Migratory Stopover of Songbirds in the Western Lake Erie Basin

THESIS

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Abstract

Songbirds use multiple stopover locations to rest and refuel for subsequent flights while migrating between breeding and non-breeding areas. Selection of high quality stopover habitat may allow migrants to minimize time and energy spent in migration and maximize fitness. Migrants should therefore attempt to select stopover habitat that affords them suitable safety, shelter, and food. A better understanding of habitat attributes that support high numbers of migrant landbirds during stopover is needed to develop conservation strategies for these species, many of which are in decline. I examined how migrant density during stopover in the Western Lake Erie Basin (WLEB) of Ohio was influenced by local- and broad-scale habitat variables, specifically: patch vegetation composition and structure, patch size and isolation, patch distance from the Lake Erie shoreline, patch distance from a river or stream, and wetland cover surrounding a patch. I used a generalized random tessellation stratified (GRTS) approach to select forested study sites within 22 km of the lakeshore along a 70 km stretch of shoreline between Toledo and Sandusky, Ohio, USA. Observers conducted over 800 point counts annually from mid-April through late May in 2011 and 2012 at a total of 135 locations. Point count data on Blackpoll Warbler (*Setophaga striata*), Black-throated Green Warbler (*S.*
and a guild of transient wood warblers (Parulidae) were analyzed using the Dail and Madsen (2011) generalized hierarchical N-mixture model. This is an open-population model that simultaneously estimates parameters that influence the abundance and detection probability of study species. Detection probabilities for transient migrants varied by survey technician, wind speed, and survey time, highlighting the importance of accounting for detectability in bird migration studies. Broad-scale variables such as distance to the lakeshore, patch isolation, and wetland cover were generally better predictors of migrant abundance than proximity to a river or stream or patch area, and local-scale variables (habitat structure and vegetation). Densities for both study species were greatest in forest patches near the lakeshore. For the transient warbler guild, densities declined about 3.4% per km from the lakeshore. Density of the transient warbler guild was greater at sites that had more emergent aquatic midges (Chironomidae) in 2012, suggesting that midges could help explain the distribution and abundance of migrants in the WLEB. While densities of transient migrants were greater near the coast, inland forests often supported more transient migrants per patch than coastal forest patches. Conservation efforts in the region should seek to protect, create, restore (1) forested areas adjacent the lakeshore and (2) any forest within 0.5–10 km of the coast, with priority given to forests that are larger (>20 ha) and closer to the lakeshore and wetlands. Results from this study should be important in developing conservation plans for migratory songbirds and for guiding decisions regarding local habitat management and the placement of wind turbines within the landscape.
For the birds
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Chapter 1 - Bird migration and migratory stopover

Study overview

Migration is a life-history strategy that allows mobile organisms to take advantage of seasonal changes in environmental conditions (i.e., more food, water, shelter, space and or fewer competitors and predators) in order to maximize their individual fitness (Dingle and Drake 2007, Pulido 2007, Ramenofsky and Wingfield 2007). Migration is an adaptation that has evolved in a large and diverse group of organisms (Bowlin et al. 2010, Dingle 1980), and is prevalent among birds, with over 50% of the world’s 10,000 known living species (roughly 50 billion individuals) undertaking some form of migration annually (Berthold 1998). Migratory birds have evolved a variety of different migration strategies (e.g., long-distance, partial, altitudinal, differential) to capitalize on seasonal resources and opportunities (Alerstam and Hedenström 1998, Chapman et al. 2011, Dingle and Drake 2007). Long-distance migration is perhaps the best-studied migration strategy, and is used by approximately 36-38% of the world’s migratory avifauna (Kirby et al. 2008, Sekercioglu 2007). Long-distance migration is believed to have been common amongst birds for over 24 million years based on evidence in the fossil record (Steadman 2005), but how this strategy evolved is not definitively known (Alerstam and Enckell 1979, Bell 2000, Bruderer and Salewski 2008, Cox 1968, Cox 1985, Rappole and Jones 2002, Salewski and Bruderer 2007).
Hundreds of species of landbirds migrate between non-breeding grounds in the tropics of Central America, South America, and the Caribbean and temperate breeding grounds in North America every spring (Greenberg 1980). These Nearctic-Neotropical (hereafter referred to as simply Neotropical) migrants, may benefit by travelling to breed in seasonally resource-rich environments in North America because with more food and space available they can support larger clutch sizes (Alerstam et al. 2003, Greenberg 1980, Jetz et al. 2008, Lack 1968, Rappole and Jones 2002, Taverner 1904). Neotropical migrants also benefit by travelling to the tropics during the winter, thereby avoiding freezing temperatures and resource scarcity common at higher latitudes, and presumably increasing their chance of survival (Alerstam et al. 2003, Greenberg 1980, Lack 1968, Taverner 1904). Thus, migrants are able to successfully “glean the best of two worlds” (Greenberg 1980). Yet, the benefits of migration, in terms of increased survival during the non-breeding period and increased reproduction during the breeding period, are balanced by the cost of high mortality associated with travelling between distant areas (Paxton et al. 2007, Sillett and Holmes 2002). These costs are likely especially high for hatch-year birds that have never experienced migration (Greenberg 1980, Moore et al. 1995).

Migration is thought to be the period of highest mortality in the annual cycle of migratory landbirds, and likely plays a major role in limiting their populations (Holmes 2007, Johnson et al. 2006, Moore and Aborn 2000, Moore et al. 2005, Sillett and Holmes 2002). Analyses on long-term datasets from Europe (Berthold et al. 1998, Sanderson et al. 2006) and North America (Robbins et al. 1989, Sauer et al. 2011) have revealed that long-distance migratory bird populations are declining significantly faster than either
resident or short-distance migrant populations. Furthermore, Sillett and Holmes (2002) estimated that 87-89% of Black-throated Blue Warblers (*Setophaga caerulescens*) die while away from the breeding and wintering grounds, presumably during migration. Similarly, Paxton et al. (2007) found that 64% of annual mortality in Southwestern-Willow Flycatchers (*Empidonax traillii extimus*) was concentrated during migratory periods. Taken together, this evidence suggests that high mortality during migration may be typical for migratory landbirds.

Long-distance migratory birds have to stop to rest and refuel in multiple locations while *en route* to their breeding or wintering grounds in order to acquire the energy needed to continue their migration (Berthold 1975, Blem 1980, Hedenström and Alerstam 1997). Migrants spend the majority of the time and energy utilized during migration in these unfamiliar stopover habitats (Catry et al. 2004, Cochran and Wikelski 2005, Hedenström and Alerstam 1997, Lindström 2005, Wikelski et al. 2003), searching for food, recuperating from long-flights, and taking shelter, before making subsequent movements toward their final destinations. Migrants that quickly refuel at a stopover location may be able to shorten the duration of their stopover (Biebach et al. 1986, Cherry 1982, Loria and Moore 1990, Matthews and Rodewald 2010, Moore and Kerlinger 1987), and consequently the time required to complete their migration (Moore et al. 1995, Newton 2006, Tøttrup et al. 2012). By shortening time spent in migration, individuals may be able to arrive earlier on the breeding grounds (Moore et al. 1995, Tøttrup et al. 2012), and secure higher quality territories (Aebischer et al. 1996, Sergio and Newton 2003, Smith and Moore 2005) and mates (Møller 1994), and experience greater reproductive success (Hochachka 1990, Lozano et al. 1996, Moore et al. 2005,

Humans have radically altered terrestrial landscapes, reducing the amount of habitat available to migratory birds during all phases of their annual cycle (Kirby et al. 2008). These changes have likely exacerbated the challenges migrants face during migratory periods (Klaassen et al. 2012). For example, stopover habitats are smaller and farther apart in fragmented landscapes, making it more difficult for migrants to locate sufficient areas of quality stopover habitat (Klaassen et al. 2012). As a consequence of limited habitat availability, migrants may become concentrated in remnant patches where they could be more apt to experience increased competition and lower food availability (Kelly et al. 2002, Moore et al. 1995), and more susceptible to disease or predation (Klaassen et al. 2012). The challenges migrants face in fragmented landscapes may delay their migration and have important consequences for their future survival and reproduction (Baker et al. 2004, Moore et al. 1995, Weber et al. 1999).

Results from long-term monitoring efforts in North America have revealed that populations of a number of Neotropical migratory bird species have declined over the last several decades (Askins et al. 1990, Peterjohn et al. 1995, Sauer et al. 2011). These findings have sparked research focused on identifying where, how, and why these species are declining. The loss and fragmentation of habitats that birds utilize on the wintering grounds (Keller and Yahner 2006, Rappole and McDonald 1994, Robbins et al. 1989,
Sherry and Holmes 1996) and on the breeding grounds (Böhning-Gaese et al. 1993, Newton 2004) are often cited as the most likely causes for population declines. However, it is now widely recognized that events occurring during migration, including the loss and degradation of habitat available to migrants *en route*, may also play role in population declines (Moore and Simons 1992, Moore et al. 1995, Newton 2006, Sherry and Holmes 1995). However, it is unlikely that declines in any population of migratory birds can be attributed solely to events occurring in any one season (Faaborg et al. 2010b, Latta and Baltz 1997, Sherry and Holmes 1995, Sherry and Holmes 1993). Consequently, conservation plans must incorporate strategies for breeding, wintering, and migratory periods to effectively manage migratory species (Faaborg et al. 2010a, Mehlman et al. 2005, Sheehy et al. 2011, Sillett and Holmes 2002), and recognize that events that occur in one season can affect events in subsequent seasons (Bearhop et al. 2004, Gunnarsson et al. 2005, Harrison et al. 2010, Holmes 2007, Marra et al. 1998, Mitchell et al. 2012, Newton 2004, Newton 2006, Norris et al. 2004, Tøttrup et al. 2012). Our ability to develop comprehensive conservation plans for migratory landbirds is currently hampered by our incomplete knowledge of their ecology, especially on the wintering grounds and during migration (Faaborg et al. 2010b, Mehlman et al. 2005, Petit 2000). Given the ongoing population declines for a number of Neotropical migrants and ongoing habitat loss throughout their ranges, there is an urgent need to identify and conserve important habitats for these populations during all phases of their annual cycle (Faaborg et al. 2010a, Mehlman et al. 2005).

The conservation of a “network of stopover sites” that encompasses the full extent of migratory routes is critical to the conservation of migratory species (Mehlman et al.
2005, Petit 2000). However, little is known about how migrants select stopover habitats (Chernetsov 2006, Moore and Aborn 2000) or which habitat attributes consistently support high numbers of migratory birds during stopover periods (Petit 2000).

