

SONGBIRD MIGRATION ECOLOGY IN EAST-CENTRAL ILLINOIS

BY

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THESIS

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ABSTRACT

Migration is a well-known phenomenon by which birds move to locations with favorable climates and abundant resources. The habitats and resources utilized by these birds throughout their annual cycle continue to be impacted by human activities, such as fragmentation and deforestation. These activities inflate the inherent consequences of migration (e.g., reduced survival, carry-over effects, and health) and contribute to the continued decline of migratory birds.

I studied passerine migration across east-central Illinois from 2012 through 2014. During this time, birds were surveyed during spring and fall migratory periods to address two research questions: 1) what habitat characteristics are indicated by different metrics of habitat quality used to evaluate stopovers for migrants? 2) which birds play a larger role in tick dispersal, and how do habitat characteristics influence infestation?

Although migrants were using fragmented study sites, I found little evidence to suggest that they were able to increase energy reserves, although I did detect a slight increase in condition among long-distance migrants in response to shrub-fruit abundance. Vegetation cover was positively related to migrant abundance and richness. I found that short-distance migrants experienced greater infestation prevalence than long-distance migrants. Birds that forage in the forest understory (< 10 m) experienced greater infestation prevalence than canopy foraging species. *Ixodes spp.* infestation prevalence was influenced by patch size and invasive shrub fruit abundance, while *H. leporispalustris* was unrelated to avian or habitat characteristics. This research indicates that variation in life-history traits among migratory birds may influence the quality and consequences of stopovers during migratory periods.

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TABLE OF CONTENTS

CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW.....	1
GENERAL INFORMATION.....	1
METRICS OF STOPOVER HABITAT QUALITY.....	5
THE SPREAD OF TICKS AND PATHOGENS DURING MIGRATION.....	7
LITERATURE CITED.....	10
CHAPTER 2: AN INTEGRATED EVALUATION OF STOPOVER HABITAT QUALITY IN ILLINOIS¹.....	23
ABSTRACT.....	23
INTRODUCTION.....	23
METHODS.....	25
RESULTS.....	32
DISCUSSION.....	36
LITERATURE CITED.....	39
TABLES.....	45
FIGURES.....	54
CHAPTER 3: THE INFLUENCE OF AVIAN AND HABITAT CHARACTERISTICS ON TICK INFESTATION AND DISPERSAL¹.....	57
ABSTRACT.....	57
INTRODUCTION.....	58
METHODS.....	59
RESULTS.....	63
DISCUSSION.....	67
LITERATURE CITED.....	72
TABLES.....	96
FIGURES.....	100
CHAPTER 4: SUMMARY.....	103
APPENDIX.....	105

CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

GENERAL INFORMATION

Migration is a phenomenon defined by Runge et al. (2014) as “a cyclic and predictable movement beyond a home range” and is common to more than 12% of the world’s wildlife species (Bowlin et al. 2010). Migration allows species to move to locations with more favorable climates (Marra et al. 2005) and track available resources throughout the year (Alerstam et al. 2003, White et al. 2007, Runge et al. 2014). Despite the benefits of a migratory strategy, numerous migratory populations are in decline (Runge et al. 2014). Efforts to reduce these declines have been relatively unsuccessful because the transient nature of these species makes them particularly difficult to study.

In the 1980s, deforestation in the breeding and wintering habitats of migratory birds was proposed as the primary cause of decline among North American species (Robbins et al. 1989). However, the year-round distribution of migrants includes stopover habitats spread across thousands of kilometers, including major ecological and anthropogenic borders. Research on passerine habitat use during the migratory period increasingly suggests that these populations are sensitive to human activities throughout their entire range, including breeding, wintering, and stopover habitats (Petit 2000). In addition to the impact of human activities on important habitats, migratory birds are vulnerable to the inherent challenges of migration such as health risks due to parasites and disease, predation risk, weather condition, carry-over effects throughout the annual cycle, and available habitat quality (Runge et al. 2014).

Migratory birds spend the majority of their annual cycle in migration, and the selection of stopover habitats during these periods have consequences that may shape events throughout the

remainder of the year (Smith and Moore 2003, Norris et al. 2004, Smith and Moore 2005, Rockwell et al. 2012). These consequences are also known as carry-over effects. For example, a migrant that uses a low-quality habitat (e.g., few food items and little cover from weather or predators) will be required to either spend more time finding food in that habitat or move on to a better quality habitat. Although dependent on bird condition (Chernetsov 2006), the decision to stay or leave a stopover may require trade-offs linked to energy and metabolism, digestive physiology, time, and risk of predation and disease-transmission – all of which may decrease optimal migration, as reviewed by Alerstam (2011). Smith and Moore (2003, 2005) found that bird condition and arrival on the breeding grounds following migration are positively correlated with reproductive success. However, the lack of site fidelity between seasons and years creates difficulty in assessing the carry-over effects of stopover conditions on the remainder of the annual cycle. Strategies to increase migrant populations typically focus on breeding habitats (e.g., management of invasive shrubs; Rodewald et al. 2010), which may directly or indirectly affect the quality of the habitat for birds throughout the duration of the annual cycle (McCusker et al. 2010). Identifying stopover use and its subsequent influence on migrant fitness requires increased use of stable isotopes, geolocators, and radar technology to establish population connectivity by tracking bird movements throughout the year (Bonter et al. 2009, Delmore et al. 2012).

Migratory birds as a whole continue to decline despite recent advances in technology that have helped researchers address knowledge gaps in the basic ecology of several migrant species (Rubenstein and Hobson 2004, Robinson et al. 2009). Robinson et al. (2009) describes a variety of techniques that are employed to study animal movement, including analyses of isotopes and genetic markers; tracking bird locations using PTT tags, radio telemetry, geolocators, satellite

telemetry, and radar. Using these methods, researchers are able to study the year-round physiology, behavior, demography, and connectivity of a species. Mehlman et al. (2005) state that until we have a complete understanding of these ecological parameters for migratory birds, the protection of key habitats for the breeding, stopover, and winter periods will face many obstacles. One such obstacle is identifying sites to conserve (Mehlman et al. 2005). Stopover use by migrants varies widely within and between seasons (Keller et al. 2009), and in response to environmental conditions (Dänhardt and Lindström 2001). This variation misleads conservationists in prioritizing habitats, and adds further confusion about the factors that increase the relative importance of a site (Mehlman et al. 2005). As it becomes evident that migratory periods may impact migrant population sizes, research focused on habitat use (Yong et al. 1998, Suthers et al. 2000), energetics (Loria and Moore 1990, Smith 2013), and other aspects of migration ecology (Faaborg et al. 2010b, a) is increasing and being used to inform conservation efforts.

Exposure to a broad range of environments during the annual cycle impacts the health of migratory birds in many ways (Merila and Svensson 1995, Wikelski et al. 2003, Hubálek 2004). Møller and Erritzøe (1998) suggest that migrants have developed advantageous immune defenses to cope with exposure to foreign parasites and pathogens. Møller et al. (2004) found that migrants arriving earlier in spring had stronger immune responses than later arrivals, and both factors have been directly related to greater reproductive success (Rockwell et al. 2012). However, immune responses also have energetic costs and are subject to trade-offs with other life-history processes such as sexual ornamentation and reproductive effort (Sheldon and Verhulst 1996). When such trade-offs occur, birds may experience greater parasitism and

infection by pathogens (Sheldon and Verhulst 1996, Knowles et al. 2009), which may then be dispersed across great distances outside their natural range (Mukherjee et al. 2014).

Dispersal of parasites and associated pathogens via birds has been well documented across the United States (Hamer et al. 2012, Schneider et al. 2014, Newman et al. 2015). Avian life-history traits such as age (Scharf 2004), feather molt (Moyer et al. 2002), and sex (Pruett-Jones and Pruett-Jones 1991) may influence parasite-bird interactions. Habitat also plays a large role in mediating interactions between birds and arthropod vectors (Marra et al. 2004, Dingler et al. 2014). Fragmentation of habitats due to human activities indirectly supports the growth of arthropod vector populations (Allan et al. 2003). Fragmentation enables invasion by non-native vegetation such as Asian honeysuckle (*Lonicera spp.*), which alters the structure and composition of the habitat it invades (Yates et al. 2004). Shewhart et al. (2014) found that exposure to *Lonicera maackii* leaf litter supported the survivorship and growth of larval *Culex pipiens*, an important vector of the West Nile virus found in migratory birds. Growth of *Lonicera spp.* and over-browsing by white-tailed deer lead to greater densities of ticks (Lubelczyk et al. 2004, Elias et al. 2006, Knight et al. 2009), such as *Ixodes scapularis* (black-legged tick). *I. scapularis* is the primary vector of the bacteria (*Borrelia burgdorferi*) that causes Lyme disease in humans, and both the tick and pathogen have been detected on birds during migration (Ginsberg et al. 2005, Brinkerhoff et al. 2011a, Schneider et al. 2014). Interactions between disease vectors and hosts will likely increase as human activities continue to alter the landscape (Gottdenker et al. 2014), and these interactions increase the risk of disease spread via the long-distance migration of songbirds (Hamer et al. 2012).

Research on migrant health, stopover quality, and survival across the United States has been focused primarily on coastal regions that experience heavy use by migrants during peak

migration (Woodrey and Moore 1997, Bonter et al. 2007, Buler and Moore 2011). Proximate to coastal regions, migratory forest-birds use forested areas to prepare for, or recover from the long flights across large water bodies (e.g., Gulf of Mexico, Great Lakes) (Bonter et al. 2009, Buler and Moore 2011). Further inland, Packett and Dunning (2009) and Liu and Swanson (2014) suggest that fragmented and isolated forest patches may also be suitable refuges for refueling birds during migration. Though, these patches are limited in number and will likely continue to be removed from the landscape as human needs lead to increasing crop conversion (Wright and Wimberly 2013) and expanding urbanization (Alig et al. 2004). En-route to the Gulf Coast in fall and the Great Lakes in spring, billions of migrants travel through the inland Midwest, and yet questions still remain about the time migrants spend in this region, the stopover selection process, health consequences, and available habitat quality. Addressing these questions in the Midwest requires further research to identify habitat and landscape attributes indicative of high-quality habitats that will support the conservation objectives for migratory bird populations (Donovan et al. 2002).

METRICS OF STOPOVER HABITAT QUALITY

Stopover-habitat quality is traditionally evaluated using direct and indirect measures of habitat use by migrants, including: migrant richness (Martin 1980, Keller and Yahner 2007), abundance (Mudrzyński and Norment 2013), and change in body condition (Winker et al. 1992, Johnson 2007). Different methodologies are used to survey migrant habitat use, and despite the known differences among the methods, a single measure is typically used to evaluate habitat quality (Remsen and Good 1996, Pagen et al. 2002, Swanson et al. 2003). As a result, the subsequent use of these measures may confound what characterizes a high-quality stopover for migrants.

High levels of migrant abundance and richness are considered indicative of high-quality stopovers. Bird surveys are conducted by a trained individual to detect the species and abundance of birds using a habitat (Ralph et al. 1995, Bibby 2000). These measures are then related to habitat characteristics, hypothesized to increase stopover habitat quality for migrants, to improve habitat conservation and restoration efforts (Bibby 2000). Yet, bird detection may vary widely in response to environmental conditions and detectability of the birds themselves (Schmidt et al. 2013). Additionally, during bouts of extreme environmental conditions (e.g., strong wind or rain; Dänhardt and Lindström 2001), or in regions with limited habitat availability or large ecological barriers, the abundance and richness of migrants in a habitat may indicate an immediate need to stop flight, rather than the selection and use of a habitat based on its resources (Van Horne 1983).

Body-condition change provides a direct physiological measure of habitat use by birds, which may then be used to deduce habitat quality (Winker et al. 1992, Dunn 2000, Horton and Morris 2012). As migrants rest and refuel, they replace fat and muscle lost during migration (Dunn 2001). The loss or gain of fat and muscle is reflected by a change in bird mass. Because mass is also influenced by age and sex (Dunn 2000), a condition index (i.e., size-corrected mass) is used to account for size differences due to age or sex by dividing mass by wing length of a given bird (Winker et al. 1992). Any change in condition thus reflects a fluctuation in energy reserves and the ability of the bird to refuel in the habitat where it was captured (Dunn 2000). However, this method is not without limitations. Sampling is limited to the vertical range of the mist-nets used (Keyes and Grue 1982), and Remsen and Good (1996) established that frequency of captures declines in response to increasing mean height of activity. However, mist nets are able to detect the presence of species that are secretive or may rarely vocalize (Remsen and Good

1996). Large sample sizes are required to detect condition change within a population (Dunn 2000), and to ensure condition change reflects the quality of the sampled habitat, birds must arrive in the habitat at or before sunrise, and capture time must be unrelated to their weight (Dunn 2000).

Although abundance, richness, and condition change are used independently, evidence to suggest that they produce similar conclusions about the characteristics of high-quality stopovers is limited. In fact, Rappole et al. (1998) and Gram and Faaborg (1997) detected a greater number of species during mist-netting than during point count surveys, while Pagen et al. (2002) and Lynch (1989) found the opposite trend. In addition to mixed results, these studies found differences in abundance and richness between the methods, but did not focus on the relationship between those measures and habitat quality. However, the differences detected indicate the need to consider the use of indirect and direct measures of habitat quality in conjunction.

