

Ixodes scapularis and *Borrelia burgdorferi* Among Diverse Habitats Within a Natural Area in East-Central Illinois

Jennifer Rydzewski,¹ Nohra Mateus-Pinilla,² Richard E. Warner,³ Sarah Hamer,⁴ and Hsin-Yi Weng⁵

Abstract

The distributions of the tick vector, *Ixodes scapularis*, and of the etiologic agent of Lyme disease, *Borrelia burgdorferi* (*Bb*), have continued expanding in Illinois over the past 20 years, but the extent of their spread is not well known. The role of multiple habitats in the establishment and maintenance of *I. scapularis* and *Bb* at local scales is not well understood, and the use of integrated approaches to evaluate local scale dynamics is rare. We evaluated habitat diversity and temporal changes of *I. scapularis* occurrence and *Bb* infection within a natural area in Piatt County, Illinois, where *I. scapularis* were first detected in 2002. Small mammals were trapped and attached ticks were collected in young forest, prairie, mature forest, and flood plain sites from 2005 to 2009. Small mammal abundance, and the prevalence (% mammals infested), mean intensity (*I. scapularis* per infested mammal), and relative density (*I. scapularis* per mammal trapped) of *I. scapularis* were computed for each habitat type and compared. Immature *I. scapularis* were tested for *Bb* infection using polymerase chain reaction techniques. Out of 2446 trapped small mammals, 388 were infested with *I. scapularis*. The prairie had the highest diversity of small mammal hosts. Prevalence, mean intensity, and relative density of *I. scapularis* and prevalence of *Bb* infection were highest for the prairie and young forest sites; in the former, all infection was associated with the prairie vole, *Microtus ochrogaster*. The minimum *Bb* infection prevalence of on-host *I. scapularis* collected in the natural area was 14% ($n=56$). Unlike previous studies solely focused on forested areas and *Peromyscus leucopus*, our study is the first to provide evidence of *I. scapularis* collected from prairie habitat and other reservoir hosts, particularly *M. ochrogaster*.

Key Words: *Borrelia*—*Ixodes*—Lyme disease—Rodents—Tick(s).

Introduction

LYME DISEASE IS CAUSED BY the spirochete *Borrelia burgdorferi sensu stricto* (*Bb*) and is transmitted by the black-legged tick, or deer tick (*Ixodes scapularis*) in the Northeast and Midwest United States (Burgdorfer et al. 1982, Davis et al. 1984, Lane et al. 1991). *I. scapularis* is a three-host generalist tick that feeds on a wide variety of hosts, primarily small mammals, during its immature stages (Mather et al. 1989). *Bb* is transmitted to immature *I. scapularis* during a blood meal from an infected host (Anderson et al. 1983). Once infected, *I. scapularis* ticks maintain the spirochete transstadially (Fish 1993). The white-footed mouse (*P. leucopus*) is a common host for feeding immature *I. scapularis* and is considered an

important reservoir host for *Bb* (Levine et al. 1985, Donahue et al. 1987, Hofmeister et al. 1999). Other small mammals, specifically rodents, also serve as hosts for immature *I. scapularis* (Anderson et al. 1985, 2006, Markowski et al. 1997, 1998); however, they are relatively less competent as reservoir hosts for *Bb* (Mather et al. 1989, LoGiudice et al. 2003).

In the Midwest, populations of both the vector tick and spirochete were once limited to southeast Minnesota and northwest Wisconsin (Davis et al. 1984, Callister et al. 1988, 1991); however, the focal endemic area has expanded farther into Illinois (Bouseman et al. 1990, Cortinas and Kitron 2006) and the surrounding states (Pinger et al. 1996, Walker et al. 1998, Lingren et al. 2005, Hamer et al. 2007) in the past 20 years. In Illinois, Lyme disease has mainly been identified in the

¹Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, Illinois.

²Illinois Natural History Survey, Institute of Natural Resource Sustainability, University of Illinois at Urbana-Champaign, Urbana, Illinois.

³Office of Sustainability, University of Illinois at Urbana-Champaign, Urbana, Illinois.

⁴Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan.

⁵Department of Pathobiology, University of Illinois at Urbana-Champaign, Urbana, Illinois.

northern third of the state (Kitron et al. 1991, Nelson et al. 1991, Jobe et al. 2006, 2007). There were 108 reported human cases in 2008 compared to only 35 cases in 2000 (IDPH 2010).

The distribution and occurrence of *I. scapularis* is typically associated with environmental factors such as tick habitat suitability (Kitron et al. 1991, Guerra et al. 2002) and small mammal host abundance (Anderson et al. 1983, Brownstein et al. 2003). Suitable habitat for *I. scapularis* has been characterized by oak-dominated forested areas with sufficient leaf litter and moist, sandy soils (Kitron et al. 1992, Schulze et al. 1998). Favorable vegetation, soil, topography, and climate are necessary for successful questing, molting, diapause, and oviposition of *I. scapularis* (Guerra et al. 2002). Although the ecological and spatial determinants of variation in *I. scapularis* distribution and habitat use are not well understood at the local-scale level (Goodwin et al. 2001), fragmentation of habitat into small forest patches has been associated with decreased vertebrate species diversity and increased densities of *P. leucopus* (Nupp and Swihart 1998, Rosenblatt et al. 1999). In some areas, the net effect of decreasing patch size is an increasing fraction of *I. scapularis* feeding on a *Bb*-competent reservoir, thus increasing the risk for high nymphal infection prevalence (Ostfeld and Keesing 2000, Allan et al. 2003).

Illinois, once dominated by tall-grass prairie, is now characterized by a highly fragmented landscape where forest patches are surrounded by urban areas, remnant prairie patches, and agricultural lands (Rosenblatt et al. 1999). The spatial variation and dynamism of the Lyme disease system highlight the need for a more comprehensive approach to study *I. scapularis* and *Bb* habitat suitability in small natural areas (Killilea et al. 2008). Both decreased biodiversity and increased habitat fragmentation are occurring throughout Illinois with potential implications for shaping Lyme disease risk.

