THE EFFECT OF URBANIZATION ON THE STOPOVER ECOLOGY OF NEOTROPICAL MIGRANT SONGBIRDS

A THESIS

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL

OF THE UNIVERSITY OF MINNESOTA

BY

Elisabeth Condon

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

MASTER OF SCIENCE

Gerald J. Niemi

April 2015

ACKNOWLEDGEMENTS

I would like to thank the U.S. Environmental Protection Agency's Coastal Monitoring Program, the University of Minnesota-Duluth, the University of Minnesota's Integrated Bioscience graduate program and the Natural Resources Research Institute for support and funding. I would also like to thank my committee members, Dr. Matthew Etterson, Dr. Richard Green, and especially my advisor, Dr. Gerald Niemi, who has been extremely supportive to me on this project. Thanks as well to my outstanding field crew, Hannah Panci, Jessica Chatterton, and Julia Luger. Thank you to Terry Brown, who created a stellar data entry system for entering and checking large amounts of point count data. The forest preserve districts of Cook, Kane, Lake and McHenry Counties gave us permission to conduct research on their properties, which was extremely helpful. Lastly, thank you to my family members, who provided housing for my field crew and who have been supportive to me throughout my life.

ABSTRACT

I conducted spring migration point counts and vegetation surveys at 29 forest patches in the Chicago, IL metropolitan area in 2012 and 2013. The forest patch selection was designed to test the effects of patch size, distance from the Lake Michigan shoreline and degree of urbanization. I conducted exploratory analysis to search for potential relationships. Vegetation structure variables, especially understory and subcanopy composition, were important factors for many models. Bird species determined to be area sensitive in previous studies were associated with large patches during migration. While path size, distance from the shoreline and urbanization were not frequently selected for models of the entire avian community, they were important in most models of individual species. No single combination benefitted all species, indicating that maintaining a variety of conditions in the region will support a diverse avifauna.

The supplementary file included in this thesis submission is the raw data from two years of point count sampling.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

For many bird species, migration may represent the largest obstacle to survival (Moore 2000). Conservation efforts for Neotropical migrants usually focus on breeding and wintering sites, but stopover habitat during the spring and fall migration is also a critical link in the conservation of birds (Mehlman et al. 2005). Stopover habitat needs during the migration period are the least understood for the Neotropical bird life-cycle (Faaborg et al. 2010) and more research is needed to understand how to conserve these species (Moore 2000).

Urbanization is continuing at a rapid rate, and many stopover sites are located in heavily urbanized areas. Despite the huge impact of cities, relatively little urban ecological research has been conducted in comparison with pristine areas (McDonnell and Pickett 1990). The impact of urbanization on migrating birds has been the subject of a few studies (Rodewald and Matthews 2005, Matthews 2008, Rodewald and Shustack 2008, Craves 2009), while more have focused on the effects of urbanization on breeding bird communities (Blair 1996, Clergeau et al. 1998, Donnelly and Marzluff 2004, Chace and Walsh 2006, Pidgeon et al. 2007, Lepczyk et al. 2008). A few studies have examined the effects of patch size on breeding bird communities embedded in an urban landscape (Crooks and Soulé 1999, Crooks 2004, Donnelly and Marzluff 2004). Most studies on birds in urban areas have been conducted during the breeding season. Relatively little is known about how urbanization and fragmentation affect stopover ecology of Neotropical migrants.

Recently, more studies have examined the effect of urbanization on migrating birds (Craves 2009, Matthews and Rodewald 2010a, Seewagen et al. 2010, 2011a). These studies used capture data, radio telemetry and stress hormone concentration to compare migrants at urban versus rural or more natural stopover sites, and found no large differences in bird behavior or mass gain between different patch types. These studies were mostly conducted on small sample sizes and examined individual bird species. We do not have an understanding of how urbanization affects migrating bird species diversity or abundance in most situations (Mehlman et al. 2005). Further research is needed to elucidate the habitat needs of migrating birds in urban areas.

In North America, the Great Lakes region is an area of rapidly expanding human development (Wolter et al. 2006). As urbanization continues to alter the Great Lakes watershed, research on its impacts to wildlife is urgent. The Great Lakes hosts one-tenth the human population of the United States and one-quarter the population of Canada (Fuller et al. 2012). Lake Michigan contains the widest range of human population density of the five Great Lakes (Niemi et al. 2007), providing a valuable opportunity to study the impacts of urbanization along a gradient. Urban and suburban sprawl, especially along the coast, continues to transform the region (Wolter et al. 2006, Lepczyk et al. 2007). Dense urbanization along the coastlines could degrade stopover sites in a number of ways. Urban forest patches tend to have a high proportion of non-native vegetation (Crooks 2004), a high concentration of mesopredators (Crooks and Soulé 1999), increased competition from a high concentration of birds (Faeth et al. 2005), decreased patch size and increased fragmentation (Theobald et al. 1997), more edge effects (Medley et al. 1995), increased anthropogenic noise (Slabbekoorn and Ripmeester 2008) and more disturbance from roads (Medley et al. 1995, Forman and Alexander 1998).

Human population density accounts for a large portion of anthropogenic stress in the Great Lakes region (Danz et al. 2007) with potential effects on stopover ecology. The Great Lakes themselves are also a formidable barrier for migrating birds. While many birds fly directly over the Great Lakes (Diehl et al. 2003), coastal stopover areas are vital to the survival of migrants (Ewert and Hamas 1995, Bonter et al. 2009, Ewert et al. 2011). The western shore of Lake Michigan may be particularly important to migrants, as it runs parallel to the direction of migration; when migrants approach the western Lake Michigan shoreline, they often follow the shore, rather than attempt a lake crossing (Diehl et al. 2003). Migrants may also use the shoreline to compensate for wind drift (Åkesson 2011) and to consume emerging aquatic insects in the spring (Ewert and Hamas 1995). All of these factors contribute to a high concentration of migrating songbirds along the western shore of Lake Michigan during spring migration.

Forest patches in the Chicago region, especially along the Lake Michigan shoreline, may provide a vital link to migrants in the region (Brawn and Stotz 2001). Bonter et al. (2009) used RADAR data to show that forest patches embedded in an urban matrix near the coastline were highly valuable to migrating birds in the Great Lakes region. However, the authors could not determine patch size differences due to the large-scale resolution of RADAR data. More intense ground surveys are needed during the migration period to answer questions about habitat use.

Very few studies have examined the effect of urbanization on Neotropical migrants during the migration season. Therefore, I did not begin this study with a set of hypotheses in mind. Rather, my intent was to search for patterns to inform hypotheses for future studies. The goal of this study was to compare diversity and abundance of migrating birds at forested stopover sites in the Chicago area, an important region for Neotropical migrating birds in the Mississippi Flyway (Brawn and Stotz 2001). My objectives included: 1) test the effect of three "fixed" landscape characteristics: patch size, level of urbanization, and distance from the lake on the response by spring migrating birds. 2) Revisit sites to determine change in species richness and abundance throughout the day. For instance, if certain habitat patches in urban areas are not suitable stopover sites for migrants, I expected to find that loss of species diversity and abundance in these sites will be higher. 3) Provide recommendations on use of this region by migrating birds on conservation and to improve habitat for migrating birds. 4) Develop a set of hypotheses for future studies.

METHODS

I used a stratified random study design and collected point count data to determine whether birds were selecting certain patch types during migration. Each forest patch was categorized in three ways, by patch size, level of urbanization in the surrounding matrix and distance from the lake. Each category had two levels. All patches were categorized as forested according to the 2002 National Land Cover Dataset, and I visited patches to ensure that they were forested before including them in the study. The Chicago region contains a mix of forest patch types, creating the opportunity for a natural experiment.

Study Area

This study was conducted in the region surrounding Chicago, Illinois, USA (city center; 41° 53' 2.9436", -87° 37' 56.6682"). The Chicago region contains a dense city center and many suburbs. Before human settlement the Chicago region was primarily composed of prairies, wetlands, and dispersed forest cover (Bowles and McBridge 2002). Today Chicago is one of the most densely populated urban centers in the United States, with the current population just over 2.7 million (U.S. Census Bureau 2012). Despite this, Cook County, the county in which Chicago is located, contains about 21% forest canopy cover (Nowak et al. 2013). County-run forest preserve districts maintain large areas of continuous forest that are free from development, and small forested lots, both privately and publicly owned, are located throughout the region. Field workers had access to housing in Glenview, Illinois, a Chicago suburb approximately 15 kilometers north of the Chicago city center. For logistical purposes, the extent of this study was limited to the Wisconsin border on the north, IL-55 (a major highway) on the south and 50 kilometers west of the Lake Michigan coastline to the west. Lake Michigan represents the eastern border of the study area (Fig. 2); an area of approximately 4600 km^2. This area contains 16 percent forest cover with a mix of forest patch sizes across a gradient of urban density and various distances from Lake Michigan (Fig. 2).

Site selection

Sample size

Using data from 10-minute point counts from the Minnesota Breeding Bird Atlas, provided to me by Dr. Gerald Niemi (personal communication, April 10th, 2012), I determined that a minimum of 32 sites, or four within each of the eight categories (Table 1), would allow the detection of a difference between sites equivalent to one standard deviation of the data. Two similar studies examining the effect of reserve size and level of urbanization had 29 (Donnelly and Marzluff 2004) and 34 (Crooks 2004) sample sites.

