Movement Ecology of an Intercontinental Migratory Bird During Spring Stopover

Emily Beth Cohen
University of Southern Mississippi

Follow this and additional works at: https://aquila.usm.edu/dissertations

Part of the Biology Commons, Ecology and Evolutionary Biology Commons, and the Zoology Commons

Recommended Citation

This Dissertation is brought to you for free and open access by The Aquila Digital Community. It has been accepted for inclusion in Dissertations by an authorized administrator of The Aquila Digital Community. For more information, please contact Joshua.Cromwell@usm.edu.
The University of Southern Mississippi

MOVEMENT ECOLOGY OF AN INTERCONTINENTAL MIGRATORY BIRD
DURING SPRING STOPOVER

by

Emily Beth Cohen

Abstract of a Dissertation
Submitted to the Graduate School
of The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy

December 2011
ABSTRACT

MOVEMENT ECOLOGY OF AN INTERCONTINENTAL MIGRATORY BIRD DURING SPRING STOPOVER

by Emily Beth Cohen

December 2011

Movement ecology is a component of nearly all aspects of animal behavior and an animal’s decision to move is likely influenced by a complex combination of exogenous and endogenous factors. Therefore, an examination of the causes and consequences of organismal movement provides a conceptual framework for understanding complex behavioral strategies. My dissertation research is focused on the movement ecology of an intercontinental migratory songbird during spring migration. I adopted experimental approaches to study the factors influencing how a songbird migrant, red-eyed vireos (Vireo olivaceus), makes decisions in unfamiliar landscapes from the initiation of spring stopover.

I simulated the arrival of nocturnal migrants at unfamiliar stopover sites to study the influence of multiple factors including energetic condition, sex, time program, habitat, landscape and conspecific song on movement patterns and stopover duration. To do this, I used radio-telemetry to follow the detailed movements of red-eyed vireos at stopover sites while quantifying vegetation structure and composition, food availability and avian predators and competitors. I found that arrival energetic condition and habitat strongly influenced movement.

In addition, migrants moved further and faster during an initial “searching” period during which they selected habitat types with greater food availability.
where they captured more prey. Migrants arriving with reduced fuel stores also remained longer at stopover sites and only migrants arriving early in the spring stayed for extended periods of time. Conspecific song did not serve as a cue for the quality of a habitat type but it did influence within-habitat selection.

Finally, I applied the results of these experiments to build individual-based models of movement according to behavioral rules and habitat-specific fuel deposition rates to measure the fitness consequences of migrant-habitat interactions during spring stopover. I applied the model and found fuel deposition rate increased as the amount of hardwood in the landscape increased and the degree of spatial aggregation of habitat decreased. The experimental and individual-based modeling approach adopted in this research provides much needed information about how migrants make decisions in unfamiliar landscapes during stopover as well as the fitness consequences of those decisions.
ACKNOWLEDGMENTS

I am especially indebted to my advisor, Frank Moore. We moved across the country so that I could work in his lab and it has been a great move for all of us. I have grown both personally and professionally as a member of the intellectually stimulating and friendly Migratory Bird Research Group at the University of Southern Mississippi. Frank’s passion for science is truly infectious. I consider myself lucky to have been a part of this productive group which is what it is because of the working environment that Frank Moore facilitates. The lab group and Frank and Cindy have been like an extended family to us.

I have benefited from the diverse background and perspectives of my committee members. Paul Hamel of the US Forest Service, Robb Diehl of the University of Southern Mississippi and then the US Geological Survey and Richard Fischer of the US Engineering Research and Development Center each provided essential guidance and professional mentoring. I additionally appreciate the assistance and mentoring of Scott Pearson at Mars Hill College with whom I worked closely on the modeling effort.

I would especially like to thank the past and current members of the migratory bird research group at USM: Rachel Bru Bolus, Jeff Buler, Kristen Covino, Robb Diehl, Rodney Felix, Jill Gautreaux, Sheri Glowinski, Sarah Wheless Hammond, Megan Hughes, Emily Lain, Zoltán Németh, Jen Owen, Eben Paxton, Kristina Paxton, Michael Sellers, Jaclyn Smolinski, Amanda Jo Williams and T. J. Zenzel. Thank you for your help and support and for creating
such a productive and intellectually stimulating environment in which to spend the last six years. It has been fun!

This work received support and cooperation from multiple state and federal agencies. Funding for this project was provided by the Department of Defense Strategic Environmental Research and Development Program, the University of Southern Mississippi and the Gulf Coast Joint Venture. Logistical support was provided by Jim Johnson and Danny Hudson at US Army Fort Polk, Lynn Bennett at Louisiana Wildlife and Fisheries and Ledon Cooley at Mississippi Department of Wildlife, Fisheries and Parks. I could not have done this work without the cooperation of personnel at the Tennessee Gas Pipeline Company, Kistachie National Forest, US Army Fort Polk, Louisiana Wildlife and Fisheries and Mississippi Department of Wildlife, Fisheries and Parks. I also thank Sarah Mabey at Hiram College for loaning me the recording equipment.

I could never have done this work without all of the hard working assistants who helped me collect data in the field: Brian Bielfelt, Mason Cline, Kristen Comolli, John Diener, Shana Everett, Clay Graham, Lizzie Goodrich, Dave Haines, Phil Heavin, Pete Hosner, Lainie LaHaye, Emijo Lain, Christopher Nicholson, Trang Nguyen, Dana Ripper, Christine Roy, Amy Scarpignato, Jaci Smolinsky, Lisa Vormvold, Brian Wilson, and Emily Zeller.

Last but not least, I would like to thank my entire family for their endless love and support. My deepest thanks go to my parents, Kenneth and Linda Cohen, for their untiring support and encouragement. I am especially grateful to
my husband, Phil Heavin, and daughter, Cora, for being enthusiastic participants on my team; providing help, friendship and encouragement when I needed it most.
TABLE OF CONTENTS

ABSTRACT .......................................................................................................................... ii

ACKNOWLEDGMENTS ...................................................................................................... iv

LIST OF TABLES .............................................................................................................. ix

LIST OF ILLUSTRATIONS ................................................................................................ x

CHAPTER

I. SYNOPSIS .................................................................................................................... 1

   Overview
   Literature Cited

II. MOVEMENT ECOLOGY OF AN INTERCONTINENTAL MIGRATORY BIRD IN RELATION TO ENDOGENOUS AND EXOGENOUS FACTORS DURING SPRING STOPOVER ........ 12

   Abstract
   Introduction
   Methods
   Results
   Discussion
   Acknowledgments
   Literature Cited

III. AN EXPERIMENTAL ASSESSMENT OF THE INFLUENCE OF ENDOGENOUS AND EXOGENOUS FACTORS ON STOPOVER DURATION DURING SPRING MIGRATION .......... 41

   Abstract
   Introduction
   Methods
   Results
   Discussion
   Acknowledgments
   Literature Cited

IV. DOES CONSPECIFIC SONG PLAY A ROLE IN HABITAT SELECTION BY SONGBIRDS DURING MIGRATORY STOPOVER? .................................................................................. 61

   Acknowledgments
   Literature Cited
Abstract
Introduction
Methods
Results
Discussion
Acknowledgments
Literature Cited

V. APPLICATION OF A SPATIALLY EXPLICIT INDIVIDUAL-BASED MODEL TO CONSERVATION OF MIGRATING SONGBIRDS .......................................................... 76

Abstract
Introduction
Methods
Results
Discussion
Conservation Implications
Acknowledgments
Literature Cited

APPENDIX: COPY OF APPROVED IACUC APPLICATION FORM .............. 103
LIST OF TABLES

Table

2.1. Comparison of the relative influence of generalized linear models in predicting the movement rate (rate) and linear displacement (distance) for all hours combined and for each two hour period of the day. ............ 25

2.2. Parameter estimates for factors in top supported generalized linear models predicting the movement rate (rate) and linear displacement (distance) for all hours combined and for each two hour period of the day. Parameter estimates shown for hour (hour), arrival energetic condition (cond), arrival habitat type (habitat), landscape (land), day of stopover (day) and day of year (date) when included in supported models. .......................................................... ........................................................ 26

3.1. Comparison of the relative influence of linear models in predicting duration of stay. .......................................................... ........................................................ 50
LIST OF ILLUSTRATIONS

Figure

2.1. Map of the state of Louisiana with translocation direction (arrow) from capture at Johnson’s Bayou on the northern border of the Gulf of Mexico (star) to the Vernon Unit of Kisatchie National Forest (star). Inset map of the study area within Kisatchie National Forest with landcover and release locations near Bundick creek (three ● on left; from left to right: hardwood, mixed pine) and Drake creek (three ● on right; from left to right: pine, hardwood, mixed). .................................................. 17

2.2. Mean number of arthropods detected in samples collected at randomly selected locations (transects) versus samples collected in areas selected by migrants (selected) in each habitat type: pine, mixed and hardwood. Means are shown and bars represent SE. ............................. 30

3.1. Duration of stay for red-eyed vireos radio-tracked in Kisatchie National Forest and the relationship between arrival energetic condition index (negative values are below lean body mass and positive are above) and the duration of stay in days. Bars represent SE. Migrants remained one (n=14), two (n=9), three (n=5), four (n=5), five (n=5) and 6 or more days (n=4). Migrants that remained ≥ six days (one remained six days, two remained seven days and one remained eight days) are combined and presented here as greater than or equal to 6 days. ........................................................................................................ 51

3.2. Boxplot of movement rate (m/ min) during two hour increments, from 6:30 to 18:30 CST, on the first day of stopover (n= 42 birds). Not all individuals were tracked all six of the two hour time periods. Migrants that remained equal to or greater than six days (one remained six days, two remained seven days and one remained eight days) are combined and presented here as greater than or equal to 6 days. .......................... 52

4.1. Time (mean ± SD) near release sites (within 200 m) in pine and hardwood habitat with and without conspecific song added to pine (n=24, n=6 for each habitat and treatment). The hardwood site naturally contained conspecific song and was not altered. ....................... 69

5.1. Graphical depiction of an individual-based model of a landscape where each shade of cell represents a habitat type and the arrow represents a model animal making stepwise movements.................................................. 82

5.2. Flow chart depicting the derivation of hourly movement distances from observations of migrant movement behavior................................................. 86
5.3. Map of translocation (arrows) from point of capture on the coast at Johnson's Bayou, LA (29° 45' N 93° 30' W) to Kisatchie National Forest, LA (30° 57' N 93° 08' W) for experiments to parameterize the model and to the Leaf River Wildlife Management area in De Soto National Forest, MS (30° 55' N 89° 02' W) to validate the model.............. 88

5.4. Map of release locations (stars) in hardwood and pine habitat in the Leaf River Wildlife Management Area (grey outline) in De Soto National Forest, MS for model validation of movement behaviors during the spring of 2011................................................................. 89

5.5. Design of the factorial experiment using nine maps with low, medium and high contagion (level of spatial aggregation of habitat; left to right column) and high (41%), medium (22%) and low (12%) amount of hardwood forest cover (top to bottom row). The map in the top left corner (low contagion, high hardwood forest cover) is a portion of the Leaf River Wildlife Management area in De Soto National Forest............. 90

5.6. Example of four model simulated movements (black lines, each ending in an arrow) and bird tracking points (circles) from the same release location (star) which were compared during the model validation process...... ................................................................................................. 91

5.7. Boxplots of fuel deposition rate (mass change/day (g)) after stopping over for one day in landscapes with a) a low, medium or high proportion of hardwood habitat. b) three levels of the degree of spatial aggregation of habitat: low, medium or high. c) after landing in hardwood, mixed or pine habitat and stopping over for one day (n = 180 simulations/ factor). Circles represent outliers (less than 3/2 times of lower quartile), box is bound by 25 and 95% quartiles with median values in center. Whiskers represent maximum and minimum values (excluding outliers)........................................................................................................... 94
CHAPTER I

SYNOPSIS

Movement ecology, or the study of why and how an organism moves from one spatial location to another, is a component of nearly all aspects of animal behavior. An animal’s decision to move is likely influenced by a complex combination of external stimuli (exogenous factors) and internal state (endogenous factors) and an examination of the causes and consequences of organismal movement provides a conceptual framework for understanding complex behavioral strategies (Nathan et al. 2008). For example, during spring migration a songbird has to resolve often conflicting demands between current survival and future reproductive success. Long-distance migrants arrive at each en route stopover site in unfamiliar surroundings and poor condition after a long flight the previous night (Blem 1990) and have to balance the need to access food resources while limiting exposure to predation risk from avian predators attracted to movement (Cimprich et al. 2005). How well a migrant solves these and other problems that arise en route will determine not only if it survives but also time of arrival and condition at its breeding site, which will influence reproductive success (Sandberg and Moore 1996, Smith and Moore 2003). Therefore, selection should act on migratory behavior to promote strategies that maximize individual fuel deposition rates while minimizing the time, energy expenditure and predation risks of migration (Alerstam and Lindström 1990).

The primary environmental factors influencing bird migration, how migrants react behaviorally to these factors and how these reactions are influenced by motivational state remain poorly understood (reviewed in Jenni and Schaub 2003). Yet, how well a migrant solves the problem of quickly finding suitable habitat while avoiding predation in each stopover landscape will determine not only if she survives but is also likely to influence her subsequent reproductive success (Sandberg and Moore 1996, Smith and
Moore 2003). Therefore, the distribution and abundance of available habitat types are likely to play a primary role in how a migrant moves at a stopover site. Largely correlative evidence suggests that habitat selection occurs during migration. Species specific patterns of habitat associations exist between years (Bairlein 1983) and multiple studies have demonstrated the distribution of migrants deviates from expected based on habitat availability (Bairlein 1983, Hutto 1985, Moore et al. 1990, Petit 2000). However, a consequence of our limited ability to follow passerines along their migratory routes is that we have little to no information about migrants during the initiation of stopover. This makes it difficult to assess when habitat selection occurs. Some selection likely occurs prior to landing as suggested by landscape-level correlations of the distribution of migrants with the amount of forest cover (Buler et al. 2007) and night-time luring of migrants using acoustic playback (Herrmans 1990, Schaub et al. 1999, Mukhin et al. 2008) but passeriform night vision probably is not good enough to make more than rough distinctions at night (Martin 1990), depending on the level of light prior to and during landing. Further, distributions of migrants captured in multiple habitat types differed from the morning to later in the day (Bairlein 1981, Degen and Jenni 1990, Spina and Bezzi 1990) and radio-tracked migrants moved further the first day (or morning) of tracking (which may or may not have been their arrival day) before settling into a more restricted area (Aborn and Moore 1997, Chernetsov 2005, Seewagen et al. 2010) suggesting that some habitat selection occurs during the first day after landing.

A migrant’s response to its environment is also likely to depend on endogenous factors including its energetic condition and time program. Energetically constrained individuals are under more pressure to replenish fuel stores (Wang and Moore 2005) and thus increase their predation risk in favor of refueling (Cimprich and Moore 2006) by foraging both more rapidly and over a greater area to access prey resources (Loria and Moore 1990, Moore and Aborn 2000, Wang and Moore 2005). The constraint to
minimize time spent on migration (Lindstrom and Alerstam 1990) implies that migrants arriving later in the season are under more pressures to replenish fuel stores quickly as is evident in the higher fuel deposition rates of late-migrating individuals (reviewed in Jenni and Schaub 2003).

Therefore, an individual's decision to move from one place to another may be influenced by a complex combination of exogenous and endogenous factors and the movement track during each stopover can be thought of as one phase embedded within an organisms' larger lifetime track, the consequences of which will carry over to subsequent phases (Nathan et al. 2008). For example, if a migratory songbird is obliged to spend more time locating suitable habitat during stopover, she may stay longer than usual to refuel and a penalty may be attached to late arrival at the next stopover site, where resource levels may have been depressed by earlier migrants (Moore and Wang 1991). If she does not make up lost time, she will arrive late on the breeding grounds potentially jeopardizing opportunities to secure a territory or a mate (Smith and Moore 2005) and if she does not regain reduced fuel stores she will arrive in poorer condition on the breeding grounds where she may suffer reduced reproductive success (Smith and Moore 2003).