Furthermore, the ways that migrants use stopover habitats may vary geographically, temporally, or in relation to habitat availability in the landscape (Andrén 1994, Mehlman et al. 2005, Petit 2000), suggesting that more research is needed during both spring and fall migration and in a variety of regions and landscape configurations. Prior stopover research has emphasized the importance of local habitat attributes (Rodewald and Brittingham 2004, Rodewald and Brittingham 2007), but very few studies have considered how patch- and broad-scale habitat features influence the abundance of migrants (Buler et al. 2007, Buler and Moore 2011). Since migrants select stopover habitat at multiple spatial-scales (Bowlin et al. 2005, Buler et al. 2007, Buler and Moore 2011, Hutto 1985b), it is important to evaluate how both broad and local features of the landscape affect the distribution and abundance of migrants (Cushman and McGarigal 2002, Moore et al. 2005, Wiens 1989).

The goal of my research was to identify local- and broad-scale attributes of stopover habitat associated with use by migrant songbirds in the Western Lake Erie Basin (WLEB) of Ohio. Migrating songbirds concentrate in immense numbers during spring and fall migration within shoreline forest patches of the WLEB (Ewert et al. 2006, Rodewald 2007). Additional data on distribution and habitat-relationships of migrants within the broader WLEB is needed as this region has been targeted for wind power development (Black Swamp Bird Observatory 2011). I examined how abundance of transient migrants varied with respect to local and broad-scale features, specifically: 1)
patch vegetation composition and structure, 2) patch size and isolation, 3) patch distance from the lakeshore, 4) patch distance from a river or stream, and 5) wetland cover surrounding a patch. Results from this study should be important in developing conservation plans for migratory songbirds and for guiding decisions regarding local habitat management and the placement of wind turbines within the landscape.
Literature Cited


Chapter 2 - The influence of local- and broad-scale habitat features on songbird abundance during migratory stopover

Introduction

Habitat selection theory and field studies suggest that migrating birds initiate the process of selecting a stopover site at a broad spatial scale, likely while descending from nocturnal migration (Bowlin et al. 2005, Chernetsov 2006, Hutto 1985b, Mukhin et al. 2008, Schaub et al. 1999), and then refine their selection through a period of exploration after making landfall (Aborn and Moore 1997, Chernetsov 2006, Hutto 1985b, Jenni and Schaub 2003, Moore and Aborn 2000). The distribution and abundance of migrants in a region can be influenced by broad-scale features of the landscape, such as proximity to geographical obstacles to migration (e.g., an ocean, large lake, desert, or mountain range) and habitat availability (Buler et al. 2007, Buler and Moore 2011, Ewert et al. 2011, France et al. 2012, McCann et al. 1993, Moore et al. 1995). At a more local scale, migrant abundance can be associated with habitat structure (Cashion 2011, Rodewald and Matthews 2005, Rodewald and Brittingham 2007), tree species within a patch (Strode 2009, Wood et al. 2012), patch size (Cox 1988, Keller and Yahner 2007, Somershoe and Chandler 2004), and the distribution of local food resources (Blake and Hoppes 1986, Buler et al. 2007, Cohen et al. 2012, Ewert et al. 2011, Martin and Karr 1986). Since both broad- and local-scale features of habitat shape patterns in the distribution and abundance of migratory birds during stopover (Buler et al. 2007, Deppe and Rotenberry 2008, Pennington et al. 2008) it is important to consider both scales in stopover research (Moore et al. 2005). A better understanding of the habitat features that influence the abundance and distribution of stopover migrant birds is needed to make informed conservation decisions for these species (Ewert et al. 2006, Mehlman et al. 2005, Moore et al. 2005, Petit 2000). This information is urgently needed as many migratory species in North America have exhibited population declines over the last several decades (Sauer et
al. 2011), which may in part be attributable to the loss of stopover habitat along their migratory routes (Newton 2006).

Stopover studies that involve the collection and analysis of survey data present several challenges. Like all avian survey data, there is the issue of imperfect detection of species and individuals that are available to be recorded (Burnham 1981, McCallum 2005), which masks the ecological patterns of scientific interest to researchers (Fiske and Chandler 2011). Individuals or species may be missed during surveys due to weather conditions, observer ability, species behavior, background noise, habitat structure, and other factors (Alldredge et al. 2007b, Johnson 2008, Simons et al. 2009). It is critical to account for imperfect detection when making inferences about the abundance of a species to limit the risk of making misguided conclusions (Gu and Swihart 2004, Kéry and Schaub 2012, Norvell et al. 2003, Royle and Dorazio 2008, Thompson 2002). However, most models designed to account for imperfect detection carry the assumption of population closure (e.g., the population does not change during the study) (Alldredge et al. 2007a, Farnsworth et al. 2002, Nichols et al. 2000, Royle 2004), which makes them inappropriate for use on migration data when populations are in a nearly continual state of flux. Dail and Madsen (2011) developed a generalized hierarchical N-mixture model that allows for simultaneous estimates of parameters that influence the abundance and detection of a species within an open-population (i.e., the population changes during the study through immigration and emigration) making it amenable to stopover data.

The Western Lake Erie Basin (WLEB) provides important stopover habitat to many migratory birds (American Bird Conservancy 2010, Ewert et al. 2006). Previous
research in the region, has documented a decline in the relative abundance of en route migrants with increasing distance from the Lake Erie shoreline (Rodewald 2007). No study to date has examined migrant use of both lakeshore forests and forests located farther inland (>5.5 kilometers from the lakeshore) while accounting for imperfect detection of these species. I studied how the abundance and arrival rates of Blackpoll Warbler (Setophaga striata), Black-throated Green Warbler (S. virens), and a guild of 24 transient wood warblers (Parulidae) varied in randomly selected forest patches in the WLEB. I examined how both local- and broad-scale habitat features influenced migrant abundance using the hierarchical N-mixture model developed by Dail and Madsen (2011). Specifically, I looked at how migrant density was influenced by 1) patch vegetation composition and structure, 2) patch size and isolation, 3) patch distance from the Lake Erie shoreline, 4) patch distance from a river or stream, and 5) wetland cover surrounding a patch. I predicted that the density of migrants would be greatest in patches that 1) were more structurally complex (Rodewald and Brittingham 2007) and contained more oak (Quercus spp.) and elm (Ulmus spp.) and fewer maple (Acer spp.) trees (Graber and Graber 1983, Wood et al. 2012), 2) were smaller and more isolated (Moore et al. 1995), 3) were closer to the Lake Erie shoreline (Buler et al. 2007, Ewert et al. 2006, Ewert et al. 2011), 4) were closer to a river or stream (Ewert et al. 2006, Skagen et al. 1998), and 5) had more wetland cover in the surrounding landscape (Ewert et al. 2011, Smith et al. 2007).
Study Area and Methods

Study area and site selection

The study was conducted in the WLEB of Ohio from 19 April to 30 May in 2011 and 2012. The study area extended from Toledo to Sandusky, Ohio, and from 0-22 km from the Lake Erie shoreline. This area includes all or portions of Erie, Huron, Lucas, Ottawa, Seneca, Sandusky, and Wood counties (Figure 2.1). Land cover in the broader WLEB is approximately 66% agriculture, 13% urban/residential, 11% grass/rural cover, 9% forest, and 1% water/wetlands (U.S. Army Corps of Engineers 2009). This region was once covered by the Great Black Swamp, a large forested wetland that was largely drained and cleared during the 19th and early 20th centuries (Kaatz 1955). Remaining forests in the WLEB are largely composed of maple, elm, oak, ash (Fraxinus spp.), hickory (Carya spp.), and eastern cottonwood (Populus deltoides). The majority of the ash trees in the region are either dead or dying as result of the emerald ash borer (Agrilus planipennis), an invasive non-native species that first arrived in this area of Ohio in 2004 (Herms et al. 2004, Herms et al. 2006).

I used the National Oceanic and Atmospheric Administration (NOAA) coastal change analysis program (C-CAP) 2006 dataset to identify all forest patches larger than 0.36 ha within the study area (NOAA 2006). I used a quantile approach to stratify all forest patches into four distance bands (0–0.57 km, 0.57–2.65 km, 2.65 km–10.09 km, 10.09–22 km) relative to the Lake Erie shoreline (shoreline defined by the U.S. Geologic Survey (USGS) National Hydrology Dataset (NHD) (USGS 1999)). I used these distance bands to perform a generalized random tessellation stratified (GRTS) draw of forest
patches with replacement for each season (Stevens and Olsen 2004) using the ‘spsurvey’ package (Kincaid and Olsen 2012) in the statistical program R (R Development Core Team 2012). I selected the nearest forested patch in the same distance band and within 0.5 km when a selected location was not forested due to a misclassification in the C-CAP dataset. Different samples of survey locations were drawn for each year in order to provide a more representative collection of forested sites within the broader study area. I identified, contacted, and received permissions from landowners, agencies, and organizations to conduct bird surveys at selected survey locations. In 2011, I evaluated 225 sites and received permission to conduct surveys at 86 locations (38.2% success rate). In 2012, I evaluated 240 sites and received permission to conduct surveys at 91 sites (37.9% success rate).

**Bird surveys**

Migrant landbird abundance during stopover can vary from day to day, with many days characterized by low numbers (DeSante 1983, Lowery Jr. 1945). I established fixed point count locations 30 m from the forest edge, where spring migrants are more likely to concentrate, to increase numbers of detections during point count surveys (Rodewald and Brittingham 2007). Whenever possible, I located survey points near eastern edges where I expected morning bird activity would be higher due to greater sunlight and insect activity (Keller et al. 2009). I established point counts at 135 locations: 86 were used in 2011, and 91 were used in 2012 (42 of which were the same locations used in 2011) (Figure 2.2). For 22 of the 135 point count locations, I could not establish the point count along an eastern edge due to inaccessibility, lack of land owner permissions, or nesting Bald Eagles (*Haliaeetus leucocephalus*). For those sites, I located point counts along southern
edges, to maintain consistent amounts of sunlight near forest edges. Point count locations were placed in the center of small woodlots to maintain a minimum distance of 20 m from all forest edges.

Point count surveys were 10 minutes long, and split into four 2.5-minute sampling periods. Observers recorded the number of individuals of each bird species detected, and estimated the distance to each individual within 3 distance bands (0–15 m, 15–30 m, >30 m) during each sampling period. In addition, observers recorded the time when the survey started and a categorical estimate for wind speed during the survey. Wind speed categories were based on the Beaufort scale: (0) = < 1 km/hr, (1) = 1–5 km/hr, (2) = 6–11 km/hr, (3) = 12–19 km/hr, (4) = 20–30 km/hr, (5) = 31–39 km/hr (Cullen 2002). During point counts in 2012, observers also recorded categorical estimates of midge abundance within 5 m of point count locations following methods developed by Smith et al. (2007). The categories used were: (0) = 0 midges, (1) = 1–10 midges, (2) = 11–100 midges, (3) = 101–500 midges, (4) = 501–1000 midges, (5) = 1001–5000 midges, (6) = >5001 midges (Smith et al. 2007).

