

MOVEMENTS, HABITAT USE, AND STOPOVER DURATION OF MIGRATORY  
SONGBIRDS IN THE WESTERN LAKE ERIE BASIN OF NORTHERN OHIO

A Thesis

Presented in Partial Fulfillment of the Requirements for  
the Degree Master of Science in the  
Graduate School of The Ohio State University

By

Ashley A. Buchanan, B.S.

\*\*\*\*\*

The Ohio State University  
2008

Master's Examination Committee:

Dr. Paul G. Rodewald, Advisor

Dr. Robert J. Gates

Dr. Amanda D. Rodewald

Approved by

---

Advisor  
Graduate Program in Natural Resources



## ABSTRACT

Migration is often considered the most energetically demanding and stressful period during the life cycle of migratory landbirds. Because migrating birds spend the majority of their time in stopover habitats rather than in flight, it is important to our understanding of migration ecology to examine spatial and temporal patterns of bird movements during stopover periods. Stopover habitats are important because they provide migratory birds a place to rest, refuel, and avoid predators. The goal of my research was to evaluate movement behavior and habitat selection of forest patches by migrant songbirds during spring stopover in a highly fragmented, agriculturally dominated landscape during spring. My specific objectives were to 1) assess patterns of movement by these migratory landbirds within and among forest patches, 2) determine how local-level (patch area, habitat type) and landscape-level (habitat connectivity) attributes influence movement rate and patch residence time, and 3) examine factors influencing stopover duration.

I used radio-telemetry to track individual Yellow-rumped Warblers (*Dendroica coronata*; YRWA) and Red-eyed Vireos (*Vireo olivaceus*; REVI) during spring migratory stopover in the western Lake Erie basin of northern Ohio from mid April to early June of 2006 and 2007. Monitoring migrants allowed me to document movement behavior, habitat selection, and stopover duration in this important region for migratory landbirds. In addition, I measured local (within patch) and landscape level habitat

characteristics to evaluate their relative importance in habitat selection. Red-eyed Vireos and Yellow-rumped Warblers were captured, color-banded, and promptly transported to one of five pre-determined release sites. Birds were fitted with a small radio transmitter and released. Experimental relocations of migrants to different sites were used to test for habitat features that influence stopover behavior and to control for arrival timing. As a control for relocated birds, REVI and YRWA were also captured at each of the five release sites, processed, fitted with a radio transmitter, and released within the same site. Location data were collected at 30-minute intervals on days 1, 2, and 3 after capture (YRWA) and days 1 and 2 after capture (REVI). Birds were checked once per day thereafter to determine minimum stopover duration.

A total of 38 YRWA and 31 REVI were radio-tracked from 20 April to 1 June in spring 2006 and 2007. Movement data were analyzed using a generalized linear mixed model with maximum likelihood estimation. The experimental unit was the bird-patch-day, and the response variable was either residence time within patch or movement rate within patch for each bird-patch-day combination. The random effect was the individual bird in both sets of analyses. Fixed effects were patch habitat type, patch area, patch connectivity, year, and translocation. Minimum stopover duration was calculated as the difference (in days) between the initial release date and the date the bird was last relocated in the study area. Data on stopover duration were analyzed for biotic and abiotic effects using a generalized linear model for categorical analysis of Poisson count

data. Following an information-theoretic approach, I used Akaike's Information Criterion with a correction factor for small sample sizes ( $AIC_c$ ) to rank candidate models for both movement behavior and stopover duration of each species.

Both species exhibited high variability in movement behavior. Mean total distance moved per day was 2.2 km for YRWA and 0.9 km for REVI. Mean movement rate ( $m\ min^{-1}$ ) per day was 3.5 for YRWA and 1.8 for REVI. Patch habitat type, area, and connectivity were important in describing variation in patch residence time and movement rate for YRWA. Patch habitat type, patch area, and translocation influenced patch residence time for REVI, but none of these factors was important in describing their movement rates. Mean minimum stopover duration for YRWA was 7.0 days ( $\pm 3.6$  S.D.) in 2006 and 4.8 days ( $\pm 2.7$  S.D.) in 2007. In contrast, mean minimum stopover duration was 1.6 days ( $\pm 0.9$  S.D.) in 2006 and 1.7 days ( $\pm 1.6$  S.D.) in 2007 for REVI. The model that best described stopover duration for YRWA included energetic condition, year, and release site. High variation in candidate models suggested that none of the models adequately described stopover duration for REVI. There was also significant variability in the movement behavior of individuals.

Spring migrants selected and spent more time in mature hardwood, beach ridge, and willow/cottonwood forest, suggesting a higher importance of these habitat types for conservation. Migrants also frequently used hedgerows as travel corridors and foraging locations, an indication that hedgerows may be an important landscape component for

migrants and should be maintained to provide connectivity between habitat patches. Stopover duration in the western Lake Erie basin can last many days for some species suggesting that this study area may significantly contribute to the energetic balance of many migrants. My study suggests that land managers should conserve and restore these important habitats (mature hardwood, willow/cottonwood, and beach ridge forests), so that migrant songbirds have more opportunities to locate resources and efficiently refuel before continuing migration.

## ACKNOWLEDGMENTS

I am grateful to Dr. Paul Rodewald for his advice and assistance throughout my graduate school endeavors and for his faith in me as a graduate student and wildlife professional. I thank my advisory committee, Drs. Robert J. Gates, Amanda D. Rodewald, and Thomas A. Waite, for valuable contributions to my research, for fostering critical thinking skills, and for support throughout the process. This work was funded by the Federal Aid in Wildlife Restoration Program (W-134-P, Wildlife Management in Ohio), and administered jointly by the U.S. Fish and Wildlife Service and the Ohio Division of Wildlife. Thank you to the Terrestrial Wildlife Ecology Lab (TWEL) and the School of Environment and Natural Resources at The Ohio State University for providing financial and logistical support. Thank you to the USFWS-Ottawa National Wildlife Refuge and ODNR-Division of Wildlife for permitting access to refuge and state lands and assisting in numerous other ways. Thank you to Black Swamp Bird Observatory for aid in capturing migrants. I am very grateful to all the graduate students in the OSU Terrestrial Wildlife Ecology Lab, especially those of the Rodewald lab, for guidance, encouragement, and friendship throughout the research process. In particular, I give a special thank you to Hunter Anderson and Steve Matthews for help with statistics and Jared Duquette and Jake Straub for help using GIS software. I also thank the many dedicated field technicians for their hard work during data collection: Luke DeGroot, Annie Lindsay, Lauren MacDade, Lisa Fitzgerald, Meg McEnroe, Kerry McGuire,

Samantha Franks, James Junda, Heather Hareza, and Jennifer Detweiler. Thank you to Ed Folts and Dennis Hull, TWEL Program Managers, for coordinating field vehicles, field assistants, and helping with numerous other project-related issues. Thank you to all OSU SENR staff for processing paperwork related to purchasing field equipment as well as hiring and paying field assistants. Thank you dear family and friends, for your patience and encouragement while conducting this research. I'd like to give a special thank you to my mom, Janet Bulloch, and dad, Randy Buchanan, for encouraging my passion for the natural world and supporting me in the pursuit of my hopes and dreams. Thank you, Dad, for assisting me with field work all over the country throughout the past several years, including field work for this graduate research. Finally, thank you Hunter Anderson for your love, support, and patient understanding and for helping make this a great experience.

## VITA

### Education

2003..... B.S. Wildlife and Fisheries Ecology, Oklahoma  
State University, Stillwater, Oklahoma

### Professional Experience

Sept 2007 – present.....SCEP Student Trainee, National Wildlife Refuge  
System, United States Fish and Wildlife Service

June – Sept 2007.....STEP Biological Science Technician, United  
States Fish and Wildlife Service

Sept 2005 – present.....Graduate Teaching and Research Associate,  
The Ohio State University, Columbus, Ohio

Apr – June 2005..... Field Biologist, The Ohio State University,  
Columbus, Ohio

Apr – Aug 2004..... Field Research Crew Leader, Kansas State  
University

Oct 2003 – Mar 2004..... Field Biologist, The Institute for Bird Populations

May – Aug 2003..... Field Biologist, Iowa State University

May – Aug 2002..... Field Biologist, Oklahoma State University

## FIELDS OF STUDY

Major Field: Environment and Natural Resources

## TABLE OF CONTENTS

	Page
Abstract.....	ii
Acknowledgments.....	vi
Vita.....	viii
List of Tables .....	xii
List of Figures.....	xiv
Chapters:	
1 Overview.....	1
Introduction.....	1
Stopover duration and timing of migration.....	3
Energetic demands of migration .....	5
Habitat selection en route.....	7
Radio telemetry.....	10
Study System .....	12
Description of study area .....	12
Landbird migration in the western Lake Erie basin.....	14
Focal species .....	15
Literature Cited .....	17
2 Movements of two songbird species during spring migration in a fragmented landscape.....	23
Introduction.....	23
Study Area .....	25
Methods.....	26
Capturing migrants.....	27
Radio-tracking.....	28
Measurement of habitat and landscape characteristics .....	30

	Statistical analyses .....	31
	Results.....	34
	Discussion.....	37
	Literature Cited.....	42
3	Influence of energetic condition and arrival date on spring stopover duration of two migratory landbird species .....	62
	Introduction.....	62
	Study Area .....	65
	Methods.....	66
	Statistical analyses .....	69
	Results .....	71
	Discussion.....	73
	Literature Cited.....	78
	Bibliography .....	88

## LIST OF TABLES

Table	Page
2.1	Sample sizes of translocated (trans) and locally-released (local) Yellow-rumped Warblers (YRWA) and Red-eyed Vireos (REVI) in each of five release sites in the western Lake Erie basin of northern Ohio in spring 2006 and 2007 .....46
2.2	Patch-level attributes of habitat types measured within 0.04-ha circular plots in the western Lake Erie basin of northern Ohio in 2006 and 2007. Summary statistics included median and range for canopy height (ft); number of snags, logs, and stumps; number of stem hits in 5 height classes (0.5-3.0 m); number of small shrubs < 2.5 cm dbh; number of large shrubs 2.5-8 cm dbh; number of small trees 8-23 cm dbh; number of medium trees 23.1-38 cm dbh; number of large trees > 38 cm dbh .....47
2.3	Log odds ratios and associated significance for the relationship between habitat use and availability conditional on habitat type. Cochran-Mantel-Haenszel tests of association were performed on each habitat type because the Breslow-Day test was significant. Results are presented for both Yellow-rumped Warblers (YRWA) and Red-eyed Vireos (REVI) in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Confidence intervals that do not contain zero indicate significant associations, suggesting habitats were used out of proportion to their availability .....48
2.4	Model selection describing patch residence time of Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Generalized linear mixed models were used. Model diagnostics include $AIC_c$ values, $\Delta AIC_c$ , and Akaike weights ( $\omega_i$ ). Abbreviations are Habitat = patch habitat type; Area = patch area; Connect = patch connectivity, Trans = translocation. Models with $\Delta AIC_c < 2$ are shown in bold text .....49
2.5	Model selection describing patch residence time of Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Generalized linear mixed models were used. Model diagnostics include $AIC_c$ values, $\Delta AIC_c$ , and Akaike weights ( $\omega_i$ ). Abbreviations are

	Habitat = patch habitat type; Area = patch area; Connect = patch connectivity; Trans = translocation. Models with $\Delta AIC_c < 2$ are shown in bold text. ....	50
2.6	Model selection describing movement rate ( $m \text{ min}^{-1}$ ) of Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Generalized linear mixed models were used. Model diagnostics include $AIC_c$ values, $\Delta AIC_c$ , and Akaike weights ( $\omega_i$ ). Abbreviations are Habitat = patch habitat type; Area = patch area; Connect = patch connectivity; Trans = translocation. Models with $\Delta AIC_c < 2$ are shown in bold text .....	51
2.7	Model selection describing movement rate ( $m \text{ min}^{-1}$ ) of Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Generalized linear mixed models were used. Model diagnostics include $AIC_c$ values, $\Delta AIC_c$ , and Akaike weights ( $\omega_i$ ). Abbreviations are Habitat = patch habitat type; Area = patch area; Connect = patch connectivity; Trans = translocation. Models with $\Delta AIC_c < 2$ are shown in bold text .....	52
3.1	Descriptive statistics for stopover duration of Yellow-rumped Warblers (YRWA) and Red-eyed Vireos (REVI) in the western Lake Erie basin of northern Ohio in spring 2006 and 2007 .....	82
3.2	Model selection describing stopover duration of Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Generalized linear models for categorical analysis of Poisson data were used. Model diagnostics include model deviance, number of parameters (K), $AIC_c$ values, $\Delta AIC_c$ , and Akaike weights ( $\omega_i$ ). Abbreviations are C = energetic condition; Y = year; R = release site, T = translocation, A = arrival date. Models with $\Delta AIC_c < 2$ are shown in bold text.....	83
3.3	Model selection describing stopover duration of Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Generalized linear models for categorical analysis of Poisson data were used. Model parameters include model deviance, number of parameters (K), $AIC_c$ values, $\Delta AIC_c$ , and Akaike weights ( $\omega_i$ ). Abbreviations are C = energetic condition; T = translocation; A = arrival date; R = release site. Models with $\Delta AIC_c < 2$ are shown in bold text.....	84

## LIST OF FIGURES

Figure	Page
2.1	Digital map depicting release locations (stars) of Yellow-rumped Warblers and Red-eyed Vireos within the study area (black outline) in northern Ohio in spring 2006 and 2007. Release locations were Crane Creek (1), Shop Woods (2), Butternut (3), MS5 Woods (4), and West Crane Creek (5). The study area was delineated by calculating a 100% Minimum Convex Polygon for all telemetry locations (circles) .....53
2.2	Stopover movements of a locally-released, second-year male Yellow-rumped Warbler in the western Lake Erie basin in April 2006. Movements were plotted on the digital map of the study area .....54
2.3	Stopover movements of a locally-released Red-eyed Vireo in the western Lake Erie basin in May 2006. Movements were plotted on the digital map of the study area .....55
2.4	Mean movement rate ( $\text{m min}^{-1}$ ) during three days following release for Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. The interquartile range is displayed, as well as minimum and maximum observations. ....56
2.5	Daily mean movement rate ( $\text{m min}^{-1}$ ) in relation to capture date for Yellow-rumped Warblers during the first three days of radio-tracking in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Mean movement rate was averaged across the first three days for each individual. No relationship was detected ( $p = 0.136$ ) .....57
2.6	Daily mean movement rate ( $\text{m min}^{-1}$ ) in relation to capture date for Red-eyed Vireos during the first day of radio-tracking in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. There was a significant, negative relationship between mean movement rate and arrival date ( $p = 0.04$ ) .....57
2.7	Percent availability of habitat types, area (ha) of available habitat types, and percent use of habitat types for Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007 .....58

2.8	Percent availability of habitat types, area (ha) of available habitat types, and percent use of habitat types for Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007.....	58
2.9	Log odds ratios indicating the direction and magnitude of association between habitat use and availability for Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Negative associations indicate avoidance, and positive associations indicate selection; significant associations noted with an asterisk. Error bars represent 95% confidence limits for the Cochran-Mantel-Haenszel estimate of association .....	59
2.10	Log odds ratios indicating the direction and magnitude of association between habitat use and availability for Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Negative associations indicate avoidance, and positive associations indicate selection; significant associations noted with an asterisk. Error bars represent 95% confidence limits for the Cochran-Mantel-Haenszel estimate of association .....	60
2.11	Patch residence time within different habitat types for Yellow-rumped Warblers in the western Lake Erie basin in spring 2006 and 2007. Patch residence time in mature hardwood forest was significantly different than in early successional forest. ....	61
2.12	Patch residence time within different habitat types for Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Patch residence time in mature hardwood forest was significantly different than in beach ridge forest and early successional forest .....	61
3.1	Map depicting release locations of Yellow-rumped Warblers and Red-eyed Vireos within Ottawa National Wildlife Refuge in northern Ohio, in spring 2006 and 2007. Release locations were Crane Creek (1), Shop Woods (2), Butternut (3), MS5 Woods (4), and West Crane Creek (5) .....	85
3.2	Stopover duration (days) of Yellow-rumped Warblers and Red-eyed Vireos in the western Lake Erie basin of northern Ohio, spring 2006 and 2007.....	86

3.3	Relationship between stopover duration (days) and energetic condition (size-adjusted body mass) for Yellow-rumped Warblers and Red-eyed Vireos in the western Lake Erie basin of northern Ohio, spring 2006 and 2007. Energetic condition was calculated using the residuals from a linear regression of the first principal component score of the multivariate associations between wing chord and tarsus measurements on body mass. Positive condition scores (i.e. residuals) indicate birds in better than average condition relative to all individuals captured for a species. Yellow-rumped Warblers in better energetic condition than expected for their body size stayed shorter durations than birds in poorer energetic condition.....	86
3.4	Relationship between stopover duration and release site for Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Bars indicate mean stopover duration ( $\pm$ S.E.) for YRWA released within five release sites.....	87

## CHAPTER 1

### INTRODUCTION

Each spring hundreds of species of migratory birds leave their southerly wintering grounds (tropical or temperate) to fly north to temperate breeding grounds. Small migratory landbirds are unable to accomplish this feat in one non-stop flight and they must stop several times along their migratory route to rest and rebuild energy reserves before they are able to continue migration (Berthold 1975, Blem 1980). Stopover habitats are important because they provide migratory birds a place to rest, refuel, and avoid predators. For migrants completing a trans-Gulf migration, stopover habitats are also utilized for muscle repair and to rebuild digestive function (Aborn and Moore 2004). Stopover habitats where migrants can safely and rapidly restore depleted fat stores must be available for migration to be successful (Moore et al. 1995), especially in areas used by very large numbers of landbird migrants, such as the Great Lakes.

Migration is often considered the most stressful and demanding period during the life cycle of migratory landbirds, because migrants encounter numerous difficulties en route and have several physiological challenges to overcome. Challenges faced by migrants include high energetic demands, balancing the trade-off between predator avoidance and foraging, competing with residents and other migrants for food, infection by parasites and pathogens, limited development of vegetation in early spring, variable

wind patterns, adverse weather (e.g. late season snow storms), and errors in navigation (reviewed by Moore et al. 1995). Challenges are greater for younger birds that are less experienced at foraging and avoiding predators (Ketterson and Nolan 1982, Alerstam 1990, Loria and Moore 1990). Although each stopover area presents new challenges that migrants must overcome, difficulties encountered during migration should be lessened by the availability of high quality stopover habitats.

Unless stopover habitat requirements are met, conservation efforts focusing on migratory birds will be compromised (Moore et al. 1995, Moore 2000, Petit 2000). This is especially important because events during the non-breeding period may influence breeding season events (Sherry and Holmes 1995, Marra et al. 1998, Sillett et al. 2000, Sillett and Holmes 2002, Newton 2004). Information on stopover ecology is needed for conservation planning for migratory birds (Woodrey 2000) and becomes more important as humans continue to modify landscapes, especially in coastal areas of North America (Simons et al. 2000). Where critical habitats occur and how they are changing in their availability as development and land conversion continues are important conservation issues (Moore and Simons 1992, Moore et al. 1995).

Research on events during migration has received insufficient attention, in part due to the difficulties of studying migrating birds (Moore et al. 1995, Petit 2000). Few studies have investigated movement behavior and habitat selection of landbirds during migratory stopover. This paucity of information is of concern because mortality during migration may be substantial (Ketterson and Nolan 1982, Newton 2004, Sillett and Holmes 2002). For example, recent long-term research suggests that as much as 85% of annual adult mortality in Black-throated Blue Warblers (*Dendroica caerulescens*) may be

attributed to events that occur during the migratory period (Sillett and Holmes 2002). Although additional research is needed, this study suggests that migration events could also limit populations of other migratory landbird species. In addition, loss or degradation of habitats used during migration could contribute to population declines of migratory birds (Moore 2000).

My research examined the movement behavior of two migratory landbird species to determine how local habitat and landscape attributes influence migratory stopover in a fragmented forest area in the western Lake Erie basin of northern Ohio. I used radio-telemetry to track individual Yellow-rumped Warblers (*Dendroica coronata*) and Red-eyed Vireos (*Vireo olivaceus*) during spring migratory stopover from mid April to early June of 2006 and 2007. Monitoring migrants allowed me to document movement behavior, habitat selection, and stopover duration in this important region for migratory landbirds. Local (within-patch) and landscape-level habitat characteristics also were measured and evaluated to determine their relative importance in habitat selection.

### Stopover duration and timing of migration

Most Nearctic-Neotropical migrants spend approximately 3-4 months on the breeding grounds, 5-6 months on the wintering grounds, and 2-4 months migrating between the two areas (Keast and Morton 1980). During migration, birds spend the majority of their time in stopover areas rather than in flight (Hedenstrom and Alerstam 1997, Wikelski et al. 2003). Where and how long a migrant stops to rest and feed depends on many factors both intrinsic and extrinsic to habitat. Intrinsic factors relate to the quality or suitability of habitat, and include resource availability, protection from

predators, and refueling potential. Extrinsic factors include those unrelated to habitat, such as overall migratory routes, innate spatiotemporal programs, weather patterns, energetic condition, and knowledge gained from past experiences (Hutto 1985b, Moore et al. 1995).

Although there is little known about which factors, whether environmental and/or endogenous, regulate stopover duration (Schaub and Jenni 2001), a few hypotheses have been proposed. First, theoretical models predict that migratory strategies differ depending on which optimization criteria birds are minimizing: time, energy, or predation risk. Speed of the migratory journey is considered the most important and widely used stopover strategy (Alerstam and Lindstrom 1990). According to optimal migration theory, if birds minimize time spent in migration then stopover duration depends on a bird's energetic condition and its ability to rapidly regain fat stores (Alerstam and Lindstrom 1990). Energetic condition upon arrival (i.e. fat stores) is considered the most important extrinsic constraint during migration (Hutto 1985b, Loria and Moore 1990, Moore et al. 1995, 2005), but other factors such as adequate resource availability, weather, age, experience and social status are also important (Moore et al. 2005). The probability of staying at a particular stopover site may also depend on habitat suitability, even for lean migrants needing to quickly gain mass during stopover (Graber and Graber 1983, Kuenzi et al. 1990). The Marginal Value Theorem predicts that time-minimizing migrants should resume migration from stopover sites when the marginal rate of gain in the distance a migrant is able to fly falls below the expected average movement speed of the migration route (Alerstam and Lindstrom 1990).