Classification techniques

In order to classify each forest patch in the region according to three categories, I used remote sensing techniques to categorize forest patches, which I then checked with a site visit prior to the start of the study. I started with a pool of candidate forest patches using Landsat imagery from 2002 (resolution 30m x 30m) that had been categorized using a system created by the Illinois Interagency Landscape Classification Project (IILCP). I grouped all forested land types (upland, partial canopy/savannah upland and coniferous) into a single new category representing forested land. This created a pool of 49,150 individual forest patches within the study area. Each patch was sorted into one of eight treatment categories based on the three binary factors: patch size, level of urbanization, and distance from Lake Michigan (Tables 1 and 2). Criteria for assignment into a category was determined by examining previous studies on urbanization and the range of patch sizes available within the study area (Table 2)(Blair 1996, Donnelly & Marzluff 2004, Marzluff 2001).

I categorized the landscape in a buffer around each patch. I used 1 kilometer buffer, as opposed to a smaller buffer, as I was most interested in the effects of the broader landscape on migrating birds. Any area within that buffer was then considered to be part of the landscape context of the habitat patch. There is little consensus between studies as to what defines an area as urban (Marzluff et al. 2001, Páez and Scott 2004). Data to define the urban gradient are often gathered through remote sensing techniques (Pidgeon et al. 2007; Lepczyk et al. 2008), but some studies also take measurements on the ground, such as pedestrian and road traffic (Blair 1996). For this study I used land cover categorization and U.S. census data to classify the urbanization level of forest patches in and around Chicago, Illinois.

To categorize sites as urban or suburban I used data on impervious surfaces, human population density and percent urbanized landcover. Impervious surfaces, such as pavement and buildings, are a strong indicator of human influence (Alberti 2005). The National Land Cover Dataset from 2006 (NLCD) contains four categories that refer to levels of human development at a 30 x 30m resolution. The defining factor of these categories is percent impervious surfaces. I calculated the mean category on a scale of 0 (no impervious surfaces) to 4 (greater than 80% impervious surfaces) to obtain a mean impervious surfaces score. This contributed to the urban/suburban categorization of each patch (Table 2). Data from the 2010 U.S. census were used to calculate the area-weighted, average population density surrounding each forest patch. Finally, to ensure that each urban patch was surrounded by urban land cover, I used IILCP data to confirm the percentage of urban land cover (high and low intensity developed categories combined) in the buffer surrounding each forest patch. I eliminated a forest patch from the "urban" category if it had less than 50% urban land cover within the 1 kilometer buffer area (Table 2). Following these steps, each forest patch was either categorized as urban or suburban. Patches that could not be categorized under this scheme eliminated from further consideration.

Distance from the Lake Michigan shoreline was calculated using the patch edge closest to the shoreline. Patch area was calculated in hectares for every forest polygon. This information was used to categorize sites as close or far from the shoreline, and as large or small (Table 2).

Table 1. Desired experimental design for this study.

	Urban	Suburban
Small	Close (n=4)	Close (n=4)
	Far (n=4)	Far (n=4)
Large	Close (n=4)	Close (n=4)
	Far (n=4)	Far (n=4)

Table 2. Categorization system for forest patches.

Patch categories	Patch characteristics
Patch size	
Small	2-5ha

Medium	>30ha
Urbanization level	
Urban	>50% impervious surface*, >15 people/ ha*, >50% urban land cover
Suburban	30-50% impervious surface*, 5-10 people/ha
Proximity to the lake	
Close	<15km from the lake shore
Far	Between 30 and 50km from the lake shore

* Based on Marzluff et al. 2001

Figure 1. Example of level of urbanization categorization for a single forest patch using a 1 kilometer buffer. (a) 2010 U.S. Census data were used to calculate an area weighted average by block, with more densely populated blocks being more shaded, (b) NLCD 2006 data were used to calculate a class value for impervious surfaces, with darker shades representing a higher percentage of impervious surfaces, (c) IILCP data were used to determine urban land cover, with urban lands shaded gray. This site was categorized as urban.

Site elimination

I used a stratified random-selection process to select sites from two levels of reserve size, two levels of urbanization, and two levels of distance from the lake to select

32 sites representing all possible combinations of these factors (Table 1). After assigning potential study sites to each of the eight categories, I had a pool of 719 sites distributed across each treatment category. I assigned a random number to each potential site and began the processes of site elimination by examining each one in numerical order. Two additional restrictions were added: 1) accessibility of the site, including such factors as ownership and parking availability, and 2) each subsequent patch had to be located greater than 1 km away from a previously selected site. Before data collection began, I scouted all sites and located the potential place where a point count could be completed near the center of each forest patch. Although understory composition varied between sites, I only included sites that had mature trees with a mostly closed canopy. Many sites were eliminated because they were no longer forested since the 2002 LANDSAT imagery. Due to accessibility issues and time constraints, some of the large sites had points that were not in the center of the patch, but were greater than 100 m from the edge of a forest patch.

This process was completed until 32 sites met the criteria of the study. During the first season of sampling, one site was dropped from the study due to its proximity to a construction site and high noise levels. I was unable to locate another suitable large site within the study area.

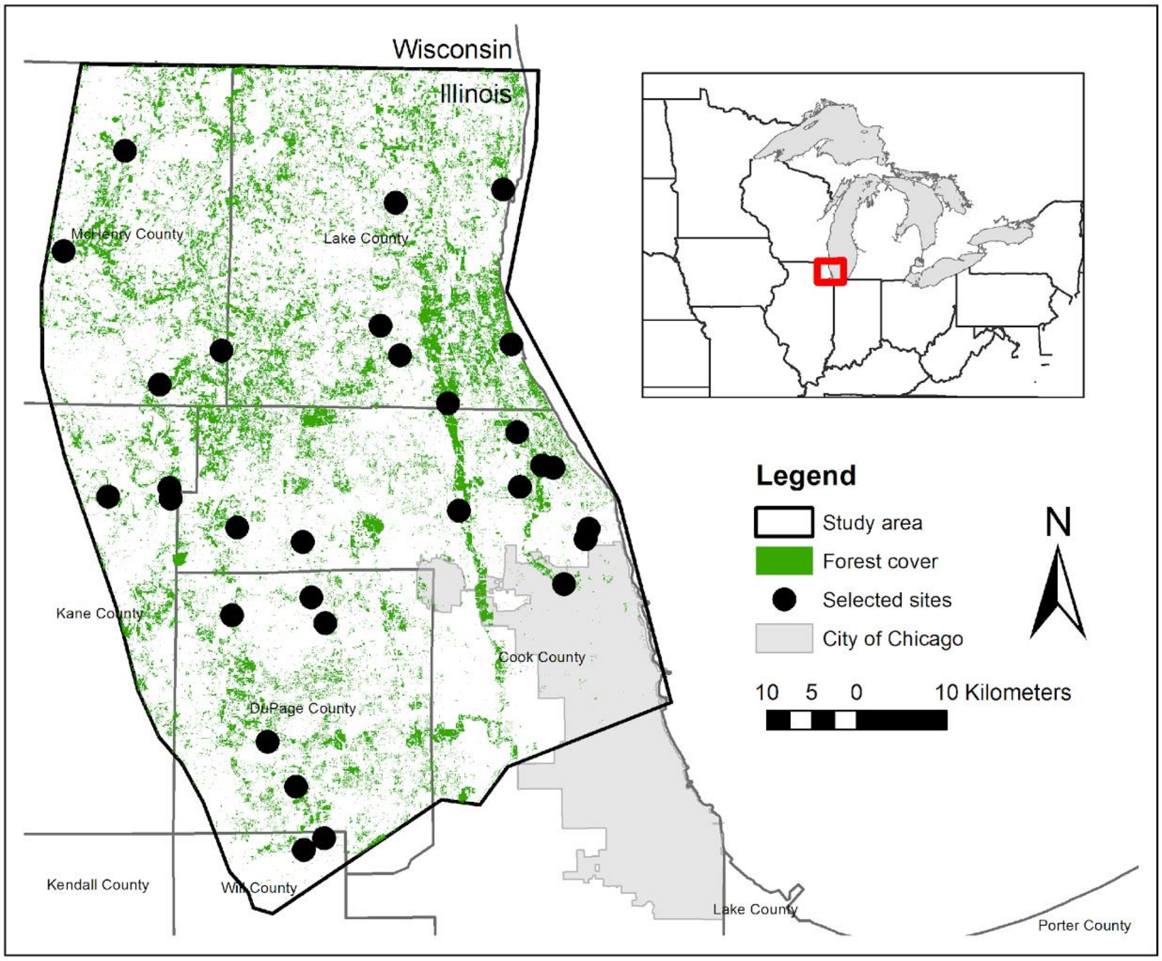

Figure 2. Final distribution of study sites.

Data collection

Data collection occurred in April and May of 2012 and May of 2013. I divided the sites into six groups that one technician could survey in one morning. A crew of three counters was able to cover all sites in two days. I randomized which blocks were covered each day with the restriction that both inland sites and coastal sites were included each day. I also randomized whether the sites within each block were surveyed from north to south or south to north for each survey day. Each two day period consisted of a single round. Each season consisted of several rounds of surveys.

The first survey set started at dawn and were completed within three hours. All surveys consisted of a 10-minute, unlimited radius circle point count. Counters were required to pass a bird identification test and also underwent distance sampling training before the start of the survey period. During the ten minute period all birds seen or heard were noted by the observer. Counters marked each detection with species, detection type (e.g. “singing”, “calling”, “observed”), minute during the count that it was first detected, and distance from the center of the count circle (within 50m, within 100m, outside 100m). Immediately after finishing each survey, the counter traveled to the next site within the survey block.