In this study, we evaluated habitat diversity and temporal changes of *I. scapularis* occurrence and the maintenance of *Bb* among small mammal hosts within a natural area in east-central Illinois. The objectives of this study were (1) to determine *I. scapularis* occurrence and *Bb* infection across four habitat types within the natural area, and (2) to evaluate differences in *I. scapularis* occurrence and *Bb* infection over a 5-year period.

Materials and Methods

Study area

The study was conducted between 2005 and 2009 in Robert Allerton Park (RAP), a 614 ha natural area owned by the University of Illinois located 6.4 km southwest of Monticello, in Piatt County, Illinois. Since initial detection of *I. scapularis* in RAP in 2002, this study represents the only *I. scapularis* surveillance effort conducted in Piatt County to date. The park is bisected by the Sangamon River; the south half is a natural area consisting of a river corridor, a flood plain, upland and bottomland forests, meadows, and prairie surrounded by an intensively farmed agricultural landscape (Fig. 1). Four sites representative of the habitats found within the park were selected. Site 1 is an upland young successional forest comprised of oak-hickory (*Quercus-Carya*) stands and heavy undergrowth (Wang et al. 2008). Site 2 is a restored tall-grass prairie mainly comprised of big bluestem and Indiangrass (*Andropogon gerardii*, *Sorghastrum nutans*). Site 3 is a mature

successional forest comprised of old-growth oak-hickory (*Quercus-Carya*) stands. Site 4 is a floodplain of the Sangamon River dominated by silver maple and green ash (*Acer saccharinum*, *Fraxinus pennsylvanica*) (Wang et al. 2008).

Sampling frame

A 90×90 m grid consisting of 100 trapping stations set 10 m apart was established within each site similar to the methods described by Kitron et al. (1991). Two 5.08×6.35×16.51 cm³ Sherman live traps (H.B. Sherman Traps, Tallahassee, FL) baited with sunflower seeds were placed 1 m apart at each trapping station for a total of 200 traps per night at each site. Traps were set in the late afternoon and retrieved the following morning. Trapping took place approximately one night every 2 weeks from June through October 2005–2009 with the exception of two trap nights in May 2007 and one in November 2008. Each site was trapped between 3 and 11 nights per year (mean=6.3, SD=2.56), and between 30 and 33 nights over the study period (mean=31.5, SD=1.29).

Small mammal processing

Captured mammals were restrained, identified, ear-tagged (National Band and Tag, Newport, KY), and examined for ticks. Ticks were removed using tweezers and placed in vials containing 70% ethanol for later identification and lab analysis. Recaptured mammals were similarly processed, and their ear tag numbers were recorded. After examination, the small mammals were released at the trapping site.

Lab analysis

Identification of the ticks to life stage and species was performed under a dissecting microscope using an identification key (Sonenshine 1979). Multiple *I. scapularis* larvae from a single host were pooled and tested as one unit, and nymphs were tested individually. Total DNA from the larval pools and nymphs was extracted using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) following a modified version of the Qiagen supplementary protocol: Purification of Total DNA from Ticks for Detection of *Borrelia* DNA.

The DNA samples were tested for *Bb* at Michigan State University using either (1) a nested polymerase chain reaction (PCR) for the 16S–23S rRNA intergenic spacer region of *Borrelia* spp. (Bunikis et al. 2004) followed by visualization with gel electrophoresis or (2) a quantitative PCR of a region of the 16S rRNA of *Bb* (Tsao et al. 2004). The intergenic spacer region primers used for PCR will amplify other *Borrelia* species. However, the only other two Midwest species detected in the lab at MSU are unlikely to be the cause of the positives. *Borrelia miyamotoi* makes a visibly smaller band on the gel, and *Borrelia andersoni* is bird-associated and has only been isolated from ticks removed from birds. A subset of the DNA samples were sequenced to confirm identification of *Bb*. The nested PCR was utilized for the first 2 years because these methods were already in place at MSU for use in other studies. The remaining 3 years of samples were tested using quantitative PCR, which is faster and more cost-effective. Preliminary experiments showed that both tests were comparable in sensitivity and were able to detect positive samples containing a minimum 10⁰–10^{−1} organisms.

