Avian Tick Burdens Across an Urban to Forest Land-Use Gradient

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at George Mason University

By

Ryan Peters
Bachelor of Science
Westminster College, 1999

Director: Larry Rockwood, Professor
Department of Environmental Science and Public Policy

Summer Semester 2009
George Mason University
Fairfax, VA

Dedication

This is dedicated to my loving mother Clara Peters and my lovable father Joseph "Buzzy" Peters.

Acknowledgments

Table of Contents

List of Tables

List of Figures

Abstract

AVIAN TICK BURDENS ACROSS AN URBAN TO FOREST LAND-USE GRADIENT

Ryan Peters, M.S.

George Mason University, 2009

Thesis Director: Dr. Larry Rockwood

Interactions between *Ixodes scapularis*, the primary vector of Lyme disease in the Eastern and Midwestern USA, and their hosts determine infection rates in ticks, and influence the human risk of infection. Several factors alter tick burdens over temporal and spatial gradients and determine the role birds play in tick-borne pathogen transmissions cycles. In the research described here, I have determined seasonal patterns of tick burdens on 23 species of birds at 16 sites along an urbanization gradient in the Mid-Atlantic, USA. Landscape and species-specific attributes, as well as questing tick abundance are examined in order to understand variability in tick burdens. Tick burdens on birds were highly seasonal, decreased with increasing urbanization of the capture site, and varied substantially between species of birds. Carolina wrens (*Thryothorus ludovicianus*) and Northern Cardinals (*Cardinalis cardinalis*) hosted 28.0% and 25.0% of all ticks obtained from birds while only comprising 4.9% and 11.9% of the avian community. Foraging height, as well as gender and age of the bird also influenced tick

burdens, but to a lesser degree. I present models to estimate or predict avian tick burdens using individual, species, and site characteristics, and the density of questing ticks. Identifying causes of variation in tick burdens on avian hosts will increase our understanding of host-parasite interactions and the role birds play in the ecology of Lyme disease.

Introduction

Globally, ticks are responsible for the transmission of multiple pathogens to both wildlife and humans. In North America, a variety of tick-borne diseases occur including babesiosis, human granulocytic ehrlichiosis, Rocky Mountain spotted fever, tularemia, Powassan virus, and Lyme disease (CDC 2007). Lyme disease, caused by the spirochete bacterium *Borrelia burgdorferi* (Burgdorfer *et al.* 1982), is the most common tick-borne disease in North America, with approximately 20,000 reported human cases a year, and an increase in the last decade in several regions of the USA (CDC 2008).

The ability of ticks to transmit a wide variety of pathogens makes the study of the environmental factors that drive and influence host-parasite interactions and disease transmission of great importance to humans. Understanding host-parasite interactions may provide insight into the impact of pathogens on host survival and potential for human infection risk. Previous host-parasite research involving ticks has focused on understanding the mechanisms that determine infection rates and tick density (LoGiudice et al. 2003, Randolph 2004, LoGiudice et al. 2008). Areas where ticks feed primarily on host species with higher host reservoir competence are likely to have higher prevalence of tick-borne pathogens and to have increased risk for human infection. Host reservoir competence varies between different animal species especially in birds (Ginsberg et al. 2005). Tick populations are influenced by host availability and density, as well as

1

environmental factors, such as temperature and humidity (Guerra et al. 2002, Brownstein et al. 2003, Randolph 2004). *I. scapularis,* the principle vector for *B. burgdorferi* in the Eastern and mid-Western USA (Steere *et al.* 1978), parasitizes a large variety of vertebrate hosts, including mammals, reptiles, and birds. Mammals are considered the primary hosts for many tick populations in the NE USA, and this is especially true for the *I. scapularis*, where a majority of ticks are found on mammals (Giardina et al. 2000, LoGiudice et al. 2003, Brisson et al. 2008). Other hosts, such as reptiles and birds, are also hosts for larval and nymph stages of ticks, although in the eastern USA they often have relatively low tick burdens compared to mammals (Levine *et al.* 1997, Eisen *et al.* 2004, Giery and Ostfeld 2007). Although birds often have smaller tick burdens than mammals, birds have larger home ranges than many small mammals and the ability to move substantial distances (e.g. 10s to 100s to 1000's of kilometers) in a short period of time (Scott *et al.* 2001). Birds' mobility may lead to the dissemination of ticks and tick-borne pathogens into previously uninhabited and/or uninfected locations, or across habitat types (Anderson and Magnarelli 1984, Battaly et al. 1987, Weisbrod and Johnson 1989, Scott et al. 2001, Ogden et al. 2008). Seasonality is also considered an important influence on host-parasite interactions through environmental factors such as temperature, rainfall, and resource availability (Altizer et al. 2006)

. *Ixodes scapularis* is an ecotoparasite that has three stages of its life cycle. Over a two year period, the black-legged tick must feed three times to complete the cycle. Larval ticks quest primarily between July through September and after obtaining a blood meal, seek refuge to digest the blood meal and molt into the nymph; this stage takes

approximately 7-8 months or until May. As a result, peak nymphal abundance occurs in early spring from May-June as nymphal ticks emerge to quest for another blood meal. After obtaining another blood meal nymphal ticks seek refuge and molt into the final stage of the *I. scapularis's* life cycle. Adults emerge and seek out larger mammalian hosts and may remain active from November through April depending on weather conditions. Adult females primarily seek out a blood meal so they can digest the blood meal and lay an egg cluster of 1000-3000 eggs in early spring (Spielman et al. 1985, Falco et al. 1999).

Borrelia burgdorferi infected nymphal *I. scapularis* ticks are thought to be the cause of most cases of Lyme disease in humans in the Eastern USA (Barbour and Fish 1993). Transovarial transmission of *B. burgdorferi* spirochete from adult female *I. scapularis* ticks to larval ticks through the egg, appears to be relatively inefficient (Magnarelli et al. 1987, Patrican 1997). Therefore, the prevalence of *Borrelia* infection in nymphs is primarily determined by the hosts on which larval *I. scapularis* ticks feed. Several studies have tried to predict the prevalence of infected nymphs by using data on host composition, host density, and host reservoir competence for transmitting *B. burgdorferi* to attached ticks and host tick burden (Giardina et al. 2000, LoGiudice et al. 2003, Madhav et al. 2004, LoGiudice et al. 2008). The host community models developed in these studies assume constant tick burdens for each species across sites and host densities. More specifically, bird tick burden in the prediction models, due to logistical constraints, could not account for species, seasonal, and spatial differences in host tick burden estimates. Birds are known not to play a major role in Lyme disease

transmission cycles (Giardina et al. 2000), but taking into account the inherent variability of bird larval tick burden could help improve current models predicting *B. burgdorferi* infected nymphs. Therefore, this study focuses on predicting seasonal bird tick burden across a spatial urban to forest land-use gradient where *I. scapularis* populations vary. Bird species, and attributes such as gender, age, and mass were also used to account for bird tick burden variability.

Habitat heterogeneity and anthropogenic land use influence host-parasite interactions of birds and ticks and have the potential to impact Lyme disease ecology. Increasing development in the past 40 years in the Mid-Atlantic region USA has lead to a reduction of agriculture and forested areas into more urbanized environments (Masek et al. 2000). Because bird communities are known to vary with urbanization, sampling tick burdens on birds and questing ticks at sites along an urbanization gradient provide an opportunity to study bird-tick interactions for a range of bird species.

Ticks are also thought to be strongly affected by urbanization. For example, forests or wooded areas often support higher tick populations than open areas such as lawns and fields (Maupin et al. 1991, Stafford 3rd and Magnarelli 1993, Ostfeld et al. 1995, Guerra et al. 2002), and fragmented landscapes with wooded lots and areas with shrub-dominated understories sometimes have higher tick abundance (Glass *et al.* 1994, Allan *et al.* 2003, Brownstein *et al.* 2005). Larval and nymphal ticks require leaf litter or other protective ground cover that retains moisture and prevents desiccation of molting, resting, or questing ticks (Stafford 1994). *Ixodes scapularis* ticks are also dependent on the presence of large mammals such as white-tailed deer (*Odocoileus virginianus)*

(Wilson *et al.* 1985, Wilson *et al.* 1988), and increasing urbanization may both increase and decrease deer populations. In highly urbanized areas without deer, ticks may be entirely absent (Wilson *et al.* 1990, Rand *et al.* 2004).

Several other species-specific and individual attributes may also influence avian tick burdens by altering contact rates between birds and microhabitats where ticks quest (Weisbrod and Johnson 1989, Battaly and Fish 1993, Slowik and Lane 2001). For example, studies in the eastern U.S. (Stafford 3rd *et al*. 1995) and California (Eisen *et al.* 2004) found that tick burdens were correlated with species' ground foraging and ground nesting behavior. Similarly, a bird's body mass may determine how long a bird forages to meet daily energy requirements (Silva *et al.* 1997); larger birds tend to move more and have larger home ranges than smaller birds (Schoener 1968). Longer foraging periods and movements over larger areas are likely to increase the likelihood of exposure to questing ticks and result in higher tick burdens. Age and sex of individual birds may also influence tick burdens by altering the habitats used by birds, the amount of time young birds spend on the ground, and the time spent preening which may remove ticks. Previous work found higher tick burdens on hatch-year birds than adults but no difference between males and females (Scharf 2004). Further research is needed to examine the collective influence of the factors that influence the abundance of ticks on birds across space. In this study, I examined patterns of avian tick burdens and questing tick abundance across 16 sites over two years to understand the factors that determine host parasite interaction and possible effects on the ecology of Lyme disease.