Point count locations were surveyed approximately twice weekly in both years when weather permitted, between 0.75 and 5.75 hours after sunrise, from 19 April through 30 May. Surveys were conducted at an average of 19.7 locations per day (range = 7–27, SD = 4.6). Survey effort was divided among locations that were in close proximity to the lakeshore, some farther inland (>6 km from the shore), and in both eastern and western parts of the study area on each day of sampling. Observers rotated among locations in both years so that only 22.6% of the time did the same observer survey the same location on the subsequent visit. A total of 808 point counts were
conducted at 86 locations in 2011, an average of 9.4 surveys per location (range = 6–12, SD = 1.4). A total of 810 point counts were conducted at 91 locations, an average of 8.9 surveys per location in 2012 (range = 6–12, SD = 0.93).

**Study species**

The Blackpoll Warbler and the Black-throated Green Warbler were selected as focal species for these analyses. The Blackpoll Warbler (BLPW) is a long-distance Neotropical-Nearctic migratory songbird, which breeds in boreal forests of the northeastern United States and Canada and winters mainly in South America (eBird 2012, Peterjohn 1989). They do not breed in Ohio, but are common transients during spring and fall migration (eBird 2012, Peterjohn 1989). The Black-throated Green Warbler (BTNW) breeds in coniferous and mixed hardwood forests of the eastern United States and Canada and winters predominantly in Central America and the Caribbean (eBird 2012, Peterjohn and Rice 1991). The BTNW breeds within eastern Ohio, but there are no breeding records within the study area, meaning all individuals surveyed were highly likely to be transients (Ohio Breeding Bird Atlas II 2012, Peterjohn and Rice 1991).

To better understand how migrant landbirds respond to landscape features during stopover, I created a guild comprised of 24 species of transient wood warblers. Migrants in the guild are taxonomically similar and likely have similar foraging strategies during stopover. Included in the guild were: Blue-winged Warbler (*Vermivora cyanoptera*), Golden-winged Warbler (*V. chrysoptera*), Tennessee Warbler (*Oreothlypis peregrina*), Orange-crowned Warbler (*O. celata*), Nashville Warbler (*O. ruficapilla*), Northern Parula (*Setophaga americana*), Chestnut-sided Warbler (*S. pensylvanica*), Magnolia Warbler (*S.
magnolia), Cape May Warbler (S. tigrina), Black-throated Blue Warbler (S. caerulescens), Yellow-rumped Warbler (S. coronata), Black-throated Green Warbler, Blackburnian Warbler (S. fusca), Yellow-throated Warbler (S. dominica), Pine Warbler (S. pinus), Prairie Warbler (S. discolor), Palm Warbler (S. palmarum), Bay-breasted Warbler (S. castanea), Blackpoll Warbler, Cerulean Warbler (S. cerulea), Hooded Warbler (S. citrina), Black-and-white Warbler (Mniotilta varia), Wilson’s Warbler (Cardellina pusilla), and Canada Warbler (C. canadensis).

Local-scale variables

I established a single 30-meter radius plot centered on each point count location to quantify local habitat characteristics. Within each plot, I recorded the number of trees by species in three diameter-at-breast-height (dbh) size classes: 8–23 cm dbh (small trees), 23–38 cm dbh (medium trees), >38 cm dbh (large trees). I recorded whether ash trees were healthy, dead, or infected by emerald ash borer following a modified version of the classification system developed by Smith (2006). I estimated understory stem density (stemhits) between 0.5–3.0 m in height by counting the number of stems touching a vertical pole every 2 m along 30 m transects that originated at the plot center and extended in each cardinal direction. I measured canopy height in meters at a minimum of two locations within the plot using a range finder in order to calculate average canopy height.

I conducted a principal components analysis (PCA) on six habitat structure variables collected at all 135 point count locations in the statistical computing program R (R Development Core Team 2012). The variables used were stemhits, number of small trees, number of medium trees, number of large trees, number of medium and large dead
ash trees, and average canopy height. I used a correlation matrix to construct the PCA (Table 2.1) and followed the latent root criterion when selecting the number of axes to interpret (McGarigal et al. 2000). The first three axes each had eigenvalues >1, but only the first two axes were retained to minimize the number of parameters in the N-mixture model (eigenvalue of third axis = 1.02). The first PCA axis accounted for 29.2% of the total variation (eigenvalue = 1.75) and described a gradient of decreasing numbers of large trees and canopy height, and increasing numbers of small and medium sized trees and medium and large dead trees (Table 2.2). The second axis accounted for an additional 28.2% of the total variation (eigenvalue = 1.69) and described a gradient of decreasing numbers of stemhits and increasing numbers of small, medium, and large trees (Table 2.2). I used the first two axes of the habitat structure PCA in subsequent N-mixture models.

I performed another PCA using the tree species data. For each point count location, I summed counts of medium and large trees for the eight most abundant species groups found in the study area. Those species groups were oaks, hickories, eastern cottonwood, elms, maples, boxelder (*Acer negundo*), walnuts (*Juglans* spp.) and dead ashes. I performed a Hellinger transformation on the raw species counts for each species group at each location using the package “vegan” (Oksanen et al. 2011) to make the data more appropriate for a PCA analysis (Legendre and Gallagher 2001). I used a correlation matrix to construct the PCA (Table 2.3) and followed the latent root criterion when selecting the number of axes to interpret (McGarigal et al. 2000). The first three axes each had eigenvalues >1, but only the first two axes were retained to minimize the number of parameters in the N-mixture model (eigenvalue of third axis = 1.25). The first
axis accounted for 27.7% of the total variation (eigenvalue = 2.22) and described a gradient of increasing numbers of oaks, hickories and walnuts and decreasing numbers of maples and cottonwoods (Table 2.4). The second axis accounted for an additional 17.8% of the total variation (eigenvalue = 1.42) and described a gradient of increasing numbers of dead ashes, hickories, and cottonwoods, and decreasing numbers of elms (Table 2.4). I used the first two axes of the species composition PCA in subsequent N-mixture models.

**Broad-scale variables**

I used data from the U.S. Fish and Wildlife Service’s (USFWS) 2012 National Wetland Inventory (NWI) (USFWS 2012) and NOAA’s 2006 C-CAP (NOAA 2006) to quantify forest cover within the study area for analyses. The 2012 NWI data were used to identify forested areas near the coast, and the 2006 coastal change analysis program (C-CAP) dataset was used to identify inland forests not covered by the NWI. The 2012 NWI data more accurately classified coastal forest patches, but was not designed to classify inland forests.

Broad-scale variables were calculated in ESRI’s ArcGIS Desktop 10 (ESRI 2011). I measured area, distance from the coast, distance from a river or stream, isolation, and wetland cover in the landscape for each point count location in the study area (Table 2.5). I used the National Hydrology Dataset (USGS 1999) to define the Lake Erie coastline and rivers and streams. I calculated the proportion of the landscape within 500 m of point count locations that was forested, as a proxy for patch isolation (Bender et al. 2003, Tischendorf et al. 2003). A 500 m scale was selected for the isolation variable based on a post-hoc analysis using the computer program Focus (Holland et al. 2004). I used Focus to assess the scale at which migrants responded to the amount of forest cover
within the landscape during stopover (Holland et al. 2004). I first calculated the proportion of the landscape surrounding point count locations that was forested at 20 different spatial scales using radii of 0.5 to 10 km, in 0.5 km increments (Buler et al. 2007). I then used Focus to create 300 samples of 14 randomly selected and spatially independent landscapes for each of the 20 spatial scales. Focus produced regressions between the proportion of the landscape that was forested and the mean abundance of migrants for the sites selected in each of the 300 samples (Buler et al. 2007, Holland et al. 2004). Focus provided mean r values (Pearson’s correlation coefficient) for the 300 correlations at each spatial scale, and for many migrants the scale with the greatest absolute r value was 0.5 km (Holland et al. 2004).

Wetlands in the study area support high concentrations of emergent aquatic midges (Diptera: Chironomidae) (MacDade et al. 2011), which are considered an important food resource to migrating birds in the Great Lakes region, particularly in spring (Ewert et al. 2011, Smith et al. 2007). Arthropod predators of midges, especially spiders, are also consumed by migrating birds (Carlisle et al. 2012, Smith et al. 2007) and their abundance can be positively correlated with midge abundance (Dreyer et al. 2012, Hoekman et al. 2011, Smith et al. 2007). Consequently, it is likely that areas near wetlands offer greater food resources to migrating birds than areas farther from wetlands (Smith et al. 2007). Wetlands were defined using the 2012 NWI data (USFWS 2012) for analyses in this study. I removed all wetlands that had special modifiers (drained/ditched, spoil, farmed, excavated, or artificial substrates), water regimes (temporarily flooded, or saturated) or subclasses (unconsolidated bottom, or unconsolidated shore) (USFWS 2012) as these wetland types are unlikely to support a high abundance of emergent
aquatic midges (Robert Gates, Personal communication). I calculated the proportion of the landscape within 200 m of each point count locations that was classified as wetland to use as a covariate in N-mixture models. A 200 m buffer was selected for this variable as midges tend to concentrate within this distance from the wetlands from where they emerge (Dreyer et al. 2012).

Statistical methods

For these analyses, I excluded data from surveys conducted prior to a species’ first detection and after a species’ last detection during each year, as those zero counts predominantly represented “false zeroes” as the species was very likely not present to be detected (Martin et al. 2005, Wenger and Freeman 2008). Several extremely high counts (>3 SD above mean) that likely were overestimates of true abundance were reduced to 2 SD above the mean. This included 5 extreme counts for Yellow-rumped Warbler and 3 for Palm Warbler, all occurred in 2011.

I used the generalized hierarchical N-mixture model created by Dail and Madsen (2011) to analyze the count data for the Blackpoll Warbler, Black-throated Green Warbler, and the transient warbler guild. This is a mechanistic open population model that allows users to estimate changes in abundance over the duration of migration using parameters for immigration (gamma - \( \gamma \)) and emigration (omega - \( \omega \)), while accounting for imperfect detection of study species (Dail and Madsen 2011). The model requires data to be collected from \( i \) independent sites, during \( j \) secondary periods within \( t \) primary periods (Dail and Madsen 2011, Royle and Chandler 2012). Primary periods were the individual point count surveys conducted at a location and secondary periods were the four 2.5-minute sub-sampling periods during each point count. Bird populations were
assumed to be closed during the 10-minute survey period at a site (a primary period), but not between surveys (Dail and Madsen 2011). The mean abundance of migrants at a location during primary period ($t = 1$) is governed in the model by the parameter lambda ($\lambda$), and changes to that abundance between subsequent visits were modeled using the parameters gamma ($\gamma$; i.e., number of new arrivals) and omega ($\omega$; i.e., apparent survivorship between surveys) (Dail and Madsen 2011). The probability of detecting the true number of individuals of a species or guild ($N_i$) present during a survey is governed by the detection probability parameter $p$ (Dail and Madsen 2011). Using these four parameters ($\lambda$, $\gamma$, $\omega$, $p$), the model can generate abundance estimates for each survey occasion, while accounting for imperfect detection of the study species (Dail and Madsen 2011). I used a Poisson distribution to model the counts of individuals detected on surveys in both single-species models for both years. Since I was modeling changes in abundance between migration surveys, it was necessary to analyze data from each year separately.