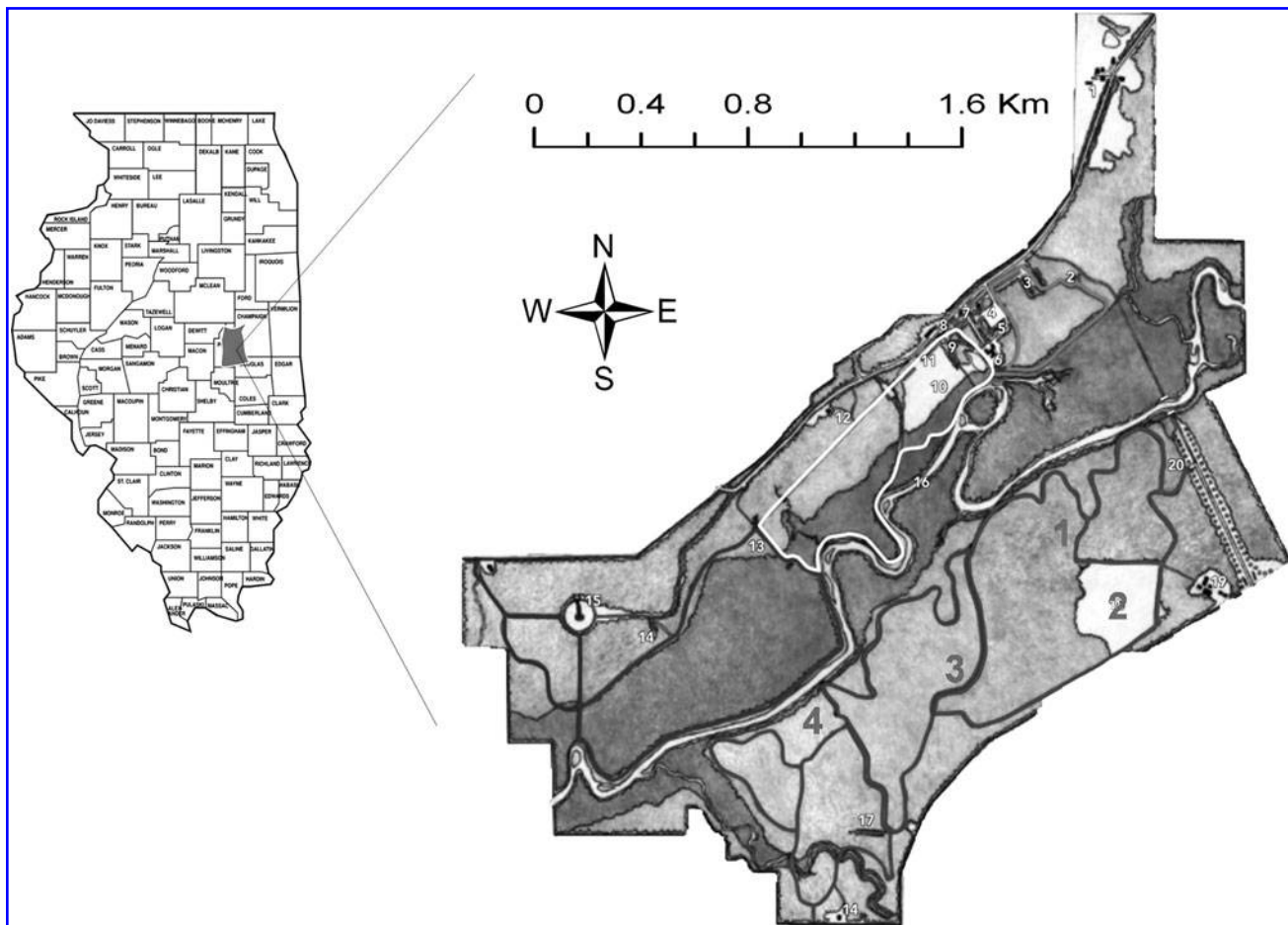


FIG. 1. Study site in east-central Illinois. Robert Allerton Park (RAP) is located 6.4 km southwest of Monticello, in Piatt County, Illinois. Site 1 = Young Forest, Site 2 = Prairie, Site 3 = Mature Forest, Site 4 = Flood Plain.

Statistical analysis

The number of captured small mammals and collected *I. scapularis* were calculated by habitat and by year. We used three measures to evaluate temporal changes of *I. scapularis* occurrence in each habitat: prevalence of *I. scapularis* infestation (proportion of mammals that were infested), mean intensity of infestation (number of *I. scapularis* per infested mammal), and *I. scapularis* relative density (number of *I. scapularis* per mammal). Prevalence of *Bb* infection in collected *I. scapularis* was quantified by the proportion of positive larval pools and nymphs from infested mammals. Differences in number of small mammals, number of *I. scapularis*, mean intensity of infestation, and *I. scapularis* relative density across habitats and years were compared using negative binomial regression. Prevalence of *I. scapularis* infestation and *Bb* infection were evaluated using logistic regression, and odds ratios (OR) were used to quantify the difference. Statistical analyses were performed using SAS software (Version 9.1.3 [2002–2004]; Statistical Analysis System Institute Inc., Cary, NC). A $p \leq 0.05$ was considered significant in this study.

Results

Small mammal abundance and species richness

Overall trapping effort amounted to 25,200 trap nights from 2005 through 2009. A total of 2446 captured small

mammals (including recaptures) were examined for ticks. The white-footed mouse (*P. leucopus*) comprised the vast majority (96%) of individuals captured in all habitats. Other species processed include the meadow jumping mouse (*Zapus hudsonius*) in the young forest, flood plain, and prairie, and the prairie vole (*Microtus ochrogaster*) and the Western harvest mouse (*Reithrodontomys megalotis*) found only in the prairie. The abundance of small mammals captured was significantly different ($p < 0.001$) across the four habitats. The abundance was highest for the flood plain (14.07 captures per 100 trap nights) followed by the mature forest (11.92 captures per 100 trap nights) and young forest (10.97 captures per 100 trap nights), then the prairie (2.17 captures per 100 trap nights). Despite the prairie having the lowest abundance of mammals captured, it had the highest species richness (Table 1).

I. scapularis occurrence

A total of 1009 immature *I. scapularis* ticks (977 larvae and 32 nymphs) were collected from the small mammals (Table 1). The number of *I. scapularis* collected was different ($p < 0.001$) across the four habitats. The young forest had the highest number of *I. scapularis* collected ($n = 676$), followed by the prairie ($n = 176$), the mature forest ($n = 127$), and the flood plain ($n = 30$).

Prevalence of *I. scapularis* infestation did not vary between the young forest and the prairie (OR = 1.0; 95% CI = 0.7, 1.5) (Table 2). However, prevalence of *I. scapularis* infestation was

TABLE 1. SUMMARY OF SMALL MAMMALS CAPTURED AND *Ixodes scapularis* COLLECTED FROM SITES IN ROBERT ALLERTON PARK, PIATT COUNTY, ILLINOIS, 2005–2009

Habitat	Species	n	Ratio ^a (95% CI)	I. scapularis	Ratio ^b (95% CI)
Young Forest	<i>Peromyscus spp.</i>	723		676	
	<i>Z. hudsonius</i>	1		0	
	Total	724	—	676	—
Prairie	<i>Microtus ochrogaster</i>	64		156	
	<i>Peromyscus spp.</i>	51		14	
	<i>Z. hudsonius</i>	15		3	
	<i>Reithrodontomys megalotis</i>	9		3	
	Total	139	0.2 (0.17, 0.32)	176	0.2 (0.1, 0.3)
Mature Forest	<i>Peromyscus spp.</i>	739	1.1 (0.9, 1.5)	127	0.1 (0.05, 0.21)
Flood Plain	<i>Peromyscus spp.</i>	832		30	
	<i>Z. hudsonius</i>	12		0	
	Total	844	1.5 (1.1, 1.9)	30	0.04 (0.02, 0.09)
Total		2446		1009	

^aRatio of mean number of mammals captured per trap night, adjusting for year and month. Young Forest served as the reference group.