Songbird migrants spend the majority of the migratory period (> 70 %) at stopover sites en route (Alerstam 2003). These periods provide ideal settings for studying movement behavior in relation to exogenous and endogenous factors for several reasons: First, energetic condition is far more variable during migration than during other phases of the annual cycle and migrants are often under pressure to replenish up to 50% of their mass as fuel reserves during stopover (Blem 1990). Therefore, a migrant's behavior is more likely to be related to its energetic condition during migration than during other times of the year and the variability in condition may make the relationship easier to detect. Second, nocturnal migrants rarely return to the
same stopover sites, unlike breeding or wintering areas where site fidelity is often high (Catry et al. 2004). Consequently, decisions made at stopover sites are more likely to be based on current information than during other phases of the annual cycle. This may not be true at breeding or wintering sites where it may be difficult to account for the effects of previous experience on movement decisions. Finally, stopover duration is restricted to anywhere from a few hours to a several days so behavior is more likely related to an assessment of the current distribution of resources than it may be during wintering or breeding periods when the duration of stay is longer and a bird may utilize an area based on an assessment of its potential for resources later in the season (Smith and Shugart 1987).

While the importance of the migratory period is widely acknowledged, the questions of when, where and how long-distance migratory passerine populations are regulated continue to focus primarily on events associated with the breeding and wintering phases of the migrant’s annual cycle (Newton 2006). Billions of landbirds engage in annual migrations of hundreds to thousands of kilometers and along that journey they must adjust to unfamiliar habitats, find enough food, resolve often conflicting demands between avoiding predators and meeting energetic requirements, correct for orientation mistakes, and cope with adverse weather. Meanwhile, they may encounter wind turbines, tall structures, light pollution, non-native predators, and increasingly smaller patches of habitat. Therefore, rapid changes in landscape configuration, resource availability, air space, and climate due to unprecedented human activity may be inflating the risks associated with migration (Wilcove and Wikelski 2008). A clear understanding of the contribution of the migratory period for long-term population change is needed if I are to conserve these populations (Moore et al. 1990) in a rapidly changing world where many migratory species are currently in decline (Wilcove and Wikelski 2008).
Overview

My dissertation research is focused on the movement ecology of an intercontinental migratory songbird during spring stopover. I adopted experimental approaches to study the factors influencing how a Nearctic-Neotropical songbird migrant makes decisions in unfamiliar landscapes from the initiation of stopover. I studied the influence of multiple factors including energetic condition, sex, time program, habitat, landscape and conspecific song on movement patterns and stopover duration. Finally, I applied the results of experiments in a spatially explicit individual-based model to determine the fitness consequences of those decisions.

In Chapter II, Migratory red-eyed vireos (*Vireo olivaceus*) were translocated to simulate arrival of nocturnal migrants at unfamiliar stopover sites. Arrival energetic condition and food abundance were controlled for by releasing migrants with and without energetic reserves in two replicates of three habitat types that differed in food abundance. Migrants were tracked continuously and the distribution of resources in the environment was sampled simultaneously. This design allowed me to a) replicate the situation of limited information that migrants likely face upon arrival at each stopover site, b) control for arrival habitat type and time of season, c) follow birds with known arrival conditions and d) continuously follow movements from the initiation of stopover using radio-telemetry. I tested expectations regarding the influence of a) features of habitat including the distribution of food, aspects of vegetation community and structure, abundance of potential competitors and the occurrence of predators, b) arrival energetic condition, and c) time of season on the spatial and temporal patterns of movement during stopover.

In Chapter III, I compared the duration of stay of a long-distance migrant recently arrived over the Gulf of Mexico at inland stopover sites. The decision of how long to stay at a stopover site may be related to internal condition, in terms of a migrant’s current fuel
reserves, rate of fuel accumulation, time pressures to continue to breeding grounds or environmental factors (review in Jenni and Schaub 2003). I examined the effects and relative influence of a migrant’s arrival energetic condition, arrival habitat type, time of season and movement rate on the amount of time they remain at the stopover site.

In Chapter IV, I used a field experiment to determine if migrating red-eyed vireos use conspecific song as a cue to assess the suitability of habitat en route. Quickly finding suitable habitat for safe and rapid refueling at each stopover site is a crucial component of a successful migration yet I still know very little about the cues used during the process of en route habitat selection. After landing at a stopover site, migrants likely use more than one cue to select among and within available habitat types while minimizing time, energy expenditure and exposure to predators (Moore and Aborn 2000). Social information is increasingly recognized for its importance in breeding habitat selection (Ahlering et al. 2010) but it has not been studied during migration. However, social information may be especially useful during stopover when migrants arrive with little or no prior information and are likely to encounter considerable environmental uncertainty at diverse stops along their route (Németh and Moore 2007). I tested the expectation that conspecific song is both a positive cue to assess the suitability of habitat and a repellent cue on a within-habitat scale upon arrival at a stopover site.

In Chapter V, I applied the experimental results from Chapter II as behavioral rules for migrant movement during stopover to build an individual-based model to measure the fitness consequences of migrant-habitat interactions during spring stopover. The model follows one individual through a stopover and predicts movement patterns and fuel deposition rate for a set of migrant characteristics in a heterogeneous landscape. Spatially explicit individual-based models are a tool uniquely suited to incorporating individual variability into behavioral responses to a changing environment. I present the model as a tool to evaluate the impact(s) of landscape context on the
refueling ability of migratory songbirds during stopover in Gulf South landscapes and test the influence of the amount of suitable habitat and the level of spatial aggregation of habitat on fuel deposition rate using a factorial experiment.
Literature Cited


CHAPTER II

MOVEMENT ECOLOGY OF AN INTERCONTINENTAL MIGRATORY BIRD IN RELATION TO ENDOGENOUS AND EXOGENOUS FACTORS DURING SPRING STOPOVER

Abstract

An experimental approach was adopted to assess the effects and relative influence of endogenous and exogenous factors on the movement ecology of a migrating songbird during stopover. An examination of how and why individuals move is fundamental to understanding the complexities of ecological systems as well as the demographics of populations they comprise. The factors influencing movement during migration are still poorly understood, despite the fitness consequences of decisions made in terms of survival, energetic condition and timing, which have carry over effects on other phases of the annual cycle. I tested expectations that migrants would behave according to simple rules driven by (a) abundance of food resources at their present location, (b) time since arrival at the stopover site, (c) arrival energetic condition and (d) time of season. Migratory red-eyed vireos (Vireo olivaceus) were translocated to simulate arrival of nocturnal migrants at unfamiliar stopover sites. Arrival energetic condition and food abundance were controlled for by releasing migrants with and without energetic reserves in two replicates of three habitat types that differed in food abundance. Migrants were tracked continuously and the distribution of resources in the environment was sampled simultaneously. Migrant movement decreased with time spent at a stopover and was influenced by an individual's arrival energetic condition and the distribution of food. Upon arrival at stopover sites, migrants moved the furthest and fastest during which time they selected habitat with greater food availability. Red-eyed vireos without fuel reserves, presumably under pressure to replenish fuel stores necessary to continue migration in a timely fashion, moved faster and further than
migrants with fuel reserves. In habitat characterized by less abundant food, movement was positively influenced by food abundance but once in habitat characterized by more food, movement was no longer influenced by the distribution of food. This work illustrates that finding habitat with abundant food at each stopover is likely a key determinant of a successful migration. However, songbird movement was not solely a function of underlying resource distributions but a complex behavioral response to a combination of endogenous and exogenous factors and these behavioral responses can be characterized by simple behavioral rules.

Introduction

The movement ecology of organisms is influenced by processes operating across vastly different spatial and temporal scales and plays a primary role in determining the fate of individuals as well as the dynamics of the populations that they comprise. Therefore, an examination of the causes and consequences of individual movement is fundamental to understanding the complexities of ecological systems. Movement tracks can be considered as a series of “phases” that are a function of the organisms’ internal motivational state, intrinsic motion and navigational capabilities, and the environment through which it is moving (Nathan et al. 2008). Long-distance migration is an extreme example of a movement phase encompassing hundreds to thousands of kilometers and comprising up to a third of a songbird’s annual cycle. Migration has the distinct goal of arriving safely at a specific seasonal destination on time and in good condition to secure local resources and/or enhance annual reproductive success (e.g., Smith & Moore 2003; Smith & Moore 2005). Successful migration requires frequent “stopover” periods between flights which cumulatively far exceed the time spent in flight and largely determine the duration of the migratory period (Alerstam 2003). Given the time and energetic constraints of migration (e.g., Alerstam & Lindström 1990), movement decisions during stopovers are likely to have fitness
consequences for individuals in terms of survival as well as time of season and energetic condition upon arrival at wintering and breeding sites (Newton 2006).

A long-distance migrant arriving at a stopover site in unfamiliar surroundings after a long flight has limited information about availability of habitat, locations of predators or distribution of food resources and must balance the need to access food resources while limiting energy expenditure and exposure to predation risk from avian predators attracted to movement (Moore, Kerlinger & Simons 1990; Chernetsov 2006). Therefore, selection should act on migratory behavior during stopover to maximize refueling rates while minimizing time, energy expenditure and exposure to predation risk (Delingat et al. 2006). Further, behavior is likely to vary with endogenous factors such as a migrant’s energetic condition (e.g., Moore & Aborn 2000; Matthews & Rodewald 2010), time program (Jenni & Schaub 2003) and sex (Paxton, van Riper III & O’Brien 2008) and exogenous factors such as abundance of food (e.g., Tietz & Johnson 2007), presence of predators (Cimprich, Woodrey & Moore 2005) and density of potential competitors (Moore & Wang 1991). Consequently, understanding the behavioral strategies for a successful migration requires a detailed examination of movement biology during stopover in relation to factors both endogenous and exogenous.

The objective of this study was to assess the effects and relative influence of internal motivational state (endogenous factors) and the distribution of resources in the environment (exogenous factors) on the detailed movement paths of a songbird species during stopover. Searching among available habitat types upon arrival at a stopover site corresponds to lost foraging time and a migrant is expected to offset risk and energy expenditure by foraging within as restricted an area as contains the necessary food resources (e.g., Lindström et al. 1990; Delingat et al. 2006). However, energetically constrained individuals are under more pressure to replenish fuel stores (Wang & Moore 2005) and may forage more rapidly and over a greater area to access prey resources
(Loria & Moore 1990; Moore & Aborn 2000). Further, the constraint to minimize time spent on migration (Alerstam & Lindström 1990) implies that migrants arriving later in the season are under more pressures to replenish fuel stores quickly (Jenni & Schaub 2003). Accordingly, I tested expectations that migrants would behave according to simple decision rules driven by (a) abundance of food resources at their present location, (b) time since arrival at the stopover site, (c) arrival energetic condition and (d) time of season.

The morning after landing the previous night, a migrant is expected to assess its surroundings by moving the greatest linear distances to select among available habitat types. When a migrant finds itself in an arrival habitat with abundant food it is expected to exhibit more area restricted movement and to select areas within those habitat types where food availability is greater. However, when a migrant finds itself in a habitat type with less abundant food it is likely to move longer initial distances in order to select habitat types characterized by greater food resources. Moreover, a migrant that arrives at a stopover site with little or no energetic reserves will move faster and further to find and acquire available resources than will a migrant arriving with greater fuel stores. In the same way, individuals arriving later in the season relative to individuals arriving earlier in the season are also expected to move further and faster to catch up. Finally, migrants may bias their daytime movements in their endogenously programmed migratory direction (Moore & Aborn 2000; Simons, Pearson & Moore 2000), so the expectation was that the directionality of daytime movements would be concentrated in a seasonally appropriate direction.

An experimental approach to simulate the initiation of stopover was taken while controlling for arrival energetic condition and quality of arrival habitat type. I continuously followed the movements of migrants released with and without energetic reserves into habitat types that differed in the abundance of food resources. The
experimental design, which controlled for both exogenous and endogenous factors, allowed me to conduct the first experimental assessment, as far as I am aware, of the relative influence of energetic condition and environmental factors on the detailed movement behavior of a migratory songbird during stopover.

Methods

Study Species

The focal species of this study was the red-eyed vireo, a Neotropical-Nearctic migratory songbird common throughout eastern deciduous forest of North America. The species is primarily a canopy foliage-gleaner of Lepidoptera larvae during the breeding season, but uses diverse substrates while foraging on a variety of arthropod taxa and berries during migration (Cimprich, Moore & Guilfoyle 2000). Red-eyed vireos are most often found in hardwood habitat during breeding (Cimprich, Moore & Guilfoyle 2000) but were detected in both bottomland hardwood and pine habitat with hardwood understory on censuses in coastal Mississippi landscapes during spring migration (Moore & Simons 1992).

Translocation experiment

Red-eyed vireos were captured in a chenier in southwestern Louisiana near Johnson’s Bayou (29° 45’ N 93° 30’ W; Fig. 2.1). Cheniers are narrow strips of coastal woodlands dominated by hackberry (Celtis laevigata) that often concentrate landbird migrants following trans-Gulf flight in spring (Moore 1999). Red-eyed vireos do not breed at Johnson’s Bayou, so individuals captured there were transient. Upon capture, migrants were banded with a US Fish and Wildlife Service band and a unique combination of colored leg bands. Subcutaneous fat was assessed (Helms & Drury 1960), weight was measured to the nearest 0.1 g with an electronic scale, and muscle score was assessed (Bairlein et al. 1985).
Red-eyed vireos were transported the afternoon or evening of the day of capture approximately 143 km to the Vernon Unit of the Calcasieu Ranger District in Kisatchie National Forest, Louisiana (30° 57' N 93° 08' W; Fig. 2.1). This site was chosen for several reasons. First, it had a variety of habitat types representative of those found throughout the East Gulf Coastal Plain (Keddy 2009), a high density of spring migrants stopping over based on weather radar observations (Gauthreaux Jr. pers. com.). Second, cover types in and around Kisatchie National Forest include upland longleaf pine savannas, bottomland hardwood, mixed pine and hardwood, planted pine, and harvested or open areas. Third, it is an inland site so habitat selection would not be
constrained by adjacency to an ecological barrier. Red-eyed vireos also commonly breed at this site so it would not have been possible to accurately establish the status (breeding or migratory) of migrants captured at the site. Migrants were held in individual cages for up to 22 hours and provided with food and water ad libitum. Red-eyed vireos were known to acclimate well to captivity (FRM pers obs, Moore, Mabey & Woodrey 2003) and lost little mass during the time I held them (1.12 ± 0.61 g for the period of captivity, n = 52 birds). The evening of the capture day migrants were fitted with radiotransmitters weighing less than 3.5% of mean lean body mass (models LB-2 and LB-2N, Holohil Systems Ltd. Ontario, Canada).

To assess how a migrant’s movement is influenced by landfall in habitat types differing in food resources red-eyed vireos were released at first light at one of six predetermined locations in three habitat types (Fig. 2.1). The most abundant habitat types also characteristic of the East Gulf Coastal Plain region and thought to differ in available food resources were chosen: upland pine savanna (pine), bottomland deciduous forests along creeks (hardwood), and an intermediate between the two (mixed). Migrants with and without fat reserves were simultaneously released at each of the six release sites and at times throughout the spring migration season (n = 50 individuals; 17 in 2007, 33 in 2008; 17 in hardwood, 16 in mixed and 17 in pine). The site at which a particular migrant was released was determined by a number of factors. First, migrants were generally not released at a site where another migrant was currently being tracked. Second, I attempted to balance the number of birds released between creeks and habitat types throughout a season and, while I did not calculate energetic condition index in the field, I also attempted to balance the number of birds released that did and did not have some fat reserves as determined by their fat score (Helm and Durury 1960).
Hardwood release sites were selected to fall within bottomland hardwood floodplains surrounding one of the predictably accessible creeks in the Vernon Unit of Kisatchie National Forest. The release sites in pine and mixed habitat were selected to be in the closest accessible locations to each hardwood release site predominately surrounded by pine and mixed habitat, respectively (Fig. 2.1). The two sets of release sites were chosen as replicates and were approximately 3 km apart. The area surrounding each set of release sites are referred to as Drake and Bundick landscapes, using the names of the creeks that pass through them.

Red-eyed vireos were continuously radio-tracked with locations taken every 15 min. To minimize impact of observer, migrants were located to within 50 m and then their locations were circled to verify the accuracy before visual observation was attempted. In 2007, migrants were tracked for the first five hours and the last hour of each day of stopover and in 2008 migrants were tracked from release to dusk for the first three days of stopover. The predominant habitat type in the 30 m surrounding each individual location was recorded. Whenever it was possible to visually observe an individual with color bands, foraging observations were taken including timing, success or failure of foraging maneuvers, prey items and other behaviors such as preening or resting.

Characterization of endogenous factors

Endogenous factors were quantified where possible for each individual. An energetic condition index was calculated for each individual to reflect the proportion of body mass attributed to fat (see Owen & Moore 2006). Therefore, a migrant with a condition index of zero was at lean body mass, a migrant with a positive condition index had fuel reserves and a migrant with a negative condition index had no fuel reserves. Mass and fat score were recorded a second time in the morning just prior to releasing individuals and used to calculate the arrival condition index. The ordinal date was used
as an estimate of relative time program. It was not possible to determine sex for the majority of individuals, but it was possible to rely on wing chord length to sex some individuals (male $\geq 82$ mm and female $\leq 76$ mm; Pyle 1997). For an assessment of the seasonally appropriate directionality of movements, the assumption was made that the migratory direction was Northeast, the direction to the majority of the breeding range (Cimprich, Moore & Guilfoyle 2000).