Other hypotheses proposed to explain stopover duration suggest that migrants may respond to an innate spatiotemporal program of flights and stopovers (Jenni and Schaub 2003), or that weather (especially wind) conditions (Akesson and Hedenstrom 2000) or predation risk may drive a bird's choice to stay or depart even under poor energetic condition (Alerstam and Lindstrom 1990). Tsvey et al. (2007) found no relationship between energetic condition and stopover duration and that migratory departures occurred under varying weather conditions (sometimes even unfavorable weather) suggesting that innate spatiotemporal programs may drive stopover duration. Fransson and Weber (1997) found that Blackcaps (*Sylvia atricapilla*) had a higher tendency to leave a stopover site after exposure to predator dummies, suggesting that predation risk also influenced stopover duration.

Lean migrants generally stay longer at stopover sites than birds in better energetic condition with fat reserves (Moore and Kerlinger 1987, Kuenzi et al. 1991) and thus, are more likely to gain mass during stopover (Loria and Moore 1990, Moore and Yong 1991). For these reasons, lean migrants may arrive later than normal on the breeding grounds. Since natural selection favors timely arrival on the breeding grounds (Francis and Cooke 1986), staying longer at stopover sites should lower the likelihood of successful reproduction.

### Energetic demands of migration

A successful migration is measured in terms of survival and subsequent reproductive success (Smith and Moore 2003). How well a migrant is able to meet demands encountered en route depends on several factors including the intrinsic

suitability and availability of stopover habitat, time and energy allotted for selecting among alternative habitats, and the probability of survival during migratory events (Moore and Simons 1992). Most migrants arrive at stopover sites with depleted fat stores and must restore them to appropriate levels before initiating another migratory flight. Birds will minimize their time spent in migration if they are able to quickly restore energy reserves through foraging. Migrants that arrive early on breeding grounds and in better energetic condition have a higher likelihood of survival and successful reproduction (Smith and Moore 2005).

When landing at a stopover site, it is adaptive for migrants to have an adequate “margin of safety” in fat reserves (Alerstam and Lindstrom 1990). Lean migrants are considered to have a smaller safety margin buffering against potential adverse conditions (e.g. poor weather, low food availability) than migrants with fat stores. However, migrants can respond to energetic demand by adjusting foraging behavior at stopover sites. For example, after crossing the Gulf of Mexico, lean Red-eyed Vireos along the northern coast expanded their use of within-patch habitat and type of foraging maneuvers, and had higher mean movement rates and turning rates compared to fat migrants (Loria and Moore 1990).

High quality stopover sites with adequate resource availability are critical for fat deposition and a timely and successful migration. However, a migrant’s ability to put on mass may also be affected by competition with residents and other migrants for limited resources, poor weather conditions, and balancing the trade-off between foraging needs and risk of predation. For example, White-eyed Vireos (*Vireo griseus*), Kentucky Warblers (*Oporornis formosus*), and Tennessee Warblers (*Vermivora peregrina*)

captured during spring stopover along the northern Gulf coast during days of low migrant abundance gained more mass than those captured on days of high migrant abundance (Moore and Yong 1991). Similarly, Wilson's Warblers (*Wilsonia pusilla*) using fall stopover areas in the Middle Rio Grande Valley of New Mexico exhibited density-dependent mass gain during stopover (Kelly et al. 2002). Cimprich et al. (2005) reported that Blue-gray Gnatcatchers (*Polioptila caerulea*) and American Redstarts (*Setophaga ruticilla*) during autumn stopover on the Alabama coast responded to predation risk by Sharp-shinned Hawks (*Accipiter striatus*). As the number of hawks increased, Blue-gray Gnatcatchers and American Redstarts responded by moving deeper into dense shrub cover and gnatcatchers also decreased their foraging and movement rates. This type of response to predation risk could negatively impact refueling rates.

#### Habitat selection *en route*

At the end of a migratory flight, one of the first decisions a migrant makes is where to settle, a decision which has consequences relating to migration timing and energetic condition (Moore et al. 2005). Migrants ending flight sometime during the night probably initially select habitat in the early morning (pre-dawn) hours (Moore et al. 1995), but mechanisms and cues used to assess habitat are largely unknown (Moore and Aborn 2000). Habitat selection by migrants in stopover areas may be innate (Barlein 1983), but Johnson (1980) and Orians and Wittenberg (1991) suggested habitat selection occurs in a hierarchical sequence of behavioral responses, with different environmental cues becoming important at different stages of selection. The hierarchy is described in four orders of habitat selection. First-order selection can be defined as selection of

physical or geographical ranges for a species. Second-order selection determines the home range of an individual or social group. Third-order selection determines usage of various habitat components within the home range. Fourth-order selection involves choosing food items from those available at site, if third-order selection determines a feeding site (Johnson 1980).

Hutto (1985b) described hierarchical habitat selection relative to migratory birds, with a migrant first settling at a new stopover site based on broad habitat features, such as vegetation structure or density. This choice, or possibly simply avoidance of other sites, may be a result of that site bearing some resemblance to habitats previously experienced. The decision to continue local movement or to search for resources within the area may depend on behavior of other migrants or on more specific habitat features (Moore and Aborn 2000). Since migrants use stopover habitat for multiple reasons, when selecting habitat en route a fat-depleted migrant may react to different habitat features compared to a migrant simply looking to rest safely (Moore and Aborn 2000). However, characteristics affecting quality of a stopover site and how those characteristics vary among species remain unknown (Dunn 2000).

Selecting suitable habitat requires time for migrants to explore and familiarize themselves with the distribution and abundance of resources (Moore et al. 1990) and also to locate places safe from predators (Aborn and Moore 1997). Exploration, characterized by infrequent crossing of paths and low turning rate, may be one way birds collect information about available resources and safe places to hide from predators (Aborn and Moore 1997). Although birds may benefit by increasing their familiarity with a stopover

site, there are costs associated with acquiring this information, such as increased predation risk (Aborn and Moore 1997).

Migrants actively select among available habitats during stopover (Moore et al. 1990, Moore and Aborn 2000, Petit 2000). Non-random patterns of habitat selection are exhibited when use of habitat is disproportional to availability. For example, of five habitat types available to Nearctic-Neotropical landbird migrants in spring along the northern Gulf coast, shrub/scrub represented only 14% of available habitat, yet had the greatest number of species and individuals, and the highest species diversity (Moore et al. 1990). During fall, migrants stopping over in central Pennsylvania consistently used mature edge-dominated and shrub-sapling forests more frequently than mature forest interior or pole-stage forests (Rodewald and Brittingham 2004).

Habitat selection is also demonstrated when changes in food availability result in seasonal shifts in use of habitat types and when species-specific patterns of distribution vary among habitats but remain similar over time. Insectivorous passerine migrants in southeastern Arizona shifted habitat use between fall and spring migratory stopovers in concert with shifts in the availability of insect prey (Hutto 1985a). Similarly, distribution, abundance, and energetic condition of migratory birds at a spring stopover site in southern Illinois were related to arthropod abundance (Graber and Graber 1983). Migrants on fall stopover in southwestern Germany demonstrated year-to-year consistency in species-specific habitat selection (Barlein 1983).

Although migrants should prefer certain stopover habitats over others if there are consequences for survival and fitness (Hutto 1985b, Moore et al. 1990, 1995), the threshold for habitat acceptance decreases over time and migrants may select less suitable

habitat if time is a constraint (Moore and Aborn 2000). Searching for alternative habitats exposes highly mobile organisms to higher predation risk, so these organisms may limit their search even when current habitat turns out to be of poorer quality than expected. Furthermore, favorable stopover habitat is considered to be limited in an absolute sense because migrating birds have little time to search for the highest quality stopover sites (Moore 2000).

### Radio telemetry

Radio telemetry has the potential to produce detailed information on the spatial and temporal movement patterns of animals and is therefore a powerful tool for researchers (Aebischer et al. 1993). Radio telemetry has recently become more commonly used in field research on the movements of small landbirds (Rappole and Tipton 1991, Sykes et al. 1990). Habitat use and breeding season movements have been documented for Ovenbirds (*Seiurus aurocapillus*) in Georgia (Lang et al. 2002). In other work with Ovenbirds, forest edge use during the breeding season (Mazerolle and Hobson 2003) and post-fledging movements (Bayne and Hobson 2001) were studied in central Saskatchewan. Movement patterns have been studied on the wintering grounds for Wood Thrush in Mexico (*Hylocichla mustelina*) (Winker et al. 1990) and for six species of grassland sparrows in Arizona (Gordon 2000).

More recently, researchers have begun to use radio telemetry to study migratory stopover. Researchers have successfully used telemetry to study movements (Aborn and Moore 1997, Moore and Aborn 2000) and activity budgets (Aborn and Moore 2004) of Summer Tanagers (*Piranga rubra*) during stopover following spring migration across the

Gulf of Mexico. Tietz and Johnson (2007) documented habitat selection during fall migration by juvenile Swainson's Thrushes (*Catharus ustulatus*) in California. Biotic and abiotic effects influencing fall migratory departure (Tsvey et al. 2007), nocturnal departure time (Bolshakov et al. 2007), movement behavior (Chernetsov and Mukhin 2006), and stopover duration (Chernetsov and Mukhin 2006, Tsvey et al. 2007) have been studied using radio-marked European robins (*Erithacus rubecula*) on the Eastern Baltic coast of Russia. Stopover duration has been estimated using radio telemetry of Orphean Warblers (*Sylvia hortensis*) in Mauritania, Africa (Bachler and Schaub 2007).

Although radio transmitters have only recently become small and light enough for attachment to small birds, our understanding of transmitter effects on small birds is rapidly improving. However, several studies have detected no apparent transmitter effects. Sykes et al. (1990) compared three different techniques for attachment of 1-g radio transmitters to captive Common Yellowthroats (*Geothlypis trichas*) and reported no short-term transmitter effects and no apparent changes in flying ability or behavior for the attachments methods. They reported that 90% of Common Yellowthroats remained in excellent physical condition for the full 30-day study period. Powell et al. (1998) found that Wood Thrushes (*Hylocichla mustelina*) successfully carried a 1.6 g radio transmitter (4% of mean body mass) for 2 years, with no apparent effects on survival or behavior. Similarly, transmitters weighing less than 4% body mass did not affect survival of fledgling Lark Buntings (*Calamospiza melanocorys*) in Colorado (Adams et al. 2006), Great Tits (*Parus major*), or Coal Tits (*P. ater*) in Switzerland when compared to fledglings marked only with color bands (Naef-Daenzer et al. 2001). There were also no apparent transmitter effects on behavior or movements of Great and Coal tits (Naef-

Daenzer et al. 2001), or Ovenbirds breeding in central Saskatchewan (Mazerolle and Hobson 2003). Bolshakov et al. (2007) reported no transmitter discomfort for radio-tagged European robins that were re-captured in mist-nets. Further, based on attributes of flight aerodynamics (i.e. body mass, flight velocity, flight power), smaller birds may be better able to carry heavier loads relative to their body size than larger birds such as waterfowl (Caccamise and Hedin 1985).

## STUDY SYSTEM

### Description of study area

My research was conducted in the western Lake Erie basin of Lucas and Ottawa counties in northwestern Ohio, a highly fragmented region dominated by agricultural and to a lesser extent urban and suburban land uses. Study sites were located within the Ottawa National Wildlife Refuge (NWR) complex which totals 3,366 ha (Ottawa NWR 2000). The refuge complex consists of Ottawa NWR, Cedar Point NWR, and West Sister Island NWR. Migrant landbirds were captured in both years at Cedar Point NWR (41° 41' N, 83° 19' W), Ottawa NWR (41° 37' N, 83° 12' W) and in 2006 within the Navarre Unit (41° 36' N, 83° 04' W) of Ottawa NWR, a 239 ha research unit where Black Swamp Bird Observatory (BSBO) has conducted long-term monitoring of landbird migrants. Cedar Point NWR (990 ha) and Ottawa NWR (1,446 ha) management units both contain coastal marshes, wetlands, wet prairies, hardwood forests, beach ridge forests, and managed and unmanaged impoundments (Ottawa NWR 2000).

This region was historically part of the 121,410 ha Great Black Swamp which formed during the Wisconsin glaciation. This extensive swamp forest was dominated by pin oak (*Quercus palustris*), swamp white oak (*Q. bicolor*), red maple (*Acer rubrum*), American elm (*Ulmus americana*) and black ash (*Fraxinus nigra*) (Cooperrider et al. 2001). After draining and clearing the region for transportation, settlement, and agriculture between 1860 and 1885 (Peacefull 1996), only 10% of original wetland habitat now remains (Ottawa NWR 2000).

Today, the remaining forest consists of small and often isolated habitat patches of various sizes. Terrestrial forest habitats include beach ridge, willow/cottonwood (*Salix/Populus*), mature hardwood, early successional, and hedgerow. Remnant beach ridge forest habitat occurs along the lake shoreline, is structurally heterogenous and dominated by willow and cottonwood trees and dogwood shrubs (*Cornus spp.*). These small forests are characterized by sandy soils, a relatively open canopy and moderate to dense understory vegetation. Willow/cottonwood forest occurs in wetlands and in pockets along diked impoundments and consists of mature and young willow and cottonwood trees and areas of understory shrubs. Mature hardwood deciduous forest consists of tall, mature broadleaf trees with a closed canopy, typically sparse understory vegetation and infrequent tree fall gaps. Ash (*Fraxinus spp.*), maple (*Acer spp.*), hickory (*Carya spp.*), and oak (*Quercus spp.*) dominate these mature forests. Early successional forest ranges in type from dense dogwood shrub thickets to younger willow and cottonwood trees and saplings mixed with dense understory shrubs. Hedgerows occur in linear strips along edges of fields and dikes and include early successional forest and willow/cottonwood forest types.

## Landbird migration in the western Lake Erie basin

Large bodies of water, such as the Great Lakes or Gulf of Mexico, or deserts, such as the Sahara, are considered ecological barriers and often present challenges to migratory birds. Wind drift, orientation errors, and inadequate energy stores are magnified when long-distance migrants face ecological barriers en route (Alerstam 1990), especially for less experienced young birds (Alerstam 1990, Loria and Moore 1990). As migrants encounter large bodies of water they either decide to land or continue their migration around or directly over water. That decision may depend on the species involved (e.g. *buteos* require thermals to migrate and rarely cross the Gulf of Mexico), but it also likely depends on the individual's energetic condition and the risk of encountering hazardous conditions while crossing (Akesson et al. 1996, Bruderer and Liechti 1998).

Migrants accumulate in high densities along the southwestern shores of Lake Erie during spring migration because many smaller birds are reluctant to cross the large expanse of open water. Migrant bird concentrations of the magnitude found in northern Ohio are rare in Midwestern states (Ottawa NWR 2000, Shieldcastle et al. 2004), making this region continentally significant for bird conservation. Because little natural habitat remains in this region, small remnant habitat patches should represent important stopover habitat for very large numbers of migrating landbirds (Ewert and Hamas 1995).

During April, May, and June, land within a few miles of the lake shore remains cooler than inland areas because lake water temperatures change more slowly than on land (Peacefull 1996). Lakeshore winds lower air temperatures, resulting in delayed development of shoreline vegetation compared to inland areas (Smith et al. 1998). This

lake effect also influences abundance and activity of insect prey, creating lower numbers of lepidopteran larvae near the shoreline relative to areas inland (Smith et al. 1998, Smith et al. 2004). Nonetheless, hatches of midges (Chironomidae) near the shoreline seem to attract migrating birds to shoreline habitats. For example, migrant Black-throated Green Warblers (*Dendroica virens*) were more abundant within shoreline habitat of Lake Huron than in inland areas most likely due to large midge hatches that occur within 0.4 km of the lakeshore (Smith et al. 1998). Midges may be an important dietary component for migrants in spring during a time when availability of other prey is low (Dallman and Smith 1995, Smith et al. 1998); this may be especially true for early migrants that often face cold temperatures and may precede leaf-out by up to 2-3 weeks (P.G. Rodewald unpubl. data). Other species of migrants have been documented foraging extensively on midges, including Palm Warblers (*Dendroica palmarum*), Yellow-rumped Warblers (Dallman and Smith 1995), Common Yellowthroat, Chestnut-sided Warblers (*Dendroica pensylvanica*), and American Redstarts (Smith et al. 1998).

#### Focal species

Yellow-rumped Warblers and Red-eyed Vireos were selected as focal species for this research because they are common in the study area during spring migration and large enough to carry small (0.43-0.66 g) radio transmitters. Yellow-rumped Warblers are short-distance (temperate) migrants, inhabiting deciduous, coniferous, and mixed forests, as well as edges of woods and thickets. The subspecies (*D.c. coronata*) breeds from northern Alaska to eastern Canada, and southeast to Michigan, West Virginia and Massachusetts. Wintering birds occur most numerous along the Atlantic and Gulf

coasts and less commonly east from Kansas through the central states to New England.

Wintering birds also occur in the West Indies, and in Mexico, rarely south as far as Panama (Hunt and Flaspohler 1998). Yellow-rumped warblers have a generalist diet, and primarily forage on insects during spring migration and the breeding season, and consume fruits and insects during fall and winter.

Red-eyed Vireos are long-distance (Nearctic-Neotropical) migrants, inhabiting deciduous and mixed forests with moderate to dense understory vegetation. This species breeds from southeast Alaska east and south throughout Canada and south through the eastern half of the United States, and winters in South America (Cimprich et al. 2000). Red-eyed Vireos primarily forage on insects during spring migration and the breeding season, and consume insects and a wide variety of small fruits during fall and winter.

## LITERATURE CITED

- Aborn, D.A., and F.R. Moore. 1997. Pattern of movement by summer tanagers (*Piranga rubra*) during migratory stopover: a telemetry study. *Behaviour* 134:1077-1100.
- Aborn, D.A., and F.R. Moore. 2004. Activity budgets of summer tanagers during spring migratory stopover. *Wilson Bulletin* 116:64-68.
- Adams, A.A., S.K. Skagen, and J.A. Savidge. 2006. Modeling post-fledging survival of lark buntings in response to ecological and biological factors. *Ecology* 87:178-188.
- Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313-1325.
- Akesson, S., and A. Hedenstrom. 2000. Wind selectivity of migratory flight departures in birds. *Behavioral Ecology and Sociobiology* 47:140-144.
- Akesson, S., L. Karlsson, G. Walinder, and T. Alerstam. 1996. Bimodal orientation and the occurrence of temporary reverse bird migration in autumn in south Scandanavia. *Behavioral Ecology and Sociobiology* 38:293-302.
- Alerstam, T. 1990. *Bird migration*. Cambridge University Press, Cambridge.
- Alerstam, T., and A. Lindstrom. 1990. Optimal bird migration: the relative importance of time, energy, and safety. Pages 331-351 *in* *Bird Migration* (E. Gwinner, Ed.). Springer, New York.
- Bachler, E., and M. Schaub. 2007. The effects of permanent and local emigration and encounter technique on stopover duration estimates as revealed by telemetry and mark-recapture. *Condor* 109:142-154.
- Barlein, F. 1983. Habitat selection and associations of species in European passerine birds during southward, post-breeding migrations. *Ornis Scandinavica* 14:239-245.
- Berthold, P. 1975. Migration: control and metabolic physiology. Pages 77-128 *in* *Avian Biology*, vol.5 (D.S. Farner and J. R. King, Eds.). Academic Press, New York.
- Blem, C.R. 1980. The energetics of migration. Pages 175-224 *in* *Animal Migration, orientation and navigation*. (S. A. Gauthreaux, Jr., Ed.). Academic Press, New York.

- Bolshakov, C.V., N. Chernetsov, A. Mukhin, V.N. Bulyuk, V. Kosarev, P. Ktitorov, D. Leoke, and A. Tsvey. 2007. Time of nocturnal departures in European robins *Erithacus rubecula* in relation to celestial cues, season, stopover duration and fat stores. *Animal Behavior* 74:855-865.
- Bruderer, B., and F. Liechti. 1998. Flight behavior of nocturnally migrating birds in coastal areas: crossing or coasting. *Journal of Avian Biology* 29:499-507.
- Caccamise, D.F., and R.S. Hedin. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bulletin* 94:306-318.
- Chernetsov, N., and A. Mukhin. 2006. Spatial behavior of European robins *Erithacus rubecula* during migratory stopovers: a telemetry study. *Wilson Journal of Ornithology* 118:364-373.
- Cimprich, D.A., M.S. Woodrey, and F.R. Moore. 2005. Passerine migrants respond to variation in predation risk during stopover. *Animal Behaviour* 69:1173-1179.
- Cimprich, D.A., F.R. Moore, and M.P. Guilfoyle. 2000. Red-eyed Vireo (*Vireo olivaceus*). *The Birds of North America*, no. 527. (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- Cooperrider, T.S., A.W. Cusick, and J.T. Kartesz. 2001. *Seventh Catalog of the Vascular Plants of Ohio*. Ohio State University Press, Columbus.
- Dallman, M., and R.J. Smith. 1995. Avian predation on Chironomids along the nearshore waters of Lake Huron. *Michigan Birds Natural History* 2:201-204.
- Dunn, E.H. 2000. Temporal and spatial patterns in daily mass gain of Magnolia Warblers during migratory stopover. *Auk* 117:12-21.
- Ewert, D.N., and M.J. Hamas. 1995. Ecology of migratory landbirds during migration in the Midwest. Pages 200-208 *in* Management of Midwestern landscapes for the conservation of Neotropical migratory birds. (F. R. Thompson III, Ed.). General Technical Report NC-187. U.S. Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.
- Francis, C.M., and F. Cooke. 1986. Differential timing of spring migration in wood warblers (Parulinae). *Auk* 103:548-556.
- Fransson, T., and T.P. Weber. 1997. Migratory fuelling in blackcaps (*Sylvia atricapilla*) under perceived risk of predation. *Behavioral Ecology and Sociobiology* 41:75-80.