Midday point counts to determine resettling behavior

I wanted to test the hypothesis that early or late morning surveys were different across different patch types. Nocturnal migrants often exhibit “morning flight” behavior, in which they spend the first part of the morning searching for good stopover habitat (Wiedner et al. 1992). This resettling behavior may be linked to stopover habitat quality. A patch that has high abundance or diversity of migrating birds early in the morning may lose abundance and diversity as the day progresses if that patch is somehow undesirable. In an effort to quantify species turnover in sites over the course of a morning, counters returned to the same woodlots after the first round of point counts and began a second set starting at three hours after dawn using the same protocol as the first round. The second round started at the first point count location as the first round. I compared the results of these point counts to the first point counts to determine if there was a loss or gain in abundance or species richness over the course of the morning.

Vegetation surveys

At each study site a vegetation survey was completed. At the center point of each count circle, surveyors collected data on tree species, basal area and vegetation structure (Table 3). Most measurements were performed within a 10m circle using two ropes set in the four cardinal directions to record measurements (Ellenberg and Mueller-Dombois 1974).

Table 3. Vegetation variables measured at each study site.

Variable	**Method**
Tree species richness	Recorded species for all trees within a 10m radius of the point count center
Average diameter at breast height	Recorded with a diameter tape for all live trees within a 10m radius of the point count center and averaged.
Estimated basal area	Measured with a 10 BAF prism from the center of each point count
Canopy density	Measurements with a convex densiometer at the center of the point count circle and at 10m away from the center point in each of the four cardinal directions. All five measurements were averaged. .
Canopy height	Surveyors chose 3 trees that were representative of average canopy height (not limited to 10m from the point count center) and used a clinometer to measure their heights. The average of these three measurements was used.
Ground cover	Visually estimated in 10% increments
Understory cover	Visually estimated in 10% increments
Subcanopy cover	Visually estimated in 10% increments
Subcanopy height	Visually estimated in meters

Statistical analyses

Very few studies have been conducted on migration in urban areas, and the few studies that do exist have not found strong relationships between the fixed effects in this study (patch size, urbanization and distance from the lake). Because of this, I chose to design an exploratory analysis. I tested twenty different dependent variables against all independent variables (Table 4). I used Akaike's Information Criterion with a correction for sample size (AIC_c) as a way to evaluate relationships; AIC_c carries a penalty for including parameters in a model. For most analyses I calculated each dependent variable (e.g. species richness, abundance or presence of individual species) for both early and late morning surveys at the same site and survey date separately. I then kept only the maximum result between the two surveys. Each site was surveyed several times, and each round of surveys contributed new data to the analysis. I removed all detections outside of a 100m radius circle from analysis.

Using several categorization schemes, I classified bird species into guilds, including urban-adapted (Bonier et al. 2007), short-distance and long-distance migrants (O'Connor 1989), permanent residents, and area-sensitive species (Herkert et al. 1993) for a total of 15 guilds (Table 4). For all these guilds I analyzed both species richness and total abundance of all species within each guild.

Variable selection and data transformation

To reduce the number of independent variables in the analysis I conducted a principle components analysis. If two variables were correlated at a level of $\rho = 0.7$ or higher I excluded the variable that was more difficult to measure or interpret.

For each dependent variable I used JMP® Version 10 (SAS Institute Inc.) to conduct a Shapiro-Wilk normality test. If the data were not normally distributed, I tried several standard transformations, including square root, negative arcsin, $\log_{10}(y+1)$ and 1/y for both dependent and independent variables. If a transformation significantly improved the normality of the data, I proceeded to analyze the transformed and untransformed data. If there was no difference in the interpretation of the results for the transformed and untransformed data results, I reported the untransformed results.

Table 4. All independent and dependent variables used in statistical analyses. For individual species I analyzed both presence/absence and abundance data.

Dependent variables		
Bird Community and guild analysis	**Individual species**	**Independent variables**
Abundance	American Goldfinch	LOG10 patch area
Species richness	American Robin	Percent urbanized landcover
Species evenness	Baltimore Oriole	Distance from lake (categorical)
Shannon-wiener Diversity Index	Black-capped Chickadee	Tree species richness
Abundance of permanent residents	Blue-gray Gnatcatcher	Estimated basal area
Species richness of permanent residents	Brown-headed Cowbird	Average DBH
Abundance of short-distance migrants	Blue Jay	Average canopy density
Species richness of short-distance migrants	Common Yellowthroat	Shrub density
Abundance of long-distance migrants	Downy Woodpecker	Subcanopy height
Species richness of long-distance migrants	Gray Catbird	Understory cover density
Abundance of birds with high area sensitivity	House Sparrow	Connectance*
Species richness of birds with high area sensitivity	Indigo Bunting	Percent forested landcover*
Abundance of birds with moderate area sensitivity	Nashville Warbler	Canopy height**
Species richness of birds with moderate area sensitivity	Northern Cardinal	Understory cover**
Species richness of birds with low area sensitivity	Northern Waterthrush	Subcanopy height**
Abundance of birds with low area sensitivity	Red-bellied Woodpecker	
Abundance of urban adapted birds	Red-eyed Vireo	
Species richness of urban adapted birds	Red-winged Blackbird	
Reduction in species richness	Song Sparrow	
Reduction in abundance	Tennessee Warbler	

*variable only used in analysis comparing early morning and late morning surveys
**variable eliminated during principle components analysis

Statistical modeling

To determine which factors had the largest effect on the bird community at each site, I fit general linear models of all possible combinations of fixed effects and covariates to each dependent variable and used model averaging to determine the relative variable importance of each dependent variable (Table 4). Initial analysis revealed that the repeated measures term of habitat patch was not supported. Therefore, I analyzed the data without repeated measures. I used three categorical variables, patch size (large or small), surrounding urban context (urban or suburban) and distance from the lake (near or far) as fixed effects. I also calculated these same variables along a continuous scale for each habitat patch. To generate results that were easily interpretable, I chose only one measurement (either categorical or continuous) from each fixed effect to be included in the analysis. Distance from the lake was categorical, whereas patch size and urbanized land cover were both included as continuous variables. I incorporated seven measurements from vegetation surveys as quantitative covariates.

I used lm() in R version 3.1 (R Core Team 2013), to fit a general linear model to all possible combinations of all independent variables against each dependent variable, then used subsets to include only models with $\Delta AIC_c < 4$. From this new set of candidate models I calculated parameter estimates and relative variable importance of each variable (w + (j)) as the sum of its AIC_c weights across all models in which it occurred in the subset of best models. I also calculated a 95% confidence interval for each parameter estimate. If a confidence interval encompassed zero, I interpreted that to mean that the parameter was not important to the model. These analyses were performed in R using a package called MuMIn.

Early and late survey comparison

Birds tend to become less detectable over the course of the morning (Sheilds 1977, Lynch 1995), but I wanted to quantify whether some patches had significantly fewer species or number of birds over the course of the morning. For all days on which we conducted both early and late morning surveys at a site, I compared the change in species richness and abundance at each site by subtracting the results of the first survey from the second survey to get a total "loss" of species richness or abundance over the course of the morning for each site. I then performed a similar procedure as the one described above, calculating a general linear model for all possible combinations of independent variables on each dependent variable and conducting model averaging on the resulting set of models with $\Delta AIC_c<4$.

I examined how connectivity and forest cover in the surrounding landscape affected whether or not a patch retained species diversity and abundance over the course of the morning. Therefore, in addition to the same fixed and quantitative covariates as the previous procedures, I used FragStats Version 4 (University of Massachusetts, Amherst) to calculate a connectance value, as a measure of connectivity, for a 1 kilometer buffer surrounding each forest patch. FragStats calculates connectance as a percentage of the maximum possible connectance given the number of patches as a user-specified distance criterion. I set the distance criterion to 250m. I also calculated percent forested land cover in a 1km buffer around each study site. The values of connectance and percent forested land cover were added as quantitative covariates in the set of all possible general linear models, then I used the same model averaging procedure described in the previous section.

RESULTS

The average area for large patches was 190 ha (minimum 30, maximum 1,343), while the average area for small patches was 3.2 ha (minimum 1.5, maximum 5.0). The average distance from the lake for sites located close to the lake was 6.5km (minimum 0.4km, maximum 14.2km), and the sites that were located far from the lake were on average 40.1 km away (minimum 31.4km, maximum 47.9km). The average percent urbanized land cover in a 1km buffer around each site for suburban sites was 35 percent (minimum 9, maximum 81), and the average for urban sites was 65 percent (minimum 33, maximum 100). There was some overlap in the proportion of urban landcover between urban and suburban sites because other factors (impervious surfaces and population density) contributed to this categorization scheme.

I completed two spring seasons of counts, each consisting of several rounds of surveys in April and May of 2012 and in May of 2013. In 2012 counters surveyed each site between three and seven times, and in 2013 each site was surveyed between two and three times. Counts in the spring of 2013 were restricted to May because bird migration was delayed due a very cold spring. With the two seasons combined we surveyed each site between seven and ten times. Some of the sites became inaccessible as the season progressed due to construction or other access issues and we were unable to survey them as expected. Most survey mornings we were able to survey all sites twice, but weather, traffic and other factors sometimes prevented us from completing both surveys. Including morning and late morning rounds, we completed 481 surveys. We detected 9,001 total birds representing 107 species. The mean species richness for all surveys was 15 (minimum 4, maximum 29), and the mean abundance was 33 (minimum 7, maximum 79).

