AN INVESTIGATION OF LYME DISEASE RISK ALONG OLD FIELD-FOREST EDGES IN SOUTHEASTERN NEW YORK

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Abstract. Past studies have shown white-footed mouse (*Peromyscus leucopus*) density to be highest within the forest, decreasing with increasing distance into old fields. Since white-footed mice are the most competent reservoir for the Lyme disease bacterium, *Borrelia burgdorferi*, and the primary host for the blacklegged tick (*Ixodes scapularis*), the vector of Lyme disease, this trend could have important epidemiological implications. It has been predicted that in areas of low white-footed mouse abundance, density of nymphs (DON), nymphal infection prevalence (NIP), and density of infected nymphs (DIN) will be lower. Therefore, we predicted that the decreasing *P. leucopus* density into old fields should be reflected in a corresponding decrease in Lyme disease risk. To test this prediction, nymphal density measurements were taken along thirty transects located at five different distances into the forest and field at six old field-forest edge sites in Dutchess County, New York. In addition, nymphal infection prevalence was calculated for four categories of distance from the forest edge. From these two measurements, density of infected nymphs was calculated for each transect. The results of this study show that both DON and DIN are significant negative functions of distance from the forest edge into old fields. These results indicate a lower Lyme disease risk in fields as compared to forests, knowledge that will be beneficial in helping humans protect themselves against exposure to Lyme disease.

INTRODUCTION

Lyme disease is the most common vector-borne disease in the United States (CDC 1997), with over 16,000 human cases reported annually (CDC 2001). Human cases of this disease have been reported in 49 states and the District of Columbia, with the highest incidence rates being found in the northeastern states (Orloski et al. 2000). Lyme disease is caused by a bacterium, *Borrelia burgdorferi*, which, in the northeastern United States, is transmitted between hosts and to humans via the bite of an infected black-legged tick, *Ixodes scapularis* (Mather et al. 1990, Fish 1993).

The Ixodid tick life cycle is made up of three post-egg stages: larva, nymph and adult. During each post-egg stage the tick receives a single blood meal from a host before molting into the next stage as a larva or nymph, or reproducing and dying as an adult. The tick has the opportunity to acquire the spirochete during any of these three blood meals, provided that it feeds off of an infected host that efficiently transmits the bacterium. With very little transovarial transmission of the spirochete, nearly all larvae hatch free of the bacterium (Piesman et al. 1986, Magnarelli et al. 1987). While they do not transmit the Lyme disease agent, larvae do play an important role in most human cases of Lyme disease because it is during the larval blood meal that ticks have the opportunity to acquire the spirochete that would enable them to infect humans as nymphs (Mather et al. 1989). This is significant because while both nymphs and adults have the ability to transmit the disease, the majority of human Lyme disease cases are acquired through bites from a nymphal tick, possibly due to its small size and its peak activity period in late spring and early summer coinciding with the peak of human outdoor activity (Piesman et al. 1987, Barbour and Fish 1993).

Since nymphal bites pose the greatest risk to humans in terms of Lyme disease transmission, measures of disease risk focus on the nymphal population (Mather 1993). The primary measure of Lyme disease risk is the density of infected nymphs (DIN), which is the product of the overall density of nymphs (DON) and the proportion of those

nymphs that are infected (the nymphal infection prevalence (NIP)) (Mather 1993, Ostfeld and Keesing 2000b). DON, NIP, and DIN, then, must be examined in order to determine disease risk.