- Gordon, C.E. 2000. Movement patterns of wintering grassland sparrows in Arizona. *Auk* 117:748-759.
- Graber, J.W., and R.R. Graber. 1983. Feeding rates of warblers in spring. *Condor* 85:139-150.
- Hedenstrom, A., and T. Alerstam. 1997. Optimal fuel loads in migratory birds: distinguishing between time and energy minimization. *Journal of Theoretical Biology* 189:227-234.
- Hunt, P.D., and D.J. Flaspohler. 1998. Yellow-rumped Warbler (*Dendroica coronata*). *The Birds of North America*, no. 376. (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- Hutto, R.L. 1985a. Seasonal changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: competition mediated? *Auk* 102:120-132.
- Hutto, R.L. 1985b. Habitat selection by nonbreeding, migratory landbirds. Pages 455-476 *in* Habitat selection in birds. (M. L. Cody, Ed.). Academic Press, California.
- Jenni, L., and M. Schaub. 2003. Behavioural and physiological reactions to environmental variables in bird migration: a review. Pages 155-171 *in* Avian Migration. (P. Berthold, E. Gwinner, and E. Sonnenschein, Eds.). Springer-Verlag, Germany.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Keast, A., and E.S. Morton, Eds. 1980. Migrant birds in the neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D. C.
- Kelly, J.F., L.S. DeLay, and D.M. Finch. 2002. Density-dependent mass gain by Wilson's Warblers during stopover. *Auk* 119:210-213.
- Ketterson, E.D., and V. Nolan, Jr. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the Dark-eyed Junco, as determined from demographic analysis of winter populations. *Auk* 99:243-259.
- Kuenzi, A., F.R. Moore, and T.R. Simons. 1991. Stopover of neotropical landbird migrants on East Ship Island following trans-gulf migration. *Condor* 93:869-883.
- Lang, J.D., L.A. Powell, D.G. Krementz, and M.J. Conroy. 2002. Wood thrush movements and habitat use: effects of forest management for red-cockaded woodpeckers. *Auk* 119:109-124.

- Loria, D.E., and F.R. Moore. 1990. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. *Behavioral Ecology* 1:24-35.
- Marra, P.P., K.A. Hobson, and R.T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884-1886.
- Mazerolle, D.F., and K.A. Hobson. 2003. Do ovenbirds (*Seiurus aurocapillus*) avoid boreal forest edges? A spatiotemporal analysis in an agricultural landscape. *Auk* 120:152-162.
- Moore, F.R. [Ed.]. 2000. Stopover ecology of Nearctic-Neotropical landbird migrants: habitat relations and conservation implications. *Studies in Avian Biology* 20.
- Moore, F.R., and D.A. Aborn. 2000. Mechanisms of *en route* habitat selection: how do migrants make habitat decisions during stopover? *Studies in Avian Biology* 20:34-42.
- Moore, F.R., S.A. Gauthreaux Jr., P. Kerlinger, and T.R. Simons. 1995. Habitat requirements during migration: important link in conservation. Pages 121-144 in *Ecology and Management of Neotropical migratory birds*. (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.
- Moore, F.R., and P. Kerlinger. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia* 74:47-54.
- Moore, F.R., P. Kerlinger, and T.R. Simons. 1990. Stopover on a Gulf coast barrier island by spring trans-Gulf migrants. *Wilson Bulletin* 102:487-500.
- Moore, F.R., and T.R. Simons. 1992. Habitat suitability and stopover ecology of Neotropical landbird migrants. Pages 345-355 in *Ecology and conservation of neotropical migrant landbirds*. (J.M. Hagan, III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D. C.
- Moore, F.R., and W. Yong. 1991. Evidence of food-based competition among passerine migrants during stopover. *Behavioral Ecology and Sociobiology* 28:85-90.
- Moore, F.R., R.J. Smith, and R. Sandberg. 2005. Stopover ecology of intercontinental migrants: en route problems and consequences for reproductive performance. Pages 251-261 in *Birds of two worlds: the ecology and evolution of migration* (R. Greenberg and P.P. Marra, Eds.). Johns Hopkins University Press, Maryland.

- Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70:730-738.
- Newton, I. 2004. Population limitation in migrants. *Ibis* 146:197-226.
- Ottawa National Wildlife Refuge Complex Comprehensive Conservation Plan. 2000.
- Orians, G.H., and J.F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137:S29-S49.
- Peacefull, L. 1996. *The Geography of Ohio*. The Kent State University Press, Ohio.
- Petit, D.R. 2000. Habitat use by landbirds along Nearctic-Neotropical migration routes: implications for conservation of stopover habitats. *Studies in Avian Biology* 20:15-33.
- Powell, L.A., D.G. Krentz, J.D. Lang, and M.J. Conroy. 1998. Effects of radio transmitters on migrating Wood Thrushes. *Journal of Field Ornithology* 69:306-315.
- Rappole, J.H., and A.R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335-337.
- Rodewald, P.G., and M.C. Brittingham. 2004. Stopover habitats of landbirds during fall: use of edge-dominated and early-successional forests. *Auk* 121:1040-1055.
- Schaub, M., and L. Jenni. 2001. Stopover durations of three warbler species along their autumn migration route. *Oecologia* 128:217-227.
- Sherry, T.W., and R.T. Holmes. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence. Pages 85-120 *in Ecology and Management of Neotropical Migratory Birds: a Synthesis and Review of Critical Issues* (T.E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.
- Shieldcastle, J., T. Kashmer, and M. Shieldcastle. 2004. Passerine habitat use during spring and fall migration. Black Swamp Bird Observatory Home Page. <http://www.bsbobird.org/spring.html>.
- Sillett, T.S., and R.T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296-308.
- Simons, T.R., S.M. Pearson, and F.R. Moore. 2000. Application of spatial models to the stopover ecology of trans-Gulf migrants. *Studies in Avian Biology* 20:4-14.

- Smith, R.J., and F.R. Moore. 2003. Arrival fat and reproductive performance in a long-distance passerine migrant. *Oecologia* 134:325-331.
- Smith, R.J., and F.R. Moore. 2005. Fat stores of American Redstarts *Setophaga ruticilla* arriving at northerly breeding grounds. *Journal of Avian Biology* 36:117-126.
- Smith, R., M. Hamas, M. Dallman, and D. Ewert. 1998. Spatial variation in foraging of the black-throated green warbler along the shoreline of northern Lake Huron. *Condor* 100:474-484.
- Smith, R.J., M.J. Hamas, D.N. Ewert, and M.E. Dallman. 2004. Spatial foraging differences in American Redstarts along the shoreline of northern Lake Huron during spring migration. *Wilson Bulletin* 116:48-55.
- Sykes, P.W., Jr., J.W. Carpenter, S. Holzman, and P.H. Geissler. 1990. Evaluation of three miniature radio transmitter attachment methods for small passerines. *Wildlife Society Bulletin* 18:41-48.
- Tietz, J.R., and M.D. Johnson. 2007. Stopover ecology and habitat selection of juvenile Swainson's thrushes during fall migration along the northern California coast. *Condor* 109:795-807.
- Tsvey, A., V.N. Bulyuk, and V. Kosarev. 2007. Influence of body condition and weather on departures of first-year European robins, *Erithacus rubecula*, from an autumn migratory stopover site. *Behavioral Ecology and Sociobiology* 61:1665-1674.
- Wikelski, M., E.M. Tarlow, A. Raim, R.H. Diehl, R.P. Larkin, and G.H. Visser. 2003. Cost of migration in free-flying songbirds. *Nature* 423:704.
- Winker, K., J.H. Rappole, and M.A. Ramos. 1990. Population dynamics of the Wood Thrush in southern Veracruz. *Condor* 92:444-460.
- Woodrey, M.S. 2000. Age-dependent aspects of stopover biology of passerine migrants. *Studies in Avian Biology* 20:43-52.

## CHAPTER 2

### MOVEMENTS OF TWO SONGBIRD SPECIES DURING SPRING MIGRATION IN A FRAGMENTED LANDSCAPE

#### INTRODUCTION

Migratory landbirds are typically unable to make one non-stop flight between wintering and breeding areas and they must stop several times along their migratory route to rest and rebuild energy reserves before they continue migration (Blem 1980). Stopover habitats are temporarily used during migration and are important because they provide migratory birds a place to rest, refuel, and avoid predators. Because migrating birds spend about 90% of their time and energy in stopover habitats rather than in flight (Hedenstrom and Alerstam 1997, Wikelski et al. 2003), it is important for our understanding of migration ecology to examine spatial and temporal patterns of bird movements during stopover. This information is especially important in highly fragmented areas and where barriers to migration result in high concentrations of migrants.

At the end of a migratory flight, one of the first decisions a migrant makes is where to settle. Several hypotheses have been proposed to explain movement behavior

and habitat selection during stopover. One view of within-site selection suggests that migrants use habitats nearest to the landing site, so the decision of where to settle upon landing at a site is most important (Jenni and Schaub 2003). Another view is that after landing migrants explore the area, making broad movements to adjust their initial choice upon landing (Moore and Aborn 2000). A third view is that migrants move in response to the distribution of food (Chernetsov 2002).

Although few studies have investigated movement behavior and habitat selection of songbirds during migratory stopover, our understanding has increased in recent years. Some migrants, such as Summer Tanagers (*Piranga rubra*), Sedge Warblers (*Acrocephalus schoenobaenus*), and Swainson's Thrush (*Catharus ustulatus*), remain localized in their movements during stopover (Aborn and Moore 1997, Chernetsov and Mukhin 2006, Tietz and Johnson 2007) and others, such as Pied Flycatchers (*Ficedula hypoleuca*) move broadly (> 2 km per day, Chernetsov et al. 2004). Variation in movement patterns within a species during stopover has been documented (Aborn and Moore 1997, 2004, Chernetsov and Mukhin 2006).

Radio telemetry can provide detailed information on the spatial and temporal movement patterns of animals and is therefore a powerful tool for researchers (Aebischer et al. 1993). Light weight radio transmitters now allow researchers to collect telemetry data for small songbirds during migration to examine patterns of movement (Aborn and Moore 1997, 2004; Chernetsov and Mukhin 2006, Tietz and Johnson 2007) and habitat selection (Tietz and Johnson 2007). The goal of my research was to evaluate movement behavior and selection of forest patches by migrants during spring stopover in a highly fragmented, agriculturally dominated landscape. I used radio telemetry to quantify

stopover behavior of two species of songbird migrants, the Yellow-rumped Warbler (*Dendroica coronata*) and Red-eyed Vireo (*Vireo olivaceus*), at a stopover area in the western Lake Erie basin of northern Ohio during spring 2006 and 2007. My specific objectives were to 1) assess patterns of movement by these migratory songbirds within and among forest patches and 2) determine how local-level (patch area, habitat type) and landscape-level (habitat connectivity) attributes influence movement rate and patch residence time.

## STUDY AREA

Research was conducted in Lucas and Ottawa counties of northwestern Ohio in the western Lake Erie basin, primarily within the Ottawa National Wildlife Refuge (NWR) complex. Migrant landbirds were captured at Cedar Point NWR and also within the Ottawa and Navarre Units of Ottawa NWR. These management units consist of coastal marshes, wetlands, wet prairies, hardwood forests, beach ridge forests, and managed and unmanaged impoundments (Ottawa NWR 2000). This highly fragmented region is dominated by agriculture and to a lesser extent urban and suburban lands. The remaining forest consists of small and often isolated tracts.

Terrestrial forest habitats include beach ridge, willow/cottonwood (*Salix/Populus*), mature hardwood, early successional, and hedgerow. Remnant beach ridge forest habitat occurred along the lake shoreline, was structurally heterogeneous and dominated by willow and cottonwood trees and dogwood shrubs (*Cornus spp.*). These forests were characterized by sandy soils, a relatively open canopy and moderate to dense understory vegetation. Willow/cottonwood forest occurred in wetlands and in pockets

along diked impoundments and consisted of mature and young willow and cottonwood trees and areas of understory shrubs. Mature hardwood deciduous forest consisted of tall, mature broadleaf trees with a closed canopy, typically sparse understory vegetation and infrequent tree fall gaps. Ash (*Fraxinus*), maple (*Acer*), hickory (*Carya*), and oak (*Quercus*) species dominated these mature forests. Early successional forest ranged from dense dogwood shrub thickets to young willow and cottonwood trees and saplings mixed with dense understory shrubs. Hedgerow habitats occurred in linear strips along edges of fields and dikes and included early successional forest and willow/cottonwood forest types.

Migrants accumulate in high densities along the southwestern shores of Lake Erie during spring migration because smaller birds are reluctant to cross the large expanse of open water. Because little natural habitat remains in this region, small remnant habitat patches should represent important stopover habitat for very large numbers of migrating landbirds (Ewert and Hamas 1995). Migrant bird concentrations of the magnitude found in northern Ohio are rare in Midwestern states (Ottawa NWR 2000, Shieldcastle et al. 2004), making this region continentally significant for bird conservation.

## METHODS

Yellow-rumped Warblers (YRWA; *Dendroica coronata*) and Red-eyed Vireos (REVI; *Vireo olivaceus*) were selected as focal species because they are common in the study area during spring migration and large enough to carry small (0.43-0.66 g) radio transmitters. Yellow-rumped Warblers are short-distance (temperate) migrants,

inhabiting deciduous, coniferous, and mixed forests, as well as edges of woods and thickets. The subspecies *D.c. coronata* breeds from northern Alaska to eastern Canada, and southeast to Michigan, West Virginia and Massachusetts. Wintering birds occur in the Atlantic and Gulf coastal states, the West Indies, and in Mexico, and less commonly east from Kansas through the central states to New England (Hunt and Flaspohler 1998). YRWA primarily forage on insects during spring migration and the breeding season, and consume fruits and insects during fall and winter.

Red-eyed Vireos are long-distance (Nearctic-Neotropical) migrants, inhabiting deciduous and mixed forests with moderate to dense understory vegetation. This species breeds from southeast Alaska east and south throughout Canada and south through the eastern half of the United States, and winters in South America (Cimprich et al. 2000). REVI primarily forage on insects during spring migration and the breeding season, and consume insects and a wide variety of small fruits during fall and winter.

#### Capturing migrants

Migrants were captured using 2.6 x 12 m mist nets (30 mm mesh) at Cedar Point National Wildlife Refuge (NWR) (10 nets), the Navarre Unit of Ottawa NWR (21 nets, but only in 2006), and at five locations within the Ottawa Unit of Ottawa NWR (5-9 nets per location). Nets were checked and captured birds were removed every 20 min or at shorter intervals when air temperatures were close to 0°C. Netting for experimental birds began 30 min before sunrise and continued for 4.5 h.

Each bird was held briefly in a cloth bag before processing. Birds were banded with a U.S.G.S. aluminum leg band. Migrants used as experimental birds were also color

banded with a unique color combination. Data on location, time of capture, age, sex, tarsus length ( $\pm 0.01$  mm), unflattened wing chord ( $\pm 0.5$  mm), and body mass ( $\pm 0.01$  gram) were recorded. Age and sex were determined using methods described in Pyle et al. (1987). Migrants were visually scored for subcutaneous body fat using the 6-point ordinal scale of Helms and Drury (1960).

### Radio-tracking

Yellow-rumped Warblers (YRWA) and Red-eyed Vireos (REVI) captured within 4 hours of sunrise and with fat scores of 3 or less (Helms and Drury 1960) were chosen as experimental birds for radio tracking. Transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) weighed 0.43 g (Model BD-2n for YRWA) and 0.66 g (Model BD-2 for REVI) which represented approximately 3% of body mass for YRWA and REVI, respectively (unpublished data). Transmitters were designed with a range of approximately 1 km and a lifespan of 7-12 days, although I failed to locate any birds whose transmitter had died prior to departure.

After banding and processing, YRWA ( $n = 23$ ) and REVI ( $n = 21$ ) used as experimental birds were promptly translocated to one of five pre-determined forest release sites at Ottawa NWR which varied in area and distance to lakeshore (Figure 2.1). Experimental translocations of individual migrants to different sites were used to examine habitat features that may influence movement behavior and to control for arrival timing. As a control for translocated birds, YRWA ( $n = 15$ ) and REVI ( $n = 12$ ) were captured within the 5 release sites, processed, and released at the same site. Each bird was fitted with a small radio transmitter and released within 50-90 minutes. Three to four

individuals of each species were released at each of the 5 release sites in each year; 62% of birds were translocated (Table 2.1). If a bird was visibly stressed (i.e. fluffing feathers, closing eyes, not alert, panting) when taken out of the holding bag, it was not fitted with a radio transmitter. Feathers in the interscapular area were parted and the radio transmitter attached using a few drops of eyelash adhesive following modified methods of Raim (1978) and Sykes et al. (1990); eyelash adhesive is water-soluble and designed for temporary attachment. For 6 birds, radio transmitters fell off within 2-11 days and were recovered in the study area.

Birds were taken to randomly selected points inside the forest patch and released in a random direction. Experimental birds were tracked using a 3-element folding Yagi Antenna (150 MHz, Advanced Telemetry Systems, Inc., Isanti, Minnesota) and 12-channel receiver (Communications Specialists, Inc., Orange, California). Radio locations were collected every 30 minutes for either 3 days (YRWA) or 2 days (REVI). All birds were checked once daily after day 2 (REVI) and day 3 (YRWA) to determine minimum stopover duration and monitor day-to-day movements. A radio location included Global Positioning System (GPS) coordinates, a compass bearing in the direction of the radio signal, and an estimated distance to the bird. Because movements may be influenced by observer presence, locations were estimated from a distance of approximately 30 meters. Since individual movements made by a bird were not independent, individual birds were treated as the sampling unit to avoid pseudoreplication (Aebischer et al. 1993). Radio telemetry was conducted primarily within the Ottawa NWR, Magee Marsh Wildlife Area, and Crane Creek State Park. When I was unable to detect a radio-marked bird, I traversed the study area for 1.5 to 2 hours searching for the bird. If the bird was still not

detected, I drove within a 4 km radius of the bird's last radio location (i.e. outside the study area), using a roof-mounted omni-directional antenna and a Yagi antenna to listen for the signal. If still undetected, the bird was assumed to have left the study area, although radio frequencies of such individuals were checked for two additional days.

### Measurement of habitat and landscape characteristics

Using a variation of the James and Shugart method (1970), local level (within patch) habitat characteristics were measured within 0.04 ha circular plots (11.3 m radius) in September of each year (Table 2.2). Within each 11.3 m radius, tree species were recorded by diameter-at-breast-height (DBH) in three classes: 8-23, 23.1-38, and >38 cm. At 2 m intervals along two perpendicular transects running through the plot center, percent coverage of understory shrubs and saplings (<8 cm DBH) was recorded using a telescoping pole marked in 5 height classes: 0.5-1, 1-1.5, 1.5-2, 2-2.5, 2.5-3 m. Within a 5 m radius, woody saplings >2 cm in DBH were recorded by species. Habitat data were collected at each radio location except where locations overlapped.

A map of the study area was produced by digitizing coverage of habitat types and land uses using ArcGIS 9.1 (Figure 2.1). The study area was delineated by calculating a 100% minimum convex polygon for all bird locations in both years (excluding a few long-distance exploratory movements) using the Animal Movement extension (Hooge and Eichenlaub 2000) in ArcView GIS 3.1. USDA color infrared aerial photographs were used to delineate habitats and land uses at the 1:2000 scale. These photographs were accurate to 1 m and taken in spring 2006. The digital map was ground-truthed for accuracy and discrepancies were corrected.

Digital habitat coverage included a variety of woody habitats (beach ridge forest, willow/cottonwood forest, mature hardwood forest, early successional forest, hedgerow) and predominately non-woody habitats (meadow, cropland, water, wetland, residential, road). Water cover types included open water of creeks and ditches. Wetland cover types included all types of wetlands occurring in the study area, such moist-soil habitats and emergent marshes, with very little to no woody vegetation. Houses, buildings, and associated lawn were considered residential. All other cover types, such as parking lots and rocky edges of dikes, were classified as “other”.

#### Statistical analyses

Only radio locations collected during days of consistent radio-tracking (first 3 days) were used in analyses for Yellow-rumped Warblers. Because mean minimum stopover duration ( $\pm$ S.D.) for Red-eyed Vireos was  $< 2$  days, only radio locations collected during the first day of tracking were used in analyses for REVI. For analyses of patch residence time, 65 individuals (35 YRWA, 30 REVI) were used. For analyses of movement rate, 63 individuals (33 YRWA, 30 REVI) were used. Birds excluded from both movement and patch residence time analyses had radio transmitters fail (2) or died of unknown cause (1). Two birds that entered patches that were off-limits due to nesting Bald Eagles were excluded from movement rate analyses. For each individual, distances traveled per day (km) were summed to quantify total distance moved. To standardize for differences in sampling effort, total distance moved was divided by time spent tracking to quantify movement rate ( $\text{m min}^{-1}$ ) for each individual.

I calculated the area of each patch visited by a bird as well as the percent of each habitat type within the study area using ArcView GIS 3.1. A patch was defined during digital map creation as a distinct area of habitat ( $> 5 \text{ m}^2$ ) with a shape other than a linear strip. The boundary of a patch was where the edge of that patch met another distinct habitat type or land use; most patches had sharp boundaries between habitat types. Hedgerows, that connected patches, occurred as linear strips of habitat and were not included as “patches” for these analyses. Connectivity of a patch was defined as the percent of woody habitat within a 100 m buffer surrounding the perimeter of a patch (Calabrese and Fagan 2004, Moilanen and Nieminen 2002), and was not necessarily a measure of the amount of habitat connected to a patch. I quantified patch connectivity for each patch visited by a bird using buffer methods in ArcGIS 9.1. Connectivity values ranged from 0 to 73%.

To test for selection among habitat types, I used two-way contingency tables stratified across habitat types. The Breslow-Day test was used to determine homogeneity of association between habitat use and availability with the Tarone correction factor (Agresti 1996). Because significant differences were detected among habitat types, the Cochran-Mantel-Haenszel (CMH) test was used to determine significant (critical  $\alpha = 0.05$ ) conditional associations (Agresti 1996). Use was defined as the percent of total radio locations within each habitat type. The percent of each habitat type that was available within the study area was considered availability.