THE SPREAD OF TICKS AND PATHOGENS DURING MIGRATION

Migratory passerines infested by ticks can facilitate the long-distance dispersal of ticks to uncolonized locations (Mukherjee et al. 2014, Scott et al. 2014). Ticks commonly found on passerines are the larvae and nymph (Brinkerhoff et al. 2011b, Schneider et al. 2014) of several genera including *Amblyomma*, *Haemaphysalis*, and *Ixodes* (Keirans et al. 1996, Kollars and Oliver 2003, Mukherjee et al. 2014). This dispersal also permits the spread of tick-borne pathogens (Hamer et al. 2011b, Scott et al. 2012). *Ixodes* ticks are key vectors of the bacteria *Borrelia*, and *Ixodes scapularis* is primarily responsible for the transmission of *Borrelia burgdorferi* among wildlife, domestic animals, and human hosts within the United States (Durden and Keirans 1996, Keirans et al. 1996). *B. burgdorferi* causes Lyme disease in humans, and incidence has continually risen since its discovery in 1981 (Burgdorfer 1991, White et al.

1991, Bacon et al. 2008). The growth of Lyme disease in the United States has been connected to the range expansion of *I. scapularis* (Stafford et al. 1998).

The range of *I. scapularis* in the United States is expanding from primary foci in the Northeast and Midwest (Dennis et al. 1998). Factors contributing to this expansion include land-use change (Killilea et al. 2008), climate change (Ogden et al. 2006, Khatchikian et al. 2012), and growing wildlife-host populations (Rooney 2001). White-tailed deer (*Odocoileus virginianus*) and other mammals with large home ranges contribute to the spread of *I. scapularis* (Bloemer and Zimmerman 1988, Madhav et al. 2004), however, birds may disperse ticks thousands of kilometers from their home range during migration (Ogden et al. 2008, Schneider et al. 2014). Some bird species have also demonstrated reservoir competence for *B. burgdorferi* and may be able to introduce the pathogen into novel environments (Ginsberg et al. 2005, Schneider et al. 2014). Other *Ixodes* spp. are also able to transmit *B. burgdorferi*, and may facilitate the introduction of the bacteria from infected hosts into new locations prior to the establishment of *I. scapularis* (Hamer et al. 2010). Hamer et al. (2010) posed three hypotheses of invasion by *I. scapularis* and *B. burgdorferi*: 1) invasion of habitat by uninfected adult *I. scapularis* via deer; 2) simultaneous invasion of habitat by *I. scapularis* and pathogen via mammal or avian hosts; 3) invasion by pathogen via other tick-vectors and reservoir hosts. Schneider et al. (2014) and Newman et al. (2015) have since found evidence of invasion by both the pathogen and *I. scapularis* and *I. pacificus* (respectively) via migrating birds, supporting the hypothesis of simultaneous invasion.

Both infestation prevalence, and reservoir competency for *B. burgdorferi* vary widely across bird species (Scharf 2004, Ginsberg et al. 2005). This variation may influence the extent to which ticks and pathogens are dispersed. Increasing awareness of the role birds play in the

dispersal of ticks and pathogens has led to research focused on the life-history traits of birds that may influence their infestation with ticks, including: age (Hamstra and Badyaev 2009, Heylen et al. 2013), sex (Pruett-Jones and Pruett-Jones 1991), foraging height (Oorebeek and Kleindorfer 2009), nesting height (Dingler et al. 2014), body size (Oorebeek and Kleindorfer 2009), molt (Moyer et al. 2002), and migration strategy (Dingler et al. 2014). The influence of avian life-history traits on tick infestation remains unclear, and we still know little about the relative importance of these traits on the probability of infection with pathogens such as *B. burgdorferi*.

The following research was focused on the influence of passerine life-history traits on two different elements of migration in east-central Illinois. Chapter 2 evaluates the merit of using multiple versus singular metrics of habitat quality to assess the value of stopovers for migrant birds. This study highlights differences in habitat quality indicated by different metrics, and among different guilds of birds. Chapter 3 examines the relative importance of songbird life-history traits that may increase tick infestation risk. Conclusions from this study provide a better understanding of the role different guilds of migrants play in the dispersal of ticks. Together, these chapters emphasize the strong influence of life-history traits on different elements of songbird migration.

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CHAPTER 2

AN INTEGRATED EVALUATION OF STOPOVER HABITAT QUALITY IN ILLINOIS¹

ABSTRACT

Measures of migrant abundance, richness, and body condition change are often used independently to evaluate stopover habitat quality. Here we compared these metrics to derive a multi-dimensional assessment of stopover quality of forest patches in east-central Illinois. We conducted avian surveys, captured birds, and measured vegetation in 14 forest patches during fall migration in 2013. Species richness and abundance of short-distance migrants and granivore-insectivores were best predicted by vegetation cover, whereas condition change among omnivores and long-distance migrants was best predicted by shrub-fruit abundance and Julian date. We found that habitats in east-central Illinois are used by a wide variety of species, and different habitat characteristics influence different metrics of habitat quality. The differences among these metric results may be indicative of the bias inherent in each method used to collect data. Therefore, we suggest caution when interpreting habitat quality based on a single measure.

INTRODUCTION

Among migrating birds the ability to refuel may be influenced by the quality of habitats used during stopover (Hutto 1998, Mehlman et al. 2005). Previous research suggests that high-quality stopovers provide migrants with abundant food items (Packett and Dunning 2009, Smith and McWilliams 2010), as well as vegetative cover for shelter from inclement weather and predators (Rodewald and Brittingham 2007, Smith and Hatch 2008). Consequently, the relationship between these habitat characteristics and some metric of habitat use is modeled to evaluate the

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quality of a stopover sites from the perspective of a migrant (Ewert and Hamas 1996, Mehlman et al. 2005). On the basis of model results, inferences are made regarding habitat characteristics that increase stopover quality for migrants and subsequently inform conservation actions for migrants, including habitat conservation and restoration, yet are often based on a single metric of habitat use by migrants.

Migrant abundance and species richness are derived from counts, either along transects or from points (Rodewald and Brittingham 2002, Packett and Dunning 2009). Point count surveys are short in duration (≤ 10 min per location) and can be conducted by a single, trained observer, making it an affordable research technique (Bibby 2000). However, observer experience, environmental conditions, and crypticity of a species may influence bird detection during surveys (Kellner and Swihart 2014). Additionally, these data are often interpreted under the assumption that birds are able to preferentially select the habitat where they are detected. Migrants, though, may exhibit less selectivity during periods of inclement weather, when suitable habitat is scarce, or when fuel reserves are diminished. In such instances the abundance or richness of migrants may be a misleading indicator of quality (Van Horne 1983).

Condition change among birds may be used as a direct measure of habitat quality (Winker et al. 1992). Condition is an index calculated by correcting the mass of a bird for its structural size (i.e., wing length), which may vary by age, sex, or species (Winker et al. 1992). Unbiased comparisons can then be made across individuals. A change in condition across individuals over time is typically used to evaluate changes in mass due to fat (i.e., energy) loss or gain (Winker et al. 1992, Dunn 2000). A change in fat stores among migrants may represent their ability to refuel in a given habitat, although captures can vary over space and time, and in response to weather conditions (Pagen et al. 2002). When capture rates are low, the ability to

detect condition change among migrants may be limited due to wide individual variation of condition (Dunn 2000). If results from a metric are limited, we propose that the use of a secondary measure may serve to support, or add to our understanding of habitat characteristics that increase stopover site quality.

To evaluate the use of different metrics of stopover quality during fall migration, we measured the abundance, richness, and condition change among different guilds of birds in forest patches across east-central Illinois (Table 1). We then modeled the relative influence of habitat factors suggested to influence stopover use by migrants in other parts of the Midwest (Rodewald and Brittingham 2002, 2004, Packett and Dunning 2009, Liu and Swanson 2014) on each metric individually. We compared the results from each metric to evaluate the potential benefit of using multiple metrics to produce more comprehensive assessments of habitat quality. Due to limited habitat availability across east-central Illinois, we expected to see similar abundance and richness patterns among all forest patches regardless of patch size (Packett and Dunning 2009). We predicted that condition change would increase in patches with greater fruit abundance, and vegetation cover, where birds were able to refuel and rest. Specifically we expected that shrub-fruit abundance (Smith and McWilliams 2010, Smith et al. 2013), successional forest (i.e., edge habitat; Rodewald and Brittingham 2004, Packett and Dunning 2009) , and forest cover (Ktitorov et al. 2008) would be included among competitive models of habitat quality metrics (Table 2).

METHODS

Site selection

We focused on 14 forest patches in Champaign, McLean, Piatt, and Vermillion counties. In each county, a cluster of one small (0.5 – 1 ha), medium (2 – 10 ha), and large (≥ 200 ha) patches located in close proximity to each other were identified in ArcGIS 10.2 (Environmental Systems

Research Institute, Redlands, California) using 2011 digital orthophotography for each county (IDOT 2011). Small and medium patches were an average of 6 km from the large patch within a cluster. Two clusters of patches, at least 20 km apart, were identified in northern and southern Vermillion County. Forest patches were ecologically similar - predominant trees included sugar maple (*Acer saccharum*), black cherry (*Prunus serotina*), and American hackberry (*Celtis occidentalis*). Predominant understory species included shrub honeysuckle (*Lonicera spp.*), multiflora rose (*Rosa multiflora*), and American hackberry saplings.

Vegetation surveys

We sought to determine vegetation and patch characteristics that influence the abundance, richness, and condition of songbirds during fall migration. During September and October of 2013 we surveyed vegetation in each patch using modified methods of Gehlhausen et al. (2000) and Bibby (2000) to quantify vegetation cover.

Vegetation surveys in each patch were conducted along four 100-m transects (Gehlhausen et al. 2000). Each transect began in the middle of each patch border (i.e. N, S, E, W) and extended toward the middle of the patch. Some patches were irregularly shaped, so mid-points in each cardinal direction were approximated using a map. Along each transect we surveyed up to 7 plots at distances of 0 (transect origin; outer edge of patch), 15, 30, 45, 70, 85, and 100-m from the patch edge (Gehlhausen et al. 2000). Transects in small and medium size patches were truncated to fit within the patch without overlapping other transects. The total number of plots surveyed per patch ranged from 6 to 28. Vegetation measurements were collected within each 5-m radius circular plot (James and Shugart Jr 1970). We visually estimated percent cover of canopy, invasive and native shrubs, herbaceous plants, leaf litter, and bare ground. We also measured diameter-at-breast height for trees greater than 5-cm in diameter

and 2-m in height, and noted minimum and maximum shrub height. Fruit abundance was estimated using a fruit abundance index (FAI). This index is based on the number of fruits observed within each plot (1 = 1-10 fruits, 2 = 11-25, 3 = 26-50, 4 = 51-100, 5 = 101-200, 6 = 201-500, 7 = 501-1000, 8 = 1001-10000; Levey 1988).

Point count surveys

Point counts were conducted in three patch clusters located in Champaign, Piatt, and northern Vermillion counties where we also captured birds during fall migration in 2013. We did not have access to the same clusters of patches for point counts and mist netting in McLean and southern Vermillion counties, therefore those point count data were not included in our analyses. Each patch was visited five times, once in each of five two-week intervals: August 19–31; September 2–13; September 15–26; September 28–October 9; October 11–22, to detect changes in bird communities throughout the season. In each patch, all birds seen and heard during a 10-minute period were recorded. Counts were conducted only during favorable weather (i.e., no precipitation and wind < 32 kph) between sunrise and 11 hours CST (Ralph et al. 1995).

Mist netting

To determine body condition of birds during fall migration of 2013, we captured birds between August 19 – October 22 using mist nets placed adjacent to streams, large shrubs, and fruiting plants (Ralph et al. 1993). Nets within a patch were opened by sunrise and monitored every 20 - 30 minutes for up to 5 hours, only in favorable weather (Ralph et al. 1993). Nets were closed immediately in the event of precipitation, or if wind speeds exceeded 32 kph.

Captured birds were extracted from mist nets, placed into individual white-cotton bags, and brought to a nearby processing station. For each bird captured we recorded species, fat score, mass, and wing chord (Pyle et al. 1997). Mass was measured with an electronic scale to the

nearest 0.1g, and time of weighing was recorded to the nearest 10 minutes. Fat score was determined using a visual estimate of subcutaneous fat (scale 1-7; Ralph et al.1993). All protocols were approved by the University of Illinois' Institutional Animal Use and Care Committee (# 12144) and the Federal Bird Banding Laboratory (# 06507 – AW).

Patch measures

Edge habitat is often used by migrating songbirds during stopover (Suthers et al. 2000, Rodewald and Brittingham 2004), however, it is unclear if the proportion of edge habitat within a forest patch influences the quality of stopover for migrants. To evaluate the influence of edge habitat on bird abundance, richness, and condition during fall migration, we determined the proportion of edge habitat within each patch using a multi-step approach (Gehlhausen et al. 2000).

First, we used a one-way ANOVA to determine the vegetation variables that changed in response to distance from the edge. Only variables with a significant response were included in further analyses, significance was evaluated at $p = 0.05$. Next, we used a least significance test to determine the plot-distance at which each variable was no longer statistically different from the ultimate plot of each transect (i.e. interior), otherwise known as the depth-of-edge influence (DEI; Gehlhausen et al. 2000). Beyond this distance, we assumed a variable was no longer influenced by distance-to-edge, and considered habitat beyond this distance as “interior.” The patch-DEI was based on the mean value of DEI for all vegetation variables (Laurance and Yensen 1991).