To account for vegetation differences between sites we conducted vegetation surveys on 29 out of 31 sites. We were unable to conduct vegetation surveys on two of sites because access was denied after our first year of sampling in 2012. Therefore, with respect to vegetation analyses, these sites were eliminated. During scouting I eliminated sites that were selected from remote sensing if they were not forested. As a result, all study sites were forested with predominately mature, deciduous trees and had a dense high canopy cover, but other vegetation factors varied greatly between sites.

Principal components analysis reduced the number of habitat variables from 14 to 10 (Table 4). Square root transformation significantly increased normality for species richness and abundance; I reported the transformed results (Table 6).

Summary of fixed effects and quantitative covariates

No single parameter showed a consistently higher relative variable importance than other parameters. Only parameters that had high relative variable importance (usually >0.75) had parameter estimates with confidence intervals that did not cross zero. There was no consistent pattern in the results for the three fixed effects of patch size, level of urbanization in a 1km buffer, and distance from the Lake Michigan shoreline. For some dependent variables the fixed effects were assigned high relative variable importance, but in others this number was low (Tables 6 and 7). A general linear model for both species richness (F=5.38, p=0.021) and individual abundance (F=9.36, p=0.002) showed a decrease from early morning counts to later morning counts.

Table 5. The twenty most abundant species. Guilds were determined from previous studies:

Code	Common name	Scientific name	Migration type*	Area sensitivity**	Urban adapted***	Avg abundance/ point count	Frequency	Maximum abundance
AMGO	American Goldfinch	*Spinus tristis*	Short-distance migrant	Low		1.38	0.73	6
AMRO	American Robin	*Turdus migratorius*	Short-distance migrant	Low	Urban adapted	2.80	0.95	8
BAOR	Baltimore Oriole	*Icterus galbula*	Long-distance migrant			0.71	0.48	4
BCCH	Black-capped Chickadee	*Poecile atricapillus*	Permanent Resident	Low	Urban adapted	1.27	0.59	10
BGGN	Blue-gray Gnatcatcher	*Polioptila caerulea*	Long-distance migrant	Moderate		0.60	0.42	3
BHCO	Brown-headed Cowbird	*Molothrus ater*	Short-distance migrant	Low		1.04	0.66	4
BLJA	Blue Jay	*Cyanocitta cristata*	Permanent Resident	Low		0.97	0.58	5
COYE	Common Yellowthroat	*Geothlypis trichas*	Long-distance migrant			0.35	0.26	3
DOWO	Downy Woodpecker	*Picoides pubescens*	Permanent Resident	Low	Urban adapted	0.59	0.50	3
GRCA	Gray Catbird	*Dumetella carolinensis*	Long-distance migrant	Low		0.53	0.40	4
HOSP	House Sparrow	*Passer domesticus*	Permanent Resident		Urban adapted	0.55	0.25	6
INBU	Indigo Bunting	*Passerina cyanea*	Long-distance migrant	Low		0.54	0.32	6
NAWA	Nashville Warbler	*Vermivora ruficapilla*	Long-distance migrant			0.40	0.23	4
NOCA	Northern Cardinal	*Cardinalis cardinalis*	Permanent Resident	Low	Urban adapted	1.91	0.88	7
NOWA	Northern Waterthrush	*Seiurus noveboracensis*	Long-distance migrant			0.38	0.23	4
RBWO	Red-bellied Woodpecker	*Melanerpes carolinus*	Permanent Resident	Low	Urban adapted	0.59	0.51	3
REVI	Red-eyed Vireo	*Vireo olivaceus*	Long-distance migrant	Moderate		0.97	0.59	4
RWBL	Red-winged Blackbird	*Agelaius phoeniceus*	Short-distance migrant	Low		1.61	0.60	12
SOSP	Song Sparrow	*Melospiza melodia*	Short-distance migrant			0.60	0.41	5
TEWA	Tennessee Warbler	*Oreothlypis peregrina*	Long-distance migrant			0.63	0.33	6

*Bonier et al. 2007, **O’Connor 1989, ***Herkert et al. 1993.

Urbanization

Urban context was an important factor for species evenness, species richness, and abundance of birds with moderate area sensitivity. Urban context was positively associated with abundance of permanent residents and negatively associated with Shannon-Wiener Diversity Index.

Percent urbanized landcover was an important factor for seven individual species. It had a positive effect on some species and a negative effect on others. Six species included in the individual species analysis were categorized as urban adapted (Table 4). Of the urban adapted species, American Robin, House Sparrow and Red-bellied Woodpecker were positively associated with urbanization, while Black-capped Chickadee, Downy Woodpecker and Northern Cardinal were unaffected by urbanization.

Percent urbanized landcover had a negative effect on change in species richness and abundance, meaning habitat patches in less urban areas tended to lose a greater number of species and individuals between the early morning and late morning surveys,

Patch size

Patch size was an important factor for nine dependent variables in bird community analyses. Dependent variables that were positively affected by patch size were species richness and abundance of urban adapted birds, species richness of long-distance migrants, species richness and abundance of short-distance migrants, species richness of birds with high area sensitivity, and species richness and abundance of birds with low area sensitivity. No dependent variables were negatively associated with patch size.

Patch size was selected as an important factor for eight individual species, having both positive and negative effects on species richness and abundance for those species. Of the twenty most abundant species, no species were categorized as having high area sensitivity. Of the two species categorized as having moderate area sensitivity, Blue-gray Gnatcatcher was unaffected by patch size and Red-eyed Vireo was positively associated with patch size (Table 7). Of the species with low area sensitivity, Northern Cardinal (presence only) and Red-bellied Woodpecker were positively associated with patch size. In contrast, American Goldfinch was negatively associated with patch size while American Robin, Brown-headed Cowbird, Black-capped Chickadee, Downy Woodpecker, Gray Catbird, Indigo Bunting and Red-winged Blackbird were not affected by patch size. Larger habitat patches tended to retain both species richness and overall abundance between the early morning and later morning surveys.

Distance from the Lake Michigan shoreline

Distance from the lake was selected as an important factor in one model of the bird community, Shannon-Wiener Diversity Index, with which it had a negative association. Distance from the lake (either continuous or categorical) was selected as an important factor in nine individual species models. It had both positive and negative effects on measures of abundance for different species.

Distance from the lake had a negative effect on loss of species richness and overall abundance between the early and late morning surveys, indicating that patches that are farther from the lake lost more species and individuals over the course of the day than those closer to the lake.

Vegetation variables

Vegetation variables from surveys conducted at the center of 29 point count sites were highly ranked in almost all models for community variables, guilds and individual species. No single vegetation variable was ranked higher than others on average across all models. Vegetation variables had both positive and negative effects, depending on the dependent variable.

Percent forested land cover had a negative effect on change in species richness and change in overall abundance, indicating that forest patches surrounded by a matrix that was highly forested tended to lose both species and individual birds over the course of the morning. Connectance was not an important variable for change in species richness, abundance or change in abundance of area sensitive species (Table 8).

Table 6. Summary of predictor variables from model averaging for all species and guild analyses. Values are relative variable importance. Values in bold had 95% confidence intervals that did not cross zero, and (+/-) indicates direction of the effect.

		Independent variables									
		Dist from the lake (cat)	Log10 patch area	Percent urbanized landcover	Shrub density	Basal area	Canopy density	DBH	Subcanopy height	Tree spp richness	Understory cover density
Dependent variables	SQRT Species richness	0.11	0.14	0.22	0.32	0.23	0.17	0.22	0.77	0.13	0.76
	SQRT Abundance	0.33	0.33	**(+)0.89**	0.61	0.41	0.47	**(-)1.00**	**(-)1.00**	**(-)1.00**	0.17
	Species evenness	0.11	0.42	0.22	0.61	0.23	0.22	0.49	**(-)0.99**	0.18	**(+)0.97**
	Shannon-wiener Diversity Index	**(-)0.99**	0.13	**(-)1.00**	0.17	0.65	**(+)0.75**	0.15	**(-)0.92**	0.37	0.66
	Species richness of urban adapted birds	0.23	**(+)0.76**	0.20	0.14	0.16	0.49	**(+)1.00**	0.22	0.54	**(+)1.00**
	Abundance of urban adapted birds	0.32	**(+)1.00**	0.15	0.22	0.28	**(+)0.79**	**(+)1.00**	0.23	0.27	**(+)1.00**
	Species richness of long-distance migrants	0.22	**(+)0.91**	0.59	0.48	**(-)0.84**	**(+)0.87**	**(-)0.86**	**(-)1.00**	**(-)0.86**	0.58
	Abundance of long-distance migrants	0.71	0.45	0.20	**(+)0.86**	0.44	0.61	**(-)1.00**	**(-)1.00**	0.78	0.29
	Species richness of short-distance migrants	0.64	**(+)0.83**	0.43	0.15	0.39	0.13	0.47	0.14	0.56	0.39
	Abundance of short-distance migrants	0.52	**(+)0.99**	0.52	0.15	0.39	0.12	0.34	0.12	0.45	0.19
	Species richness of permanent residents	0.18	**(-)1.00**	0.18	**(+)1.00**	0.60	**(-)1.00**	0.50	0.29	0.49	0.76
	Abundance of permanent residents	0.17	0.74	**(+)0.99**	0.69	**(+)0.83**	**(-)1.00**	0.37	0.37	0.36	0.31
	Species richness of birds with high area sensitivity	0.17	**(+)0.93**	0.16	0.18	0.24	0.38	0.22	**(-)0.94**	0.59	**(+)1.00**
	Abundance of birds with high area sensitivity	0.29	0.63	0.15	0.21	0.13	0.19	0.30	0.31	0.80	**(+)1.00**
	Species richness of birds with moderate area sensitivity	0.17	0.29	0.13	0.63	0.15	0.24	0.62	**(-)0.99**	0.17	**(+)0.90**
	Abundance of birds with moderate area sensitivity	0.14	0.27	0.14	0.68	0.17	0.22	0.62	**(-)0.99**	0.15	**(+)0.88**
	Species richness of birds with low area sensitivity	0.21	**(+)1.00**	0.40	0.17	0.31	**(+)1.00**	**(+)0.89**	0.77	0.30	**(+)1.00**
	Abundance of birds with low area sensitivity	0.36	**(+)1.00**	0.51	0.73	**(-)0.85**	**(+)1.00**	0.42	**(-)0.92**	**(-)0.87**	**(+)0.85**