An important influence on DON and NIP is larval host availability (Van Buskirk and Ostfeld 1998), so an understanding of *I. scapularis*-host relationships is essential to understanding any spatial variation in Lyme disease risk. In the northeast, the primary host of juvenile black-legged ticks and the primary reservoir of B. burgdorferi is the white-footed mouse, *Peromyscus leucopus* (Levine et al. 1985, Mather et al. 1989). To be considered an epidemiologically important reservoir for Lyme disease an animal must occur in high numbers in areas with *I. scapularis* populations, host a large number of juvenile *I. scapularis*, be frequently infected with *B. burgdorferi*, and be highly infectious to the feeding ticks (Mather et al. 1989, Lane et al. 1991). The white-footed mouse demonstrates all of these characteristics (Mather et al. 1989). *P. leucopus* host a high number of larval and nymphal *I. scapularis* (Levine et al. 1985, Mather et al. 1989, Adler et al. 1992), and are populous in the forest (Morris 1991, Markowski et al. 1998) where *I. scapularis* density has been shown to be highest (Maupin et al. 1991, Schmidtmann et al. 1994, Ostfeld et al. 1996). Past studies have found that the white-footed mouse is the most infectious host, with about 90% of ticks feeding off of these mice receiving the spirochete (Mather et al. 1990, Mather 1993). Furthermore, larvae that feed on white-footed mice are more likely to successfully molt into nymphs than those receiving their blood meals from other animals (Mather and Ginsberg 1994).

Because other hosts do not share the reservoir characteristics of white-footed mice, it has been predicted that habitat-related variation in mouse density could result in variation in Lyme disease risk between habitats (Ostfeld and Keesing 2000a, Schmidt and Ostfeld 2001). The dilution effect proposed by Ostfeld and Keesing (2000a) states that the lower the host representation by white-footed mice, the higher the proportion of larvae that must feed on less competent reservoirs; therefore, DIN should be lower in areas with fewer white-footed mice. This possibility of a dilution effect in habitats with a low representation by white-footed mice, combined with the current lack of knowledge about variation in NIP and DIN between habitats, suggested the need for a study of variation in Lyme disease risk across habitats.

With an abandonment of agriculture in parts of the northeast in the 1900's, old fields surrounded by forest patches of varying size have become a prominent landscape feature (Glitzenstein et al. 1990, Lane et al. 1991). Because they bring together a variety of habitats (forest, herbaceous or shrubby fields, and edge habitat) in a small area, and because much is known about the small mammal population at the interface (Grant 1972, Ostfeld et al. 1997, Manson et al. 1998), it was decided that old field-forest edges would be ideal sites for studying variation in Lyme disease risk across habitats. Since people utilize forest, field, and edge habitats, it would be beneficial for them to know in which environment(s) they are most at risk for acquiring Lyme disease so that they can take the proper precautions to minimize such risk.

Thus, the purpose of this study was to discover what variation exists in Lyme disease risk (defined by DIN) or its components, DON and NIP, along old field-forest edges. We hypothesized that the observed risk pattern would reflect the known white-footed mouse population gradient, being highest in the forest, lower near the edge, and still lower out into the field (Grant 1972, M'Closkey and Fieldwick 1975, M'Closkey and LaJoie 1975).

METHODS

Six old field-forest edge sites were selected in Dutchess County, New York, a county with one of the highest incidence rates of Lyme disease in the United States (Orloski et al. 2000). All sites were located at or near the Institute of Ecosystem Studies (41° 50′ N, 73° 45′ W). The dominant species in the forests and fields varied between sites, as did the successional stage of the fields. The predominant vegetation types found at the primarily herbaceous field sites were *Schizachyrium scoparium, Bromus inermis, Phleum pratense, Galium tincturum, Solidago juncea, S. rugosa, Vicia cracca, Centuria maculosa,* and *Carex sp.*, while *Lonicera morrowi, Cornus racemosa,* and *Rosa multiflora* were also present at the shrubbier sites (Ostfeld et al. 1997).

At each of the sites, five 80 m long transects were established, running parallel to the forest edge. The transects were 2 m wide, centered at 4 m into the forest and 1, 11, 21, and 34 m into the field. Between 10 am and 4 pm from June 25 through June 30, 2001, a single nymphal density measurement was taken along each transect. A one m^2 white corduroy drag cloth was pulled along each transect with the cloth kept as close to the ground as possible. The cloth and the researcher's clothing were examined for ticks every 20 m. Nymphal ticks were counted, removed, and maintained alive for later analysis. These systematic counts allowed us to express DON as the number of nymphs captured per m^2 at each distance category. This method of estimating nymphal density has been shown to be both reliable and effective (Falco and Fish 1992).