Then, we determined a shape index value (SI) for each patch. The distribution of edge effects within a perfectly circular patch is expected to be distributed evenly (Laurance and Yensen 1991). However, irregularly shaped patches may experience an uneven distribution of edge effects (Laurance and Yensen 1991), and the *SI* provides an estimation of patch deviation

from circularity. We calculated the *SI* for each patch using the equation of Laurance and Yensen (1991):

$$SI = \frac{P}{200 [(\pi TA)^{0.5}]}$$

where *P* is the perimeter length of the patch and *TA* is the total area of the patch in hectares, determined using ArcGIS (Redlands, CA). Subsequently, we calculated the edge and interior area for each patch following Laurance and Yensen (1991):

$$EA = \{(3.5)(DEI)(SI)[(TA/10000)^{0.5}]\}$$

$$IA = TA - EA$$

where *EA* is area of edge habitat in a patch and *IA* is the interior area of a patch. Biased estimates of edge area may result from nonlinearities between DEI and the interior area for patches with a circular shape (i.e., *SI* of 1.5 or less). To reduce this bias, we calculated an adjusted *EA* value using Laurance and Yensen (1991):

$$EA_{adj} = EA \times \left[1 - \left(\frac{0.265(EA/TA)}{(SI)^{1.5}} \right) \right]$$

Finally, the *EA_{adj}*, *IA*, and *TA* values for each patch were used as predictor variables in models to evaluate the relative importance of each variable on stopover quality for migratory songbirds (Table 2).

Condition change

Data were analyzed under the assumption that migrants arrived in the patch at or prior to sunrise, and that the time of capture was independent of bird weight (Winker et al. 1992, Dunn 2000). If these conditions were met, any change in the average condition of birds captured in a patch over the course of a day represents the change in condition of birds that used the patch (Winker et al.

1992, Dunn 2000). Condition change among birds was then modeled in relation to habitat characteristics that have been demonstrated to influence condition change and habitat use.

Sixteen species included in these analyses were represented by at least five individuals. While this was not sufficient for species-level analyses, it supported more robust analyses of migratory and foraging guilds. Each species was assigned to a specific migratory and foraging guild (Poole 2005, Rappole 2013) prior to analyses. For each bird, we used the mass and wing chord measurements to calculate an index of body condition following Winker et al. (1992):

$$Condition = \left(\frac{mass}{wing\ chord^3} \right) * 10000$$

This calculation adjusts mass by differences in wing chord to account for variation in mass that is due to age and sex, rather than condition. The resulting index measures variation in energy reserves among captured birds, which is an indirect indication of how well birds are able to refuel in the habitats where they are captured. We regressed condition indices on fat scores to confirm that change in body condition reflected change in fat levels observed in captured birds. We also regressed bird mass against time of day to ensure there was no bias in the size of birds captured throughout the day. We then used the average change in condition among captured birds to evaluate the relative importance of patch, vegetation, and temporal variables that we presumed to be indicative of high quality stopovers based on previous research and our own observations.

Statistical analyses

Each species detected was assigned to a specific migratory and foraging guild (Table 1) to determine how stopover habitat quality may vary among birds with different migration strategies and foraging requirements (Poole 2005, Rappole 2013). To evaluate the stopover quality of forest patches across east-central Illinois, we derived models based on patch, vegetation, and

temporal variables that we hypothesized would influence condition change, richness, and abundance among bird guilds (Table 2).

Data from the point count surveys were used to calculate measures of guild abundance and richness for each patch. These measures included only birds detected within 50-m of the point to minimize the detection bias associated with increasing distance from a sampling point and to exclude birds that were detected flying over or outside a forest patch (Bibby 2000). The 50-m restriction also ensured the same amount of area was sampled within patches of different sizes. We used generalized linear models of richness and abundance of each guild, and for all species pooled using distributions that best fit the data. Gaussian and poisson models were tested using the stats package v3.0.2 for R v3.1.1 (R Development Core 2014) and negative binomial models were tested using the MASS package v7.3-29 for R v3.1.1 (R Development Core 2014). AIC_c tables were generated using the MuMIn package v1.12.1 for R v3.1.1 (R Development Core 2014).

For each guild, and among all birds pooled, condition was used as the response variable in mixed model regressions conducted using the lme4 package v1.1-7 for R v3.1.1 (R Development Core 2014). In each model, ‘species’ was included as a random variable to account for any species-specific variation. ‘Hours-since-sunrise’ was included in interaction terms with each predictor variable to produce estimates of condition change over time in response to each predictor variable within a model. AIC_c tables were generated using the AICcmodavg package v2.00 for R v3.1.1 (R Development Core 2014). All models were ranked using Akaike’s Information Criterion adjusted for small sample sizes (AIC_c) and AIC_c weights were calculated to determine support for models of body condition change (Burnham and Anderson 2002).

Models of condition, richness, and abundance with $\Delta AIC_c \leq 2$ were considered competitive. To assess support for each competing model relative to the top model, we calculated evidence ratios (w_i / w_j ; Burnham and Anderson 2002) using AIC_c weights (w_i). We conducted a bootstrap analysis (1000 steps) using the `pbkrtest` package v0.4-1 for R v3.1.1 (R Development Core 2014) to reduce model selection uncertainty among models of condition when the null model was within the top model set (Burnham and Anderson 2002). Finally, we compared the results from each metric of habitat quality to assess the potential benefit of combining methods to estimate habitat quality for birds during migration.

RESULTS

Patch characterization

Total area of forest patches ranged from 0.63 ha to > 1400 ha, and area of edge habitat within patches ranged from 0.62 ha to 169.68 ha (Table 3). The DEI values used to determine the area of edge in each patch ranged from 15 m to 45 m, with a mean DEI value of 21 m \pm 10 m [SD] among all patches. Vegetation variables responded differently to distance-from-edge among all patches (Table 3).

Model selection: species richness and abundance

A total of 45 point counts were conducted during fall migration, resulting in a total of 281 detections among 45 species. Non-migratory birds were the most abundant migratory guild (Fig. 1), and omnivorous birds were more abundant than granivore-insectivores (Fig. 2). Patch models were the only well-supported models of total abundance (Table 4), whereas well-supported models of total richness included patch (Table 4) and vegetation models (Table 5).

Competitive models of abundance and species richness for long-distance migrants (Table 5) suggested that fewer birds ($\beta = -0.02 \pm 0.01$ [SE]) were detected in patches with greater

amounts of canopy cover, whereas more birds ($\beta = 0.06 \pm 0.03$ [SE]) and species ($\beta = 0.09 \pm 0.02$ [SE]) were detected in patches with greater amounts of herbaceous cover. More species of long-distance migrants were detected in patches of smaller size relative to larger forests (small patches: $\beta = 0.40 \pm 0.64$ [SE]; medium patches: $\beta = 1.09 \pm 0.57$ [SE]), and fewer long-distance migrants were detected as the fall season progressed ($\beta = -0.02 \pm 0.01$ [SE]; Table 6).

Competitive models of abundance and species richness among short-distance migrants also indicated that more birds ($\beta = 0.04 \pm 0.02$ [SE]) and species ($\beta = 0.04 \pm 0.02$ [SE]) were present in patches with greater amounts of herbaceous cover (Table 5). Additionally, fewer short-distance migrants were present in patches with greater amounts of litter cover ($\beta = -0.02 \pm 0.007$ [SE]), bare ground ($\beta = -0.03 \pm 0.02$ [SE]), and invasive shrub fruit ($\beta = -0.24 \pm 0.16$ [SE]).

The best models for abundance and species richness (Table 4B) of non-migrants suggested that fewer birds were present in patches with greater native-shrub cover ($\beta = -0.04 \pm 0.01$ [SE]; Table 5). A decline in abundance ($\beta = -1.02 \pm 0.52$ [SE]) and richness ($\beta = -0.90 \pm 0.32$ [SE]) among non-migrants was detected in smaller patches relative to larger patches (Table 4), whereas more birds ($\beta = 0.30 \pm 0.35$ [SE]) and species ($\beta = 0.08 \pm 0.24$ [SE]) were detected in medium patches relative to larger patches.

Competitive patch models of omnivorous bird abundance (Table 7) indicated that more birds were detected in patches with greater area ($\beta = 0.0003 \pm 0.0002$ [SE]), edge habitat area ($\beta = 0.003 \pm 0.001$ [SE]), and interior habitat area ($\beta = 0.0003 \pm 0.0002$ [SE]). Best fitting models of omnivore species richness (Table 7) suggested that more species were present in medium-sized patches ($\beta = 0.17 \pm 0.18$ [SE]) and fewer species were present in smaller sized patches relative to larger patches ($\beta = -0.35 \pm 0.21$ [SE]). Competitive vegetation models for granivore

abundance and richness (Table 8) indicated that more birds ($\beta = 0.06 \pm 0.03$ [SE]) and species ($\beta = 0.08 \pm 0.02$ [SE]) are present in patches with greater herbaceous cover. The second-best vegetation model for granivore-insectivores indicated that fewer birds were present in patches with greater amounts of litter cover ($\beta = -0.01 \pm 0.01$ [SE]) and bare ground ($\beta = -0.07 \pm 0.03$ [SE]). The top temporal model for both abundance ($\beta = -0.03 \pm 0.01$ [SE]) and richness ($\beta = -0.01 \pm 0.01$ [SE]) of granivore-insectivores was Julian date (Table 6), which revealed a reduction in abundance as the season progressed.

Model selection: body condition

Among all patches, sampling effort totaled 497.5 net hours, and mass and wing-chord data were collected from 172 birds of 16 species. Captures were not influenced by mass during sampling events ($\beta = -0.22$, $p = 0.76$). A positive relationship between fat scores of captured birds and body condition indices confirmed that change in condition reflected change in energy (i.e., fat) reserves ($\beta = 1.22$, $p = 0.0058$). Average body condition among all captures was 0.47 g/mm^3 , and ranged from 0.25 to 1.27 g/mm^3 . Average condition of long-distance migrants was also significantly less than average condition of short-distance migrants ($z = -2.5$, $p = 0.012$) and non-migrants ($z = -2.37$, $p = 0.018$; Fig 3). Mean condition of granivore-insectivores ($\beta = 0.55$) was greater than omnivores ($\beta = 0.43$, $p < 0.001$); Fig. 4). The best model of condition change among all species pooled was the single-variable model of shrub-fruit abundance (Table 5).

Change in body condition indicated little model selection uncertainty among patch (Table 4), vegetation (Table 5), or temporal models (Table 6) for any migrant guild, although few models were well-supported relative to the null. Best-supported models differed between guilds. Some model selection uncertainty did occur between top vegetation models of condition change among long-distance migrants. However, a bootstrap analyses provided additional support for

the shrub-fruit abundance as the top model for long-distance migrants (PBtest statistic = 8.6848, $p = 0.046$). Julian date was also a well-supported model of condition change among long-distance migrants ($\beta = 0.001 \pm 0.0008$ [SE]), whereas models of total patch, edge and interior habitat area lacked support. We found no support for models of condition change among short-distance migrants.

Patch (Table 4), vegetation (Table 5), and temporal models (Table 6) among non-migrants were well supported, although results suggest effects on condition are mixed. Competitive patch models included area of edge habitat ($\beta = 0.0007 \pm 0.0003$ [SE]), area of interior habitat ($\beta = 0.00002 \pm 0.00001$ [SE]), and total patch area ($\beta = 0.00002 \pm 0.00001$ [SE]), each of which indicated a weak effect on condition change. Vegetation models that were well-supported for non-migrants included: native-shrub cover ($\beta = 0.008 \pm 0.002$ [SE]), herbaceous cover ($\beta = -0.001 \pm 0.0007$ [SE]), native-shrub fruit abundance ($\beta = -0.045 \pm 0.017$ [SE]), and tree fruit abundance ($\beta = -0.233 \pm 0.09$ [SE]). Among non-migrants in general, condition change declined in response to hours-since-sunrise ($\beta = -0.037 \pm 0.005$ [SE]).

Models of condition change among foraging guilds indicated support for only the shrub-fruit abundance model of omnivore condition change, which indicated slight decline in omnivore condition change ($\beta = -0.0067 \pm 0.005$ [SE]). We found no support for models of condition change among granivore-insectivores.

Metric comparison

The best supported patch, vegetation, and temporal models differed in their relative importance for abundance, richness, and condition change, and among guilds (Table 9). Patch models of characteristics and vegetation cover were generally better predictors of abundance and richness, whereas shrub fruit abundance was the primary predictor of condition change. Only the non-

migrant guild had similar support for models from each metric of habitat quality, although similarities between best supported models of abundance and richness did occur for other guilds.

DISCUSSION

Our results suggest that metrics of habitat quality suggest that characteristics of stopover habitats influence metrics of habitat quality differently. Although migrants used these fragmented and scattered patches, we were unable to detect meaningful increases in condition among the birds sampled. Of the habitat characteristics we evaluated, patch size, understory vegetation, and invasive-shrub fruit had mixed effects on abundance and species richness, whereas shrub-fruit abundance was related to increased condition change during fall migration. From our results we have drawn conclusions about stopover quality for a broad range of migrants. Despite the limitations of condition analyses, models of migrant abundance and richness revealed compelling information about vegetation characteristics that may increase habitat quality among migratory and forage guilds.