I modeled count data for the transient warbler guild using an exponential model described by Fiske and Chandler (2011), a modified version of the Dail and Madsen model (2011). This model integrates immigration and emigration parameters into a single parameter gamma ($\gamma$) that represents population growth/loss (Fiske and Chandler 2011). In this model, the number of individuals at site $i$ on occasion $t$ is equal to the number in the previous period multiplied by $\gamma$ or the finite rate of increase (Fiske and Chandler 2011). My decision to use the exponential model over the Dail and Madsen (2011) model for the guild data was validated by improved Akaike Information Criterion (AIC) scores.
For the guild models, I used a Poisson distribution in 2011, and a negative binomial distribution in 2012, as this distribution was favored by AIC.

Each of the parameters in the Dail and Madsen model ($\lambda$, $\gamma$, $G\bar{J}$, $p$) and the exponential model ($\lambda$, $\gamma$, $p$) can be modeled as functions of covariates. Only variables for which there was an a priori reason to believe influenced a given parameter were considered. I used an information-theoretic approach to select appropriate variables for each parameter (Burnham and Anderson 2002), and all continuous variables were scaled and centered before being fit to any parameter by subtracting the mean of a variable from all of its values and then dividing that number by the SD of the variable. I first modeled candidate sets for detection probability, and identified the model with the greatest AIC support. I then used the top detection model when testing the candidate set for gamma. The most parsimonious model from the gamma set was considered the top overall model. To plot relationships between variables and abundance, I created a model set of all plausible models (< 2 AIC from the most parsimonious model) to use in generating model-averaged predictions of relevant variables and parameters (Burnham and Anderson 2002).

I modeled the initial counts of migrants at study sites ($\lambda$ – lambda) as a constant because there were very few detections of migrants early in migration, so modeling these sparse data were not appropriate. I modeled immigration rates and population growth (gamma - $\gamma$), using local- and broad-scale variables known to influence migrant landbird abundance during stopover. A set of 60 candidate models were developed using the following variables: patch area (Cox 1988, Martin 1980, Somershoe and Chandler 2004), isolation (Buler et al. 2007, Martin 1980), distance from the coast (Buler et al. 2007,
Buler and Moore 2011, Ewert et al. 2011, Rodewald 2007), patch distance from rivers and streams (Ewert et al. 2006, Skagen et al. 1998, Skagen et al. 2005), wetland cover (Ewert et al. 2006, Ewert et al. 2011, Smith et al. 2004, Smith et al. 2007), tree species composition (Graber and Graber 1983, Strode 2009, Wood et al. 2012), and habitat structure (Rodewald and Brittingham 2007). Each of the 60 models included Julian date and a quadratic term for Julian date because the abundance of the study species and the guild was unimodal as counts generally peaked during mid-migration. Two variables (area and isolation) were strongly correlated (|Pearson’s r| > 0.7), and so were not included in the same models. Interactions were not considered in the analysis, as understanding main effects in this novel framework was the primary focus of the study.

I modeled apparent survivorship of individuals between visits to a site (Ω – omega) as a constant because I believed measured variables were not appropriate in predicting the apparent survivorship of migrants. For the detection probability parameter (p), I considered time of day, a quadratic effect for time of day, a categorical estimate of wind speed, and the survey observer. Previous research has shown that the ability to detect an individual bird that is present in an area during a survey can be influenced by: observer skill and experience (Alldredge et al. 2007b, Diefenbach et al. 2003, Faanes and Bystrak 1981, Farmer et al. 2012), observer age and hearing ability (Cyr 1981, Emlen and Dejong 1992, Ramsey and Scott 1981, Saunders 1934), observer attentiveness (Farmer et al. 2012, McCallum 2005, Robbins and Stallcup 1981), and observer expectations (Balph and Balph 1983). Detection probabilities can also be influenced by background noise (Alldredge et al. 2007b, Simons et al. 2007), time of day (Bart and Herrick 1984), number of individuals present to be detected (Bart and Schoutz 1984, Kéry 2002,
Simons et al. 2007) and weather conditions (e.g., precipitation and wind) (Dawson 1981, Emlen and Dejong 1981, Simons et al. 2009, Simons et al. 2007). Detectability also depends on the behavior of the species itself, and how frequently species make themselves available for detection (Alldredge et al. 2007b, Johnson 2008, McCallum 2005, Simons et al. 2009). I created a set of 12 candidate models using the variables of interest for each of three distributions (Poisson, Negative Binomial, Zero-inflated Poisson) and then tested each set for the detection parameter for each species and guild.

I assessed model fit using a parametric bootstrap procedure (Dixon 2002). The procedure generated 250 replicate data sets for the single-species models with the greatest support and 125 for the guild models, estimated parameters for those data, and computed a fit statistic (Freeman-Tukey for the Dail and Madsen models and a Chi-square for the exponential models) for each dataset (Fiske and Chandler 2011, Kéry et al. 2005). I compared the fit statistic from the model with greatest support (observed) to the distribution of the fit statistic created from the parametric bootstrap procedure (expected) and then reported the proportion of the expected distribution greater than the observed statistic (P-value) to assess the overall model fit (Fiske and Chandler 2011, Kéry and Schaub 2012, Kéry et al. 2005). All model fitting, parameter estimations, and goodness of fit testing were carried out in the program R version 2.15.1 (R Development Core Team 2012) using the package ‘unmarked’ version 0.9-9 (Fiske and Chandler 2011).

Maps

I created maps to show how the density of migrants varied in forest patches across the landscape and to identify the forest patches that were most used by transient migrants during spring migration. I made a raster of all forested locations using the NWI (USFWS
2012) and C-CAP (NOAA 2006) data. For each 1 ha cell of the raster, I assigned a value for all variables within each top model that I was able to map (distance from the coast, distance from a river or stream, patch isolation, wetland cover, patch area, and date). I scaled and mapped all variables for each day of migration using the “raster” package (Hijmans and van Etten 2012) in R (R Development Core Team 2012). I then used the top model for each species or guild in each year to make area-weighted predictions of bird abundance for each forest cell for each day of migration (Fiske and Chandler 2011). I assumed that all individuals within 75 m of point count locations were exposed to sampling in order to calculate densities. Given that surveyed areas were equal to 1.77 ha, I divided predicted estimates by 1.77 before assigning estimated abundances to raster cells that had areas of 1 ha. I also assumed that bird density was constant across the patch. I extrapolated area-weighted predictions to the total area of the forest patch to estimate numbers of individuals per patch.

**Results**

*Blackpoll Warbler*

In 2011, I detected a total of 95 BLPW during 514 surveys at 86 sites between 5 May and 29 May (0.18 BLPW/survey). There were four equally plausible models for the detection parameter. The detection model with the greatest support included terms for observer, time of day, and a quadratic of time of day. Detection probability was positively correlated with time of day for all observers (Figure 2.3). There were three equally plausible models for gamma (arrival rate of BLPW) (Table 2.6). The best-
supported model included terms for Julian date, a quadratic of Julian date, isolation, and wetland cover, and showed moderate fit \( P = 0.29 \). Arrival rates of BLPW in 2011 were higher at sites with more wetland cover in the landscape, and at sites with less surrounding forest cover (Figure 2.4). Arrival rates for BLPW peaked around 15 May in 2011 (Figure 2.5).

In 2012, I detected a total of 73 BLPW during 409 surveys at 91 sites between 9 May and 28 May \( (0.18 \text{ BLPW/survey}) \). There were three equally plausible models for the detection parameter, with the best-supported model including a term for wind. There was a general pattern of decreasing detection probability with increasing wind speed (Figure 2.6). There were seven equally plausible models for gamma (arrival rate of BLPW) (Table 2.7). The model with the greatest support included terms for Julian date, a quadratic term for Julian date, distance from the coast, patch area, and wetland cover in the surrounding landscape, and showed moderate fit \( P = 0.38 \). Arrival rates in 2012 were higher at sites that had greater wetland cover, that were closer to the lakeshore (Figure 2.7), and that were smaller in area, although this effect was marginal (Figure 2.8; Table 2.8). Arrival rates for BLPW peaked around 15 May in 2012.

Arrival rates for BLPW in 2011 and 2012 were influenced largely by date, wetland cover, patch isolation, and distance to the coast (Figure 2.8; Table 2.8). Forest patches adjacent the Lake Erie shoreline and wetlands supported average densities that were 9.9 to 144 times greater than forests that were 22 km inland and isolated from wetlands (Figure 2.9). The forest patches that supported the highest average numbers of BLPW during migration were within 9 km of the Lake Erie shoreline and were larger than 15 ha (Figure 2.10). In many cases, smaller patches near the lakeshore supported as
many BLPW as large inland patches. For example, the average number of BLPW in a 8
ha patch adjacent to the lakeshore was approximately equal to the number supported in an
87 ha patch located 22 km inland.

**Black-throated Green Warbler**

In 2011, I detected a total of 202 BTNW during 727 surveys at 86 sites between
21 April and 29 May (0.28 BTNW/survey). There were four equally plausible models for
the detection parameter. The detection model with the greatest support included terms for
observer, time of day, and a quadratic term for time of day. Detection probability for
BTNW peaked mid-morning for all observers (Figure 2.1). There were seven equally
plausible models for gamma (arrival rate of BTNW) (Table 2.9). The model with the
greatest support included Julian date, a quadratic term for Julian date, distance from a
river or stream, species composition PC1, and species composition PC2 and showed
marginal fit (P = 0.12). Arrival rates of BTNWs in 2011 were most closely associated
with Julian date, with other variables showing little association (Figure 2.8; Table 2.8).
BTNW arrivals peaked around 6 May in 2011 (Figure 2.12).

In 2012, I detected a total of 202 BTNW during 753 surveys at 91 sites between
22 April and 28 May (0.27 BTNW/survey). There were two equally plausible models for
the detection parameter. The detection model with the greatest support included a term
for the survey observer, although parameter estimates overlapped zero (Figure 2.13).
There were six plausible models for gamma (Table 2.10). The model with the greatest
support included Julian date, a quadratic term for Julian date, distance from the lakeshore,
habitat structure PC1, habitat structure PC2, and patch isolation, and showed marginal fit
(P = 0.06). Arrival rates were primarily related to distance from the lakeshore (Figure
2.14) and date, as habitat structure and patch isolation were weakly associated with arrival rates (Figure 2.8; Table 2.8). The peak in arrival rate was around 4 May in 2012 (Figure 2.15).