^bRatio of mean number of *Ixodes scapularis* collected per trap night, adjusting for year and month. Young Forest served as the reference group.

higher in the young forest than in the mature forest (OR=0.2; 95% CI=0.16, 0.28) and the flood plain (OR=0.03; 95% CI=0.02, 0.05) (Table 2). Intensity of infestation showed the same pattern with the greatest number of *I. scapularis* per infested mammal found in the prairie and the young forest. These two habitats had, on average, twice as high an intensity of infestation as both the mature forest and the flood plain (Table 2). Based on the outcome of the previous measures, the density of *I. scapularis* was highest for the prairie and the young forest, followed by the mature forest, and finally the flood plain (Table 2).

There was an increasing trend ($p < 0.001$) in the prevalence of *I. scapularis* infestation over the study period (Fig. 2). The most recent year, 2009, had the highest prevalence (21%) of infestation and relative density (0.6 *I. scapularis* per mammal), and the second highest mean intensity (3.0 *I. scapularis* per infested mammal) (Fig. 2).

Bb infection

In total, 356 *I. scapularis* larval pools and 32 nymphs were tested for *Bb* by PCR ($n = 388$), of which 53 larval pools and 3 nymphs were positive ($n = 56$), for an overall infection prevalence of 14% for collected *I. scapularis* (95% CI = 11%, 18%) (Table 3). The 3 positive nymphs were removed from captured small mammals in the young forest. The highest pro-

portion of positive *I. scapularis* was found in the prairie (27%; 95% CI = 16%, 41%). Of additional interest in this study, all positive *I. scapularis* from the prairie were larval pools collected from the prairie vole, *M. ochrogaster*. The odds of *I. scapularis* testing positive in the prairie were twice as high as the young forest (OR=2.2; 95% CI=1.0, 4.5) (Table 3). The small numbers of *I. scapularis* testing positive for *Bb* in the mature forest ($n = 5$) and the flood plain ($n = 1$) made it difficult to draw conclusions from these two sites (Table 3). The prevalence of *Bb* infection within RAP did not significantly vary over the study period ($p = 0.992$), despite a lack of detectable infection in 2006 (Fig. 3), and significant variation in abundance of *I. scapularis* across years ($p < 0.001$).

Discussion

In the highly fragmented region of east-central Illinois, the Sangamon River is a vital riparian corridor among small forest and remnant prairie patches surrounded by agricultural fields and urban areas (Rosenblatt et al. 1999). This landscape produces a complex but relatively small network of habitat diversity within RAP with unknown effects on the dynamics of *I. scapularis* occurrence and *Bb* infection among small mammal hosts. The significant increasing trend (2005 to 2009) in prevalence of *I. scapularis* infestation in RAP in this study, compared to the initial reports in 2002 of 9 adult

TABLE 2. *IXODES SCAPULARIS* OCCURRENCE IN ROBERT ALLERTON PARK, PIATT COUNTY, ILLINOIS, 2005–2009

Habitat	Prevalence ^a % (n)	Odds ratio ^b (95% CI)	Mean intensity ^c (I)	Ratio ^b (95% CI)	Relative density ^d	Ratio ^b (95% CI)
Young Forest	32.7 (724)	—	2.9 (237)	—	0.9	—
Prairie	39.6 (139)	1.0 (0.7, 1.5)	3.2 (55)	1.1 (0.9, 1.4)	1.3	1.0 (0.7, 1.5)
Mature Forest	10.8 ^e (739)	0.2 (0.16, 0.28)	1.6 ^e (80)	0.6 (0.4, 0.7)	0.2 ^e	0.2 (0.12, 0.22)
Flood Plain	1.9 ^e (844)	0.03 (0.02, 0.05)	1.9 ^e (16)	0.5 (0.3, 0.9)	0.04 ^e	0.03 (0.02, 0.05)

^aPrevalence = infested mammals/trapped mammals, n is number of trapped mammals.

^bOdds Ratio is value per mammal, Ratio is value per trap night, both adjusting for year and month. Young Forest served as the reference group.

^cMean Intensity = *I. scapularis*/infested mammals. I is number of infested mammals.

^dRelative Density = *I. scapularis*/trapped mammals.

^eValue significantly lower than young forest and prairie ($p \leq 0.001$).