Between foraging guilds, we found that habitat use by granivorous and insectivorous migrants in the fall increased in forest patches with greater herbaceous cover in the understory. Diverse herbaceous cover provides habitat for arthropods (Maleque et al. 2009, Ulyshen 2011), such as beetles, flies, and spiders (Robinson and Holmes 1982), which serve as prey items for foraging birds. Though arthropods provide a good source of protein for migrants (Bell 1990), successful arthropod foraging may require a greater time and energy investment than searching for fruits (Schmidt-Nielsen 1972, Catterall 1985). Consequently, insectivorous species may require a longer sampling period to detect condition change, particularly in habitats where arthropod abundance is reduced. This may explain why we did not see support for herbaceous cover among the top models of migrant condition change.

Models of condition change indicated that shrub-fruit abundance increases habitat quality of forest patches in east-central Illinois. Omnivores, including long-distance and non-migrants specifically, body condition increased in patches with greater fruit abundance, and did not change in patches with lower fruit abundance. Other studies also emphasize the value of fruit for refueling migrants (Buler et al. 2007, Smith and McWilliams 2010), though the degree of frugivory may be influenced by avian digestive abilities and nutritional needs which vary widely among species (Levey and Rio 2001, Mudrzynski and Norment 2013). Furthermore, the nutrition gained from native and invasive shrub fruits may differ; native fruits have greater fat content, energy density, and are assumed to be of better quality for refueling birds (Smith et al. 2013). However, fruit quality from the anthropocentric perspective may not translate to fruit choice among foraging birds (Whelan and Willson 1994). In fact, birds may consume fruits that are abundant yet considered poor quality from the anthropocentric view, such as exotic honeysuckle (*Lonicera spp.*) and buckthorn (*Rhamnus cathartica*). Both species are prevalent among Midwestern forests (Heneghan et al. 2002, Yates et al. 2004).

Exotic-shrub fruits provide an abundant resource for omnivorous birds during fall migration, however exotic shrubs are tied to a number of negative ecological impacts. Invasion by exotic shrubs may alter forest understory structure (Hartman and McCarthy 2008), depress understory vegetation growth (Miller and Gorchoy 2004), and reduce arthropod diversity (Christopher and Cameron 2012). These impacts may subsequently diminish food availability and preferred foraging habitat for insectivores and granivores. Thus habitats invaded by exotic shrubs may serve as poor-quality stopovers for insectivores and granivores, but provide fruit for omnivores during fall migration. The potential value of these fruiting shrubs for omnivorous migrants should be considered prior to their removal in habitats that may be used as a stopover.

Abundance and richness of non-migrants varied among different patch sizes (Table 2a) and condition increased in response to greater habitat area. Habitat quality for non-migrants was also influenced by native-shrub and herbaceous cover, and fruit abundance of native shrubs and trees. Because their movements are typically limited to foraging or dispersal (Rappole 2013), any change in non-migrant physical condition would potentially reflect the quality of habitat where they reside (Mörtberg 2001). Furthermore, evidence suggests that migrating birds may use resident social information to infer habitat quality (Németh and Moore 2007) and although our study was not designed to test this relationship, we detected similar characteristics of high-quality habitats between top models of non-migrant and migrant metrics (i.e., condition change, abundance, and richness).

We found that models of migrant abundance, richness, and condition change identified different habitat characteristics that influence stopover quality. We determined that shrub-fruit abundance was a driving factor of habitat quality of migrant condition change, whereas models of abundance and richness offered insights about the use of habitats in response to vegetation cover. These differences provide support for the use of multiple metrics of habitat quality to reduce the influence of methodological and analytical biases on the inferences derived from the data. The use of both metrics provides an overview of factors that influence stopover quality for a broad scope of species (Pagen et al. 2002).

For future studies of inland stopover ecology, we recommend that researchers incorporate the use of both condition change and richness/abundance metrics to evaluate stopover habitat quality. We detected condition change among omnivores, including long-distance migrants, in response to shrub-fruit abundance. This relationship did not appear among models of bird richness and abundance. Instead these models revealed the importance of vegetation cover for

granivore-insectivores, which we presume influences food availability. Overall, it is clear that food availability is an important variable to consider when evaluating stopover habitat quality (Rodewald and Brittingham 2004, Buler et al. 2007, Smith and McWilliams 2010). Fruit from exotic shrubs are often more abundant in edge-dominated patches and may serve as an important resource for refueling songbirds. Yet shrub fruit and edge area were included in well-supported models of different habitat quality metrics for frugivores and long-distance migrants. Furthermore, no models of condition were well-supported for short-distance migrants or granivore-insectivores, whereas models of abundance and richness provided evidence for the relative importance of vegetation cover. These differences validate the benefit of using collective metrics of habitat quality to provide a more comprehensive understanding of the factors that create high quality stopovers for migratory songbirds.

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TABLES

Table 1. Descriptions of migratory and foraging guilds used for species classification, as modified from Rappole (2013) and Birds of North America Online.

Guild	Migration range
Local movement, non-migratory	Local seasonal movements including: post-breeding dispersal, distance foraging, and flocking.
Short-distance migration	All individuals of a population move < 2000 km outside the breeding range.
Long-distance migration	All individuals of a population move > 2000 km outside the breeding range.
Granivore - Insectivore	Food items primarily consist of grains, insects, or both during migration.
Omnivore	Food items primarily consist of fruits, insects, nectar, or any combination of these items during migration.

Table 2. A priori determined candidate models used to examine habitat quality of forest patches for birds in east-central Illinois during fall migration in 2013.

Patch models	Vegetation models	Temporal models
Patch edge area	Invasive fruit index (shrub)	Julian date
Total patch area	Native fruit index (shrub)	Hours since sunrise
Patch interior area	Invasive shrub cover	Hours since sunrise x Julian
Patch cluster	Native shrub cover	Null
Categorical patch size (s,m,l)	Canopy cover	
Patch cluster x size	Canopy + herb cover	
Null	Canopy + herb + shrub cover	
	Canopy + shrub cover	
	Herb cover	
	Herb + shrub cover	
	Shrub cover	
	Shrub fruit index	
	Tree fruit index	
	Litter + bare cover	
	Null	

Table 3. The vegetation variable and patch depth-of-edge influence values, and patch characteristics for each patch studied across east-central Illinois during fall migration, 2013. (CHAM = Champaign County; FORG = Vermillion County, south; MCLE = McLean County; PIAT = Piatt County; VERM = Vermillion County, north)

Variable	Site	CHAM			FORG			MCLE		PIAT			VERM		
	Point	L	M	S	L	M	S	M	S	L	M	S	L	M	S
Canopy cover								45			15		30		
Dbh		45				15	15			45	15		15		15
Shrub cover			15												
Herbaceous cover					15								15		
Tree fruit abundance		15											15		
Shrub fruit abundance															
Litter cover				15	15								15		
Invasive shrub cover		15							15						
Native shrub cover			15												
Bare ground			30												
Shrub species richness		45	85				15	15						15	
Patch DEI		30.0	36.3	15.0	15.0	15.0	15.0	30.0	15.0	45.0	15.0	15.0	18.0	15.0	15.0
Total patch area		117.3	9.3	0.6	1204.5	19.4	2.9	18.8	1.1	1445.5	8.6	1.2	237.2	4.4	1.3
Patch perimeter		7800.0	1306.4	476.6	24648.6	2293.3	1351.4	2119.9	550.9	37895.6	1844.9	524.4	14269.7	841.8	727.1
Patch shape index		2.0	1.2	1.7	2.0	1.5	2.2	1.4	1.5	2.8	1.8	1.3	2.6	1.1	1.8
Patch affected area (edge)		23.4	4.7	0.7	37.0	3.4	2.0	6.4	0.8	170.8	2.8	0.8	25.7	1.3	1.1
Patch core area (interior)		93.9	4.5	-0.1	1167.4	16.0	0.9	12.5	0.2	1274.6	5.8	0.4	211.5	3.1	0.2
Adjusted affected area		23.0	4.3	0.6	36.9	3.4	1.9	6.0	0.7	169.7	2.7	0.7	25.6	1.2	1.0
Adjusted core area		94.3	5.0	0.0	1167.5	16.0	1.0	12.8	0.3	1275.8	5.9	0.5	211.6	3.2	0.3

Table 4. Competitive patch models of metrics used to determine stopover quality for migrant guilds across east-central Illinois during fall migration, 2013.

Patch models	K	AIC _c	Δ AIC _c	w _i	Cum. w _i	LL	Evidence ratio
ABUNDANCE							
<i>All species</i>							
Patch edge	3	246.70	0.00	0.20	0.20	-120.07	1.00
Total patch area	3	246.80	0.12	0.19	0.39	-120.13	1.06
Patch interior	3	246.90	0.14	0.19	0.58	-120.14	1.07
<i>Non-migrant</i>							
Patch size	3	156.20	0.00	0.99	0.99	-74.81	1.00
RICHNESS							
<i>All species</i>							
Patch size	3	183.30	0.00	0.37	0.37	-88.36	1.00
Patch edge	2	185.20	1.86	0.15	0.52	-90.44	2.53
Total patch area	2	185.20	1.93	0.14	0.66	-90.48	2.62
Patch interior	2	185.20	1.94	0.14	0.80	-90.48	2.64
<i>Long-distance</i>							
Patch size	3	86.60	0.00	0.22	0.22	-40.03	1.00
<i>Non-migrant</i>							
Patch size	3	132.10	0.00	0.79	0.79	-62.74	1.00
CONDITION CHANGE							
<i>Non-migrant</i>							
Patch edge	6	-55.17	0.00	0.48	0.48	36.82	1.00
Total patch area	6	-53.81	1.36	0.24	0.73	36.13	2.00
Patch interior	6	-53.76	1.41	0.24	0.96	36.11	2.00

Table 5. Competitive vegetation models of metrics used to determine stopover quality for migrant guilds across east-central Illinois during fall migration, 2013.

Vegetation models	K	AIC _c	Δ AIC _c	w _i	Cum. w _i	LL	Evidence ratio
ABUNDANCE							
<i>Long-distance</i>							
Canopy cover	3	112.00	0.00	0.21	0.21	-52.70	1.00
Herb cover	3	112.70	0.70	0.15	0.35	-53.05	1.42
Canopy herb cover	4	113.30	1.32	0.11	0.46	-52.15	1.93
<i>Short-distance</i>							
Litter bare cover	3	105.90	0.00	0.41	0.41	-49.66	1.00
<i>Non-migrant</i>							
Native shrub cover	2	165.90	0.00	0.40	0.40	-80.82	1.00
RICHNESS							
<i>All species</i>							
Canopy cover	2	183.80	0.00	0.14	0.14	-89.76	1.00
Herb cover	2	183.90	0.13	0.13	0.27	-89.83	1.07
Canopy shrub cover	3	184.00	0.20	0.13	0.40	-88.71	1.11
Canopy herb cover	3	184.50	0.68	0.10	0.50	-88.95	1.40
Herb shrub cover	3	184.50	0.73	0.10	0.60	-88.98	1.44
Shrub cover	2	185.20	1.41	0.07	0.67	-90.47	2.02
Invasive shrub cover	2	185.20	1.42	0.07	0.74	-90.47	2.03
Canopy herb shrub cover	4	185.30	1.51	0.07	0.80	-88.16	2.13
<i>Long-distance</i>							
Herb cover	2	79.40	0.00	0.44	0.44	-37.54	1.00
Canopy herb cover	3	81.10	1.72	0.18	0.62	-37.25	2.36
<i>Short-distance</i>							
Herb cover	2	89.00	0.00	0.14	0.14	-42.35	1.00
<i>Non-migrant</i>							
Native shrub cover	2	139.20	0.00	0.16	0.16	-67.47	1.00
CONDITION CHANGE							
<i>All species</i>							
Shrub fruit abundance	6	-324.22	0.00	0.39	0.39	168.36	1.00
<i>Long-distance</i>							
Shrub fruit abundance	6	-130.38	0.00	0.36	0.36	72.03	1.00
<i>Non-migrant</i>							
Native shrub cover	6	-53.36	0.00	0.31	0.31	35.91	1.00
Herbaceous cover	6	-52.45	0.91	0.20	0.51	35.46	1.55
Native shrub fruit	6	-52.24	1.12	0.18	0.68	35.35	1.72
Tree fruit	6	-51.60	1.76	0.13	0.81	35.03	2.38

Table 6. Competitive temporal models of metrics used to determine stopover quality for migrant and forage guilds across east-central Illinois during fall migration, 2013.

Temporal models	K	AIC _c	Δ AIC _c	w _i	Cum. w _i	LL	Evidence ratio
ABUNDANCE							
<i>Long-distance</i>							
Julian date	3	111	0	0.79	0.79	-52.22	1.00
<i>Granivore-Insectivore</i>							
Julian date	4	117.7	0	0.77	0.77	-55.57	1.00
RICHNESS							
<i>Granivore-Insectivore</i>							
Julian date	2	95	0	0.39	0.39	-45.34	1.00
CONDITION CHANGE							
<i>Long-distance</i>							
Julian date	4	-131.44	0.00	0.60	0.60	70.10	1.00
<i>Non-migrant</i>							
Hours-since-sunrise	4	-53.91	0.00	0.83	0.83	32.29	1.00

Table 7. Competitive patch models of metrics used to determine stopover quality for forage guilds across east-central Illinois during fall migration, 2013.