Arrival rates for BTNW in 2011 and 2012 were most strongly related to distance from the lakeshore and date (Figure 2.8; Table 2.8). Predictive maps show that forest patches within ~2 km of the Lake Erie shoreline supported densities of BTNW that were between 1.5 and 2 times greater than forested areas 22 km inland (Figure 2.16). The patches that supported the highest average numbers of BTNW per patch were larger than 58 ha and within 9 km of the lakeshore (Figure 2.17).

**Transient warbler guild**

In 2011, I detected a total of 3802 individuals in the transient warbler guild during 808 surveys at 86 sites between 19 April and 30 May (4.7 individuals/survey). The most abundant transient migrant observed was the Yellow-rumped Warbler (50% of total), followed by Palm Warbler (8%), Black-throated Green Warbler (7%), and Nashville Warbler (6%) (Figure 2.18). The only probable model for the detection probability parameter included terms for observer, time of day, a quadratic of time of day, and wind. For all observers, detection probability generally declined with increasing wind speed (Figure 2.19) and increased with time of day (Figure 2.20). There were five equally plausible models for the finite rate of increase (Table 2.11). The model with the greatest support included terms for Julian date, a quadratic of Julian date, and distance from the coast and exhibited moderate fit ($P = 0.16$). The finite rate of increase was negatively related to distance from the coast, and the 95% confidence interval for the estimate of the coefficient overlapped zero (estimate for coefficient = -0.014, 95% confidence interval: 0.014).
The average density of the transient warbler guild during migration was 2.2 times greater in forest patches at the lakeshore compared to sites 22 km inland, and declined by about 3.2% per km from the lakeshore.

In 2012, I detected a total of 1413 individuals in the transient warbler guild during 810 surveys at 91 sites between 19 April and 28 May (1.74 individuals/survey). The most abundant transient migrant was the Yellow-rumped Warbler (36% of total), followed by Black-throated Green Warbler (13%), Magnolia Warbler (6%), Nashville Warbler (6%), and Tennessee Warbler (6%) (Figure 2.18). The one plausible model for the detection probability parameter included terms for observer, time of day, a quadratic of time of day, and wind. For all observers, detection probability generally declined with increasing wind speeds (Figure 2.21), and increased with time of day (Figure 2.22). There were four equally plausible models for the finite rate of increase (Table 2.12). The model with the greatest support included terms for Julian date, a quadratic of Julian date, and distance from the coast and exhibited moderate fit (P = 0.18). The finite rate of increase was negatively related to distance from the coast, and the 95% confidence interval for the estimate of the coefficient overlapped zero (estimate for coefficient = -0.019, 95% confidence interval: -0.022 to 0.012). Mean density of the transient warbler guild was about 2.4 times greater at sites within a km of the lakeshore than at sites 22 km inland, declining about 3.9% with each km from the lakeshore.

Abundance of transient warblers in the WLEB in 2011 and 2012 was most strongly related to the distance from the lakeshore. Mean density of transient warblers during 2011 and 2012 was 2.2 times higher within a km of the lakeshore compared with forests 22 km inland, and declined about 3.4% per km from the lakeshore (Figure 2.23).
The patches that supported the highest average number of guild members during migration were larger than 58 ha and within 9 km of the lakeshore (Figure 2.24).

*Midges*

Categorical estimates of midge abundance in 2012 increased with Julian date (Figure 2.25), wetland cover (Figure 2.26), and proximity to the coast (Figure 2.27). I used empirical Bayes methods to estimate the number of transient warblers present at each point count location during each survey period using the top model for the transient warbler guild in 2012 (Fiske and Chandler 2011). I conducted a post-hoc ANOVA where abundance of transient warblers was predicted using midge scores, Julian date, and a quadratic of Julian date. There was a difference in the mean abundance of transient warblers among midge classes ($F_{6, 801} = 1.835, P = 0.0895$). I found that surveys that had midge scores of 3, 2, or 1 had significantly more transient warblers than surveys that had midge scores of 0, and that surveys that had midge scores of 3 had significantly more transient warblers than surveys that had midge scores of 1 (Figure 2.28).

**Discussion**

*Broad-scale variables*

Proximity to the coast was one of the strongest predictors of arrival rates for Blackpoll Warblers in 2012 and Black-throated Green Warblers in 2012; it was also the lone habitat variable in the top model for the finite rate of increase for the transient warbler guild in both years, although confidence intervals for coefficient of the relationship overlapped zero in both years. The generally higher arrival rates and finite
rates of increase near the shoreline led to higher predicted densities of migrants in lakeshore forest patches compared with more inland forests. These results are consistent with other studies in the Great Lakes region (Bonter et al. 2009, Ewert et al. 2011, France et al. 2012), along the Atlantic coast (McCann et al. 1993), and along the Gulf of Mexico (Buler et al. 2007, Buler and Moore 2011), where migrant densities were consistently found to be greatest in close proximity to large bodies of water. Although the decline in migrant density with increasing distance from the Lake Erie coast was expected (Ewert et al. 2006), no study had quantified this decline at distances more than 5.5 km from the coast using on the ground surveys. The nature of the decline varied by species. For example, BLPW abundance was more concentrated along the coast than BTNW or the transient warbler guild. Migrants that are closer to their breeding grounds may respond differently to features of the landscape than migrants that breed farther away (Keller and Yahner 2007). Given that Yellow-rumped Warblers (the most abundant species in the transient warbler guild) and BTNWs are closer to their breeding grounds in northwestern Ohio than BLPW, they may be more apt to explore the local landscape in search of food or potential breeding habitat than would BLPW. This would help explain differences in the way the species responded to Lake Erie.

Why migrants concentrated near the shoreline is not entirely clear, but several factors likely are involved. Migrants may encounter the lake and then decide to land in lakeshore habitats in order to rest and refuel before attempting to cross (Ewert et al. 2006, Ewert et al. 2011, Fortin et al. 1999). Concentrations of migrants may also build in lakeshore habitats if migrants are circumventing the lake in order to minimize risk and energy associated with directly crossing the water where there are few suitable locations
to land (Alerstam 2001, Sandberg and Moore 1996b). A local radar study of nocturnal migration found that spring migrant landbirds largely fly northwest (parallel to the coast) when they encounter the Lake Erie shoreline, suggesting that migrants are hesitant to cross the Lake at night (Jeremy Ross, Personal communication). If spring migrants east of the study area also head west when they reach Lake Erie, this would result in many birds being directed into my study area, and would explain why this region hosts such enormous numbers of migratory birds during spring migration (Ewert et al. 2006). More research is needed to understand movements of migratory birds in relation to Lake Erie at various locations along its shoreline and farther inland (Ewert et al. 2006).

Migrants may also be concentrating in lakeshore forest patches because these areas offer greater food resources in the form of emergent aquatic midges and possibly arthropods (Ewert et al. 2006, Ewert et al. 2011, Smith et al. 2007). Food is a critical resource to migrating birds, and several studies have shown migrant abundance to be positively correlated with food abundance during stopover across habitats (Cohen et al. 2012, Hutto 1985a, Smith and Hatch 2008) and within a habitat (Buler et al. 2007, Ewert et al. 2011, Martin and Karr 1986). Migrant densities may increase in lakeshore habitats over a period of several days if individual migrants stopover longer in these areas due to high food availability and an increased opportunity to refuel rapidly (Martin and Karr 1986, Moore et al. 2005). Several pieces of evidence suggest that migrant abundance was positively related to midge abundance in this study. Midge abundances along with transient warbler abundance and 2012 BLPW and BTNW arrival rates were higher at sites near the Lake Erie shoreline. In addition, midges were more abundant at sites with more wetland cover in the landscape and so were BLPW arrival rates in both 2011 and
2012. Furthermore, a post-hoc analysis revealed that surveys during 2012 that had higher estimates of midges also had significantly more transient warblers. However, because distance to the lakeshore and wetland cover variables were correlated ($|r| = 0.52$), it was not possible to tease apart whether migrants concentrated near the lake in response to the ecological obstacle, the increased food abundance, or both. Yet, it is clear from this study that lakeshore forest sites received high use by migrating birds in the WLEB and therefore have high conservation value (Mehlman et al. 2005).

The amount of forest cover in the landscape was an important factor influencing the abundance and arrival rates of BLPW in 2011. In that year, BLPWs were more abundant in patches that were more isolated. This finding is in contrast to Buler et al. (2007) who found that migrant abundance in the Gulf of Mexico was positively related to increasing forest cover in the landscape at the 5 km scale. However, the landscape where Buler et al. (2007) worked was 70% forested, whereas my study area was only 5.3% forested. The lack of available habitat may have forced migrants to concentrate into remnant patches at high densities (Moore et al. 1995). These densities may cause migrants to experience greater competition and lower food availability (Kelly et al. 2002, Moore et al. 1995), or be more exposed to disease or predation (Klaassen et al. 2012), which in turn could influence their future survival and reproductive success (Baker et al. 2004, Moore et al. 1995). More research is needed to discern the influences of stopover habitat quality and availability on the future reproductive success and survivorship of migratory birds.

Patch proximity to a river or stream did not seem to strongly influence transient migrant arrival rates or abundances. The variable was found in only one top model
(BTNW in 2012), but the 95% confidence interval for the coefficient overlapped zero. However, inland point count locations (>10 km from the lakeshore) along rivers and streams often had more migrants than other inland locations that were not situated along rivers and streams. In contrast, migrants heavily used all lakeshore point count locations (< 2 km from the lake), regardless of their proximity to a river or stream. This suggests that distance to a river or stream may be a better predictor of migrant abundance and arrival rates at inland sites (>10 km from the lakeshore) than at lakeshore sites. Future research that examines abundance of migrants in relation to rivers and streams should consider interaction-effects with larger-scale landscape features, especially obstacles to migration such as large lakes, oceans, and mountains, as patterns in habitat-use by migrants may shift with proximity to large-scale geographical features.