During the remainder of nymphal peak, using the method described above, additional nymphs were collected from transects to increase sample size for determining infection prevalence. Due to problems collecting an acceptable number of ticks from the two transects farthest into the field, the five distance categories used for DON measurements were combined into four categories for NIP analysis – forest (-4 m), edge (1m), 11 m, and 21+ m – and nymphs from the same distance category were pooled across sites. This pooling was necessary to have a sufficient number of nymphs from each distance for determining NIP.

Collected nymphs were washed in 70% ethanol and deionized water, and crushed in an Eppendorf tube containing phosphate-buffered saline (PBS) solution. The PBS-tick solution from each tick filled three separate wells of a multi-well slide, which was then fixed in cold acetone. Fluorescein conjugate was added to each well, and the slides were incubated at 37° C for 45 minutes. They were then washed in PBS solution and deionized water, dried, and mounted in fluorescent-antibody mounting medium. Wells were examined for spirochetes under a fluorescent microscope at 400x magnification, with each tick being classified as positive or negative for the presence of *B. burgdorferi*. If a nymph was not immediately classified as positive then all three wells for that tick were methodically scanned. A minimum of ten nymphs was examined from each distance category, and the proportion infected was the NIP for that category.

From the DON and NIP measurements, DIN was calculated for the five original categories (forest, edge, 11 m, 21 m, and 34 m), using the NIP for the 21+ m category in calculations of DIN at both 21 m and 34 m. Regression analyses were performed to determine whether DON, NIP, and DIN were significant functions of distance from the forest. ANOVA tests with post hoc comparisons were also performed to determine which distances from the forest differed significantly in terms of DON and DIN.

RESULTS

A regression showed DON to be a significant negative linear function of distance from forest ($R^2 = 0.27$, $P = 0.004$, $N = 30$; Figure 1A). A one-way ANOVA with Tukey HSD Multiple Comparisons revealed that density of nymphs within the forest (-4 m) was significantly higher than DON at 21 or 34 m into the field ($P = 0.011, 0.015$; Figure 2A). Nymphal density was two times higher in the forest than it was at any of the measured distances away from the forest (Table 1). A regression indicated that NIP was not a significant function of distance from forest ($R^2 = 0.59$, $P = 0.23$, $N = 4$). However, a notable negative trend was observed between NIP and distance with 40% of the nymphs captured in the forest being infected and between 20 and 25% of the nymphs captured at varying distances into the field being infected (Figure 2B). A regression did reveal DIN to be a significant negative linear function of distance from forest ($R^2 = 0.31$, $P = 0.001$, $N = 30$; Figure 1B). A one-way ANOVA with Tukey HSD Multiple Comparisons revealed that density of infected nymphs was significantly higher within the forest than it was at any of the other transect locations ($P < 0.01$ for all distances; Figure 2C). Density of infected nymphs was more than four times higher within the forest than it was at 1 or 11 m into the field and more than 36 times higher within the forest than it was at 21 or 34 m (Table 1).

DISCUSSION

While past studies have found DON to be highest within the forest (Ginsberg and Ewing 1989, Maupin et al. 1991, Siegel et al. 1991, Stafford and Magnarelli 1993, Ostfeld et al. 1995, Carroll and Schmidtmann 1996, Ostfeld et al. 1996), prior studies have not examined DON as a function of distance from forest edges. In the present study, DON was found to be highest in the forest; in addition, it was found to be a significant negative function of distance from the forest. Likely, this density gradient is the result of a combination of abiotic and biotic factors. Ixodid ticks are very vulnerable to desiccation (Balashov 1972, Schulze et al. 1984); therefore, they are limited to microclimates with sufficient humidity. Tick mortality is higher in dry, open habitats (Milne 1950), conditions characteristic of many old fields. However, forests have a canopy and leaf litter, which can buffer adverse weather effects such as direct sunlight and drying winds. These characteristics are likely to be at least partially responsible for the higher DON we observed in the forest.