Characterization of environment

To quantify arthropod and avian abundance and distribution in relation to the three habitat type, landscape and time of season, six 1200 m transects were laid out passing through each release site and remaining within the same habitat type. Twelve samples were taken every 100 m along each of the six transects three times per year during a week in early (13 to 18 April), middle (26 April to 2 May), and late (7 to 12 May) spring. Canopy branch clipping was used, a method that has been shown to be effective in measuring arthropod prey density on and near vegetation used by foliage-gleaning birds (Johnson 2000). Samples were collected at the same locations along transects, but were not collected from the same branches or necessarily from the same trees at those locations. The same methodology was used to sample arthropods at locations along migrants’ movement paths in order to compare arthropod abundance at locations selected by migrants to areas systematically sampled on transects. Arthropod samples were taken at a subset of locations along the first day movement track of the majority of migrants. Samples were collected no less than ten days after tracking at the first location of every other hour on the first day of stopover.

To determine the number of transient migrants and avian predators associated with each release site, daily avian surveys were conducted along 500 m sections of the six transects passing through the release sites in 2008. The same surveyor conducted all surveys. Each morning, three transects in one landscape were surveyed and
alternated daily between landscapes, systematically rotating the order of habitat types surveyed (16 sets of surveys at Drake and 17 at Bundick).

Data analysis

Multiple factors were expected to influence migrant behavior and the interest was in their relative influence as well as their effects, so multi-model inference and an information-theoretic approach was used (Burnham & Anderson 2002) to analyze the relative explanatory power of six factors on movement patterns. Movement patterns were quantified during two hour increments from 6:30 to 18:30 for each individual during the first three days of stopover. Two parameters were used to quantify movement patterns: linear displacement (the linear distance between the first and last location of the time period; m) and rate (the cumulative distance between all locations divided by the time in a time period; m min$^{-1}$). To measure the relative influence of factors on movement, 43 biologically plausible models were created and compared composed of six fixed effects: hour of day (hour), arrival energetic condition (condition), habitat type of the release site (habitat), landscape of the release site (landscape), day of season (date), and day of stopover (day) as well as one interaction term, arrival energetic condition by release habitat type. A subset of the same set of models, excluding hour (28 candidate models), was used to assess the differential influence of the five remaining fixed effects (condition, habitat, landscape, date and day) and interaction term (condition * habitat) on movement during each time period throughout the day. To allow for correlations between observations from the same individual, linear mixed-effects models were fitted (REML function in library nlme for R) with the individual as the random component. Exploratory analyses revealed no differences between years (linear displacement $t_{48, 332} = -0.40, P = 0.69$, rate $t_{48, 332} = -1.17, P = 0.25$), consequently year was not included in candidate models. Data transformation ($\log [x +1]$) was used to meet the assumption of normality for movement rate and linear displacement.
Akaike’s Information Criterion for small sample sizes (AICc) was used to rank, compare, and evaluate all candidate model sets. All models with a $\Delta$AICc $\leq 2$ are presented as plausible competing models (considered the subset of best supported models, Burnham and Anderson 2002). The null (intercept only) model is also presented for comparison with the relative explanatory power of the plausible models. For variables occurring in more than one top model ($\Delta$AICc $\leq 2$) parameter estimates were averaged across models containing each explanatory variable (Burnham & Anderson 2002).

To test for differences in movement based on habitat use, linear mixed-effects models with the individual as the random component were used. A one-way ANOVA was used to test the effects of habitat use on foraging attack rate. Only observations when at least one prey was captured were included. This conservative approach was taken to eliminate all non-foraging behavioral observations but inclusion of observations of unsuccessful foraging bouts did not change the results.

Differences in movement between the sexes were assessed using the subset of migrants for which the sex was known. Mixed-effects models for all time periods with the individual as a random component and sex as a fixed effect were built and t-tests were used to test for differences in movement rate and linear displacement between male and female individuals. To test the prediction that migrants moved in a seasonally appropriate direction during stopover, consistency and directionality in the mean vector angle ($\mu$) during the first day of stopover (the bearing from the release location to the last location of the first day) were tested. Rayleigh’s Uniformity Test was used to test for a uniform Northeast distribution of vectors for all individuals and for individuals released at each site. Oriana (version 3.2) was used to calculate circular statistics.

Effects of habitat type, landscape, time of season (early, middle or late) and type of sample (transect versus selected) on the total number of arthropods detected were
tested. The last factor (transect versus selected) was included to test for differences in the number of arthropods in areas selected by migrants versus at random locations on transects. Lepidoptera larvae are known to be a preferred food source for this species during breeding (Cimprich, Moore & Guilfoyle 2000) so effects of habitat type, landscape, time of season and type of sample were also tested for on the distribution of Lepidoptera larvae. A zero-altered negative-binomial model (ZANB, with logit link) for count data (hurdle function in library pscl for R) was used to test for effects of factors on number of arthropods and a multiple logistic regression model (glm function with logit link and binomial distribution in library stats for R) was used to test for effects of factors on presence or absence of Lepidoptera larvae.

Effects of landscape, habitat type and day of season on the number of transient Nearctic-Neotropical passerine migrants detected were also tested for. To determine the number of transient migrants for species that migrate through the region but also breed there, I took the minimum number of each species detected on each transect on any given day during the season and considered that to be an estimate of the number of breeding individuals of each species within each transect sampling area. I calculated the daily number of transient migrants on each transect by subtracting species and transect specific estimates from the total daily detections of each species on each transect. It was not possible to account for differences in detectability between habitat types with my methods but because the count data were zero-inflated and positive-skewed, a two-component poisson regression model for count data via maximum likelihood (ZAP, hurdle function) was used.

I used a permutational multivariate analysis of variance (adonis function in R library vegan) to test for differences in vegetation structure and tree community composition between the three habitat types and the habitat type replicates. Analyses
were conducted in R version 2.11.1 (R Development Core Team 2010). Except where stated otherwise I report means ± standard deviation throughout.

Results

Migrants were rarely stationary (14 % of \( n = 2177 \) locations with behavior recorded), moving up to 2,347 m linear distances from release locations during the first day of stopover (618 ± 519 m, \( n = 50 \)), and several exogenous and endogenous factors influenced the movement of individuals. All variables included in candidate models influenced migrant movement to some extent but movement patterns were most strongly influenced by a migrant’s arrival energetic condition and the landscape in which it stopped over (Table 2.1). There was also a temporal pattern to migrant movement during stopover; the furthest and fastest movements occurred during the first two hours of the arrival day and then gradually decreased with the hour of the day and the day of stopover (Table 2.1). Migrants moved less during the afternoon hours and none of the variables included in candidate models influenced linear displacement after 12:30 or movement rate after 14:30 (Table 2.1). The time of season did not influence movement patterns.

Influence of exogenous factors

Both the arrival habitat type and landscape influenced migrant movement patterns during stopover. Arrival habitat type influenced initial dispersal distances. During the first two hours after arrival migrants released in pine moved further (pine 405 ± 348 m) than those released in mixed (197 ± 224 m) or in hardwood habitat (147 ± 178 m; Table 2.2). After the first two hours, the release landscape also consistently explained variability in movement (Table 2.2). Migrants moved both faster and further in the Bundick landscape than they did in the Drake landscape (Bundick displacement 157 ± 195 m and rate 2.44 ± 2.19 m min\(^{-1}\) m for two hour periods; Drake displacement 116 ±
Table 2.1

Comparison of the relative influence of generalized linear models in predicting the movement rate (rate) and linear displacement (distance) for all hours combined and for each two hour period of the day.

<table>
<thead>
<tr>
<th>Period</th>
<th>Response</th>
<th>Model</th>
<th>ΔAICc</th>
<th>K</th>
<th>wi</th>
<th>Obs</th>
<th>Birds</th>
</tr>
</thead>
<tbody>
<tr>
<td>All hours</td>
<td>Distance</td>
<td>hour, cond, land, day</td>
<td>0.0</td>
<td>7</td>
<td>0.92</td>
<td>382</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>null</td>
<td>33.9</td>
<td>3</td>
<td>&lt; 0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rate</td>
<td>hour, cond, land, day</td>
<td>0.0</td>
<td>7</td>
<td>0.99</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>null</td>
<td>43.3</td>
<td>3</td>
<td>&lt; 0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6:30 - 8:30</td>
<td>Distance</td>
<td>habitat, cond</td>
<td>0.0</td>
<td>5</td>
<td>0.48</td>
<td>74</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td></td>
<td>null</td>
<td>8.2</td>
<td>3</td>
<td>&lt; 0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rate</td>
<td>habitat</td>
<td>0.0</td>
<td>4</td>
<td>0.27</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>null</td>
<td>0.0</td>
<td>3</td>
<td>0.26</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>cond, land</td>
<td>1.4</td>
<td>5</td>
<td>0.13</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>land</td>
<td>1.9</td>
<td>4</td>
<td>0.11</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8:31 - 10:30</td>
<td>Distance</td>
<td>cond, land</td>
<td>0.0</td>
<td>5</td>
<td>0.46</td>
<td>94</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td></td>
<td>cond</td>
<td>0.4</td>
<td>4</td>
<td>0.37</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>null</td>
<td>10.4</td>
<td>3</td>
<td>&lt; 0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rate</td>
<td>cond, land</td>
<td>0.0</td>
<td>5</td>
<td>0.95</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>null</td>
<td>13.0</td>
<td>3</td>
<td>&lt; 0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10:31 - 12:30</td>
<td>Distance</td>
<td>cond, land</td>
<td>0.0</td>
<td>5</td>
<td>0.66</td>
<td>71</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td></td>
<td>null</td>
<td>7.1</td>
<td>3</td>
<td>0.02</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rate</td>
<td>cond, land</td>
<td>0.0</td>
<td>5</td>
<td>0.68</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>null</td>
<td>6.3</td>
<td>3</td>
<td>0.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12:31 - 14:30</td>
<td>Distance</td>
<td>date</td>
<td>0.0</td>
<td>4</td>
<td>0.23</td>
<td>59</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>null</td>
<td>1.9</td>
<td>3</td>
<td>0.16</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rate</td>
<td>date</td>
<td>0.0</td>
<td>5</td>
<td>0.41</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>null</td>
<td>2.8</td>
<td>3</td>
<td>0.09</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. The number of parameters (K), differences in AICc values (ΔAICc) and Akaike weights (wi) for all top models (ΔAICc ≤ 2 considered equally plausible) and the null (intercept only) model are shown. Modeled factors were hour (hour), arrival energetic condition (cond), arrival habitat type (habitat), landscape (land), day of stopover (day) and day of year (date). Null models were top models from 14:31 to 18:30 so these time periods are not presented.
Table 2.2

Parameter estimates for factors in top supported generalized linear models predicting
the movement rate (rate) and linear displacement (distance) for all hours combined and
for each two hour period of the day. Parameter estimates shown for hour (hour), arrival
energetic condition (cond), arrival habitat type (habitat), landscape (land), day of
stopover (day) and day of year (date) when included in supported models.

<table>
<thead>
<tr>
<th>Period</th>
<th>Response</th>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Hours</td>
<td>Distance</td>
<td>cond</td>
<td>-0.32</td>
<td>0.08</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td></td>
<td>hour</td>
<td>-0.12</td>
<td>0.02</td>
<td>330</td>
</tr>
<tr>
<td></td>
<td></td>
<td>land a</td>
<td>1.54</td>
<td>0.31</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td></td>
<td>day</td>
<td>-0.24</td>
<td>0.10</td>
<td>330</td>
</tr>
<tr>
<td>Rate</td>
<td>cond</td>
<td>-0.14</td>
<td>0.03</td>
<td>47</td>
<td></td>
</tr>
<tr>
<td></td>
<td>hour</td>
<td>-0.05</td>
<td>0.01</td>
<td>330</td>
<td></td>
</tr>
<tr>
<td></td>
<td>land</td>
<td>0.59</td>
<td>0.10</td>
<td>47</td>
<td></td>
</tr>
<tr>
<td></td>
<td>day</td>
<td>-0.09</td>
<td>0.03</td>
<td>330</td>
<td></td>
</tr>
<tr>
<td>6:30 to 8:30</td>
<td>Distance</td>
<td>cond</td>
<td>-0.23</td>
<td>0.07</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td></td>
<td>habitat b</td>
<td>-0.43</td>
<td>0.16</td>
<td>45</td>
</tr>
<tr>
<td>8:31 to 10:30</td>
<td>Distance</td>
<td>cond</td>
<td>-0.36</td>
<td>0.10</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td></td>
<td>land</td>
<td>1.14</td>
<td>0.41</td>
<td>46</td>
</tr>
<tr>
<td>Rate</td>
<td>cond</td>
<td>-0.16</td>
<td>0.03</td>
<td>46</td>
<td></td>
</tr>
<tr>
<td></td>
<td>land</td>
<td>0.59</td>
<td>0.12</td>
<td>46</td>
<td></td>
</tr>
<tr>
<td>10:31 to 12:30</td>
<td>Distance</td>
<td>cond</td>
<td>-0.36</td>
<td>0.12</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>land</td>
<td>2.49</td>
<td>0.48</td>
<td>36</td>
</tr>
<tr>
<td>Rate</td>
<td>cond</td>
<td>-0.13</td>
<td>0.03</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td></td>
<td>land</td>
<td>0.64</td>
<td>0.13</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td>12:31 to 14:30</td>
<td>Rate</td>
<td>cond</td>
<td>-0.15</td>
<td>0.04</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>land</td>
<td>0.66</td>
<td>0.15</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>date</td>
<td>0.03</td>
<td>0.01</td>
<td>25</td>
</tr>
</tbody>
</table>

a Values for landscape are Drake = 1 and Bundick = 2
b Values for habitat are pine = 1, mixed = 2 and hardwood = 3

Note. The parameter estimates and errors for arrival condition from 8:31 to 10:30 is model weighted and averaged from
the top two models. No parameters influenced linear displacement from 12:31 to 18:30 or movement rate from 6:30 to
8:30 and 14:31 to 18:30; the null model was a top model. The signs represent the directionality of the relationship.
167 m and rate $1.49 \pm 1.76 \text{ m min}^{-1}$). Although the release habitat type influenced initial displacement distance, when all periods of the day were combined there was no difference in movement patterns between migrants using pine versus mixed (displacement $t = -1.32$, $P = 0.19$; rate $t = -1.08$, $P = 0.28$; df = 327, $n = 50$ [individuals], 90 [pine locations], 112 [mixed locations]) or pine versus hardwood habitat (displacement $t = -1.09$, $P = 0.28$; rate $t = -0.77$, $P = 0.44$; df = 327, $n = 50$ [individuals], 90 [pine locations], 180 [hardwood locations]).

Migrants gradually moved out of poorer quality habitat types and into habitat types characterized by greater food resources (pine < mixed < hardwood) during the morning of the first day. After two hours, the majority of migrants were still in their release habitat type (2.65 ± 1.88 hours in release habitat prior to changing habitat types). However, after eight hours in the landscape (14:30), as well as on subsequent days of stopover, the majority of migrants released in all habitat types were in either mixed or hardwood habitat. This pattern was true in both landscapes.

There was no evidence of a stationary acclimation period prior to flying or foraging after release. Individuals were observed foraging as early as one minute after release in hardwood, 22 min. after release in mixed and 48 min. after release in pine. Foraging was successful as early as one minute after release in hardwood, 32 min. after release in mixed and an hour after release in pine. Migrants caught prey more quickly in habitat types characterized by greater food resources ($F_{2,26}=3.37$, $P = 0.04$, $n = 29$ observations from 14 individuals). Capture rates in pine were significantly less than in hardwood ($P = 0.04$), but capture rates did not differ between mixed (0.04 ± 0.02 prey s$^{-1}$, $n = 5$) and pine (0.01 ± 0.003 prey s$^{-1}$, $n = 15$, $P = 0.41$) or mixed and hardwood (0.05 ± 0.02 prey s$^{-1}$, $n = 9$, $P = 0.72$).
**Influence of endogenous factors**

Migrants had a range of energetic conditions (-2.28 to 6.3) that were well correlated with visual estimation of fat scores for the migrants released \((R^2 = 0.562, p < 0.001)\). A migrant’s arrival energetic condition strongly influenced how he/she moved during stopover (Table 2.1). Migrants in poorer energetic condition moved faster and further than migrants with greater fuel reserves (Table 2.2). The time of season was not highly influential (Table 2.1); individuals released later in the season did not move any faster or further than did individuals released earlier. It was possible to estimate sex for 17 individuals: nine males and eight females. There were no differences in movement between sexes (linear displacement \(t_{15, 115} = -1.28, P = 0.22\); rate \(t_{15, 115} = -1.33, P = 0.20\)). Migrants did not move in a uniform direction during the first day of stopover \((Z = 0.17, P > 0.50)\) nor did migrants released at the same site consistently move in the same direction (all \(P > 0.25\)).