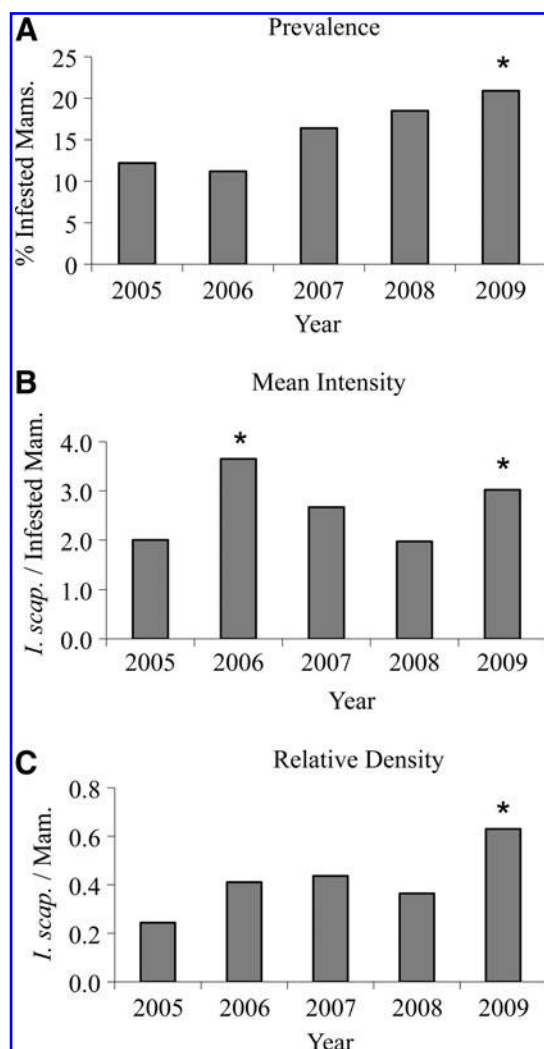


FIG. 2. (A–C) Temporal changes in *I. scapularis* occurrence (Prevalence, Mean Intensity, and Relative Density) in RAP, Piatt County, Illinois, 2005–2009. *Value significantly higher compared to 2005 as the reference group ($p \leq 0.001$).

I. scapularis ticks from a deer-harvest county-surveillance effort, support the hypothesis that *I. scapularis* distribution continues to expand in Illinois (Cortinas and Kitron 2006, IDPH 2009). All three measures of *I. scapularis* occurrence were significantly higher in 2009, the final year of this study, resulting in an upward trend of infested hosts with higher tick burdens. If this pattern continues in coming years, an increase in *Bb* infection of *I. scapularis* in RAP is a conceivable possibility.

The data of this study indicate differences in *I. scapularis* prevalence, mean intensity, and relative density among habitats, with greater measures of *I. scapularis* occurrence in the prairie and young forest compared to both the mature forest and the flood plain. The prevalence of *I. scapularis* infestation among trapped small mammals ranged from 40% in the prairie to 33% in the young forest, 11% in the mature forest, and 2% in the flood plain. Although these results are comparable to small mammal studies in forest patches in northwestern Illinois (Kitron et al. 1991, Mannelli et al. 1994, Slajchert et al. 1997), this study is the first to report a prairie

TABLE 3. *IXODES SCAPULARIS* LARVAL POOLS AND NYMPHS FROM INFESTED SMALL MAMMALS TESTED FOR *BORRELIA BURGDORFERI* IN ROBERT ALLERTON PARK, PIATT COUNTY, ILLINOIS, 2005–2009

Habitat	No. of infested mammals	<i>Bb</i> positive <i>I. scapularis</i> % (n)	Odds ratio ^a (95% CI)
Young Forest	237	14.8 (35)	—
Prairie	55	27.3 (15)	2.2 (1.0,4.5)
Mature Forest	80	6.3 (5)	×
Flood Plain	16	6.3 (1)	×
Total	388	14.4 (56)	

Only three nymphs from the young forest tested positive for *Bb*.

^aOdds ratio of *B. burgdorferi* infection prevalence per infested mammal, adjusting for year and month. Young Forest served as the reference group; ×, small sample size of Mature Forest ($n=5$) and Flood Plain ($n=1$) did not allow precise estimates.

habitat supporting the highest prevalence of *I. scapularis* infestation compared to the forested sites within the same natural area. In addition, we are the first to report evidence that *M. ochrogaster* may potentially serve as a competent reservoir host for *Bb*. Further research is needed to verify the suitability of prairie habitat for *I. scapularis* population dynamics and of *M. ochrogaster* for *Bb* maintenance and transmission. If multiple habitat types populated by competent reservoir host species are suitable for supporting *I. scapularis* vectors, Lyme disease transmission could increase in RAP and in the east-central region of the state.

This study indicates that *Bb* is present in the park. This result is of pivotal importance to evaluate the risk of Lyme disease transmission in an area where the mechanisms of host–vector coexistence and the maintenance of *Bb* remain equivocal. The highest prevalence of *Bb* infection was found in on-host *I. scapularis* larval pools from the prairie (27%) fol-

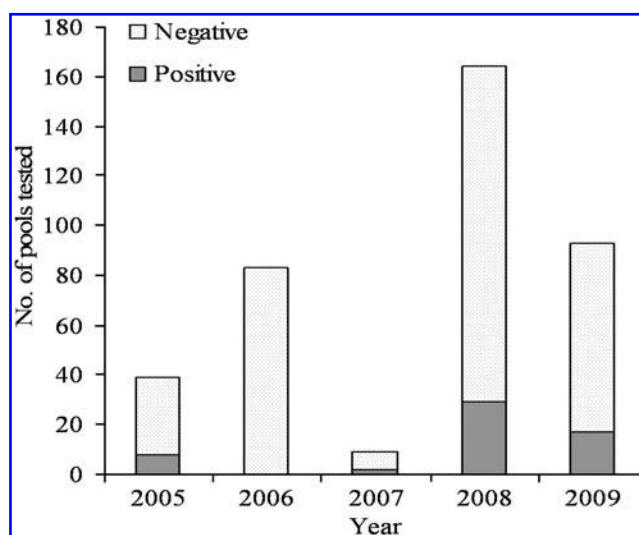


FIG. 3. *I. scapularis* larval pools and nymphs tested for *Borrelia burgdorferi* in RAP, Piatt County, Illinois, 2005–2009. % positive *I. scapularis* did not vary significantly ($p=0.992$) across years.

lowed by the young forest (15%), the mature forest (6%), and the flood plain (6%). Because of the small sample size of *Bb*-positive *I. scapularis*, more data are needed to increase precision of these point estimates.

Whereas *I. scapularis* is typically associated with sandy, oak, upland deciduous forest (Guerra et al. 2002), we found that the prairie had the highest occurrence of *I. scapularis* (although not statistically different from occurrence in the young forest), despite having the lowest abundance of small mammals. The prairie also had the highest observed species richness of small mammals, including *Peromyscus* spp. as well as *M. ochrogaster*, *R. megalotis*, and *Z. hudsonius*. These additional species may serve as substitute or additional hosts for *I. scapularis* where *P. leucopus* is less abundant (Mannelli et al. 1993, Markowski et al. 1997).

