happen to be deposited in appropriate soils have the greatest likelihood of hatching and developing successfully. In contrast to the nonegg stages of the tick, the eggs may be more protected from desiccation, and more susceptible to colonization by molds. A sandy soil would allow the eggs to settle in an insulated layer of soil just below the surface. This would both protect the eggs from excessive moisture, and also discourage the presence of herbaceous plant growth conducive to insects and other animals that may prey on tick eggs.

Of the 75 sites within the SSURGO subset that had the more detailed soil data available, the three with the greatest tick abundances were located in the coastal plain of New Jersey on sandy, acidic soils. Soil at the site where the greatest number of ticks ($n = 16$) were collected is of the order Spodosols, suborder Aquods, greatgroup Haplaquods, subgroup typic, series Berryland sand. This extremely acidic soil is siliceous and sandy, and is frequently flooded. Drainage is very poor, and the depth to the water table is less than one foot. Permeability is moderately rapid, while surface runoff is slow. Parent material is composed of sandy marine sediments. Vegetation consists of a dense understory of blueberry, sweet pepperbush, bay magnolia, leather leaf, gallberry, and greenbriar, and the trees pitch pine, widely spaced Atlantic white cedar, red maple and black gum. This soil series is found in the coastal plain of New Jersey, Maryland, Delaware, Maine, and possibly Long Island, NY.

Sites within the SSURGO subset with the next highest numbers of ticks ($n = 12$, $n = 11$) were characterized by soils of the Hammonton series. Parent material consists of sandy and loamy marine sediments. They are in the order Ultisols, which along with Spodosols, are generally low in fertility. Like Berryland soils, permeability is moderate to moderately rapid, while surface runoff is very slow. These coarse-loamy, siliceous soils are similarly very strongly acidic. The biological significance of acidity interacting with soil moisture may create biochemical cues for successful egg development; e.g., trace metal nutrients are more readily leached from geologic sources with increased acidity, making them more bioavailable to tick eggs.

We believe that the association between soil and ticks is a direct one because the available water capacity (AWC) was positively correlated with tick abundance only within a narrow range of values (0.267–0.406 cm water per cm soil) (Table 3). This result is consistent with the humidity requirements for *I. scapularis:* they run the risk of dessication in dry conditions, but are subject to fungal attack if conditions are too wet.

We speculate that there is an important interaction, however, between soil texture and climate; viz. rainfall, humidity, or other factors that affect soil moisture, such that well-drained soils are positively correlated with tick abundance provided that there is high rainfall and limited annual flooding. Previous studies have noted positive correlations between tick abundance and sandy, well-drained soils (Glass et al. 1994, 1995), and high soil and vegetation moisture (Dister et al. 1997). Sutherst et al. (1999) also noted that high rainfall at well-drained sights favored cattle tick (*Boophilus microplus*) (Canestrini) survival. The present analysis reveals that poorly drained soils, too, are associated with high tick abundances, but only with frequent annual flooding and probably low rainfall. Climate factors may account for some of the substantial variation in tick abundance patterns within similar habitats (Schulze and Jordan 1996).

Future models may be improved by incorporating variable climatic factors. The dynamics of temperature and precipitation during winter months when eggs or juveniles are in the soil, roughly 18 mo previous to the year when adults are collected by flagging, may account for significant variation in the outcome. Future studies can use the present analysis to design laboratory and field experiments to test the hypothesis that soil texture in conjunction with moisture availability during the egg stage exerts direct pressure on tick generational survival success.

Mouse and deer reservoir population distributions should be studied in similar analyses to establish their relationship to environmental correlates, at appropriate scales; the current study focuses exclusively on the vector. While *I. scapularis* ticks may be transported over large distances by *Odocoileus virginianus* (Zimmermann), the white-tailed deer, with ranges up to 50 km, as well as by migratory birds, they probably do not move far under their own locomotion from where the eggs were deposited (Sonenshine et al. 1995). More complete understanding of how environmental factors influence vector distribution patterns should improve prevention and control strategies for human Lyme borreliosis and other emerging vector-borne diseases.

Acknowledgments

The authors wish to gratefully acknowledge the expert technical and logistical assistance provided by Subhash R. Lele, J. Stephen Dumler, Jonathan Patz, Stephen C. Guptill, Doug Wysocki, and James Brown. We thank the State Park Superintendents from the states of Delaware, Maryland, and New Jersey, and the commonwealths of Pennsylvania and

Virginia. Funding was obtained from U.S. EPA ORD grant 96-NCERQA-1B, NASA grant NCC5–305, and the First Ralph and Sylvia Barr Fellowship in Medical Entomology awarded to Bunnell in 1998. This work was completed in partial fulfillment of Bunnell's doctoral degree in the Department of Molecular Microbiology and Immunology at the Johns Hopkins University Bloomberg School of Public Health.

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Received for publication 13 December 2001; accepted 11 October 2002.