**Characterization of environment**

As expected, the number of arthropods varied with habitat. I collected 800 arthropod samples, 396 on transects and 404 in locations selected by migrants. Five samples were excluded from analyses due to missing factors. There were more arthropods in mixed than in pine \((\beta = 0.76 \pm 0.13 [SE], P < 0.01)\), in hardwood than in pine \((\beta = 1.11 \pm 0.12, P < 0.01)\) and in areas selected by migrants than in randomly sampled locations \((\beta = 0.70 \pm 0.19, P < 0.01)\). There were no difference in arthropods between landscapes \((X^2 = 0.08, df = 1, P = 0.77)\) or times of season \((X^2 = 0.45, df = 2, P = 0.80)\). Within pine habitat, there were more arthropods in areas selected by migrants \((4.24 \pm 7.23, n = 37)\) than on transects \((2.75 \pm 2.29, n = 133)\), whereas in mixed and hardwood habitat, there were fewer arthropods in selected areas (mixed \(4.44 \pm 3.47, n = 150\); hardwood \(5.54 \pm 4.55, n = 213\)) versus on transects (mixed \(5.01 \pm 5.82, n = 130\); hardwood \(7.51 \pm 6.91, n = 132\); Fig. 2.2). Lepidoptera larvae presence varied with
habitat ($X^2 = 28.93, df = 4, P < 0.01$) but not with time of season ($X^2 = 5.39, df = 2, P = 0.07$), landscape ($X^2 = 3.56, df = 1, P = 0.06$) or type of sample ($X^2 = 4.80, df = 3, P = 0.19$). There were fewer Lepidoptera larvae in pine habitat than in hardwood ($\beta = 1.22 \pm 0.30, P < 0.01$) but mixed did not differ in Lepidoptera larvae ($\beta = 0.45 \pm 0.32, P = 0.16$).

The number of transient migrants varied with habitat ($X^2 = 14.58, df = 2, P < 0.01$) and landscape ($X^2 = 9.70, df = 1, P < 0.01$). Transient migrants were less abundant in pine than in hardwood ($\beta = 1.21 \pm 0.40, P < 0.01$) and less frequent in pine than in mixed ($\beta = 2.06 \pm 0.80, P = 0.01$) and less abundant in the Bundick than in the Drake landscape ($\beta = 0.88 \pm 0.31, P = 0.01$). There were more hawks detected on transects in the Bundick ($n = 13$) than in the Drake landscape ($n = 5$) but detections were in all three habitats ($n = 12$ hardwood, $n = 2$ in mixed, $n = 4$ in pine) on both sets of transects.

The vegetation structure was different in the three habitat types ($pseudo-F_{2,35} = 26.02, P < 0.001$; permutational multivariate analysis of variance, adonis function in R library vegan) but not in the habitat type replicates ($pseudo-F_{1,35} = -0.33, P = 0.999$). The tree community composition also differed between habitat types ($pseudo-F_{2,35} = 15.831, P < 0.001$) but not between replicates ($pseudo-F_{1,35} = 1.367, P = 0.244$). The area surrounding each of the release sites in the three habitat types did not differ in canopy height, herbaceous layer height or total basal area but pine habitat had less shrub layer cover and more live ground cover, mixed habitat had more shrubs, and hardwood habitat had greater canopy cover. Landscapes are inherently variable and the area surrounding the three release sites in the Bundick landscape contained comparatively more mixed (50% versus 39% at Drake) and hardwood (24% versus 17% at Drake) and the area surrounding the Drake release sites contained comparatively more pine (29% versus 19% at Bundick).
Figure 2.2. Mean number of arthropods detected in samples collected at randomly selected locations (transects) versus samples collected in areas selected by migrants (selected) in each habitat type: pine, mixed and hardwood. Means are shown and bars represent SE.

Discussion

The experimental design enabled me to draw strong inferences about the effects and effect sizes of exogenous and endogenous factors on the movement ecology of an intercontinental migratory songbird during spring stopover in a field setting. Stopover periods are uniquely suited to drawing inferences about the influence of internal state and distribution of resources on avian movement because individuals arrive with vastly different energetic reserves and have a short period of time to accomplish their goals (rest or refuel) in an unfamiliar landscape. Migrant movement during stopover showed considerable variability. Nevertheless, red-eyed vireos responded to their environment in consistent ways that were habitat and condition dependent.
Influence of exogenous factors

There was support for the expectation that migrants exhibit exploratory movement the morning after arrival and that movement would be greater in habitat types characterized by reduced food resources. The amount of exploration and time until attempted and successful foraging was also habitat-dependent and negatively related to food abundance. There are energetic and time costs associated with a requisite initial period prior to foraging at stopover sites. If necessary at each stop along a migrant’s journey, non-foraging periods would affect the optimal energy load and duration of stay (Alerstam & Lindström 1990; Alerstam & Hedenström 1998) and would cumulatively result in a significant energetic and/or time cost to migration (Lindström 1991). There is mixed evidence for a non-foraging period cost from banding data in the form of an observed mass loss after initial capture (reviewed in Schwilch & Jenni 2001), though the effect of the capture handling time could not be eliminated in these studies (Delingat et al. 2006). There was no evidence for a requisite period for the purpose of physical acclimation prior to foraging; stationary behaviors were observed only slightly more often during the first two hours of the day and migrants began foraging almost immediately upon release in habitat with abundant food. Delingat et al. (2006) also observed foraging from one minute to half an hour after moving and releasing Northern wheatears (Oenanthe oenanthe), presumably into habitat with abundant food.

The prediction that migrants would move into habitat types characterized by greater food resources was supported. Migrants released in hardwood largely stayed in hardwood whereas migrants released in mixed and pine moved into hardwood. This pattern was consistent in both landscapes and characterized migrants with greater fuel reserves, presumably under less pressure to locate food resources (cf. Loria & Moore 1990; Wang & Moore 2005). The results suggest that it is beneficial to a migrant to
search for high quality habitat characterized by greater food even with potential costs of energy expenditure or exposure to avian predators attracted to movement.

The necessity of finding food implies that migrant movement would be primarily influenced by the distribution of food resources. This is supported by correlative evidence for habitat selection based on food abundance (Hutto 1985; Blake & Hoppes 1986; Johnson & Sherry 2001) and migrant distributions in relation to changes in food availability at different scales (reviewed in Moore et al. 1995; Buler, Moore & Woltmann 2007). If movement of migratory songbirds during stopover is largely a function of the distribution of food resources, then migrants would not only select habitat types with greater food resources but would also select areas within habitat types where food availability was greater. When migrants were in habitat characterized by less abundant food (pine), they selected locations within that habitat type with greater food abundance than was present at random locations. Conversely, once in habitat characterized by more abundant food (hardwood), red-eyed vireos selected locations with considerably less abundant food than expected by chance alone. Champlin, Kilgo and Moorman (2009) also did not find migrant habitat use changed with food abundance within hardwood habitat. This implies migrants may be searching for areas with sufficient food as opposed to areas with the most abundant food supply. Further, migrants gradually moved through the landscape and did not show any indication of defending territories once in high quality habitat.

Counter to my expectations, movement was not more area restricted within hardwood habitat. Movement did differ between the two landscapes. Red-eyed vireos moved further and faster in the Bundick landscape which had comparatively more hardwood habitat, avian predators and en route migrants but did not differ in food or vegetation structure. These results suggest that once red-eyed vireos located high quality habitat, factors other than to the distribution of food influenced movement.
decisions. Further experimental work is needed on how predators and the density of migrants influence movement patterns during stopover, especially within habitat where food may not be limited.

**Influence of endogenous factors**

Energetic condition upon arrival strongly influenced movement of red-eyed vireos during stopover. As predicted, migrants with reduced fuel stores moved further and faster during stopover (see also Moore & Aborn 2000; Matthews & Rodewald 2010), consistent with pressure to replenish depleted fuel stores necessary to continue migration in a timely fashion (Alerstam & Lindström 1990). Fatter migrants may move at a slower rate and over shorter distance to conserve fat stores and reduce risk of predation (see Wang & Moore 2005, Cimprich & Moore 2006). However, two other species tracked during stopover did not exhibit condition-dependent movement (Chernetsov & Mukhin 2006; Paxton, van Riper III & O’Brien 2008). At the within-habitat scale, energetically constrained red-eyed vireos and thrushes foraged at faster rates using more diverse substrates and maneuvers relative to individuals with greater fuel stores (Loria & Moore 1990; Wang & Moore 2005).

Although movement of migrants arriving late in relation to their destination are expected to reflect higher fuel deposition rates during stopover (Jenni and Schaub 2003), there was no support for a relationship between time of spring and movement patterns of red-eyed vireos. That expectation assumes that red-eyed vireos tracked late in the season are late in relation to their time program, and it was not possible to determine the remaining distance a migrant had to travel relative to the time of season. Wilson’s warblers (*Wilsonia pusilla*) moved faster and further later in the spring, which may have been related to reduced availability of food resources late in the season (Paxton, van Riper III & O’Brien 2008). However, there was no support for a seasonal pattern in abundance or distribution of food in this study. Therefore, movement likely did
not change with time of season due to exogenous factors such as food, which I did not find to vary at my sites, but may have varied in relation to an individual’s time program which I could not accurately assess with my methods.

There was no difference in movement between male and female red-eyed vireos, though it was only possible to identify sex for a subset of individuals. There is reason to believe males are under increased pressure to migrate faster and arrive to breeding areas earlier than females in some species (Morbey & Ydenberg 2001; Moore, Mabey & Woodrey 2003), but there is less reason to expect faster migration or protandry in the case of less sexually dimorphic species such as the red-eyed vireo (see Rubolini, Spina & Saino 2004; Hatch & Smith 2009). It was not possible to differentiate age in this study but more experienced migrants may be more successful at overcoming the challenges of migration. However, age may not determine dominance for red-eyed vireos (Moore, Mabey & Woodrey 2003).

The expectation that daytime movements would be concentrated in a seasonally appropriate north-northeastern direction was also tested. Contrary to my prediction, directionality varied widely among individuals and release sites. The initial direction of movement after release at dawn in an unfamiliar landscape was essentially random. Migrants also did not move consistently in a north-northeastern direction by the end of the first day. This implies migrants prioritize local scale information about the distribution of resources over larger scale information about directionality to destination during stopover. The relatively short distance of movement during stopover periods may not be long enough to incur sufficient costs, either in terms of distance or energy, to make directionality beneficial during stopover.

In conclusion, songbird movement decisions during stopovers are not solely a function of underlying resource distributions but are more complex behavioral responses to a combination of endogenous and exogenous factors. The movement track during
each stopover can be thought of as one phase embedded within an organisms’ larger lifetime track, the consequences of which will carry over to subsequent phases (Nathan et al. 2008). For example, if a migratory songbird is obliged to spend more time locating suitable habitat during stopover, she may stay longer than usual to refuel and a penalty may be attached to late arrival at the next stopover site, where resource levels may have been depressed by earlier migrants (Moore & Wang 1991). Alternatively, if she departs “on time” but with lower fat stores, she will need to stay longer or refuel faster at the next stopover to maintain a “margin of safety” vis-a-vis anticipated energetic demands. If she does not make up lost time, she will arrive late on the breeding grounds potentially jeopardizing opportunities to secure a territory or a mate (Smith & Moore 2005) and if she does not regain reduced fuel stores she will arrive in poorer condition on the breeding grounds where she may suffer reduced reproductive success (Smith & Moore 2003).

Acknowledgments

This manuscript was improved by comments from Z. Németh, J. Gautreaux and K. Paxton. Logistical support was provided by J. Johnson and D. Hudson at Fort Polk and L. Bennett Louisiana at Wildlife and Fisheries. I would especially like to thank the members of the migratory bird research group at USM and all of the hard working assistants who helped us collect data in the field: B. Bielfelt, M. Cline, K. Comolli, S. Everett, D. Haines, P. Heavin, P. Hosner, L. LaHaye, E. Lain, C. Nicholson, D. Ripper, C. Roy, A. Scarpignato, J. Smolinsky, L. Vormvold and B. Wilson. Funding for this project was provided by the Department of Defense Strategic Environmental Research and Development Program.
Literature Cited


CHAPTER III
AN EXPERIMENTAL ASSESSMENT OF THE INFLUENCE OF ENDOGENOUS AND EXOGENOUS FACTORS ON STOPOVER DURATION DURING SPRING MIGRATION

Abstract

Knowledge of the relative influence of factors affecting stopover duration remains poorly understood despite its importance for understanding the spatiotemporal organization of migration. I took an experimental approach to measure stopover duration in relation to the time of season, energetic condition, arrival habitat type and movement behavior on the duration of stay at spring stopover. I controlled for arrival time, condition and habitat quality at a stopover site by translocating transient nocturnal migrants with varying amounts of fuel reserves to one of two unfamiliar landscapes and released them in one of three habitat types that varied in food availability. I continuously radio-tracked individuals until departure and assessed the accuracy of estimates of duration of stay with annual aerial surveys. Migrants remained at the stopover sites from one to eight days (2.86 ± 0.3 days). Migrants arriving with reduced fuel stores remained longer and only migrants arriving early in the spring stayed for extended periods of time (≥ 6 days). Previous work in this system found migrants arriving in poorer quality habitat had a longer searching period prior to foraging and that migrants arriving with reduced fuel reserves move faster during stopover, presumably under increased pressure to refuel. However, neither arrival habitat quality nor movement rate during stopover influenced how long migrants remained in the landscape. Further, no factors examined influenced remaining at stopover for an intermediate period (> 3 days and < 6 days). Arrival energetic condition is a strong determinant of duration of stay at stopover but two days may have been sufficient time to replenish fuel stores in these landscapes and migrants may need to adjust the speed and duration of spring migration for optimal arrival and breeding sites.
Introduction

Over half of the birds that breed in North America are migratory species, spending up to a third of their annual cycle traversing hundreds to thousands of kilometers of land and water for which they have limited information. Long-distance migration is characterized by alternating periods of flight, when energy stores are consumed, and periods of stopover, when energy stores are replenished. Stopover periods are particularly important because migration is energetically costly (e.g., Blem 1980, Alerstam 1990) and foraging at stopover sites is essential for a successful migration. In fact, the cumulative amount of time songbirds spend refueling at stopover sites far exceeds the time spent in flight and largely determines the duration of the migratory period (Alerstam 2003). Yet, knowledge of the relative influence of factors affecting stopover duration remains poorly understood despite its importance for understanding the spatiotemporal organization of migration (Schaub and Jenni 2001, Jenni and Schaub 2003).

The amount of time spent at each stopover site is likely to be influenced by a complex interplay of internal state, including a migrant’s energetic condition upon arrival, pressure to arrive at a destination in a timely fashion, and with external factors that influence the rate of fuel deposition such as food abundance, competition and predation pressure (Jenni and Schaub 2003). For example, a landscape with plentiful food may lead to a longer stay for a migrant with low fuel reserves while food availability may not influence duration of stay for migrants with plentiful fuel reserves. Pressures to arrive early to breeding locations should act to minimize time spent migrating and these pressures should increase as the season progresses (Weber et al. 1998). However, migration is a time of exceptional energetic demands (Blem 1980) and migrants with lower fuel reserves may require more time for refueling at stopover sites (e.g., Kuenzi et al. 1991, Yong and Moore 1993). That said, energetically constrained individuals are
under more pressure to replenish fuel stores rapidly (Wang and Moore 2005).
Energetically constrained migrants increase their predation risk in favor of refueling
(Cimprich and Moore 2006) and forage both more rapidly and over a greater area to
access prey resources (Loria and Moore 1990, Moore and Aborn 2000, Wang and
Moore 2005).