Methods

We studied bird–tick interactions at 16 sites in the Mid-Atlantic region, USA. These sites span an urbanization gradient, where urbanization is defined by the conversion of forest into residential and urban areas. Because the process of urbanization occurs over time scales of decades, this study employed a space-for-time substitution and examined sites at different stages of urbanization. The sites included: 1) three nearly intact forested sites at SERC, the Smithsonian Environmental Research Center in Edgewater, MD, Jug Bay Wetland Sanctuary in Lothian, MD, and Patuxent National Wildlife Refuge in Laurel, MD; 2) three sites that have large wooded parks surrounded by residential or urban areas, including Fort Dupont Park, in Washington DC, Rock Creek Stream Valley Park in Rockville, MD, and Wheaton Regional Park, in Wheaton MD; 3) six sites that were located in residential areas including two sites in Takoma Park MD, two in Bethesda MD, one in Millersville MD, and one in Crofton MD; and 4) three sites in urban areas including the National Mall in Washington DC, Foggy Bottom, Washington DC, and Arlington, VA (Figure 1). Sixteen sites were sampled in 2007 and eleven in 2006 (Arlington, Wheaton, Patuxent, Millersville, and Crofton were not sampled in 2006) (Table 1).

I used 30m resolution forest cover and impermeable surface (e.g. pavement, buildings, roads) data layers (USGS. National Land Cover Database. http://www.mrlc.gov/.) and ESRI ArcGIS software and Hawth's Analysis Tools for ArcGIS (Beyer 2004) to estimate a continuous Urbanization Index (UI) for each site (Gomez *et al.* 2008) (Figure 2):

6

UI = (100% – % Canopy Cover + % Impervious Surface)/2 (1)

This index ranges from 0 to 100 with a value of zero indicating a completely forested site and a value of 100 indicating a landscape completely impervious to water. Urbanization Index values for each site were calculated using a radius of 500m around the site center (Table 1).

I sampled birds from May to October in both 2006 and 2007. Birds were captured in mist-nests for 2-3 days at each site once a month. Birds were aged, and sexed, based on plumage, breeding characteristics, and skull ossification (Pyle 1997). I examined each bird for attached ticks by visual observation and blowing to part feathers. I initially examined the head, neck, legs, and the body, but found over 99% of all ticks on the head and neck. Subsequent searches focused on the head and neck region of each bird. Ticks were removed with a pair of fine-point forceps and placed in 95% ethanol for subsequent identification. Ticks were identified to stage and species with a 40x dissecting microscope using illustrated and non-illustrated keys (Clifford *et al.* 1961, Clifford *et al.* 1973, Keirans and Litwak 1989, Keirans and Durden 1998).

I estimated questing tick abundance using the standard drag-cloth method (Falco and Fish 1992), using a 1m x 1m white corduroy cloth with a 4cm x 1.5cm x 1.1m pine board secured into a slot of the fabric in the front, and four pairs of 3cm washers wrapped in duct tape and sewn into the terminal edge. Ten 30m linear sampling transects at each site were distributed throughout the landscape and stratified to reflect the various types of

ground substrate. Sampling occurred bi-weekly from May through October and once in

November and December. I collected adult and nymphal ticks attached to the cloth with

forceps and placed them in 95% ethanol. Clear packaging tape was used to collect larval

ticks attached to the drag cloth. I estimated the relative questing abundance of each life

stage (larvae, nymph, adult) for each tick species as (Daniels *et al.* 2000):

Tick density = Number of Ticks/Distance of Drag Transect (Meters) = (# Ticks/m^2)   (2)

Bird species were placed in foraging and nesting guilds to determine if these

behaviors that might be associated with contact rates with tick questing substrate on the

ground could explain variation in tick burdens. Foraging guilds were separated into four

categories based on broad classifications for North American birds (Ehrlich et al. 1988).

The classifications were based on bird's primary and/or secondary foraging techniques

during the breeding season. Birds in the first foraging guild represented birds that had

one primary foraging technique as ground gleaners. Birds in the second guild were

considered ground gleaners as their primary foraging technique and foliage gleaners as

their secondary foraging technique, where some time was spent foraging in the mid to

upper canopy. The third foraging guild consisted of birds that spent a minority of time

foraging on the ground. The primary foraging technique for this group was foliage

gleaning and the secondary foraging technique was ground gleaning, therefore a majority

of time is spent foraging in the mid to upper canopy. Birds in the fourth foraging guild

spend primarily all of their time in the mid to upper canopy foraging. The primary

8

foraging technique for the fourth foraging guild was foliage gleaners.   Birds were placed

in nesting guilds based on the Birds of North America accounts (Poole 2005), with four

nesting categories: ground nesters, shrub or mid-canopy nesters, canopy nesters and

cavity nesters.

Statistical analyses

As in other studies of parasites, tick burdens on birds were highly aggregated

making analyses based on normal distributions inappropriate (Shaw and Dobson 1995). I

used a generalized linear model (GLM) with a negative binomial distribution and log link

function in SPSS, v15.0. I restricted analysis to species of birds where I examined ($\geq$5)

individuals. In addition, because negative binomial distributions are strictly positive, it

was necessary to eliminate from the analysis species of birds that did not have at least one

tick. These species were not included and including them by adding a single tick in the

analysis would have made the models with species effect stronger.

I focused on larval *I. scapularis* tick burdens since this is the most important

stage in Lyme disease ecology. Categorical variables included year of sampling (2006 or

2007), species of bird, age (Hatch Year or After Hatch Year) gender (male or female),

foraging guild, and nesting guild. Continuous predictors included urbanization,

seasonality (modeled using a cubic function of Julian date (January 1 = 1) to account for

the fast increase and slower decline in my data as seen elsewhere), questing tick

abundance, and mass (in grams) of each bird (Randolph 2004, Brunner and Ostfeld

2008).

9

Larval ticks remain on hosts for an average of 6 (range 3-8) days following initial attachment. As a result, the ideal period to estimate questing tick abundance to predict avian tick burdens would be over the 6 days before capture. I used the bi-weekly questing tick abundance measurements to estimate questing tick abundance 3 days (the midpoint of the attachment period) before the bird sampling visit by averaging relative tick questing samples from tick drags within ten days prior and ten days after the focal date and weighting by the time difference between the focal date and the date of the flagging.

I performed an additional analysis that focused on the tick burden for the six most well sampled species that include American Robin (*Turdus migratorius*), Carolina Wren (*Thryothorus ludovicianus*), Eastern Towee (*Pipilo erythrophthalmus*), Northern Cardinal (*Cardinalis cardinalis*), Ovenbird (*Seiurus aurocapilla*), and Wood Thrush (*Hylocichla mustelina*). For these species I examined the interaction between urbanization and species of bird. I used a generalized linear model with a negative binomial distribution and log link function in SPSS, v15.0 to determine if there was a different effect of urbanization on tick burden for different species of birds.

My goal was to build four models that describe factors that best predict tick burden on birds. First, I attempted to use factors that best described my local dataset and including in this model the local seasonality (cubic date function), species, UI, age, sex, and mass. Second, I built a model based on species traits, rather than the specific species (which could be used to estimate tick burdens on other unsampled species). This model included the same predictors as the first model, but substituted foraging and nesting guild

10

for the species predictor. The third and fourth models were attempts to predict tick

burdens using questing tick abundance and either species (model 3) or species' traits

(model 4). These models could be used to estimate tick burdens on birds at other sites

where questing tick abundance was measured.   In building these models I also tested

hypotheses about which factors are useful in predicting bird tick burden. The models

were compared using AIC (Akaike's information criterion; (Burnham and Anderson

2002).

Results

I examined 10,289 birds of 70 species at 16 sites (Table 2). Of the 70 bird species

examined with at least 11 individuals, only 23 species had *I. scapularis* larval ticks. Tick

burdens on birds vary among species. Carolina Wrens (*Thryothorus ludovicianus*) and

Northern Cardinals (*Cardinalis cardinalis*) represented 4.9% and 11.9% of captured birds

but hosted 28.0% and 25.0% of *I. scapularis* larvae, respectively. In contrast, Acadian

Flycatchers (*Empidonax virescens*) and House sparrows (*Passer domesticus*) were only

1.4 % and 24 % of captured birds but hosted 0% and 0.5 % of *I. scapularis* larvae.

Although *I. scapularis* larvae were the most common ticks on birds, five additional

species of larval and nymphal ticks were also found (Table 2**,** Table 9).

My goal was to build models to determine what parameters best predict tick

burden with our particular localized data set and determine what parameters could best be

used outside the regional scope of the study where species of birds and seasonal measures

may vary.   In models 1 and 2 the coefficients of the cubic date function indicated a

highly seasonal pattern with a quick rise during July and decreased more slowly

afterward (Figure 3). In model 1, the factors that explained tick burden included seasonality, urbanization, bird species, age, sex and mass (Table 3; Model 1). Birds captured at forested sites had higher burdens than birds of the same species at more urban sites (Figure 4). At the Smithsonian Environmental Research Center (SERC) peak (July 1-August 15) tick burdens on Carolina Wren (*T. ludovicianus*) and Northern Cardinal (*C. cardinalis*) were the highest and Red-eyed Vireos (*Vireo olivaceus*) and Eastern Tufted Titmouse (*Baeolophus bicolor*) had the lowest tick burdens (Figure 5).