Table 7. Summary of predictor variables from model averaging for the top twenty most abundant species. Values are relative variable importance. Values in bold had 95% confidence intervals that did not cross zero, and (+/-) indicates direction of the effect.

		Independent variables									
		Dist from the lake (cat)	Log10 patch area	Percent urbanized landcover	Basal area	Canopy density	DBH	Shrub density	Subcanopy height	Tree spp richness	Understory cover density
Dependent variables	AMGO Abundance	0.30	**(-)1.00**	**(-)1.00**	0.17	**(-)1.00**	0.73	0.19	**(+)0.80**	**(+)0.98**	0.26
	AMGO Presence	0.13	0.70	0.42	0.66	**(-)0.98**	0.22	0.13	**(+)0.94**	**(+)0.96**	0.12
	AMRO Abundance	**(-)1.00**	0.18	**(+)1.00**	0.15	0.31	**(+)1.00**	**(-)1.00**	**(+)1.00**	0.31	0.21
	AMRO Presence	0.14	0.20	0.50	0.24	0.48	0.13	0.30	0.62	0.27	0.13
	BAOR Abundance	0.48	0.68	0.19	0.26	0.17	0.12	0.15	0.15	0.23	**(+)1.00**
	BAOR Presence	0.40	0.64	0.12	0.36	0.67	0.17	0.14	0.54	0.24	**(+)0.99**
	BCCH Abundance	**(+)0.99**	0.37	0.67	0.19	0.62	**(-)0.93**	0.14	0.37	0.67	0.45
	BCCH Presence	**(+)0.91**	0.25	0.40	0.18	**(-)0.91**	0.14	0.32	0.74	0.14	0.42
	BGGN Abundance	0.37	0.11	0.13	0.17	0.62	0.26	0.11	0.18	0.59	**(+)0.99**
	BGGN Presence	0.75	0.31	0.18	0.11	0.18	0.16	0.11	0.35	0.57	0.57
	BHCO Abundance	**(-)0.98**	0.14	0.17	**(-)0.96**	0.26	0.11	0.13	0.21	0.19	0.12
	BHCO Presence	0.37	0.32	0.38	0.47	**(-)0.96**	0.23	0.14	0.26	0.62	0.49
	BLJA Abundance	0.16	0.19	**(-)1.00**	0.25	0.18	**(+)1.00**	0.55	0.16	**(+)1.00**	0.25
	BLJA Presence	0.15	**(+)0.85**	0.65	0.14	0.59	0.25	0.21	0.64	0.34	0.39
	COYE Abundance	**(+)1.00**	0.56	0.31	0.26	0.26	0.80	0.70	0.28	0.20	0.13
	COYE Presence	**(+)1.00**	**(-)0.90**	0.34	0.26	0.57	0.37	0.31	0.19	0.15	0.16
	DOWO Abundance	0.14	0.24	0.16	0.48	0.32	0.46	0.14	**(-)1.00**	0.20	0.30
	DOWO Presence	0.18	0.11	0.15	0.25	0.28	0.35	0.12	**(-)1.00**	0.15	0.18
	GRCA Abundance	0.15	0.22	0.21	0.39	0.14	0.24	**(+)1.00**	0.56	0.14	**(+)1.00**

	Independent variables									
	Dist from the lake (cat)	Log10 patch area	Percent urbanized landcover	Basal area	Canopy density	DBH	Shrub density	Subcanopy height	Tree spp richness	Understory cover density
GRCA Presence	0.11	0.12	0.28	0.33	0.12	0.11	**(+)0.95**	0.34	0.11	**(+)1.00**
HOSP Abundance	0.19	0.15	**(+)1.00**	0.66	0.28	**(-)1.00**	**(+)1.00**	**(-)1.00**	**(-)1.00**	0.19
HOSP Presence	0.18	0.21	**(+)1.00**	0.75	0.30	**(-)1.00**	**(+)0.80**	**(-)1.00**	**(-)1.00**	0.17
INBU Abundance	0.17	0.27	0.42	**(+)0.78**	**(-)0.94**	0.16	**(-)1.00**	0.24	**(+)1.00**	**(+)1.00**
INBU Presence	0.16	0.26	0.28	**(+)0.94**	**(-)1.00**	0.18	**(-)1.00**	0.25	**(+)1.00**	**(+)1.00**
NAWA Abundance	0.38	0.66	0.48	0.54	0.25	**(+)1.00**	0.13	0.27	0.39	0.17
NAWA Presence	0.21	**(+)0.81**	0.50	0.44	0.30	**(+)0.98**	0.31	0.22	0.42	0.17
NOCA Abundance	**(+)0.76**	0.23	0.53	0.24	0.61	**(-)1.00**	0.39	**(-)0.88**	0.22	0.30
NOCA Presence	0.32	**(+)0.97**	0.18	0.15	0.23	**(-)1.00**	0.37	**(-)0.97**	0.64	0.27
NOWA Presence	**(-)0.91**	0.15	**(-)0.88**	0.36	0.27	0.10	0.14	0.34	0.13	0.43
NOWA Abundance	0.52	0.12	0.75	0.18	0.21	0.27	0.12	0.15	0.13	0.81
RBWO Abundance	0.19	**(+)1.00**	**(+)1.00**	0.45	**(+)1.00**	0.35	0.21	**(-)1.00**	**(-)1.00**	**(+)0.96**
RBWO Presence	0.16	**(+)1.00**	**(+)1.00**	**(-)0.84**	**(+)1.00**	0.56	0.19	**(-)1.00**	**(-)1.00**	**(+)0.92**
REVI Abundance	**(+)1.00**	**(+)1.00**	0.74	0.63	**(+)1.00**	**(+)0.96**	**(-)0.95**	0.26	0.22	0.22
REVI Presence	**(+)0.96**	**(+)1.00**	0.49	0.69	**(+)1.00**	0.64	0.48	0.21	0.33	0.55
RWBL Abundance	**(+)1.00**	0.23	**(+)1.00**	**(+)1.00**	**(-)0.96**	**(-)1.00**	**(+)1.00**	0.56	**(-)1.00**	0.27
RWBL Presence	**(+)1.00**	0.43	**(+)1.00**	**(+)1.00**	0.71	**(-)0.97**	**(+)1.00**	**(-)0.77**	**(-)1.00**	0.23
SOSP Abundance	0.30	**(-)1.00**	0.21	**(+)1.00**	**(-)1.00**	0.37	0.50	**(+)1.00**	**(+)1.00**	0.20
SOSP Presence	**(+)1.00**	**(-)1.00**	0.18	**(+)1.00**	**(-)1.00**	0.33	0.20	**(+)1.00**	**(+)0.94**	0.24
TEWA Abundance	0.75	0.23	0.20	0.21	0.10	0.16	0.17	0.11	0.12	0.12
TEWA Presence	0.12	0.14	0.23	0.75	0.29	0.17	0.10	0.10	0.14	0.21

Table 8. Results of the change in species richness and abundance between early and late morning surveys. Values are relative variable importance. Values in bold had 95% confidence intervals that did not cross zero, and (+/-) indicates direction of the effect.

		Independent variables											
		Dist from the lake (cat)	Log10 patch area	Percent urbanized landcover	Percent forested landcover	Connectance	Basal area	Canopy density	DBH	Shrub density	Subcanopy height	Tree spp richness	Understory cover density
Dependent variables	Change in abundance	**(-)1.00**	**(-)1.00**	**(-)1.00**	**(-)1.00**	0.35	0.13	0.29	**(+)1.00**	0.13	**(+)0.97**	**(-)1.00**	0.16
	Change in abundance of area sensitive birds	0.28	0.13	0.18	0.11	0.15	0.72	0.69	0.49	0.11	0.16	0.72	0.09
	Change in species richness	**(+)1.00**	0.14	**(-)1.00**	0.74	**(-)0.69**	0.56	0.55	**(+)1.00**	0.23	**(-)0.98**	**(-)1.00**	0.41

DISCUSSION

One of the objectives of this study was to develop a set of hypotheses for future research based on the patterns identified in this study. Throughout this discussion I will point to hypotheses that I recommend for future testing on bird abundance and diversity in the urban environment.