Movement data were analyzed using a generalized linear mixed model, with maximum likelihood (ML) estimation. The mixed-effect model uses a random intercept that accounts for unbalanced sample sizes among individuals (i.e. unequal number of

telemetry locations per individual), so the inference for the population is independent of individual sampling intensity (Gillies et al. 2006). The experimental unit was the bird-patch-day, and each patch that a bird visited was considered. I used only the first instance of a bird visiting a particular patch, not each time it visited that patch, because prior knowledge of a patch could influence behavior on subsequent visits to that patch. The response variable was either residence time within patch or movement rate within patch for each bird-patch-day combination. The random effect was the individual bird in both sets of analyses. Fixed effects were patch habitat type, patch area, patch connectivity, year, and translocation (i.e. 1 = translocated, 0 = not translocated). Following an information-theoretic approach, I used Akaike's Information Criterion (AIC) with a correction factor for small sample sizes ( $AIC_c$ ) to rank candidate models for YRWA and REVI (Burnham and Anderson 2002). Difference in  $AIC_c$ , or simply  $\Delta_i$ , was used to select "good" models from the set of candidate models. These differences were obtained by subtracting  $AIC_c$  of model under consideration from the top-ranked model. Candidate models were chosen *a priori* and included main effects and their combinations, 2-way interactions, and the null model (a total of 25 models). The same set of candidate models was used in analyses for both response variables and for each species. Models with  $\Delta_i < 2.0$  relative to the model with the lowest  $AIC_c$  were considered "good" models. "Good" models were then evaluated for goodness-of-fit. After ranking candidate models, models with  $\Delta_i < 2.0$  were re-analyzed using restricted/residual maximum likelihood (REML) estimation. The variance components structure, which models a variance structure for the random effect, was determined to be optimal for the observed covariance correlation (SAS Institute 1996). Multiple comparisons among significant main effects

were performed using the Tukey-Kramer adjustment for experiment-wise error and considered significant at an overall experiment-wise error of  $\alpha = 0.05$ . All statistical analyses were performed using SAS version 9.1 for Windows (SAS Institute 1996).

## RESULTS

A total of 38 Yellow-rumped Warblers and 31 Red-eyed Vireos were radio-tracked from 20 April to 1 June in 2006 and 2007. The final dataset included 2,499 telemetry locations collected across both years, and 1,164 hours of radio-tracking (YRWA = 938 hours, REVI = 226 hours). Mean number of telemetry locations per individual was 55.2 (range 21 to 71) for YRWA and 17.1 (range 12 to 22) for REVI. Mean tracking time (hours) per individual was 29.9 (range 9.7 to 34.7) for YRWA and 8.2 (range 5.5 to 10.5) for REVI.

Mean total distance moved (km) per day for YRWA was 2.2 (S.D. = 1.2; range 0.3 to 4.6 km). In contrast, mean total distance moved (km) per day for REVI was 0.9 (S.D. = 0.8; range 0.3 to 3.9 km). Mean movement rate ( $\text{m min}^{-1}$ ) per day was 3.5 ( $\pm 1.9$  S.D.) for YRWA and 1.8 ( $\pm 1.4$  S.D.) for REVI. For YRWA, both mean movement rate and standard deviation increased from day 1 to day 3, indicating higher movement and variability in movement with each day of radio-tracking (Figure 2.4). YRWA showed a negative, but non-significant relationship between movement rate and date of capture ( $p = 0.136$ , Figure 2.5); there was a negative relationship between mean movement rate and date of capture for REVI ( $p = 0.04$ , Figure 2.6).

During a three day period, individual YRWA visited 1 to 12 unique habitat patches (mean = 5.0, median = 5) and 1 to 5 (mean = 2.5, median = 2) different habitat types, whereas REVI only visited 1 to 3 unique patches (mean = 1.5, median = 1) and 1 to 2 (mean = 1.4, median = 1) different habitat types during their shorter stopover. YRWA spent 87.5 % of their time within forest habitat patches and 12.5% of their time in hedgerows (Figure 2.7). Similarly, REVI spent 86% of their time in patches and 14% of their time in hedgerows (Figure 2.8).

The 95% confidence interval for the log odds ratio did not contain zero, indicating that both YRWA and REVI avoided early successional forest, but selected for mature hardwood forest (Table 2.3, Figures 2.9 and 2.10). YRWA also selected willow/cottonwood forest, whereas REVI used this forest type proportional to its availability. REVI selected beach ridge forest but YRWA used beach ridge forest proportional to its availability. Use of hedgerows was proportional to availability of hedgerow habitats for both species.

For analyses of patch residence time, the model for YRWA with greatest support (lowest AIC<sub>c</sub>) included patch habitat type, patch area, and patch connectivity ( $\omega_i = 0.269$ ; Table 2.4). Using REML estimation, the variance component estimate was 9,056 (S.E. = 5759.71,  $p = 0.06$ ) indicating marginally significant inter-bird variation independent of environmental factors. YRWA spent more time ( $F_{4,219} = 2.71$ ,  $p = 0.03$ ) in mature hardwood forest than any other habitat type, and that patch residence time in mature hardwood forest was greater than in early successional forest ( $p = 0.02$ ). As patch area increased, patch residence time increased ( $F_{1,219} = 5.12$ ,  $p = 0.02$ , estimate = 6.08), and as

patch connectivity increased, patch residence time decreased ( $F_{1,227} = 6.10, p = 0.01$ , estimate = -309.65).

For REVI, the model that best described patch residence time included patch habitat type, patch area, and translocation ( $\omega_i = 0.354$ ; Table 2.5). The variance component estimate was 18,846 (S.E. = 6813.24,  $p = 0.003$ ) indicating significant inter-bird variation. REVI spent more time ( $F_{3,23.5} = 5.89, p = 0.004$ ) in mature hardwood forest than any other habitat type, which was greater than in both early successional forest ( $p = 0.024$ ) and beach ridge forest ( $p = 0.007$ ). As patch area increased, patch residence time of REVI increased ( $F_{1,24.3} = 15.93, p < 0.001$ , estimate = 16.99), similar to YRWA. However, patch residence time also increased with translocation ( $F_{1,34.8} = 8.14, p = 0.007$ , estimate = -155.86).

For analyses of movement rates, the model with most support for YRWA included habitat type, patch connectivity, and an interaction between habitat type and patch connectivity ( $\omega_i = 0.217$ ; Table 2.6). The variance component estimate was 4,369 (S.E. = 7,781.62,  $p = 0.287$ ) indicating no significant inter-bird variation. The interaction between patch habitat type and connectivity ( $F_{4,205} = 2.91, p = 0.023$ ) suggested that movement rates within a habitat type depended on patch connectivity. For REVI, the model that best described variation in movement rates was the null model ( $\omega_i = 0.227$ ; Table 2.7), suggesting that none of the factors adequately explained movement rates. The variance component estimate was 656 (S.E. = 367.28,  $p = 0.037$ ), indicating significant inter-bird variation for REVI.

## DISCUSSION

In my study, Yellow-rumped Warblers and Red-eyed Vireos exhibited high variation in movement behavior during stopover. The majority of individuals of both species moved widely within the study area, used a range of habitats, and frequently used vegetated dikes as corridors for travelling between forest patches and as foraging locations. Most migrants arrive at stopover sites with depleted fat stores and energetic condition is thought to influence activity budgets, time spent at stopover sites, and flight distance following departure (Alerstam and Lindstrom 1990). Bird movements within a stopover area also likely depend upon several other factors such as type and amount of available habitat, proximity to breeding grounds, and behavior of the species (i.e. some species are inherently more sedentary than others). For example, radio telemetry of Swainson's Thrush during fall stopover indicated low movement rates and distances traveled, and this likely reflects the sedentary nature of this species (Tietz and Johnson 2007).

YRWA and REVI are less sedentary than most species studied to date, so we should expect higher movement rates and distances traveled for these species than more sedentary species. Both YRWA and REVI traveled greater distances but did not move at higher rates ( $\text{m min}^{-1}$ ) relative to other studies (e.g. Aborn and Moore 1997, Chernetsov et al. 2006, Tietz and Johnson 2007). Summer Tanagers along the northern Gulf coast moved an average of 0.5 km linear distance, and no more than 1 km total distance during their brief (< 2 day) spring stopover (Aborn and Moore 1997). In contrast, YRWA in northern Ohio moved twice that amount, an average of 2.19 km per day within the first 3 days of radio-tracking. Summer Tanagers along the coast moved an average of 9.0 m

min<sup>-1</sup>, whereas both YRWA and REVI averaged lower movement rates in northern Ohio. It should be noted that one translocated YRWA flew back to an area very near the original capture site on the morning of the third day (a distance >8 km), but this individual was not included in movement rate analyses. In contrast to YRWA, REVI did not move great distances during stopover, but this was likely a reflection of their brief stopover in northern Ohio during spring, similar to REVI (Loria and Moore 1990) and Summer Tanagers (Aborn and Moore 1997) along the Gulf coast. In Russia, Pied Flycatchers (*Ficedula hypoleuca*) moved broadly (more than 2 km per day), compared to Sedge Warblers, which remained very localized (Chernetsov et al. 2004).

Several studies have documented that migrants actively select among available habitats during stopover (e.g. Moore et al. 1990, Moore and Aborn 2000). Non-random patterns of habitat selection are suggested when use of habitat is disproportional to availability (Hutto 1985b). For example, of five habitat types available to Nearctic-Neotropical landbird migrants in spring along the northern Gulf Coast, shrub/scrub represented only 14% of available habitat, yet had the greatest number of species and individuals (Moore et al. 1990). During spring, migrants stopping over in central Pennsylvania consistently used mature edge-dominated forests more frequently than mature forest interior or pole-stage forests (Rodewald and Brittingham 2007). Of the five habitat types available in my study, YRWA selected mature hardwood and willow/cottonwood forest and avoided early successional forest. Similarly, REVI selected mature hardwood and beach ridge forest and also avoided early successional forest. Although individuals of both species spent time in all wooded habitats, hedgerow was the only type used in proportion to its availability. Both YRWA and REVI spent

almost 15% of their time in hedgerows, which they frequently used as travel corridors and foraging locations.

All three attributes of patches that I examined (habitat type, area, and connectivity) were important in describing variation in patch residence time for YRWA and habitat type and connectivity were important in describing variation in their movement rate. Birds spent more time in larger patches and in mature hardwood forest patch types. They spent less time and moved at higher rates in patches that were more connected. These relationships are perhaps expected, since translocation and year were not related to either patch residence time or movement rate for YRWA. However, there was significant variability in patch residence time among individual YRWA. This individual variability is consistent with other studies (i.e. Aborn and Moore 1997, 2004, Chernetsov and Mukhin 2006) and should be considered for studies modeling movement behavior of birds during stopover. Since migrants use stopover habitat for multiple reasons, when selecting habitat en route a fat-depleted migrant may react to different habitat features compared to a migrant simply looking to rest safely (Moore and Aborn 2000).

Patch habitat type, patch area, and translocation influenced patch residence time for REVI, but none of the factors were important in describing their movement rates. As with YRWA, the variance component estimate was significant in analyses of patch residence time and movement rate for REVI, indicating high variability among individual birds. I failed to find evidence of annual variation in movement rates for REVI. It makes sense to find few to no relationships for REVI, as I only had one day of telemetry data to include in analyses for REVI. The possibility remains that variables that I did not

measure may better describe variation in movement behavior. For example, factors such as food availability, predation risk, and weather conditions, also are expected to influence patch residence time and movement rate.

Given that small, light weight radio transmitters have only recently become available, relatively few data have been published on the response of individuals to radio-marking. I found that radio-marked birds behaved similar to individuals without radios. Upon release, radio-marked individuals resumed flying and foraging and otherwise normal behavior within minutes. I found no differences between translocated birds and locally released birds for either species, with the exception of higher patch residence times for translocated REVI. This translocation did not appear to strongly alter bird behavior, a finding consistent with several other studies (Mazerolle and Hobson 2003, Naef-Daenzer et al. 2001, Powell et al. 1998, Sykes et al. 1990).

To effectively conserve stopover habitats, we must learn which habitats and habitat attributes are most critical for conservation and management efforts. Where those critical habitats occur and how they are changing in their availability as development and land conversion continues is an important conservation issue (Moore and Simons 1992, Moore et al. 1995). Relatively little published data exist on the spatial and temporal use of patches by birds during stopover, especially with regard to patch residence time and movement rates within fragmented landscapes. In northern Ohio, spring migrant Yellow-rumped Warblers and Red-eyed Vireos selected and spent more time in mature hardwood, beach ridge, and willow/cottonwood forest, suggesting a higher importance of these habitat types for conservation. Migrants also frequently used hedgerow habitat as traveling corridors and foraging locations, an indication that hedgerows are also an

important landscape component for migrants and should be maintained to provide connectivity between patches. Although spring migrants in my study used early successional forests less often than other habitat types, these habitats are important during fall (Rodewald and Brittingham 2004) and for transient and breeding species that prefer shrub-dominated habitats. My study suggests that land managers should conserve and restore mature hardwood, willow/cottonwood, and beach ridge forests, so that spring migrant songbirds have more opportunities to locate resources and efficiently refuel before continuing migration. Additional information on the ecology and behavior of migratory birds during stopover is needed to address which habitats and habitat attributes are most critical for conservation and management efforts.

## LITERATURE CITED

- Aborn, D.A., and F.R. Moore. 1997. Pattern of movement by summer tanagers (*Piranga rubra*) during migratory stopover: a telemetry study. *Behaviour* 134:1077-1100.
- Aborn, D.A., and F.R. Moore. 2004. Activity budgets of summer tanagers during spring migratory stopover. *Wilson Bulletin* 116:64-68.
- Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313-1325.
- Agresti, A. 1996. An introduction to categorical data analysis. John Wiley and Sons, Inc., New York.
- Alerstam, T., and A. Lindstrom. 1990. Optimal bird migration: the relative importance of time, energy, and safety. Pages 331-351 *in* Bird Migration (E. Gwinner, Ed.). Springer, New York.
- Blem, C.R. 1980. The energetics of migration. Pages 175-224 *in* Animal Migration, orientation and navigation. (S. A. Gauthreaux, Jr., Ed.). Academic Press, New York.
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach, 2<sup>nd</sup> Ed. Springer-Verlag, New York.
- Calabrese, J.M., and W.F. Fagan. 2004. A comparison shopper's guide to connectivity metrics. *Frontiers in Ecology and the Environment* 2:529-536.
- Chernetsov, N. 2002. Spatial behavior of first-year Blackcaps (*Sylvia atricapilla*) during the pre-migratory period and during autumn migratory stopovers. *Journal of Ornithology* 143:424-429.
- Chernetsov, N., and A. Mukhin. 2006. Spatial behavior of European robins *Erithacus rubecula* during migratory stopovers: a telemetry study. *Wilson Journal of Ornithology* 118:364-373.
- Chernetsov, N., A. Mukhin, and P. Ktitorov. 2004. Contrasting spatial behavior of two long-distance passerine migrants at spring stopovers. *Avian Ecology and Behaviour* 12:53-61.
- Cimprich, D.A., F.R. Moore, and M.P. Guilfoyle. 2000. Red-eyed Vireo (*Vireo olivaceus*). *The Birds of North America*, no. 527. (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

- Ewert, D.N., and M.J. Hamas. 1995. Ecology of migratory landbirds during migration in the Midwest. Pages 200-208 *in* Management of Midwestern landscapes for the conservation of Neotropical migratory birds. (F. R. Thompson III, Ed.). General Technical Report NC-187. U.S. Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.
- Gillies, C.S., M. Hebblewhite, S.E. Nielsen, M.A. Krawchuk, C.L. Aldridge, J.L. Frair, D.J. Saher, C.E. Stevens, and C.L. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75: 887-898.
- Hedenstrom, A., and T. Alerstam. 1997. Optimal fuel loads in migratory birds: distinguishing between time and energy minimization. *Journal of Theoretical Biology* 189:227-234.
- Helms, C.W., and W.H. Drury. 1960. Winter and migratory weight and fat field studies on some North American buntings. *Bird Banding* 31:1-40.
- Hunt, P.D., and D.J. Flaspohler. 1998. Yellow-rumped Warbler (*Dendroica coronata*). *The Birds of North America*, no. 376. (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- Hooge, P.N., and B. Eichenlaub. 2000. Animal movement extension to ArcView. Version 2.0. Alaska Science Center, Biological Science Office, U.S. Geological Survey, Anchorage, A.K.
- James, F.C. and H.H. Shugart Jr. 1970. A quantitative method of habitat description. *Audobon Field Notes* 24:727-736.
- Jenni, L., and M. Schaub. 2003. Behavioural and physiological reactions to environmental variables in bird migration: a review. Pages 155-171 *in* Avian Migration. (P. Berthold, E. Gwinner, and E. Sonnenschein, Eds.). Springer-Verlag, Germany.
- Loria, D.E., and F.R. Moore. 1990. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. *Behavioral Ecology* 1:24-35.
- Mazerolle, D.F., and K.A. Hobson. 2003. Do ovenbirds (*Seiurus aurocapillus*) avoid boreal forest edges? A spatiotemporal analysis in an agricultural landscape. *Auk* 120:152-162.
- Moilanen, A. and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. *Ecology* 83:1131-1145.

- Moore, F.R., P. Kerlinger, and T.R. Simons. 1990. Stopover on a Gulf coast barrier island by spring trans-Gulf migrants. *Wilson Bulletin* 102:487-500.
- Moore, F.R., and D.A. Aborn. 2000. Mechanisms of *en route* habitat selection: how do migrants make habitat decisions during stopover? *Studies in Avian Biology* 20:34-42.
- Moore, F.R., and T.R. Simons. 1992. Habitat suitability and stopover ecology of Neotropical landbird migrants. Pages 345-355 *in* Ecology and conservation of neotropical migrant landbirds. (J.M. Hagan, III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D. C.
- Moore, F.R., S.A. Gauthreaux Jr., P. Kerlinger, and T.R. Simons. 1995. Habitat requirements during migration: important link in conservation. Pages 121-144 *in* Ecology and Management of Neotropical migratory birds. (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.
- Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70:730-738.
- Ottawa National Wildlife Refuge Complex Comprehensive Conservation Plan. 2000
- Petit, D. R. 2000. Habitat use by landbirds along Nearctic-Neotropical migration routes: implications for conservation of stopover habitats. *Studies in Avian Biology* 20:15-33.
- Powell, L.A., D.G. Krentz, J.D. Lang, and M.J. Conroy. 1998. Effects of radio transmitters on migrating Wood Thrushes. *Journal of Field Ornithology* 69:306-315.
- Pyle, P., S.N.G. Howell, R.P. Yunick, and D.F. DeSante. 1987. Identification guide to North American passerines. Slate Creek Press, California.
- Raim, A. 1978. A radio transmitter attachment for small passerine birds. *Bird Banding* 49:326-332.
- Rodewald, P.G., and M.C. Brittingham. 2004. Stopover habitats of landbirds during fall: use of edge-dominated and early-successional forests. *Auk* 121:1040-1055.
- Rodewald, P.G., and M.C. Brittingham. 2007. Stopover habitat use by spring migrant landbirds: the roles of habitat structure, leaf development, and food availability. *Auk* 124:1063-1074.

- SAS Institute. 1996. SAS/STAT User's Guide, Version 9.1. SAS Institute, Cary, North Carolina.
- Shieldcastle, J., T. Kashmer, and M. Shieldcastle. 2004. Passerine habitat use during spring and fall migration. Black Swamp Bird Observatory Home Page. <http://www.bsbobird.org/spring.html>.
- Sykes, P.W., Jr., J.W. Carpenter, S. Holzman, and P.H. Geissler. 1990. Evaluation of three miniature radio transmitter attachment methods for small passerines. *Wildlife Society Bulletin* 18:41-48.
- Tietz, J.R., and M.D. Johnson. 2007. Stopover ecology and habitat selection of juvenile Swainson's thrushes during fall migration along the northern California coast. *Condor* 109:795-807.
- Wikelski, M., E.M. Tarlow, A. Raim, R.H. Diehl, R.P. Larkin, and G.H. Visser. 2003. Cost of migration in free-flying songbirds. *Nature* 423:704.

Release Site	Year	Number of YRWA		Number of REVI		Total
		Trans	Local	Trans	Local	
Crane Creek	2006	3	1	3	1	8
	2007	2	2	1	2	7
Shop Woods	2006	3	1	3	1	8
	2007	2	2	2	1	7
Butternut	2006	2	2	2	2	8
	2007	2	2	2	0	6
MS5 Woods	2006	3	1	3	0	7
	2007	2	1	1	1	5
West Crane Creek	2006	2	2	2	1	7
	2007	2	1	2	1	6
Total		23	15	21	10	69

Table 2.1. Sample sizes for translocated (trans) and locally-released (local) radio-tagged Yellow-rumped Warblers (YRWA) and Red-eyed Vireos (REVI) in each of five release sites in the western Lake Erie basin of northern Ohio in spring 2006 and 2007.

	Beach ridge		Early successional		Hedgerow		Mature hardwood		Willow/cottonwood	
	Median	Range	Median	Range	Median	Range	Median	Range	Median	Range
Canopy height	38	30-45	20	6-45	30	8-40	54	12-80	32	20-40
Snags	0	0-6	0	0-6	0	0-6	1	0-8	0	0-8
Logs	10	0-39	1	0-31	3	0-30	20	0-76	8	0-25
Stumps	0	0-4	0	0-7	0	0-7	1	0-21	1	0-4
Stems	27	0-106	37	0-148	59	0-186	9	0-160	37	0-150
Small shrubs	1	0-60	17	0-155	24	0-135	3	0-79	8	0-92
Large shrubs	2	0-14	15	0-130	15	0-105	4	0-40	6	0-37
Small trees	5	0-31	11	0-69	7	0-60	14	0-39	11	0-40
Medium trees	4	0-10	0	0-7	2	0-13	4	0-18	4	0-18
Large trees	1	0-3	0	0-5	0	0-4	2	0-10	0	0-8

47

Table 2.2. Patch-level attributes of habitat types measured within 0.04-ha circular plots in the western Lake Erie basin of northern Ohio in 2006 and 2007. Summary statistics included median and range for canopy height (ft); number of snags, logs, and stumps; number of stem hits in 5 height classes (0.5-3.0 m); number of small shrubs < 2.5 cm dbh; number of large shrubs 2.5-8 cm dbh; number of small trees 8-23 cm dbh; number of medium trees 23.1-38 cm dbh; number of large trees > 38 cm dbh.