Both species habitat distributions and other species-specific traits played a role in species tick burdens. For example, species such as the House sparrow (*Passer domesticus*), have low tick burdens overall, partly because they are found in primarily urban and residential sites. However, they also had low tick burdens at sites where they occur with other species that show higher tick burdens, such as Northern Cardinals and Carolina wrens (Figure 4).

In model 2, species attributes such as primary foraging guild and nesting guild were also significant indicators of variability of tick burden (Table 3; Model 2). Birds that spent all or a majority of time foraging on the ground had higher larval tick burdens than birds that spent less time foraging on the ground (Figure 5). Birds in the ground nesting guilds also had higher tick burden.

Although they were less powerful predictors of tick burdens (Table 4-5), the sex and age of the bird were also significant predictors and included in the best fitting models (Table 3; Model 3). For example, the observed *I. scapularis* larval tick burdens on the Northern Cardinal at Rockcreek Stream Valley Park indicated higher tick burden on male

12

birds than female birds (Figure 1) and slightly higher tick burdens on hatch year (HY) birds than after hatch year or adult birds.

In models 3 and 4, questing larval tick abundance was also a strong predictor of avian tick burdens with species (Table 3; Model 3) and species attributes (Table 3; Model 4) as predictors. Local seasonality and urbanization however were more powerful predictors (Table 3; Model 3). In fact, in a model with questing larval tick abundance, site urbanization (UI) explained additional variation in tick burden.

Questing larval tick abundance was a significant predictor of bird tick burden, (Table 3; Models 3-4). In this study, however, seasonality explained more variability in *I. scapularis* larvae tick burden then questing tick abundance on birds. I examined the relationship between the observed mean tick burden on the Northern Cardinal across the urbanization gradient and the measure of larval questing tick abundance. Sampling of birds and questing tick abundance between July 1 through August 15 of 2006 and 2007 were averaged and placed on Figure 6. The six week time frame represents the predicted peak for *I. scapularis* larval tick burden across our sampling sites. Residential populations of Northern Cardinal span most of the sampling sites along the gradient and they experience increased tick burden with increasing questing tick abundance (Figure 6).

The final analysis examined if bird larval tick burden increased or decreased with increasing urbanization among six bird species (Table 5). Tick burdens for six species show predicted declines with increasing urbanization, but burdens decline at different rates for different species. Burdens on Northern Cardinal and Eastern Towhee show similar decline and are the steepest of all the six species examined. Burdens on Wood

Thrush and Carolina Wren have a similar pattern of decline but not as steep as N.
Cardinal and Eastern Towhee. Burdens on American Robin and Ovenbird show
shallower declines with increasing urbanization. Finally, burdens on Ovenbird decreased
slightly but non-significantly with urbanization (Figure 7).

Discussion

Previous studies examining bird and mammal tick burdens have focused sampling
in one or two habitat types or at banding stations during migration (Anderson and
Magnarelli 1984, Battaly et al. 1987, Weisbrod and Johnson 1989, Maupin et al. 1991,
Scott et al. 2001, LoGiudice et al. 2003, Brunner and Ostfeld 2008, LoGiudice et al.
2008). Perhaps as result, models of the contribution of each host to *Borrelia* infection in
ticks frequently assume fixed tick burdens (LoGiudice et al. 2003, LoGiudice et al.
2008). Our study is the first to simultaneously sample multiple hosts across an urban to
forest land-use gradient and over multiple years. I found that *I. scapularis* larval tick
burdens on hosts decreased substantially from forest to urban sites, but in a complex way,
such that the relative importance of different hosts in feeding ticks varied significantly
(Figure 7). A clear illustration of the decrease in tick burden with urbanization came
from examining individual bird species across a range of sites. For example, resident
Northern Cardinals occurred at all 16 sites, and tick burdens on Northern Cardinal
showed a strong decrease with increased urbanization, with few if any ticks on cardinals
at urban sites (Figure 4). Although all species showed this general trend, the rate of
decrease with urbanization differed among species. At the most forested site, burdens on

14

Northern cardinals were the highest of the six species in the urbanization-species interaction analysis, whereas cardinals had only the 4th highest tick burdens at the residential sites (Figure 7; UI = 50). This is an important finding, because it demonstrates that the relative burdens on hosts may change across a habitat gradient. If the same finding holds true for mammals, then models that assume constant tick burdens (or constant relative contributions to the total population of ticks fed) will be inaccurate (LoGiudice et al. 2003, LoGiudice et al. 2008)

Strong temporal patterns in tick burdens were also evident in our study. I found an asymmetrically quick rise in larval *I. scapularis* tick burden at the end of July and a slow decline into the month of August (Figure 3). Previous studies on birds and mammals have also shown a seasonal rise and fall in both percent infestation (i.e. fraction of hosts with any ticks) and mean tick burdens (Battaly et al. 1987, Battaly and Fish 1993, Stafford 3rd et al. 1995, Durden et al. 2001, Randolph 2004, Brunner and Ostfeld 2008).

Temporal and spatial patterns of tick burdens are thought to be driven primarily by changes in questing tick abundance (Randolph 2004, Brunner and Ostfeld 2008). For example, the quick temporal increase in tick burden on hosts is thought to correspond with the emergence of larval ticks from eggs and the slow decline in tick burden is thought to be the combination of tick mortality or attachment to hosts (Randolph 2004). I found that spatio-temporal variability in tick burdens on birds was correlated with questing tick abundance (Table 3, Model 3-4). Nonetheless relative questing tick abundance did not explain as much variation in bird tick burden as a cubic function of the

15

sampling date, even after accounting for differences in the number of parameters (Table 3; Models 2 and 4). This may have resulted from difficulties in accurately estimating questing tick abundance over the 6 days prior to when the birds were sampled when ticks would have attached to the birds. Potential sources of error in our estimates include our frequency of sampling and the heterogeneous landscapes features at many of the sites. Although our tick drag sampling included ten to twelve 30m drags it may not have accurately measured the density of questing ticks. Thus, while measuring questing tick densities by dragging is useful in predicting tick burdens on hosts, estimates contain significant variability.

One strong source of variability in tick burdens was host species. Bird species was a significant predictor of tick burden and models with host species produced the two top models (Table 3; Models 1-3). Two species attributes, primary foraging guilds and primary nesting guilds, had substantial explanatory power and this result suggests that they might play a causal role in the differences in tick burden between different species of birds. Both these attributes were used as estimates of contact rates with potential tick questing substrate, as in previous studies of birds and larval *I. pacificus* ticks (Eisen et al. 2004). One shortcoming of these measures, and a possible explanation for the difference in model fit between models with species and species attributes (Table 3, Models 2-4) is that they were fixed in time and in space, and it is well known that birds change their foraging habitat between seasons (DeGraff and Wentworth 1986). Future analyses could quantify foraging time and behavior at local sites across multiple habitat types, or could include additional species attributes.

16

Finally, the individual attributes of gender, age, and mass of birds explained some additional variability in tick burdens. I found that tick burdens on male birds were generally higher then burdens on female birds which contrasts with a previous study (which had much smaller sample sizes) which found no differences in tick burdens by gender (Scharf 2004). Two potential explanations for our result are differences in preening behavior and use of different microhabitats when foraging. Preening is thought to allow birds and other animals to remove ecotoparasites like ticks. Male birds, however, generally spend more time preening compared to female birds (Cotgreave and Clayton 1994) which should result in fewer ticks on males (the opposite of what I found). The other explanation would be that males may spend more time moving around guarding their territory and helping fledglings that have just left the nest, and therefore spending more time in microhabitats where questing ticks are active.

I also found that juvenile or hatch-year birds had higher burdens then adult birds of the same species, which was the same result as a previous study on birds in the central Piedmont region of Maryland (Scharf 2004). Like gender, increased tick burden on young birds may result from differences in behavioral traits such as spending extended periods of time on the ground foraging or waiting for parental feedings, or poor preening skills. However, for both gender and age differences other traits, such as differences in immune response (Menten-Dedoyart et al. 2008), cannot be discounted.

The final individual attribute that explained a significant portion of variation in tick burden in some models (1 and 3; Table 3) was the mass of the bird. This was somewhat surprising, given that species was already a factor in these models, and thus

this effect resulted from larger birds, within a species, having higher tick burden. This might have resulted from increased foraging time for larger birds (Nagy et al. 1999), greater surface area (Calder 1984) for ticks to attach to, or some other unknown factor.

In conclusion, I have demonstrated that tick burdens on birds vary significantly among species, gender, age, and mass, and with seasonality and land use. These findings suggest that models that are based on constant tick burdens or even constant relative tick burdens are likely to be inaccurate and potentially problematic, in ascribing undo importance to a host in *Borrelia* transmission. To refine these Lyme disease risk models, I have presented four models of tick-host associations. Model 1 was the best fitting model, but is limited in scope to our specific bird species sampled and the phenology of ticks in the sampling region. Model 2 uses species attributes (foraging and nesting guild) to allow for predictions of tick burden for other unsampled species but is again limited to specific sampling dates and local sites. Model 3, indicated that measuring questing tick abundance is a useful predictor for ticks on birds and model 3 could be used regionally with the same bird species used in the analysis. Our results in model 4, indicate that using questing tick abundance as the seasonality measure and the species attributes of foraging and nesting guilds as a surrogate for individual bird species could significantly predict tick burdens on species that I did not sample in different regions where bird host communities are different.

I have also shown that species attributes, such the location of foraging and nesting activities, offer substantial insight into species differences. Our results could help improve current bird tick burden estimates used in host community models for predicting

B. burgdorferi infected nymphs. They also suggest that models using single estimates of

tick burdens may not be correctly characterizing the most important hosts for ticks.

