EXPLAINING MIGRATORY BEHAVIORS USING OPTIMAL MIGRATION THEORY

By

Jennifer D. McCabe

B.S. The University of Vermont, 2003

A DISSERTATION

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Ecology and Environmental Science)

The Graduate School

The University of Maine

December 2015

Advisory committee:

Brian J. Olsen, Associate Professor, School of Biology and Ecology, Advisor

Peter Koons, Professor, School of Earth and Climate Sciences

Glen Mittelhauser, Executive Director, Maine Natural History Observatory

Sean Birkel, Research Assistant Professor, Climate Change Institute

Shawn T. McKinney, Assistant Professor and Assistant Unit Leader, Maine Cooperative Fish and Wildlife Research Unit, Department of Wildlife, Fisheries, and Conservation Biology

DISSERTATION ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Jennifer D. McCabe I affirm that this manuscript is the final and accepted dissertation. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

Dr. Brian J. Olsen, Associate Professor Date

ACKNOWLEDGMENTS

Data was collected under USGS banding permit #s 23613 and 22055 and Maine state wildlife scientific collection permit #270. All research with direct handling of animals was covered by the University of Maine IACUC Permit A2013-08-01. I am grateful to The Nature Conservancy, College of the Atlantic, U.S. Fish and Wildlife Service's Maine Coastal Islands National Wildlife Refuge, and Acadia National Park for allowing access to their lands. Thank you to all people and organizations that allowed me to incorporate their data into my analyses; Biodiversity Research Institute, U.S. Fish and Wildlife Service's Maine Coastal Islands National Wildlife Refuge, Rebecca Holberton, Adrienne Leppold, and Kristen Covino. I would also like to thank all the funding sources contributed to the field data collection: the National Park Service's Northeast Temperate Network, Acadia National Park, the University of Maine, the Maine Agriculture and Forest Experimental Station, the U.S. Fish and Wildlife Service's Maine Coastal Islands National Wildlife Refuge. I want to especially thank Bruce Connery, Sara Williams, Adrienne Leppold, Keegan Tranquillo, and Jeff Roelke for all their help getting the fieldwork off the ground and keeping sane during the banding seasons.

Thank you to Peter Koons for making the second portion of this dissertation happen. I am forever grateful for your ability to tolerate a non-physicist, non-fluid dynamics, biologist bothering you with elementary questions! It was also a joy watching you get excited about birds and all the awesome things they do.

Thank you to David Hiebeler, Huijie Xue, and especially Bipush Osti for their hours and hours of coding help, without them the birds would never have flown. Thank

you to my committee, Sean Birkel, Peter Koons, Glen Mittlehauser, and Shawn McKinney for their input along the way. William Halteman deserves a massive thank you for the many hours we spent sitting in his office discussing my data and statistical analyses.

I'd like to thank all the members of the Olsen and McGill labs for listening and providing helpful suggestions on this work, particularly Jenny Shrum, Evan Adams, Allie Byrd, Mo Correll, Dave Grunzel, Adrienne Leppold, and Kate Ruskin.

Thank you to my family and Morgan Graham who provided support through countless care packages and encouraging phone calls. I cannot adequately thank Allie Byrd, Mo Correll, Dave Grunzel, and Kate Ruskin for being such awesome friends; I couldn't have done this without you! Wren and D. Rosco, thank you for the napping couch cuddles and forever making the office a more entertaining place to work.

Finally, I want to thank Brian Olsen for all his patients and understanding. Brian, I can't thank you enough for all the runs, whiteboard outlines, hours of editing, and extremely loud laughs. I couldn't have asked for a better advisor, teacher, and mentor. Thank you for everything.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIBRARY RIGHTS STATEMENT

In presenting this dissertation in partial fulfillment of the requirements for an advanced degree at the University of Maine, I agree that the Library shall make it freely available for inspection. I further agree that permission for “fair use” copying of this dissertation for scholarly purposes may be granted by the Librarian. It is understood that any copying or publication of this dissertation for financial gain shall not be allowed without my written permission

Signature:

Date:

EXPLAINING MIGRATORY BEHAVIORS USING OPTIMAL MIGRATION THEORY

By Jennifer D. McCabe

Dissertation Advisor: Dr. Brian J. Olsen

An Abstract of the Dissertation Presented
in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
'in Ecology and Environmental Science'
December 2015

Bird migration is the regular seasonal movements between breeding and nonbreeding grounds. In general, birds that breed in the Northern Hemisphere tend to migrate northward in the spring to take advantage of increasing insect populations and lower predation pressures and fly south when food availability and weather conditions decline. Embarking on a journey that can stretch a thousand miles round trip is a dangerous and arduous undertaking. While en route migrants must stop and feed to replenish their depleted energy reserves, often in unfamiliar locations with unknown predation pressures. They also must react to weather conditions during flight and while on the ground. Additionally, areas of high quality habitats where birds can refuel efficiently and safely may be few and far between. Therefore, it's not surprising that mortality rates can be higher during migration than at any other period of the year. Behavioral decisions such as when and where to stop, how long to stay, and when to leave all involve costs and benefits with an ultimate goal to balance the costs and benefits on order to achieve a successful and efficient migration. Optimal migration theory, aims

to explain how migrants balance behavioral and physiological parameters of migration that minimize total time spent on migration, total energy expended, or mortality risk. The eventual result of these optimization pressures is thought to be a gradient of behavioral strategies that optimize different combinations of the three currencies: time, energy, and risk. I investigated how migratory behaviors of North American songbirds in the autumn balance the three currencies. More specifically I 1) explored how stopover site selection varies across migratory strategies at the landscape (Chapter 2) and habitat-patch (Chapter 3) scale; 2) investigated the importance of wind for the evolution and maintenance of migratory routes (Chapter 4); and 3) explored how selection of wind conditions for migratory departure affects overall behavioral strategies (Chapter 5). With this research, I hope to further our predictive abilities of migratory behaviors under various environmental and geographic situations using an optimal migration framework.

CHAPTER 1: INTRODUCTION

1.1. Overview of migration

Migration differs from ordinary flight in both the greater length of the journey and in the greater altitude at which it usually occurs (Newton 2008). Further, while en route migrants must stop and feed to replenish their depleted energy reserves, often in unfamiliar locations with unknown predation pressures (Moore and Aborn 2000). They must also respond plastically to prevailing weather during flight and while on the ground. Moreover, areas of favorable habitat where birds can refuel efficiently and safely may be few and far between. It’s not surprising that mortality rates can be higher during migration than at any other period of the year (Sillett and Holmes 2002).

One of the main advantages of flight over other modes of migratory locomotion is speed (Newton 2008), which facilitates longer distance travel. Nevertheless, the lengths and types of migratory flights can be greatly modified by endogenous factors (e.g., genetics, body size, morphology, physiology) and exogenous factors (e.g., prevailing weather conditions, geography) (Moore et al. 2005). The above factors can constrain the decisions birds make during migration, thereby affecting migratory route, airspeed, the length of re-fueling breaks between bouts of migratory movements (i.e., stopover), and fuel load. All decisions involve costs and benefits, and the goal of migration ecology broadly is to predict the behaviors birds use to balance the costs and benefits to achieve a successful migration.

1.2. Optimal migration theory

The use of optimization approaches to bird migration was pioneered by Pennycuick (1969) and has since been a cornerstone for interpreting flight adaptations and strategies in migrating birds (Alerstam and Lindstrom 1990). In coining the term “Optimal Migration Theory”, Alerstam and Lindstrom (1990) aimed to establish relationships between the main behavioral and physiological parameters of migration (stopover duration, frequency, and flight energy consumption) that minimize the expenditure of total time spent on migration, total energy expended, or mortality risk (Chernetsov 2012).

Generally, birds that gain an advantage in arriving to their wintering or breeding grounds before competitors employ a time-minimizing strategy. These species are predicted to exhibit shorter stopover durations, faster refueling rates, and higher fuel loads upon departure (which allow for longer flights between stopovers). Birds migrating under the energy-minimization strategy, on the other hand, should exhibit behaviors that reduce the rate of energy expenditure (Chernetsov 2012; Hedenstrom and Alerstam 1997). Typical behaviors include longer stopover durations, slower refueling rates, and lower fuel loads (to increase flight efficiency). Minimization for overall mortality risk is discussed less in the literature probably because it is a difficult parameter to quantify (Chernetsov 2012). Much of the theoretical and empirical studies are centered on minimization of predation risk. However, as Alerstam and Lindstrom (1990) state, in a risk minimization strategy birds should reduce the total mortality risk during migration as low as possible.

For my dissertation, I investigated how migratory behaviors of North American songbirds in the autumn balance the three aforementioned currencies: time, energy, and risk. With this research, I hope to further our predictive abilities of migratory behaviors under various environmental and geographic situations using an optimal migration framework. More specifically I 1) explored how stopover site selection varies across migratory strategies at the landscape (Chapter 2) and habitat-patch (Chapter 3) scale; 2) investigated the importance of wind for the evolution and maintenance of migratory routes (Chapter 4); and 3) explored how selection of wind conditions for migratory departure affects overall behavioral strategies (Chapter 5).

1.3. Stopover site selection

A successful migration depends heavily on stopover habitat. Stopover habitat provides birds with a place to rest, refuel, and avoid predation, and stopover site selection thus has consequences for all three of the main migration currencies (time, energy, and risk, respectively). Factors influencing habitat selection, however, is most often scale dependent (Hutto 1985). At large regional scales, stopover habitat use is primarily governed by extrinsic factors, those factors unrelated to habitat, such as wind patterns and individual energetic status (Gauthreaux 1980, Kerlinger and Moore 1989). As spatial scales become smaller, intrinsic factors, such as food availability, habitat structure (Buler, Moore, and Woltmann 2007), and predator abundance (Moore and Aborn 2000) likely become increasingly important in decisions of habitat use (Hutto 1985).

Much of the total time spent on migration is spent on stopover (Dänhardt and Lindström 2001, Hedenstrom and Alerstam 1997). Therefore, stopover site selection likely plays a significant role in balancing the total costs of migration for all three migratory currencies. Many factors contribute to a migrants choice in where to stopover, including 1) the migratory strategies employed by the migratory community, 2) local geography, 3) landscape composition and configuration, 4) predation risk, and 5) interactions among these factors.

First, migratory strategies vary among species as a function of their energetic constraints (Moore et al. 1995). For example, long-distance migrants, generally considered time-minimizers, may have substantially different stopover habitat requirements than short-distance migrants (i.e., energy-minimizers) due to the constraints of longer flight distances and the associated cumulative energy requirements and risk along the migratory route.

Second, geography and landscape composition and configuration are widely used predictors of habitat use more broadly. For example, major landscape features (e.g., coastlines, water resources) are known to concentrate both migrating landbirds and raptors (Aborn 1994, Valeix et al. 2009), affecting stopover site selection. The success of these characteristics in predicting bird behavior, however, is tightly dependent on scale. At large spatial scales, the proportion of vegetated lands versus un-vegetated lands may be a significant driver of stopover site use. Conversely, at finer scales habitat type, such as hardwood forest cover (Buler et al. 2007), has been shown to be a significant predictor of stopover site use (Hutto 1985, Moore et al. 1995).

Additionally, predation risk can be a strong contributor to stopover habitat selection (Lindström 1990). Optimal foraging theory (after which optimal migration theory was modeled) predicts that birds choose feeding sites and habitats that allow them to meet their energetic requirements while minimizing predation risk (Chernetsov 2012). Individuals are predicted to avoid areas with high predation risk, even if these areas would maximize foraging efficiency. In times of high energetic demand, such as migration, added predation risk may be outweighed by the costs of decreased foraging efficiency in safer habitats. These added challenges during migration are likely to alter the optimal solution to the foraging versus predator-avoidance trade-off. Studies of landbirds (Moore 1994, Cimprich et al. 2005) and shorebirds (Metcalfe and Furness 1984) have demonstrated that individuals in migratory condition decrease predator avoidance behavior relative to individuals that are not migrating.