Species	Habitat type	Log odds ratio	95% LCB	95% UCB	$\chi^2$	$p$
YRWA	Early successional	-0.613	-0.907	-0.319	17.80	< 0.001
YRWA	Hedgerow	-0.177	-0.523	0.170	1.00	0.317
YRWA	Residential	0.000	-1.210	1.210	0.00	1.00
YRWA	Beach ridge	0.119	-0.328	0.566	0.27	0.603
YRWA	Willow/cottonwood	0.334	0.021	0.647	4.48	0.034
YRWA	Mature hardwood	0.417	0.138	0.696	8.81	0.003
REVI	Early successional	-1.139	-1.565	-0.712	37.90	< 0.001
REVI	Hedgerow	-0.100	-0.434	0.234	0.34	0.559
REVI	Willow/cottonwood	0.213	-0.109	0.535	1.69	0.194
REVI	Mature hardwood	0.399	0.119	0.678	7.99	0.005
REVI	Beach ridge	0.599	0.209	0.989	9.99	0.002

Table 2.3. Log odds ratios and associated significance for the relationship between habitat use and availability conditional on habitat type. Cochran-Mantel-Haenszel tests of association were performed on each habitat type because the Breslow-Day test was significant. Results are presented for both Yellow-rumped Warblers (YRWA) and Red-eyed Vireos (REVI) in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Confidence intervals that do not contain zero indicate significant associations, suggesting that habitats were used out of proportion to their availability.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	ω <sub>i</sub>
<b>Habitat + Connect + Area</b>	<b>3245.1</b>	<b>0.0</b>	<b>0.269</b>
<b>Habitat + Connect + Area + Year + Trans</b>	<b>3246.8</b>	<b>1.7</b>	<b>0.115</b>
Habitat + Connect + Area + (Connect * Area)	3247.2	2.1	0.094
Habitat + Connect + Area + Trans	3247.2	2.1	0.094
Connect + Area	3247.4	2.3	0.085
Connect + Area + (Connect * Area)	3247.9	2.8	0.066
Habitat + Connect	3248.2	3.1	0.057
Habitat + Area	3248.9	3.8	0.040
Habitat + Connect + Year + Trans	3249.4	4.3	0.031
Habitat + Area + Year + Trans	3249.9	4.8	0.024
Habitat	3250.1	5.0	0.022
Habitat + Connect + Area + (Habitat * Area)	3250.3	5.2	0.020
Area	3250.7	5.6	0.016
Habitat + Year + Trans	3250.8	5.7	0.016
Habitat + Area + Trans	3251.0	5.9	0.014
Area + Year + Trans	3251.3	6.2	0.012
Habitat + Connect + Area + (Habitat * Connect)	3252.1	7.0	0.008
Habitat + Connect + (Habitat * Connect)	3252.8	7.7	0.006
Year	3254.2	9.1	0.003
Null (Intercept)	3255.3	10.2	0.002
Connect	3255.6	10.5	0.001
Year + Trans	3255.7	10.6	0.001
Habitat + Area + (Habitat * Area)	3255.8	10.7	0.001
Trans	3257.0	11.9	0.001
Global	3259.8	14.7	0.000

Table 2.4. Model selection describing patch residence time of Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Generalized linear mixed models were used. Model diagnostics include AIC<sub>c</sub> values, ΔAIC<sub>c</sub>, and Akaike weights (ω<sub>i</sub>). Abbreviations are Habitat = patch habitat type; Area = patch area; Connect = patch connectivity, Trans = translocation. Models with ΔAIC<sub>c</sub> < 2 are shown in bold text.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	ω <sub>i</sub>
<b>Habitat + Area + Trans</b>	<b>605.7</b>	<b>0.0</b>	<b>0.354</b>
<b>Habitat + Connect + Area + Trans</b>	<b>607.0</b>	<b>1.3</b>	<b>0.185</b>
Habitat + Connect + (Habitat * Connect)	608.0	2.3	0.112
Habitat + Connect + Area + (Habitat * Area)	608.7	3.0	0.079
Habitat + Area + Year + Trans	608.7	3.0	0.079
Habitat + Connect + Area + (Habitat * Connect)	609.1	3.4	0.065
Habitat + Connect + Area + (Connect * Area)	610.1	4.4	0.039
Habitat + Connect + Area + Year + Trans	610.2	4.5	0.037
Habitat + Area	611.2	5.5	0.023
Habitat + Connect + Area	611.6	5.9	0.019
Habitat + Area + (Habitat * Area)	614.0	8.3	0.006
Area + Year + Trans	616.1	10.4	0.002
Habitat	619.2	13.5	0.000
Area	619.2	13.5	0.000
Connect + Area (Connect * Area)	619.4	13.7	0.000
Habitat + Year + Trans	621.0	15.3	0.000
Habitat + Connect	621.1	15.4	0.000
Global	621.7	16.0	0.000
Connect + Area	621.7	16.0	0.000
Habitat + Connect + Year + Trans	624.0	18.3	0.000
Trans	626.6	20.9	0.000
Null (Intercept)	627.0	21.3	0.000
Year	628.7	23.0	0.000
Year + Trans	628.9	23.2	0.000
Connect	629.1	23.4	0.000

Table 2.5. Model selection describing patch residence time of Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Generalized linear mixed models were used. Model diagnostics include AIC<sub>c</sub> values, ΔAIC<sub>c</sub>, and Akaike weights (ω<sub>i</sub>). Abbreviations are Habitat = patch habitat type; Area = patch area; Connect = patch connectivity; Trans = translocation. Models with ΔAIC<sub>c</sub> < 2 are shown in bold text.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	ω <sub>i</sub>
<b>Habitat + Connect + (Habitat * Connect)</b>	<b>3260.9</b>	<b>0.0</b>	<b>0.217</b>
<b>Habitat + Connect + Area + (Habitat * Area)</b>	<b>3261.1</b>	<b>0.2</b>	<b>0.196</b>
<b>Habitat + Connect</b>	<b>3261.5</b>	<b>0.6</b>	<b>0.160</b>
<b>Habitat + Connect + Area + (Habitat * Connect)</b>	<b>3261.9</b>	<b>1.0</b>	<b>0.131</b>
Habitat + Connect + Area	3263.6	2.7	0.056
Habitat + Area + (Habitat * Area)	3263.7	2.8	0.053
Habitat + Connect + Year + Trans	3264.1	3.2	0.044
Habitat + Connect + Area + Trans	3264.5	3.6	0.036
Habitat + Area	3266.0	5.1	0.017
Habitat	3266.0	5.1	0.017
Habitat + Year + Trans	3266.0	5.1	0.017
Habitat + Connect + Area + Year + Trans	3266.2	5.3	0.015
Habitat + Area + Trans	3266.3	5.4	0.015
Habitat + Connect + Area + (Connect * Area)	3266.6	5.7	0.013
Global	3267.9	7.0	0.007
Habitat + Area + Year + Trans	3268.1	7.2	0.006
Trans	3275.3	14.4	0.000
Null (Intercept)	3275.3	14.4	0.000
Year + Trans	3276.4	15.5	0.000
Connect	3277.0	16.1	0.000
Year	3277.0	16.1	0.000
Area	3277.3	16.4	0.000
Area + Year + Trans	3278.4	17.5	0.000
Connect + Area + (Connect * Area)	3278.5	17.6	0.000
Connect + Area	3279.1	18.2	0.000

Table 2.6. Model selection describing movement rate ( $m \text{ min}^{-1}$ ) of Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Generalized linear mixed models were used. Model diagnostics include AIC<sub>c</sub> values, ΔAIC<sub>c</sub>, and Akaike weights (ω<sub>i</sub>). Abbreviations are Habitat = patch habitat type; Area = patch area; Connect = patch connectivity; Trans = translocation. Models with ΔAIC<sub>c</sub> < 2 are shown in bold text.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	ω <sub>i</sub>
<b>Null (Intercept)</b>	<b>496.2</b>	<b>0.0</b>	<b>0.227</b>
<b>Habitat</b>	<b>497.5</b>	<b>1.3</b>	<b>0.119</b>
<b>Habitat + Area + (Habitat * Area)</b>	<b>497.6</b>	<b>1.4</b>	<b>0.113</b>
<b>Connect</b>	<b>498.0</b>	<b>1.8</b>	<b>0.092</b>
Year	498.5	2.3	0.072
Area	498.5	2.3	0.072
Trans	498.6	2.4	0.068
Habitat + Connect + Area + (Habitat * Area)	499.8	3.6	0.038
Habitat + Connect	500.0	3.8	0.034
Habitat + Area	500.1	3.9	0.032
Connect + Area	500.5	4.3	0.026
Habitat + Connect + Area + (Habitat * Connect)	500.6	4.4	0.025
Year + Trans	501.0	4.8	0.021
Habitat + Connect + (Habitat * Connect)	501.7	5.5	0.015
Habitat + Year + Trans	502.5	6.3	0.010
Habitat + Connect + Area	502.9	6.7	0.008
Connect + Area + (Connect * Area)	502.9	6.7	0.008
Habitat + Area + Trans	503.1	6.9	0.007
Area + Year + Trans	503.6	7.4	0.006
Habitat + Connect + Year + Trans	505.3	9.1	0.002
Habitat + Area + Year + Trans	505.6	9.4	0.002
Habitat + Connect + Area + (Connect * Area)	505.9	9.7	0.002
Habitat + Connect + Area + Trans	506.0	9.8	0.002
Habitat + Connect + Area + Year + Trans	508.6	12.4	0.000
Global	523.3	27.1	0.000

Table 2.7. Model selection describing movement rate ( $m \text{ min}^{-1}$ ) of Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Generalized linear mixed models were used. Model diagnostics include AIC<sub>c</sub> values, ΔAIC<sub>c</sub>, and Akaike weights (ω<sub>i</sub>). Abbreviations are Habitat = patch habitat type; Area = patch area; Connect = patch connectivity; Trans = translocation. Models with ΔAIC<sub>c</sub> < 2 are shown in bold text.

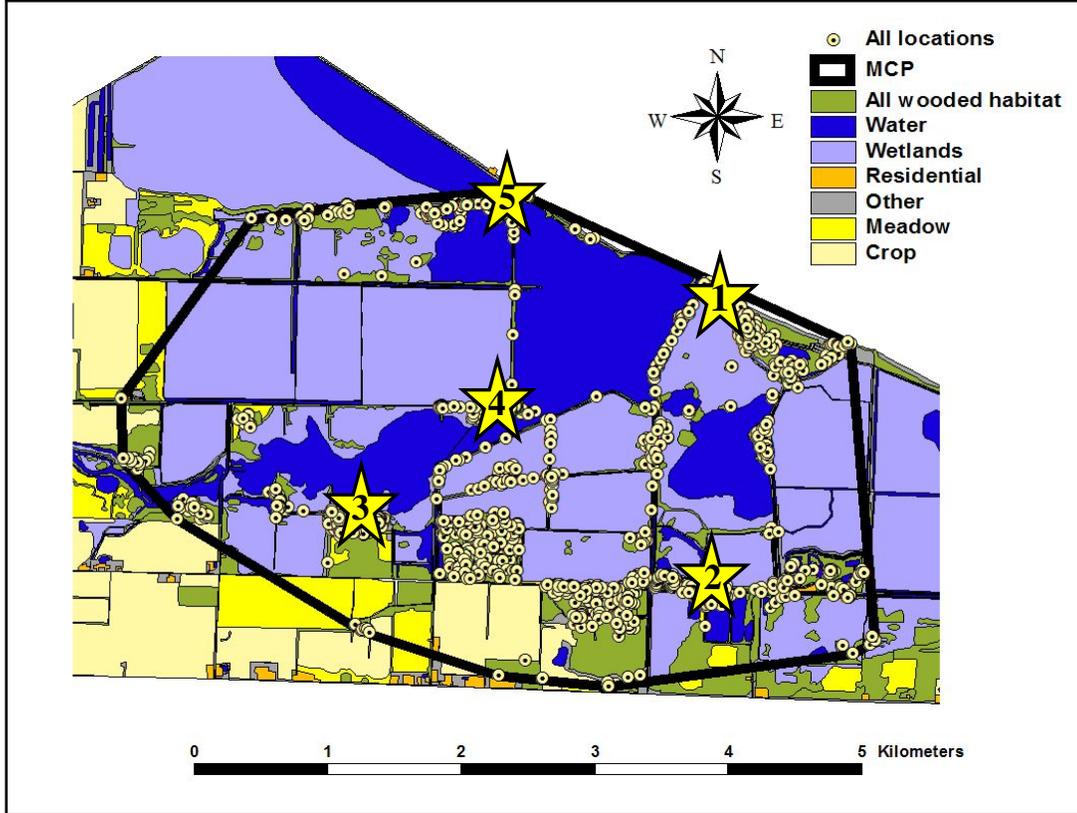


Figure 2.1. Digital map depicting release locations (stars) of Yellow-rumped Warblers and Red-eyed Vireos within the study area (black outline) in northern Ohio in spring 2006 and 2007. Release locations were Crane Creek (1), Shop Woods (2), Butternut (3), MS5 Woods (4), and West Crane Creek (5). The study area was delineated by calculating a 100% Minimum Convex Polygon for all telemetry locations (circles).

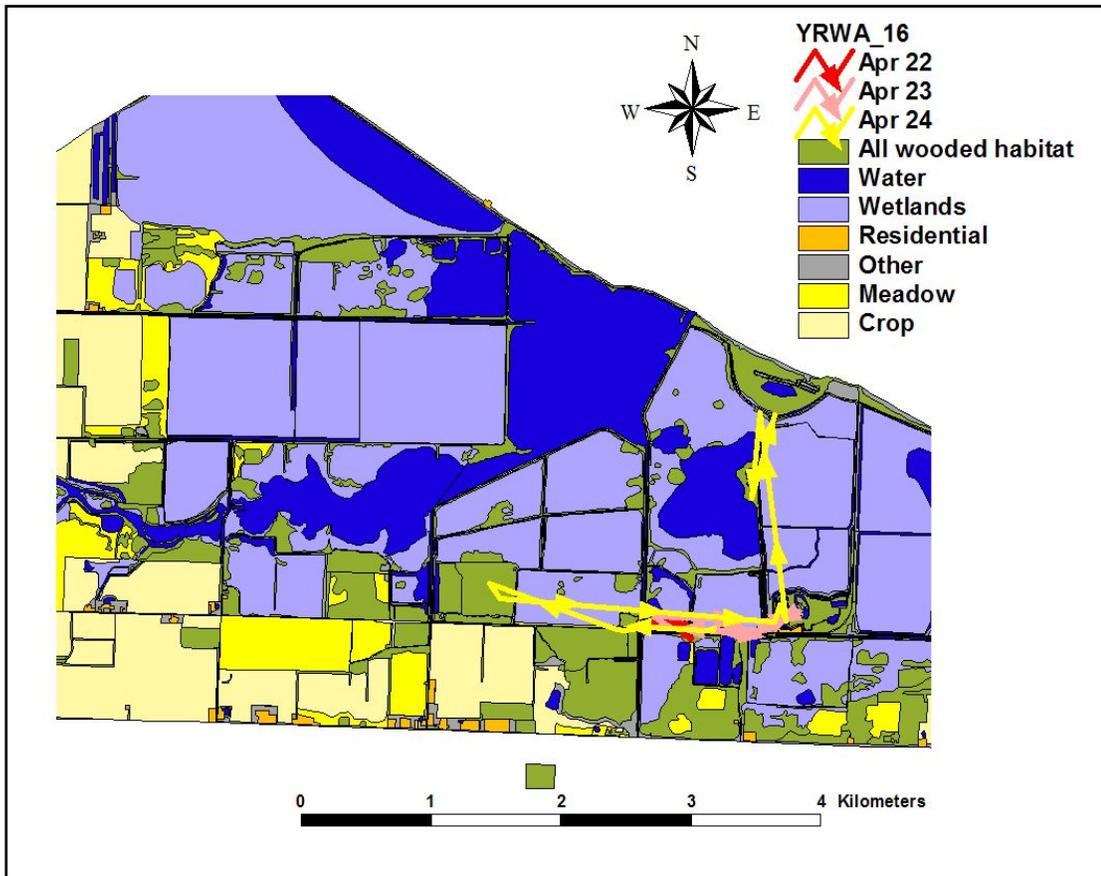


Figure 2.2. Stopover movements of a locally-released, second-year male Yellow-rumped Warbler in the western Lake Erie basin in April 2006. Movements were plotted on the digital map of the study area.

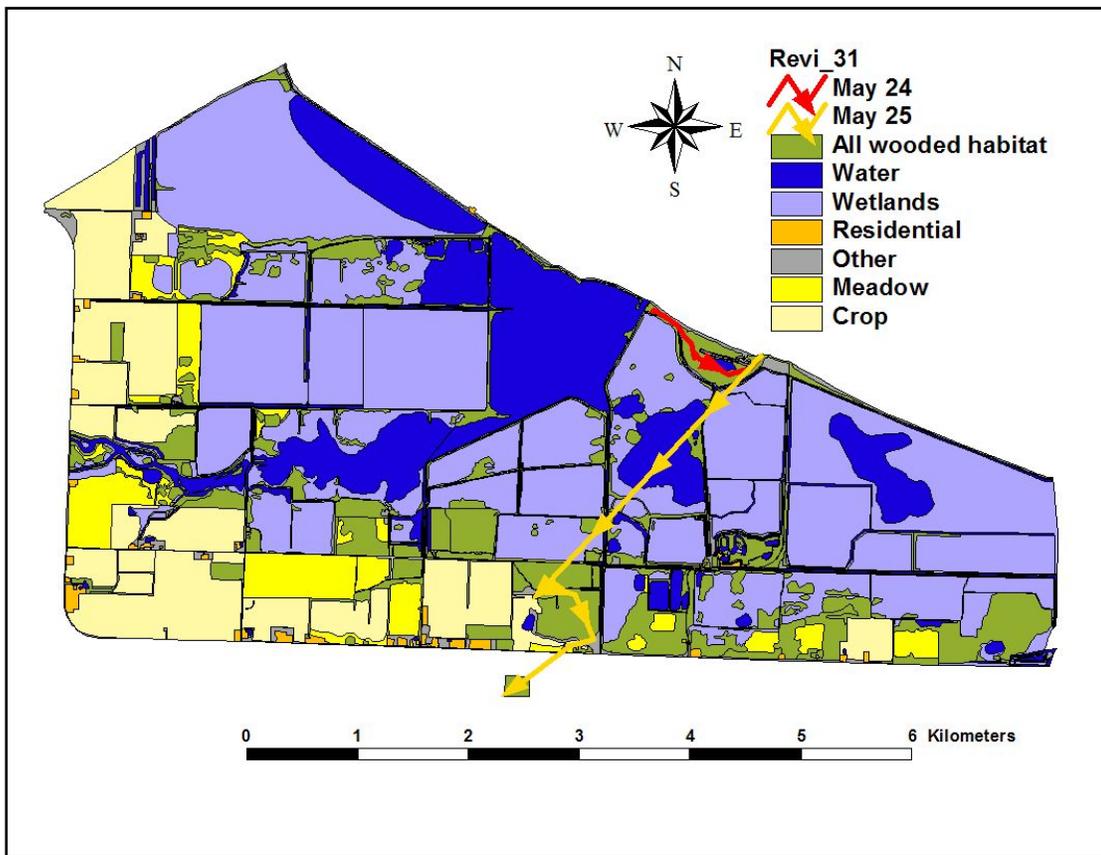


Figure 2.3. Stopover movements of a locally-released Red-eyed Vireo in the western Lake Erie basin in May 2006. Movements were plotted on the digital map of the study area.

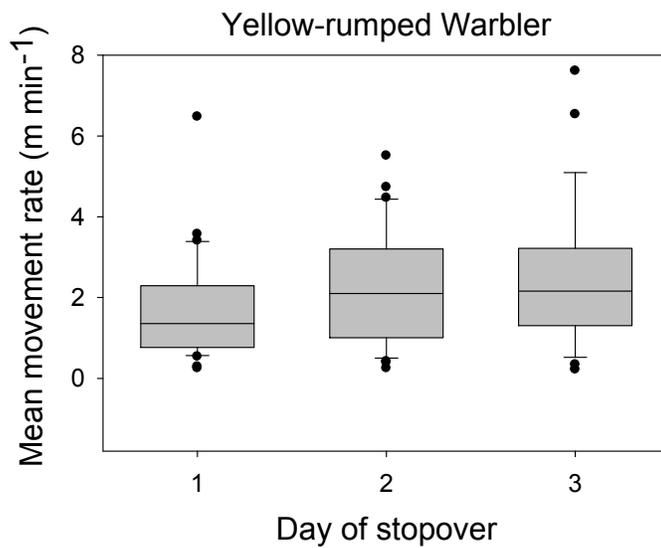


Figure 2.4. Mean movement rate ( $\text{m min}^{-1}$ ) during three days following release for Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. The interquartile range is displayed, as well as minimum and maximum observations.

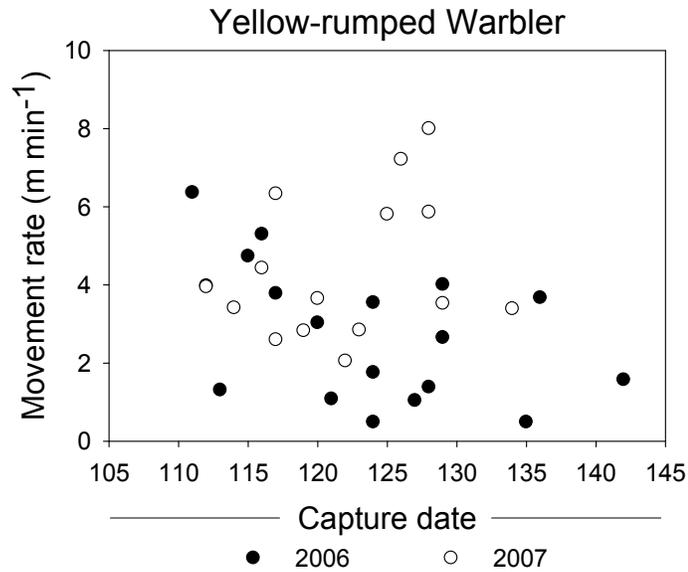


Figure 2.5. Daily mean movement rate ( $\text{m min}^{-1}$ ) in relation to capture date for Yellow-rumped Warblers during the first three days of radio-tracking in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Mean movement rate was averaged across the first three days for each individual. No relationship was detected ( $p = 0.136$ ).