These findings could help improve our understanding of the role of birds in Lyme disease

ecology.

Tables and Figures

Figure 1: Regional map of the Mid-Atlantic with sites located in Maryland, Virginia, and District of Columbia

Urbanization Gradient

Urbanization Index = (100-% Forest Cover+% Impermeable Surfaces)/2

Forest   **Residential**   **Urban**
0 ◄───► 100

-Jug Bay, MD
-SERC, MD
-Patuxent, MD

-Fort Dupont
 Park, SE DC
-Rock Creek
 Stream Valley
 Park, MD
-Wheaton, MD

-Bethesda, MD
 (2 Sites)
-Takoma
 Park, MD (2 Sites)
-Crofton, MD
-Millersville, MD

-The National Mall, DC
-Foggy Bottom, DC
-Baltimore, MD
-Arlington, VA

Forest
3 sites

Suburban
Parks 3 sites

Residential
6 sites
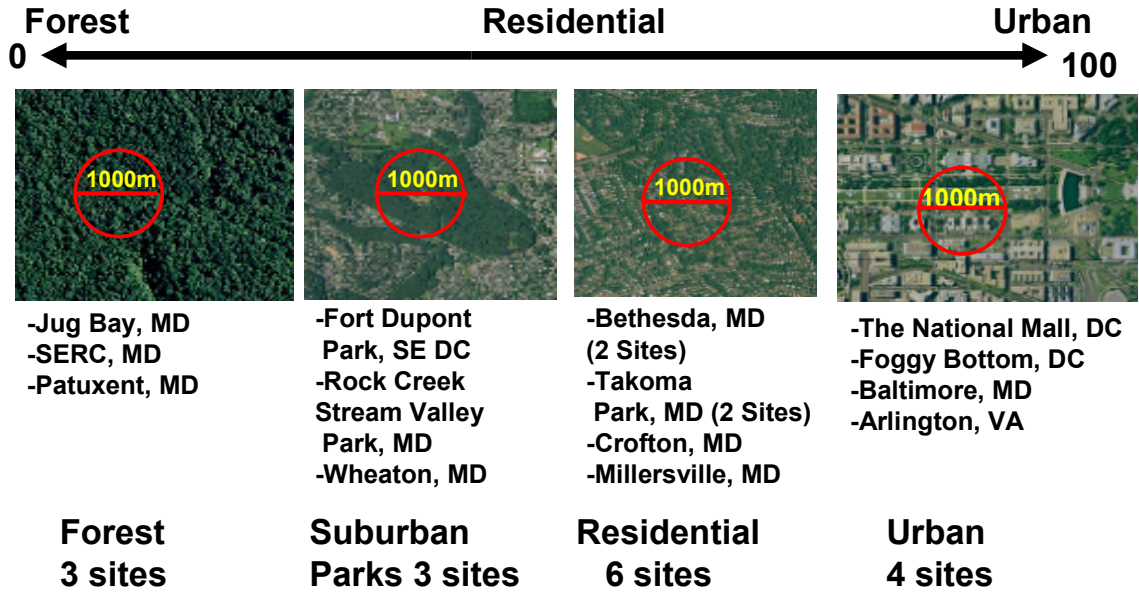
Urban
4 sites

Figure 2: Diagram of Urbanization Index (UI) equation and a list of four land-use types along with the field site names.

Table 1: Site locations, site codes and years that avian tick burden and tick density were sampled. Also indicates Urbanization Index value (UI) generated for each sampling site with circular buffer around the site center with a radius of 500m.

SITES	Site Code	Sampling Year		UI Values
Wheaton Regional Park, MD	WH	N/A	2007	6.7
Patuxent NWR, MD	PX	N/A	2007	12.9
Jug Bay Wetland Sanctuary, MD	JB	2006	2007	13.0
Rock Creek SV Park, MD	RC	2006	2007	13.2
Fort Dupont Park, DC	FD	2006	2007	15.4
SERC, MD	SC	2006	2007	16.2
Bethesda, MD (Site A)	BEA	2006	2007	28.0
Millersville, MD	MI	N/A	2007	36.1
Bethesda, MD (Site B)	BEB	2006	2007	36.5
Crofton, MD	CR	N/A	2007	36.7
Takoma Park, MD (Site A)	TPA	2006	2007	46.9
Takoma Park, MD (Site B)	TPB	2006	2007	49.3
Arlington, VA	AR	N/A	2007	71.8
The National Mall, DC	NH	2006	2007	76.5
Foggy Bottom, DC	BR	2006	2007	81.8
Baltimore, MD	BA	2006	2007	90.1

Table 2: Number of birds examined for *I. scapularis* ticks, in each of three habitat types (with urbanization index (UI) ranges given), predicted peak tick burdens from model 1 (Julian Date = July 22) and total number of *I. scapularis* larvae collected from that species.

Bird Species	Number of Birds Examined			Fitted Values For Peak Tick Burden (July 22)			Number Ticks Collected
	Forest and Park UI = (0-16)	Residential UI = (17-50)	Urban UI =(51-100)	Forest and Park UI=(12.9)	Residential UI=(40.9)	Urban UI=(80.1)	
American Robin (*Turdus migratorius*)	214	300	290	2.951	0.553	0.053	278
Brown-headed Cowbird (*Molothrus ater*)	17	29	4	11.421	2.139	0.207	47
Blue Jay (*Cyanocitta cristata*)	22	46	9	1.120	0.210	0.020	9
Brown Thrasher (*Toxostoma rufum*)	9	1	2	3.727	0.698	0.068	2
Carolina Chickadee (*Poecile carolinensis*)	167	100	11	0.049	0.009	0.001	2
Carolina Wren (*Thryothorus ludovicianus*)	339	135	29	8.158	1.528	0.148	1088
Common Grackle (*Quiscalus quiscula*)	3	10	51	6.670	1.249	0.121	1
Eastern Bluebird (*Sialia sialis*)	13	0	0	0.343	0.064	0.006	4
Eastern Towhee (*Pipilo erythrophthalmus*)	127	10	0	4.688	0.878	0.085	175

Species							
Eastern Tufted Titmouse (*Baeolophus bicolor*)	248	145	10	0.369	0.069	0.007	33
Gray Catbird (*Dumetella carolinensis*)	231	433	228	0.304	0.057	0.006	31
House Finch (*Carpodacus mexicanus*)	26	102	54	0.129	0.024	0.002	2
House Sparrow (*Passer domesticus*)	3	1084	1346	0.029	0.005	0.001	2
Hooded Warbler (*Wilsonia citrina*)	11	0	0	4.719	0.884	0.086	16
House Wren (*Troglodytes aedon*)	15	20	1	3.483	0.652	0.063	21
Indigo Bunting (*Passerina cyanea*)	28	0	0	0.533	0.100	0.010	4
Northern Cardinal (*Cardinalis cardinalis*)	589	592	47	4.207	0.788	0.076	960
Ovenbird (*Seiurus aurocapilla*)	225	1	2	9.577	1.794	0.174	500
Red-eyed Vireo (*Vireo olivaceus*)	199	3	0	0.040	0.008	0.001	2
Song Sparrow (*Melospiza melodia*)	11	129	53	0.255	0.048	0.005	3
Veery (*Catharus fuscescens*)	21	0	1	39.595	7.416	0.718	39
White-breasted Nuthatch (*Sitta carolinensis*)	60	59	1	0.148	0.028	0.003	2
Wood Thrush (*Hylocichla mustelina*)	534	44	0	3.402	0.637	0.062	636
Species Without Ticks							
Downy Woodpecker (*Picoides pubescens*)	109	68	12	-	-	-	0
European Starling (*Sturnus vulgaris*)	0	45	513	-	-	-	0

Species						
Eastern Wood-Pewee (*Contopus virens*)	41	2	0	-	-	0
Hairy Woodpecker (*Picoides villosus*)	26	3	0	-	-	0
Mourning Dove (*Zenaida macroura*)	21	60	131	-	-	0
Northern Mockingbird (*Mimus polyglottos*)	1	11	96	-	-	0
Red-bellied Woodpecker (*Melanerpes carolinus*)	23	14	0	-	-	0
Rock Pigeon (*Columba livia*)	0	0	125	-	-	0
Scarlet Tanager (*Piranga olivacea*)	33	1	0	-	-	0
Yellow-Shafted Flicker (*Colaptes auratus*)	12	9	0	-	-	0
American Goldfinch (*Carduelis tristis*)	96	85	9	-	-	0