1.4. Evolution of migration divides

All else being equal, energy costs should favor birds taking the shortest, most direct route between breeding and wintering grounds, yet many birds take longer, circuitous routes (Newton 2008). An example of a circuitous migratory pattern can be found along the many migratory divides around the world. Migratory divides are where hybrid zones or areas of contact between sister species overlap across taxa (Helbig 1996, Bensch, Andersson, and Akesson 1999, Delmore, Fox, and Irwin 2012, Ruegg and Smith 2002, Rohwer and Irwin 2011, Møller et al. 2011) but have very different headings and migratory routes.

One such divide can be found in Central Europe. Along this divide populations migrate either southwest or southeast to circumvent the Mediterranean Sea to the west or east, respectively, on their way to their wintering grounds in Africa (Helbig 1991, Helbig 1992, Helbig 1996, Berthold and Helbig 1992, Berthold and Terrill 1988). Another is the

Siberian divide north of the Tibetan Plateau (Irwin and Irwin 2005) where the two pathways circumvent the inhospitable terrain of the Plateau. The Canadian Rockies in North America also possess a divide where eastern and western species breed adjacent to one another yet exhibit different migration routes (Ruegg 2008, Ruegg and Smith 2002, Delmore, Fox, and Irwin 2012, Kelly and Hutto 2005, Toews, Brelsford, and Irwin 2011, Rohwer and Irwin 2011).

Hypotheses concerning the formation of migratory divides and the evolution of circuitous migratory routes in general posit a range of potential causes, including post-glacial range expansions out of shared refugia (Remington, Charles 1968, Swenson and Howard 2005, Anderson 1948), proximity to geographic barriers (Remington, Charles 1968, Swenson and Howard 2005), and meteorological factors such as wind patterns (Richardson 1978, Alerstam 1979, Gauthreaux et al. 2005). The ultimate cause of each of the above-mentioned selection pressures, however, is likely the differential costs of migration in terms of time, energy, or risk (Helbig 1996).

1.5. Wind selectivity

Currents can be strong selective forces on the movements of migratory animals (Kemp et al. 2012, Richardson 1990, Chapman et al. 2010, Melià et al. 2013, Xue et al. 2008, Incze et al. 2010, Alerstam et al. 2011, Srygley and Dudley 2007). Wind is thought to be one of the most important factors affecting bird migration timing, orientation, energy expenditure, and flight speed (Alerstam and Lindstrom 1990, Erni et al. 2002; McLaren, Shamoun-Baranes, and Bouten 2012).

Winds flowing in the intended migratory direction can increase flight speed dramatically (Bruderer and Liechti 1998). Thus, birds can almost double flight speed and save half the energy required for its migratory journey if they can take advantage of wind assist (Liechti and Bruderer 1998). Selectivity of wind conditions should be behaviors that are under strong selection, although the precise form of this selection should be dependent upon which migratory behavioral strategy they employ. To minimize flight time and energy, a bird should migrate only in favorable winds. High selectivity, however, restricts departure opportunities and potentially increases the cumulative time spent on migration (Alerstam 2011, Bruderer, Underhill, and Liechti 1995, McLaren, Shamoun-Baranes, and Bouten 2012).

In the chapters that follow, I use a diversity of empirical and modeling approaches to investigate migratory behavior in an optimal migration framework. The over-arching goal of this work is to predict behavior under varying geographic, environmental, and taxonomic conditions. Specifically, I address the factors that influence stopover site selection at both regional (Chapter 2) and local (Chapter 3) scales, those that explain differences in migration route along a migratory divide (Chapter 4), and factors that explain variation in wind selectivity across varying taxa and migration strategies (Chapter 5).

CHAPTER 2: LANDSCAPE-SCALE HABITAT AVAILABILITY, AND NOT LOCAL GEOGRAPHY, PREDICTS MIGRATORY LANDBIRD STOPOVER ACROSS THE GULF OF MAINE

2.1. Summary

While it is clear that many migratory behaviors are shared across taxa, generalizable models that predict the distribution and abundance of migrating taxa at the landscape scale are rare. In migratory landbirds, ephemeral concentrations of refueling birds indicate that individual behaviors sometimes produce large epiphenomena in particular geographic locations. Identifying landscape factors that predict the distribution and abundance of birds during migratory stopover will both improve our understanding of the migratory process and assist in broad, regionally relevant conservation. In this study we used autumnal passerine stopover data from a five-year period and eleven stopover sites across coastal Maine, USA, to test four broad hypotheses of migrant distribution and abundance that have been supported in other regions: a) the community characteristics of the pool of potential migrants, b) a site's local geography, c) landscape composition and configuration measured at different spatial scales, and d) interactions between these factors. Our final model revealed that birds concentrate at "habitat islands", sites that possess a disproportionate percentage of the vegetated habitat in the 4-km surrounding landscape. The strength of this pattern, however, was inversely proportional to a species' remaining migratory distance. Our results corroborate several studies that emphasize the importance of land cover composition at finer spatial scales (<80 km^2) for predicting the stopover distribution and abundances of migratory birds. This suggests that different migrants likely assess stopover sites with similar mechanisms

along their migratory route, and these commonalities may be broadly applied to identify stopover locations of conservation importance across the continent.

2.2. Introduction

Stopover sites are extraordinarily important for birds making the costly journey from breeding grounds to nonbreeding grounds. The majority of total migration time for passerines is spent on stopover (Dänhardt and Lindström 2001, Hedenstrom and Alerstam 1997), although stopover habitat selection has only recently been explicitly modeled (Cohen et al. 2014). To predict the effects of future landscape alteration on migratory birds, we need to understand how individual choices made during migratory stopover produce population and community-level patterns of abundance. Here we present a community-scale comparison of stopover habitat use over five years across eleven monitoring stations spanning a 15,000 km^2 region of coastal Maine, USA. We use this broad-scale dataset to test the efficacy of a number of hypothesized drivers of stopover abundance that have been identified by previous studies along the major North American migratory flyways. These factors include a) the characteristics of the taxa that are available to use a site for stopover (hereafter the "migratory community"), b) local site position relative to major landforms (i.e. local geography), c) the landscape characteristics at multiple spatial scales, and d) interactions among these various factors (Table 2.1). Together, these taxa-, landscape-, and site-related factors likely combine to determine stopover site use each migratory season. Using a suite of previously unstudied stopover locations, we tested whether a set of these factors could predict the integrated seasonal use of a site by the entire landbird migratory community over the autumnal migratory season. Integrated seasonal use is an estimate of the total number of migrants that stop at a given site throughout an entire migratory season, and it is thus a proxy for a site's importance to a migratory bird taxon or regional community.

One potential determinant of the distribution of migrants during stopover at a locale is the variety of migratory strategies employed by the migratory community. Landbirds differ in their energetic constraints and consequently in their need for migratory stopover (Moore et al. 1995) as a function of the distance to their non-breeding locale (Table 2.1: Migratory Strategy Hypothesis 1, M1), foraging guild (Table 2.1: M2), and other unique characteristics of their phylogeny (taxonomic family) (Table 2.1: M3). Ultimately, however, these strategies affect whether an individual will use a specific stopover site, and the integrated use of a site by all migrants should be partially determined by the composite strategies of the entire migratory community. For example, species traveling over 5,000 km may have considerably different stopover habitat requirements than species spending the non-breeding season within 1,500 km of their breeding grounds (M1). Similarly, site use is influenced by energetic constraints, and migrants that are plastic in their dietary behavior (Parrish 2000) may exhibit different stopover choices than birds that are dietary specialists (M2). In New Jersey, broad stopover habitat use was similar by taxonomic family, with most families preferring similar successional stages and different families choosing different habitat types (M3) (Suthers et al. 2000).

Migrant use of a locale during stopover may also be determined by local geography, including a site's distance from a major coastline (Table 2.1: Geographical Hypothesis 1, G1), its position along a coastline (Table 2.1: G2), and whether or not the site is found on an island (Table 2.1: G3) of a given size (Table 2.1: G4). Coastlines, for one, are known to concentrate migrant landbirds unwilling to cross open water without suitable weather conditions (Gauthreaux 1971a). Even in favorable weather conditions, however, migrants use coastal habitats in large numbers (Kuenzi et al. 1991), especially during the fall in eastern North America, when the prevailing winds drive migrants toward the coast (Williams et al. 1977, Moore et al. 1995). This effect may be augmented in the fall because the migratory community is dominated by young of the year, which use the coast to visually orient during their first passage south (Ralph 1981). We might expect then, that distance from the coast would correlate inversely with stopover site use (G1). Further, the northeast–southwest orientation of Maine's coastline has the potential to concentrate large numbers of birds. As birds traveling from the northwestern US reach the coast at various points, but all continue southwest along the coastline (Drury and Keith 1962, Richardson 1978), we may detect more birds at sites within the southwestern extent of the region than within the more northeastern extent (G2). Islands may produce different patterns of stopover relative to continuous coastal shorelines as well (G3), as has been reported along two different stretches of North American shoreline (McCann et al. 1993). Similarly, island size may be correlated with bird abundance in migration (Suomala et al. 2010, Martin 1980) (G4), as it is in the breeding season (Freemark and Merriam 1986, Blake and Karr 1987, Suomala et al. 2010).

Landscape characteristics are a third broad category of factors that have been found to predict patterns of migrant stopover. Landscape characteristics can be broken into two, more specific groups; landscape composition and landscape configuration.

Landscape composition includes variables describing the relative amount of various land cover types such as the total percentage of vegetated lands (Table 2.1: Landscape Characteristic Hypothesis, L1), the total percentage of various broad land cover types found within the landscape (Table 2.1: L2), and the proportional habitat availability (the proportion of any type of land cover versus all other cover types: L3 & L4). To our knowledge, habitat availability has not been tested directly as a driver of migrant stopover behavior, but it is a keystone of habitat selection theory more broadly (e.g. Johnson 1980, McDonald et al. 2005). There is considerably more research on the importance of the landscape configuration for migrants. In landscapes where resources are patchy, migrant foraging and habitat use can vary by patch size or patch density (Table 2.1: L5). Several studies in the Midwestern US have found differential use of habitat patches and their edges during migration (Wilson et al. 1982, Vitz and Rodewald 2007).

Landscape composition and configuration are widely used predictors of habitat use more broadly, but success in their use is tightly dependent on scale. At large spatial scales (> 450 km^2), the proportion of vegetated lands versus un-vegetated lands may be a significant driver of stopover site use (L3). Many authors have recognized the importance of finer scale habitat availability in predicting migrant habitat use (Hutto 1985, Moore et al. 1995). Buler et al. (2007) reasoned that hardwood forest cover in the northern Gulf of Mexico region might be a proximate cue for birds selecting a stopover site. Mathematical formulations have confirmed these predictions (Farmer and Wiens 1998, Simons et al. 2000), although empirical support is lacking (Buler et al. 2007). If birds use vegetation composition as a cue for habitat use at finer scales, migrant stopover distribution may vary by the local availability of certain land cover types relative to the availability in the larger region (L4).

Patterns of migratory stopover may also be influenced by the interactions among factors (Table 2.1: Interaction Hypothesis 1, I1). In a review of migratory habitat selection studies, Petit (2000) reported an interaction between stopover habitat use and foraging guild in three of five studies. During fall migration in the Rocky Mountains, Carlisle et al. (2004) found differential habitat use between neotropical and temperate migrants, suggesting an interaction between migration distance and habitat type.