It is possible that these abiotic factors do not fully explain the difference in DON; biotic factors are likely involved as well. Other determinants of DON include larval abundance and the proportion of larvae that find a host and feed successfully (Hazler and Ostfeld 1995). The first of these, larval abundance, is a function of the abundance of white-tailed deer, the primary host for adult blacklegged ticks (Wilson et al. 1988, Duffy et al. 1994). Numerous studies have shown that larval density is higher in the forest than in fields (Maupin et al. 1991, Ostfeld et al. 1996), a finding that would likely contribute to the higher number of nymphs found in the forest in this study. The other determinant of nymphal abundance, the proportion of larvae finding hosts and feeding successfully would be expected to be highest in areas with a high abundance of the primary host for juvenile ticks, the white-footed mouse. As mentioned earlier, white-footed mice host more ticks than most other animals (Levine et al. 1985, Mather et al. 1989, Adler et al. 1992), and larvae that feed off them are more likely to molt into nymphs successfully (Mather and Ginsberg 1994). Therefore, the higher DON in the forest can likely be partially attributed to white-footed mice being most abundant in the forest (Morris 1991, Markowski et al. 1998).

The other factor involved in calculating Lyme disease risk, NIP, did not vary significantly between locations; however, it did show a decreasing trend from the forest into the field. Due to difficulty acquiring nymphs from the transects farthest away from the forest, the sample size for determining infection prevalence was small. Had we not had to pool the nymphs from same-distance transects in calculating NIP, there is a possibility that with the increased sample size, the decreasing trend we observed might be statistically significant.

While not significant on its own, the downward trend in NIP combined with the significant decrease in DON as a function of distance from the forest resulted in a highly significant decrease in DIN from the forest to the field. This decrease corresponds to what would be expected based on what is known about the composition of the small mammal community at old field-forest edges and what is known about the dilution effect. In herbaceous old fields, such as the majority of the sites utilized in this study, meadow voles are the dominant small mammal species (Lobue and Darnell 1959, Rose and Birney 1985, Ostfeld and Manson 1996). Since voles are dominant to white-footed mice (Grant 1972, Ostfeld et al. 1997, Manson et al. 1998), their presence in fields tends to restrict the mice to the forest, where they are the dominant small mammal species (Grant 1972, Ostfeld et al. 1997, Baker 1968, Morris 1991). In studies done by Ostfeld and colleagues (1997) at the same sites used in this study, vole activity was found to be more common at 5, 10, and 20 meters into the field than at the edge or 5 m into the forest. Therefore, the distances from the forest edge observed to have higher vole activity in the past correspond with those having the lowest DIN in this study. This result supports the idea of a dilution effect because the field, a habitat associated with a lower abundance of white-footed mice was shown to have a lower DIN than the forest, with the DIN gradient reflecting the previously observed gradient in white-footed mouse abundance across the edge.

Since DIN, the primary measure of Lyme disease risk, was several times higher in the forest than at or near the edge and many times higher than distances greater than 10 m from the forest, it is apparent that people run the greatest risk of being exposed to an infected nymph, and hence to the Lyme disease bacterium, in the forest. Thus, people should take proper precautions when entering the forest and should very thoroughly check themselves for

ticks upon exiting. However, it should be noted that infected nymphs were present at all distances into the field as well; therefore, risk is not limited to the forest.

Future study is warranted in this area. First, since the only forest measurements taken extended just 5 m into the forest, further study should be done to clarify whether risk is constant throughout the forest. It is possible that risk is highest near the edges of the forest, as Schmidtmann and colleagues (1994) found nymphal density to be highest in the shallow woods and Allan et al. found DIN to be highest in smaller forest fragments (Allan et al., in review). Also, since this study combined many forest and field types, further study should be done comparing Lyme disease risk between forests and fields of differing vegetation composition and successional stage. These additional studies could help in clarifying where "hot spots" for Lyme disease risk occur, knowledge which hopefully would lead to increased awareness and precaution, and, as a result, less human Lyme disease cases.