Patch models	K	AIC _c	Δ AIC _c	w _i	Cum. w _i	LL	Evidence ratio
ABUNDANCE							
<i>Omnivore</i>							
Patch edge	4	233.20	0.00	0.20	0.20	-113.33	1.00
Patch area	4	233.30	0.09	0.19	0.39	-113.37	1.05
Patch interior	4	233.30	0.10	0.19	0.58	-113.38	1.05
RICHNESS							
<i>Omnivore</i>							
Patch size	3	175.50	0.00	0.44	0.44	-84.48	1.00

Table 8. Competitive vegetation models of metrics used to determine stopover quality for forage guilds across east-central Illinois during fall migration, 2013.

Vegetation models	K	AIC _c	Δ AIC _c	w _i	Cum. w _i	LL	Evidence ratio
ABUNDANCE							
<i>Granivore-Insectivore</i>							
Herb cover	4	120.50	0.00	0.20	0.20	-56.95	1.00
Litter, bare cover	5	121.40	0.92	0.13	0.32	-56.20	1.58
RICHNESS							
<i>Granivore-Insectivore</i>							
Herb cover	2	87.50	0.00	0.39	0.39	-41.59	1.00
Canopy, herb cover	3	88.80	1.29	0.21	0.60	-41.09	1.91
CONDITION CHANGE							
<i>Omnivore</i>							
Shrub fruit abundance	6	-327.18	0.00	0.29	0.29	169.90	1.00

Table 9. Comparison of best supported patch, vegetation, and temporal models of guild abundance, richness, and condition change, and effect direction, across east-central Illinois during fall migration, 2013.

Guild	Abundance	Richness	Condition change
All species	Edge area (+) Total patch area (+) Interior area (+)	Canopy cover (-) Herbaceous cover (+) Canopy cover (-) Canopy cover (-) + herbaceous cover (+) Herbaceous cover (+) + shrub cover (-) Shrub cover (-) Invasive shrub cover (-) Canopy (-) + herbaceous (+) + shrub (-)	Shrub fruit (-)
Long-distance	Canopy cover (-) Herbaceous cover (+) Canopy cover (-) + herbaceous cover (+) Julian date (-)	Patch size (M [+]; S [+]) Herbaceous cover (+) Canopy (-) + herbaceous (+)	Shrub fruit (-) Julian date (+)
Short-distance	Litter cover (-) + Bare ground (-) Herbaceous cover (+) Invasive shrub fruit abundance (-)	Herbaceous cover (+)	
Non-migrant	Patch size (M [+]; S [-]) Native shrub cover (-)	Patch size (M [+]; S [-]) Native shrub cover (-)	Edge area (+) Interior area (+) Total patch area (+)
Omnivore	Edge area (+) Total patch area (+)	Patch size (M [+]; S [-])	Shrub fruit abundance (-)

Table 9. cont.

Guild	Abundance	Richness	Condition change
	Interior area (+)		
Granivore- insectivore	Herbaceous cover (+)	Herbaceous cover (+)	
	Litter cover (-) + bare ground (-)	Canopy cover (-) + herbaceous cover (+)	
	Julian date (-)	Julian date (-)	

FIGURES

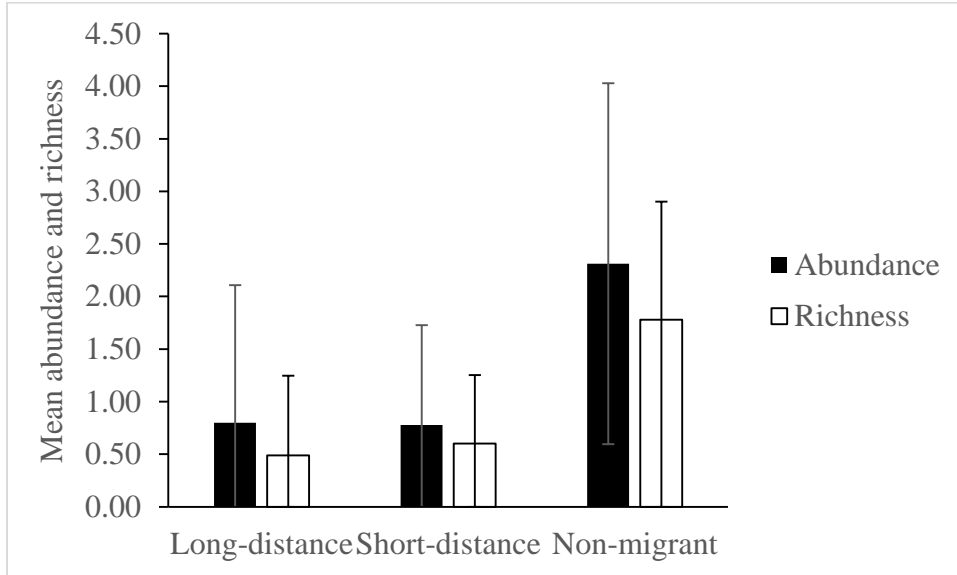


Figure 1. Mean relative abundance and richness (\pm SD) of migrant guilds detected across east-central Illinois during fall migration in 2013.

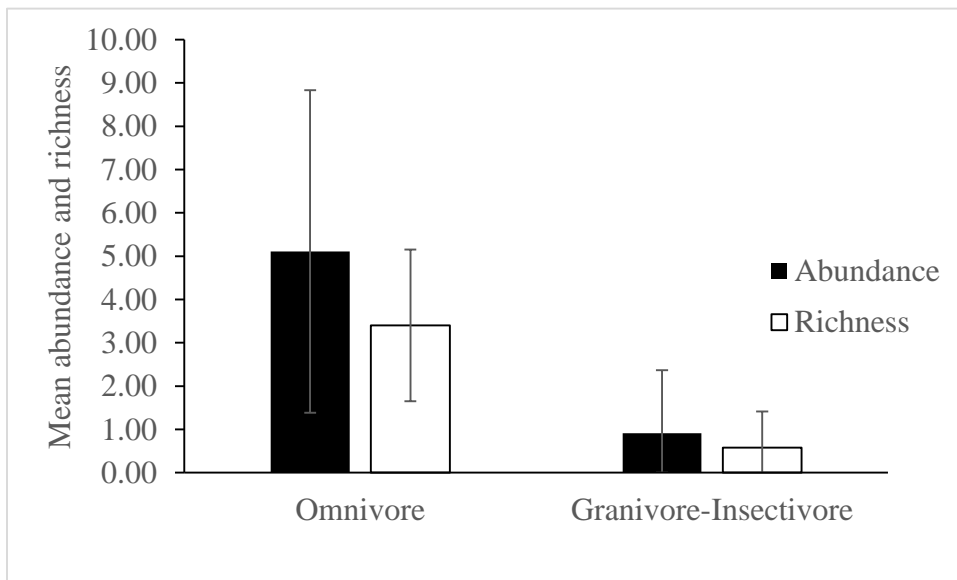


Figure 2. Mean relative abundance and richness (\pm SD) of forage guilds detected across east-central Illinois during fall migration in 2013.

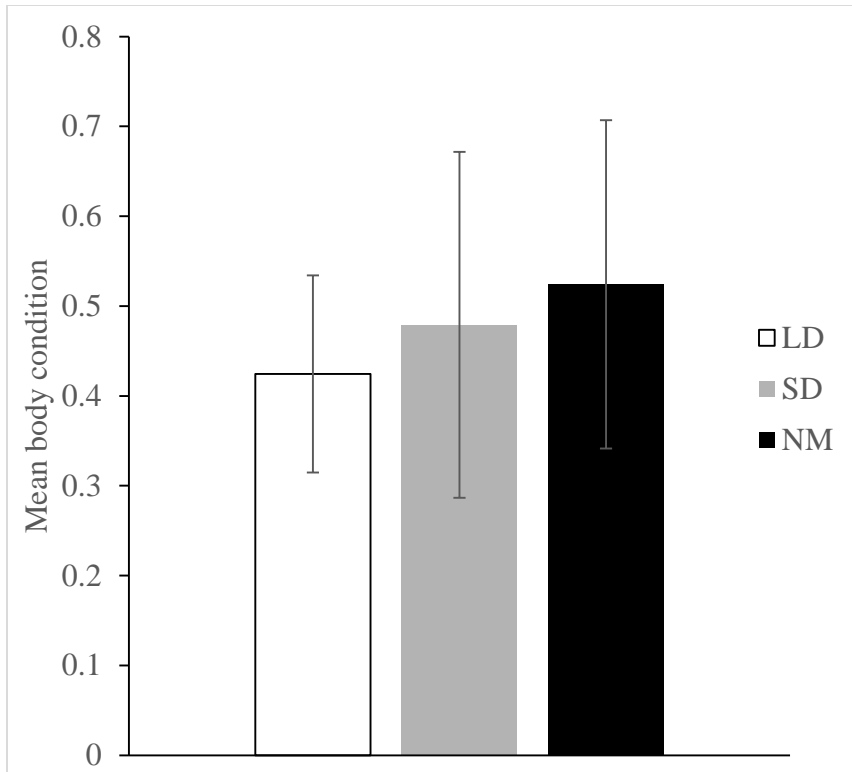


Figure 3. Mean body condition (\pm SD) among long-distance, short-distance, and non-migratory birds captured during fall migration of 2013 in east-central Illinois.

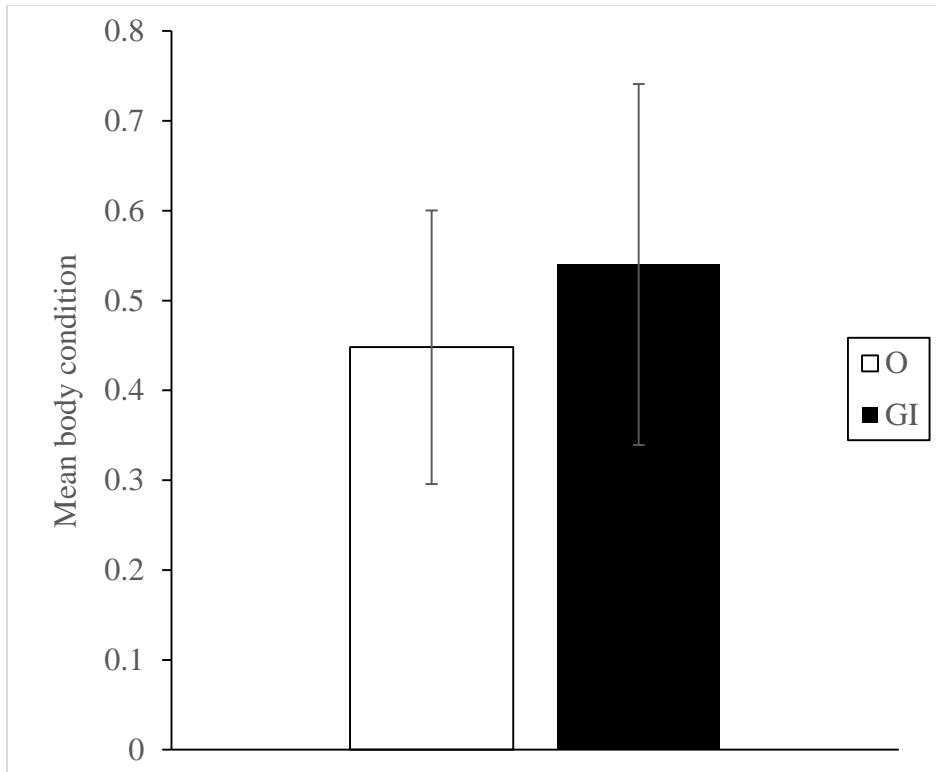


Figure 4. Mean body condition (\pm SD) among omnivores and granivore-insectivores captured during fall migration of 2013 in east-central Illinois.

CHAPTER 3

THE INFLUENCE OF AVIAN AND HABITAT CHARACTERISTICS ON TICK INFESTATION AND DISPERSAL ¹

ABSTRACT

A mechanism by which ticks and associated pathogens are able to colonize new locations is bird migration. Most tick species found on birds are host specialists, yet infestation varies among bird species. To determine which birds are disproportionately infested and the habitat characteristics that may influence infestation, captured birds were examined during migratory periods in fall of 2012 and 2013, and spring of 2013 and 2014 in 22 remnant forest patches across east-central Illinois. We examined 78 species and 1028 birds; 136 (13.2%) individuals representing 33 (42.3%) species were infested with at least one tick. Analyses of the probability of tick infestation as a function of average foraging height indicated that species foraging in the forest understory (i.e., < 10 m) experienced greater infestation prevalence, though canopy foraging species were occasionally infested. Analysis of infestation among migratory guilds indicated that short-distance migrants had greater infestation prevalence than long-distance migrants during spring migration, but not fall. Among all migrants pooled, infestation prevalence was not different from prevalence among resident birds. We also found that patch size and invasive shrub fruit influenced infestation prevalence among songbirds. Our findings highlight the importance of avian life-history and habitat characteristics that may influence tick infestation among songbirds.