Urbanization

Based on published studies, I expected urbanization to have a negative impact on species diversity. For instance, several studies during the breeding season have found that urbanization has a negative effect on bird species diversity (Friesen et al. 1995, Blair 1996, van Rensburg et al. 2009), or that intermediate levels of disturbance produce a peak in species richness (Lepczyk et al. 2008). These results indicate that the level of urbanization in the surrounding matrix does not have an effect on most metrics of bird communities during the migration period. Urbanization was not assigned a high relative variable importance in either species-specific analyses or in guild analyses. Urbanization did have a positive effect on overall abundance of birds. This follows past studies, which found that urbanization can actually increase overall abundance of bird species (Lancaster and Reese 1979). Supporting the results of past studies, Shannon-Wiener Diversity Index did decrease with urbanization (Clergeau et al. 1998, Marzluff 2001). Certain bird species benefit from manmade features in urban habitats, such as bird feeders and nesting spots on buildings (Marzluff 2001), increasing the abundance of a few species that can exploit these aspects of the human environment. This causes an overall increase in abundance of birds while simultaneously decreasing evenness in association with urbanization. The results of this study support this theory, although not all birds that were categorized as urban-adapted responded positively to increasing levels of urbanization.

Recently, telemetry studies have found that urbanization has little effect on migratory behavior (Craves 2009, Matthews and Rodewald 2010b, Seewagen et al. 2010, 2011b). A study using RADAR data found that areas with high concentrations of migrants in the Great Lakes region also had high levels of urban land cover, but the authors could not determine whether this was due to the high value of urban lands as stopover areas or because urban areas fall within migratory pathways (Bonter et al. 2009). My results indicate that the effects of urbanization are unimportant to any of the migrating guilds, but urbanization does have a large impact on many individual bird species; some species select patches embedded in an urban landscape, while others avoid them.

Urbanization did have an effect on change in species richness and abundance over the course of a morning, with sites embedded in a more urbanized matrix retaining bird species diversity and abundance between the early morning and late morning surveys. This is a hypothesis deserves further investigation, probably involving the tracking of individual birds at similar forest patches embedded in landscapes with varying levels of urbanization.

Abundance of permanent residents was positively associated with urbanization. Many permanent residents in cities, such as Northern Cardinals and Black-capped Chickadees, are considered to be urban-adapted (Table 5), so there was some overlap in these two guilds. I expected urban-adapted species to be positively associated with increasing urbanization in the surrounding landscape, but they were not. This disagrees with past literature, which has found that increasing levels of urbanization in the surrounding landscape increases the abundance of urban-adapted bird species (Blair 1996, Marzluff 1997, 2001, Donnelly and Marzluff 2004, van Rensburg et al. 2009). Blair (1996) found that House sparrow, an urban adapted species found in many of my surveys, is an "urban exploiter", and Donnelly and Marzluff (2004) also categorized House sparrow as a synanthropic species, along with American Crow. In individual species analysis, House Sparrows had a positive association with percent urbanized landcover had a positive association, agreeing with Blair's (1996) study, but many urban adapted species, including American Crow, had no association with urbanization (Table 7). Most studies examining the effect of urbanization on birds have been conducted during breeding season, but birds that specialize on urban areas tend to be non-migratory species (Partecke & Gwinner, 2007).

I may not have found similar results to past studies on the effect of urbanization on the abundance of urban-adapted birds. First, I concentrated on forest patches, whereas most past studies have included very different environments, such as open parks and golf courses. Forest patches, even small ones, may not be ideal habitat for many bird species that exploit the urban environment. Second, the greater Chicago region contains little area that is unaffected by urbanization. Despite this, my sites covered a wide gradient of urbanized land cover from 9% to 99% in a 1 kilometer buffer surrounding each forest patch. The surrounding land cover at sites with low levels of urbanization varied greatly from rural to open space to grassland. Unfortunately, this comparison is not possible in the Chicago area, and not possible in most urban areas.

Patch size

My results indicate that patch size had no effect on species richness, bird abundance or Shannon-Wiener Diversity index during the migration period at the point count level. Past studies during the breeding season have found mixed results for the effect of patch size in an urban environment on measures of bird abundance and diversity. Donnelly and Marzluff (2004) found that increasing patch size in urban areas increases species richness, but had no effect on bird abundance. A study conducted in southern California found that avian species diversity peaked in fragmented habitat located within an urban landscape (Crooks 2004) and suggested an interaction effect between urbanization and patch size.

Many past studies have examined the relationship between Neoptropical migrant species diversity and abundance during the breeding season and found that decreasing patch size has a negative effect on species diversity (Ambuel and Temple 1983, Wilcove 1985, Remsen Jr and Robinson 1990, Donnelly and Marzluff 2004), as well as a negative effect on breeding density of Neotropical migrants (Askins et al. 1990). Bonter et al. (2009) using RADAR data found that populations of migrating birds were highest in landscapes with a high percentage of forested habitat, but that the patch sizes in those landscapes were not significantly different than forest patch sizes in areas with lower concentrations of migrating birds. They concluded that further research is warranted to determine which patches within a forested landscape are most used.

Forest patch size was not selected as an important factor for metrics involving species richness or abundance of the migrating bird community at the point count level. This could be interpreted to mean that patch size is not important to the larger bird community during the migration period. However, I sampled an equivalent area (one point count) at all forest patches. For example, my surveys had an average of 2.8 American Robins per survey circle (Table 5). The area of a 100-m survey circle is 3.14 hectares. Hence, on average a forest patch in the Chicago region during the migration period had a density of 0.9 American Robins per hectare. Many of the forest patches in this study were about the size of a point count circle, while some of the larger patches were over 1000 hectares. A small patch may only support about three American Robins, while larger patches could support many more. I cannot make similar assumptions about species richness; if I had sampled a larger area within each patch it is likely that I would have detected more species, but it would not be directly proportional to the area sampled.

Species richness of birds with high area sensitivity and species richness and abundance of birds with low area sensitivity were positively associated with increasing patch size on a point count basis. Species categorized as having moderate area sensitivity had no association with changes in patch size on a point count basis. These results suggest that birds with area sensitivity on the breeding grounds may be selecting larger patches during migration. A study conducted in southern Wisconsin, near my study area, found that larger patches had higher species diversity during the breeding season mostly due to the absence of long-distance migrants in smaller patches (Ambuel and Temple 1983). The authors attributed this effect not to an increased diversity of habitat within larger patches, but to increased competition from forest edge and farmland birds in smaller patches. In my study, abundance of species with high area sensitivity was not higher in point counts within patches of different size. The mixed results of my findings on the effect of patch size on migrating birds categorized as area sensitive warrants further study. Because birds with high area sensitivity are of conservation concern, it would be helpful to pursue the hypothesis that birds that exhibit high area sensitivity on the breeding grounds select larger patches during the breeding season.

Distance from the lake

There is strong evidence from past studies that nocturnal migrating birds use coastlines to navigate and compensate for wind drift (Akesson 2011). Bonter et al. (2009) found that large concentrations of migrating birds were associated with bodies of water in the Great Lakes region (2009). Distance from the lake was selected as an important factor in nine of twenty individual species. Some species were more abundant closer to the shoreline, but there were no overall patterns in species diversity or abundance related to distance from the coast. The only dependent variable in multiple species analysis associated with distance from the lake was Shannon-Wiener Diversity Index, which had a negative association with distance from the lake. This indicates that the bird community had a higher degree of evenness in sites that were closer to the lake.

My study examined distance from the lake on a large scale (from zero to fifty kilometers). It is possible that the effect of the coastline may operate on a much smaller scale (e.g., a few kilometers or less). Little forested habitat is available near the Lake Michigan shoreline but further study could find effects at a smaller scale.

Changes in species richness and abundance between early and late morning surveys

We tested the hypothesis that early or late morning surveys were different across different patch types. All three fixed effects were important to change in species richness and abundance in a patch over the course of a single morning, and all three effects had a negative association with the dependent variables. Since the metrics used were “loss” of species, this indicates that larger patches in more urbanized areas that were farther from the lake tended to retain bird species and individuals as the day progressed.

Vegetation characteristics

In addition to fixed effects, vegetation structure within a patch likely affected the migratory bird community. Past studies have shown that forest structure can have large effects on bird community composition (Emlen 1974, Gavareski 1976, Cody 1981, Beissinger and Osborne 1982, Mills et al. 1989, King and DeGraaf 2000, Cleeton 2012). In this study subcanopy height was negatively associated with abundance, species evenness and Shannon-Wiener Diversity Index. This could indicate that a low subcanopy is preferable to forested bird species in urban areas. Other vegetation variables had mixed effects, some with positive or negative effects depending on the species.

Understory cover density was an important factor in nine models of bird community diversity and abundance. In all models it had a positive effect. We did not record understory species on vegetation surveys, but it may be related to invasive shrubs, such as buckthorn. Understory composition in the Chicago area is strongly related to invasive shrubs, an issue of major concern in the region (Chicago Wilderness 1999). European Buckthorn (*Rhamnus cathartica*), an invasive shrub, was present at all of my sites at varying levels. At some sites it created a nearly closed subcanopy. A recent study on breeding birds in the Chicago region found that invasive species, and buckthorn in particular, have a negative impact on bird species richness (Cleeton 2012). My study supports the idea that a thick understory is beneficial to bird species in urban environments. Although there are ongoing efforts to limit the spread of buckthorn and other invasive shrubs in the region, it may be important to consider replacing invasive shrubs with native ones to provide proper foraging opportunities for the bird community.