Amount of fat carried by a migrant upon arrival at a stopover site, as fuel for
continued migration, is thought to be a key determinant of how long migrants remain at a
site but problems with accurately assessing the duration of stay has made it difficult to
draw strong inferences about the influence of arrival condition. Lean migrants without fat
stores are more likely to be recaptured at the same site during migration than are
migrants with fat reserves suggesting that they remain at sites longer (e.g., Cherry 1982,
However, lean migrants may also be more active during the day than fatter migrants
(Yong and Moore 1993, Chapter II) and therefore may be more likely to be recaptured.
When an increased probability of recapture was included as a factor in models of
stopover duration, the influence of arrival condition on duration was less than previously
thought (Bächler and Schaub 2007, Salewski and Schaub 2007). Radio-tracking of
migrants does not rely on recapture to estimate departure therefore it provides a more
accurate estimate of departure time and hence of stopover duration. This technique has
for the most part supported the influence of arrival energetic condition on duration of stay
(Chernetsov and Mukhin 2006, Goymann et al. 2010, Matthews and Rodewald 2010,
Seewagen and Gugliemo 2010; but see Tsvey et al. 2007, Tietz and Johnson 2007,
Seewagen et al. 2010). However, with the exception of one study (Matthews and
Rodewald 2010) only minimum stopover duration of individuals has been measured
because migrants were captured and tracked at the same site making the time from
arrival to capture unknown. Further, limitations in the spatial and temporal scope of sampling efforts may have resulted in underestimation of the duration of stay.

I took an experimental approach to measure stopover duration from the time of arrival to departure for individuals with known arrival energetic conditions. I controlled for arrival time, condition and habitat type at a stopover site by translocating transient nocturnal migrants with varying amounts of fuel reserves to one of two unfamiliar landscapes and releasing them before dawn in one of three habitat types that varied in food availability (see Chapter II). I continuously radio-tracked individuals until departure and used annual aerial surveys to verify that my tracking methods accurately assessed length of stay.

My objective was to assess the relative influence of time of season, arrival energetic condition, arrival habitat type, and movement behavior during stopover on the duration of stay. I expected migrants stopping over later in the season to spend less time at stopover sites than those arriving earlier in the season. I also expected migrants that arrived in better energetic condition to stay for a shorter time than migrants arriving in poorer energetic condition. I assume that finding suitable habitat is key to a successful stopover and that time spent searching for suitable habitat influences the duration of stay (Alerstam and Lindström 1990, Alerstam and Hedenström 1998). Therefore, I expected migrants that arrived in habitat characterized by greater food availability to remain for a shorter time than migrants that arrived in less suitable habitat. Finally, leaner migrants are also known to forage more intensely than fatter migrants during stopover (Loria and Moore 1990), which increases the rate of fuel deposition (Wang and Moore 2005) and presumably shortens duration of stopover. Therefore, I expected migrants with faster daily movement rates to have shorter stopover duration. Arrival energetic condition and food abundance were controlled for by releasing migrants
with and without energetic reserves in two replicates of three habitats types that differed in food abundance.

Methods

The red-eyed vireo (*Vireo olivaceus*) was chosen as focal species because it is one of the most common long-distance Nearctic-Neotropical migratory songbirds in eastern deciduous forests, was common during spring surveys at the study sites (Fischer et al. 2011), individuals are large enough to carry transmitters, and vary their behavior in relation to energetic condition (Loria and Moore 1990; Sandberg and Moore 1996). I captured red-eyed vireos in a chenier in coastal southwestern Louisiana near Johnson’s Bayou (29° 45’ N 93° 30’ W). Cheniers are narrow strips of coastal woodlands dominated by hackberry (*Celtis laevigata*) along the northern coast of the Gulf of Mexico and are the first wooded habitat available to songbirds following the trans-Gulf flight (Moore 1999). Red-eyed vireos do not breed at Johnson’s Bayou so I knew that migrants captured there were transient individuals. Upon capture, migrants were banded with a U.S. Fish and Wildlife Service band and a unique combination of one or two colored leg bands. I also assessed weight, wing chord and amount of subcutaneous fat (Helms and Drury 1960). I calculated an energetic condition index to reflect the proportion of body mass attributed to fat (see Owen and Moore 2006). Size specific fat-free masses for captured red-eyed vireos were estimated from a regression of wing chord length on mass for all red-eyed vireos with no visible fat (score of zero; Helms and Drury 1960) captured from 1998 to 2006 at Johnson’s Bayou (n= 1775). Therefore, a migrant with a condition index of zero was at lean body mass, a migrant with a positive condition index had fuel reserves while a migrant with a negative condition index was below lean body mass. I recorded the mass and fat score a second time the morning after capture just prior to release and used this to calculate the arrival condition index. A migrant’s energetic condition upon arrival was calculated as their
release mass (with the attached transmitter) less the fat-free mass specific to their wing chord length.

Red-eyed vireos captured at Johnson’s Bayou were transported the afternoon or evening of the day of capture approximately 143 km to the Vernon Unit of the Calcasieu Ranger District in Kisatchie National Forest, Louisiana (30° 57’ N 93° 08’ W). This site was chosen because it is used by a high density of spring migrants (Fischer et al. 2011) and forest cover types are characteristic of those found throughout the region. Migrants were held in individual cages and provided with food and water ad libitum. The evening of the capture day migrants were fitted with radio-transmitters weighing less than 3.5% of mean lean body mass (models LB-2 and LB-2N, Holohil Systems Ltd. Ontario, Canada). Feathers were removed from the synsacrum and the transmitter was glued to the exposed area using nontoxic glue. I placed transmitters the evening of the capture day to give migrants time for acclimation prior to releasing them the next morning.

Red-eyed vireos with variable energetic reserves were released at first light at one of six predetermined locations in two landscapes that are approximately 3 km apart and contain similar compositions of habitat types (see Chapter II for a more detailed description of landscapes and release sites). Migrants were released in two replicates of three habitat types characteristic of habitat likely to be encountered by migrants moving through this region: upland longleaf pine (*Pinus palustris*) savanna (pine), bottomland deciduous forests along creeks (hardwood), and an intermediate between the two (mixed). To quantify food resources, I took arthropod canopy samples near each of the six release sites during early, middle and late spring (see Chapter II). Hardwood habitat was characterized by the greatest food abundance and pine habitat the least but there were no seasonal differences in food abundance (see Chapter II). Replicates of release habitat types also did not differ in food abundance, vegetation structure or tree community composition (see Chapter II).
Red-eyed vireos were radio-tracked continuously with locations taken every 15 min. I approached the signal to about 50 m and then circled to verify the location before attempting to resight the bird from a distance, so as not to alter behavior. In 2007 I tracked migrants the first five hours and last hour of each day of stopover and in 2008 I tracked migrants for 12 hrs each of the first three days of stopover and after that I located migrants once or twice daily to determine the duration of stay at the study site. My equipment did not allow me to follow movements of migrants during rain but I was able to verify if migrants remained in the landscape during rain. I defined the duration of stay as the as the number of days from release to the last day a migrant was located. Searching for a bird tracked the previous day began at first light at the last known location. When an individual was not detected I searched systematically surrounding the last known location. I also used a set of locations surrounding the entire study site to conduct systematic searched for lost signals daily. Once per season, personnel from the adjacent military installation checked a subset of my signals from a helicopter flown over the Vernon Unit of Kistachie National Forest to verify that signals not detected on the ground were no longer in the landscape. The signals checked from the air included migrants currently present in the landscapes and migrants no longer detected on the ground. In each case, the aerial surveys verified that the signals detected on the ground were also detected in the air and the signals not detected on the ground during systematic searches also were not detected from the air. One migrant stopped over for at least thirteen days. I excluded this bird from analyses because the duration may have been extended due to an unseasonably cold week and because thirteen days is also within the range of the transmitter life so transmitter failure may alternatively have underestimated duration of stay.

It is possible that attaching transmitters and moving migrants could have affected their behavior. However, I did not observe any behavioral differences during extensive
detailed foraging observations (see Chapter II). Further, during the spring of 2006 I used
the same methods to attach radio-transmitters to four red-eyed vireos captured at
Johnson’s Bayou. I released migrants at their capture location and followed them
continuously to measure stopover duration. They exhibited the same behavior with
regard to arrival condition in that the three migrants with positive energetic condition
index (above lean body mass) remained one day while the one migrant below lean body
mass remained three days. This duration and behavior in relation to condition is not
inconsistent with two similar coastal sites where mean stopover duration was 2.0 days
for banded-only migrants (Moore and Simons 1992).

Data analyses

To analyze the relative influence of time of season, arrival energetic condition,
arrival habitat, and landscape on the duration of stay I constructed and compared 15
biologically plausible linear models. The arrival energetic condition was calculated for
each individual as described above, the time of season was the ordinal day of the year,
the release habitat type was either pine, mixed or hardwood and the landscape was one
of the two sets of replicate release sites. There were no differences between years in
the duration of stay \( (t=1.20, P = 0.25, n_1 = 14, n_2 = 28) \), consequently year was not
included in candidate models. I employed an information-theoretic approach because I
expected multiple factors to influence migrant behavior, and I was interested in their
relative influence as well as their effects. I used Akaike’s Information Criterion for small
sample sizes (AICc) to rank, compare, and evaluate all candidate model sets (Burnham
and Anderson 2002). I present all models with a \( \Delta \text{AICc} \leq 2 \) as plausible competing
models (considered the subset of best supported models, Burnham and Anderson
2002). I also present the null (intercept only) model for assessment of the relative
explanatory power of the plausible models. For variables in more than one top model
(\( \Delta \text{AICc} \leq 2 \)) parameter estimates were averaged across models containing each
explanatory variable and standard errors were calculated from conditional variances to incorporate model selection uncertainty (Burnham and Anderson 2002). Relative importance of variables and model-averaged parameter estimates were calculated in Excel according to Burnham and Anderson (2002).

To assess the influence of daily movement rate on how long migrants remained at the site, I quantified movement rate for each individual by dividing the cumulative distance between all locations by the time period of tracking (m min⁻¹) during two hour increments from 6:30 to 18:30 CST on the first three days of stopover. Movement rate was transformed (log [x +1]) to meet assumptions of normality. Individual movement rate varied considerably both within and between stopover days (Chapter II) and I did not have data for every two hour increment for all migrants tracked each day because of rain and differences in sampling schemes between the two years of the study. Therefore, to control for the influence of for correlations between observations from the same individual throughout the day, I fitted linear mixed-effects models with the daily movement rates as a fixed effect and the individual as the random component and analyzed the influence of movement rate on stopover duration separately for each of the first three days of stopover. Analyses were conducted in R version 2.11.1 (R Development Core Team 2010). I present means ± SE throughout.

Results

During early April to mid-May, I released 42 red-eyed vireos in a range of energetic conditions (-2.3 to 6.3 index values) into my test landscapes. Migrants remained at the stopover sites from one to eight days (2.86 ± 0.3 days; n= 14 in 2007 and 28 in 2008). One third of migrants left the night of the release day (n = 14), close to a quarter remained only two days (n = 9), and four birds stayed six or more nights. Two top supported models for stopover duration which explained 61 % of the variation in the data; both included energetic condition and one included day of season (Table 3.1). The
model averaged parameter estimate for energetic condition ($\beta = -0.40 \pm 0.16$) reflects increasing duration of stay with decreasing arrival energetic condition (Figure 3.1). In addition, as the spring progressed, migrants spent less time at the stopover site ($\beta = -0.05 \pm 0.03$). This relationship was due to the four birds that stayed longer than five days, all of which occurred during the first three weeks of April. Without these four individuals, day of season was no longer a supported variable.

Table 3.1

*Comparison of the relative influence of linear models in predicting duration of stay.*

<table>
<thead>
<tr>
<th>Model description</th>
<th>$\Delta$AICc</th>
<th>K</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>condition, day</td>
<td>0.0</td>
<td>4</td>
<td>0.366</td>
</tr>
<tr>
<td>condition</td>
<td>0.8</td>
<td>3</td>
<td>0.244</td>
</tr>
<tr>
<td>condition, day, landscape</td>
<td>2.5</td>
<td>5</td>
<td>0.103</td>
</tr>
<tr>
<td>condition, landscape</td>
<td>3.2</td>
<td>4</td>
<td>0.075</td>
</tr>
<tr>
<td>day</td>
<td>4.3</td>
<td>3</td>
<td>0.043</td>
</tr>
<tr>
<td>condition, day, habitat</td>
<td>4.6</td>
<td>6</td>
<td>0.036</td>
</tr>
<tr>
<td>condition, habitat</td>
<td>4.8</td>
<td>5</td>
<td>0.034</td>
</tr>
<tr>
<td>NULL</td>
<td>4.8</td>
<td>2</td>
<td>0.034</td>
</tr>
<tr>
<td>landscape</td>
<td>6.2</td>
<td>3</td>
<td>0.017</td>
</tr>
<tr>
<td>day, landscape</td>
<td>6.4</td>
<td>4</td>
<td>0.015</td>
</tr>
<tr>
<td>condition, day, habitat, landscape</td>
<td>7.5</td>
<td>7</td>
<td>0.009</td>
</tr>
<tr>
<td>condition, habitat, landscape</td>
<td>7.5</td>
<td>6</td>
<td>0.009</td>
</tr>
<tr>
<td>habitat</td>
<td>8.1</td>
<td>4</td>
<td>0.006</td>
</tr>
<tr>
<td>day, habitat</td>
<td>8.3</td>
<td>5</td>
<td>0.006</td>
</tr>
<tr>
<td>habitat, landscape</td>
<td>10</td>
<td>5</td>
<td>0.002</td>
</tr>
<tr>
<td>day, habitat, landscape</td>
<td>10.8</td>
<td>6</td>
<td>0.002</td>
</tr>
</tbody>
</table>

Note. The differences in AICc values ($\Delta$AICc), number of parameters (K) and Akaike weights ($w_i$) are shown for all models as well as the null (intercept only) model. All models with $\Delta$AICc ≤ 2 are considered equally plausible.
Figure 3.1. Duration of stay for red-eyed vireos radio-tracked in Kistachie National Forest and the relationship between arrival energetic condition index (negative values are below lean body mass and positive are above) and the duration of stay in days. Bars represent SE. Migrants remained one (n=14), two (n=9), three (n=5), four (n=5), five (n=5) and 6 or more days (n=4). Migrants that remained ≥ six days (one remained six days, two remained seven days and one remained eight days) are combined and presented here as greater than or equal to 6 days.

A migrant’s rate of movement on the first, second and third day of stopover did not influence how long it remained at the stopover site (all P > 0.65, Figure 3.2).

Because arrival energetic condition was highly influential in explaining the duration of stay I ran post-hoc two-way ANOVAs to test for the influence of arrival condition, movement rate and their interaction during each of the first three days of stopover on the stopover duration. I tested for the influence of individual movement rate during the first two hours of the day (0630 to 0830 CST) because that is the time period when most movement occurred (see Chapter II). I found movement rate during the first two hours of each of the first three days of stopover did not influence how long migrants remained in the landscape (all P > 0.34). Arrival energetic condition continued to positively influence the duration of stay for migrants remaining in the landscape after the first day (F_{1,20} =
6.39, \( P = 0.002 \)) but did not influence the duration of stay for migrants that remained in the landscape beyond the second day (\( F_{1,13} = 1.85, P = 0.20 \)).

![Boxplot of movement rate (m/ min) during two hour increments, from 6:30 to 18:30 CST, on the first day of stopover (n= 42 birds). Not all individuals were tracked all six of the two hour time periods. Migrants that remained equal to or greater than six days (one remained six days, two remained seven days and one remained eight days) are combined and presented here as greater than or equal to 6 days.](image)

**Figure 3.2.** Boxplot of movement rate (m/ min) during two hour increments, from 6:30 to 18:30 CST, on the first day of stopover (n= 42 birds). Not all individuals were tracked all six of the two hour time periods. Migrants that remained equal to or greater than six days (one remained six days, two remained seven days and one remained eight days) are combined and presented here as greater than or equal to 6 days.

**Discussion**

I present evidence from carefully controlled experiments with known arrival dates, that arrival energetic condition is the most influential determinant of stopover duration. Migrants that arrived in better energetic condition were more likely to leave
after the first and second day of stopover than were migrants in poorer energetic condition. However, arrival energetic condition did not influence stopover duration for migrants that remained three or more days. This work confirms evidence from other radio-telemetry studies that arrival energetic condition is the most consistently important determinant of how long migrants remain at stopover sites (Chernetsov and Mukhin 2006, Goymann et al. 2010, Matthews and Rodewald 2010, Seewagen and Gugliemo 2010). Matthews and Rodewald (2010) also moved migrants to new sites and found support for negative relationships between day of season and arrival condition on duration of stay at stopover sites not near geographic barriers in spring. Seewagen and Guglielmo (2010) used magnetic resonance analysis to attribute a proportion of body mass to fat and found migrants with more fat mass did not remain as long at stopover but they did not find a relationship between stopover duration and lean body mass. Results of several radio-telemetry studies that did not find a relationship between stopover duration and arrival energetic condition (Tsvey et al. 2007, Tietz and Johnson 2007, Seewagen et al. 2010) may be compromised because they relied on an estimate of minimum duration. This is because migrants were tracked at their capture location which meant that the amount of time between arrival and capture was unknown. While capture-recapture studies have largely supported a negative relationship between arrival condition and stopover duration (Cherry 1982, Moore and Kerlinger 1987, Arizaga et al. 2008, Schaub et al. 2008, Arizaga et al. 2011), these results may be confounded by violations of model assumptions regarding equal catchability (Bächler and Schaub 2007, Salewski and Schaub 2007, Salewski et al. 2007). My work supports energetic condition as a key physiological determinant of stopover duration and emphasizes the value of knowing the true arrival and departure days as well as accurately assessing condition.