¹Christine Parker, James R. Miller, and Brian Allan; Target journal: Ticks and Tick-borne Diseases

INTRODUCTION

Migrating birds serve are known to facilitate the long-distance dispersal of ticks and associated pathogens (Hamer et al. 2010, Heffernan et al. 2014). In North America, migrants have been implicated in the range expansion of *Borrelia burgdorferi* – the Lyme disease pathogen – and its primary vector *Ixodes scapularis* (black-legged tick; Schneider et al. 2014, Scott et al. 2014) . *Ixodes scapularis* infestation of birds is reported frequently (Kinsey et al. 2000, Durden et al. 2001, Morris et al. 2007), yet parasitism by other tick species is also important to note (Weisbrod and Johnson 1989, Nicholls 1996, Schneider et al. 2014). For example, *I. dentatus* poses less risk to humans than *I. scapularis*, yet is capable of maintaining *B. burgdorferi* in a wildlife-tick cycle that includes songbirds (Telford and Spielman 1989, Hamer et al. 2011b, Scott et al. 2012). Interest in the role birds play in the Lyme disease system is growing as it becomes apparent that bird hosts are more involved than previously thought (Hamer et al. 2011b, Dingler et al. 2014). To fully understand the role of songbirds in the Lyme disease system and their influence on tick dispersal, it is necessary to understand which bird species experience greater infestation prevalence.

Tick species detected on birds are considered host-specialists (Scharf 2004, Dingler et al. 2014). Among bird hosts, infestation prevalence varies among species and individuals (Kollars et al. 1999, Kollars and Oliver 2003). This variation may be due to host life-history traits that influence host interactions with vectors (Beveroth et al. 2006, Roulin et al. 2007, Hamer et al. 2011a). Bird age (Scharf 2004), sex (Pruett-Jones and Pruett-Jones 1991, Dingler et al. 2014), foraging height (Oorebeek and Kleindorfer 2009), nesting height (Dingler et al. 2014), body size (Oorebeek and Kleindorfer 2009), molt (Moyer et al. 2002), and migration strategy (Dingler et al. 2014) have been proposed to explain differential infestation. Infestation prevalence may also

be influenced by the habitats used by hosts. Among small mammals that used habitats with greater woody vegetation cover infestation prevalence was greater (Adler et al. 1992, Prusinski et al. 2006). Invasion by non-native vegetation (Lubelczyk et al. 2004) and habitat fragmentation (Ogrzewalska et al. 2011) may increase tick abundance and subsequent interactions with hosts, leading to greater infestation. Disproportionate infestation among avian hosts may influence the extent to which ticks are able to disperse across a landscape.

We investigated the influence of avian traits and habitat characteristics on tick infestation prevalence among songbirds during migratory periods. We hypothesized that: (1) prevalence would be greatest among ground-foraging species because host-seeking ticks are typically located in vegetation of less than one meter in height; (2) prevalence would be greater among migratory species because they may forego preening to spend more time on necessary life-history traits such as foraging to store or replace fat; (3) prevalence would be greater among birds captured in smaller patches because tick densities may be greater; (4) prevalence would be greater among birds captured in patches with greater invasive vegetation cover that provides questing habitat for ticks and may be used by foraging or resting birds during stopover. We also evaluated the role of songbird hosts between seasons to determine the feeding phenology of larval and nymphal ticks. Synchronous feeding periods of the immature tick stages may influence the prevalence of the Lyme disease pathogen in host-seeking ticks. Increased dispersal of these ticks and associated pathogens may ultimately increase disease risk to humans.

METHODS

Study sites

This research was conducted in 22 remnant forest patches in Champaign, McLean, Piatt, and Vermillion Counties in east-central Illinois, and Putnam County in north-central Illinois. Survey

data suggest that *I. scapularis* establishment occurred between 1988 and 1998 in Putnam County (Bouseman et al. 1990, Guerra et al. 2002), and prior to 2005 in Vermillion County (Diuk-Wasser et al. 2006); McLean, Piatt, and Champaign Counties were invaded more recently (Illinois Department of Public Health 2014).

Patch size (0.5 - 200+ ha), and proximity among patches (avg. distance 6000m) were determined in ArcGIS 10.2 (Environmental Systems Research Institute, Redlands, California) using 2011 digital orthophotography for each county (Illinois Department of Transportation). Patches were then classified by size as small (0.5 – 1 ha), medium (2 – 10 ha), and large (\geq 200 ha), with one patch of each size located in each county. Sampling in Putnam County also occurred in two additional small and medium sized patches, and sampling in Vermillion County occurred in one additional large, medium, and small patch. Predominant forest cover included sugar maple (*Acer saccharum*), black cherry (*Prunus serotina*), and American hackberry (*Celtis occidentalis*); predominant shrub cover included honeysuckle (*Lonicera spp.*), multiflora rose (*Rosa multiflora*), and American hackberry.

Bird captures and tick collection

To assess tick infestation of avian hosts during migration, we captured birds from August through October in 2012 and 2013, and from April through May in 2013 and 2014. Sampling in 2012 occurred only in Putnam and Champaign counties as part of a pilot study (Schneider et al. 2014). In each patch, we captured birds using 3-5 mist nets that were opened by sunrise and observed every 20 – 30 minutes for up to 5 hours in only “good” weather (e.g., nets were closed immediately in the event of precipitation or wind speeds exceeding 32 kph; Ralph et al. 1993).

For each bird captured, we recorded the location and date of capture, species, age (Pyle et al. 1997), presence of body molt, and tick burden. During extreme heat or cold, and if symptoms

of stress were evident, the data collected for each bird were limited to band number, species, and tick burden. We searched only the head and neck for ticks, as these are the primary attachment locations for feeding ticks (Pruett-Jones and Pruett-Jones 1991, Mitra et al. 2010). A subsample of birds was examined more thoroughly and no ticks were found in other body locations. All ticks were counted, removed using needle forceps, and placed in vials containing 70% ethanol; vials were stored in a -20° C freezer. We subsequently identified ticks morphologically to genus and species (Durden and Keirans 1996) using a Leica MZ 12.5 stereomicroscope. Each tick removed was classified as fully engorged, partially fed, or unfed. Engorgement classification data were used in our analyses under the assumption that unfed or partially fed ticks were acquired locally, whereas engorged ticks were acquired prior to a bird's arrival in our study sites. We evaluated the relationship between infestation prevalence by unfed or partially fed ticks and habitat characteristics of the patches where birds were captured. All protocols were approved by the University of Illinois' Institutional Animal Use and Care Committee (# 12144) and the Federal Bird Banding Laboratory (# 06507 – AW).

Vegetation surveys

We sought to determine the understory-vegetation and patch characteristics that may influence the infestation prevalence of songbirds during migration. Therefore, during September and October of 2013 we surveyed vegetation in each patch using modified methods of Gehlhausen et al. (2000), Bibby (2000) and, James and Shugart Jr (1970). Vegetation surveys in each patch were conducted along four 100-m transects (Gehlhausen et al. 2000). Each transect began in the middle of each patch border (i.e. N, S, E, W) and extended toward the center of the patch. Some patches were irregularly shaped, so mid-points in each cardinal direction were approximated using a map. Along each transect, we surveyed up to 7 5-m radius plots at distances of 0 (transect

origin; outer edge of patch), 15, 30, 45, 70, 85, and 100 m from the patch edge (Gehlhausen et al. 2000). Transects in small and medium size patches were truncated to fit within the patch without overlapping other transects. The total number of plots surveyed per patch ranged from 6 to 28. We visually estimated percent cover of invasive shrubs and noted minimum and maximum shrub height. Fruit abundance was estimated using a fruit abundance index (FAI) based on the number of fruits observed in each plot (1 = 1-10 fruits, 2 = 11-25, 3 = 26-50, 4 = 51-100, 5 = 101-200, 6 = 201-500, 7 = 501-1000, 8 = 1001-10000; Levey 1988).

Statistical analyses

Migration strategy and average foraging height for each species were based on published records (Poole 2005). All birds were assigned to one of five migration strategies (Table 10; Rappole 2013): (1) NM – non migratory; (2) FM – facultative; (3) PM – partial (4) SD – short-distance; (5) LD – long-distance. We used average foraging heights to calculate a foraging height index (FHI) for each species, as described by Pruett-Jones and Pruett-Jones (1991). The FHI is used to represent the strata within a forest where a given species forages. Four strata were considered: 1: ground (< 0.5 m); 2: understory (0.5-2 m); 3: lower canopy (2-10 m); and 4: upper canopy (> 10 m). If the foraging range of a species overlapped two or more strata, a mean index score was calculated. More captures of species that utilize understory and low-canopy layers in the forest is an inherent bias associated with capture-related studies. Therefore, we calculated the proportion of infested birds at each FHI level, out of the total number of birds examined at each level. While this does not eliminate the issue of biased captures, it presents a capture-weighted estimate of infestation at each level. For analyses presented here, we considered species with an FHI of three or less as understory foragers, and those with an FHI of 3.5 or 4 as canopy foragers.

We calculated measures of infestation prevalence and intensity by ticks to compare our results with those obtained in previous studies (Bush et al. 1997, Dingler et al. 2014). Infestation prevalence was reported as the proportion of individuals checked for ticks that were infested by at least one tick. The mean intensity of infestation was based on the mean number of ticks detected on infested birds. We also calculated the relative intensity of infestation as the average number of ticks detected among all birds examined. We then used generalized linear models to evaluate infestation prevalence among bird guilds and in relation to habitat characteristics. We also modeled the influence of habitat characteristics on infestation prevalence among birds by all ticks, and individual tick species. We repeated these analyses by season to determine if there were any differences in prevalence between fall and spring migration.

RESULTS

Bird captures

From fall 2012 to spring 2014, we captured 1056 individuals, 21 of which were previously banded, representing 83 species. Of these captures, we examined 1028 birds of 78 species for ticks. The majority of birds examined were migratory, including partial, short-distance, long-distance, and facultative migrants (88.5%, n = 910). Non-migratory species comprised 11.5% (n = 118) of examined birds. A greater number of captured birds had FHI values of 1 – 3 (i.e., primarily understory foragers; 86.5% (n = 889)), while the remaining 13.5% (n = 139) had FHI values of 3.5 – 4. The most frequently captured species included gray catbirds (*Dumetella carolinensis*), American robins (*Turdus migratorius*), and myrtle warblers (*Dendroica coronata coronata*).

Infested birds

Of the birds examined, 136 (13.7%) individuals of 33 (41%) species were infested with ticks (Table 11). The species most frequently infested were the white-throated sparrow (*Zonotrichia albicollis*; 24.5%), Northern cardinal (*Cardinalis cardinalis*; 25.4%), and gray catbird (*Dumetella carolinensis*; 14.1%). We found ticks on 74 birds during spring and 61 birds during fall. Mean infestation intensity was greater in fall versus spring ($t = 4.00$, $p < 0.0001$), although infestation prevalence did not differ between seasons ($\chi^2 = 1.09$, $p = 0.34$). Mean intensity of infestation of all parasitized individuals was 2.73 ticks per bird, and the relative intensity of infestation across all individuals examined was 0.37 ticks per bird.

Ticks sampled

A total of 368 ticks were detected on birds, of which 309 were collected and identified (Fig. 5). All ticks collected were juveniles and were identified as *Amblyomma spp.* (0.6%), *Haemaphysalis leporispalustris* (45%), *I. scapularis* (19.7%), *I. dentatus* (10.4%), and *Ixodes spp.* (18.8%); 5.5% were damaged and unidentifiable to genus. Some *Ixodes spp.* were unable to be identified to species due to damaged or missing mouthparts, although we expect that these ticks were likely *I. scapularis* or *I. dentatus* because we did not collect any other *Ixodes spp.* Larvae represented the majority of ticks collected (64.7%), followed by nymphs (31.1%); 4.2% were unidentifiable to life stage. Between seasons, we found that nymphal infestation prevalence was greater during spring ($\chi^2 = 4.34$, $p = 0.037$), and larval infestation prevalence did not change ($\chi^2 = 0.58$, $p = 0.445$).

Ixodes scapularis were collected from 40 birds of 15 species. Species most frequently infested by *I. scapularis* included house wrens (*Troglodytes aedon*; $n = 5$), brown thrashers (*Toxostoma rufum*; $n = 4$), Swainson's thrushes (*Catharus ustulatus*; $n = 4$), and Northern cardinals ($n = 4$). *Haemaphysalis leporispalustris* were collected from 47 individuals of 19

species; white-throated sparrows ($n = 9$), Swainson's thrushes ($n = 7$), and gray catbirds ($n = 5$) were the most frequently infested. Other tick species detected on birds included *Amblyomma spp.* on a myrtle warbler and a Northern cardinal, *I. dentatus* on 20 birds of 12 species, and *Ixodes spp.* on 49 birds of 32 species. Seventeen ticks from 12 birds of 8 species were damaged and could not be identified.

Guild infestation prevalence

We detected a strong effect of migration strategy on infestation prevalence ($\chi^2 = 10.18$, $p = 0.03$), and non-migrants had the greatest prevalence overall (17.5%). Among migratory groups, infestation prevalence was greatest among short-distance migrants (16.1%), followed by partial (11.1%) and long-distance migrants (10.6%). We did not detect any difference in the probability of infestation as a function of migration strategy in fall ($\chi^2 = 2.84$, $p = 0.58$), but during spring, long-distance migrants were less likely to be infested than short-distance ($\beta = -0.79$, $p = 0.001$) and non-migrant birds ($\beta = -0.88$, $p = 0.03$). We did not find any difference in infestation prevalence between migratory birds (i.e., all migratory guilds pooled) and residents ($\chi^2 = 1.59$, $p = 0.206$). We found a similar lack of difference in prevalence between migratory birds infested by *I. scapularis* ($\chi^2 = 0.19$, $p = 0.659$) and *H. leporispalustris* ($\chi^2 = 0.04$, $p = 0.838$), yet resident birds experienced greater infestation prevalence by *Ixodes spp.* ticks than migratory birds ($\chi^2 = 4.90$, $p = 0.026$).