In this study we test the ability of these four broad, previously identified factors (Migrant Community, Geography, Landscape Characteristics, and their Interactions) to predict the distribution and abundance of 50 common migratory landbird species among 11 previously unstudied stopover locations across five autumn migration seasons.

Table 2.1. Citations that found support for each general hypothesis of migrant distribution tested in this study (non-exhaustive). The right column indicates whether or not our study supported the referenced hypothesis.

Hypothesis	**Explanatory Variables**	**Citation**	**Supported**
Migratory community characteristics (M)	M1: Migration strategy	Carlisle et al. 2004	Yes
	M2: Foraging guild	Parrish 2000 Rodewald & Brittingham 2004 Wilson et al. 1982	No
	M3: Taxonomic group	Suthers et al. 2000	Yes
Local geography (G)	G1: Distance from the coastline	Bonter et al. 2009 Buler and Moore 2011 Ralph 1981 (Stewart, R.M., Mewaldt, L.R., and Kaiser 1974) Alerstam and Petterson 1977	No
	G2: NE to SW position within the Gulf of Maine	Drury and Keith 1962 McCann et al. 1993	No
	G3: Mainland vs. island site	McCann et al. 1993	No
	G4: Island size	Suomala et al. 2010 Martin 1980	No
Landscape characteristics (L)	***Landscape Composition*** L1: Total percentage of vegetated habitat	This study	No
	L2: Total percentage of four land cover types	Bonter et al. 2009 Buler and Moore 2011 Buler et al. 2007 Moore et al. 1990 Cohen et al. 2014	No
	L3: Proportional vegetated habitat availability	This study	Yes
	L4: Proportional availability of four land cover types	This study	No
	Landscape Configuration L5: Vegetation patch dynamics (patch density & patch area)	Martin & Karr 1986 Rodewald and Brittingham 2004 Vitz and Rodewald 2007 Matthews and Rodewald 2010 Wilson et al. 1982 Cohen et al. 2014	No
Combinations and interactions of above hypotheses (I)	I1: Combination of variables	Bonter et al. 2009 Vitz and Rodewald 2007 Wislon et al. 1982 Buler and Moore 2011	Yes

2.3. Methods

2.3.1. Study region and sites

We used fall migrating-landbird data from eleven monitoring stations in the Downeast and Midcoast regions of Maine, USA from August – October 2007 – 2012 (excluding 2008) that used regionally standardized, passive mist-netting (Table 2.2). The stations are located along 180 km of coastline (Figure 2.1). These sites span both sides of the mouth of the Penobscot River (the longest river system within Maine and the second longest river system that enters the Gulf of Maine). Birds often utilize rivers as migratory corridors (Skagen et al. 1998, Bagg 1923, Lehnen and Krementz 2005, Martell et al. 2001), and with its north-south orientation the Penobscot River may serve as an important landmark for birds migrating along the Atlantic flyway. Wherever possible, nets were erected in five main habitat types (forest, shrub, mowed or grazed field, and transitional edges in field-shrub and shrub-forest) within each site to prevent confounding the habitat of capture with the stopover site of capture. One of our eleven sites did not possess a field component (Cross Island) and two sites did not possess forest components (Seal and Petit Manan islands).

Five of the eleven monitoring sites were located on the mainland or on islands separated from the mainland by less than 1/20 of their width (Figure 2.1). The site furthest from the coast, McFarland Hill, is located 3 km west of Frenchman Bay (9 km from the Gulf of Maine) in the interior of Mount Desert Island (MDI). Mount Desert Island has an area of 280 km^2, is the largest island off the coast of Maine, and is located only 800 m from the mainland at its closest. Our second mainland site, Seawall, is located on the headlands of the southernmost tip of MDI, 16 km southwest of McFarland Hill. Three additional mainland sites, Petit Manan Point, Schoodic Point, and Schoodic Head, are located on peninsulas to the northeast of MDI.

We monitored migrants on six, off-shore islands (Figure 2.1). Great Duck Island is a 0.75-km² island located 11 km further out into the Gulf of Maine from the Seawall site. Petit Manan Island and Cross Island are both located northeast of MDI (Figure 2.1). All other island sites (Isle Au Haut, Seal Island, and Metinic Island) are located to the southwest of MDI at varying distances from the mainland.

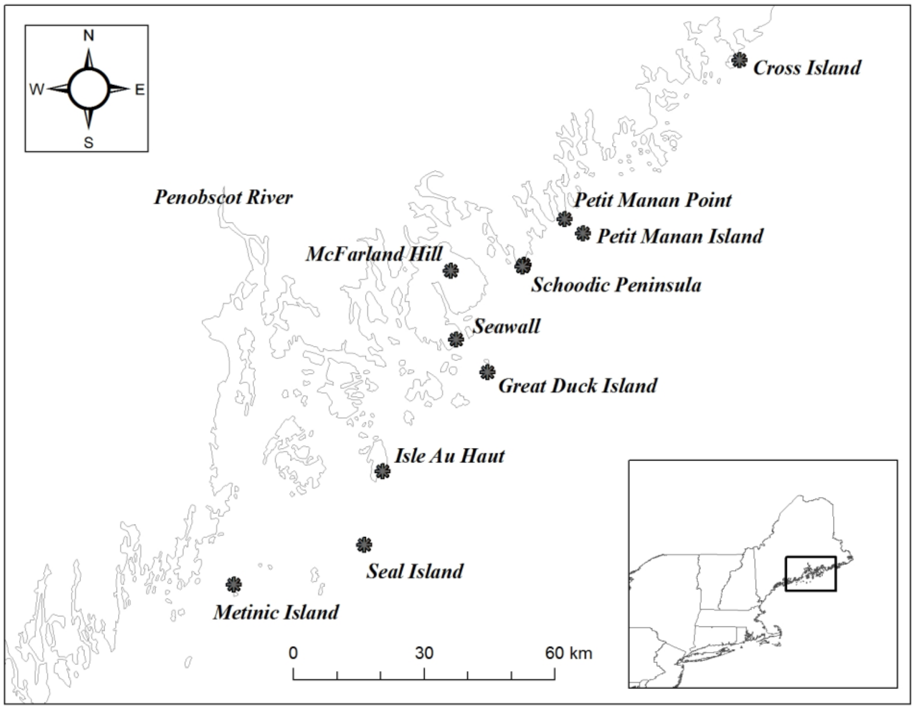


Figure 2.1. Diagram of our coastal transect of migration monitoring stations in the Downeast and Midcoast regions of Maine, USA. Note there are two migration monitoring stations located on Schoodic Peninsula.

2.3.2. Bird captures

Each fall mist-nets were opened 30 minutes before sunrise and closed six hours after opening, when the conditions permitted. The number of nets opened on any given day varied by weather conditions (e.g. wind and rain), and we therefore used normalized daily capture rates with each site's daily total net-hours (the time each net was open summed daily across all nets at a site) instead of raw number of birds captured. We banded all birds with uniquely numbered aluminum bands during their initial capture.

We described patterns of bird abundance across our sampling region using "integrated seasonal use", which we define as the mean detection rate of each species ($n = 50$) at each site during each year a site was operated. We only included a species' seasonal use when it was not present in our region year round and we captured > 10 individuals across all sites within a given year. Not all commonly captured species were captured at each site during each year. Specifically, the individual sampling unit ($n = 667$) was measured as the detection rate (captures divided by net-hours) of each species detected within each site per year ($n = 20$ site-years: Table 2.2).

Because habitat selection and the integrated use of the community is partially a function of the number of individuals available for stopover, we calculated the integrated seasonal use using only detections during the "peak" of migration for each species and year. To standardize our estimate of peak-migration time, we pooled daily capture rates for each species from all sites operated in a specific year, obtained the quartile passage dates (the date at which 25% and 75% of the individuals of a particular species had been captured), and calculated site-specific annual mean capture rates using only the two middle observation quartiles. Because the assigned inner-quartile passage window (“peak”) varied for each species with each year, this method not only centers our analyses of habitat use during the periods when more of the preferred habitats will be filled, it also controls for variation in migratory phenology among both years and species. Table 2.3 describes variation in the number of days for the “peak” migration of each year across all species.

Table 2.2. Operating organization, years of operation, and percentage of broad land cover types within the site (100 meter buffer surrounding all mist-nets). Also included is the value of proportional habitat availability (vegetated versus non-vegetated spaces) at the 4 km scale. Organizational abbreviations: University of Maine (UMaine), Acadia National Park (ANP), Maine Coastal Island National Wildlife Refuge (MCINWR), Biodiversity Research Institute (BRI).

Site	**Operating Organization(s)**	**Year(s) Operated**	**% Conifer forest**	**% Mixed forest**	**% Human development**	**% Shrub-land**	**% Grass-land**	**% Non -habitat**	**Proportional Hab. Avail. (4 km)**
Cross Island	UMaine MCINWR	2013	65	0	0	3	0	32	9.65
Great Duck Island	UMaine ANP	2010-2011	8	29	0	0	22	41	34.64
Isle Au Haut	BRI	2009	85	6	0	0	0	9	3.08
McFarland Hill (MDI)	UMaine ANP	2010-2011	1	74	3	8	10	4	1.11
Metinic Island	UMaine MCINWR	2009-2011	41	0	0	0	59	< 1	36.84
Petit Manan Island	MCINWR	2009	0	0	0	0	29	71	106.31
Petit Manan Point	MCINWR	2010-2012	0	90	0	0	10	0	4.76
Seal Island	MCINWR	2007 & 2009	0	0	0	14	1	85	61.28
Seawall (MDI)	UMaine ANP	2010-2012	18	59	12	1	0	10	2.32
Schoodic Peninsula 1	UMaine	2009	63	0	24	0	0	13	3.88
Schoodic Peninsula 2	UMaine ANP	2012	46	49	0	0	0	5	3.76

Table 2.3. The range of capture days and the species corresponding to the range for "peak" migration for each year and the yearly median of capture days.

Year	**Minimum # of days (species)**	**Maximum # of days (species)**	**Median # of days**
2007	1 (Traill's flycatcher)	28 (Hermit thrush)	11
2009	4 (Black-throated green warbler)	24 (Yellow-shafted flicker)	13
2010	6 (Chestnut-sided warbler)	38 (Song sparrow)	18
2011	7 (Palm warbler)	49 (Song sparrow)	20
2012	6 (Myrtle warbler)	44 (Hermit thrush)	22

2.3.3. Migratory community characteristics

We tested for the ability of three metrics of the migratory community to predict habitat use: migratory strategy (Table 2.1: M1), foraging guild (M2), and taxonomic group (M3). As an additive effect, each of these three variables tests whether the average relative use across our entire region differs by taxa. We used migration distance as an index for migratory strategy (M1) by calculating the difference between the latitude at the center of our region (MDI) and the latitudinal midpoint of the nonbreeding range (as defined by Erickson et al. 2011). This method estimates the median distance remaining in migration for each species and provides a continuous variable for migratory distance as birds pass through our region. Species were further grouped based on their diet during fall migration (M2) as insectivores, granivores, frugivores, and generalists using previous categorizations created from three sources (Parrish 1997, Suomala et al. 2010, Erickson et al. 2011). Finally, we included taxonomic family (M3) as a covariate to control for phylogenetic differences in stopover behavior independent of the other species characteristics.

2.3.4. Local geographic characteristics

We tested for the ability of four geographic variables to predict stopover distribution and abundance: distance from the coastline (Table 2.1: G1), the northeast-southwest position of each site along the coast of the Gulf of Maine (G2), mainland versus island (G3), and island size for island sites (G4). These four variables each attempt to explain variation in bird use among sites within our sampled region. Each site's distance from the coast and distance from a reference point along a northeast-southwest axis was calculated using the linear referencing toolbox within ArcGIS 10 (ESRI 2011). Island sizes (m^2) were obtained from Maine Coastal Island National Wildlife Refuge and Acadia National Park. We nested island size within the binomial, dummy variable for island so that island size was only included in the model when the dummy variable equaled one (island).