Surprisingly, patch area had little influence on the finite rate of increase in the guild models, or arrival rate in either of the single-species models. In 2012, the only year in which patch area was in a top model, BLPW arrival rates were generally higher in smaller patches, but the effect was marginal as the confidence interval for the coefficient of the relationship overlapped zero. The influence of patch area on both migrant arrival rates and the finite rate of increase may be more complex than initially expected. For example, a large inland forest patch likely has lower density of migrants than a smaller patch located at the same distance from lakeshore (Martin 1980). However, near the lakeshore (< 2 km) all patches, both large and small, may have equally high densities of migrants because there is limited remaining habitat in this area. Thus, the effect of patch area on migrant abundance may vary in relation to distance from the lakeshore, such that patch area has a weaker influence on migrant density closer to the lakeshore.
Local-scale variables

Counter to my predictions, local-scale vegetation variables, patch composition, and structure had little influence on transient migrant abundance or arrival rates. Previous research has demonstrated that *en route* migrants selectively forage in oak and elm trees and avoid maples during migration (Graber and Graber 1983, Strode 2009, Wood et al. 2012), likely because oaks (Summerville et al. 2003) and elms support greater abundances of food resources (Graber and Graber 1983, Wood et al. 2012). Therefore, I expected migrants would exhibit higher densities at sites that contained more oak and elms and exhibit lower densities at sites that contained more maples. In 2012, the only year in which patch composition was in a top model, BTNW arrival rates were negatively related to PC1, suggesting greater arrival rates at sites with more maples and cottonwoods and lower arrival rates at sites with more oak and hickory, but the relationship was not strong. I also found that BTNW arrival rates were negatively related to PC2, suggesting greater arrival rates at sites with more elms and lower arrival rates at sites with more dead ash and hickory. Although the confidence interval on the coefficient did not overlap zero, the influence of PC2 on arrival rates was marginal. The reason I found no relationship between migrant abundance and species composition may have been related to the nature of my data. I did not record which tree species migrants were foraging in during point counts and so my data could only identify correlations between the abundance of tree species and the abundance of migrants, but likely not preferences by migrants for particular tree species.

Habitat structure also seemed to have little influence on migrant abundance and arrival rates. Some studies have found that *en route* migrants seem to prefer sites with
complex and diverse vegetative structure (Cashion 2011, Rodewald and Brittingham 2007), but others have found structure to be weakly related to en route migrant abundance during spring migration (Buler et al. 2007, Martin 1980, Packett and Dunning 2009, Somershoe and Chandler 2004). In the one model in which patch structure was a top variable, BTNWW arrival rates slightly declined with increasing values of PC1, suggesting lower arrival rates at less mature sites (sites with more small and medium trees and fewer large trees). However, the coefficient for the estimate of the relationship overlapped zero. BTNWW arrival rates showed a positive relationship with PC2, suggesting higher arrival rates at sites with more trees (of all sizes) and denser understories. While the 95% CI for the coefficient of that relationship did not overlap zero, habitat structure (PC2) was not as strongly related to BTNWW arrival rates as was patch distance to the coast. Spring migrants in the WLEB have been shown to respond to vegetation structure (Rodewald 2007), but that the pattern was not detected in this study. There may have been too little variation in habitat structure across study sites to detect a pattern between migrant abundance and structural variables. Furthermore, I focused modeling efforts on arrival rates and abundance, which may be more strongly related to broad-scale landscape features than local features (Buler et al. 2007). Fine-scale habitat selection by migrants may be better addressed by focusing modeling efforts on omega or apparent survivorship or alternatively by using radio-telemetry methods. Future efforts could explore how apparent survivorship and stopover duration relates to various local- and broad-scale habitat features.
Detection probability

Observer, time of day, and wind strongly influenced detection rates for transient migrants. Other studies have shown that detection probability can vary among survey observers (Diefenbach et al. 2003, Sauer et al. 1994) and decline with increasing wind conditions (Simons et al. 2007). I found that detection probabilities during migration generally increased with time of day, which is in contrast to numerous other studies that have documented declines in detection probability over the course of morning surveys (Farnsworth et al. 2002, Marques et al. 2007). A decline in detection probability as the morning progresses is expected during the breeding season, as avian singing rates generally decline from sunrise to noon (Bart and Herrick 1984). Since the majority of detections during avian surveys are aural (Brewster and Simons 2009, Dawson and Efford 2009), it is not surprising that this would lead to lower detection probabilities for these species. The lower detection probability that was observed in my study during early morning surveys may have been due to observers being exposed to high singing rates of territorial breeding and transient birds at those times. Observers exposed to a high volume of acoustic cues may have lower detection probabilities than observers exposed to fewer signals (Bart and Schoultz 1984, Simons et al. 2007). For example, Simons et al. (2007) found that observers detected 41 ± 5.2% fewer birds on simulated point counts when there were 3 additional species of birds singing in the background. I also found dramatically different detection probabilities among observers in 2011, which likely resulted from a lower ability of one observer to hear high frequency vocalizations of some species (Emlen and Dejong 1992).
Using guilds can be an effective way to make inferences about a suite of species and to utilize data collected on rarer species for which counts were too low to use in more detailed analyses (Mattsson and Marshall 2009). However, grouping similar species together can also mask species-level variability to environmental gradients, especially for less common species in the guild. I created and used a transient warbler guild in order to understand more general patterns in the stopover habitat-use of transient migrants in the WLEB. I recognize that species in this guild may have had different detection probabilities (Diefenbach et al. 2003, Mattsson and Marshall 2009, Moore et al. 2004, Reidy et al. 2011), which could lead to misleading results. However, I believe differences in detection probability among species were marginal because species in the transient warbler guild were taxonomically similar and shared similar foraging strategies during migration. Moreover, others have had some success using guilds in an occupancy framework while accounting for imperfect detection probability (Mattsson and Marshall 2009). While detection probability was lower for the guild than for single-species models, the presence of larger numbers of guild members on surveys likely made it difficult for observers to track all individuals, resulting in the observed lower detection rates (Bart and Schoultz 1984, Simons et al. 2007).

**Conclusions and management recommendations**

The abundance and distribution of migrants in the WLEB during spring migration was primarily shaped by broad-scale variables including wetland cover, patch isolation, and especially proximity to the coast. There was some year-to-year variability in the raw count totals for some species and in the variables that most strongly influenced the arrival rates and abundance of migrants, which may have resulted, in part, from annual variation.
in weather conditions. In general, lakeshore forests hosted the highest densities of migrants, but this does not necessarily indicate that these areas are of higher quality habitat than more inland forests (Johnson 2007, Van Horne 1983). However, lakeshore forest sites consistently received high use for stopover in both 2011 and 2012 and thus are of conservation value (Mehlman et al. 2005). Larger patches of forest (>20 ha) located between 0.5 to 10 km from the lakeshore are also of high conservation value, particularly those nearer the coast and wetlands, as these patches consistently supported the greatest seasonal abundance of transient migrants in both years. Habitat conservation away from the lakeshore could seek to provide a network of forest patches and potentially travel corridors (e.g., along streams and rivers) that should benefit stopover migrants (Ewert et al. 2006, Mehlman et al. 2005). With limited habitat remaining in the WLEB, the conservation of any forested habitats will likely benefit migratory forest birds. Future conservation efforts should prioritize the protection and restoration of (1) forested areas adjacent the coastline and (2) forested areas within 0.5–10 km of the coast, with priority given to forests that are larger than 20 ha and closer to wetlands and the lakeshore.
Literature Cited


Table 2.1 - Correlation matrix of habitat structure variables used in constructing habitat structure PCA. Habitat structure variables were measured within 30 m of each of the 135 point count locations within the Western Lake Erie Basin of Ohio, USA. The habitat variables used in the matrix were: stemhits = number of understory stems between 0.5 and 3.0 m, small trees = number of trees between 8–23 cm dbh, medium trees = number of trees between 23–38 cm dbh, large trees = number of trees >38 cm dbh, medium and large dead trees = number of medium (23–38 cm dbh), and large (>38 cm dbh) dead ash trees, and average canopy height (m).

<table>
<thead>
<tr>
<th></th>
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<th>medium trees</th>
<th>large trees</th>
<th>stemhits</th>
<th>medium and large dead trees</th>
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<td>medium and large dead trees</td>
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Table 2.2- Factor loadings for the first and second principal component axes (PC1 and PC2) in the habitat structure PCA. The first axis explained 29.2% of the total variation (eigenvalue = 1.75). The second axis explained an additional 28.2% of the total variation (eigenvalue = 1.69). The variables represent components of the habitat structure at each of the 135 point count locations in the Western Lake Erie Basin, Ohio, USA. Variables were measured within 30m of each point count location. The variables are: stemhits = number of understory stems between 0.5 and 3.0 m, small trees = number of trees between 8–23 cm dbh, medium trees = number of trees between 23–38 cm dbh, large trees = number of trees >38 cm dbh, medium and large dead trees = number of medium (23–38 cm dbh), and large (>38 cm dbh) dead ash trees, and average canopy height (m).

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<td>-0.08</td>
<td>0.07</td>
</tr>
<tr>
<td>elm</td>
<td>0.13</td>
<td>-0.07</td>
</tr>
</tbody>
</table>

Table 2.3 - Correlation matrix of counts of trees >23 cm dbh in the eight most abundant tree species groups used in constructing the species composition PCA. Counts of trees by species were made within 30 m of each of the 135 point count locations in the Western Lake Erie Basin of Ohio, USA. The species groups used in the matrix were: oaks (*Quercus* spp.), maples (*Acer* spp.), boxelder (*A. negundo*), eastern cottonwood (*Populus deltoides*), walnuts (*Juglans* spp.), hickories (*Carya* spp.), dead ashes (*Fraxinus* spp.), and elm (*Ulmus* spp.). A Hellinger transformation was performed on the raw species counts to make the data more appropriate for the PCA.
<table>
<thead>
<tr>
<th>Variables</th>
<th>PC1</th>
<th>PC2</th>
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<tbody>
<tr>
<td>oaks</td>
<td>0.741</td>
<td>-0.114</td>
</tr>
<tr>
<td>maples</td>
<td>-0.774</td>
<td>-0.087</td>
</tr>
<tr>
<td>boxelder</td>
<td>0.177</td>
<td>-0.179</td>
</tr>
<tr>
<td>cottonwood</td>
<td>-0.522</td>
<td>0.329</td>
</tr>
<tr>
<td>walnuts</td>
<td>0.699</td>
<td>0.036</td>
</tr>
<tr>
<td>hickories</td>
<td>0.487</td>
<td>0.37</td>
</tr>
<tr>
<td>dead ashes</td>
<td>0.147</td>
<td>0.787</td>
</tr>
<tr>
<td>elms</td>
<td>0.142</td>
<td>-0.709</td>
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</tbody>
</table>