The probability of tick infestation, by all tick species pooled, among understory foragers was nearly twice as high ($\beta = -1.98$, $p = 0.0008$; Fig. 6) as canopy foragers. The probability of infestation among canopy foragers was also less during both fall ($\beta = -2.61$, $p = 0.01$) and spring ($\beta = -1.57$, $p = 0.03$). Understory foragers experienced greater infestation prevalence by *I.*

scapularis and *Ixodes spp.* ($\chi^2 = 5.02$, $p = 0.0251$; Fig. 7), however there was no difference between forage guilds in infestation prevalence by *H. leporispalustris* ($\chi^2 = 0.00$, $p = 0.999$).

Influence of habitat characteristics on infestation prevalence

Shrub honeysuckle (*Lonicera spp.*), multiflora rose (*Rosa multiflora*), and Missouri gooseberry (*Ribes missouriense*) were the most commonly detected invasive shrubs among all forest patches. Honeysuckle ranged in height from 0.5 to 6 m, and mean maximum height was 1.65 m. Multiflora rose ranged in height from 0.5 to 3 m, and mean maximum height was 1.47 m. Missouri gooseberry ranged in height from 1 to 1.5 m, and mean maximum height was 1.06 m. No fruits of Missouri gooseberry or multiflora rose were detected, and the mean fruit abundance index for honeysuckle was 2.51, indicating abundance ranged from 11- 25 fruits per plot.

Of the birds parasitized by partially or unfed ticks, infestation prevalence was greater among birds captured in large ($z = 2.67$, $p = 0.007$) or small forest patches ($z = -3.03$, $p = 0.0024$), relative to medium size patches. Among birds captured in large and small patches, there was no difference in infestation prevalence by all tick species ($z = 0.06$, $p = 0.950$), *I. scapularis* ($z = 0.60$, $p = 0.548$), or *Ixodes spp.* ($z = -0.05$, $p = 0.961$). Infestation prevalence by *H. leporispalustris* was not influenced by patch size ($\chi^2 = 0.05$, $p = 0.973$). We found no response of infestation prevalence by partially or unfed ticks to mean invasive shrub cover ($\chi^2 = 0.09$, $p = 0.770$), or mean invasive shrub fruit abundance ($\chi^2 = 2.19$, $p = 0.138$). Infestation prevalence by *I. scapularis* did not respond to mean invasive shrub cover ($\chi^2 = 0.27$, $p = 0.605$), yet declined in response to increasing shrub fruit abundance ($\beta = -0.33$, $\chi^2 = 4.41$, $p = 0.035$). Infestation by *Ixodes spp.* also declined in response to increasing fruit abundance ($\beta = -0.268$, $\chi^2 = 5.64$, $p = 0.017$), yet was not influenced by invasive shrub cover ($\chi^2 = 0.05$, $p = 0.823$). Infestation

prevalence by *H. leporispalustris* was not influenced by invasive shrub cover ($X^2 = 0.32$, $p = 0.57$) or invasive shrub fruit abundance ($X^2 = 0.03$, $p = 0.872$).

DISCUSSION

Our results confirmed the influence of foraging height on infestation by ticks generally, and by individual tick species (Scott et al. 2012, Dingler et al. 2014, Mukherjee et al. 2014). Infestation prevalence by *Ixodes spp.* was greater among non-migratory bird species, and declined in habitats with greater abundance of invasive shrub fruits. Infestation by *H. leporispalustris* was not influenced by avian traits or habitat characteristics. We found that among migratory birds, short-distance migrants may serve an important role in the long-distance dispersal of ticks, particularly during spring migration, whereas resident species may be participating in the local dispersal of ticks. Our data confirm the synchronous feeding activity of larval and nymphal ticks during spring and fall seasons (Gatewood et al. 2009), which may increase pathogen transmission between larvae and infected nymphs, and subsequently increase disease risk for humans.

Long-distance tick dispersal by migratory birds

The involvement of migratory birds in the long-distance dispersal of ticks is well-documented (Scott et al. 2012, Schneider et al. 2014). Our data suggest that short-distance, rather than long-distance migrants, may be more important for tick dispersal during migration in spring (Mohr 1961). One possible explanation for this result is the influence of foraging strategy. Among the long-distance species we captured, 35% are considered partially or primarily insectivorous. These species often forage aerially or from a perch, and may thus spend less time foraging in tick habitat (Dingler et al. 2014). We did not have sufficient evidence to suggest that infestation

prevalence by *H. leporispalustris* differed among migratory guilds, likely because it is a common tick species with a wide ranging distribution from Alaska to Argentina (Labruna et al. 2000).

Additionally, our analyses indicated that infestation prevalence by *I. scapularis* was not significantly different between migratory and resident birds. Newman et al. (2015) reported a similar result among birds infested by *I. pacificus*. However, we also found that resident birds experienced greater infestation prevalence by *Ixodes spp.* than migratory birds, which suggests that *Ixodes spp.* populations are likely present in the forest patches we studied. Although migrants may have acquired ticks in east-central Illinois, our engorgement data suggest that some of these birds may have become infested prior to stopover in east-central Illinois, further emphasizing the participation of migrants in the long-distance dispersal of ticks.

The influence of foraging height on tick infestation

Avian foraging height strongly influences *Ixodes spp.* infestation prevalence among birds (Scott et al. 2012, Dingler et al. 2014, Mukherjee et al. 2014), and our results supported this idea. Infestation prevalence by *H. leporispalustris* occurred only among bird species that forage below 10 m, in the forest understory, whereas some species with higher foraging heights were infested by *Ixodes spp.* We presume this may be a factor of the low height (< 0.25 m) at which *H. leporispalustris* (Camin and Drenner 1978) quests, or seeks, hosts. Foraging birds that use lower forest-strata are at greater risk of infestation because those substrates often serve as questing habitat for host-seeking ticks (Anderson and Magnarelli 2008). Ticks reduce their risk of desiccation by remaining in close proximity to a humid refuge, such as leaf litter (Vail and Smith 2002), and are therefore dependent on passive interactions with hosts using the habitat. These interactions may be further influenced by environmental factors, such as temperature, which may increase tick travel distance and time spent questing for hosts (Randolph and Storey 1999, Vail

and Smith 2002). Temperature and humidity are regulated by understory vegetation (Chen et al. 1999, Parker et al. 2009, Watling et al. 2011), which may also influence tick burden and pathogen transmission in hosts (Adler et al. 1992, Prusinski et al. 2006).

Influence of habitat characteristics on infestation prevalence

Forest understories in the Midwest are often subject to invasion by exotic vegetation such as honeysuckle (*Lonicera spp.*; Miller et al. 2004) and buckthorn (*Rhamnus spp.*; Heimpel et al. 2010). Greater prevalence of these invasive species may increase the abundance of ubiquitous reservoir species of *B. burgdorferi*, such as the American robin (*Turdus migratorius*; McCusker et al. 2010), and appears to provide suitable microclimate conditions for *I. scapularis* (Lubelczyk et al. 2004, Christopher and Cameron 2012). We detected *I. scapularis* infestation among captured birds, however its prevalence appeared unrelated to cover by invasive shrubs, and declined in response to increasing native shrub fruit abundance. We presume this was related to the range of invasive shrub heights because we noticed (anecdotally) that shrub fruits were often located across the crown of shrubs, which could reduce bird interactions with ticks if ticks aren't questing on the top of fruiting shrubs. So although tick densities may be greater in locations with greater invasive cover, the birds using those habitats may be foraging out of tick questing range (approximately 1 meter; Goddard 1992).

Tick infestation prevalence, in general and by *Ixodes spp.*, was greater in small and large patches, relative to medium-size patches. Decreasing patch area may lead to increased population densities of *I. scapularis* and small mammals such as the white-footed mouse (*Peromyscus leucopus*; Allan et al. 2003, Anderson et al. 2003), the primary reservoir host of *B. burgdorferi* in the United States (Durden and Keirans 1996, Keirans et al. 1996). Larger forest patches may experience greater use by large-bodied mammals, such as the white-tailed deer, which play a

vital role in the population regulation of *I. scapularis* (Deblinger et al. 1993). White-tailed deer often serve as a host to adult ticks seeking a blood meal to enable reproduction (Keirans et al. 1996) As a result, greater tick density may lead to greater infestation prevalence among bird hosts using the habitats.

Habitat, tick infestation, and highly mobile wildlife

Evaluating the relationship between tick infestation of migrating birds, or other highly-mobile species, and stopover habitat is challenging for several reasons: 1) we are generally unable to determine where and when a bird became infested; 2) determining the rate of infestation among birds in specific patches is logistically difficult because stopover length varies widely due to a number of intrinsic and extrinsic factors (Schaub et al. 2008); 3) recapture attempts typically result in small sample sizes (Scharf 2004). Here we used an engorgement classification to determine if birds become infested locally or prior to stopover in our study sites. Based on our engorgement data and similar infestation prevalence between migrant and resident birds, it appears that many of the ticks detected on birds may have been acquired locally. Immature ticks feed on average from 2.5 to 8 days (Anderson and Magnarelli 2008), therefore ticks may have also been acquired in a location from which a bird departed about a week prior to its arrival in east-central Illinois. Migrants may exhibit a settling period following initial stopover during which time they may sample different habitats (Aborn and Moore 1997, Mills et al. 2011), in which case the use of engorgement data may not provide a reliable indication of when ticks were acquired. However, infestation prevalence among the non-migratory birds captured should also provide some indication, or baseline of questing tick abundance in the habitat. Lower prevalence among non-migrants may indicate that migrant infestation occurred in a previous stopover location.

Overall, the infested bird species we encountered encompass a broad range of life-history traits which may influence the geographic extent of tick dispersal. Ticks feeding on long or short-distance migrants may cross numerous state or country borders, whereas ticks feeding on resident species may be transported just a few kilometers from its natal habitat. The behavior and subsequent interactions of both hosts and ticks are also affected by habitat conditions (abiotic and biotic; Rodewald and Brittingham 2004, Allan et al. 2010). Contrary to our expectations, invasive shrub-fruit abundance appeared to reduce infestation prevalence among birds, despite the positive relationship between invasive shrubs and tick densities found in other studies (Elias et al. 2006, Christopher and Cameron 2012). Our results highlight the need to consider host life-history traits, and habitat characteristics that may increase interactions between ticks and potential hosts.

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TABLES

Table 10. Descriptions of migration strategies as adapted from Rappole (2013)

Migrant strategy	Description
(NM) Local movement, non-migratory	Includes seasonal movements such as post-breeding dispersal, inter- and intra-species flocking, and distant foraging in species that are otherwise considered non-migratory.
(FM) Facultative migration	Includes nonbreeding season movements influenced by extrinsic factors such as weather, variable food supply, and social hierarchies. Movements range in distance from breeding locations.
(PM) Partial migration	Includes species for which the population is comprised of individuals that remain at the breeding location during the nonbreeding season, and individuals that migrate elsewhere during the nonbreeding season.
(SD) Short-distance migration	The entire population migrates less than 2,000 km outside the breeding range.
(LD) Long-distance migration	The entire population migrates a distance of greater than 2,000 km outside the breeding range.

Table 11. Avian traits, infestation parameters, tick species, and life stages (L: larvae; N: nymph; U: unknown) collected from captured birds during spring of 2013-2014 and fall of 2012-2013 in east-central Illinois.

Species	FHI	Migrant strategy	No. infested	No. checked	I. dentatus	I. scapularis	Ixodes spp.	H. leporispalustris	Amblyomma spp.	Unknown spp.
American robin	1.5	PM	4	77	1 N	3L, 1N				
Black-capped chickadee	3.5	FM	1	14						1U
Blue jay	2.5	PM	5	16	4L	3L	3L	5L		1U
Brown thrasher	1	SD	7	20	2L	7L, 1N	4L, 2N	3L		
Brown-headed cowbird	1	SD	2	24			1N	1L		
Canada warbler	2	LD	1	1	2N					
Carolina chickadee	3.5	NM	1	6			3L			
Carolina wren	2	NM	3	9	1L		1N	1L		
Common yellowthroat	2	LD	1	8			1L			
Eastern towhee	1.5	SD	2	7		1L	2N			
Gray catbird	2	SD	11	78	1L	2L, 1N	2L, 1N	6L, 4N		
Gray-cheeked thrush	1	LD	8	17		1N	3N	8L, 6N		2L, 2U
Hermit thrush	2	SD	9	20	12L	3L, 1N	3L, 1N	1L		1L

Table 11. cont.

Species	FHI	Migrant strategy	No. infested	No. checked	I. dentatus	I. scapularis	Ixodes spp.	H. leporispalustris	Amblyomma spp.	Unknown spp.
House wren	2.5	SD	8	23		1L, 7N	6N	9L, 8N, 1U		1N, 1U
Indigo bunting	2	LD	7	71			1L, 3N	5L, 1N		
Kentucky warbler	2	LD	2	4			1N	2L		
Lincoln's sparrow	1.5	SD	3	13	3L		1L, 1U			1N
Myrtle warbler	3	SD	2	69					1L	1L
Northern cardinal	2	NM	13	51	3L	6N	2L, 4N	48L	1L	
Northern waterthrush	1.5	LD	2	18			1N	1L		
Ovenbird	2	LD	2	36	1L	9L	1L			
Rose-breasted grosbeak	3.5	LD	1	15		1N	1N			
Song sparrow	2	PM	5	24		3N	5N	7L		
Swainson's thrush	2	LD	11	59	1L	3L, 2N		12L, 2N		
Swamp sparrow	2	PM	3	10			1N	2L, 2N		
Tufted titmouse	2.5	NM	2	23		3N	2N			
Veery	2	LD	1	2				1L		

Table 11. cont.