Although the meadow vole (*Microtus pennsylvanicus*) has been reported as a competent reservoir for *Bb* (Anderson 1988, Markowski et al. 1998), no reports to date describe *M. ochrogaster* as a potential reservoir host for *Bb*. Mather et al. (1989) reported that the prairie does not qualify as suitable habitat for *I. scapularis* populations, so the potential for small mammal reservoir hosts of *Bb* in this habitat (specifically *M. ochrogaster* in this study) may have been overlooked. All *I. scapularis* testing positive for *Bb* in the prairie were larvae collected from *M. ochrogaster*, which implies the larvae acquired infection from *M. ochrogaster* as their first blood meal. It must be noted that larval feeding can become interrupted and larvae may seek out an additional blood meal as a result. Nymphs could also acquire infection during a previous blood meal, but none were found on *M. ochrogaster*. Based on evidence from this study and the fact that *M. ochrogaster* and *M. pennsylvanicus* are closely related, it is plausible for *M. ochrogaster* to serve as a competent zoonotic reservoir for *Bb*.

Previous studies suggest that decreased biodiversity and increased habitat fragmentation appear to have significant roles in the overpopulation of *P. leucopus* (Rosenblatt et al. 1999), the establishment of *I. scapularis* (Ginsberg 1994), and the risk of Lyme disease (Van Buskirk and Ostfeld 1995, Logiudice et al. 2003). Conclusions from prior studies indicate that an increase in species diversity within host communities leads to a "dilution effect" of immature *I. scapularis* acquiring *Bb* infection because of more ticks feeding on inefficient reservoir hosts (Van Buskirk and Ostfeld 1995, Ostfeld and Keesing 2000). In other words, increased biodiversity of small mammals leads to *I. scapularis* feeding on a wider variety of hosts that have low *Bb* reservoir competency thus decreasing the chance of the feeding tick to become infected and reducing risk of human exposure to Lyme disease. The result is less infected *I. scapularis* in habitats with greater biodiversity. In contrast, our study shows an increase in *I. scapularis* occurrence and *Bb* infection in the prairie, where small mammal species richness is greatest. The presence of *M. ochrogaster* in the prairie may serve as a competent reservoir that is not found within other habitat types. In this manner, the vole may amplify the abundance of infected *I. scapularis*, as Ogden and Tsao (2009) alternatively suggest.

The observation made by Brown and Burgess (2001) that habitat heterogeneity leads to increased host diversity and increased rodent density may explain why the occurrence of *I. scapularis* is highest in the prairie as well as the young forest. Given the relatively small size of RAP (614 ha), *I. scapularis* occurrence and *Bb* prevalence may be dynamic, or continue to

shift and change within and among the habitats of the park. The diverse habitats of this natural area are clustered within a close range and bordered by agriculture fields and urban areas (Rosenblatt et al. 1999). Such habitat composition favors a high degree of connectivity, enabling vertebrate host movements between suitable habitat patches, which, based on literature, is an important factor correlated with *I. scapularis* distribution and abundance (Estrada-Peña 2003). For example, this landscape could facilitate deer movement between habitats, enabling them to utilize the riparian corridor of the Sangamon River near the young forest as a dispersal route, the prairie as a bedding area, and the agriculture fields as a food source. Such deer habitat use could explain the high occurrence of *I. scapularis* in the prairie and young forest. As habitat patches become smaller in size due to changes in land use toward agriculture and urbanization, *I. scapularis* may increase in abundance and density in remaining patches (Ginsberg 1994).

We identified the occurrence of *I. scapularis* within habitats other than forested areas. These findings are supported by a number of exceptions to generalized tick-habitat associations (Piesman and Gray 1994), and the concept that landscape context can influence the abundance of *I. scapularis* (Madhav et al. 2004, Estrada-Peña 2009). Given the caution associated with surveying only one study site, our findings reveal a need to further investigate potential suitability of habitats other than forested areas and reservoir hosts, particularly *M. ochrogaster*, for *I. scapularis* population establishment and *Bb* transmission at a local scale in a dynamic fragmented landscape.

Acknowledgments

The authors acknowledge M. Buhnerkempe, J. Teisburg, L. Kammin, and S. Rao for their contributions to the initial stages of this study; N. Beccue, D. Becker, and Allerton Park Staff for access to study sites and facilities; and field and lab technicians and volunteers for data collection. The authors also thank Drs. L. Haramis and J. Nelson for providing valuable input to this study. Funding for this project was provided by the University of Illinois at Urbana-Champaign: Earth and Society Initiative, James Scholar Program, Department of Natural Resources and Environmental Sciences, Illinois Natural History Survey, and the Federal Aid in Wildlife Restoration Project W-146-R. This project was conducted under protocols approved by University of Illinois Biosafety and Institutional Animal Care and Use protocols.

Disclosure Statement

No competing financial interests exist.

References

- Allan, BF, Keesing, F, Ostfeld, RS. Effect of forest fragmentation on Lyme disease risk. *Conserv Biol* 2003; 17:267–272.
- Anderson, J. Mammalian and avian reservoirs for *Borrelia burgdorferi*. *Ann NY Acad Sci* 1988; 539:180–191.
- Anderson, JF, Johnson, RC, Magnarelli, LA, Hyde, FW. Identification of endemic foci of Lyme disease: isolation of *Borrelia burgdorferi* from feral rodents and ticks (*Dermacentor variabilis*). *J Clin Microbiol* 1985; 22:36–38.
- Anderson, JF, Magnarelli, LA, Burgdorfer, W, Barbour, AG. Spirochetes in *Ixodes dammini* and mammals from Connecticut. *Am J Trop Med Hyg* 1983; 32:818–824.