Average diameter at breast height was the most commonly selected vegetation variable for species-specific analyses (Table 10), although it had different effects for different species and models. Past studies have found that an increase in DBH due to a higher proportion of mature trees can increase bird species richness (Berg 1997), or that species richness peaks in forests with intermediate average DBH (King and DeGraaf 2000). Many Neotropical migrant birds specialize on mature forests, but birds that have been identified as mature-forest dependent species in past studies had different reactions to average DBH in my study. Red-eyed vireos were positively associated with high average DBH, while Northern Waterthrushes had no association with average DBH (Table 7). Both are considered mature forest birds (Therres 1992). This indicates that some mature forest species may select habitat patches with a higher proportion of mature trees on migration, while others may not.

I explored the use of connectance and percent forested landcover as covariates as part of the habitat analysis even though they were measured with remote sensing. While evaluating patches for inclusion in this study, I found many candidate patches that were categorized as contiguous forest patches but upon visiting them were actually boulevards of trees lining neighborhood streets. I eliminated these candidate sites from inclusion because I decided that ecologically they did not function as a “forest” in the same way that a forest patch with undergrowth and subcanopy layers. I had expected a high proportion of forested landcover around the patch and a high connectance would cause birds to “leak” from a forest patch into the surrounding landscape. Connectance was negatively associated with loss of abundance, and percent forested landcover was negatively associated with a loss of species richness. Forest patches embedded in a landscape with high connectivity tended to retain species, and forest patches embedded in a landscape with a higher percentage of forest cover tended to retain abundance. This may indicate that the forest cover and connectivity of the surrounding landscape has a positive effect on the bird community in a forest patch. This hypothesis merits further research with a study that controls for patch size in the surrounding matrix.

Conclusions

The effects of urbanization, forest patch size, and distance from Lake Michigan were not important in most bird community-level models, but many were significant factors in individual species models. This indicates that their effects contribute to their distribution within this landscape, but there are species-specific responses to these factors. For example, Nashville Warbler responded positively to increasing patch size, but another long-distance migrant, Baltimore Oriole, had no association with patch size. The differential response of each species to these variables indicates that there is no simple combination of habitat or landscape variables that will benefit all species. Urbanization, patch size and distance from the lake were positively and negatively associated with some species and had different associations even for those species that occur within the same guild. My results suggest maintaining a diverse array of habitat patches scattered throughout the region. Habitat needs for species of conservation concern may also serve as a focal point towards the conservation of certain patch types.

Many past studies conducted during the breeding or wintering season have found large effects due to patch size and urbanization. The effects of these factors on avian species richness and abundance may be dampened during the migration period for several reasons. Passerines migrate at night, and when the sun rises they search for stopover habitat (Moore and Aborn 2000). If at sunrise a migrant lands in the Chicago metropolitan area, all stopover habitat will likely be in a highly urbanized landscape. There is evidence that passerine migrants tend to be less "choosy" during migration, picking stopover habitats that may be suboptimal compared with the breeding or wintering periods and tending towards more generalist behavior (Chernetsov 2006). Migrating birds passing through regions with poor stopover habitat, especially where habitat patches are isolated, may condense in poor habitat (Martin 1980, Shochat et al. 2002). This could ultimately have negative impacts on a bird's ability to survive migration.

Unfortunately, due to already high levels of development in Chicago, land managers may not select where to set aside forested habitat patches, and most large habitat patches have already become fragmented. My study and others have found that improving vegetation characteristics within urban woodlots can have large impacts on the bird community (Askins et al. 1990, Tilghman 1987, Mills et al. 1989). Managing vegetation characteristics within existing forest patches, such as planting native shrubs to increase foraging opportunities for some birds, could possibly make urban forest patches more hospitable to migrating birds. The hypothesis that changing vegetation within a patch, for example, manipulating understory cover density, can produce changes in the migrating bird community, merits further research. Land managers would benefit if we understood how they can change the vegetation characteristics of a patch to benefit certain species or guilds of birds during the migration period.

The results of this study do not indicate that certain types of urban forest patches are “better” for the entire migrant community, or that urbanization is necessarily negative for all migrating bird species. However, presence or abundance of certain bird species during migration may not be indicative of their ability to gain energy from foraging in a forest patch. Distance from the coastline and level of urbanization had a small impact on avian species richness or abundance during migration, but we still do not fully understand the energetics of urban forest patches for migrating birds. The stress of feeding in a poor quality habitat patch may decrease a bird’s ability to complete migration, a measurement that is difficult to quantify with any prevailing techniques for smaller-bodied bird species. Geolocators are one exception, but the individuals need to be recaptured; this is very difficult for migratory species. Future research on bird migration in urban areas should focus on food consumption, food availability, survival, and a greater focus on the quality of stopover habitats.

BIBLIOGRAPHY

Åkesson, S. 2011. Coastal migration and wind drift compensation passerine migrants. Oikos 24:87–94.

Alberti, M. 2005. The effects of urban patterns on ecosystem function. International Regional Science Review 28:168–192.

Ambuel, B., and S. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057–1068.

Askins, R.A., Lynch, J.F. and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. Pages 1-53 in D.M. Power, editor. Current Ornithology volume 7. Plenum Press, New York, United States.

Beissinger, S., and D. Osborne. 1982. Effects of urbanization on avian community organization. Condor 84:75–83.

Berg, Å. 1997. Diversity and abundance of birds in relation to forest fragmentation, habitat quality and heterogeneity. Bird Study 44:355–366.

Blair, R. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506–519.

Blair, R. 2004. The effects of urban sprawl on birds at multiple levels of biological organization. Ecology and Society 9:2.

Blake, J. 1992. Temporal variation in point counts of birds in a lowland wet forest in Costa Rica. Condor 94:265–275.

Bonier, F., P. R. Martin, and J. C. Wingfield. 2007. Urban birds have broader environmental tolerance. Biology Letters 3:670–3.

Bonter, D. N., S. A. Gauthreaux, and T. M. Donovan. 2009. Characteristics of important stopover locations for migrating birds: remote sensing with radar in the Great Lakes basin. Conservation Biology 23:440–8.

Bowles, M., and J. McBridge. 2002. Pre-European Settlement Vegetation of Cook County, Illinois. Morton Arboretum, Lisle, Illinois, USA.

Brawn, J. D., and D. F. Stotz. 2001. The importance of the Chicago region and the “Chicago Wilderness” initiative for avian conservation. Pages 509–522 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic, Massachusetts, United States.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edition. Springer-Verlag New York, Inc., New York, New York.

Chernetsov, N. 2006. Habitat selection by nocturnal passerine migrants en route: mechanisms and results. Journal of Ornithology 147:185–191.

Chicago Wilderness. 1999. Executive Summary Chicago Wilderness and Its Biodiversity Recovery Plan. Chicago Wilderness, Chicago, Illinois, USA.

Cleeton, S. H. 2012. Songbird community ecology and habitat selection in the Chicago area. Thesis.

Cody, M. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and productivity. BioScience 31:107–113.

Clergeau, P., Savard, J.-P. L., Mennechez, G., and Falardeau, G. 1998. Bird abundance and diversity along an urban-rural gradient: a comparative study between two cities on different continents. The Condor, 100: 413–425.

Craves, J. 2009. A fifteen-year study of fall stopover patterns of Catharus thrushes at an inland, urban site. The Wilson Journal of Ornithology 121:112–118.

Crooks, K. 2004. Avian assemblages along a gradient of urbanization in a highly fragmented landscape. Biological Conservation 115:451–462.

Crooks, K., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Danz, N. P., G. J. Niemi, R. R. Regal, T. Hollenhorst, L. B. Johnson, J. M. Hanowski, R. P. Axler, J. J. H. Ciborowski, T. Hrabik, V. J. Brady, J. R. Kelly, J. A. Morrice, J. C. Brazner, R. W. Howe, C. A. Johnston, and G. E. Host. 2007. Integrated measures of anthropogenic stress in the U.S. Great lakes basin. Environmental Management 39:631–47.

Danz, N. P., R. R. Regal, G. J. Niemi, V. J. Brady, T. Hollenhorst, L. B. Johnson, G. E. Host, J. M. Hanowski, C. A. Johnston, T. Brown, J. Kingston, and J. R. Kelly. 2005. Environmentally stratified sampling design for the development of Great Lakes environmental indicators. Environmental Monitoring and Assessment 102:41–65.

Diehl, R., R. Larkin, and J. Black. 2003. Radar observations of bird migration over the Great Lakes. The Auk 120:278–290.

Donnelly, R., and J. M. Marzluff. 2004. Importance of reserve size and landscape context to urban bird conservation. Conservation Biology 18:733–745.

Ellenberg, D., and D. Mueller-Dombois. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, New York.

Emlen, J. 1974. An urban bird community in Tucson, Arizona: derivation, structure, regulation. Condor 76:184–197.

Ewert, D., and M. Hamas. 1995. Ecology of migratory landbirds during migration in the Midwest. Pages 200–208 Management of Midwestern Landscapes for the Conservation of Neotropical Migratory Birds. U.S. Department of Agriculture, Forest Service, St. Paul, Minnesota, USA.