Note: *I. scapularis* larvae were also found on (# ticks, # birds examined): Canada warbler (1,1), Common yellowthroat (1,1), Worm-eating warbler (7,3). *Ixodes dentatus* larvae were also found on (# ticks, # birds examined): C. wren (5,5), N. Cardinal (3, 3), Gray catbird, (1,1), E. Towhee (1,1), Hermit thrush (1,1). *I. dentatus* nymphs were found on the following species A. Robin (3,3), C. Wren (1,1), and Wood thrush (1,1). *Amblyomma americanum* larvae were found on Brown Thrusher (1,1), and Wood Thrush (1,1). *A. americanum* nymphs found on American Robin (1,1) and Carolina Wren (1,1). *Dermacentor variabilis* larvae found on C. Wren (4,1) and *Haemaphysalis chordeilis* larvae were found on C. Wren (4,1).
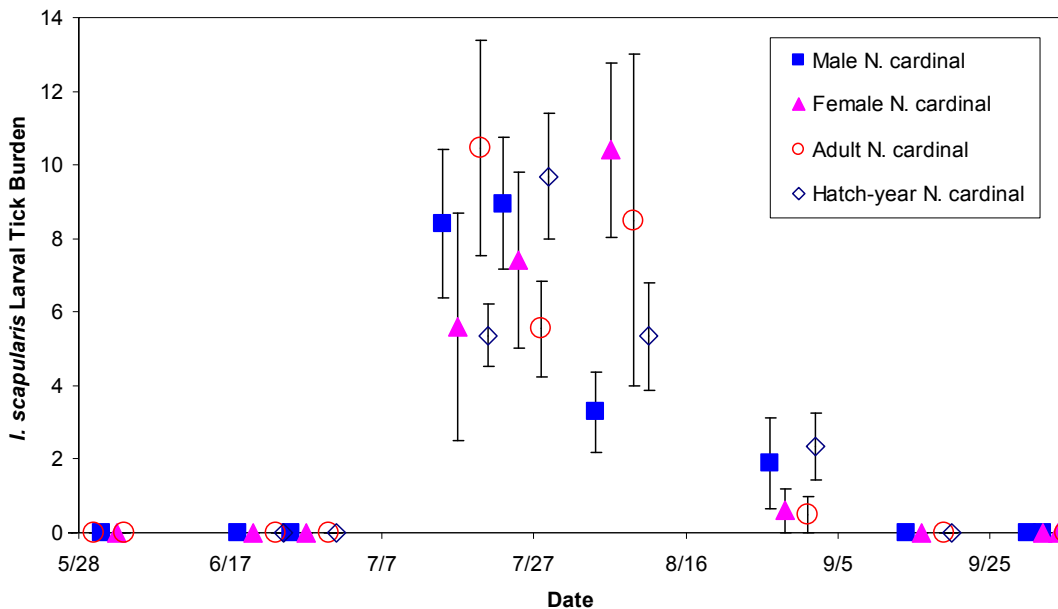
Figure 3: Observed *I. scapularis* Laval Tick Burden (±SE) for Male and Female and adult and hatch-year N. Cardinals at Rockcreek Stream Valley Park, Maryland averaged across the 2006 and 2007 sampling years. Points have been staggered 1-3 days around the sampling date for clarity of presentation. Female is the actual date, male is 2 days prior to actual date, adult is 1 day after actual date, and hatch year is 2 days after actual date except for the data point on 8/10 which is 3 days after the actual date for clarity..
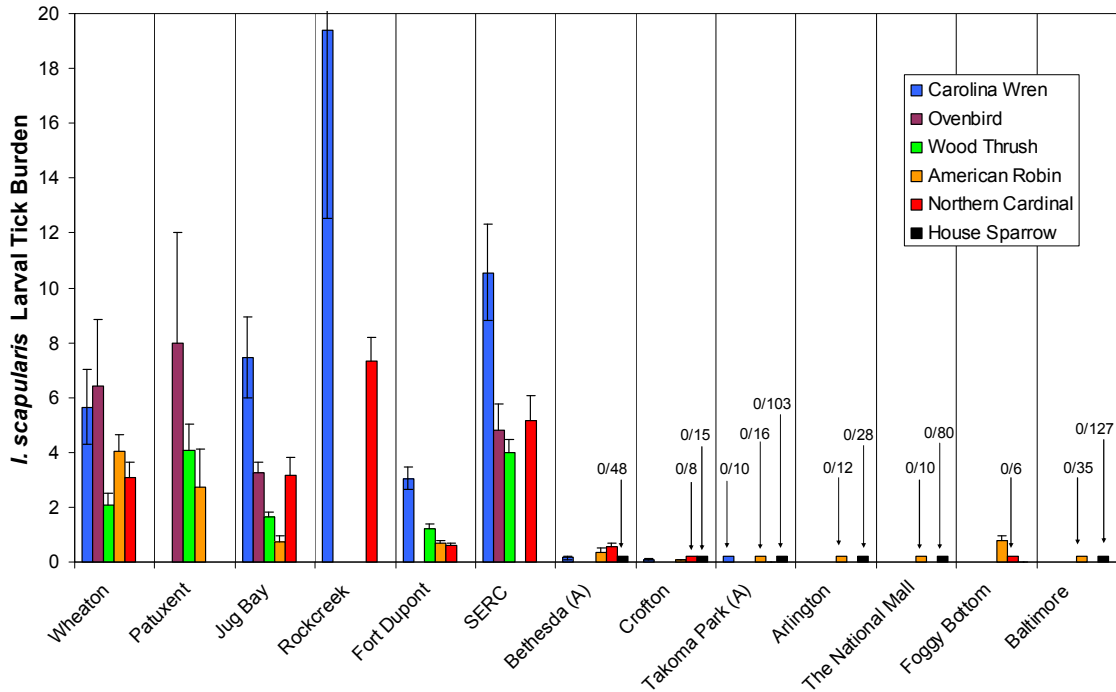
Figure 4: Observed mean *I. scapularis* larvae tick burden (±SE) for years (2006 and 2007) during peak larval abundance (July 1-August 15) on 6 species of birds across urbanization land-use gradient. Sites arranged from most forested to most urban based on urbanization index. Observed mean tick burden does not differentiate between sex or age class of bird. Arrows indicate species where observed mean tick burden was zero along with sample of birds examined, (mean burden, number of birds examined).
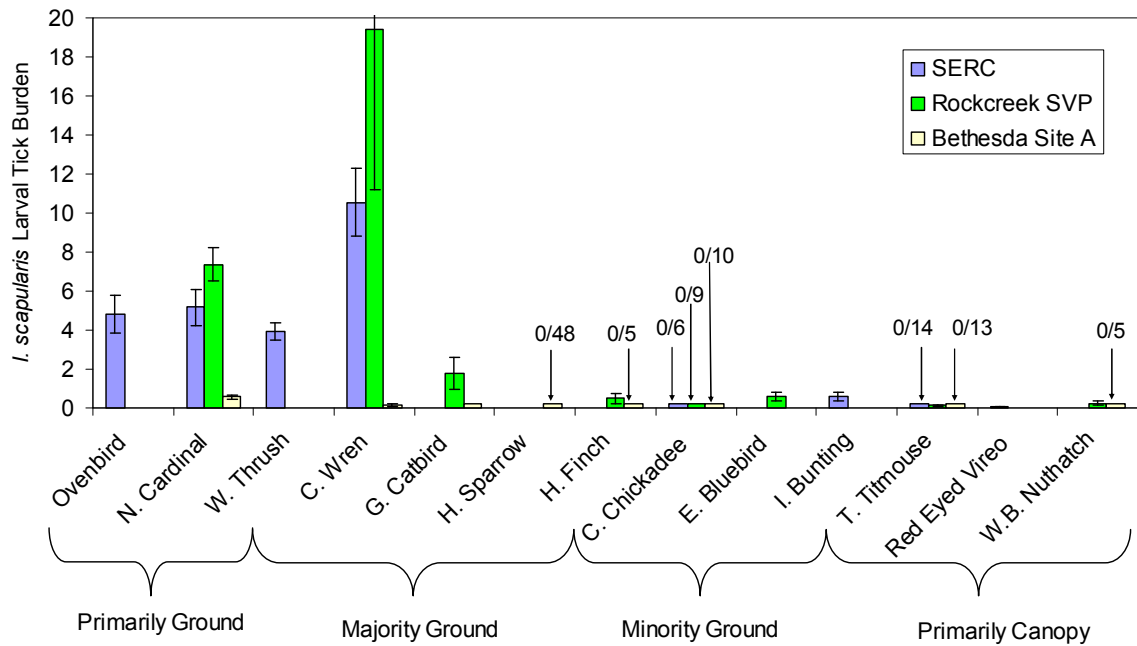
Figure 5: Observed mean *I. scapularis* larval tick burden (±SE) on 12 species of birds over 2 years (2006-2007) during peak larval abundance (July 1- August 15) at three sites, the Smithsonian Environmental Research Center (SERC), a forested site, Rockcreek Stream Valley Park, a park site, and Bethesda site A, a residential site. Bird species are arranged based on foraging guild: Primarily Ground foragers: Ovenbird and N. Cardinal; Majority Ground foragers: Wood Thrush, Carolina Wren, Grey Catbird, House Sparrow, and House Finch. Minority Ground Foragers: Carolina Chickadee, Eastern Bluebird, and Indigo Bunting. Primarily Canopy Forager: Eastern Tufted Titmouse, Red-eyed Vireo, and White-breasted Nuthatch. Observed mean tick burden for birds does not differentiate between sex or age class of bird. Arrows indicate species where observed mean tick burden was zero and sample size of birds examined is indicated.

Table 3: Results of model comparisons using Akaike's information criterion (AIC) for predicting *I. scapularis* larval tick burden on bird hosts across an urbanization land-use gradient. See Methods for additional discussion of models.

Model	Parameters	Log Likelihood(a)	Akaike's Information Criterion (AIC)	Δ AIC	Degrees of Freedom
1	Species, Age, Sex, Mass, UI, Date (Cubic Function)	-3127.1	6316.3	0	30
2	Primary Foraging Guild, Nesting Guild, Age, Sex, Mass, UI, Date (Cubic Function)	-3397.8	6825.5	509	13
3	Species, Age, Sex, Mass, UI, Year, Questing Tick Abundance	-3954.7	7969.5	1653.2	29
4	Primary Foraging Guild, Nesting Guild, Age, Sex, UI, Questing Tick Abundance, Year	-4259.7	8545.5	2229.2	11

Table 4: Parameter coefficients (±SE) from models 1 and 3. Asterisks indicate the reference levels, and dashes indicate that that model did not include that parameter.