- Anderson, JM, Swanson, KI, Schwartz, TR, Glass, GE, et al. Mammal diversity and infection prevalence in the maintenance of enzootic *Borrelia burgdorferi* along the Western Coastal Plains of Maryland. *Vector Borne Zoonot Dis* 2006; 6:411–422.
- Bouseman, JK, Kitron, U, Kirkpatrick, CE, Siegel, J, et al. Status of *Ixodes dammini* (Acari: Ixodidae) in Illinois. *J Med Entomol* 1990; 27:556–560.
- Brown, RN, Burgess, EC. Lyme borreliosis. In: Williams, ES, Barker, IK, eds. *Infectious Diseases of Wild Mammals*. Iowa: Iowa State University Press, 2001:434–454.
- Brownstein, JS, Holford, TR, Fish, D. A climate-based model predicts the spatial distribution of the Lyme disease vector *Ixodes scapularis* in the United States. *Environ Health Perspect* 2003; 111:1152–1157.
- Bunikis, J, Garpmo, U, Tsao, J, Berglund, J, et al. Sequence typing reveals extensive strain diversity of the Lyme borreliosis agents *Borrelia burgdorferi* in North America and *Borrelia afzelii* in Europe. *Microbiology* 2004; 150:1741–1755.
- Burgdorfer, W, Barbour, AG, Hayes, SF, Benach, JL, et al. Lyme disease—a tick-borne spirochetosis? *Science* 1982; 216:1317–1319.
- Callister, S, Nelson, J, Schell, R, Jobe, D, et al. Survey for *Ixodes* spp. and *Borrelia burgdorferi* in southeastern Wisconsin and northeastern Illinois. *J Clin Microbiol* 1991; 29:403–406.
- Callister, SM, Agger, WA, Schell, RF, Ellingson, JLE. *Borrelia burgdorferi* infection surrounding La Crosse, Wis. *J Clin Microbiol* 1988; 26:2632–2636.
- Cortinas, MR, Kitron, U. County-level surveillance of white-tailed deer infestation by *Ixodes scapularis* and *Dermacentor albipictus* (Acari: Ixodidae) along the Illinois river. *J Med Entomol* 2006; 43:810–819.
- Davis, JP, Schell, WL, Amundson, TE, Godsey, MJ, et al. Lyme disease in Wisconsin: epidemiologic, clinical, serologic, and entomologic findings. *J Biol Med* 1984; 57:685–696.
- Donahue, JG, Piesman, J, Spielman, A. Reservoir competence of white-footed mice for Lyme disease spirochetes. *Am J Trop Med Hyg* 1987; 36:92–96.
- Estrada-Peña, A. The relationships between habitat topology, critical scales of connectivity and tick abundance *Ixodes ricinus* in a heterogeneous landscape in northern Spain. *Ecography* 2003; 26:661–671.
- Estrada-Peña, A. Diluting the dilution effect: a spatial Lyme model provides evidence for the importance of habitat fragmentation with regard to the risk of infection. *Geospatial Health* 2009; 3:143.
- Fish, D. Population ecology of *Ixodes dammini*. In: Ginsberg, H, ed. *Ecology and Environmental Management of Lyme Disease*. New Jersey: Rutgers University Press; 1993:25–42.
- Ginsberg, HS. Lyme disease and conservation. *Conserv Biol* 1994; 8:343–353.
- Goodwin, BJ, Ostfeld, RS, Schaubert, EM. Spatiotemporal variation in a Lyme disease host and vector: black-legged ticks on white-footed mice. *Vector Borne Zoonot Dis* 2001; 1:129–138.
- Guerra, ME, Jones, C, Paskewitz, S, Cortinas, MR, et al. Predicting the risk of Lyme disease: habitat suitability for *Ixodes scapularis* in the north central United States. *Emerg Infect Dis* 2002; 8:289–297.
- Hamer, SA, Roy, PL, Hickling, GJ, Walker, ED, et al. Zoonotic pathogens in *Ixodes scapularis*, Michigan. *Emerg Infect Dis* 2007; 13:1131–1133.
- Hofmeister, EK, Ellis, BA, Glass, GE, Childs, JE. Longitudinal study of infection with *Borrelia burgdorferi* in a population of *Peromyscus leucopus* at a Lyme disease-enzootic site in Maryland. *Am J Trop Med Hyg* 1999; 60:598–609.
- Illinois Department of Public Health (IDPH). Known geographic distribution of *Ixodes scapularis* by county in Illinois 2008. 2009. Available at www.idph.state.il.us/envhealth/pdf/Deer_Tick_Range.pdf; accessed February 18, 2010.
- Illinois Department of Public Health (IDPH). Reportable Communicable Disease Cases, 2000–2008. 2010. Available at www.idph.state.il.us/health/infect/communicabledisease00_09.htm; accessed February 18, 2010.
- Jobe, DA, Lovrich, SD, Nelson, JA, Velat, TC, et al. *Borrelia burgdorferi* in *Ixodes scapularis* ticks, Chicago Area. *Emerg Infect Dis* 2006; 12:1039–1041.
- Jobe, DA, Nelson, JA, Adam, MD, Martin, SA. Lyme disease in urban areas, Chicago. *Emerg Infect Dis* 2007; 13:1799–1800.
- Killilea, ME, Swee, A, Lane, RS, Briggs, CJ, et al. Spatial dynamics of Lyme disease: a review. *Ecohealth* 2008; 5:167–195.
- Kitron, U, Jones, CJ, Bouseman, JK. Spatial and temporal dispersion of immature *Ixodes dammini* on *Peromyscus leucopus* in northwestern Illinois. *J Parasitol* 1991; 77:945–949.
- Kitron, U, Jones, CJ, Bouseman, JK, Nelson, JA, et al. Spatial analysis of the distribution of *Ixodes dammini* (Acari: Ixodidae) on white-tailed deer in Ogle County, IL. *J Med Entomol* 1992; 29:259–266.
- Lane, RS, Piesman, J, Burgdorfer, W. Lyme borreliosis: relation of its causative agent to its vectors and hosts in North America and Europe. *Annu Rev Entomol* 1991; 36:587–609.
- Levine, JF, Wilson, ML, Spielman, A. Mice as reservoirs of the Lyme disease spirochete. *Am J Trop Med Hyg* 1985; 34:355–360.
- Lingren, M, Rowley, WA, Thompson, C, Gilchrist, M. Geographic distribution of ticks (Acari: Ixodidae) in Iowa with emphasis on *Ixodes scapularis* and their infection with *Borrelia burgdorferi*. *Vector Borne Zoonot Dis* 2005; 5:219–226.
- LoGiudice, K, Ostfeld, RS, Schmidt, K, et al. The ecology of infectious disease: effects of host diversity and community composition on Lyme disease risk. *Proc Natl Acad Sci USA* 2003; 100:567–571.
- Madhav, N, Brownstein, J, Tsao, J, Fish, D. A dispersal model for the range expansion of blacklegged tick (Acari: Ixodidae). *J Med Entomol* 2004; 41:842–852.
- Mannelli, A, Kitron, U, Jones, CJ, Slajchert, TL. Role of the eastern chipmunk as a host for immature *Ixodes dammini* (Acari: Ixodidae) in northwestern Illinois. *J Med Entomol* 1993; 30:87–93.
- Mannelli, A, Kitron, U, Jones, CJ, Slajchert, TL. Influence of season and habitat on *Ixodes scapularis* infestation on white-footed mice in northwestern Illinois. *J Parasitol* 1994; 80:1038–1043.
- Markowski, D, Ginsberg, HS, Hyland, K, Hu, R. Reservoir competence of the meadow vole (Rodentia: Cricetidae) for the Lyme disease spirochete *Borrelia burgdorferi*. *J Med Entomol* 1998; 35:804–808.
- Markowski, D, Hyland, KE, Ginsberg, HS, Hu, R. Spatial distribution of larval *Ixodes scapularis* (Acari: Ixodidae) on *Peromyscus leucopus* and *Microtus pennsylvanicus* at two island sites. *J Parasitol* 1997; 83:207–211.
- Mather, TN, Wilson, M, Moore, S, Ribiero, JM, et al. Comparing the relative potential of rodents as reservoirs of the Lyme disease spirochete (*Borrelia burgdorferi*). *Am J Epidemiol* 1989; 130:143–150.
- Nelson, J, Bouseman, J, Kitron, U, Callister, S, et al. Isolation and characterization of *Borrelia burgdorferi* from Illinois *Ixodes dammini*. *J Clin Microbiol* 1991; 29:1732–1734.