Ewert, D. N., M. J. Hamas, R. J. Smith, M. E. Dallman, and S. W. Jorgensen. 2011. Distribution of migratory landbirds along the northern Lake Huron shoreline. The Wilson Journal of Ornithology 123:536–547.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, P. P. Marra, C. L. Merkord, E. Nol, S. I. Rothstein, T. W. Sherry, T. S. Sillett, F. R. Thompson, and N. Warnock. 2010. Conserving migratory land birds in the new world: do we know enough? Ecological Applications 20:398–418.

Faeth, S. H., P. S. Warren, E. Shochat, and W. A. Marussich. 2005. Trophic dynamics in urban communities. BioScience 55:399–407.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207–231.

Fotso, J. C., A. C. Ezeh, J. N. Madise, and J. Ciera. 2011. Population Distribution, Urbanization, Internal Migration and Development: an International Perspective. United Nations Department of Economic and Social Affairs Population Division.

Friesen, L., P. Eagles, and R. Mackay. 1995. Effects of residential development on forest-dwelling Neotropical migrant songbirds. Conservation Biology 9:1408–1414.

Fuller, K., H. Shear, and J. Wittig (Eds.). 2012. The Great Lakes: An Environmental Atlas. U.S. Environmental Protection Agency and Environment Canada, 3rd edition. U.S. EPA Great Lakes National Program Office and Government of Canada, Toronto, Ontario, Canada and Chicago, Illinois, USA.

Gavareski, C. 1976. Relation of park size and vegetation to urban bird populations in Seattle, Washington. Condor 78:375–382.

Herkert, J. R., R. E. Szafoni, V. M. Kleen, and J. E. Schwegman. 1993. Habitat establishment, enhancement and management for forest and grassland birds in Illinois. Division of Natural Heritage, Illinois Department of Conservation, Springfield, Illinois, USA.

King, D. I., and R. M. DeGraaf. 2000. Bird species diversity and nesting success in mature, clearcut and shelterwood forest in northern New Hampshire, USA. Forest Ecology and Management 129:227–235.

Lancaster, R.K. and Rees, W.E. 1979. Bird communities and the structure of urban habitats. Canadian Journal of Zoology 57: 2358-2368.

Lepczyk, C. A., C. H. Flather, V. C. Radeloff, A. M. Pidgeon, R. B. Hammer, and J. Liu. 2008. Human impacts on regional avian diversity and abundance. Conservation Biology 22:405–16.

Lepczyk, C. A., R. B. Hammer, S. I. Stewart, and V. C. Radeloff. 2007. Spatiotemporal dynamics of housing growth hotspots in the North Central U.S. from 1940 to 2000. Landscape Ecology 22:939–952.

Lynch, J. 1995. Effects of point count duration, time-of-day, and aural stimuli on detectability of migratory and resident bird species in Quintana Roo, Mexico. USDA Forest Service.

Martin, T. 1980. Diversity and abundance of spring migratory birds using habitat islands on the Great Plains. Condor 82:530–439.

Marzluff, J. M. 1997. Effects of urbanization and recreation on songbirds. Pages 89–102 in W. M. Block and D. M. Finch, editors. Songbird Ecology in Southwestern Ponderosa Pine Forests: A Literature Review. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19–48 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizingworld. Kluwer Academic, New York City, NY.

Marzluff, J. M., R. Bowman, and R. Donnelly. 2001. A historical perspective on urban bird research: trends, terms and approaches. Pages 1–17 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic Publisheres, Boston.

Matthews, S. N. 2008. Stopover habitat utilization by migratory landbirds within urbanizing landscapes of central Ohio. The Ohio State University, Colombus, Ohio, USA.

Matthews, S. N., and P. G. Rodewald. 2010. Movement behaviour of a forest songbird in an urbanized landscape: the relative importance of patch-level effects and body condition during migratory stopover. Landscape Ecology 25:955–965.

McDonnell, M. J., and S. T. A. Pickett. 1990. Ecosystem structure and function along urban-rural gradients : an unexploited opportunity for ecology. Ecology 71:1232–1237.

Medley, K., M. J. McDonnell, and S. T. A. Pickett. 1995. Forest-landscape structure along an urban-to-rural gradient. Professional Geographer 47:159–169.

Mehlman, D. W., S. E. Mabey, D. N. Ewert, C. Duncan, B. Abel, D. Cimprich, R. D. Sutter, and M. Woodrey. 2005. Conserving stopover sites for forest-dwelling migratory landbirds. The Auk 122:1281–1290.

Mills, G. S., J. B. Dunning, and J. M. Bates. 1989. Effects of urbanization on breeding bird community structure in Southwestern desert habitats. The Condor 91:416.

Moore, F. R. 2000. Preface. Pages 1–3 in F. R. Moore, editor. Stopover Ecology of Nearctic-neotropical Landbird Migrants: Habitat Relations and Conservation Implications. Cooper Ornithological Society.

Moore, F. R., and D. A. Aborn. 2000. Mechanisms of en route habitat selection: how do migrants make habitat decisions during stopover? Studies in Avian Biology 20:34–42.

Niemi, G. J., J. R. Kelly, and N. P. Danz. 2007. Environmental indicators for the coastal region of the North American Great Lakes : introduction and prospectus. Journal of Great Lakes Research 33:1–12.

Nowak, D. J., R. E. Hoehn, A. R. Bodine, D. E. Crane, J. F. Dwyer, G. Watson, G. Deresinski, A. Edwards, G. Fischer, E. Injerd, L. Maenpaa, J. Van Someren, P. Watson, and E. Wisniewski. 2013. Urban Trees and Forests of the Chicago Region. United States Department of Agriculture Forest Service, Newton Square, Pennsylvania, USA.

O’Connor, R. J. 1989. Population variation in relation to migrancy status in some North American birds. Pages 64–74 in J. M. Hagan and D. W. Johnston, editors. Ecology and Conservation of Neotropical Migrant Landbirds. Smithsonian Institution Press, Washington, D.C.

Páez, A., and D. Scott. 2004. Spatial statistics for urban analysis: a review of techniques with examples. GeoJournal 61:53–67.

Partecke, J., and E. Gwinner. 2007. Increased sedentariness in European Blackbirds following urbanization: a consequence of local adaptation? Ecology 88:882–90.

Pidgeon, A. M., V. C. Radeloff, C. H. Flather, C. A. Lepczyk, M. K. Clayton, T. J. Hawbaker, and R. B. Hammer. 2007. Associations of forest bird species richness with housing and landscape patterns across the USA. Ecological Applications 17:1989–2010.

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org/.

Ribic CA, Guzy MJ, Sample DW (2009) Grassland bird use of remnant prairie and

Remsen Jr, J., and S. K. Robinson. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Studies in Avian Biology 13:144–160.

Van Rensburg, B. J., D. S. Peacock, and M. P. Robertson. 2009. Biotic homogenization and alien bird species along an urban gradient in South Africa. Landscape and Urban Planning 92:233–241.

Rodewald, A. D., and D. P. Shustack. 2008. Urban flight: understanding individual and population-level responses of Nearctic-Neotropical migratory birds to urbanization. The Journal of Animal Ecology 77:83–91.

Rodewald, P. G., and S. N. Matthews. 2005. Landbird use of riparian and upland forest stopover habitats in an urban landscape. The Condor 107:259–268.

Schaub, M., R. Pradel, L. Jenni, and J. D. Lebreton. 2001. Migrating birds stop over longer than usually thought: an improved capture–recapture analysis. Ecology 82:852–859.

Seewagen, C. L., C. D. Sheppard, E. J. Slayton, and C. G. Guglielmo. 2011. Plasma metabolites and mass changes of migratory landbirds indicate adequate stopover refueling in a heavily urbanized landscape. The Condor 113:284–297.

Seewagen, C. L., E. J. Slayton, and C. G. Guglielmo. 2010. Passerine migrant stopover duration and spatial behaviour at an urban stopover site. Acta Oecologica 36:484–492.

Shields, W. 1977. The effect of time of day on avian census results. The Auk 94:380–383.

Shochat, E., Z. Abramsky, B. Pinshow, and M. E. A. Whitehouse. 2002. Density-dependent habitat selection in migratory passerines during stopover: what causes the deviation from IFD? Evolutionary Ecology 16:469–488.

Slabbekoorn, H., and E. a P. Ripmeester. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Molecular Ecology 17:72–83.

Theobald, D. M., J. R. Miller, and N. T. Hobbs. 1997. Estimating the cumulative effects of development on wildlife habitat. Landscape and Urban Planning 39:25–36.

Therres, G. D. 1992. Integrating management of forest interior migratory birds with game in the Northeast. Pages 402–407 in D. Finch and P. Stangel, editors. Status and management of Neotropical migratory birds. U.S. Forest Service General Technical Report RM-229. Fort Collins, CO.

Tilghman, N. G. 1987. Characteristics of urban woodlands affecting breeding bird diversity and abundance. Landscape and Urban Planning 14:481–495.

U.S. Census Bureau. 2012. State and County QuickFacts Cook County, Illinois. United States Census Bureau. Washington, D.C.

Wiedner, D. S., P. Kerlinger, D. A. Sibley, P. Holt, J. Hough, S. Url, and R. Crossley. 1992. Visible Morning Flight of Neotropical Landbird Migrants at Cape May. The Auk 109:500–510.

Wilcove, D. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214.

Wolter, P. T., C. A. Johnston, and G. J. Niemi. 2006. Land use land cover change in the U.S. Great Lakes basin 1992 to 2001. Journal of Great Lakes Research 32:607–628.