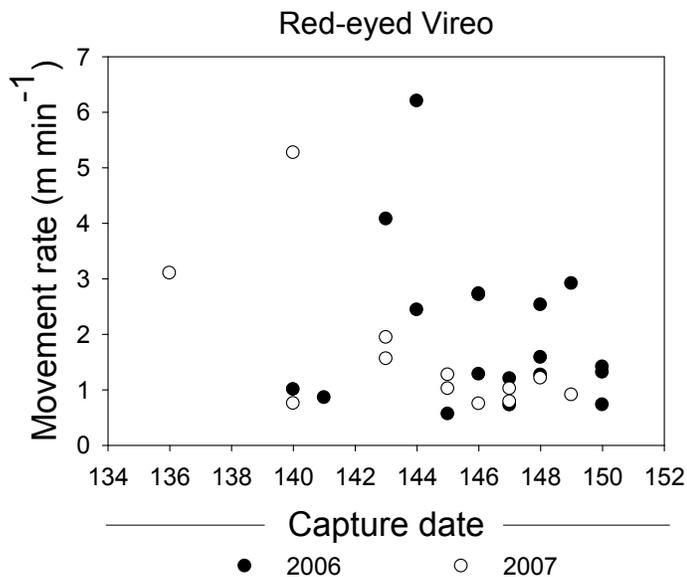


Figure 2.6. Daily mean movement rate ( $\text{m min}^{-1}$ ) in relation to capture date for Red-eyed Vireos during the first day of radio-tracking in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. There was a significant, negative relationship between mean movement rate and arrival date ( $p = 0.04$ ).

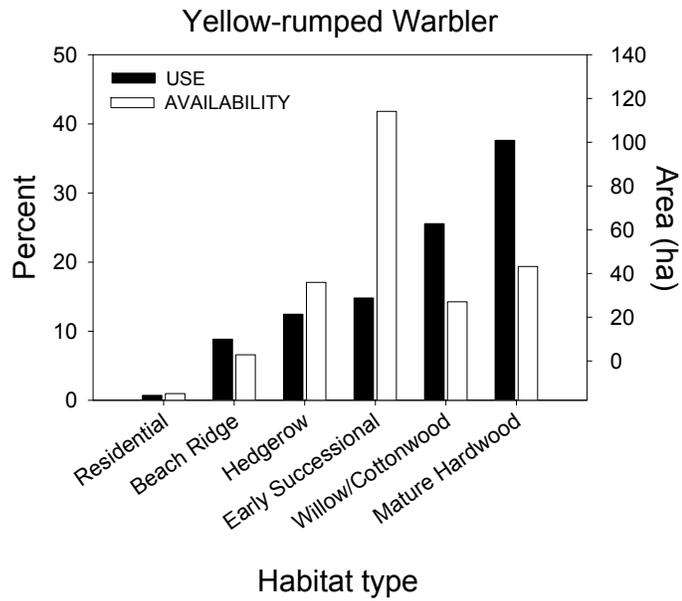


Figure 2.7. Percent availability of habitat types, area (ha) of available habitat types, and percent use of habitat types for Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007.

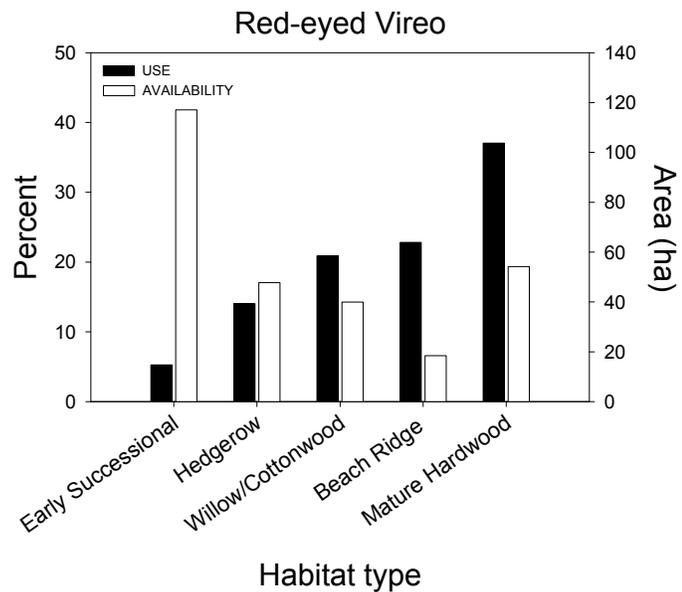


Figure 2.8. Percent availability of habitat types, area (ha) of available habitat types, and percent use of habitat types for Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007.

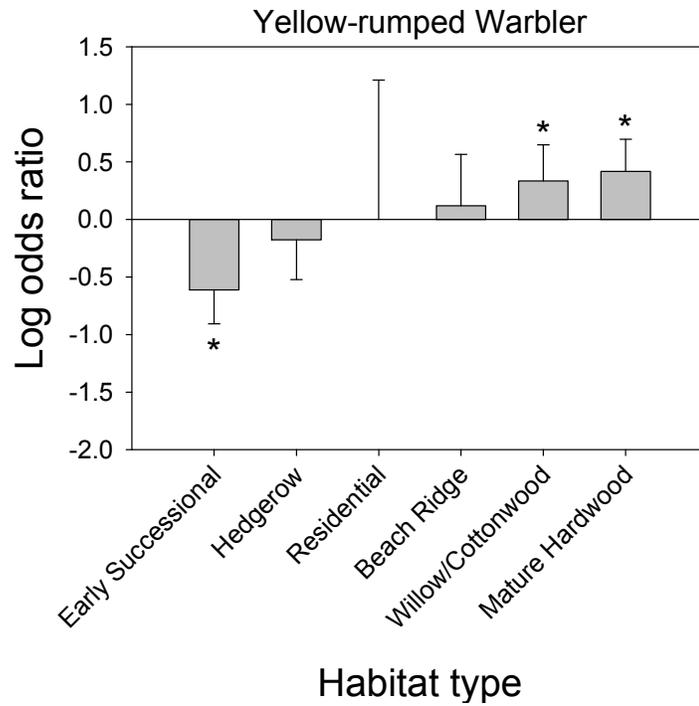


Figure 2.9. Log odds ratios indicating the direction and magnitude of association between habitat use and availability for Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Negative associations indicate avoidance, and positive associations indicate selection; significant associations noted with an asterisk. Error bars represent 95% confidence limits for the Cochran-Mantel-Haenszel estimate of association.

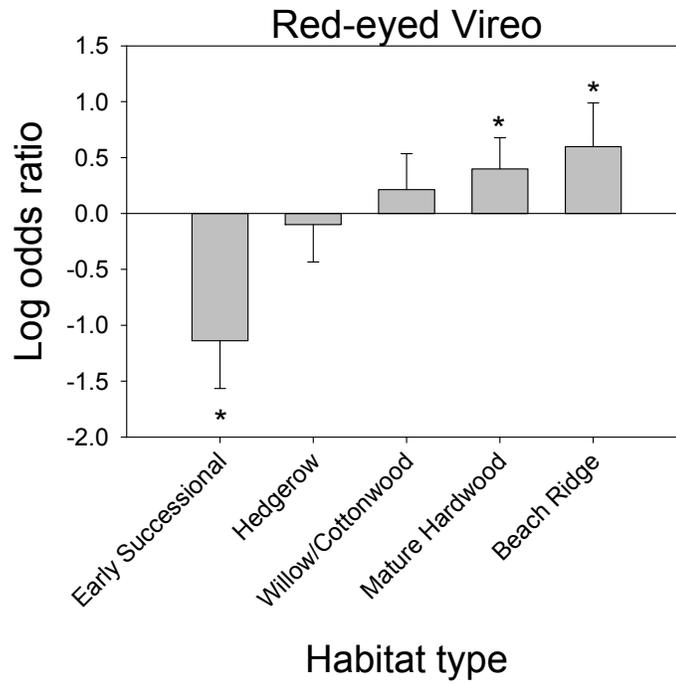


Figure 2.10. Log odds ratios indicating the direction and magnitude of association between habitat use and availability for Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Negative associations indicate avoidance, and positive associations indicate selection; significant associations noted with an asterisk. Error bars represent 95% confidence limits for the Cochran-Mantel-Haenszel estimate of association.

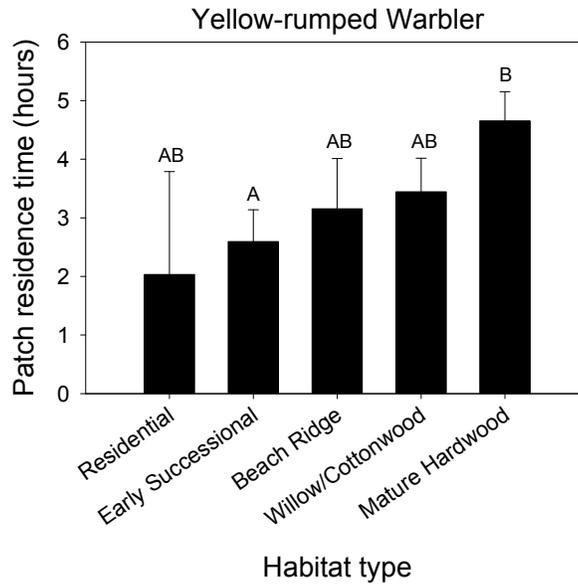


Figure 2.11. Patch residence time within different habitat types for Yellow-rumped Warblers in the western Lake Erie basin in spring 2006 and 2007. Patch residence time in mature hardwood forest was significantly different than in early successional forest.

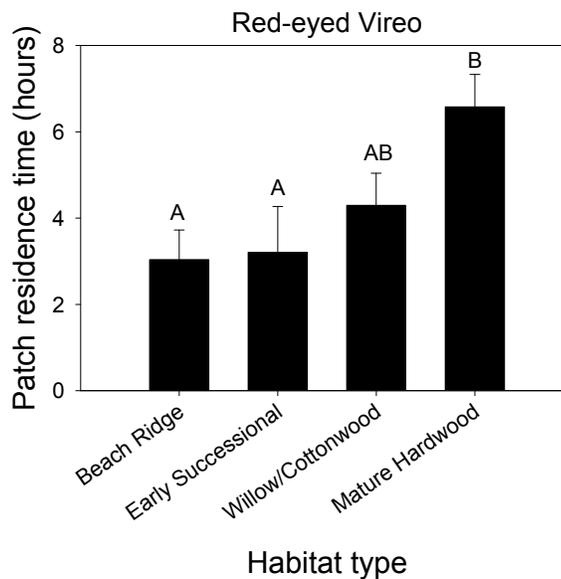


Figure 2.12. Patch residence time within different habitat types for Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Patch residence time in mature hardwood forest was significantly different than in beach ridge forest and early successional forest.

## CHAPTER 3

### INFLUENCE OF ENERGETIC CONDITION AND ARRIVAL DATE ON SPRING STOPOVER DURATION OF TWO MIGRATORY SONGBIRD SPECIES

#### INTRODUCTION

Migration is often considered the most stressful and demanding period during the life cycle of migratory landbirds. Even so, research on events occurring during migration has received insufficient attention, in part due to the difficulties of studying migrating birds (Moore et al. 1995, Petit 2000). Stopover habitats are temporarily used during migration and are important because they provide migratory birds a place to rest, refuel, and avoid predators. Stopover habitats where migrants can safely and rapidly restore depleted fat stores must be available for migration to be successful (Moore et al. 1995). Since natural selection favors a timely arrival on the breeding grounds (Francis and Cooke 1986), staying longer at stopover sites should lower the likelihood of successful reproduction.

During migration, birds spend the majority of their time in stopover areas rather than in flight (Hedenstrom and Alerstam 1997, Wikelski et al. 2003), so examining where, when, and how long birds choose to stopover is important for understanding the

ecology of migration (Alerstam and Lindstrom 1990, Jenni and Schaub 2003). At multiple points along their migratory journey species may respond differently or have different migration strategies altogether, especially when faced with geographical barriers, such as large bodies of water or deserts. Understanding how migratory birds respond to stopover habitat conditions and how behavior varies among species and seasons is necessary to identify and conserve important stopover areas.

Fundamental for assessing the importance of a stopover location is the ability to accurately quantify how long birds are utilizing stopover habitats. Until recently, stopover duration has been estimated from mark-recapture techniques (e.g. Kuenzi et al. 1991, Loria and Moore 1990, Schaub and Jenni 2001). Because these estimates rely on recapturing marked individuals and are based on the assumption that birds not recaptured have left the study area, they potentially underestimate true stopover durations (Bachler and Schaub 2007). While these estimates of stopover duration are informative, estimates from radio telemetry should be more accurate. For example, estimates of stopover duration based on relocations of radio-marked Orphean Warblers (*Sylvia hortensis*) during spring migration in West Africa were twice as long as estimates from mark-recapture and resighting data (Bachler and Schaub 2007). Beyond stopover duration, radio telemetry can provide detailed information on spatial and temporal movement patterns of animals and is therefore a powerful tool for researchers (Aebischer et al. 1993). Light weight radio transmitters now allow researchers to collect telemetry data for small landbirds during migration to examine patterns of movement (Aborn and Moore

1997, 2004; Chernetsov and Mukhin 2006, Tietz and Johnson 2007) and habitat selection (Tietz and Johnson 2007).

Although factors regulating stopover duration are poorly understood (Schaub and Jenni 2001), several hypotheses have been proposed. Theoretical models predict that migratory strategies differ depending on which optimization criteria birds are minimizing: time, energy, or predation risk. Speed of the migratory journey is considered the most important and widely used stopover strategy (Alerstam and Lindstrom 1990). According to optimal migration theory, if birds minimize time spent in migration then stopover duration depends on a bird's energetic condition and its ability to rapidly regain fat stores (Alerstam and Lindstrom 1990). Other hypotheses proposed to explain stopover duration suggest that migrants may respond to an innate spatiotemporal program of flights and stopovers (Jenni and Schaub 2003), or that weather (especially wind) conditions (Akesson and Hedenstrom 2000) or predation risk may drive a bird's decision to stay or depart (Alerstam and Lindstrom 1990).

Most migrants arrive at stopover sites with depleted fat stores and energetic condition is thought to influence activity budgets, flight distance, and time spent at stopover sites (Alerstam and Lindstrom 1990). Although energetic condition upon arrival is often considered the most important extrinsic (unrelated to habitat) constraint during migration (Hutto 1985, Loria and Moore 1990, Moore et al. 1995, 2005), most studies examining stopover duration based on telemetry data have reported no relationship between energetic condition at capture and stopover duration (e.g. Bolshakov et al. 2007, Dierschke and Delingat 2001, Tietz and Johnson 2007, Tsvey et al. 2007). However,

Chernetsov and Mukhin (2006) did report a non-significant, negative relationship between energetic condition and stopover duration for European Robins (*Erithacus rubecula*).

Information on the timing and rate of migration is needed to better understand the migratory schedules of birds. The goal of my research was to examine factors influencing the stopover duration of migrant songbirds in a highly fragmented, agriculturally dominated landscape with high concentrations of migratory birds in spring. I used radio telemetry to estimate minimum stopover duration for two species of landbird migrants, the Yellow-rumped Warbler (*Dendroica coronata*) and Red-eyed Vireo (*Vireo olivaceus*), in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. My specific objectives were to assess how energetic condition (size-adjusted body mass) at capture, date of arrival, release site and year may influence stopover duration.

## STUDY AREA

Research was conducted in Lucas and Ottawa counties of northwestern Ohio in the western Lake Erie basin, primarily within the Ottawa National Wildlife Refuge (NWR) complex. Migrant landbirds were captured at Cedar Point NWR and also within the Ottawa and Navarre Units of Ottawa NWR. These management units consist of coastal marshes, wetlands, wet prairies, hardwood forests, beach ridge forests, and managed and unmanaged impoundments (Ottawa NWR 2000). In this highly fragmented region dominated by agriculture and to a lesser extent urban and suburban land cover, the

remaining forest consists of small and often isolated tracts. Terrestrial forest habitats include beach ridge, willow/cottonwood, mature hardwood, early successional, and hedgerow.

Migrants accumulate in high densities along the southwestern shores of Lake Erie during spring migration because smaller birds are reluctant to cross the large expanse of open water. Because little natural habitat remains in this region, small remnant habitat patches should represent important stopover habitat for very large numbers of migrating landbirds (Ewert and Hamas 1995). Migrant bird concentrations of the magnitude found in northern Ohio are rare in Midwestern states (Ottawa NWR 2000, Shieldcastle et al. 2004), making this region continentally significant for bird conservation.

## METHODS

Yellow-rumped Warblers and Red-eyed Vireos were selected as focal species because they are common in the study area during spring migration and large enough to carry small (0.43-0.66g) radio transmitters. Yellow-rumped Warblers are short-distance (temperate) migrants, inhabiting deciduous, coniferous, and mixed forests, as well as edges of woods and thickets. The subspecies *D.c. coronata* breeds from northern Alaska to eastern Canada, and southeast to Michigan, West Virginia and Massachusetts. Wintering birds occur in the Atlantic and Gulf coastal states, the West Indies, and in Mexico, and less commonly east from Kansas through the central states to New England (Hunt and Flaspohler 1998). YRWA primarily forage on insects during spring migration

and the breeding season, and consume fruits and insects during fall and winter.

Red-eyed Vireos are long-distance (Nearctic-Neotropical) migrants, inhabiting deciduous and mixed forests with moderate to dense understory vegetation. This species breeds from southeast Alaska east and south throughout Canada and south through the eastern half of the United States, and winters in South America (Cimprich et al. 2000). REVI primarily forage on insects during spring migration and the breeding season, and consume insects and a wide variety of small fruits during fall and winter.

Migrants were captured using 2.6 x 12 m mist nets (30 mm mesh) at Cedar Point National Wildlife Refuge (10 nets), the Navarre Unit of Ottawa NWR (21 nets, but only in 2006), and at five locations within the Ottawa Unit of Ottawa NWR (5-9 nets each location). Nets were checked and captured birds were removed every 20 minutes or at shorter intervals when air temperatures were close to 0°C. Netting for experimental birds began 30 minutes before sunrise and continued for 4.5 hours.

Each bird was held briefly in a cloth bag before processing. Birds were banded with a U.S.G.S. aluminum leg band. Migrants used as experimental birds were also color banded with a unique color combination. Data on location, time of capture, age, sex, tarsus length ( $\pm 0.01$  mm), unflattened wing chord ( $\pm 0.5$  mm), and body mass ( $\pm 0.01$  gram) were recorded. Age and sex were determined using methods described in Pyle et al. (1987). Migrants were visually scored for subcutaneous body fat using the 6-point ordinal scale of Helms and Drury (1960).

Yellow-rumped Warblers and Red-eyed Vireos captured within 4 hours of sunrise and with fat scores of 3 or less (Helms and Drury 1960) were chosen as experimental

birds for radio tracking. Transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) weighed 0.43 g (Model BD-2n for YRWA) and 0.66 g (Model BD-2 for REVI) which represented approximately 3% of body mass for YRWA and REVI, respectively (unpublished data). Transmitters were designed with a range of approximately 1 km and a lifespan of 7-12 days, although I failed to locate any birds whose transmitter had died prior to departure.

After banding and processing, YRWA (n = 23) and REVI (n = 21) used as experimental birds were promptly translocated to one of five pre-determined forest release sites at Ottawa NWR which varied in area and distance to lakeshore (Figure 3.1). Experimental relocations of individual migrants to different sites were used to examine habitat features that may influence movement behavior and to control for arrival timing. As a control for translocated birds, YRWA (n = 15) and REVI (n = 12) were also captured within the 5 release sites, processed, and released at the same site. Each bird was fitted with a small radio transmitter and released within 50-90 minutes. Three to four individuals of each species were released at each of the 5 release sites in each year; 62% of birds were translocated. If a bird was visibly stressed (i.e. fluffing feathers, closing eyes, not alert, panting) when taken out of the holding bag, it was not fitted with a radio transmitter. Feathers in the interscapular area were parted and the radio transmitter attached using a few drops of eyelash adhesive using modified methods of Raim (1978) and Sykes et al. (1990); eyelash adhesive is water-soluble and designed for temporary attachment. For 6 birds, radio transmitters fell off within 2-11 days and were recovered in the study area. These 6 individuals were not used in duration analyses.

Birds were taken to randomly selected points inside the forest patch and released in a random direction. Experimental birds were tracked using a 3-element folding Yagi Antenna (150 MHz, Advanced Telemetry Systems, Inc., Isanti, Minnesota) and 12-channel receiver (Communications Specialists, Inc., Orange, California). Radio locations were collected every 30 minutes for 3 days (YRWA) and 2 days (REVI). All birds were checked once daily after day 3 (YRWA) and day 2 (REVI) to determine minimum stopover duration and monitor day-to-day movements. When I was unable to detect a radio-marked bird, I traversed the study area (Ottawa NWR) for 1.5 to 2 hours searching for the bird. If the bird was still not detected, I drove within a 4 km radius of the bird's last location, using a roof-mounted omni-directional antenna and a Yagi antenna to listen for the signal. If still undetected, the bird was assumed to have left the study area, although radio frequencies of such individuals were checked for two additional days.

#### Statistical analyses

Minimum stopover duration of each experimental bird was calculated as the difference (in days) between the initial release date and the date the bird was last relocated in the study area. Although the exact arrival date is unknown, captured migrants were assumed to be new arrivals for these analyses. Sites were netted regularly to increase the probability of capturing birds on arrival day. Migrant activity was observed daily so migrant movements into and out of the study area were well known, suggesting that in many cases experimental birds were captured on arrival day.

I used all individuals captured in 2006 and 2007 to build an index of energetic condition. For each species, a principal components analysis was used to reduce structural measurements (wing chord and tarsus) of each bird captured to a single factor. Scores from the first principal component represented a standardized metric for each individual. Principal component scores were then regressed against the mass values of these individuals and the residuals of this regression were used as an index of energetic condition (Green 2001). Positive condition scores (i.e. residuals) indicated birds in better than average condition relative to all individuals captured.