- Nupp, TE, Swihart, RK. Effects of forest fragmentation on population attributes of white-footed mice and Eastern chipmunks. *J Mammal* 1998; 79:1234–1243.
- Ogden, NH, Tsao, JI. Biodiversity and Lyme disease: dilution or amplification? *Epidemics* 2009; 1:196–206.
- Ostfeld, RS, Keesing, F. Biodiversity and disease risk: the case of Lyme disease. *Conserv Biol* 2000; 14:722–728.
- Piesman, J, Gray, JS. Lyme disease/Lyme borreliosis. In: Sonenshine, DE, Mather, TN, eds. *Ecological Dynamics of Tick-Borne Zoonoses*. NY: Oxford University Press, 1994:327–350.
- Pinger, R, Timmons, RL, Karris, K. Spread of *Ixodes scapularis* (Acari: Ixodidae) in Indiana: collections of adults in 1991–1994 and description of a *Borrelia burgdorferi*-infected population. *J Med Entomol* 1996; 33:852–855.
- Rosenblatt, DL, Heske, EJ, Nelson, SL, Barber, DM, et al. Forest fragments in east-central Illinois: islands or habitat patches for mammals? *Am Midl Nat* 1999; 141:115–123.
- Schalze, TL, Jordani, RA, Hung, RW. Comparison of *Ixodes scapularis* (Acari: Ixodidae) populations and their habitats in established and emerging Lyme disease areas in New Jersey. *J Med Entomol* 1998; 35:64–70.
- Slajchert, T, Kitron, UD, Jones, CJ, Mannelli, A. Role of the eastern chipmunk (*Tamias striatus*) in the epizootiology of Lyme borreliosis in northwestern Illinois, USA. *J Wildl Dis* 1997; 33:40–46.
- Sonenshine, DE. *Insects of Virginia* No. 13. Ticks of Virginia (Acari: Metastigmata). Research Division Bulletin 139. Virginia: Virginia Polytechnic Institute and State University Press, 1979.
- Tsao, JI, Wootton, JT, Bunikis, J, Luna, MG, et al. An ecological approach to preventing human infection: vaccinating wild mouse reservoirs intervenes in the Lyme disease cycle. *Proc Natl Acad Sci USA* 2004; 101:18159–18164.
- Van Buskirk, J, Ostfeld, RS. Controlling Lyme disease by modifying the density and species composition of tick hosts. *Ecol Appl* 1995; 5:1133–1140.
- Walker, ED, Stobierski, MG, Poplar, ML, Smith, TW, et al. Geographic distribution of ticks (Acari: Ixodidae) in Michigan, with emphasis on *Ixodes scapularis* and *Borrelia burgdorferi*. *J Med Entomol* 1998; 35:872–882.
- Wang, J, Grimley, DA, Xu, C, Dawson, JO. Soil magnetic susceptibility reflects soil moisture regimes and the adaptability of tree species to these regimes. *Ecol Manag* 2008; 255:1664–1673.

Address correspondence to:

Nohra Mateus-Pinilla

Illinois Natural History Survey

Institute of Natural Resource Sustainability

University of Illinois at Urbana-Champaign

1816 S. Oak Street

Urbana, IL 61820

E-mail: nohram@illinois.edu