Table 2.4- Factor loadings for the first and second principal component axes (PC1 and PC2) of the species composition PCA. The first axis explained 27.7% of the total variation (eigenvalue = 2.22). The second axis explained an additional 17.8% of the total variation (eigenvalue = 1.42). The variables represent counts of trees >23 cm dbh within the eight most abundant tree species groups. Counts were made within 30 m of each of the 135 point count locations in the Western Lake Erie Basin, Ohio, USA. The species groups are: oaks (*Quercus* spp.), maples (*Acer* spp.), boxelder (*Acer negundo*), eastern cottonwood (*Populus deltoides*), walnuts (*Juglans* spp.), hickories (*Carya* spp.), dead ashes (*Fraxinus* spp.), and elms (*Ulmus* spp.).
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<th>median</th>
<th>minimum</th>
<th>maximum</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>area</td>
<td>30 ha</td>
<td>12 ha</td>
<td>1 ha</td>
<td>498 ha</td>
<td>64 ha</td>
</tr>
<tr>
<td>distance to river</td>
<td>4.5 km</td>
<td>1.6 km</td>
<td>0 km</td>
<td>19 km</td>
<td>4.8 km</td>
</tr>
<tr>
<td>distance to coast</td>
<td>5.6 km</td>
<td>2.9 km</td>
<td>0.03 km</td>
<td>21.8 km</td>
<td>6.4 km</td>
</tr>
<tr>
<td>isolation</td>
<td>0.29</td>
<td>0.23</td>
<td>0</td>
<td>0.89</td>
<td>0.21</td>
</tr>
<tr>
<td>wetland cover</td>
<td>0.36</td>
<td>0.32</td>
<td>0</td>
<td>1</td>
<td>0.35</td>
</tr>
</tbody>
</table>

Table 2.5- Summary statistics for broad-scale variables for the 135 point count locations used in 2011 and 2012. The variables are: area = area (ha) of the forest patch in which the point count was conducted, distance to a river = distance (km) from point count location to the nearest stream or river, distance to coast = distance (km) from point count location to the nearest point of Lake Erie coastline, isolation = proportion of the landscape within 0.5 km of point count location classified as forest, wetland cover = proportion of the landscape within 0.2 km of point count location classified as wetland.
<table>
<thead>
<tr>
<th>Model</th>
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<th>AIC</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>patch isolation + wetland cover</td>
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<td>873.06</td>
<td>0</td>
</tr>
<tr>
<td>distance to coast + isolation + wetland cover</td>
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<td>distance to river + isolation + wetland cover + composition PC1 + composition PC2 + isolation + wetland cover</td>
<td>13</td>
<td>874.27</td>
<td>1.21</td>
</tr>
<tr>
<td>composition PC1 + composition PC2 + isolation + wetland cover</td>
<td>14</td>
<td>875.48</td>
<td>2.42</td>
</tr>
<tr>
<td>structure PC1 + structure PC2 + isolation + wetland cover</td>
<td>14</td>
<td>877.05</td>
<td>3.99</td>
</tr>
<tr>
<td>FULL model (minus area)</td>
<td>18</td>
<td>881.67</td>
<td>8.61</td>
</tr>
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</table>

Table 2.6 - Top models for gamma (arrival rate) for Blackpoll Warbler in 2011. nPars = number of parameters in the model. AIC = Akaike Information Criterion. ΔAIC = Difference in AIC between top-ranked model and specified model. Note that all models include Julian date and a quadratic term for Julian date and that only models with ΔAIC < 10 are shown. Variables in the models are: area = area (ha) of the forest patch in which the point count was conducted, distance to river = distance (km) from point count location to nearest stream or river, distance to coast = distance (km) from point count location to nearest point of Lake Erie coastline, isolation = proportion of the landscape within 0.5 km of point count location classified as forest, wetland cover = proportion of the landscape within 0.2 km of point count location classified as wetland, composition PC1 = species composition PC1, composition PC2 = species composition PC2, structure PC1 = habitat structure PC1, structure PC2 = habitat Structure PC2. FULL model (minus area) = a model with all variables included except patch area (ha).
Table 2.7 - Top models for gamma (arrival rate) for Blackpoll Warbler in 2012. nPars = number of parameters in the model. AIC = Akaike Information Criterion. ΔAIC = Difference in AIC between top-ranked model and specified model. Note that all models include Julian date and a quadratic term for Julian date and that only models with ΔAIC < 5 are shown. Variables in the models are: area = area (ha) of the forest patch in which the point count was conducted, distance to river = distance (km) from point count location to nearest stream or river, distance to coast = distance (km) from point count location to nearest point of Lake Erie coastline, isolation = proportion of the landscape within 0.5 km of point count location classified as forest, wetland cover = proportion of the landscape within 0.2 km of point count location classified as wetland, composition PC1 = species composition PC1, composition PC2 = species composition PC2, structure PC1 = habitat structure PC1, structure PC2 = habitat Structure PC2. FULL model = a model with all variables included except the variable inside the parentheses.
<table>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>distance to coast</td>
<td>-3.61 (-5.29 to -1.93)</td>
<td>-0.27 (-0.46 to -0.1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>distance to river</td>
<td>-0.13 (-0.28 to 0.02)</td>
<td>-0.84 (-1.13 to -0.54)</td>
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<tr>
<td>Julian date</td>
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<td>-1.09 (-1.81 to -0.36)</td>
<td>-1.43 (-1.82 to -1.05)</td>
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</tr>
<tr>
<td>Julian date (quadratic)</td>
<td>-0.87 (-1.32 to -0.43)</td>
<td>-1.08 (-1.35 to -0.81)</td>
<td>-0.95 (-1.54 to -0.36)</td>
<td>-1.1 (-1.4 to -0.79)</td>
</tr>
<tr>
<td>area</td>
<td>-0.9 (-2.1 to 0.3)</td>
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</tr>
<tr>
<td>composition PC1</td>
<td>-0.14 (-0.27 to 0)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>composition PC2</td>
<td>-0.15 (-0.3 to -0.01)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>isolation</td>
<td>-0.71 (-1.01 to -0.41)</td>
<td>-0.14 (-0.29 to 0.02)</td>
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</tr>
<tr>
<td>structure PC1</td>
<td>-0.03 (-0.18 to 0.1)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>structure PC2</td>
<td>0.16 (0.02 to 0.3)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>wetland cover</td>
<td>0.64 (0.4 to 0.89)</td>
<td>0.47 (0.17 to 0.76)</td>
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</table>

Table 2.8- Coefficients for the top variables in the single-species models in each year. 95% confidence intervals for estimates are given inside the parentheses. Note that the data are scaled and centered so interpretation of coefficients should be for strength and direction of relationship. BLPW = Blackpoll Warbler. BTNW = Black-throated Green Warbler. The variables are: area = area (ha) of the forest patch in which the point count was conducted, distance to river = distance (km) from point count location to the nearest stream or river, distance to coast = distance (km) from point count location to nearest point of Lake Erie coastline, isolation = proportion of the landscape within 0.5 km of point count location classified as forest, wetland cover = proportion of the landscape within 0.2 km of point count location classified as wetland, composition PC1 = species composition PC1, composition PC2 = species composition PC2, structure PC1 = habitat structure PC1, structure PC2 = habitat Structure PC2.
<table>
<thead>
<tr>
<th>Model</th>
<th>nPars</th>
<th>AIC</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>distance to river + composition PC1 + composition PC2</td>
<td>13</td>
<td>1855.72</td>
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</tr>
<tr>
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<td>1856.67</td>
<td>0.96</td>
</tr>
<tr>
<td>composition PC1 + composition PC2</td>
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<td>1856.87</td>
<td>1.16</td>
</tr>
<tr>
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<td>14</td>
<td>1857.14</td>
<td>1.43</td>
</tr>
<tr>
<td>distance to river + distance to coast + composition PC1 + composition PC2</td>
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<td>1857.33</td>
<td>1.61</td>
</tr>
<tr>
<td>distance to river + composition PC1 + composition PC2 + isolation</td>
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<td>1857.34</td>
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<tr>
<td>distance to river + composition PC1 + composition PC2 + area</td>
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<td>1857.44</td>
<td>1.73</td>
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<td>wetland cover</td>
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<td>2.65</td>
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<tr>
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<td>1858.63</td>
<td>2.91</td>
</tr>
<tr>
<td>composition PC1 + composition PC2 + area + wetland cover</td>
<td>14</td>
<td>1858.67</td>
<td>2.95</td>
</tr>
<tr>
<td>composition PC1 + composition PC2 + isolation + wetland cover</td>
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<td>1858.67</td>
<td>2.96</td>
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<tr>
<td>composition PC1 + composition PC2 + area</td>
<td>13</td>
<td>1858.72</td>
<td>3.00</td>
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<tr>
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<td>1858.80</td>
<td>3.08</td>
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<td>3.41</td>
</tr>
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<td>1859.13</td>
<td>3.42</td>
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<tr>
<td>distance to river + wetland cover</td>
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<td>1859.21</td>
<td>3.49</td>
</tr>
<tr>
<td>distance to river + distance to coast + area</td>
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<td>1859.40</td>
<td>3.69</td>
</tr>
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</tr>
<tr>
<td>distance to coast + wetland cover</td>
<td>12</td>
<td>1859.62</td>
<td>3.90</td>
</tr>
</tbody>
</table>

Table 2.9 - Top models for gamma (arrival rate) for Black-throated Green Warbler in 2011. nPars = number of parameters in the model. AIC = Akaike Information Criterion. ΔAIC = Difference in AIC between top-ranked model and specified model. Note that all models include Julian date and a quadratic term for Julian date and that only models with ΔAIC < 4 are shown. Variables in the models are: area = area (ha) of the forest patch in which the point count was conducted, distance to river = distance (km) from point count location to nearest stream or river, distance to coast = distance (km) from point count location to nearest point of Lake Erie coastline, isolation = proportion of the landscape within 0.5 km of point count location classified as forest, wetland cover = proportion of the landscape within 0.2 km of point count location classified as wetland, composition PC1 = species composition PC1, composition PC2 = species composition PC2, structure PC1 = habitat structure PC1, structure PC2 = habitat Structure PC2.
Table 2.10 - Top models for gamma (arrival rate) for Black-throated Green Warbler in 2012. nPars = number of parameters in the model. AIC = Akaike Information Criterion. ΔAIC = Difference in AIC between top-ranked model and specified model. Note that all models include Julian date and a quadratic term for Julian date and that only models with ΔAIC < 5 are shown. Variables in the models are: area = area (ha) of the forest patch in which the point count was conducted, distance to river = distance (km) from point count location to nearest stream or river, distance to coast = distance (km) from point count location to nearest point of Lake Erie coastline, isolation = proportion of the landscape within 0.5 km of point count location classified as forest, wetland cover = proportion of the landscape within 0.2 km of point count location classified as wetland, composition PC1 = species composition PC1, composition PC2 = species composition PC2, structure PC1 = habitat structure PC1, structure PC2 = habitat Structure PC2.
<table>
<thead>
<tr>
<th>Model</th>
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<th>ΔAIC</th>
</tr>
</thead>
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<tr>
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<td>1.96</td>
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<td>distance to coast + area</td>
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<td>1.99</td>
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<td>distance to coast + wetland cover</td>
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</tr>
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<td>distance to river</td>
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<td>3.62</td>
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</table>