Duration was represented as counts of the number of birds that stayed per day. The frequency distribution is non-Gaussian (Figure 3.2); therefore, duration was modeled using the Poisson probability distribution. Data on stopover duration were analyzed for biotic and abiotic effects using a generalized linear model for categorical analysis of Poisson count data. Sixty individuals (32 YRWA, 28 REVI) were used in analyses of stopover duration (Table 3.1). Because I was unable to determine their stopover duration, I excluded from analyses birds that had radio transmitters fail (1), were depredated (1), died of unknown cause (1), or had radio transmitters fall off in the study area (6). Following an information-theoretic approach, I used Akaike's Information Criterion (AIC) with a correction factor for small samples sizes ( $AIC_c$ ) to rank candidate models for YRWA and REVI (Burnham and Anderson 2002). Difference in  $AIC_c$ , or simply  $\Delta_i$ , was used to select "good" models from the set of candidate models. These differences were obtained by subtracting  $AIC_c$  of model under consideration from the top-ranked

model. Candidate models were chosen *a priori* and included main effects and their combinations, 2-way interactions, and the null model (a total of 33 models). Models with  $\Delta_i < 2.0$  relative to the model with the lowest  $AIC_c$  were considered “good” models. “Good” models were then evaluated for goodness-of-fit.

Due to small sample sizes within age-sex classes, age and sex were not included as factors. However, because the model for YRWA with the most support included condition, I divided the dataset into 4 subsets of age-sex classes [after-second-year (ASY) males, ASY females, second-year (SY) males, and SY females] and tested for differences in stopover duration among groups for YRWA using the Mann-Whitney U test. Then, using simple linear regression, I regressed stopover duration against energetic condition separately for each age-sex class. All statistical analyses were performed using SAS version 9.1 for Windows (SAS Institute 1996).

## RESULTS

A total of 38 Yellow-rumped Warblers and 31 Red-eyed Vireos were radio-tracked from 20 April to 1 June in spring 2006 and 2007. Mean stopover duration was surprisingly long for YRWA and far shorter for REVI. For YRWA, mean minimum stopover duration ( $\pm$ S.D.) was 7.0 days ( $\pm$ 3.6;  $n = 17$ ) in 2006 and 4.8 days ( $\pm$ 2.7;  $n = 15$ ) in 2007 (Table 3.1). In contrast, mean minimum stopover duration ( $\pm$ S.D.) for REVI was 1.6 days ( $\pm$ 0.9;  $n = 18$ ) in 2006 and 1.7 days ( $\pm$ 1.6;  $n = 10$ ) in 2007 (Table 3.1).

The model that best described stopover duration (lowest AIC<sub>c</sub>) for YRWA included energetic condition, year, and release site ( $\omega_i = 0.383$ ; Table 3.2). The parameter estimate was  $-0.33 \pm 0.08$  S.E. ( $X^2_1 = 15.35$ ;  $p < 0.001$ ) for energetic condition, indicating a negative relationship between condition and stopover duration for YRWA (Figure 3.3). YRWA stopped over 42% longer in 2006 than in 2007; parameter estimate for year was  $0.42 \pm 0.15$  S.E. ( $X^2_1 = 7.86$ ;  $p = 0.005$ ). There was also a relationship between release site ( $X^2_4 = 13.45$ ;  $p = 0.009$ ) and duration, suggesting that YRWA released in larger patches had shorter durations than those released in small patches (Figure 3.4). The only other competing model for YRWA indicated that energetic condition and year best described stopover duration ( $\Delta_i=1.64$ ;  $\omega_i = 0.168$ ; Table 3.2). Because the evidence ratio for top-ranked and second-ranked models was large ( $\omega_1/\omega_2 = 2.28$ ), we should expect high variation in the model that best describes stopover duration for YRWA (Burnham and Anderson 2002).

After-second-year males ( $n = 3$ ) had significantly shorter stopovers than other YRWA age-sex classes ( $n = 29$ ,  $p = 0.019$ ). After adjusting for energetic condition, these ASY males did not have significantly shorter stopovers ( $p = 0.05$ ). Stopover duration was strongly condition dependent for ASY males ( $r^2 = 0.995$ ,  $p = 0.04$ ), but not for ASY females ( $r^2 = 0.397$ ,  $p = 0.25$ ), SY males ( $r^2 = 0.121$ ,  $p = 0.29$ ), or SY females ( $r^2 = 0.064$ ,  $p = 0.40$ ).

High variation in candidate models suggested that none of the models adequately described stopover duration for REVI (Table 3.3). The model with the most support for REVI was the null model (intercept alone); parameter estimate was  $0.47 \pm 0.15$  S.E.

( $X^2_1 = 10.13$ ;  $p = 0.002$ ). Other models with  $\Delta_i < 2.0$  were a model with only energetic condition ( $\Delta_i = 1.36$ ;  $\omega_i = 0.103$ ) and a model with only translocation ( $\Delta_i = 1.38$ ;  $\omega_i = 0.102$ ; Table 3.3), neither of which strongly contributed to explaining variation in REVI stopover duration.

## DISCUSSION

In my study, stopover duration of Yellow-rumped Warblers was influenced by energetic condition at capture, year, and release site. Birds in better energetic condition than expected for their body size had shorter stopover durations. These results are consistent with theoretical models of time-minimization, which predict that if birds minimize time then stopover duration depends on energetic condition and ability to rapidly regain fat stores (Alerstam and Lindstrom 1990). However, my results contrast with studies that reported no clear relationships between energetic condition at capture and stopover duration (e.g. Bolshakov et al. 2007, Dierschke and Delingat 2001, Tsvey et al. 2007). The inconsistencies among studies suggest that factors influencing stopover duration are highly variable and difficult to generalize across migratory species.

Interestingly, stopover duration was very strongly condition dependent, with after-second year (ASY) male YRWA making the shortest stopovers. This pattern is consistent with the idea that if sexual selection drives protandry, males should leave the wintering grounds sooner, make shorter stopovers relative to their energetic condition, and arrive on the breeding grounds earlier to acquire the best territories. Although there

were only 3 ASY male YRWA in my dataset, a pattern of condition-dependent stopover duration was strong.

Stopover duration of YRWA was 42% longer in 2006 than in 2007, indicating that differences between years can provide important information for modeling stopover duration. This interannual variation is consistent with some studies of stopover duration (e.g. Schaub and Jenni 2001), but not others (e.g. Tsvey et al. 2007). High variability in stopover duration between years could be expected due to variable weather en route and fluctuations in resource availability.

The effect of release site suggests that YRWA released in larger forest sites had shorter durations. In both years, YRWA that were released in the largest release site (Butternut) had the shortest durations. Similarly, birds released in the two next largest sites (Shop Woods and MS5 Woods) also had shorter stopover than birds released in the smallest sites (Crane Creek and West Crane Creek) in 2006 but not in 2007. Between years, mean stopover duration was consistent for Butternut, Shop Woods, and MS5 Woods, but not for Crane Creek and West Crane Creek. YRWA released in Crane Creek and West Crane Creek in 2006 had the longest durations, but in 2007 this was not the case. Larger sites might be expected to have more resources available and allow more protection from predators compared to smaller sites, possibly enabling migrants to refuel more quickly. However, because area of release site was confounded with habitat type and distance to lake, elucidating which release site characteristics were most influential on stopover duration is a challenge.

For Red-eyed Vireo, mean minimum stopover duration was less than 2 days, an estimate similar to that by Loria and Moore (1990), who reported that 85% of REVI along the northern Gulf Coast stopped over for only 1 day in spring. However, none of the models effectively explained duration behavior of REVI in my study area. REVI is a long-distance Nearctic-Neotropical migrant wintering in South America. Because this species must migrate very long distances from wintering areas, it may exhibit a migration strategy that does not involve long stopovers but favors many shorter stopovers. Long-distance (tropical) migrants may travel for longer periods than short-distance (temperate) migrants, and at higher speeds (Alerstam and Lindstrom 1990), so this pattern of short stopovers could be expected. Another possibility is that migrating REVI arriving in my study area in late spring have to compete with other late migrants and local breeders for resources and may choose to continue migration instead of stopping over in an area with possibly low refueling potential. Optimal migration theory suggests that when fat depleted migrants are unable to find adequate food they may be prone to continuing migration (Alerstam and Lindstrom 1990). On the other hand, migrant REVI in my study may simply be able to rebuild fuel stores within one to two days and are thus able to leave sooner for the next migratory flight, especially if the flight is short. Because I developed a set of candidate models *a priori*, the possibility remains that unmeasured variables (e.g. weather, food availability, predation risk) may better explain variation in stopover duration for REVI. For example, relationships between stopover duration and weather conditions, food availability, or predation risk may also affect stopover duration.

Given that small, light weight radio transmitters have only recently become available, there are relatively few published estimates of stopover duration based on radio-marked individuals to compare for this species or for many others. I found that radio-marked individuals behaved similar to individuals without radio transmitters. Upon release, experimental birds resumed flying and foraging and otherwise normal behavior within minutes. I found no differences in stopover duration between translocated birds and locally released birds for either species in either year, suggesting that this did not strongly alter bird behavior, a finding consistent with other studies (Mazerolle and Hobson 2003, Naef-Daenzer et al. 2001, Powell et al. 1998, Sykes et al. 1990).

I detected no relationship between arrival date and stopover duration for either species, suggesting that late arriving individuals in northern Ohio did not stop over for shorter periods. This discovery was not consistent with the idea that the pace of migration increases as the season progresses (Alerstam and Lindstrom 1990). Although little data exist regarding the true timing of migration, Dierschke and Delingat (2001) found that Northern Wheatears (*Oenanthe oenanthe*) migrating to Scandinavia tended to make shorter stopovers in the second half of the spring migration season. No relationship between arrival date and stopover duration was expected for REVI, considering their narrow migratory window in northern Ohio.

Understanding where, when, and how long birds stay in different stopover areas is fundamental for conserving and managing important stopover areas. My research contributes to our understanding of the timing and rate of migration, by examining factors that influenced stopover duration in a highly fragmented, agriculturally dominated

landscape. My results suggest that land managers should be aware of the variability in stopover duration among birds and stopover areas, and that stopover duration in the western Lake Erie basin can last many days for some species. Such lengthy stopover periods suggest that this study area may significantly contribute to the energetic balance of many migrants. Further, since release site and energetic condition were important factors influencing stopover duration, land managers should provide sufficient habitat resources for migrants to efficiently refuel before continuing migration. In the western Lake Erie basin, I suggest that increasing the size of forest patches may benefit landbirds during migration.

## LITERATURE CITED

- Aborn, D.A., and F.R. Moore. 1997. Pattern of movement by summer tanagers (*Piranga rubra*) during migratory stopover: a telemetry study. *Behaviour* 134:1077-1100.
- Aborn, D.A., and F.R. Moore. 2004. Activity budgets of summer tanagers during spring migratory stopover. *Wilson Bulletin* 116:64-68.
- Aebischer, N. J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313-1325.
- Akesson, S., and A. Hedenstrom. 2000. Wind selectivity of migratory flight departures in birds. *Behavioral Ecology and Sociobiology* 47:140-144.
- Alerstam, T., and A. Lindstrom. 1990. Optimal bird migration: the relative importance of time, energy, and safety. Pages 331-351 *in* Bird Migration (E. Gwinner, Ed.). Springer, New York.
- Bachler, E., and M. Schaub. 2007. The effects of permanent and local emigration and encounter technique on stopover duration estimates as revealed by telemetry and mark-recapture. *Condor* 109:142-154.
- Bolshakov, C.V., N. Chernetsov, A. Mukhin, V.N. Bulyuk, V. Kosarev, P. Ktitorov, D. Leoke, and A. Tsvey. 2007. Time of nocturnal departures in European robins *Erithacus rubecula* in relation to celestial cues, season, stopover duration and fat stores. *Animal Behavior* 74:855-865.
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach, 2<sup>nd</sup> Ed. Springer-Verlag, New York.
- Chernetsov, N., and A. Mukhin. 2006. Spatial behavior of European robins *Erithacus rubecula* during migratory stopovers: a telemetry study. *Wilson Journal of Ornithology* 118:364-373.
- Cimprich, D.A., F.R. Moore, and M.P. Guilfoyle. 2000. Red-eyed Vireo (*Vireo olivaceus*). *The Birds of North America*, no. 527. (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- Dierschke, V. and J. Delingat. 2001. Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. *Behavioral Ecology and Sociobiology* 50:535-545.
- Ewert, D.N., and M.J. Hamas. 1995. Ecology of migratory landbirds during migration in the Midwest. Pages 200-208 *in* Management of Midwestern landscapes for the

conservation of Neotropical migratory birds. (F. R. Thompson III, Ed.). General Technical Report NC-187. U.S. Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.

- Francis, C.M., and F. Cooke. 1986. Differential timing of spring migration in wood warblers (Parulinae). *Auk* 103:548-556.
- Green, A.J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? *Ecology* 82:1473-1483.
- Hedenstrom, A., and T. Alerstam. 1997. Optimal fuel loads in migratory birds: distinguishing between time and energy minimization. *Journal of Theoretical Biology* 189:227-234.
- Helms, C.W., and W.H. Drury. 1960. Winter and migratory weight and fat field studies on some North American buntings. *Bird Banding* 31:1-40.
- Hunt, P.D., and D.J. Flaspohler. 1998. Yellow-rumped Warbler (*Dendroica coronata*). *The Birds of North America*, no. 376. (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- Hutto, R.L. 1985. Habitat selection by nonbreeding, migratory landbirds. Pages 455-476 *in* Habitat selection in birds. (M. L. Cody, Ed.). Academic Press, California.
- Jenni, L., and M. Schaub. 2003. Behavioural and physiological reactions to environmental variables in bird migration: a review. Pages 155-171 *in* Avian Migration. (P. Berthold, E. Gwinner, and E. Sonnenschein, Eds.). Springer-Verlag, Germany.
- Kuenzi, A., F.R. Moore, and T.R. Simons. 1991. Stopover of neotropical landbird migrants on East Ship Island following trans-gulf migration. *Condor* 93:869-883.
- Loria, D.E., and F.R. Moore. 1990. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. *Behavioral Ecology* 1:24-35.
- Mazerolle, D.F., and K.A. Hobson. 2003. Do ovenbirds (*Seiurus aurocapillus*) avoid boreal forest edges? A spatiotemporal analysis in an agricultural landscape. *Auk* 120:152-162.
- Moore, F.R., S.A. Gauthreaux Jr., P. Kerlinger, and T.R. Simons. 1995. Habitat requirements during migration: important link in conservation. Pages 121-144 *in* Ecology and Management of Neotropical migratory birds. (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.

- Moore, F.R., R.J. Smith, and R. Sandberg. 2005. Stopover ecology of intercontinental migrants: en route problems and consequences for reproductive performance. Pages 251-261 *in* Birds of two worlds: the ecology and evolution of migration (R. Greenberg and P.P. Marra, Eds.). Johns Hopkins University Press, Maryland.
- Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70:730-738.
- Ottawa National Wildlife Refuge Complex Comprehensive Conservation Plan. 2000.
- Petit, D. R. 2000. Habitat use by landbirds along Nearctic-Neotropical migration routes: implications for conservation of stopover habitats. *Studies in Avian Biology* 20:15-33.
- Powell, L.A., D.G. Krementz, J.D. Lang, and M.J. Conroy. 1998. Effects of radio transmitters on migrating Wood Thrushes. *Journal of Field Ornithology* 69:306-315.
- Pyle, P., S.N.G. Howell, R.P. Yunick, and D.F. DeSante. 1987. Identification guide to North American passerines. Slate Creek Press, California.
- Raim, A. 1978. A radio transmitter attachment for small passerine birds. *Bird Banding* 49:326-332.
- SAS Institute. 1996. SAS/STAT User's Guide, Version 9.1. SAS Institute, Cary, North Carolina.
- Schaub, M., and L. Jenni. 2001. Stopover durations of three warbler species along their autumn migration route. *Oecologia* 128:217-227.
- Shieldcastle, J., T. Kashmer, and M. Shieldcastle. 2004. Passerine habitat use during spring and fall migration. Black Swamp Bird Observatory Home Page. <http://www.bsbobird.org/spring.html>.
- Sykes, P.W., Jr., J. W. Carpenter, S. Holzman, and P.H. Geissler. 1990. Evaluation of three miniature radio transmitter attachment methods for small passerines. *Wildlife Society Bulletin* 18:41-48.
- Tietz, J.R., and M.D. Johnson. 2007. Stopover ecology and habitat selection of juvenile Swainson's thrushes during fall migration along the northern California coast. *Condor* 109:795-807.

Tsvey, A., V.N. Bulyuk, and V. Kosarev. 2007. Influence of body condition and weather on departures of first-year European robins, *Erithacus rubecula*, from an autumn migratory stopover site. *Behavioral Ecology and Sociobiology* 61:1665-1674.

Wikelski, M., E.M. Tarlow, A. Raim, R.H. Diehl, R.P. Larkin, and G.H. Visser. 2003. Cost of migration in free-flying songbirds. *Nature* 423:704.

Species	Year	<sup>†</sup> n <sub>1</sub>	<sup>‡</sup> n <sub>2</sub>	Mean Duration (days)	Std Dev	Min	Max
YRWA	2006	20	17	7.0	3.60	1	13
YRWA	2007	18	15	4.8	2.68	2	10
REVI	2006	18	18	1.6	0.98	1	4
REVI	2007	13	10	1.7	1.57	1	6
Total		69	60				

<sup>†</sup> Indicates number of individuals radio-tagged

<sup>‡</sup> Indicates number of individuals used in analyses of stopover duration. Individuals excluded from analyses had radio transmitters that fell off in the study area (6), had radio transmitters fail (1), were depredated (1), or died of unknown cause (1).

Table 3.1. Descriptive statistics for stopover duration of Yellow-rumped Warblers (YRWA) and Red-eyed Vireos (REVI) in the western Lake Erie basin of northern Ohio in spring 2006 and 2007.

Model	Deviance	K	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	ω <sub>i</sub>
<b>C + Y + R</b>	<b>25.30</b>	<b>7</b>	<b>-315.71</b>	<b>0.00</b>	<b>0.383</b>
<b>C + Y</b>	<b>38.75</b>	<b>3</b>	<b>-314.07</b>	<b>1.64</b>	<b>0.168</b>
C + Y + T	37.54	4	-312.65	3.06	0.083
C + Y + A + R	25.07	8	-312.35	3.37	0.071
C + Y + A	37.87	4	-312.33	3.39	0.070
C + Y + T + R	25.22	8	-312.19	3.52	0.066
C + Y + (C * Y)	38.57	4	-311.62	4.09	0.050
T + C + A + Y	36.10	5	-311.26	4.45	0.041
R + C	33.38	6	-310.94	4.78	0.035
C + Y + A + R + T	24.94	9	-308.55	7.16	0.011
C	47.51	2	-307.75	7.97	0.007
T + C	46.42	3	-306.40	9.32	0.004
C + A	46.84	3	-305.98	9.74	0.003
T + C + A	45.29	4	-304.90	10.81	0.002
Y + T + (Y * T)	45.64	4	-304.56	11.16	0.001
T + C + (T * C)	45.79	4	-304.40	11.31	0.001
C + A + (C * A)	46.39	4	-303.81	11.91	0.001
Y	52.67	2	-302.59	13.12	0.001
Y + R	41.85	6	-302.46	13.25	0.001
C + R + (C * R)	27.40	10	-301.80	13.91	0.000
Y + A	51.67	3	-301.15	14.57	0.000
Y + T	51.69	3	-301.13	14.59	0.000
Null (Intercept)	59.22	0	-300.46	15.26	0.000
Y + T + A	50.02	4	-300.18	15.54	0.000
R	48.25	5	-299.11	16.60	0.000
Y + A + (Y * A)	51.67	4	-298.53	17.19	0.000
T	57.60	2	-297.67	18.05	0.000
Y + R + (Y * R)	32.25	10	-296.95	18.76	0.000
A	58.65	2	-296.61	19.11	0.000
T + A	56.33	3	-296.49	19.23	0.000
T + R + (T * R)	41.54	10	-287.66	28.05	0.000
A + R + (A * R)	44.16	10	-285.04	30.67	0.000
Global	1.76	30	1511.15	1826.86	0.000

Table 3.2. Model selection describing stopover duration of Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Generalized linear models for categorical analysis of Poisson data were used. Model diagnostics include model deviance, number of parameters (K), AIC<sub>c</sub> values, ΔAIC<sub>c</sub>, and Akaike weights (ω<sub>i</sub>). Abbreviations are C = energetic condition; Y = year; R = release site; T = translocation; A = arrival date. Models with ΔAIC<sub>c</sub> < 2 are shown in bold text.

Model	Deviance	K	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	ω <sub>i</sub>
<b>Null (Intercept)</b>	<b>17.98</b>	<b>1</b>	<b>49.45</b>	<b>0.00</b>	<b>0.203</b>
<b>C</b>	<b>17.02</b>	<b>2</b>	<b>50.81</b>	<b>1.36</b>	<b>0.103</b>
<b>T</b>	<b>17.04</b>	<b>2</b>	<b>50.84</b>	<b>1.38</b>	<b>0.102</b>
A	17.85	2	51.65	2.20	0.068
Y	17.90	2	51.70	2.24	0.066
T + C	15.66	3	51.97	2.52	0.058
R	10.08	5	52.12	2.67	0.053
T + C + (T * C)	13.10	4	52.15	2.70	0.053
T + A	16.75	3	53.06	3.61	0.033
Y + T	16.78	3	53.09	3.64	0.033
C + A	16.87	3	53.19	3.73	0.031
Y + C	17.01	3	53.33	3.87	0.029
Y + A	17.82	3	54.14	4.69	0.019
T + C + A	15.31	4	54.37	4.91	0.017
C + R	9.06	6	54.38	4.93	0.017
Y + T + C	15.60	4	54.65	5.20	0.015
T + R	9.68	6	54.99	5.54	0.013
A + R	10.03	6	55.35	5.90	0.011
Y + T + (Y * T)	16.30	4	55.35	5.90	0.011
Y + R	10.08	6	55.39	5.94	0.010
Y + T + A	16.61	4	55.67	6.21	0.009
T + A + (T * A)	16.70	4	55.76	6.31	0.009
C + A + (C * A)	16.85	4	55.90	6.45	0.008
Y + C + A	16.86	4	55.92	6.47	0.008
Y + C + (Y * C)	17.00	4	56.06	6.61	0.007
Y + A + (Y * A)	17.67	4	56.73	7.28	0.005
T + C + A + Y	15.31	5	57.35	7.90	0.004
C + Y + R	9.03	7	57.95	8.50	0.003
C + A + T + Y + R	8.46	9	65.78	16.32	0.000
C + R + (C * R)	4.54	10	66.80	17.35	0.000
T + R + (T * R)	7.32	10	69.57	20.12	0.000
Y + R + (Y * R)	9.33	10	71.58	22.13	0.000
Global	0.34	25	958.88	909.43	0.000

Table 3.3. Model selection describing stopover duration of Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Generalized linear models for categorical analysis of Poisson data were used. Model diagnostics include model deviance, number of parameters (K), AIC<sub>c</sub> values, ΔAIC<sub>c</sub>, and Akaike weights (ω<sub>i</sub>). Abbreviations are C = energetic condition; T = translocation; A = arrival date; R = release site; Y = year. Models with ΔAIC<sub>c</sub> < 2 are in shown bold text.