Parameter	Model 1		Model 3	
	B	**SE**	**B**	**SE**
Intercept	-411.59	18.90	1.47	0.40
Species				
American Robin	-0.88	0.27	0.48	0.23
Brown-headed Cowbird	1.46	0.36	0.82	0.27
Blue Jay	-2.22	0.57	-0.40	0.50
Brown Thrasher	-0.48	0.93	-0.40	0.86
Carolina Chickadee	-3.08	0.81	-5.38	0.78
Carolina wren	1.75	0.29	0.07	0.24
Common Grackle	-1.09	1.22	0.51	1.17
Eastern Bluebird	-1.69	0.70	-2.23	0.68
Eastern Towhee	0.56	0.19	0.16	0.16
Eastern Tufted Titmouse	-1.41	0.33	-2.94	0.29
Gray Catbird	-2.03	0.24	-2.53	0.23
House Finch	-2.44	0.78	-3.96	0.75
House Sparrow	-4.10	0.74	-5.23	0.73
Hooded Warbler	1.47	0.58	-0.69	0.51
House Wren	1.15	0.52	-0.49	0.44
Indigo Bunting	-0.84	0.67	-2.19	0.62
Northern Cardinal	0.45	0.12	0.24	0.10
Ovenbird	1.94	0.31	0.01	0.26
Red-eyed Vireo	-3.49	0.78	-5.45	0.76
Song Sparrow	-1.75	0.66	-3.13	0.64
Veery	2.89	0.81	-0.30	0.42
White-breasted Nuthatch	-2.28	0.78	-3.90	0.76
Wood Thrush	0*	.	0*	.
Species Attributes				
Age				
Hatch Year	0.37	0.10	0.66	0.087
Adult	0*	.	0*	.
Gender				
Unknown	0.15	0.12	0.15	0.10
Female	-0.277	0.089	-0.333	0.075
Male	0*	.	0*	.
Mass	0.030	0.010	-0.025	0.008

Seasonality Parameters				
Date (Cubic Function)				
Julian Date	5.48	0.26	-	-
Julian Date^2	-0.024	0.0012	-	-
Julian Date^3	0.000034	0.0000017	-	-
Questing Tick Abundance Per m^2	-	-	2.65	0.15
Year of Sampling				
2006	-	-	-0.61	0.067
2007	-	-	0*	.
Spatial Parameter				
Urbanization Index	-0.060	0.0029	-0.055	0.0029

Table 5: Parameter coefficients (±SE) from models 2 and 4. Asterisks indicate the reference levels, and dashes indicate that that model did not include that parameter.

| Parameter	Model 2		Model 4	
	B	**SE**	**B**	**SE**
Intercept	-401.21	17.99	-2.14	0.20
Species Attributes				
Foraging Guilds				
Primarily Ground	4.46	0.22	4.40	0.21
Majority Ground	2.92	0.19	3.034	0.18
Minority Ground	-0.24	0.406	-0.29	0.39
Primarily Canopy	0*	.	0*	.
Nesting Guilds				
Ground Nester	-0.57	0.13	-0.58	0.11
Shrub Nester	-1.75	0.15	-1.28	0.11
Canopy Nester	-0.72	0.14	-0.45	0.074
Cavity Nester	0*	.	0*	.
Age				
Hatch Year	0.24	0.093	0.63	0.079
Adult	0*	.	0*	.
Gender				
Unknown	0.35	0.10	0.30	0.087
Female	-0.22	0.085	-0.26	0.073
Male	0*	.	0*	.
Seasonality Parameters				
Date (Cubic Function)				
Julian Date	5.33	0.25	-	-
Julian Date^2	-0.023	0.0011	-	-
Julian Date^3	0.000033	0.0000017	-	-
Questing Tick Abundance Per m^2	-	-	2.88	0.15
Spatial Parameter				
Urbanization Index	-0.088	0.00302	-0.083	0.00298

31
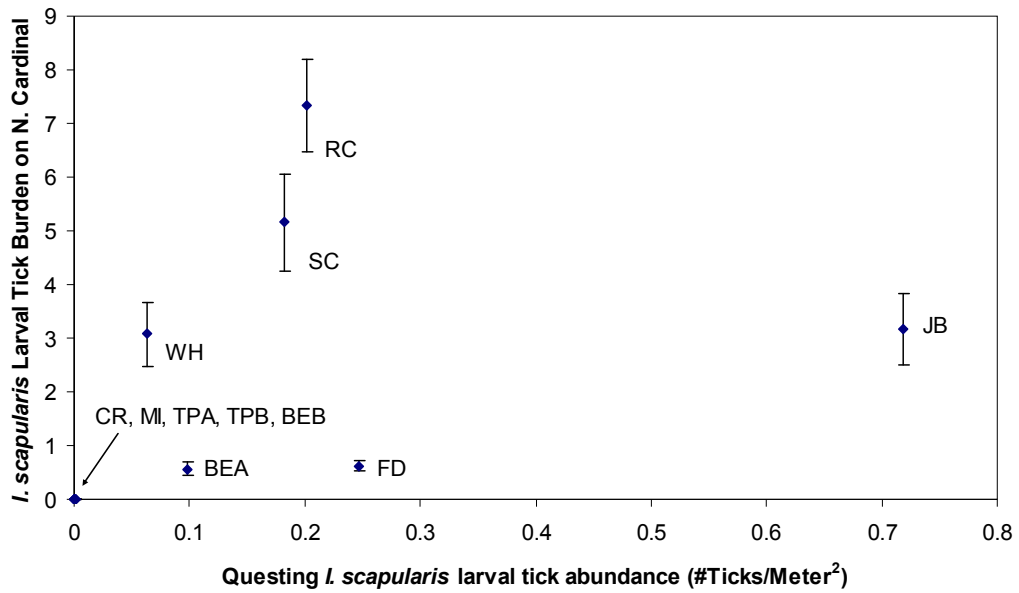
Figure 6: *I. scapularis* larval tick burden on Northern Cardinal vs. questing larval *I. scapularis* abundance at 11 sites along an urbanization land-use gradient (Values averaged from July 1-August 15 for years 2006-2007 combined). 8-84 birds were sampled per site. Raw values ignore effects of age, sex, and date of capture. Site abbreviations are given in table 1.

Table 6: Analysis of species by urbanization interaction analysis. The interaction term had strong explanatory power (Δ AIC = 155.1), as did all other model effects (species, age, sex, and cubic date function), as in Table 3 above.

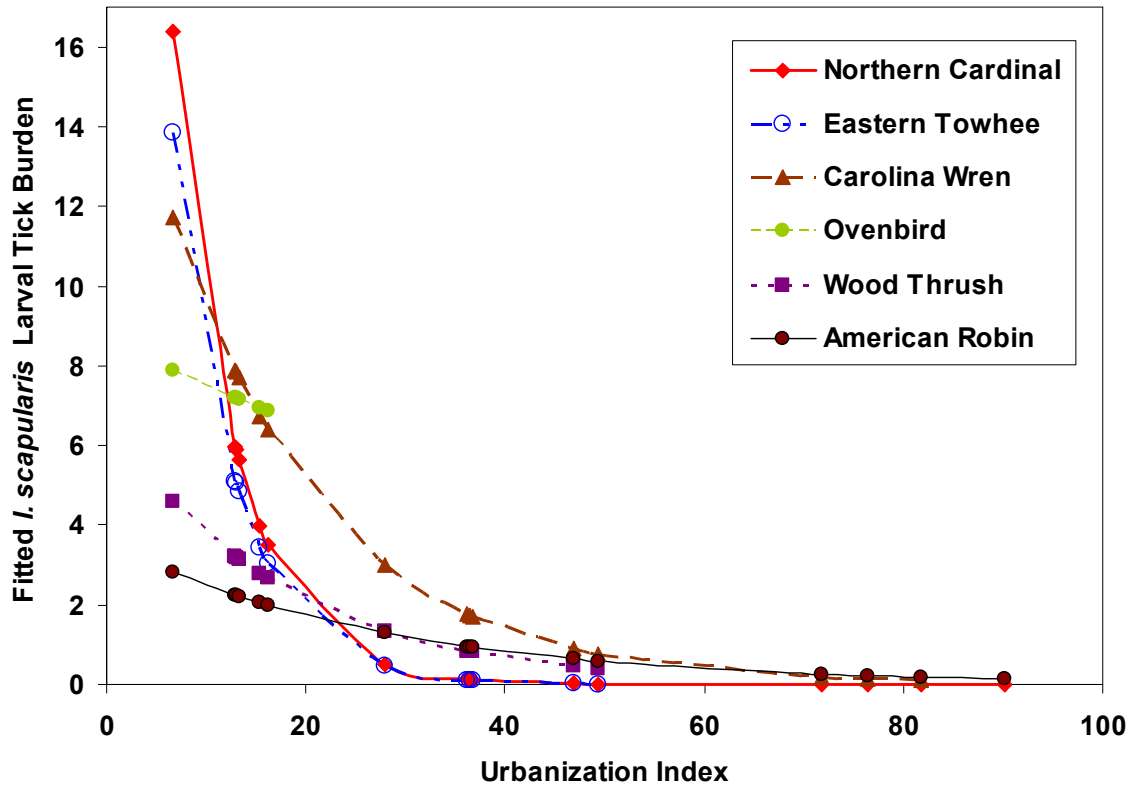| Urbanization Slope	B	SE
American robin	-0.037	0.015
Carolina wren	-0.064	0.016
Eastern towhee	-0.161	0.044
Northern cardinal	-0.163	0.018
Ovenbird	-0.015	0.044
Wood thrush	-0.058	0.014

Figure 7: Fitted *I. scapularis* larval tick burden from interaction analysis on six species with increasing urbanization. Markers indicate urbanization indices of actual sampling sites and lines extend to sites where species were sampled.