2.3.5. Landscape characteristics

We also attempted to explain variation in bird use among sites using landscape composition and landscape configuration metrics. Our eighteen landscape-characteristic variables included the total percentage of vegetated lands (Table 2.1: L1), total percentage of each of four land cover types (coniferous forest, mixed coniferous-hardwood forest, shrubland, and human development: L2), the proportional availability of all vegetated habitats (L3) and of each of the four more specific land cover types (L4) within the sampled site versus the surrounding landscape, and indices for patch size and patch density for each of the four cover types (L5).

We assessed each of these eighteen metrics at multiple spatial scales, given that birds may respond to landscape features while landing (Ktitorov et al. 2008) from a variety of altitudes. To do so, we first defined each stopover site as the area within a 100 m buffer of all mist-nets. Because of uncertainty in the appropriate spatial extent to consider as available habitat for migrants moving through an area, we then calculated land cover percentage and proportional habitat availability for each of the eighteen landscape-characteristic variables at four scales. The largest scale was established using a buffer of the maximum visibility (16 km) gathered from a weather station centrally located within the study region and along the coast (Hancock County - Bar Harbor Airport), and we defined three finer scales at 75% (12 km), 50% (8 km), and 25% (4 km) of this distance.

We delineated land cover types using the Maine Land Cover Dataset (MeLCD). The MeLCD dataset is the most current layer with the highest resolution encompassing the entire study region. The MeLCD layer was derived from Landsat Thematic Mapper 5 and 7 imagery (1999-2001) and refined to the State of Maine requirements using SPOT 5 panchromatic imagery from 2004 with a spatial resolution of 5 x 5 m to create a land cover classification with 23 land cover types. We aggregated land cover from the 22 MeLCD classes by similarity in vegetation height (i.e. how they would presumably appear to a bird from the air) and the vegetation descriptions provided in the layer's metadata (www.maine.gov/megis/catalog/metadata/melcd.html). This resulted in six broad land cover types (coniferous forest, mixed coniferous-hardwood forest, shrubland, human development, grassland, and non-habitat). We did not calculate either raw percentages or proportional availabilities for both the grassland (which included agricultural lands) and non-habitat cover types (e.g. open water, bare land, roadway/runway), because they comprise such a small percentage of the landscape relative to other habitats (4.5% and 3.2% respectively). Further, grasslands do not provide similar quality and abundance of food resources for autumnal landbird migrants relative to the other habitat types (Yong et al. 1998, Hutto 1998).

Total percentage of land cover for each coverage type was calculated by dividing the area of each type by the total area of all land within each of the four spatial scales. Proportional habitat availability was calculated by dividing the percent of each land cover type within a site (the 100 m buffer around nets) by the percent of each land cover type found within each of the four spatial scales (including the area within the site). We calculated patch size and density using FRAGSTATS (McGarigal et al. 2012). Specifically we determined the degree of fragmentation (patch density) and patch size (patch area weighted mean) for each of our four habitat types within each stopover site and spatial scale described previously.

2.3.6. Interactions

Regional patterns of migratory stopover are most likely driven by an assortment of factors interacting together. For example, different foraging guilds may be captured differently among sites. For this reason we considered all possible two-way interactions between migratory community characteristics and both the local geography variables and the landscape characteristics (Table 2.1: I1).

2.3.7. Statistical analysis

To test the ability of parameters identified by past migration studies to explain migratory habitat use within an untested region (the Gulf of Maine), we initially calculated 79 explanatory variables within our hypotheses as described above. To reduce this initial candidate set of fixed effects for model selection, we performed a random forest analysis (Liaw and Wiener 2002, R Development Core Team 2012).

While also used for regression and machine learning, random forests can rank candidate variable importance by quantifying each variable's ability to classify a dependent variable ($\log_{10}$-transformed mean annual species capture rate, in this case) using iterative subsets of a data set (Cutler et al. 2007). Random forests show high predictive accuracy and are applicable even in high-dimensional problems with correlated variables. Because random forests are constructed with regression trees, they inherently account for interactions by allowing variables to occur multiple times within a tree at different nodal levels. We selected variables to include in our final model selection by identifying a cut-off in the scree plot of variable importance values produced by a random forest. We tested all variables that produced a decrease in nodal purity greater than 4.0 (Figure 2.2).

We then constructed a series of linear mixed-effects models ($n = 6$) using maximum likelihood (package 'nmle' in R; Pinheiro et al. 2012). We used all single variables and all possible combinations of the interactions between the highly ranked migratory community characteristics (migratory distance and foraging guild) and landscape variables (proportional vegetated habitat availability at 4 km). Capture rates and proportional habitat availability at 4 km were $\log_{10}$ transformed to meet model assumptions. All models, including the null, included taxonomic family as a fixed effect to account for family-specific capture probabilities. Since we are trying to predict site use, site was our primary sampling unit. Since site is pseudoreplicated across years we included year as a fixed effect (along with family) in all models and site as the highest-level random effect to control for the pseudoreplication. Further we sampled species within each site as indicators of the use of that site by the entire migratory community. Species nested within site was included as a random variable in all models as we considered each species a random sample of all the species that were likely to use that site in a given year. We than selected the top model using AIC model selection (Burnham and Anderson 2004).

To validate this model ranking (and account for ranking stability), we used a bootstrap method on each model with AIC < 5.0 ($n = 3$). Each of the three top models were bootstrapped twenty times, using a different bootstrapped dataset (with replacement). The AIC scores for each, twenty-model iteration were then averaged before we compared mean AIC scores to determine our final model ranking. Because our initial variable reduction technique (the random forest) removed all of our candidate variables representing local geography, we added each geographic variable into the final model separately and examined the resulting model performance using AIC scores as a test of our geographic hypotheses.

2.4. Results

On average, 36 species with sufficient detections were observed each fall season (range of species = 18 – 47; range of the number of detections per species per year = 10 – 4072). Of the species detected, approximately 70% were neotropical migrants. We operated mist-nets for a total of 58,304 hours over 20 site-years.

The random forest technique identified four single variables: migratory distance, taxonomic family, foraging guild, and proportional vegetated habitat availability (at the finest spatial scale – 4 km) for use in our candidate model set (Figure 2.2). Our bootstrapped model selection process identified one top model (Table 2.4) that included five fixed effects (in addition to the random effect of species nested within site). This top-ranked model included four single variables (taxonomic family, year, migratory distance, and proportional vegetated habitat availability at the 4-km scale) and one interaction term (migration strategy by habitat availability). No single geographic variable (i.e., distance from mainland, island versus mainland, or island size) improved the fit of the final model; in fact, all geographic variables increased the AIC value of the final model (ΔAIC = 0.8 – 1.9). Our top model contained five variables predicting $\log_{10}$-transformed detection rates of migrant bird species (Table 2.4). Of the five variables, all had significant effects: taxonomic family, year, migratory distance, vegetated habitat availability at the 4 km scale, and the interaction between migratory distance and vegetated habitat availability (Table 2.5).

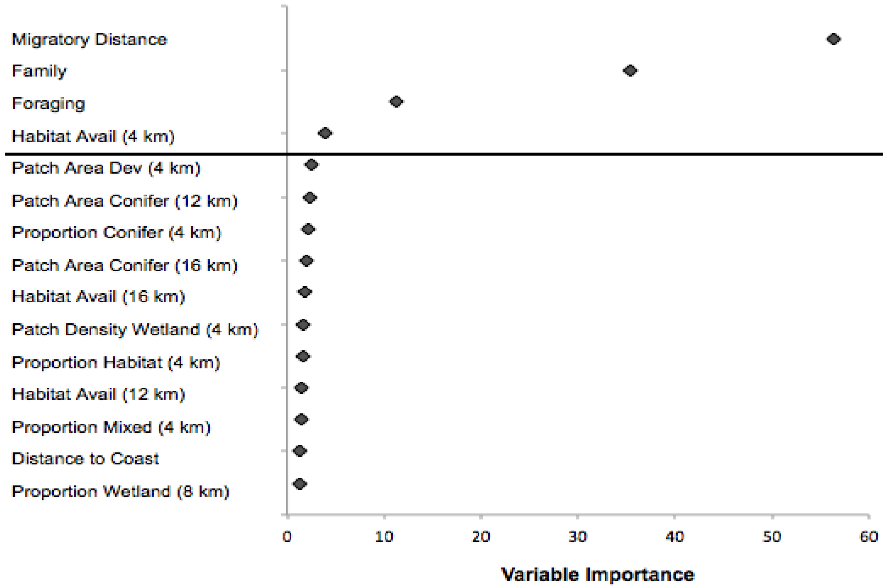


Figure 2.2. Random forest scree plot indicating variable importance. Depicts the top 15 predictors of yearly detection rates of each species at each site (of 79 variables explored) produced by a random forest of 500 regression trees.

Table 2.4. AIC model selection results for all bootstrapped models and the null model predicting migrant stopover site selection within the coastal region of Maine, United States (2007, 2009-2012). Also shown is the difference in AIC relative to the top model and number of model parameters (*k*). Distances within parentheses following the variables below indicate the scale at which they were calculated.

model	***AIC***	***ΔAIC***	***k***
Taxonomic Family + Year + Migratory Distance + Habitat Availability (4 km) + Migratory Distance x Habitat Availability (4 km)	857.5	0	5
Taxonomic Family + Year + Migratory Distance + Habitat Availability (4 km)	859.7	2.2	4
Taxonomic Family + Year + Migratory Distance + Habitat Availability (4 km) + Foraging Guild+ Migratory Distance x Habitat Availability (4 km) x Foraging Guild x Habitat Availability (4 km)	872.1	14.6	7
Null: Taxonomic Family + Year	883.2	25.7	2

Table 2.5. Comparison of parameter estimates and 95% confidence intervals of the final selected model. Parameter estimates are based on the $\log_{10}$-transformed detection rates. Parameter estimates of categorical variables are calculated in reference to the baseline listed. The number of species within each categorical variable is shown in the parentheses. Significant parameters are indicated by *.

		Final model			
Variable		**Parameter Estimate**	**95% Confidence Interval**		
Migration Distance		7.75×10^{-08}	2.09×10^{-09},	1.53×10^{-07}	*
Proportional habitat avail. 4-km		0.42	0.21,	0.64	*
Year					
	2007	Reference			
	2009	-0.20	-0.42,	0.03	
	2010	-0.40	-0.63,	-0.17	*
	2011	-0.46	-0.69,	-0.23	*
	2012	-0.43	-0.67,	-0.19	*
Family					
	Cardinalidae (n = 2)	Reference			
	Cuculidae (n = 1)	-1.89	-1.18,	0.20	
	Emberizidae (n = 8)	-0.14	-0.58,	0.31	
	Fringillidae (n = 1)	-0.30	-0.93,	0.33	
	Icteridae (n= 1)	-0.39	-1.00,	0.21	
	Mimidae (n = 1)	-0.52	-1.07,	0.03	
	Parulidae (n = 20)	-0.32	-0.73,	0.10	
	Picidae (n = 2)	-0.38	-0.88,	0.12	
	Regulidae (n = 1)	0.18	-0.36,	0.71	
	Tryglodytidae (n = 1)	-0.85	-1.76,	0.05	
	Turdidae (n = 5)	-0.45	-0.89,	-0.02	*
	Tyrannidae (n = 4)	-0.32	-0.76,	0.12	
	Vireonidae (n = 3)	-0.20	-0.67,	-0.19	
	Migration strategy x habitat 4-km	-8.05×10^{-8}	-1.40×10^{-7},	-2.16×10^{-8}	*

Proportional vegetated habitat availability at the 4-km scale was significant as a single predictor (Table 2.5 and Figure 2.3). As proportional habitat availability increased, so did captures of the total migratory community, regardless of migratory distance, such that use was highest at sites that possessed high amounts of habitat in a landscape relatively devoid of habitat (i.e. habitat islands). We also found a significant interaction between migratory distance and vegetated habitat availability. Stopover habitat use for the shortest distance migrants was most strongly associated with proportional vegetated habitat availability. As the median migratory distance of a species increased, however, the funneling effect of vegetated habitat availability decreased (Table 2.5 and Figure 2.4).