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APPENDIX

TABLE 1. A comparison of mean density of nymphs and mean density of infected nymphs at different distances from the forest edge.

Distance (m)	DON (nymphs/m^2)	DIN (infected nymphs/m^2)
-4	0.2260	0.0904
1	0.0750	0.0176
11	0.0833	0.0208
21	0.0052	0.0010
34	0.0125	0.0025

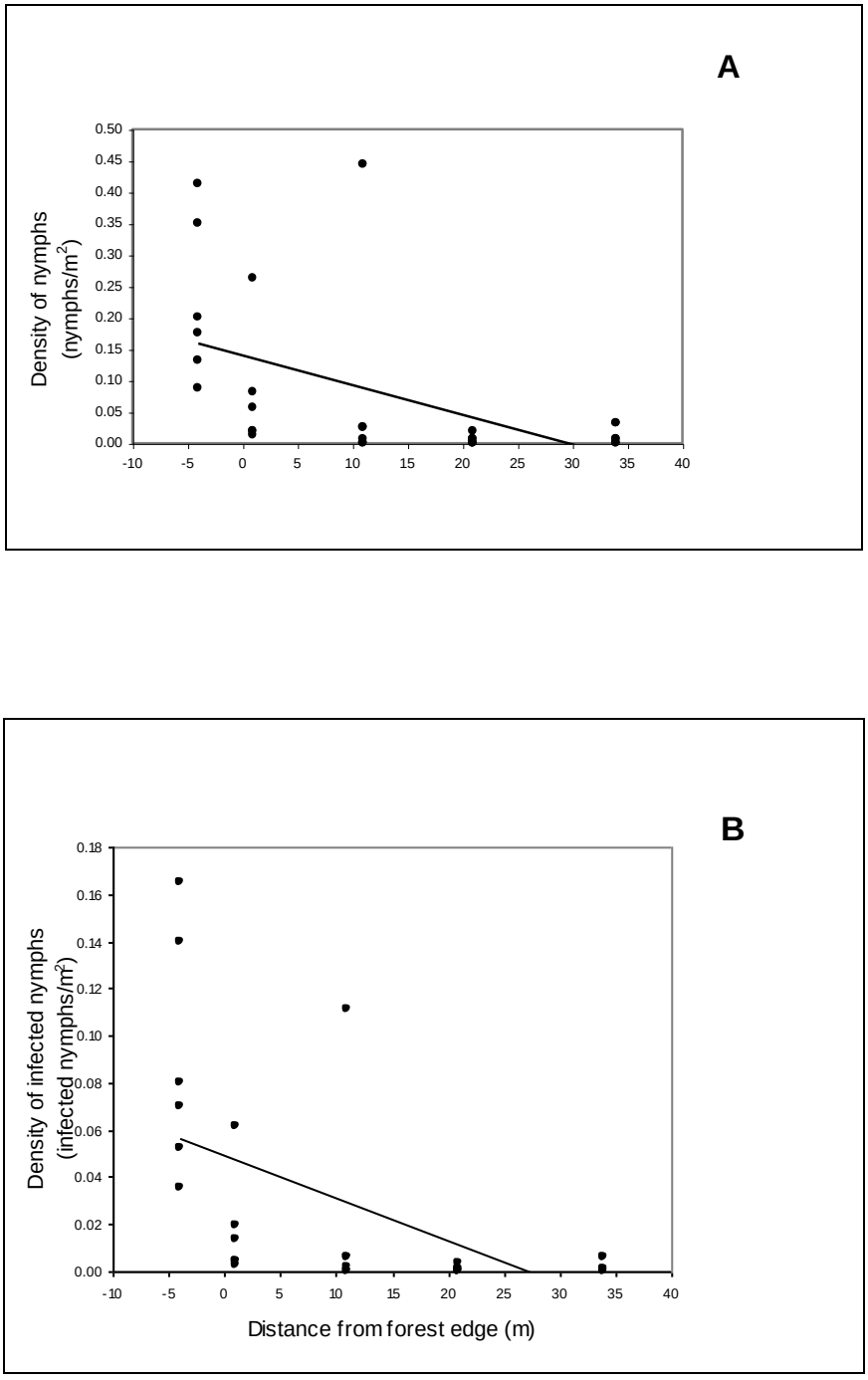

FIGURE 1. Relationship between two components of Lyme disease risk and distance from the forest edge into old fields in Dutchess County, NY. (A) Density of nymphs plotted against distance from