Species	FHI	Migrant strategy	No. infested	No. checked	I. dentatus	I. scapularis	Ixodes spp.	H. leporispalustris	Amblyomma spp.	Unknown spp.
White-breasted nuthatch	3.5	NM	1	3			1N			
White-crowned sparrow	1.5	SD	1	9				1N		
White-throated sparrow	2	SD	14	57		1L, 1N	1L	11L, 3N		6U
Winter wren	1.5	SD	1	1	1L					
Wood thrush	1.5	LD	1	4				3L, 1N		
Yellow-shafted flicker	1	PM	1	1						

FIGURES

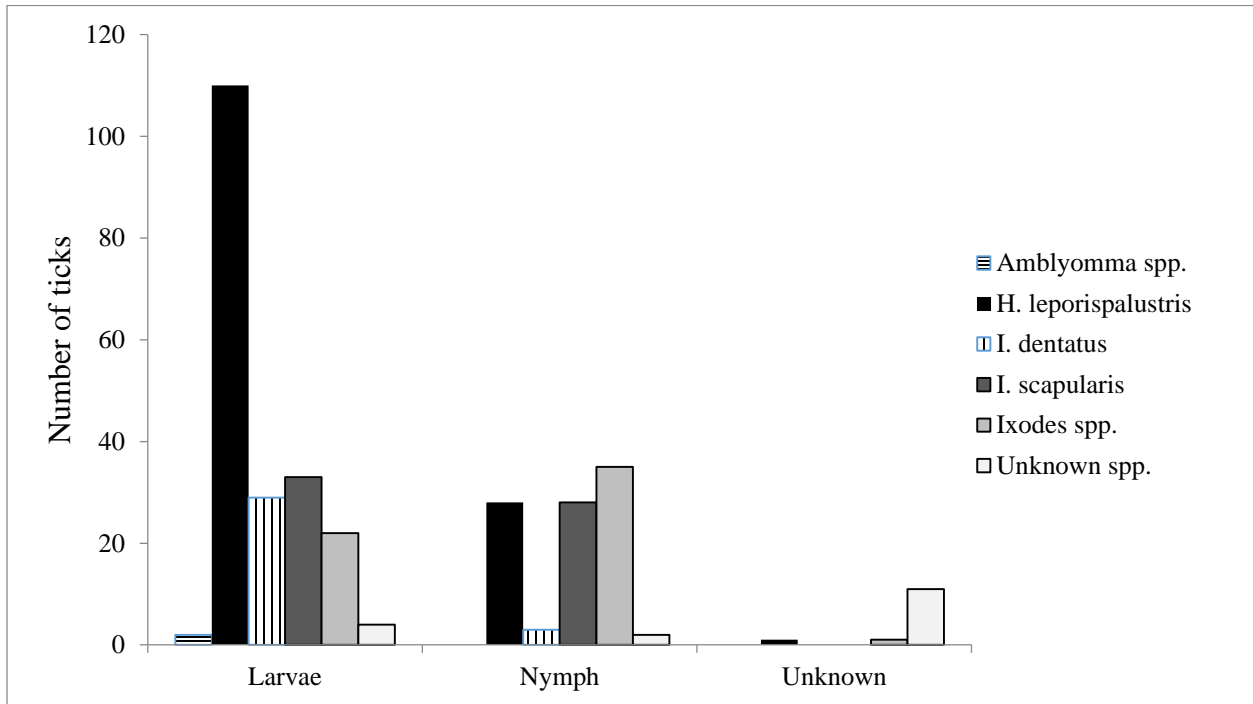


Figure 5. Distribution of species and life stage of ticks sampled from birds captured in east-central Illinois from 2012 to 2014.

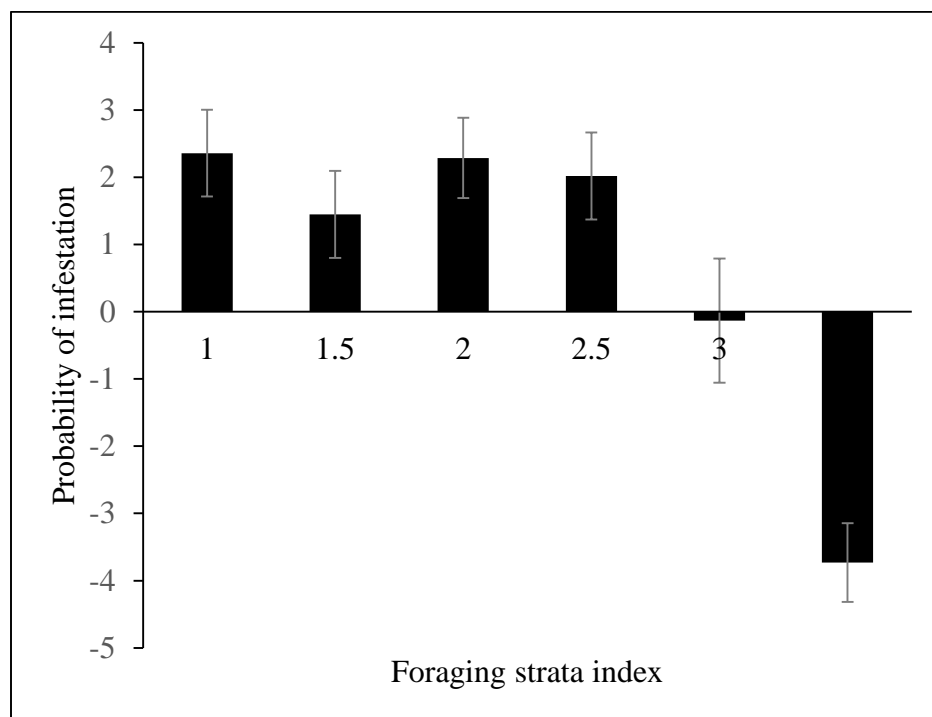


Figure 6. Estimated probabilities and standard errors of tick infestation among birds with different FHI levels that were captured in east-central Illinois from 2012 to 2014.

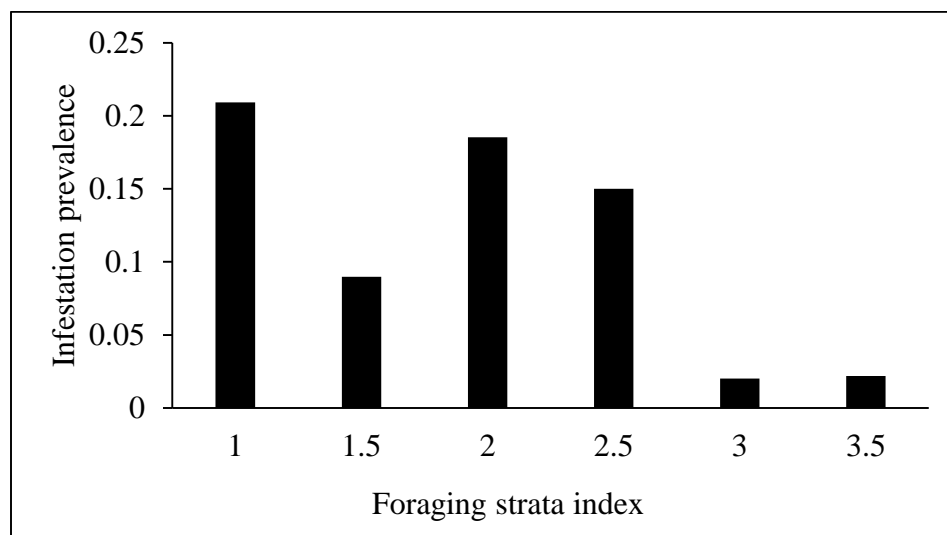


Figure 7. Infestation prevalence among examined birds of different FHI levels that were captured in east-central Illinois from 2012 to 2014.

CHAPTER 4

SUMMARY

The primary objective of this research was to gain a better understanding of how life-history traits may influence different aspects of stopover ecology among migratory birds. The primary conclusion from the second chapter was metrics of habitat quality suggest different habitat characteristics increase stopover quality. Using multiple metrics to evaluate stopover quality may therefore provide an enhanced perspective of important habitat features for different guilds of birds. Patches in east-central Illinois were used by migrants, but little evidence suggested they were able to increase energy reserves. Condition change among long-distance migrants was best predicted by shrub-fruit abundance, and no variables were good predictors of condition change among short-distance migrants. Alternatively, short-distance migrant abundance and richness were best predicted by ground cover, including herbs, leaf litter, and bare ground. I presume the differences observed between these metrics are indicative of the biases inherent to different survey methods. Therefore, I recommend using multiple measures of habitat use to improve the inferences made about habitat quality among all migratory strategies.

The main finding from the third chapter was that migration and foraging strategies influence infestation prevalence among songbirds. Short-distance migrants had greater infestation prevalence than long-distance migrants. Additionally species that forage in the forest understory (< 10 m), versus the canopy, had greater infestation prevalence. I found no support for age or molt as predictors of infestation prevalence among songbirds. Overall, my findings

provide support for the influence of life-history on risk of infestation by ticks, and also interpretations of habitat quality.

APPENDIX

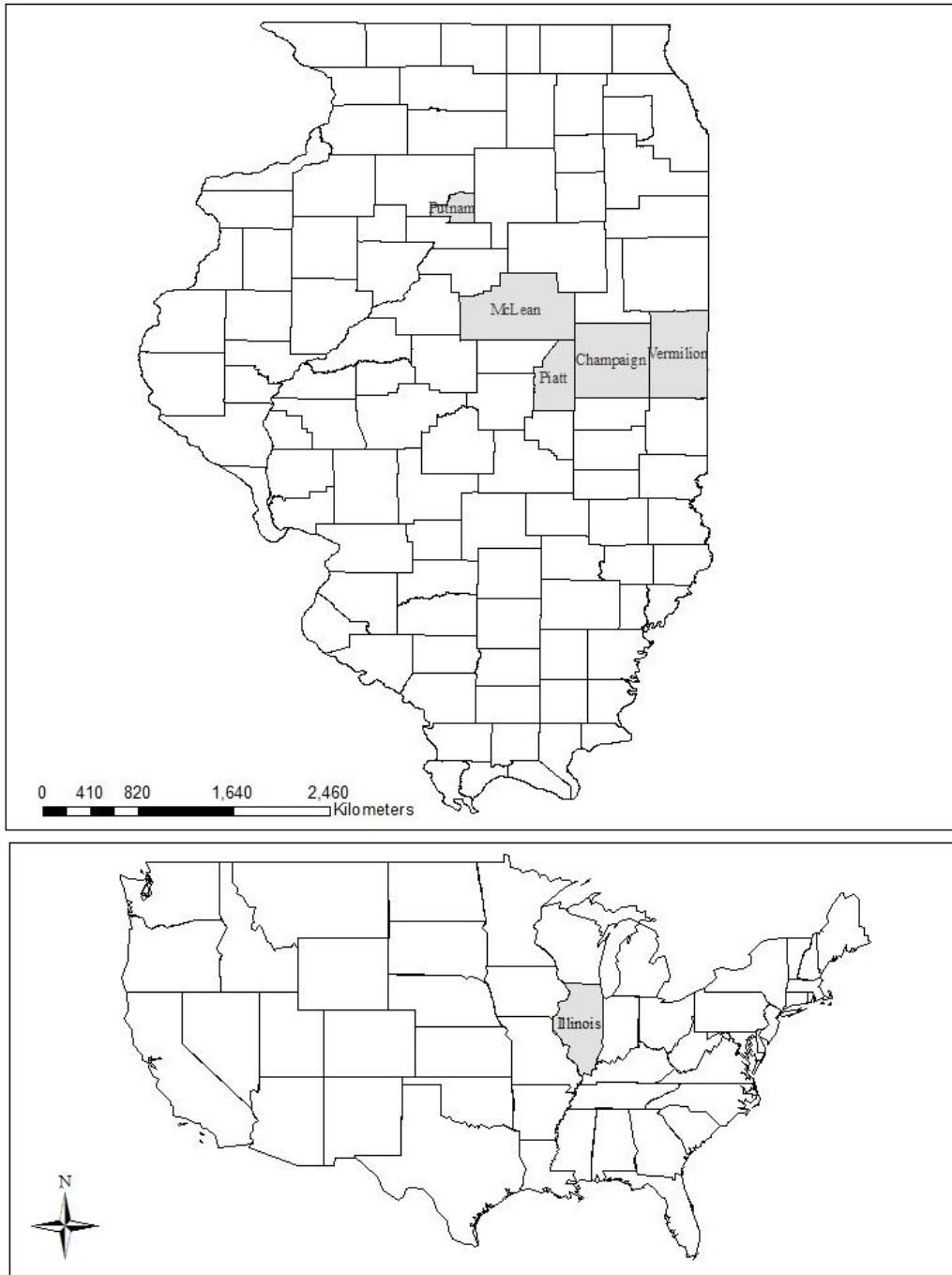


Figure 8. Map of counties in Illinois where sampling occurred from 2012 to 2014.