The only migrants that remained at the stopover sites for extended periods did so early in the spring indicating that timing may be especially important in early spring when
temperatures are cooler and migrants need to fine-tune their arrival to breeding areas. Earlier in the season migrants are more likely to be affected by cooler temperatures and more variable weather (Tøttrup et al. 2010). Early migrants may need to stop longer because arthropods are less abundant when temperatures are cooler. Temperatures were cooler earlier in the spring (pers obs) but food abundance did not vary with time of spring at my sites (see Chapter II). However, early migrants may have adjusted their stopover durations in response to local environmental conditions to fine-tune arrival time to breeding, especially as they approach their breeding latitudes (Marra et al. 2005, Tøttrup et al. 2010). These adjustments may be why none of the factors examined were important in explaining why migrants remained a moderate amount of time at stopover, more than two but less than six days. Some of the unexplained variability was also likely due to the influence of weather on nightly departure decisions (Tsvey et al. 2007), which I did not include in analyses. Weather is unlikely to have influenced the factors that were examined. It is also possible that cooler temperatures had other costs for migrants such as increased basal metabolic rate (Piersma et al. 1995). More work is needed on the influence of local environmental conditions on stopover durations across a latitudinal gradient (Marra et al. 2005).

Migrants that moved faster during stopover did not leave earlier. I expected movement rate during stopover to reflect foraging intensity which is known to be greater for migrants in poorer condition in terms of foraging speed, diversity of maneuvers and diversity of substrates (Loria and Moore 1990, Wang and Moore 2005). Therefore, I expected foraging rate to reflect differences in foraging intensity and to be greater for migrants that are under more pressure to continue migration. Movement rate varied between individuals and temporally during stopover (Chapter II). However, when I controlled for arrival condition I did not find foraging rate influenced stopover duration. The variability in movement rate appears to have been attributed largely to energetic
condition (Chapter II). It is also possible that at this scale movement rate may not have been a good indicator of foraging effort or of foraging success, which is more likely to be related to fuel deposition rates.

The arrival habitat type also did not influence the duration of stay. Searching and settling costs are thought to exert strong influence on stopover duration in that they delay the initiation of foraging and, therefore, fuel deposition rates during stopover (Delingat et al. 2006). I expected searching time to increase as arrival habitat quality, in terms of food abundance, decreased. Therefore, I expected stopover duration to be greater for migrants arriving in poorer quality habitat. Searching time was greater for migrants arriving in poorer quality habitat (see Chapter II) but this did not influence the duration of stay. This may have been because most migrants left the poorer quality habitat within two hours and moved into habitat with more abundant food (Chapter II). Therefore, the proximity to high quality habitat within these landscapes may have been low enough so as not to influence fuel deposition rates.

In conclusion, I found support for the influence of a combination of endogenous and exogenous factors on stopover duration when arrival time and condition were experimentally controlled and departure day were known. Arrival energetic condition most strongly influenced the duration of stay at stopover sites. However, arrival condition did not influence the decision to remain more than three days. Food may have been relatively abundant at these inland sites where high quality habitat was not limited (see Chapter II). Therefore, it may have been possible to replenish fuel stores within two days. Many migrants did stay longer than two days and early in the spring migrants remained for extended periods. I also did not find any indication of an influence of searching costs due to arrival habitat quality or movement behavior during stopover on stopover duration. Migratory songbirds must successfully rest and refuel at stopover sites along their routes but they may also need to adjust how long they stay at each site
during spring for optimal timing of arrival at breeding sites. An understanding of the multiple and interrelated factors influencing how long migrants stay at stopover sites remains poorly understood. Yet, quantifying how migratory songbirds respond to the landscapes through which they must pass is essential especially in the face of increasing temperature and phonological variability due to global warming.

Acknowledgments

Logistical support was provided by J. Johnson and D. Hudson at Fort Polk and L. Bennett Louisiana at Wildlife and Fisheries. I would especially like to thank the members of the migratory bird research group at USM and all of the hard working assistants who helped us collect data in the field: B. Bielfelt, M. Cline, K. Comolli, S. Everett, D. Haines, P. Heavin, P. Hosner, L. LaHaye, E. Lain, C. Nicholson, D. Ripper, C. Roy, A. Scarpignato, J. Smolinsky, L. Vormvold and B. Wilson. Funding for this project was provided by the Department of Defense Strategic Environmental Research and Development Program.
Literature Cited


Yong, W., and F. R. Moore. 1993. Relation between migratory activity and energetic condition among thrushes (Turdinae) following passage across the Gulf of Mexico.


CHAPTER IV

DOES CONSPECIFIC SONG PLAY A ROLE IN HABITAT SELECTION BY SONGBIRDS DURING MIGRATORY STOPOVER?

Abstract

Migrants are likely to use simple cues to quickly find suitable habitat for safe and rapid refueling at each stopover along their migratory route. Conspecific song is a cue likely to be common to the many landscapes encountered by migratory birds, especially during vernal passage when breeding conspecifics are setting up territories and, therefore, singing prolifically. I designed a field experiment to determine if migrating red-eyed vireos use conspecific song as a cue to assess the suitability of habitat en route. I simulated the initiation of stopover by translocating transient red-eyed vireos to predetermined locations in pine habitat, which is less preferred habitat and where the species was not detected singing, and hardwood habitat, which is preferred habitat and where red-eyed vireos sang prolifically. I released individuals in pine with and without pre-recorded conspecific song playback to test the expectation that migrants would (a) remain longer within pine with song if song is a positive cue for habitat selection and (b) spend less time near an arrival site paired with song if conspecific song is a negative cue on a within-habitat scale. The presence of conspecific song did not increase the amount of time migrants spent in pine habitat. However, migrants moved away from the release site more quickly when it was paired with conspecific song. Although the cues used during stopover habitat selection are poorly understood, my findings suggest migrants may not use conspecific song to assess habitat suitability during stopover, rather song may provide information about the increased likelihood of competitive interactions.

Introduction

How well a songbird migrant overcomes the challenge of arriving with little or no information about resources and sources of stress in the diverse landscapes
encountered during their migratory journey will affect not only their survival but also their subsequent reproductive success (Moore et al. 2005). Avoiding predation while locating habitat with sufficient food resources may be the most important factor determining success at each stopover site, yet the mechanisms of en route habitat selection are poorly understood (Moore and Aborn 2000, Chernetsov 2006). Habitat selection during migration is a hierarchical process with different cues becoming more or less important at each spatial scale (Hutto 1985, Moore et al. 1995, Buler et al. 2007). After landing at a stopover site, migrants may use more than one cue to select among and within available habitat types while minimizing time, energy expenditure and exposure to predators (Moore and Aborn 2000). Direct sampling of food resources is the most accurate measure of habitat suitability but time and energetic constraints may require migrants to rely on other, less direct cues such as vegetation structure or socially acquired information (Németh and Moore 2007, McGrath et al. 2009). The publically available landscape of sounds, or “soundscape,” provides information that is not costly to acquire and is increasingly recognized for its influence on the orientation and navigation of multiple taxa (Slabbekoorn and Bouton 2008).

Social information may be especially useful during stopover when migrants arrive with little or no prior information and are likely to encounter considerable environmental uncertainty at diverse stops along their route (Németh and Moore 2007). I expected conspecific song to be an important cue for habitat selection during spring migration because it is a simple cue likely to be common across the many landscapes encountered along the migratory route (Morton 1990). Indeed, migratory songbirds are known to respond to nocturnal calls, both conspecific and heterospecific, when ceasing migratory flights (Herrmans 1990, Schaub et al. 1999, Mukhin et al. 2008, Alessi et al. 2010). For example, two habitat specialist species were lured into atypical habitat during
nighttime landfall by the addition of conspecific song (Mukhin et al. 2008), suggesting that conspecific song provides habitat related information during migration.

Migrants may respond positively to the presence of conspecific individuals because better habitat may attract more individuals (Moore and Simons 1992), although migrants may also respond negatively to the presence of conspecific individuals because they may indicate depleted resources and an increased likelihood of competitive interactions (Lindström et al. 1990, Moore and Wang 1991). Results of previous work with migratory red-eyed vireos (*Vireo olivaceus*) suggested that conspecific song may be both a positive and a negative cue for habitat selection (see Chapter II). The red-eyed vireo is one of the most common long-distance Nearctic-Neotropical migratory songbirds in eastern deciduous forests (Cimprich et al. 2000). Consequently, transient migrants are likely to encounter conspecific song upon arrival at southern stopover sites, especially in spring when breeding red-eyed vireos are singing prolifically during territory establishment (Cimprich et al. 2000). Two primary habitat types at my study site, longleaf pine (*Pinus palustris*) savannas (pine) and bottomland hardwood (hardwood), differed in the presence of singing red-eyed vireos and the abundance of food (see Chapter II). Hardwood habitat was characterized by the greatest abundance of Lepidoptera larvae, the primary food source of red-eyed vireos (Cimprich et al. 2000), and by singing red-eyed vireos (see Chapter II). I experimentally released red-eyed vireos during spring migration at sites in pine where no red-eyed vireos could be heard singing and at sites in hardwood where up to four red-eyed vireos could frequently be heard singing. I found migrants released in hardwood remained in that habitat type while migrants released in pine left it to preferentially select hardwood. The same individuals released in pine initially remained close to their release location while individuals released in hardwood moved away from their release location more quickly (E. Cohen unpublished data). Given that migratory red-eyed vireos arrived with
no information about habitat suitability, yet consistently moved into hardwood habitat, which was/is characterized by greater food abundance and where there were abundant singing red-eyed vireos, I suspected that conspecific song was a readily available cue for locating hardwood habitat. However, I also found red-eyed vireos more quickly moving away from their release site in hardwood habitat, suggesting that song may also be a repellant cue on a smaller within-habitat scale.

Conspecific song is increasingly recognized for its role in avian breeding habitat selection (see Ahlering et al. 2010) but the role of conspecific song in habitat selection during migration has not yet been studied. Here I was interested in determining if migrating red-eyed vireos used conspecific song as a cue to assess the suitability of habitat upon arrival at a stopover site during migration. To examine this question, I took an experimental approach to simulate the initiation of stopover by translocating transient red-eyed vireos and releasing them at two predetermined locations; one in hardwood and one in pine. If song is a positive cue for habitat selection, I expected migrants to remain within pine longer when conspecific song was experimentally added to that habitat. Additionally, if conspecific song is a negative cue on a within-habitat scale then I expected migrants to spend less time near an arrival site in pine when song was added. Because migrants use multiple environmental cues when selecting habitat, I controlled for environmental variation by releasing migrants at the same locations varied only by the addition of conspecific song to the pine site.

Methods

I captured red-eyed vireos at a long-term banding station in coastal southwestern Louisiana (29° 45' N 93° 30' W, Moore 1999). The species does not breed at the capture site, ensuring that individuals captured there were transient (Cimprich et al. 2000). I transported migrants the afternoon or evening of capture approximately 143 km and held them overnight in individual cages for up to 22 hours with food and water ad
The evening of the capture day I fitted individuals with radio-transmitters weighing less than 3.5% of mean lean body mass (models LB-2 and LB-2N, Holohil Systems Ltd. Ontario, Canada). I used mass and wing chord to calculate an index of energetic condition for each individual (Owen and Moore 2006). Before first light the next morning I released migrants in the Vernon Unit of the Calcasieu Ranger District in Kisatchie National Forest (30° 57’ N 93° 08’ W). I chose the study site because it is a high density stopover site (S. A. Gauthreaux, Clemson University, unpublished data) and because forest cover types found there are characteristic of those throughout the Gulf Coastal Plain region (Keddy 2009). During the springs of 2008 and 2009, I released red-eyed vireos at one location each in pine and hardwood, approximately 1.65 km apart. Sites were chosen to be predominately surrounded by upland longleaf pine savanna and bottomland deciduous forest, respectively. I did not observe any obvious vegetation differences at the pine site between years and food abundance in pine did not differ between 2007 and 2008 (see Chapter II).

To determine the difference in available conspecific social information at the pine and hardwood sites, I used the results of transect surveys (from 2008; see Chapter II) and point counts. Three singing red-eyed vireos were consistently detected within 100 m of the hardwood release site and no red-eyed vireos were ever detected near the pine release site, singing or otherwise. During extended point counts (in April 2009), I recorded the distance and direction from the release point to each singing red-eyed vireo surrounding the hardwood release site. On a single day during the early spring of 2009 I used a Sennheiser ® ME-65 omnidirectional microphone, a Telinga® Pro parabola, and an Olympus ® WS-110 WMA digital voice recorder to record the three red-eyed vireos singing near the hardwood release site. I was reasonably certain that I recorded different individuals based on locations and counter-singing. I minimally edited the
recordings to reduce background noise and then chose the one minute with the least background noise and most song clarity for each of the three individuals.

During the spring of 2008, translocated individuals were released prior to first light (n= 6 pairs) and tracked continuously for the first five hours of the day with locations taken every 15 min. To minimize the impact of the observer, I located birds to within 50 m and then circled the locations to verify the accuracy. During the spring of 2009, I conducted releases at the same two sites using the same methods but conspecific song added to pine (n= 6 in each habitat). I placed three sets of iPods (Apple ®) with folding amplified speakers (RadioShack ®) surrounding the pine release site in the same distances and directions as the detected red-eyed vireos surrounding the hardwood release site (I refer to this artificially added song as “playback”). I situated each set of playback equipment as high in the vegetation as logistically possible to replicate the height of red-eyed vireos, which predominately use the hardwood canopy (Cimprich et al. 2000) and broadcast songs at full volume. Playback could be heard consistently by human observers standing up to 150 m from the source. Each playback setup looped a one minute recording of a single individual and played continuously as long as the tracked migrant remained within 300 m of the release site.

**Statistical analyses**

I quantified the amount of time migrants remained within their release habitat and within 200 m of their release site. I chose 200 m as a conservative response distance because it was the furthest distance that humans could consistently hear the song playback. I tested for mean differences in behavior between migrants released in pine without added playback and in pine with added playback. I also compared the difference between the behavior of migrants released in pine and hardwood when pine did and did not have added playback. I expected the difference in behavior between migrants released in pine and migrants released in hardwood to be less when conspecific song
was added to pine. Energetic condition is known to influence the behavior of red-eyed vireos during stopover (Sandberg and Moore 1996, Loria and Moore 1990, Chapter II) so I also tested for a correlation between arrival energetic condition index and each of the two response variables, time in release habitat and time near release site, using a Pearson's product moment correlation coefficient. I considered $P \leq 0.05$ statistically significant, used independent one-tailed $t$-tests because predictions were directional and report means ± SD.

Results

There was no difference in the amount of time transient red-eyed vireos remained in pine with and without added conspecific song (with song 2.23 ± 1.71 hr; without song 2.02 ±1.53 hr; $t_{14} = 1.33, P = 0.10$). The difference between the mean time to change habitat types for migrants released in hardwood and pine was the same (2.34 hr) regardless of whether conspecific song was present in pine (2009) or not (2008). I did find a difference in the amount of time migrants remained within 200 m of their release site in pine habitat when conspecific song was present (pine without playback 2.99 ± 1.68 hr; pine with playback 2.63 ± 1.95 hr; $t_{13} = 2.5, P = 0.01$, Fig. 4.1). Moreover, this difference in the amount of time migrants spent near their release site was less apparent between hardwood and pine habitat with conspecific song added (Fig. 1).

There was no correlation between energetic condition and time near the release site ($r = -0.03, P = 0.92$) but there was a positive correlation between energetic condition and time in release habitat ($r = 0.59, P = 0.04$). I did not observe the released migrants approaching or responding vocally to the playback.
**FIGURE 4.1.** Time (mean ± SD) near release sites (within 200 m) in pine and hardwood habitat with and without conspecific song added to pine (n=24, n=6 for each habitat and treatment). The hardwood site naturally contained conspecific song and was not altered.