Appendix

Table 7: Additional bird species examined in each habitat type that had no *I. scapularis* larval tick burden and sample size was less then 20.

Bird Species	Number of Birds Examined		
	Forest and Park UI = (0-16)	Residential UI = (17-50)	Urban UI =(51-100)
Baltimore Oriole (*Icterus galbula*)	0	1	0
Black-and-white Warbler (*Mniotilta varia*)	1	0	0
Brown Creeper (*Certhia americana*)	1	0	0
Cerulean Warbler (*Dendroica cerulea*)	0	0	1
Cooper's Hawk (*Accipiter cooperii*)	1	0	0
Fish Crow (*Corvus ossifragus*)	0	0	1
Hermit Thrush (*Catharus guttatus*)	0	1	0
Mourning Warbler (*Oporornis philadelphia*)	1	0	0
Northern Parula (*Parula americana*)	1	0	0
Prothonotary Warbler (*Protonotaria citrea*)	1	0	0
Red-shouldered Hawk (*Buteo lineatus*)	1	0	0
Sharp-shinned Hawk (*Accipiter striatus*)	1	0	0
White-throated Sparrow (*Zonotrichia albicollis*)	0	0	1
Eastern Kingbird (*Tyrannus tyrannus*)	0	0	2
Red-winged Blackbird (Agelaius phoeniceus)	1	1	0
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	1	0	1
Yellow breasted Chat (*Porzana flaviventer*)	1	0	1
Cedar Waxwing (*Bombycilla cedrorum*)	0	0	3
Chipping Sparrow (*Spizella passerina*)	2	1	0
Kentucky Warbler (*Oporornis formosus*)	3	0	0
Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	0	0	3
Pileated Woodpecker (*Dryocopus pileatus*)	3	0	0
Swainson's Thrush (*Catharus ustulatus*)	3	0	0

Red-breasted Nuthatch (*Sitta canadensis*)	3	1	0
White-eyed Vireo (*Vireo griseus*)	5	0	0
Yellow-billed Cuckoo (*Coccyzus americanus*)	5	0	0
Yellow-throated Vireo (*Vireo flavifrons*)	5	0	0
Blue-gray Gnatcatcher (*Polioptila caerulea*)	6	0	0
Eastern Phobe (*Sayornis phoebe*)	6	0	0
Summer Tanager (*Piranga rubra*)	6	0	0
Great Crested Flycatcher (*Myiarchus crinitus*)	7	3	0
Lousiana Waterthrush (*Seiurus motacilla*)	10	1	0

Table 8: Additional bird species infested with larval and nymphal *Haemaphysalis leporispalustris* (Packard) ticks, commonly known as Rabbit ticks.

Bird Species	Examined	*Haemaphysalis leporispalustris*			
		Larvae		Nymphs	
		Number Infested	Number Collected	Number Infested	Number Collected
American Robin (*Turdus migratorius*)	804	13	47	17	21
Brown-headed Cowbird (*Molothrus ater*)	50	1	1	1	1
Blue Jay (*Cyanocitta cristata*)	77	3	15	1	1
Brown Thrasher (*Toxostoma rufum*)	12	0	0	1	1
Carolina Wren (*Thryothorus ludovicianus*)	503	30	289	35	54
Common Grackle (*Quiscalus quiscula*)	64	0	0	1	1
Eastern Towhee (Pipilo erythrophthalmus)	137	6	21	0	0
Eastern Tufted Titmouse (Baeolophus bicolor)	403	4	6	0	0
Gray Catbird (*Dumetella carolinensis*)	892	24	93	12	17
House Finch (*Carpodacus mexicanus*)	182	0	0	1	1
House Sparrow (*Passer domesticus*)	2433	12	51	7	8

Species					
House Wren (*Troglodytes aedon*)	36	2	12	0	0
Mourning Dove (*Zenaida macroura*)	212	1	2	0	0
Mourning Warbler (*Oporornis philadelphia*)	1	0	0	1	1
Northern Cardinal (*Cardinalis cardinalis*)	1228	59	717	39	56
Northern Mockingbird (*Mimus polyglottos*)	108	3	18	0	0
Ovenbird (*Seiurus aurocapilla*)	228	2	7	3	3
Song Sparrow (*Melospiza melodia*)	193	16	119	9	12
Wood Thrush (Hylocichla mustelina)	578	10	50	7	8

References

References

Allan, B. F., F. Keesing, and R. S. Ostfeld. 2003. Effect of Forest Fragmentation on Lyme Disease Risk. Conservation Biology **17**:267-272.

Altizer, S., A. Dobson, P. Hosseini, P. Hudson, M. Pascual, and P. Rohani. 2006. Seasonality and the dynamics of infectious diseases. Ecology Letters **9**:467-484.

Anderson, J. F., and L. A. Magnarelli. 1984. Avian and mammalian hosts for spirochete-infected ticks and insects in a Lyme disease focus in Connecticut. Yale J Biol Med **57**:627-641.

Barbour, A. G., and D. Fish. 1993. The biological and social phenomenon of Lyme disease. Science **260**:1610-1616.

Battaly, G. R., and D. Fish. 1993. Relative importance of bird species as hosts for immature Ixodes dammini (Acari: Ixodidae) in a suburban residential landscape of southern New York State. J Med Entomol **30**:740-747.

Battaly, G. R., D. Fish, and R. C. Dowler. 1987. The seasonal occurrence of Ixodes dammini and Ixodes dentatus(Acari: Ixodidae) on birds in a Lyme disease endemic area of southeastern New York State. Journal of the New York Entomological Society **95**:461-468.

Beyer. 2004. Hawth's Analysis Tools for ArcGIS.

Brisson, D., D. E. Dykhuizen, and R. S. Ostfeld. 2008. Conspicuous impacts of inconspicuous hosts on the Lyme disease epidemic. Proceedings of the Royal Society B: Biological Sciences **275**:227-227.

Brownstein, J. S., T. R. Holford, and D. Fish. 2003. A climate-based model predicts the spatial distribution of the Lyme disease vector Ixodes scapularis in the United States. Environmental Health Perspectives **111**:1152–1157-1152–1157.

Brownstein, J. S., T. R. Holford, and D. Fish. 2005. Effect of Climate Change on Lyme Disease Risk in North America. EcoHealth **2**:38-46.

Brunner, J. L., and R. S. Ostfeld. 2008. Multiple causes of variable tick burdens on small-mammal hosts. Ecology **89**:2259-2272.

Burgdorfer, W., A. G. Barbour, S. F. Hayes, J. L. Benach, E. Grunwaldt, and J. P. Davis. 1982. Lyme Disease--A Tick-Borne Spirochetosis? Science **216**:1317-1319.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. A practical information-theoretic approach.

Calder, W. A. 1984. Size, Function, and Life History. Cambridge, Mass.: Harvard University Press.

CDC. 2007. Infectious Disease Information, Tickborne Diseases.*in* C. f. D. Control, editor., Atlanta.

CDC. 2008. Surveillance for Lyme Disease United States, 1992-2006.*in* C. f. D. Control, editor. Division of Vector-Borne Infectious Diseases, National Center for Zoonotic Vector-Borne and Enteric Diseases, Fort Collins.

Clifford, C. M., G. Anastos, and A. Elbl. 1961. The larval ixodid ticks of the eastern United States. Misc. Publ. Entomol. Soc. Am **2**:215-244.

Clifford, C. M., D. E. Sonenshine, J. E. Keirans, and G. M. Kohls. 1973. Systematics of the subfamily Ixodinae (Acarina: Ixodidae). I. The subgenera of Ixodes. Ann Entomol Soc Am **66**:489-500.

Cotgreave, P., and D. H. Clayton. 1994. Comparative analysis of time spent grooming by birds in relation to parasite load. Behaviour:171-187.

Daniels, T. J., R. C. Falco, and D. Fish. 2000. Estimating Population Size and Drag Sampling Efficiency for the Blacklegged Tick (Acari: Ixodidae). J. Med. Entomol **37**:357Ñ363-357Ñ363.

DeGraff, R. M., and J. M. Wentworth. 1986. Avian guild structure and habitat associations in suburban bird communities. Urban Ecosystems **9**:399-412.

Durden, L. A., J. H. Oliver, and A. A. Kinsey. 2001. Ticks (Acari: Ixodidae) and spirochetes (spirochaetaceae: spirochaetales) recovered from birds on a Georgia Barrier Island. Journal of Medical Entomology **38**:231-236.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook: a field guide to the natural history of North American birds. Simon and Shuster. Inc., New York. 785 pp.

Eisen, L., R. J. Eisen, and R. S. Lane. 2004. The roles of birds, lizards, and rodents as hosts for the western black-legged tick Ixodes pacificus. Journal of Vector Ecology: Journal of the Society for Vector Ecology **29**:295-308.

Falco, R. C., and D. Fish. 1992. A comparison of methods for sampling the deer tick,Ixodes dammini, in a Lyme disease endemic area. Experimental and Applied Acarology **14**:165-173.

Falco, R. C., D. F. McKenna, T. J. Daniels, R. B. Nadelman, J. Nowakowski, D. Fish, and G. P. Wormser. 1999. Temporal relation between Ixodes scapularis abundance and risk for Lyme disease associated with erythema migrans. American Journal of Epidemiology **149**:771-776.