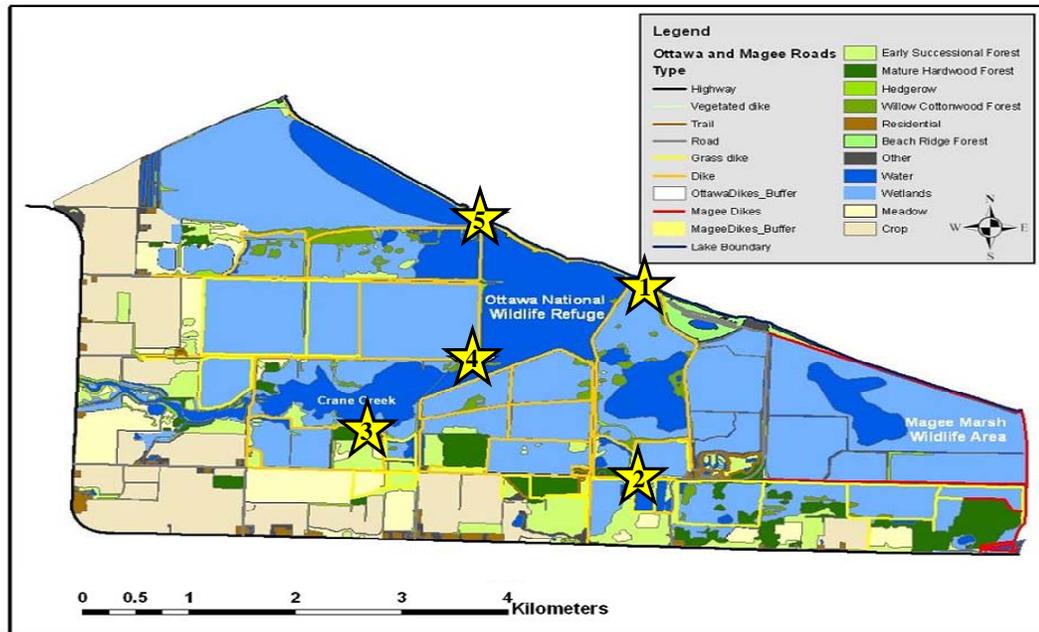


Figure 3.1. Map depicting release locations of Yellow-rumped Warblers and Red-eyed Vireos within Ottawa National Wildlife Refuge in northern Ohio, spring 2006 and 2007. Release locations were Crane Creek (1), Shop Woods (2), Butternut (3), MS5 Woods (4), and West Crane Creek (5).

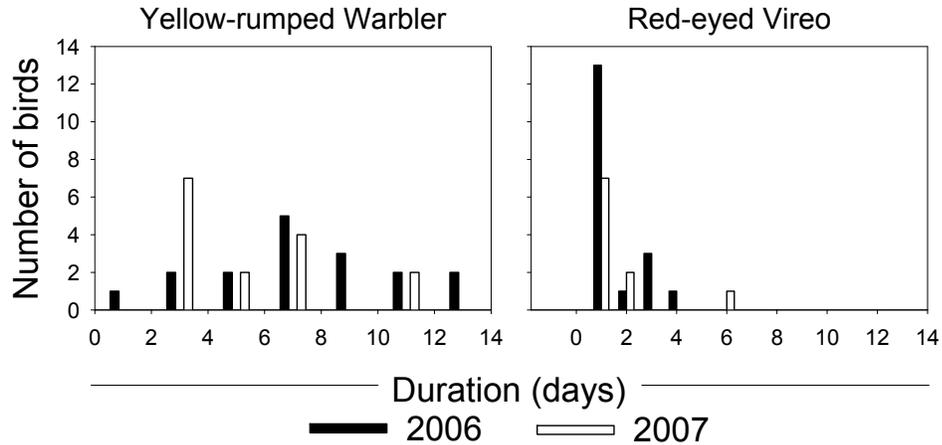


Figure 3.2. Stopover duration (days) of Yellow-rumped Warblers and Red-eyed Vireos in the western Lake Erie basin of northern Ohio in spring 2006 and 2007.

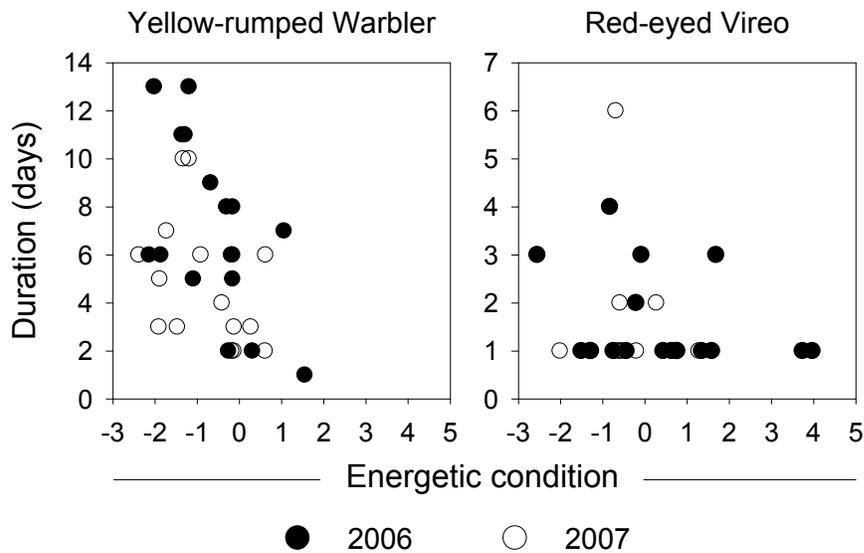


Figure 3.3. Relationship between stopover duration (days) and energetic condition (size-adjusted body mass) for Yellow-rumped Warblers and Red-eyed Vireos in the western Lake Erie basin of northern Ohio, spring 2006 and 2007. Energetic condition was calculated using the residuals from a linear regression of the first principal component score of the multivariate associations between wing chord and tarsus measurements on body mass. Positive condition scores (i.e. residuals) indicate birds in better than average condition relative to all individuals captured for a species. Yellow-rumped Warblers in better energetic condition than expected for their body size stayed shorter durations than birds in poorer energetic condition.

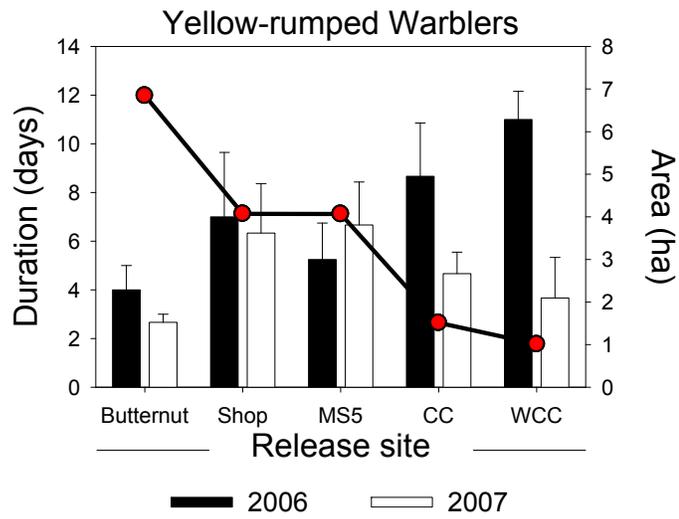


Figure 3.4. Stopover duration in relation to area of release site for Yellow-rumped Warblers in the western Lake Erie basin of northern Ohio in spring 2006 and 2007. Bars indicate mean stopover duration ( $\pm$ S.E.) for YRWA released within five release sites.

## BIBLIOGRAPHY

- Aborn, D.A., and F.R. Moore. 1997. Pattern of movement by summer tanagers (*Piranga rubra*) during migratory stopover: a telemetry study. *Behaviour* 134:1077-1100.
- Aborn, D.A., and F.R. Moore. 2004. Activity budgets of summer tanagers during spring migratory stopover. *Wilson Bulletin* 116:64-68.
- Adams, A.A., S.K. Skagen, and J.A. Savidge. 2006. Modeling post-fledging survival of lark buntings in response to ecological and biological factors. *Ecology* 87:178-188.
- Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313-1325.
- Agresti, A. 1996. An introduction to categorical data analysis. John Wiley and Sons, Inc., New York.
- Akesson, S., and A. Hedenstrom. 2000. Wind selectivity of migratory flight departures in birds. *Behavioral Ecology and Sociobiology* 47:140-144.
- Akesson, S., L. Karlsson, G. Walinder, and T. Alerstam. 1996. Bimodal orientation and the occurrence of temporary reverse bird migration in autumn in south Scandinavia. *Behavioral Ecology and Sociobiology* 38:293-302.
- Alerstam, T. 1990. Bird migration. Cambridge University Press, Cambridge.
- Alerstam, T., and A. Lindstrom. 1990. Optimal bird migration: the relative importance of time, energy, and safety. Pages 331-351 *in* Bird Migration (E. Gwinner, Ed.). Springer, New York.
- Bachler, E., and M. Schaub. 2007. The effects of permanent and local emigration and encounter technique on stopover duration estimates as revealed by telemetry and mark-recapture. *Condor* 109:142-154.
- Barlein, F. 1983. Habitat selection and associations of species in European passerine birds during southward, post-breeding migrations. *Ornis Scandinavica* 14:239-245.

- Berthold, P. 1975. Migration: control and metabolic physiology. Pages 77-128 *in* Avian Biology, vol.5 (D.S. Farner and J. R. King, Eds.). Academic Press, New York.
- Blem, C. R. 1980. The energetics of migration. Pages 175-224 *in* Animal Migration, orientation and navigation. (S. A. Gauthreaux, Jr., Ed.). Academic Press, New York.
- Bolshakov, C.V., N. Chernetsov, A. Mukhin, V.N. Bulyuk, V. Kosarev, P. Ktitorov, D. Leoke, and A. Tsvey. 2007. Time of nocturnal departures in European robins *Erithacus rubecula* in relation to celestial cues, season, stopover duration and fat stores. *Animal Behavior* 74:855-865.
- Bruderer, B., and F. Liechti. 1998. Flight behavior of nocturnally migrating birds in coastal areas: crossing or coasting. *Journal of Avian Biology* 29:499-507.
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach, 2<sup>nd</sup> Ed. Springer-Verlag, New York.
- Caccamise, D.F., and R.S. Hedin. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bulletin* 94:306-318.
- Calabrese, J.M., and W.F. Fagan. 2004. A comparison shopper's guide to connectivity metrics. *Frontiers in Ecology and the Environment* 2:529-536.
- Chernetsov, N. 2002. Spatial behavior of first-year Blackcaps (*Sylvia atricapilla*) during the pre-migratory period and during autumn migratory stopovers. *Journal of Ornithology* 143:424-429.
- Chernetsov, N., A. Mukhin, and P. Ktitorov. 2004. Contrasting spatial behavior of two long-distance passerine migrants at spring stopovers. *Avian Ecology and Behaviour* 12:53-61.
- Chernetsov, N., and A. Mukhin. 2006. Spatial behavior of European robins *Erithacus rubecula* during migratory stopovers: a telemetry study. *Wilson Journal of Ornithology* 118:364-373.
- Cimprich, D.A., M.S. Woodrey, and F.R. Moore. 2005. Passerine migrants respond to variation in predation risk during stopover. *Animal Behaviour* 69:1173-1179.
- Cimprich, D.A., F.R. Moore, and M.P. Guilfoyle. 2000. Red-eyed Vireo (*Vireo olivaceus*). *The Birds of North America*, no. 527. (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

- Cooperrider, T.S., A.W. Cusick, and J.T. Kartesz. 2001. Seventh Catalog of the Vascular Plants of Ohio. Ohio State University Press, Columbus.
- Dallman, M., and R. J. Smith. 1995. Avian predation on Chironomids along the nearshore waters of Lake Huron. Michigan Birds Natural History 2:201-204.
- Dierschke, V., and J. Delingat. 2001. Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behavioral Ecology and Sociobiology 50:535-545.
- Dunn, E.H. 2000. Temporal and spatial patterns in daily mass gain of Magnolia Warblers during migratory stopover. Auk 117:12-21.
- Ewert, D.N., and M.J. Hamas. 1995. Ecology of migratory landbirds during migration in the Midwest. Pages 200-208 in Management of Midwestern landscapes for the conservation of Neotropical migratory birds. (F. R. Thompson III, Ed.). General Technical Report NC-187. U.S. Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.
- Francis, C.M., and F. Cooke. 1986. Differential timing of spring migration in wood warblers (Parulinae). Auk 103:548-556.
- Fransson, T., and T.P. Weber. 1997. Migratory fuelling in blackcaps (*Sylvia atricapilla*) under perceived risk of predation. Behavioral Ecology and Sociobiology 41:75-80.
- Gillies, C.S., M. Hebblewhite, S.E. Nielsen, M.A. Krawchuk, C.L. Aldridge, J.L. Frair, D.J. Saher, C.E. Stevens, and C.L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75: 887-898.
- Gordon, C.E. 2000. Movement patterns of wintering grassland sparrows in Arizona. Auk 117:748-759.
- Graber, J. W., and R. R. Graber. 1983. Feeding rates of warblers in spring. Condor 85:139-150.
- Green, A.J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? Ecology 82:1473-1483.
- Hedenstrom, A., and T. Alerstam. 1997. Optimal fuel loads in migratory birds: distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227-234.

- Helms, C.W., and W.H. Drury. 1960. Winter and migratory weight and fat field studies on some North American buntings. *Bird Banding* 31:1-40.
- Hooge, P.N., and B. Eichenlaub. 2000. Animal movement extension to ArcView. Version 2.0. Alaska Science Center, Biological Science Office, U.S. Geological Survey, Anchorage, A.K.
- Hunt, P.D., and D.J. Flaspohler. 1998. Yellow-rumped Warbler (*Dendroica coronata*). *The Birds of North America*, no. 376. (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- Hutto, R.L. 1985a. Seasonal changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: competition mediated? *Auk* 102:120-132.
- Hutto, R.L. 1985b. Habitat selection by nonbreeding, migratory landbirds. Pages 455-476 *in* *Habitat selection in birds*. (M. L. Cody, Ed.). Academic Press, California.
- James, F.C. and H.H. Shugart Jr. 1970. A quantitative method of habitat description. *Audobon Field Notes* 24:727-736.
- Jenni, L., and M. Schaub. 2003. Behavioural and physiological reactions to environmental variables in bird migration: a review. Pages 155-171 *in* *Avian Migration*. (P. Berthold, E. Gwinner, and E. Sonnenschein, Eds.). Springer-Verlag, Germany.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Keast, A., and E.S. Morton, Eds. 1980. *Migrant birds in the neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, D. C.
- Kelly, J.F., L.S. DeLay, and D.M. Finch. 2002. Density-dependent mass gain by Wilson's Warblers during stopover. *Auk* 119:210-213.
- Ketterson, E.D., and V. Nolan, Jr. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the Dark-eyed Junco, as determined from demographic analysis of winter populations. *Auk* 99:243-259.
- Kuenzi, A., F.R. Moore, and T.R. Simons. 1991. Stopover of neotropical landbird migrants on East Ship Island following trans-gulf migration. *Condor* 93:869-883.

- Lang, J.D., L.A. Powell, D.G. Krentz, and M.J. Conroy. 2002. Wood thrush movements and habitat use: effects of forest management for red-cockaded woodpeckers. *Auk* 119:109-124.
- Loria, D.E., and F.R. Moore. 1990. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. *Behavioral Ecology* 1:24-35.
- Marra, P.P., K.A. Hobson, and R.T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884-1886.
- Mazerolle, D.F., and K.A. Hobson. 2003. Do ovenbirds (*Seiurus aurocapillus*) avoid boreal forest edges? A spatiotemporal analysis in an agricultural landscape. *Auk* 120:152-162.
- Moilanen, A. and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. *Ecology* 83:1131-1145.
- Moore, F.R. [Ed.]. 2000. Stopover ecology of Nearctic-Neotropical landbird migrants: habitat relations and conservation implications. *Studies in Avian Biology* 20.
- Moore, F.R., and D.A. Aborn. 2000. Mechanisms of *en route* habitat selection: how do migrants make habitat decisions during stopover? *Studies in Avian Biology* 20:34-42.
- Moore, F.R., S.A. Gauthreaux Jr., P. Kerlinger, and T.R. Simons. 1995. Habitat requirements during migration: important link in conservation. Pages 121-144 in *Ecology and Management of Neotropical migratory birds*. (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.
- Moore, F.R., and P. Kerlinger. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia* 74:47-54.
- Moore, F.R., P. Kerlinger, and T.R. Simons. 1990. Stopover on a Gulf coast barrier island by spring trans-Gulf migrants. *Wilson Bulletin* 102:487-500.
- Moore, F.R., and T.R. Simons. 1992. Habitat suitability and stopover ecology of Neotropical landbird migrants. Pages 345-355 in *Ecology and conservation of neotropical migrant landbirds*. (J.M. Hagan, III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D. C.
- Moore, F. R., and W. Yong. 1991. Evidence of food-based competition among passerine migrants during stopover. *Behavioral Ecology and Sociobiology* 28:85-90.

- Moore, F.R., R. J. Smith, and R. Sandberg. 2005. Stopover ecology of intercontinental migrants: en route problems and consequences for reproductive performance. Pages 251-261 *in* *Birds of two worlds: the ecology and evolution of migration* (R. Greenberg and P.P. Marra, Eds.). Johns Hopkins University Press, Maryland.
- Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70:730-738.
- Newton, I. 2004. Population limitation in migrants. *Ibis* 146:197-226.
- Ottawa National Wildlife Refuge Complex Comprehensive Conservation Plan. 2000.
- Orians, G.H., and J.F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137:S29-S49.
- Peacefull, L. 1996. *The Geography of Ohio*. The Kent State University Press, Ohio.
- Petit, D.R. 2000. Habitat use by landbirds along Nearctic-Neotropical migration routes: implications for conservation of stopover habitats. *Studies in Avian Biology* 20:15-33.
- Powell, L.A., D.G. Krementz, J.D. Lang, and M.J. Conroy. 1998. Effects of radio transmitters on migrating Wood Thrushes. *Journal of Field Ornithology* 69:306-315.
- Pyle, P., S.N.G. Howell, R.P. Yunick, and D.F. DeSante. 1987. *Identification guide to North American passerines*. Slate Creek Press, California.
- Raim, A. 1978. A radio transmitter attachment for small passerine birds. *Bird Banding* 49:326-332.
- Rappole, J.H., and A.R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335-337.
- Rodewald, P.G., and M.C. Brittingham. 2004. Stopover habitats of landbirds during fall: use of edge-dominated and early-successional forests. *Auk* 121:1040-1055.
- Rodewald, P.G., and M.C. Brittingham. 2007. Stopover habitat use by spring migrant landbirds: the roles of habitat structure, leaf development, and food availability. *Auk* 124:1063-1074.
- SAS Institute. 1996. *SAS/STAT User's Guide, Version 9.1*. SAS Institute, Cary, North Carolina.

- Schaub, M., and L. Jenni. 2001. Stopover durations of three warbler species along their autumn migration route. *Oecologia* 128:217-227.
- Sherry, T.W., and R.T. Holmes. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence. Pages 85-120 *in Ecology and Management of Neotropical Migratory Birds: a Synthesis and Review of Critical Issues* (T.E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.
- Shieldcastle, J., T. Kashmer, and M. Shieldcastle. 2004. Passerine habitat use during spring and fall migration. Black Swamp Bird Observatory Home Page. <http://www.bsbobird.org/spring.html>.
- Sillett, T.S., and R.T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296-308.
- Simons, T.R., S.M. Pearson, and F.R. Moore. 2000. Application of spatial models to the stopover ecology of trans-Gulf migrants. *Studies in Avian Biology* 20:4-14.
- Smith, R.J., and F.R. Moore. 2003. Arrival fat and reproductive performance in a long-distance passerine migrant. *Oecologia* 134:325-331.
- Smith, R.J., and F.R. Moore. 2005. Fat stores of American Redstarts *Setophaga ruticilla* arriving at northerly breeding grounds. *Journal of Avian Biology* 36:117-126.
- Smith, R., M. Hamas, M. Dallman, and D. Ewert. 1998. Spatial variation in foraging of the black-throated green warbler along the shoreline of northern Lake Huron. *Condor* 100:474-484.
- Smith, R.J., M.J. Hamas, D.N. Ewert, and M.E. Dallman. 2004. Spatial foraging differences in American Redstarts along the shoreline of northern Lake Huron during spring migration. *Wilson Bulletin* 116:48-55.
- Sykes, P.W., Jr., J. W. Carpenter, S. Holzman, and P.H. Geissler. 1990. Evaluation of three miniature radio transmitter attachment methods for small passerines. *Wildlife Society Bulletin* 18:41-48.
- Tietz, J.R., and M.D. Johnson. 2007. Stopover ecology and habitat selection of juvenile Swainson's thrushes during fall migration along the northern California coast. *Condor* 109:795-807.
- Tsvey, A., V.N. Bulyuk, and V. Kosarev. 2007. Influence of body condition and weather on departures of first-year European robins, *Erithacus rubecula*, from an autumn migratory stopover site. *Behavioral Ecology and Sociobiology* 61:1665-1674.

- Wikelski, M., E.M. Tarlow, A. Raim, R.H. Diehl, R.P. Larkin, and G.H. Visser. 2003. Cost of migration in free-flying songbirds. *Nature* 423:704.
- Winker, K., J.H. Rappole, and M.A. Ramos. 1990. Population dynamics of the Wood Thrush in southern Veracruz. *Condor* 92:444-460.
- Woodrey, M.S. 2000. Age-dependent aspects of stopover biology of passerine migrants. *Studies in Avian Biology* 20:43-52.