Table 2.11 – Top gamma (finite rate of increase) models for the transient warbler guild in 2011. nPars = number of parameters in the model. AIC = Akaike Information Criterion. ΔAIC = Difference in AIC between top-ranked model and specified model. Note that all models include Julian date and a quadratic term for Julian date and that only models with ΔAIC < 5 are shown. Variables in the models are: area = area (ha) of the forest patch in which the point count was conducted, distance to river = distance (km) from point count location to nearest stream or river, distance to coast = distance (km) from point count location to nearest point of Lake Erie coastline, isolation = proportion of the landscape within 0.5 km of point count location classified as forest, wetland cover = proportion of the landscape within 0.2 km of point count location classified as wetland, composition PC1 = species composition PC1, composition PC2 = species composition PC2, structure PC1 = habitat structure PC1, structure PC2 = habitat Structure PC2.
<table>
<thead>
<tr>
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<th>ΔAIC</th>
</tr>
</thead>
<tbody>
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<tr>
<td>isolation</td>
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<td>16</td>
<td>8142.37</td>
<td>4.23</td>
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<td>structure PC1 + structure PC2</td>
<td>16</td>
<td>8142.76</td>
<td>4.61</td>
</tr>
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Table 2.12 – Top gamma (finite rate of increase) models for the transient warbler guild in 2012. nPars = number of parameters in the model. AIC = Akaike Information Criterion. ΔAIC = Difference in AIC between top-ranked model and specified model. Note that all models include Julian date and a quadratic term for Julian date and that only models with ΔAIC < 5 are shown. Variables in the models are: area = area (ha) of the forest patch in which the point count was conducted, distance to river = distance (km) from point count location to nearest stream or river, distance to coast = distance (km) from point count location to nearest point of Lake Erie coastline, isolation = proportion of the landscape within 0.5 km of point count location classified as forest, wetland cover = proportion of the landscape within 0.2 km of point count location classified as wetland, composition PC1 = species composition PC1, composition PC2 = species composition PC2, structure PC1 = habitat structure PC1, structure PC2 = habitat Structure PC2.
Figure 2.1 – Location of the study area (defined in purple in the upper right and bottom) in the Western Lake Erie Basin, Ohio, USA. In the upper left and right, darker grey areas bordered in black represent the state of Ohio. Yellow areas in the upper right and left represent the counties in which the study took place.
Figure 2.2 - Point count locations (dots) used in 2011 (grey), in 2012 (white), and in both years (black) within the study area in the Western Lake Erie Basin, Ohio, USA. Distance bands used in the stratified GRTS sampling are shown in yellow (0–0.573 km), orange (0.573–2.648 km), pink (2.648–10.09 km), and blue (10.09–22 km). Forest patches within the study area are shown in green.
Figure 2.3 - Detection probability for Blackpoll Warbler in 2011 as a function of observer and time of day. Grey areas represent 95% confidence intervals for estimated detection probabilities for each observer (colored lines).
Figure 2.4 - Number of Blackpoll Warblers gained between visits to a site (new arrivals) in the Western Lake Erie Basin, Ohio, USA as a function of patch isolation in 2011. The grey area represents the 95% confidence interval of the predicted estimate (black line).
Figure 2.5 - Number of Blackpoll Warblers gained between visits to a site (new arrivals) in the Western Lake Erie Basin, Ohio, USA as a function of date in 2011. The grey area represents the 95% confidence interval of the predicted estimate (black line).
Figure 2.6 - Detection probability for Blackpoll Warblers in the Western Lake Erie Basin, Ohio, USA in 2012 as a function of a categorical estimate for wind speed. Dots represent estimates for detection probability and whiskers represent 95% confidence intervals of the estimates.
Figure 2.7 - Number of Blackpoll Warblers gained between visits to a site (new arrivals) in the Western Lake Erie Basin, Ohio, USA as a function of patch distance from the lakeshore in 2012. The grey area represents the 95% confidence interval of the predicted estimate (black line).
Figure 2.8 - Coefficient estimates and 95% confidence intervals for variables influencing gamma (arrival rate) in the top models for Blackpoll Warbler and Black-throated Green Warbler in 2011 and 2012. The red-dotted line is at X = 0. Variables are: Structure 1 = habitat structure PC1, Structure 2 = habitat Structure PC2, Distance from coast = distance (km) from point count location to nearest point of Lake Erie coastline, Area = area (ha) of the forest patch in which the point count was conducted, Composition 2 = species composition PC2, Composition 1 = species composition PC1, Distance to a River = distance (km) from point count location to nearest stream or river, Date - squared = quadratic of Julian Date, Patch isolation = proportion of the landscape within 0.5 km of point count location classified as forest, Date = Julian date, Wetland cover = proportion of the landscape within 0.2 km of point count location classified as wetland.
Figure 2.9 - Average density of Blackpoll Warblers (individuals per hectare) in forest patches of the Western Lake Erie Basin, Ohio, USA, during each day of 2011 and 2012 spring migrations (approximately 5 May to 30 May annually).
Figure 2.10 - Average number of Blackpoll Warblers per forest patch in the Western Lake Erie Basin, Ohio, USA, during each day of 2011 and 2012 spring migrations (approximately 5 May to 30 May annually).
Figure 2.11- Detection probability for Black-throated Green Warblers in the Western Lake Erie Basin, Ohio, USA in 2011 as a function of observer and time of day. Grey areas represent 95% confidence intervals for estimated detection probabilities for each observer (colored lines).
Figure 2.12 - Number of Black-throated Green Warblers gained between visits to a site (new arrivals) in the Western Lake Erie Basin, Ohio, USA as a function of date in 2011. The grey area represents the 95% confidence interval of the predicted estimate (black line).
Figure 2.13 - Estimated detection probabilities for Black-throated Green Warbler for different observers in the Western Lake Erie Basin, Ohio, USA in 2012. Lines coming off of estimates represent 95% Confidence intervals.
Figure 2.14 - Number of Black-throated Green Warblers gained between visits to a site (new arrivals) in the Western Lake Erie Basin, Ohio, USA in 2012 as a function of distance from the coast. The grey area represents the 95% confidence interval of the predicted estimate (black line).
Figure 2.15 - Number of Black-throated Green Warblers gained between visits to a site (new arrivals) in the Western Lake Erie Basin, Ohio, USA in 2012 as a function of date. The grey area represents the 95% confidence interval of the predicted estimate (black line).
Figure 2.16- Average density of Black-throated Green Warblers (individuals per hectare) within forest patches of the Western Lake Erie Basin, Ohio, USA, during each day of 2011 and 2012 spring migrations (approximately 21 April – 29 May annually).
Figure 2.17- Average number of Black-throated Green Warblers per forest patch in the Western Lake Erie Basin, Ohio, USA, during each day of 2011 and 2012 spring migrations (approximately 21 April to 29 May annually).
Figure 2.18 – Raw counts of individuals in the transient warbler guild by species and year. Counts were made during spring migration in the Western Lake Erie Basin, Ohio, USA. The species are: Black-and-white Warbler (BAWW), Bay-breasted Warbler (BBWA), Blackburnian Warbler (BLBW), Blackpoll Warbler (BLPW), Black-throated Blue Warbler (BTBW), Black-throated Green Warbler (BTNW), Blue-winged Warbler (BWWA), Canada Warbler (CAWA), Chestnut-sided Warbler (CSWA), Cerulean Warbler (CERW), Cape May Warbler (CMWA), Golden-winged Warbler (GWWA), Hooded Warbler (HOWA), Magnolia Warbler (MAWA), Yellow-rumped Warbler (MYWA), Nashville Warbler (NAWA), Northern Parula (NOPA), Orange-crowned Warbler (OCWA), Palm Warbler (PAWA), Pine Warbler (PIWA), Prairie Warbler (PRAW), Tennessee Warbler (TEWA), Wilson’s Warbler (WIWA), and Yellow-throated Warbler (YTWA).
Figure 2.19 - Detection probability for the transient warbler guild in the Western Lake Erie Basin, Ohio, USA as a function of wind speed and observer in 2011. (0) = no wind, (5) = high wind. Whiskers indicate 95% confidence intervals of estimates.
Figure 2.20 - Detection probability for transient warbler guild in the Western Lake Erie Basin, Ohio, USA as a function of time of day and observer in 2011. Grey areas represent 95% confidence intervals for estimated detection probabilities for each observer (colored lines).
Figure 2.21 - Detection probability for the transient warbler guild in the Western Lake Erie Basin, Ohio, USA as a function of wind speed and observer in 2012. (0) = no wind, (4) = high wind. Whiskers indicate 95% confidence intervals of estimates.
Figure 2.22 - Detection probability for the transient warbler guild in the Western Lake Erie Basin, Ohio, USA as a function of time of day and observer in 2012. Grey areas represent 95% confidence intervals for estimated detection probabilities for each observer (colored lines).
Figure 2.23 – Average density of guild members (individuals per hectare) within forest patches of the Western Lake Erie Basin, Ohio, USA, during each day of 2011 and 2012 spring migrations (approximately 19 April to 30 May annually).
Figure 2.24 - Average number of guild members per forest patch within the Western Lake Erie Basin, Ohio, USA, during each day of 2011 and 2012 spring migrations (approximately 19 April to 30 May annually).
Figure 2.25 - Boxplot showing estimated midge abundance at survey locations in the Western Lake Erie Basin, Ohio, USA, in relation to survey date in 2012. Categories used to estimate midge abundance were: (0) = 0 midges, (1) = 1–10 midges, (2) = 11–100 midges, (3) = 101–500 midges, (4) = 501–1000 midges, (5) = 1001–5000 midges, (6) = >5001 midges.
Figure 2.26 – Boxplot showing estimated midge abundance at survey locations in the Western Lake Erie Basin, Ohio, USA, in relation to wetland cover in the landscape in 2012. Categories used to estimate midge abundance were: (0) = 0 midges, (1) = 1–10 midges, (2) = 11–100 midges, (3) = 101–500 midges, (4) = 501–1000 midges, (5) = 1001–5000 midges, (6) = >5001 midges.
Figure 2.27- Boxplot showing estimated midge abundance at survey locations in the Western Lake Erie Basin, Ohio, USA, in relation to distance to coast in 2012. Categories used to estimate midge abundance were: (0) = 0 midges, (1) = 1-10 midges, (2) = 11-100 midges, (3) = 101-500 midges, (4) = 501-1000 midges, (5) = 1000-5000 midges, (6) = >5001 midges.
Figure 2.28 – Pairwise comparisons between transient warbler abundance in each midge abundance category while accounting for Julian date and a quadratic of Julian date. Estimates for the difference in transient warbler abundance between midge abundance categories (Y-axis) are shown on the plot as dots. 95% Tukey family-wise confidence intervals extend from estimated differences. Categories used to estimate midge abundance were: (0) = 0 midges, (1) = 1-10 midges, (2) = 11-100 midges, (3) = 101-500 midges, (4) = 501-1000 midges, (5) = 1000-5000 midges, (6) = >5001 midges. A dotted line is at X = 0. ‘*’ = P < 0.05, ‘**’ = P < 0.01, ‘***’ = P < 0.001.
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