Giardina, A. R., K. A. Schmidt, E. M. Schauber, and R. S. Ostfeld. 2000. Modeling the role of songbirds and rodents in the ecology of Lyme disease. Can. J. Zool./Rev. Can. Zool **78**:2184-2197.

Giery, S. T., and R. S. Ostfeld. 2007. The role of lizards in the ecology of Lyme disease in two endemic zones of the Northeastern United States. Journal of Parasitology **93**:511-517.

Ginsberg, H. S., P. A. Buckley, M. G. Balmforth, E. Zhioua, S. Mitra, and F. G. Buckley. 2005. Reservoir Competence of Native North American Birds for the Lyme Disease Spirochete, Borrelia burgdorferi. Journal of Medical Entomology **42**:445-449.

Glass, G. E., F. P. Amerasinghe, J. M. Morgan Iii, and T. W. Scott. 1994. Predicting Ixodes scapularis Abundance on White-Tailed Deer Using Geographic Information Systems. The American Journal of Tropical Medicine and Hygiene **51**:538-538.

Gomez, A., A. M. Kilpatrick, L. D. Kramer, I. A. P. Dupuis, J. G. Maffei, S. J. Goetz, P. P. Marra, P. Daszak, and A. A. Aguirre. 2008. Land Use and West Nile Virus Seroprevalence in Wild Mammals. Emerg Infect Dis **14**:962-965.

Guerra, M., E. Walker, C. Jones, S. Paskewitz, M. R. Cortinas, A. Stancil, L. Beck, M. Bobo, and U. Kitron. 2002. Predicting the risk of Lyme disease: habitat suitability for Ixodes scapularis in the north central United States. Emerg Infect Dis **8**:289-297.

Keirans, J. E., and L. A. Durden. 1998. Illustrated key to nymphs of the tick genus Amblyomma (Acari: Ixodidae) found in the United States. J Med Entomol **35**:489-495.

Keirans, J. E., and T. R. Litwak. 1989. Pictorial key to the adults of hard ticks, family Ixodidae (Ixodida: Ixodoidea), east of the Mississippi River. J. Med. Entomol **26**:435-448.

Levine, J. F., C. S. Apperson, P. Howard, M. Washburn, and A. L. Braswell. 1997. Lizards as hosts for immature Ixodes scapularis (Acari: Ixodidae) in North Carolina. J Med Entomol **34**:594-598.

LoGiudice, K., S. T. K. Duerr, M. J. Newhouse, K. A. Schmidt, M. E. Killilea, and R. S. Ostfeld. 2008. Impact of host community composition on lyme disease risk. Ecology **89**:2841-2849.

LoGiudice, K., R. S. Ostfeld, K. A. Schmidt, and F. Keesing. 2003. The ecology of infectious disease: Effects of host diversity and community composition on Lyme disease risk. PNAS **100**:567-571.

Madhav, N. K., J. S. Brownstein, J. I. Tsao, and D. Fish. 2004. A Dispersal Model for the Range Expansion of Blacklegged Tick (Acari: Ixodidae). Journal of Medical Entomology **41**:842-852.

Magnarelli, L. A., J. F. Anderson, and D. Fish. 1987. Transovarial transmission of Borrelia burgdorferi in Ixodes dammini(Acari: Ixodidae). Journal of Infectious Diseases **156**:234-236.

Masek, J. G., F. E. Lindsay, and S. N. Goward. 2000. Dynamics of urban growth in the Washington DC metropolitan are, 1973-1996, from Landsat observations. International Journal of Remote Sensing **21**:3473-3486.

Maupin, G. O., D. Fish, J. Zultowsky, E. G. Campos, and J. Piesman. 1991. Landscape Ecology of Lyme Disease in a Residential Area of Westchester County, New York. American Journal of Epidemiology **133**:1105-1113.

Menten-Dedoyart, C., B. Couvreur, O. Thellin, P. V. Drion, M. Herry, O. Jolois, and E. Heinen. 2008. Influence of the Ixodes ricinus tick blood-feeding on the antigen-specific antibody response in vivo. Vaccine **26**:6956-6964.

Nagy, K. A., I. A. Girard, and T. K. Brown. 1999. Energetics of free-ranging mammals, reptiles, and birds. Annual review of nutrition **19**:247-247.

Ogden, N. H., L. R. Lindsay, K. Hanincov , I. K. Barker, M. Bigras-Poulin, D. F. Charron, A. Heagy, C. M. Francis, C. J. O'Callaghan, I. Schwartz, and R. A. Thompson. 2008. Role of migratory birds in introduction and range expansion of Ixodes scapularis ticks and of Borrelia burgdorferi and Anaplasma phagocytophilum in Canada. Applied and Environmental Microbiology **74**:1780-1790.

Ostfeld, R. S., O. M. Cepeda, K. R. Hazler, and M. C. Miller. 1995. Ecology of Lyme disease: Habitat associations of ticks(Ixodes scapularis) in a rural landscape. Ecological Applications **5**:353-361.

Patrican, L. A. 1997. Absence of Lyme disease spirochetes in larval progeny of naturally infected Ixodes scapularis (Acari: Ixodidae) fed on dogs. Journal of Medical Entomology (USA).

Poole, A. 2005. The Birds of North America Online.*in* A. Poole, editor. Cornell
      Laboratory of Ornithology, Ithaca N.Y.

Pyle. 1997. Identification guide to North American birds Part 1, Columbidae to
      Ploceidae. Slate Creek Press, Bolinas, California.

Rand, P. W., C. Lubelczyk, M. S. Holman, E. H. Lacombe, and R. P. Smith Jr. 2004.
      Abundance of Ixodes scapularis (Acari: Ixodidae) after the complete removal of
      deer from an isolated offshore island, endemic for Lyme Disease. J Med Entomol
      41:779-784.

Randolph, S. E. 2004. Tick ecology: processes and patterns behind the epidemiological
      risk posed by ixodid ticks as vectors. Parasitology **129**:S37-S65-S37-S65.

Scharf, W. C. 2004. Immature Ticks on Birds: Temporal Abundance and Reinfestation.
      Northeastern Naturalist **11**:143-150.

Schoener, T. W. 1968. Sizes of Feeding Territories among Birds. Ecology **49**:123-141.

Scott, J. D., K. Fernando, S. N. Banerjee, L. A. Durden, S. K. Byrne, M. Banerjee, R. B.
      Mann, and M. G. Morshed. 2001. Birds disperse ixodid (Acari: Ixodidae) and
      Borrelia burgdorferi-infected ticks in Canada. J Med Entomol **38**:493-500.

Shaw, D. J., and A. P. Dobson. 1995. Patterns of macroparasite abundance and
      aggregation in wildlife populations: a quantitative review. Ecology of Wildlife
      Host-Parasite Interactions.

Silva, M., J. H. Brown, and J. A. Downing. 1997. Differences in population density and
      energy use between birds and mammals: a macroecological perspective. Journal
      of Animal Ecology **66**:327-340.

Slowik, T. J., and R. S. Lane. 2001. Birds and Their Ticks in Northwestern California:
      Minimal Contribution to Borrelia Burgdorferi Enzootiology. Journal of
      Parasitology **87**:755-761.

Spielman, A., M. L. Wilson, J. F. Levine, and J. Piesman. 1985. Ecology of Ixodes dammini-borne human babesiosis and Lyme disease. Annual Review of Entomology **30**:439-460.

Stafford 3rd, K. C., V. C. Bladen, and L. A. Magnarelli. 1995. Ticks (Acari: Ixodidae) infesting wild birds (Aves) and white-footed mice in Lyme, CT. J Med Entomol **32**:453-466.

Stafford 3rd, K. C., and L. A. Magnarelli. 1993. Spatial and temporal patterns of Ixodes scapularis (Acari: Ixodidae) in southeastern Connecticut. J Med Entomol **30**:762-771.

Stafford, K. C. 1994. Survival of immature Ixodes scapularis (Acari: Ixodidae) at different relative humidities. Journal of Medical Entomology **32**.

Steere, A. C., T. F. Broderick, and S. E. Malawista. 1978. Erythema chronicum migrans and Lyme arthritis: epidemiologic evidence for a tick vector. Am J Epidemiol **108**:312-321.

Weisbrod, A. R., and R. C. Johnson. 1989. Lyme disease and migrating birds in the Saint Croix River Valley. Appl. Environ. Microbiol. **55**:1921-1924.

Wilson, M. L., G. H. Adler, and A. Spielman. 1985. Correlation between abundance of deer and that of the deer tick, Ixodes dammini(Acari: Ixodidae). Annals of the Entomological Society of America **78**:172-176.

Wilson, M. L., A. M. Ducey, T. S. Litwin, T. A. Gavin, and A. Spielman. 1990. Microgeographic distribution of immature Ixodes dammini ticks correlated with that of deer. Medical and Veterinary Entomology **4**:151-159.

Wilson, M. L., S. R. Telford 3rd, J. Piesman, and A. Spielman. 1988. Reduced abundance of immature Ixodes dammini (Acari: Ixodidae) following elimination of deer. J Med Entomol **25**:224-228.

Curriculum Vitae

Ryan Peters graduated from Norwin High School, North Huntingdon, Pennsylvania 1995. He received his Bachelor of Arts from Westminster College in 1999. He was employed as a field assistant by a variety of research institutions and later received his Master of Science in Environmental Science and Policy from George Mason University in 2009.