**Discussion**

We know little about the proximate cues used by migrants to select habitat upon arrival at stopover sites despite the fact that those decisions are likely to have consequences in terms of survival, timing and energetic condition (Newton 2006), given the time and energetic requirements of migration (Alerstam and Lindström 1990). Resident or breeding conspecifics may have had more time to locate the most suitable areas in landscapes or habitat patches and therefore may provide inadvertent information about resources and sources of stress. I took an experimental approach in a field setting to ask for the first time if conspecific song is used by migrating songbirds as a source of information about habitat suitability during spring stopover. I found
conspecific song did not serve as a cue for the quality of a habitat type but it did influence within-habitat selection.

At one scale conspecific song may have attractant qualities (i.e., a cue to high quality habitat) as is true for many songbird species upon arrival at breeding sites (Ward and Schlossberg 2004, Fletcher 2007, Ahlering et al. 2010, Nocera and Betts 2010, Ward et al. 2010, but see Cornell and Donovan 2010). However, I did not find support for the use of conspecific song as a cue to locate high quality habitat in the context of migration. Migrants likely make movement decisions at multiple scales (e.g., region, landscape, patch; Buler et al. 2007) and different cues may be important at each scale (Moore and Aborn 2000). Therefore, at the landscape scale previous experience in pine habitat or innate preferences for hardwood habitat, as defined by aspects of vegetation (Berthold 1990), may have superseded the false cue of conspecific song in pine habitat. Alternatively, many of the migrants released in pine eventually moved into small hardwood patches characterized by seasonal creeks and similar plant compositions to bottomland hardwood habitat but were smaller in area and surrounded by upland longleaf pine habitat. There were few breeding red-eyed vireos detected in these patches, which suggests that these habitat types may provide resources valuable for the short-term needs of stopover but not sufficient for a breeding red-eyed vireo. In which case, heterospecific song may be a more important cue for locating habitat during stopover (Mönkkönen et al. 1990, Mönkkönen and Forsman 2002).

Within habitat, conspecific song may be a repellant cue in that a high density of breeding birds may also represent more competition for the same food resources (Moore and Wang 1991). I found that migrants spent less time near their release site when conspecific song was present. I also observed aggressive interactions on several occasions between migratory individuals that I was tracking and presumed residents -- unbanded singing red-eyed vireos in hardwood habitat. One transient individual had a
total of three interactions with resident breeders during stopover in different locations in hardwood habitat. The aggressive interactions I observed resembled territorial disputes including chasing, supplanting, grappling and pecking (Cimprich et al. 2000). In all cases when I observed an interaction, the migrant being tracked subsequently moved away from the area of the aggressive interaction. My experimental results coupled with these observations suggest that conspecific song may be used as a deterrent at the patch level (i.e. information about the likelihood of an aggressive encounter). Given the high energetic requirements of migration (Blem 1990), a migrant is motivated to improve its energetic condition and to avoid energetically expensive, and potentially injurious aggressive encounters. In contrast, breeding residents are more likely to be better informed about local resources and sources of stress, in better condition, and more invested in establishing or maintaining a territory than a transient individual (Tobias 1997). Further, by virtue of residency breeding birds may have priority access to resources and be more likely to win an aggressive encounter with a migrant, which is consistent with my behavioral observations. Clearly, more work is needed on how residents impact the behavior of transients, including their fuel deposition rates during stopover.

Habitat selection during stopover is also known to be condition-dependent (Moore and Aborn 2000, Chernetsov 2006). Migrants in poorer energetic condition may be more likely to take advantage of social information because it is public and, therefore, less costly to acquire (Németh and Moore 2007). For example, hooded warblers (Wilsonia citrina) were more likely to join flocks when they were in poorer energetic condition (Nemeth and Moore 2007). I did not find a relationship between arrival energetic condition and amount of time migrants remained close to their release location in pine habitat with or without added conspecific song. Migrants in better condition did
remain longer in their release habitat type, but this behavior was not influenced by the addition of conspecific song.

In conclusion, migrating birds are under pressure to locate suitable habitat quickly and to do so with little, or no, information about the distribution of resources in diverse landscapes along a migrant’s route (Hutto 1985, Moore and Aborn 2000). Under those conditions, publically available information such as conspecific song may be valuable because it is a low-cost and readily available source of information about the distribution of resources (Nocera et al. 2008, Nocera and Ratcliffe 2010). I attempted to “upgrade” the perceived quality of a poor quality habitat by adding conspecific song and found no evidence that migrating red-eyed vireos use conspecific song as a cue for selecting among habitat types; I did find that conspecific song may be a cue to avoid potentially costly aggressive interactions with territorial conspecifics. My work also highlights how little is known about how transient migrants interact with the conspecific residents they encounter en route.

Acknowledgments

Funding for this project was provided by Department of Defense Strategic Environmental Research and Development Program and The University of Southern Mississippi. Logistical support was provided by Jim Johnson and Danny Hudson (U.S. Army Fort Polk) and Lynn Bennett (Louisiana Wildlife and Fisheries). I thank Sarah Mabey at Hiram College for loaning us the recording equipment. I would especially like to thank Clay Graham and the members of the migratory bird research group at the University of Southern Mississippi for their help in the field.


Herremans, M., 1990. Can night migrants use interspecific song recognition to assess habitat?
Le Gerfaut 80:141–148.


CHAPTER V

APPLICATION OF A SPATIALLY EXPLICIT INDIVIDUAL-BASED MODEL TO CONSERVATION OF MIGRATING SONGBIRDS

Abstract

Whereas the importance of migration in the annual cycle of migratory birds is widely recognized, we have had difficulty quantifying how migratory songbirds respond to the landscapes through which they must pass. For example, long-distance migrants stopover in diverse landscapes during their migratory journey and must quickly and safely replenish up to half of their weight as fuel with little or no information about resources and sources of stress yet little is known about how resources at stopover sites affect fuel deposition rates (FDR). My objectives were to understand the effects on nocturnally migrating songbirds of moving through and refueling in Gulf South landscapes during spring migration. Successful refueling during migration is influenced by a variety of factors, and spatially explicit individual-based models are a tool uniquely suited to incorporating individual variability into behavioral responses to a changing environment. I conducted field experiments to assess the effects and relative influence of endogenous and exogenous factors on songbird movement during spring stopover and used the results of these experiments to parameterize a spatially explicit individual-based model of forest songbird movement and refueling. I present this model as a tool to evaluate the impact(s) of landscape context on the refueling ability of migratory songbirds during stopover. I first apply the model to test the expectation that FDR would decrease in landscapes with less hardwood habitat and less habitat contagion, or spatial aggregation of habitat. I used a factorial design with three levels of two factors, the proportion and the contagion of hardwood habitat. I found FDR decreased as the amount of hardwood in the landscape decreased from 42 to 22 to 12 %. Counter to my expectation, FDR was higher in the landscapes with low contagion as compared to the
landscapes with high contagion. Quickly locating habitat with sufficient food resources may be the most important factor determining a successful migration and migrants that arrived in higher quality habitat types gained more mass. Therefore, differences in FDR may be most influenced by whether or not an individual experiences an initial searching cost after landing in poor quality habitat. The model presented here is a tool for identifying features of landscapes that influence their fitness value for migratory songbirds, and conserving landscapes with increased hardwood forest cover may be especially important.

Introduction

Over half of all birds breeding in the forests of eastern North America migrate from more tropical wintering areas in the Caribbean, Mexico, and Central and South America (Rappole 1995). While it is presumed that the costs of migration are balanced by the benefits of exploiting seasonally abundant resources (Greenberg 1980), our inability to track the fates of individuals across the spatial and temporal extent of migratory routes has lead to a lack of empirical data on the demographic effects of the migratory period. Many long-distance intercontinental landbird migrant species are currently declining (Robbins et al. 1989, Askins et al. 1990, Marchant 1992, Berthold et al. 1998, Sokolov et al. 2001, Sauer et al. 2007) and migratory species appear to be declining faster than resident breeding species (Robbins et al. 1989, Askins et al. 1990, Sanderson et al. 2006) suggesting events outside of the breeding period may be limiting populations (Sillett and Holmes 2002, Newton 2006). However, the questions of when, where and how long-distance migratory passerine populations are regulated continue to focus primarily on events associated with the breeding and wintering phases of the migrant's annual cycle (e.g., Terborgh 1989, Sherry and Holmes 1995, Newton 2004). Still, billions of landbirds engage in annual migrations of hundreds to thousands of kilometers and along that journey they must adjust to unfamiliar habitats, find enough
food, resolve often conflicting demands between predator avoidance and meeting energetic requirements, correct for orientation mistakes, and cope with adverse weather. Meanwhile, they may encounter wind turbines, tall structures, light pollution, non-native predators, and increasingly smaller patches of habitat. Therefore, rapid changes in landscape configuration, resource availability, air space, and climate due to unprecedented human activity may be inflating the risks associated with migration (Wilcove and Wikelski 2008), making it critical to incorporate the migratory period into studies of where, when and how migratory songbird populations are limited (Moore et al. 1995).

Migration is energetically costly (Blem 1980). Consequently, successful migration typically requires frequent stopover periods for refueling between flights, the duration of which cumulatively far exceed time spent in flight and largely determine the duration of the migratory period (Hedenström and Alerstam 1997, Alerstam 2003). Therefore, how well a migrant solves the problem of finding suitable habitat while avoiding predation in each stopover landscape will determine not only if she survives but also her subsequent reproductive success (Sandberg and Moore 1996, Smith and Moore 2003). Nevertheless, there is surprisingly little information about the influence of environmental factors on fuel deposition rates (FDR), recognized as the currency of migration, during stopover (Jenni and Schaub 2003, Schaub et al. 2008).

Incorporating the migratory period into comprehensive conservation strategies requires identifying and protecting important stopover sites (Mehlman et al 2005). However, prioritizing stopover sites for protection necessitates an understanding of their value to migrating songbirds. It is essential to establish how factors including landscape context translate into the refueling value of stopping over at a site. Forested areas across the eastern US are declining largely due to urban growth, timber harvesting and other development, particularly in coastal areas (Drummond and Loveland 2010). Here I
examine how the abundance and configuration of suitable habitat in a landscape affect FDR of nocturnal migrants during stopover. The consequences of landscape composition and configuration have been well studied for breeding birds (e.g., Andrén 1994, Smith et al. 2011) but the effects of landscape context on songbirds during stopover remains poorly understood (Ktitorov et al. 2008).

Selection of a stopover site may be the greatest determinant of refueling rates (Schaub and Jenni 2001, Dunn 2002) suggesting that characteristics of sites, exclusive of their geography (Schaub and Jenni 2001), strongly influence FDR. The amount of hardwood forest cover positively influenced the distribution of spring migrants in Gulf South landscapes (Buler et al. 2007) and FDR for two songbird species in Europe were higher at sites with more forest cover (Ktitorov et al. 2008). Moreover, when suitable habitat is less fragmented, migrants may increase FDR by reducing the energetic or time costs associated with an initial searching period prior to foraging (Alerstam and Lindstrom 1990, Alerstam and Hedenstrom 1998) and spending more time foraging successfully with less movement (see Graber and Graber 1983). I tested the expectations that FDR would be positively related to the amount of hardwood forest cover and the level of habitat contagion, a measure of spatial aggregation, in a landscape. Further, because safely finding suitable habitat in a timely manner is essential for a successful stopover, I expected FDR to be greater for migrants landing in hardwood habitat. I applied the constructed model to test these predictions about the influence of landscape context on FDR in a factorial experiment.

My goal was to quantify the impacts of landscape pattern on migrating songbirds during stopover in Gulf South landscapes. Successful refueling during migration is influenced by a variety of factors and spatially explicit individual-based models are a tool uniquely suited to incorporating individual variability into behavioral responses to a changing environment (McLane et al. 2011). Previous work (Simons et al. 2000,
Pearson and Simons 2002) demonstrated the predictive ability of models for this period when migrants are thought to be most at risk but no subsequent attempt has been made to build empirically derived individual-based models of stopover. To achieve my objective, I constructed a spatially explicit individual-based model of migratory songbirds moving through and refueling in heterogeneous landscapes. The specific objectives of this research were to build an empirically derived model about stopover ecology, calibrate and validate the model using field data, and use the model assess the impacts of change landscape pattern on migrant birds.

Methods

An individual-based model for stopover migrant behavior was developed to simulate the movement of virtual migrant birds on a raster map of forest habitats found in the Gulf South region of the U.S. As birds move, they gain and lose energy, measured as body mass, according to the foraging opportunities presented by different habitat types. The research reported herein uses field data on radio-tagged birds to adjust the rates of body mass gain (FDR) and to modify the movement rules. The objective was to produce a more realistic and accurate model of stopover ecology for a common and representative migrant bird species then to use this model to assess the impacts of landscape pattern of habitats on migrant birds.

Derivation of model parameters from field data

I parameterized the model based on the results of field experiments conducted in Kisatchie National Forest, LA (30° 57' N 93° 08' W) during the springs of 2007 and 2008 (Chapter II). This site was chosen because a high density of spring migrants stopover there (Fischer et al. 2011) and it contains forest types characteristic of those found throughout the Gulf South region including longleaf pine savannas and bottomland hardwood forests (Evans 1994, Keddy 2009). I present the principal data collection...
methodologies and results here because they were used to parameterize the model and
in the next section (model construction) I discuss how I applied them in the model.

I chose the red-eyed vireo (*Vireo olivaceus*) as a model species representative of
canopy foraging songbirds of eastern North America (Cimprich et al. 2000). The red-
eyed vireo is a long distance migrant wintering in South America and is one of the most
common species breeding extensively in deciduous forests across Canada and eastern
North America. I captured known migratory individuals, recently arrived across the Gulf
of Mexico (captured at Johnson’s Bayou, LA, 29° 45’ N 93° 30’ W). On the day of
capture I attached a radio-transmitter weighing less than 3 % of mean body mass to
each bird (model BD-2A, Holohil, Ontario, Canada). The following morning, red-eyed
vireos were released in one of six predetermined locations surrounded predominately by
one of three habitat types: upland longleaf pine (*Pinus palustris*) savanna (pine),
bottomland hardwood forest (hardwood), and an intermediate between the two (mixed)
in two landscapes. I continuously followed the movements of migrants from release until
they left to continue migration. I simultaneously characterized the environment through
which migrants were moving by measuring the distribution of food, avian predators and
other migrants. I found predictable responses to endogenous and exogenous factors
during stopover (see Chapter II for more detail).

Movement during stopover varied with time since arrival at the stopover site and
was most strongly influenced by energetic condition and habitat. Red-eyed vireos
moved the furthest and fastest upon arrival at a stopover site during which time they
selected hardwood and mixed habitat, characterized by greater food availability. Once
in habitat characterized by more abundant food they also captured more food items
when observed foraging. Moreover, migrants arriving in habitat characterized by less
abundant food initially moved further and faster presumably while they were searching
for food/ better habitat. Finally, red-eyed vireos without fuel reserves, under pressure to
replenish fuel stores necessary to continue migration in a timely fashion, moved faster and further throughout stopover than migrants with fuel reserves.

**Model structure**

The model simulates the movement and energy status of songbirds during stopover. Each simulation follows one individual and predicts habitat associations, movement patterns and FDR. Movement rules depend on energetic status for a set of migrant characteristics in a heterogeneous landscape. Each daylight hour (12-hour days) for the duration of stopover the model migrant makes step-wise movement decisions through a heterogeneous landscape composed of 28.5 m square cells representative of habitat types of variable quality (Figure 5.1).

![Figure 5.1. Graphical depiction of an individual-based model of a landscape where each shade of cell represents a habitat type and the arrow represents a model animal making stepwise movements.](image)

The model structure reflects the behavior observed during field experiments. During each hour, the migrant moves a specified number of map cells. The number of
cells crossed is specific for the hour of the day and day of stopover as well as the bird’s condition and habitat type occupied at the end of the previous hour (see Chapter II). Energetic condition is updated based on the number of cells crossed and the habitat type of the last cell (see below for calculation of energetic gain). Migrants preferentially selected habitat with greater food abundance but did not bias their movements in a seasonally appropriate direction (Chapter II). Therefore, directionality of model migrants are determined by habitat (hardwood > mixed > pine > unforested) in the 24 surrounding cells. I used the 24 surrounding cells for three reasons. First, model migrant movement did not reflect observed migrant movement when I used the adjacent eight surrounding cells. Second, I considered the distance across two 28.5 m cells to be a distance across which migrants could reasonably assess resources whereas the distance across three cells was likely beyond a biologically reasonable range of perception. Finally, model migrant movement reflected observed movement when the 24 surrounding cells were used. When adjacent cells are of equal quality, the migrant preferentially selects those not previously visited and otherwise selects randomly among adjacent cells of equal or greater habitat quality. Migrants cannot revisit cells except when all surrounding cells having been visited. In this situation, migrants can pass through an adjacent cell that was previously visited if there is a cell across it that has not been previously visited.