Migratory distance and year were also significant single predictors of site use. We captured, on average more short distance than long distance migrants and more birds per unit effort in 2007 and 2009 than in later years (Table 2.5).

The mean detection rates of taxonomic families were remarkably similar, despite wide variation in the total number of individuals captured for each species. Among all of the species considered, only capture rates of the Turdidae were different than those of the reference family (Cardinalidae: Table 2.5). We suggest that this pattern occurred because of two major reasons. First, variation among species within each category dampened the variation among species overall. Second, our calculations for detection rate using only “peak” migration periods (the middle two quartiles of passage time for each year) was successful in creating directly comparable detection rates at the family scale. In general, longer distance migrants are assumed to migrate faster than short distance migrants (Ellegren 1993). In support of this, species with lower total capture abundances tended to pass through the study region in a shorter time period, such that capture rates during their brief peak were similar to more abundant species during their wider migratory peak (Table 2.3).

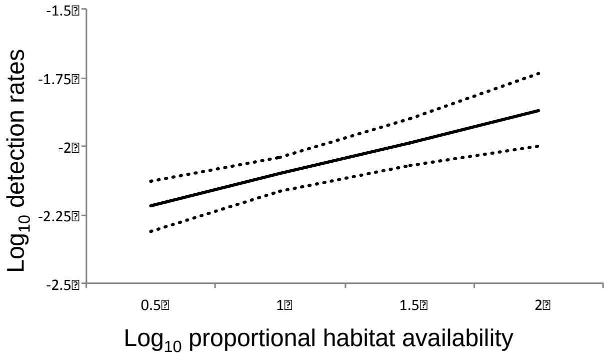


Figure 2.3. The predicted $\log_{10}$-transformed detection rates (± 95% CI) of migratory songbirds as a function of the proportional availability of habitat (versus non-vegetated spaces) across eleven migration monitoring stations.

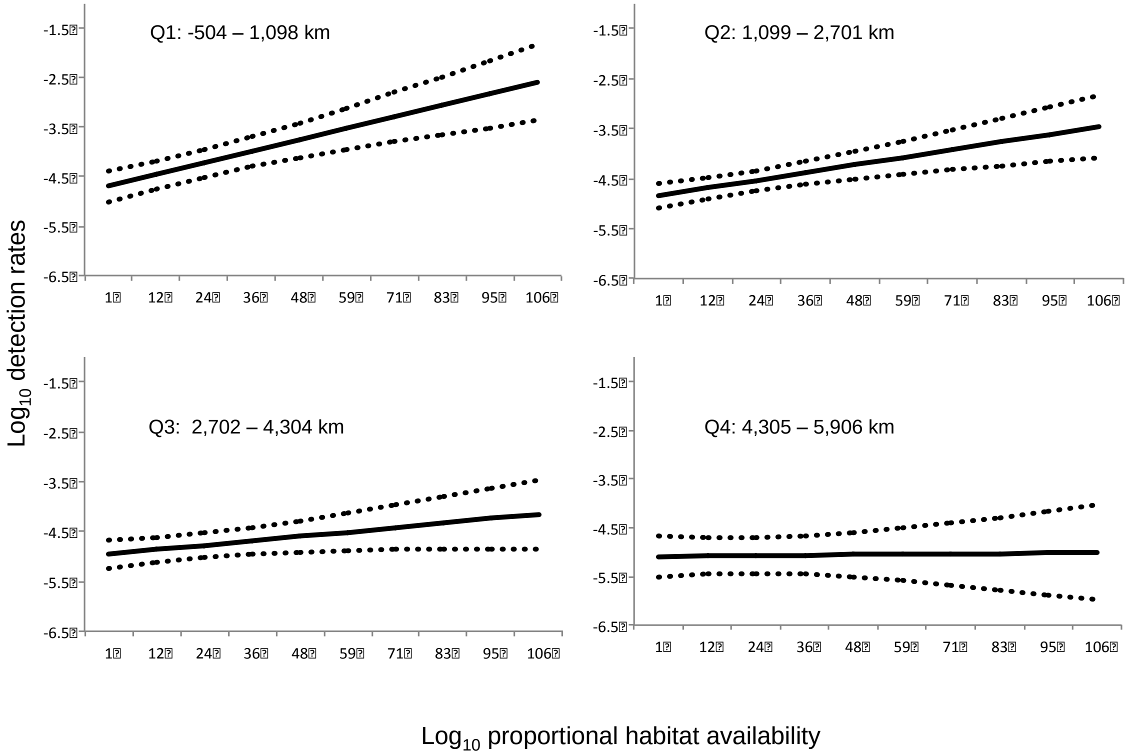


Figure 2.4. The predicted $\log_{10}$-transformed detection rates (± 95% CI) of migratory songbirds as a function of the proportional availability of habitat (versus non-vegetated spaces). Data from eleven migration monitoring stations for species in each of the four quartiles of migratory distance (the distance from the region of capture to the midpoint of the nonbreeding range).

2.5. Discussion

Our analysis of migrant landbird stopover patterns in coastal Maine revealed that landscape composition at fine spatial scales (< 4 km, i.e. close to landing) in combination with a species' relative remaining migratory distance explained stopover site use across space and among years. Our predictive abilities were not improved by considering larger scale landscape variables or a site's local geographical position. Specifically, more isolated habitat patches (i.e. habitat islands) concentrated migrants, and this pattern was strongest among shorter distance migrants. This pattern was not driven by an oceanic island effect, as islands of habitat showed similar patterns of bird use regardless of the specific make-up of the non-vegetated matrix (e.g., open water, bare ground, & roads). Further, models with an indicator variable for oceanic island did not perform better than those with the habitat availability metric. Studies in urban parks such as Central Park in New York City (Seewagen and Slayton 2008) and desert oases in North Africa (Bairlein 1988) have revealed that habitat islands in any non-vegetated matrix are important stopover sites, which suggests that proportional habitat availability may be widely applicable for predicting stopover distributions globally.

The importance of habitat at the 4-km scale supports the broader hypothesis that migratory animal decision-making is hierarchical (Hutto 1985, Moore et al. 1995). At large regional scales, this migratory paradigm suggests that the primary drivers of stopover habitat are factors extrinsic to habitat, such as weather and individual energetic status (Moore et al. 1995). Our results agree; we found no relationship between larger landscape characteristics and stopover site use within our region. At finer spatial scales, like the one we have identified here, factors intrinsic to the habitat itself, such as food availability (Olsen et al. 2015), structure (Sherry and Holmes 1985, Moore and Aborn 2000, Winker et al.1992), and predator risk likely become increasingly important in decisions of habitat use (Hutto 1985). It is reasonable to assume that the important landscape characteristics in our model are very coarse cues for these intrinsic habitat factors, as seen in studies conducted along the Gulf of Mexico (Buler and Moore 2011, Buler, Moore, and Woltmann 2007). Buler et al.'s (2007) work found that hardwood forest cover at a finer (5 km radius) spatial scale predicted migrant use best. While our study corroborates the fine spatial scale at which migrants are making decisions, we found that proportional habitat availability and not forest cover is most important for migrants in the Gulf of Maine. This leaves open the possibility that even finer scale selection occurs within stopover sites (although we did not measure that explicitly in this study). We hypothesize that gross, vegetated habitat availability within a few kilometers influences site selection upon landing, and this selection is further refined among habitat patches at finer spatial scales during stopover (Hutto 1985, Martin and Karr 1986).

In a similar way to spatial scale, habitat use is also controlled by additional factors at shorter time scales than the seasonal use metrics investigated here. Nightly weather conditions such as the magnitude and direction of wind, precipitation, and cloud cover have all been shown to affect the numbers of birds stopping over at a particular site (Moore et al. 1995, Dänhardt and Lindström 2001, Adams 2014), especially off-shore islands where its thought many birds using them were blown there (Richardson 1978a). Unless weather conditions are consistently different among sites, which is unlikely given the spatial scale of our study, daily variation in these weather conditions and their associated effects on migrant behavior should cancel out over the length of a migration season. Previous study within the Gulf of Maine, however, has hypothesized that site-specific variation in weather produces consistent differences in stopover behavior. Specifically, off-shore islands should concentrate birds more than other sites as birds are blown off course into the Gulf (Richardson 1978). Our study found no evidence for meteorological forcing in this way over a migratory season, as an indicator variable for island and the distance of islands to the coast did not improve our predictions of site use over our top models. While it remains possible that particular storm systems could produce this pattern in the short term, our results suggest that these events do not drive site use by landbird migrants at the scale of a full migratory season. From a land prioritization and conservation standpoint, local habitat availability should do a better job at maximizing benefit for migratory populations.

Our results are also consistent with the hypothesis that landbird migration occurs as a broad front over both land and water at sub-continental scales (Nisbet 1970, Richardson 1976 and 1978, Alerstam and Pettersson 1977). The ability of relatively rare habitats to concentrate birds is expected when spatially homogeneous migrating flocks are attracted to the nearest visible landscape features prior to stopover. If birds were distributed more heterogeneously during migratory flights (i.e. not in a "broad front"), this concentrating effect could still occur, but local geography would also be needed to explain site use due to the initial heterogeneity in birds available for stopover. We found no support for such a two-step explanation across our coastal transect.

We recognize that bird use of a stopover site occurs not only directly after a nocturnal migratory flight but also after relocation flights during stopover within the broader landscape as individuals search for more suitable habitat (Mills et al. 2011, Taylor et al. 2011, Woodworth, Francis, and Taylor 2014, Chernetsov, Bulyuk, and Ktitorov 2007). Our study confounds these various types of use. Both categories of movement, however, are important contributors to overall site use and should be considered in discussions of stopover habitat use at any scale.

Many predictors of stopover habitat use from previous studies were not important for the Gulf of Maine. These factors are thus not universal predictors, but they could still be important regionally (Table 2.1). For instance, we did not find a difference between migrant abundance on islands versus the mainland as McCann et al. (1993) did. The proportional habitat availability effect we show here, however, predicts higher use for any relatively rare habitat on the landscape, which would include islands of habitat in water as well as islands in any other non-vegetated landscapes. We might have found a similar island effect as McCann et al. (1993) had we not controlled for landscape characteristics (which they did not). The overall inability of other local geographic variables to predict site use may be a function of the scale of our region. For instance, we may have detected an effect of distance to the coast on site use if we had monitored areas further inland.

2.5.1 Landscape characteristics and migratory distance

The ability of stopover oases to concentrate shorter distance migrants more readily than longer distance migrants, as we show here, remains untested elsewhere. Our reported concentration in site use was attributable to all vegetated habitat types and not to any specific vegetation component (unlike Buler et al. 2007). Our results suggest that the conservation consequences of habitat fragmentation, at least in our region, are likely different for shorter versus longer distance migrants as a result of their habitat selection behaviors during migration.