the forest edge (R^2 = 0.27, P = 0.004, N = 30); (B) Density of infected nymphs plotted against distance from the forest edge (R^2 = 0.31, P = 0.001, N = 30).

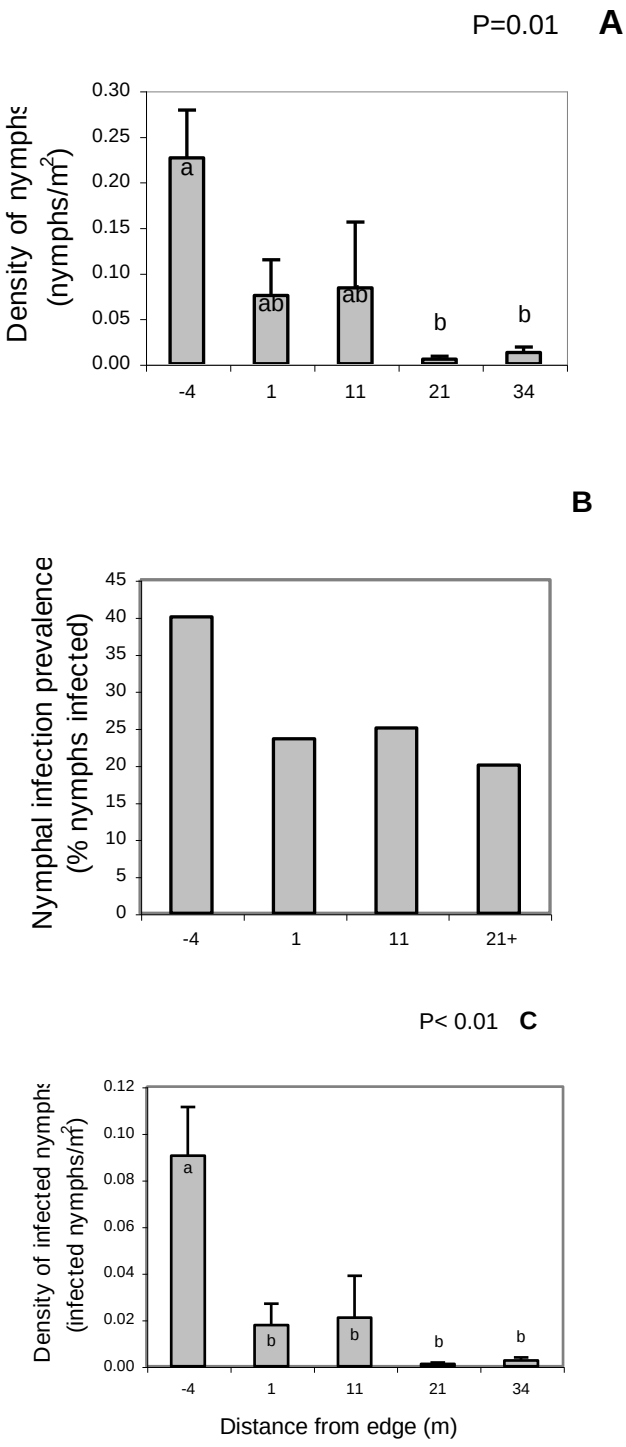

FIGURE 2. Comparison of the components of Lyme disease risk at different distances from the forest edge. Data shows means + 1 SE (A) Density of nymphs collected at different distances from the forest edge (B) Nymphal infection prevalence at different distances from the forest edge (C) Density of infected nymphs collected at different distances from the forest edge.