Energetic costs are reflected in the proportion of each hour not spent foraging because the energetic cost of flying the relatively short distances moved during stopover is likely to be minimal (see Lindström 1991). The time not spent foraging is determined by the number of cells crossed which were calculated from the mean time it took observed migrants moving linearly, and not observed foraging, to move 28.5 m. I assume that foraging occurred in the last cell of the movement at each time-step and the energetic gain is based on the habitat type of that cell (see below for determination of habitat-specific rates). Therefore, prior to each movement the energetic condition index
of each migrant is updated by adding mass change from the time spent foraging in the last cell of the movement as follows:

Foraging time = one hour - (number of cells crossed * time to cross a cell)

Energetic condition = current condition + (foraging time * habitat specific mass change rate of the last cell of time step)

I summarize the attributes of the model “migrant” and the landscape which must be specified for each simulation and the parameters generated from each simulation. The model migrant is initialized with a body mass in grams, a start location, and a set of movement values that vary with the hours of the day and day of stopover. The landscape is initialized with a set of gain values for the habitat types in the map. The start location can be selected at random by the modeling environment or specified as an cartesian coordinate in the map. Random start locations are selected from forested (hardwood, pine or mixed) cells migrants are not known to land in unforested habitat types (see Chernetsov 2006). The movement values are specified as a set of integers listing the number of map cells to move between hourly time steps. Movement distance is a function of habitat and body mass and depends on the day and hour of stopover (see Chapter II).

The gain values are a vector of values corresponding to the habitat types in the landscape (hardwood, mixed, pine, unforested). Maximum FDR are determined by food availability, capture rates and digestive rates (Lindstrom 1991). My experimental work found food availability was related to habitat type in Kisatchie National Forest. I used the observed difference in foraging success between habitat types (number of successful attacks per time spent foraging, see Chapter II) to determine the relative foraging benefit of time spent in a pine, mixed or hardwood cell. The gain value of unforested habitat was assumed to be zero. Frank Moore’s lab at The University of Southern Mississippi has been banding spring migrants near Johnson’s Bayou for over 15 years. This site is
adjacent to an ecological barrier and mean mass change rates may be quite different there. Therefore, I did not use mean mass change values (likely specific to habitat) but I did I use red-eyed vireo recapture records (n=115) to determine the range of reasonable mass change values (see Loria and Moore 1990). I confirmed that the departure masses resulting from the assigned habitat-specific gain values fell within the range observed from the recapture data. While mass change rates at the banding station may not be representative of mean rates at Kisatchie National Forest, I assume the range of variability to be reflective of those experienced by the species in general during spring stopover.

The model generates a movement path for each simulation with cartesian locations for each movement step and body mass in grams at end of each time step. The number and location of cells visited during each step of the simulation are used to calculate the movement rate and linear displacement. FDR is calculated as mass change, the mass at the end of each time period, or at the end of stopover, minus the arrival mass. A status for the simulation is also recorded (normal operation or abnormal run) so that the simulation can be discarded in the rare case of an error (migrant moved off the map or was boxed into a corner).

**Model development**

Following the initial construction, completion of the model required calibration, verification and validation. During calibration, I iteratively compared the model generated patterns to those observed from the radio-tracking data and reparameterized the movement values until I minimized the difference (Figure 5.2). The patterns of habitat selection were reflected in the model output and did not need to be adjusted. I compared the model generated displacement distances (linear distance between the first and last point of each hour, n = 500) simulations to the radio-tracking data (n=50 migrants). I adjusted the movement values, which define the number of cells to cross
(not the linear distance) until the difference in linear displacement was minimized. I followed the same iterative process to adjust the habitat-specific gain values.

Figure 5.2. Flow chart depicting the derivation of hourly movement distances from observations of migrant movement behavior.

Once the difference between the model and observed migrant behavior had been minimized, I verified the model using a smaller sample of migrants tracked using the same methods in Kistachie National Forest during the spring of 2009 (n=6). These migrants were not included in the data used for model parameterization and calibration.
I simulated migratory movements (n = 60) from the same location where migrants were released. I tested for differences in and that the linear displacement of the migrants tracked and the model generated hourly displacement.

Finally, to be able to apply the model across the Gulf South region, I needed to determine the generality of the behaviors observed in Kisatchie National Forest. To accomplish this objective/goal, I quantitatively compared actual migrant behavior to simulated migrant behavior at a second site in another state. During the spring of 2011, I conducted subsequent translocation experiments and tracking in the Leaf River Wildlife Management Area (LRWMA) of De Soto National Forest, MS (30° 55' N 89° 02' W; Figure 5.3). De Soto National Forest was selected because the latitude is very similar to Kisatchie National Forest and because it contains the hardwood, mixed and pine habitat characteristic of the region. I released migratory red-eyed vireos in a range of energetic conditions (-3.0 to 3.5 condition index) into two replicates of pine (n = 5) and hardwood (n = 5) habitat (Figure 5.4). Translocation experiments followed the methods used at Kisatchie National Forest (see above, Derivation of model parameters from field data); migrants were transported from Johnson’s Bayou, fitted with radio-transmitters, held overnight, released before first light and followed continuously for ten hours on one day.

I tested for differences between the behavior of migrants stopping over in LRWMA and model generated movement patterns of simulated migrants “released” at the same locations. I tested for similarity in (a) hourly linear displacement patterns, (b) the influence of release habitat, (c) the influence of release condition, and (d) habitat selection.
Figure 5.3. Map of translocation (arrows) from point of capture on the coast at Johnson’s Bayou, LA (29° 45’ N 93° 30’ W) to Kisatchie National Forest, LA (30° 57’ N 93° 08’ W) for experiments to parameterize the model and to the Leaf River Wildlife Management area in De Soto National Forest, MS (30° 55’ N 89° 02’ W) to validate the model.

Landscape pattern and stopover performance

I used a factorial experiment to test for effects of the amount of hardwood forest cover and contagion on migrant FDR. I further tested for effects of arrival habitat type and arrival energetic condition on FDR. I altered one raster (gridded) map, a portion of LRWMA, using focal statistics tools in ArcMap (v. 9.3, © ESRI, Redlands, CA) to create nine maps; three levels of hardwood abundance (41 %, 22 %, and 12 %) and three levels of spatial aggregation (high, medium and low) (Figure 5.5). The LRWMA landscape contained only the three habitat types: pine (30 %), mixed (31 %) and hardwood habitat (40 %) and was naturally low in contagion. When altering this
Figure 5.4. Map of release locations (stars) in hardwood and pine habitat in the Leaf River Wildlife Management Area (grey outline) in De Soto National Forest, MS for model validation of movement behaviors during the spring of 2011.

I held the amount of mixed habitat constant (31%) and increased the amount of pine habitat while decreasing hardwood habitat.

I simulated 60 migrants landing in each of the nine landscapes and stopping over for one 12 hr day. The simulated birds arrived in each landscape at random locations with the range of masses observed for the species (12 to 23 g). I calculated FDR by subtracting each individual’s arrival mass from the end of day mass. I used ANOVA and post-hoc Tukey’s HSD to test for differences in mass change for each variable (level of contagion, amount of hardwood, arrival habitat type and arrival condition) and an interaction between contagion and amount of hardwood.
Figure 5.5. Design of the factorial experiment using nine maps with low, medium and high contagion (level of spatial aggregation of habitat; left to right column) and high (41%), medium (22%) and low (12%) amount of hardwood forest cover (top to bottom row). The map in the top left corner (low contagion, high hardwood forest cover) is a portion of the Leaf River Wildlife Management area in De Soto National Forest.

Results

Model development

I verified that the linear displacement distances of six migrants released in hardwood habitat did not differ from the linear displacement of simulations from the same release location ($F = 0.005, df = 1, P = 0.94$). The validation showed a high level of agreement between the simulated behavior and the behavior of the birds that I released and tracked (see example in Figure 5.6). The hourly movement pattern of actual migrants was similar to the hourly movement pattern of simulated migrants. In fact, there was no difference in hourly linear displacement (all $P > 0.05$) except during
the first 2 hrs when the tracked migrants moved further than simulated (P = 0.02). The release habitat type influenced initial linear displacement distances in similar ways; migrants released in pine moved further than those released in hardwood during the first hour (P < 0.01) but not during second hour (P = 0.38). Arrival energetic condition influenced linear displacement in similar ways; migrants in poorer energetic condition moved further from their release sites than migrants in better condition (P=0.01). Finally, migrants showed the same patterns of habitat selection; by the end of the day all migrants tracked in LRWMA had moved into either mixed or hardwood habitat but predominately into hardwood.

Figure 5.6. Example of four model simulated movements (black lines, each ending in an arrow) and bird tracking points (circles) from the same release location (star) which were compared during the model validation process.
**Landscape pattern and stopover performance**

FDR (mass change/day) increased with the amount of hardwood forest cover (F= 30.03, df= 2, P< 0.01; all comparisons P < 0.05; Figure 5.7a) but decreased as habitat became more aggregated (F= 13.65, df= 2, P< 0.01, Figure 5.7b). FDR was higher in the landscape with low contagion, or little spatial aggregation of habitat, than in the landscape with high contagion, high spatial aggregation of habitat (P< 0.01) but was not different between landscapes with medium versus low or high contagion (P > 0.10). There was no interaction between the amount of hardwood and level of contagion (F= 0.73, df= 4, P= 0.57). FDR was also influenced by the arrival habitat type (F= 54.26, df= 2, P< 0.01). Migrants arriving in pine habitat had lower FDR during the first day of stopover than those arriving in mixed or hardwood (all comparisons P< 0.01; Figure 5.7c). Finally, leaner migrants gained more mass on the first day of stopover than fatter migrants (F= 4.35, df= 1, P< 0.05).

**Discussion**

Despite its central importance to our understanding of migration, there is surprisingly little information about the influence of environmental factors on fuel deposition rates during stopover (Jenni and Schaub 2003, Schaub et al. 2008). I found the amount of hardwood forest at a stopover site positively influenced refueling rate. Buler et al. (2007) found the strongest predictor of migrant density in southern Mississippi and Louisiana was the abundance of hardwood habitat in a landscape which was positively correlated with arthropod abundance. Ktitorov et al. (2008) found fuel deposition rates of two songbird species (Willow Warbler, *Phylloscopus trochilus* and Eurasian Redstart, *Phoenicurus phoenicurus*) captured at netting stations across Europe were highest at sites with more forest cover. My work supports the suggestion that migrants may use hardwood as a cue to select high quality landscapes (Buler et al.
2007) because I found fuel deposition rates to be higher in landscapes with more hardwood cover.

Fragmentation of habitat may only affect birds and mammals when the amount of suitable habitat covers < 30% of the landscape (Andrén 1994). I reduced the amount of high quality habitat from approximately 40 to 20 and 10% and, counter to my expectations, I found increasing fragmentation was beneficial for refueling migrants. Actually, an intermediate amount of fragmentation did not impact FDR but migrants had higher FDR in the landscape with low, versus high, contagion. Quickly locating habitat with sufficient food resources may be the most important factor determining a successful migration and migrants that arrived in higher quality habitat types gained more mass. Therefore, differences in FDR may be most influenced by whether or not an individual experiences an initial searching cost. Migrants arriving at random in a landscape where hardwood habitat is less spatially aggregated are more likely to find hardwood habitat and quickly benefit from increased foraging success in that habitat type (Simons et al. 2000). Evidence of searching costs, in the form of an observed mass loss after initial capture, from banding data is mixed (reviewed in Schwilch & Jenni 2001). I found no evidence for an acclimation period prior to foraging; migrants began foraging almost immediately upon release in habitat with abundant food (see Chapter II). Delingat et al. (2006) also observed foraging from one minute to half an hour after moving and releasing Northern wheatears (*Oenanthe oenanthe*), presumably into habitat with abundant food. There are expected to be energetic costs associated with an increased searching period prior to foraging upon arrival at stopover sites. If necessary at each stop along a migrants’ journey, these initial periods would affect the refueling rate or duration of stay at each stopover (Alerstam and Lindstrom 1990, Alerstam and Hedenstrom 1998) and would cumulatively result in a significant energetic or time cost to migration (Lindstrom 1991).
Figure 5.7. Boxplots of fuel deposition rate (mass change/day in g) after stopping over for one day in landscapes with (a) a low, medium or high proportion of hardwood habitat, (b) three levels of the degree of spatial aggregation of habitat: low, medium or high, (c) after landing in hardwood, mixed or pine habitat and stopping over for one day (n = 180 simulations/ factor). Circles represent outliers (less than 3/2 times of lower quartile), box is bound by 25 and 95% quartiles with median values in center. Whiskers represent maximum and minimum values (excluding outliers).
Migrants arriving in poorer condition are the most likely to be negatively impacted by reduced habitat availability at stopover sites because of their increased energetic demands and reduced margin of safety. I found migrants that arrived in poorer energetic condition gained more mass during stopover than migrants that arrived with greater fuel reserves. A migrant’s behavior during stopover is expected to be strongly influenced by its energetic condition because they are often under pressure to replenish up to 50% of their mass as fuel reserves during stopover (Blem 1980). For example, leaner migrants move further and faster during stopover (Moore and Aborn 2000, Chernetsov 2006, Matthews and Rodewald 2010) likely because they are under more pressure to quickly replenish depleted fuel stores. Further, the conditions of long-distance spring migrants arriving at stopover sites are likely to be influenced by the environment they experienced in their over-wintering areas in the Neotropics (Wolfe and Ralph 2009, K. Paxton unpublished data) many of which are rapidly being converted to landscapes dominated by agricultural land uses (Houghton 1994, Foley et al. 2005) thereby increasing the likelihood that migrants will arrive in increasingly poorer condition.

Conservation Implications

The experimental and individual-based modeling approach adopted in this study provides much needed information about how migrants make decisions in unfamiliar landscapes during stopover as well as the fitness consequences of those decisions. This information is necessary to evaluate the contribution of the migratory period to long-term population change or to forecast how demography of migrants relates to changes in the composition and configuration of human actions. There is every reason to believe that events during migration influence fitness (Sandberg and Moore 1996, Sillet and Holmes 2002, Smith and Moore 2003), but we have difficulty quantifying impacts of the landscape through which migrants must pass. This model is a tool for assessing the effects of the factors influencing migratory refueling during stopover. For example, the
model can be used to derive the difference in FDR between (a) alternative landscapes, (b) in one landscape before and after the addition of suitable habitat (c) through time, or (d) as a consequence of habitat loss. Most intercontinental songbirds migrate at night and stop only briefly during the day to rest and refuel and for this reason much of migratory natural history remains poorly understood. Nevertheless, a clear understanding of the contribution of the migratory period for long-term population change is needed if we are to conserve these populations (Moore et al. 1990) in a rapidly changing world where many migratory species are currently in decline (Wilcove and Wikelski 2008).

Acknowledgments

Scott Pearson at Mars Hill College worked closely with me on this model. Logistical support was provided by Ledon Cooley of the Mississippi Department of Wildlife, Fisheries and Parks. I would like to thank the members of the migratory bird research group at The University of Southern Mississippi and the hard working assistants who helped us collect data in the field: Trang Nguyen, John Diener, Lizzie Goodrich, and Emily Zeller. Funding for this project was provided by the Gulf Coast Joint Venture and The University of Southern Mississippi.
Literature Cited


Cooper, R. J., P. J. Martinat, and R. C. Whitmore. 1990. Dietary similarity among insectivorous birds: influence of taxonomic versus ecological categorization of prey. Pages 104-109 in


APPENDIX

COPY OF APPROVED IACUC APPLICATION FORM

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE
NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER: 11092210
PROJECT TITLE: Migratory Connectivity and the En Route Migration Strategies of Migratory Birds
PROPOSED PROJECT DATES: 10/01/2011 to 09/30/2014
PROJECT TYPE: Renewal/Continuation of a Previously Approved Project
PRINCIPAL INVESTIGATOR(S): Frank R. Moore, Ph.D.
COLLEGE/DEPARTMENT: College of Science & Technology
DEPARTMENT: Biological Sciences
FUNDING AGENCY/SPONSOR: National Science Foundation, Moore Basic Research, National Geographic Society
IACUC COMMITTEE ACTION: Full Committee Review Approval
PROTOCOL EXPIRATION DATE: 09/30/2014

Jodie M. Jawor, Ph.D.
IACUC Chair