Because our sites are relatively close to the breeding grounds for many species captured within the Gulf of Maine, the longest distance migrants may be less energetically strained early in their migration, and thus not driven to stop in landscapes where suitable habitat is rare. Short to medium distance migrants, however, stop more frequently along their routes (Newton 2008) and thus may be more likely to search for habitat even in areas where it is less available. This behavioral difference (likely produced by different physiological constraints) would cause areas with less available habitat to concentrate shorter distance migrants more. As longer distance migrants travel further south and become increasingly energetically compromised, we would predict that the relationship between proportional habitat availability and stopover site use would approximate the pattern we show here for shorter distance migrants. Indeed, the concentrated use of North African oases by longer distance migrants after crossing a water barrier (Bairlein 1988) appears to support this prediction.

2.5.2. Conservation implications

Moore et al. (2005) emphasized that the conservation of migratory habitat should be scale dependent. Our study found migratory landbirds were strongly associated with habitat characteristics at scales where governmental and other agencies are able to focus their conservation efforts. The greatest gains for stopover use by all bird guilds are thus to be made by maximizing vegetated habitats (vs. non-habitat). This also means that in areas where there is little vegetated habitat (urban landscapes and offshore islands), the remaining small patches may be disproportionately important for the local migratory community relative to similarly sized patches in areas of more contiguous habitat. When increasing habitat widely across the landscape is not possible, the conservation of these small patches should be a priority for migratory stopover habitat use.

CHAPTER 3: TRADEOFFS BETWEEN PREDATION RISK AND FRUIT RESOURCES SHAPE HABITAT USE OF LANDBIRDS DURING AUTUMN MIGRATION

3.1. Summary

While foraging, animals often trade off between food and safety, reducing feeding in response to increased predation risk. This response, however, may not be a viable option for animals that are energetically compromised. Many single-species studies have shown that hungry animals select habitats where foraging opportunities are greater even if predation pressures are higher, but it is unclear how generalizable these patterns are to entire communities. Here we examined the stopover habitat use of 28 frugivorous landbird species along the coast of Maine, USA, during an energetically demanding period of the annual cycle, fall migration. Across six stopover sites we determined whether or not a trade-off existed between safe habitat patches (patches with high plant stem density) and patches with high food resources (patches with high fruit abundance). Controlling for raptor abundance at a site, landbird migrants were captured at higher rates at sites without a trade-off, suggesting that birds avoid staying at sites were there is a predation risk – foraging trade-off. At all sites, regardless of the presence of a trade-off, longer distance migrants used patches with high food availability more frequently, whereas patch use by shorter distance migrants was explained by habitat cover alone. Our findings suggest that for the Gulf of Maine birds alleviate predation risk at the scale of a stopover site, and differences in habitat selection at finer patch scales are mediated by migratory strategy.

3.2. Introduction

Food acquisition and predator avoidance are fundamental components of the survival strategies of most animals (Houston, McNamara, and Hutchinson 1993, Hebblewhite and Merrill 2009, Brown and Kotler 2004, Metcalfe and Furness 1984, Cowlishaw 1997). To maximize fitness, animals often trade off between foraging and either increased vigilance for predators (Brown et al. 1999), flocking behaviors (Lindström 1989), time spent in a patch (Ydenberg et al. 2004), or crypsis (reduced rates of movement or protective cover: Thaler et al. 2012). In situations where animals are energetically constrained, however, the costs of reducing time spent foraging to decrease predation risk may be prohibitively high (Krebs 1980).

Predation risk can be a strong modifier of animal habitat selection (e.g., Gotceitas 1990, Hebblewhite and Merrill 2009, Lima 1988a, Lindström 1990, Thaler et al. 2012, Yasué et al. 2003). As a rule, animals choose feeding habitats that allow them to meet their energetic requirements while minimizing predation risk (Yasué, Quinn, and Cresswell 2003), avoiding areas with high predation risk, even if these areas would maximize foraging efficiency (Gotceitas 1990, Pomeroy, Butler, and Ydenberg 2006). In times of higher than average energetic demand, however, added predation risk may be outweighed by the costs of decreased foraging efficiency in safer habitats.

Migration may be such a period where the trade-off between foraging and predation risk shifts predictably. Migration is energetically expensive and suitable habitats for rest and refueling are critical for a successful migration (Hutto 1985, Moore et al. 1995, Rodewald and Brittingham 2007). The large scale of migration further increases risks to survival, because individuals find themselves in unfamiliar environments with unknown predation pressures while trying to balance predator evasion (Moore 1994) and food acquisition (Moore and Aborn 2000) under higher than average energetic demand. Predation risk varies both spatially and temporally (Sih 1992), so migrating animals must renegotiate the trade-off between predation risk and energetic demand across an abundance of sites en route. Further, major landscape features (e.g., coastlines, water resources) are known to concentrate both migratory animals and their predators (Aborn 1994, Valeix et al. 2009). Therefore, the benefits of optimal behaviors are likely greatest at these choke points, as they concentrate landbirds (often before over-water flights) and their aerial predators (Aborn 1994, DeSorbo et al. 2012, Schmaljohann and Dierschke 2004). Predator risk is thus increased at the same time as energetic demand.

Together, these added challenges during migration are likely to shift the optimal solution to the foraging vs. predator avoidance trade-off. For example, studies of both Passerine songbirds (Moore 1994, Cimprich et al. 2005) and Charadriiform shorebirds (Metcalfe and Furness 1984) demonstrate that individuals in migratory condition decrease crypsis and vigilance relative to individuals that are not migrating.

Further, the high energetic demands of migration affect an individual's energy stores, which control behavioral responses to the predation risk – foraging trade-off (Pomeroy et al. 2008, Cimprich and Moore 1999). Fat stores can alter flight performance (Hedenström 1992, Cimprich and Moore 2006) and motivation to forage (Krebs 1980), such that fatter birds increase vigilance while leaner birds take more risks (Koivula, Rytkonen, and Orell 1995, Lima and Dill 1990, Cimprich and Moore 2006). Lindström and Alerstam (1992), however, state that each individual may have a "set point" or optimal fuel load at which point their motivation to forage decreases, which may disrupt any correlation between fuel load and anti-predator behavior.

In this study we assessed stopover habitat use for 28 species of Passeriform and Piciform birds (hereafter, “landbirds”) under the increased risk and energetic demand of migration along the coast. While single-species studies are invaluable in determining specific behavioral and physiological reactions to predation, it is difficult to translate that information into multi-species migratory habitat conservation and management efforts. To understand the community-level response to trade-offs between predation risk and foraging demand, we examined the habitat use of the entire migratory landbird community during fall migration along the coast of Maine, USA at two types of stopover sites: 1) sites where the local habitat composition forces birds to trade-off predator avoidance and food availability, and 2) sites where such a trade-off does not exist. In sites of the first type, habitat patches with the highest food availability have relatively little protective cover. In the second site type, birds do not experience a trade-off between predation avoidance and foraging, because patches with the highest food availability are also patches with the highest structural cover at the site. We used weekly relationships between fruit and cover to allow the presence (or absence) of a trade-off between fruit availability and cover at a particular site to vary throughout the season as fruit availability changes.

Our study design explicitly tests how well fruit availability predicts habitat patch use within a stopover site each week as a function of A) the structural cover present within the same patch, B) whether the stopover site as a whole possesses or lacks a trade-off between cover and fruit availability, and C) the site-level abundance of avian predators. Further, because we examined all 28, commonly caught species in our migrant community, we are able to assess whether migratory distance, which likely varies with energetic demand (Bairlein and Gwinner 1994), affects the interactions among these three patch- and site-level covariates.

More specifically, we predicted that birds presented with a trade-off between fruit availability and cover would accept more risk (use patches with relatively less cover) than those not facing such a trade-off, given the high energetic demand of migration. Further, we expected that low raptor abundances should increase the impact of fruit availability on patch use within sites with a trade-off, relative to sites with no such trade-off. Finally, we predicted that these two differences between trade-off and non trade-off sites would be greatest for species with longer migratory distances, as they are presented with the greatest energetic constraints.

3.3. Methods

3.3.1. Study location and general design

We sampled fall-migrating landbirds and their stopover habitat in the Downeast and Midcoast regions of Maine during 2011-2012 at six monitoring stations, including two coastal headland and four island sites (Figure 3.1). We considered each monitoring station as a largely independent stopover site. Each station was no closer than 10 km to the nearest station (mean nearest station distance ± SE is 23 ± 10 km; mean pairwise distance among all stations is 46 ± 9 km). Within each of our monitoring sites we sampled habitat use through bird captures, using passive mist-nets placed in a variety of different habitat types (see below).

We defined a 4-m buffered area around each mist net as a habitat patch within the stopover site. Within each site, nets were placed 4 – 398 m apart (μ ± SE = 119 ± 3 m). Four-meter-wide belt transects were established parallel to each net. While capture within a patch does not require that an individual be using a patch for foraging or crypsis (e.g., passage use during movement between other patches), capture rates should increase as individuals spend longer within a patch, and there is no reason to suspect that any other type of use would correlate with either structural cover or fruit availability. Capture rates should thus serve as an adequate index of patch use.

We sampled three islands ranging in size from 0.75 km² (Great Duck Island: 2011) to 1.30 km² (Metinic Island: 2011) to 280 km² (Mount Desert Island). We sampled two locations on Mount Desert Island: one at the most southern coastal headland (Seawall: 2011-2012) and one 16-km to the north in the interior of the island (McFarland Hill: 2011). The three islands vary in their distance from the nearest mainland (Mount Desert Island = 1 km, Metinic Island = 8 km, Great Duck Island = 23 km). We also sampled the headlands of two peninsulas: Schoodic Peninsula (2012) and Petit Manan Point (2011-2012). The entire sampled region stretches 114 km from Metinic Island in the southeast to Petit Manan Point to the northeast. All six migration stations possess four broad vegetation types: forest dominated by *Picea* species (with *Alnus, Larix, Betula, Acer,* and *Populus* species); shrubland dominated by *Alnus, Aronia, Sorbus*, and *Ilex* species; mowed or grazed grassland; and a mixture of edge habitats among these broader types. These stations were all located on protected conservation lands and operated in collaboration with researchers at Acadia National Park, the Maine Coastal Islands National Wildlife Refuge, The Nature Conservancy, and the University of Maine.

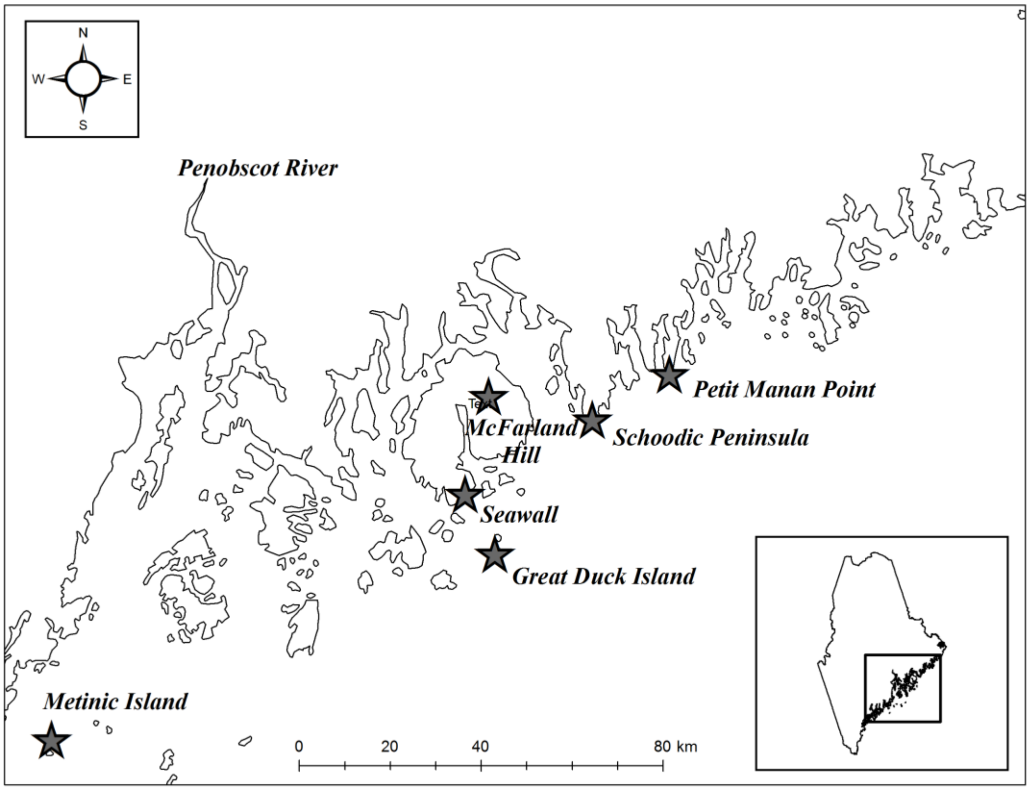


Figure 3.1. Diagram of six migration monitoring site locations within the Downeast and Midcoast regions of Maine.

3.3.2. Bird surveys

We surveyed migrant landbirds during fall migration in 2011 (16 August to 28 October), and 2012 (18 August to 18 October) using passive mist-netting. Nets were opened 30 minutes before sunrise and closed six hours after opening, weather conditions permitting. The specific nets and the total number of nets opened on any given day varied with weather conditions, most commonly with the presence of strong winds or rain. Number of nets at the sites ranged from 14 – 20. The range of site area (summed 4-meter buffer areas around all nets) was 2143 – 2912 m^2. We fit all captured birds with a uniquely numbered aluminum band.

Foraging habitat use was defined as the number of birds caught per week for each species, patch, and year. Birds recaptured within the same season were excluded from the dataset. Due to the difficulty of separating resident individuals from migratory, we removed all species found year-round at our sites from analyses. We also removed all species whose migratory diet did not include fruit, because we used fruit availability as our index of food resources. Species' diets were determined using previous categorizations created from three sources (Erickson et al. 2011, Parrish 1997, Suomala et al. 2010). We further excluded species when we captured fewer than 50 birds across all sites and years, because rare species introduced many zero weekly capture counts, causing overdispersion. To account for the hierarchical nature of habitat selection in migratory birds (Hutto 1985), we kept all zero counts at nets when species were caught at that net sometime during the migratory season (i.e., birds are available to use the patch, but the patch was not selected during a given time period). However, we dropped all zero counts at nets when a given species was either never captured at that site during a given year (i.e., birds never selected the site and were therefore unavailable to select a patch secondarily) or never captured at that net during any time period within the year (i.e., birds may have selected the site, but it is impossible to distinguish between the lack of patch selection due to a preference for another patch or the lack of patch selection due to its unsuitability to the species' niche more broadly).

Together with species, age, sex, and morphological measurements, the amount of subcutaneous fat in the furculum and abdomen was recorded. Fat was scored on a scale of 0-5; 0 = none; 0.5 = trace; 1 = lining furculum; 2 = filling furculum; 3 = mounded in furculum and beginning to cover abdomen; 4 = mounded on breast and sides of abdomen;

5 = covering breast and abdomen (no or very little skin visible). Although individual fat load has been shown to affect anti-predator behavior and foraging in other migration studies, we did not include a metric for individual energy reserves in our analysis. Preliminary data exploration indicated that there is not a biologically significant difference in the mean fat scores across trade-off versus non trade-off sites (μ ± SD: trade-off group 1.46 ± 1.75, non trade-off group 1.06 ± 1.37). Therefore, any reported differences between patch use at trade-off and non trade-off sites cannot be due to a difference in the mean energy reserves of the population selecting patches.

3.3.3. Migratory distance

Landbird species differ in their energetic constraints and consequently in their habitat needs at migratory stopover (Moore et al. 1995). These energetic differences may drive differential habitat use by species. We included each species' migratory distance as a potential predictor of habitat use to capture this variation with energetic demand. Migratory distance was calculated by obtaining each species' most northern and southern non-breeding range limits based on Cornell Lab of Ornithology range maps (Erickson et al. 2011), determining the latitudinal midpoint of each species non-breeding range, and calculating the latitudinal distance from the capture region to this midpoint (McCabe and Olsen 2015). This method provides a continuous estimate of the median distance left to travel for each species.

3.3.4. Raptor abundance

Predation pressure was measured in the field by recording all birds of prey seen utilizing, not merely flying over, the migration banding stations during hours of banding operation. Our raptor abundance variable is a weekly raptor total for each banding site divided by the total number of hours nets were open at each site to control for the varying effort. The most common avian predator species observed at our sites were merlin (*Falco columbarius*), sharp-shinned hawk (*Accipiter striatus*), and peregrine falcon (*F. peregrinus*), predators that do not hunt in dense cover (Fransson and Weber 1997, Niles, Burger, and Clark 1996, Raim, Cochran, and Applegate 1989).

3.3.5. Habitat patch measurements

Within each habitat patch, two 4-m wide belt transects running parallel to the net were established. The transects were placed outside the areas directly affected by the maintenance of the net lanes.

Woody stem density was measured down the center of each 4-m belt transact by counting stems in one-meter intervals at two heights (0.5 m and 1.5 m). We then summed the stem counts across both transects along each net for each height and averaged the sums from the two heights to provide us with a single continuous stem density count per patch.

We used ripe fruit abundance as a measure of food availability. While the use of patches with high fruit abundance does not necessitate that birds are foraging on fruit, there are few obvious alternative behavioral mechanisms that could produce a positive relationship between patch use and fruit availability among frugivorous birds that are not related to foraging behavior (or flocking with those species that are), especially once we control for habitat structure (using the multivariate approaches described below).

We recorded ripe fruit abundance weekly along the two belt transects for each mist net. We assessed fruit abundance for several shrub species, including chokeberry (*Photinia melanocarpa*), wild raisin (*Viburnum* sp.), pin cherry (*Prunus pensylvanica*), low and high bush blueberry (*Vaccinium* sp.), huckleberry (*Gaylussacia* sp.*)* and two *Rubus* species. We excluded bayberry (*Myrica pensylvanica*) because only one species, Yellow-rumped Warbler, is able to digest its waxy fruits (Borgmann et al. 2004, Place and Stiles 1992). Chokeberry, wild raisin, and pin cherry were the majority of fruiting species at all sites. The numbers of individual fruits were estimated for each species using a modified scale with eight abundance categories, first developed by Smith and McWilliams (2009). Abundance categories where defined as 1 (≤ 10 ripe fruits), 2 (11-25 ripe fruits), 3 (26-100 ripe fruits), 4 (101-250 ripe fruits), 5 (251-1,000 ripe fruits), 6 (1,001-3,000 ripe fruits), 7 (3,001-10,000 ripe fruits), and 8 (≥ 10,000 ripe fruits). To attain our continuous fruit availability variable we summed the categorical midpoints of estimated ripe fruit abundance across both transects for each week.

3.3.6. Statistical analysis

3.3.6.1 Identifying site trade-offs

For each week we modeled ripe fruit availability as a function of stem density across all habitat patches for each site using quantile regression ($\tau = 0.80$), using the R package “quantreg” (Koenker 2013, R Development Core Team 2012). We used quantile regression to describe the relationship between the 80th percentile of fruit availability for a given stem density. This allowed us to identify sites with patches that had both high cover and abundant fruit versus sites that lacked such patches during a given week. Site-weeks (hereafter "sites") for which there was a negative relationship between fruit availability and stem density were labeled as trade-off sites, and sites with a positive relationship were categorized as non trade-off sites. Although banding stations have similar broad habitats, fruiting plant species diversity, abundance, and fruiting phenology differ within and among sites. By modeling weekly relationships between fruit and cover, we thus allow patches to exhibit trade-offs between fruit availability and cover variously through time with patch fruiting phenology.

3.3.6.2. Model selection

Based on *a priori* hypotheses about the differences in foraging habitat use between trade-off and non trade-off sites, we constructed a set of candidate models. We then used model selection to determine which combination of predictors explained patch use best and whether use differed for sites with or without a trade-off between food and cover. To test our hypotheses we constructed a series of generalized linear mixed effects models with weekly species counts modeled as a negative binomial distribution with a log-link function and an offset of weekly net hours (to account for effort). We used a negative binomial distribution to account for overdispersion and zero-inflation in our capture data. We repeatedly measured captures of 28 species at 144 patches weekly over two years; therefore, species and patch identity were included as random effects. We fit the generalized linear negative binomial mixed models with the R package "lme4" (Bates et al. 2014). All models included year and week as fixed effects accounting for the differences between years and to control for variation in the phenology of the migratory community. Weekly fruit availability measurements were heavily skewed, thus we square-root transformed the variable. The relationship between bird abundance and week is non-linear; therefore we added a quadratic term for week in all models. As our hypotheses were concerned only with relative foraging patch use for the migratory community in sites with and without a trade-off between food and cover, we did not disentangle differences in captures due to true abundance versus detection probability. We should note, however, that our methods assume that detection probability is similar within a given site, year, and species for all nets within a site.

The candidate model set consisted of eight models (Table 3.1). All models aside from the null model included year (2011 or 2012), week (linear and quadratic terms), fruit availability, trade-off (yes or no), raptor abundance, stem density, and migratory distance as single variables. Additive models of these single variables describe each variable's overall effect on patch use. For example, fruit availability as a single variable only explains whether more or fewer birds were captured at patches with varying fruit availability. To test our hypotheses that the relationship between bird use and fruit availability varies with risk and migratory strategy, we used a series of two and three-way interactions.

Specifically the model set contained: A) three models, each with one two-way interaction between fruit availability and either stem density, migratory distance, or raptor abundance; B) three, three-way interaction models formed by interacting trade-off with each of the two-way interactions above (plus their associated two-way interactions and main effects); C) one model containing only the single variables: fruit availability, migratory distance, trade-off status, stem density, and raptor abundance; and D) a null model, containing only year and week as fixed effects. The three two-way interactions test whether the relationship between fruit availability and patch use varies by risk (indicated by raptor abundance and the inverse of stem density) and energetic strategy (indicated by migratory distance). The three-way interactions then test whether any of these relationships differ between sites with and without a tradeoff between food and cover.

We standardized all of our continuous candidate variables by subtracting the mean and dividing them by the standard deviation. By standardizing the variables we can directly compare the parameter estimates among our candidate variables to describe the strength of the difference between trade-off and non trade-off sites.

We used Akaike's Information Criterion (AIC) to rank models based on their ability to explain variance in the data and used Akaike weights (w_i) to estimate the relative likelihood of each model given the data (Burnham and Anderson 2002). We considered models with ΔAIC < 2.0 to be equivalent (Burnham and Anderson 2002). We assessed model fit (including the random variables) by calculating the conditional R^2. We used the "Wald" method to calculate 95% confidence intervals around the parameter estimates of the top model.

3.4. Results

During the 2011 and 2012 fall migration seasons, we captured 9,649 migrant birds belonging to 28 species of 7 families. We operated nets for 27,544 hours over 144 net-years. The number of sampling days for each site during a given year ranged from 33 –

55 days (μ ± SE = 43 ± 3.1 days). Yearly net effort for individual banding stations ranged from 2,122 – 4,363 net hours. The weekly predation pressure averaged 0.033 (SD=0.004, n=24 site-weeks, range=0-50 raptors per site-week) and 0.005 (SD=0.036, n=35 site/weeks, range=0-11 raptors per site/week) raptors per net hour for 2011 and 2012 respectively.

A trade-off between cover and fruit availability was present during 15 site-weeks and the trade-off was absent during 46 site-weeks. Fruit availability and stem density differed between years and by trade-off group. Stem density varied between years because the sites operated varied between the two years. Fruit availability was higher in 2011 (μ ± SE = 21.76 ± 1.56 fruit/effort) than 2012 (6.74 ± 0.72) and higher among trade-off sites (22.17 ± 2.44) versus non trade-off sites (13.27 ± 1.02). Stem density was slightly lower among patches measured during 2011 (7.29 ± 0.22 stems) than 2012 (7.97 ± 0.22) and lower at the trade-off sites (6.19 ± 0.30) versus the non trade-off sites (8.05 ± 0.18).

Our top-ranked model predicting variation in patch use contained a two-way interaction between fruit availability and migratory distance (and the associated main effects), controlling for the single variables for raptor abundance, trade-off status, stem density, year, and week (model weight = 0.82: Table 3.1). Our final model fit the data reasonably well (conditional $R^2 = 0.40$) and was not overdispersed, with a ratio of the sum of squared Pearson's residuals to residual degrees of freedom of 1.08.

Within the top-ranked model we found important effects of week, year, trade-off status, raptor abundance, stem density, and the interaction between fruit availability and migratory distance (Table 3.2). The largest effect on predicted capture rates was week; as the season progressed, captures increased toward the beginning at all sites and decreased at the end (Table 3.2). Model-predicted capture rates were higher at non trade-off sites (μ ± SE = 0.018 ± 0.0001) versus trade-off sites (0.011 ± 0.00007) during 2011 and 2012 (non trade-off: 0.011 ± 0.00006 versus trade-off sites: 0.009 ± 0.00006), and at sites with high raptor abundances (Table 3.2). Controlling for all other factors, birds preferred patches with higher stem density (Table 3.2). Fruit had little effect on the capture rates of shorter distance migrants; however, as migration distance increased, species were captured more and more preferentially in patches with high fruit availability (Table 3.2 and Figure 3.2).

Table 3.1. AIC model selection results for all models explaining migrant landbird stopover use of patches. All models include the variable "year" and "week". "Fruit Avail." is an index of ripe fruit abundance within a habitat patch; "Trade-off" indicates whether or not there is a negative relationship between stem density and fruit abundance among patches within a site during a given week; "Stem Den." is an index of vegetative cover within a patch; "Migration Dist." is the median latitudinal distance left to travel for each species; and "Raptor Abund." is an index of predation risk to landbirds at each site during a given week.

Model	*AIC*	ΔAIC	w_i
1. Fruit Avail. + Trade-off + Stem Den. + Migration Dist. + Raptor Abund. + (Fruit Avail. x Migratory Dist.)	24816.7	0	0.815
2. Fruit Avail. + Trade-off + Stem Den. + Migration Dist. + Raptor Abund. + (Fruit Avail. x Migratory Dist. x Trade-off) + (Fruit Avail. x Migratory Dist.) + (Trade-off x Fruit Avail.) + (Trade-off x Migratory Dist.)	24819.8	3.1	0.173
3. Fruit Avail. + Trade-off + Stem Den. + Migration Dist. + Raptor Abund + (Fruit Avail. x Raptor Abund.)	24825.6	8.9	0.010
4. Fruit Avail. + Trade-off + Stem Den. + Migration Dist. + Raptor Abund. + (Fruit Avail. x Raptor Abund. x Trade-off) + (Fruit Avail. x Raptor Abund.) + (Trade-off x Fruit Avail.) + (Trade-off x Raptor Abund.)	24828.9	12.2	0.002
5. Fruit Avail. + Trade-off + Stem Den. + Migration Dist. + Raptor Abund. + (Fruit Avail. x Stem Den.)	24831.8	15	<0.0001
6. Fruit Avail. + Trade-off + Stem Den. + Migration Dist. + Raptor Abund. + Stem Density	24832.2	15.5	<0.0001
7. Fruit Avail. + Trade-off + Stem Den. + Migration Dist. + Raptor Abund. + (Fruit Avail. x Stem Den. x Trade-off) + (Trade-off x Fruit Avail.) + (Trade-off x Stem Den.)	24836.3	19.5	< 0.0001
8. Null	24904.9	88.2	< 0.0001

Table 3.2. Parameter estimates with 95% confidence intervals for all variables within the top model predicting capture rates at migratory stopover sites within the Gulf of Maine. Bold represents parameters where the 95% confidence intervals do not bound zero.

Parameter	***Estimate***	***95% CI***
Intercept	-4.28	(-4.53 -4.03)
Week (linear)	**0.73**	**(0.55, 0.90)**
Week (quadratic)	**-0.39**	**(-0.57, -0.21)**
Year	**-0.15**	**(-0.26, -0.04)**
Stem Density	**0.08**	**(0.01, 0.15)**
Trade-off Status	**-0.24**	**(-0.34, -0.13)**
Raptor Abundance	**0.22**	**(0.17, 0.28)**
Fruit Availability	-0.01	(-0.05, 0.04)
Migratory Distance	-0.05	(-0.30, 0.19)
Fruit Avail. x Migration Dist.	**0.08**	**(0.04, 0.11)**

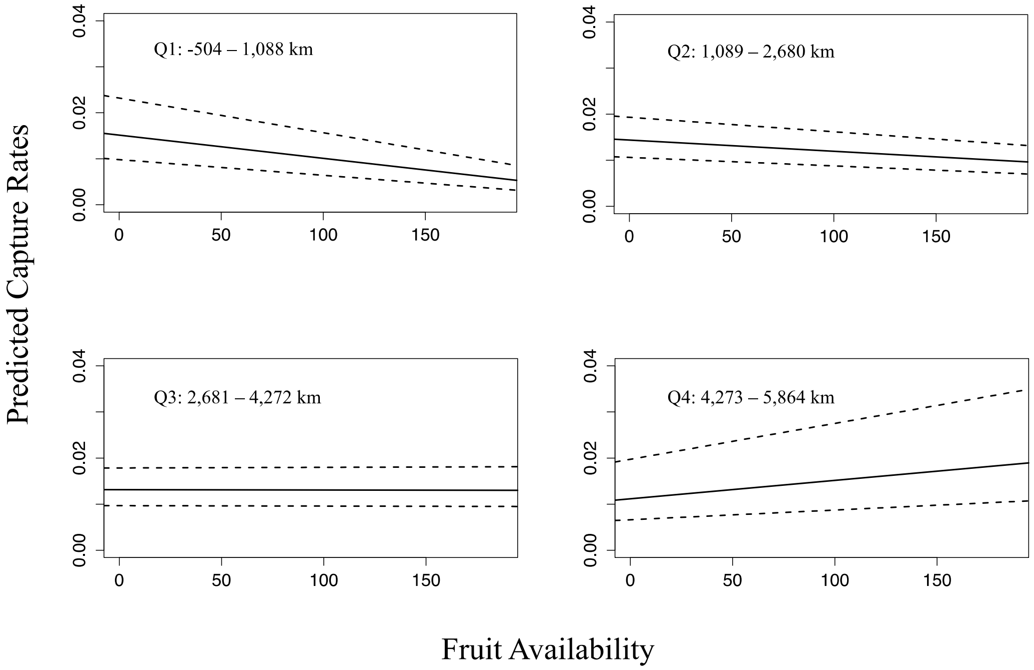


Figure 3.2. Effect of fruit availability (square-root transformed) on predicted capture rates (± 95% CI) for four different migratory guilds (split by quartiles of the latitudinal distance from our study region to the mid-point of the non-breeding range) at all stopover sites.

3.5. Discussion

Animals have been repeatedly shown to modify their foraging choices to reflect both foraging success and predation risk (Lima and Dill 1990). In situations where individuals are food deprived or engaged in energetically costly events, however, they may make more “risky” foraging decisions (Pomeroy et al. 2008, Metcalfe and Furness 1984). In a community of species actively engaged in migration, we predicted that capture rates would be higher at patches with higher fruit abundance among sites where individuals had to choose between patches with high food availability or high cover. Further, we predicted that at sites without a trade-off, capture rates would be positively correlated with both fruit abundance and cover. Instead we found that birds preferentially used patches with high cover regardless of the presence (or absence) of a trade-off at the site, once we controlled for predator abundance. Further, fruit availability was only predictive of patch use among the longest distance migrants, again regardless of the presence of a trade-off between food availability and cover. Overall bird abundance, however, was highest at sites without a trade-off.

Migrants approaching stopover are constantly assessing their surroundings and making decisions at finer and finer spatial scales (Hutto 1985). Our results are consistent with this hierarchical stopover decision-making process and suggest that site selection may be more important than patch selection to explain habitat use at time scales of a week or greater. We hypothesize that migrants rapidly assess the relative safety and productivity of a site, departing sites more rapidly if there is a trade-off between foraging and safety. Assuming similar landing densities among our sites, longer stopover times at higher quality sites would explain the patterns we report here.

Patch use among longer distance migrants was explained by fruit availability across all sites (Figure 3.2), which is concordant with our assumption that these birds have higher energetic demands (i.e., are likely to accept more risk during foraging). This pattern could also be explained by a bias in more specialized frugivory (during migration) among the longest distance migrants. Given the advantages of a more frugivorous diet during stopover that have been reported in a number of landbird species (Bairlein 1998, Long and Stouffer 2003, Newton 2008, Parrish 1997, 2000), long-distance migrants may select habitats higher in fruit resources, regardless of their diet during non-migratory periods, in order to gain weight more efficiently during stopover. Such behavior minimizes the time spent on stopover, in turn shortening total migratory passage time, and is one of the hallmarks of a "time minimizer" migration strategy (Alerstam and Lindström 1990, Hedenström and Alerstam 1997). Short-distance migrants are generally assumed to be less constrained by time and to depart stopover sites with lower mass loads (Hedenström and Alerstam 1997). Doing so allows them both to be more cautious on stopover (Metcalfe and Furness 1984) and increases their escape velocity and maneuverability (Kullberg, Fransson, and Jakobsson 1996), both of which lessen predation risk at a cost to migration time (Alerstam and Lindström 1990, Seewagen and Guglielmo 2010). Here we support this overall paradigm, showing that shorter distance migrants prioritized patches with high cover (low predation risk) at all sites, whereas longer distance migrants compromised between cover and food availability when presented with a trade-off.

It's important to note that our measure of fruit availability was a weekly calculation, and the timing and composition of fruiting plants at a stopover site may vary at even finer time scales. However, using similar data collected at the same sites as this study, Olsen et al. (2015) found that food resource phenology, along with other ephemeral resources (deciduous leaf drop and soil moisture), predicted patch use throughout the migratory season better than static habitat structure (i.e., vegetation cover and height). Ripe fruit abundance was positively associated with the capture rates of Parulidae, Emberizidae, and Vireonidae but was unrelated to capture rates of Tyrannidae. Results from Olsen et al. (2015) and this study confirm the importance of within-season variation in resource availability for predicting migrating songbird habitat use.

Vegetation structure is an essential factor shaping birds' habitat choices (Wiens and Rotenberry 1981), as it can provide information regarding shelter from predators (Deppe and Rotenberry 2008, Sapir et al. 2004). To assess habitat use of the migrant community, we used woody stem density as a proxy for protection from predation risk, where high stem density was assumed to equate to lower predation risk (Savino and Stein 1989). It is possible that individuals utilize other characteristics to select cover, such as percent vegetation cover or height, when searching out protection. Vegetation cover, height, and density, however, are often highly correlated (Vitz and Rodewald 2007), although this remains untested at our study sites. Previous fall migratory studies have found correlations between stem density and bird abundances (Suthers, Bickal, and Rodewald 2000, Rodewald and Brittingham 2002), although whether these correlations can be attributed to perceived protection or an association with food resources is unknown. Cimprich et al. (2005) found that both American redstarts (*Setophaga ruticilla*) and blue-gray gnatcatchers (*Poliopitla carerulea*) moved deeper into the shrubs when presented with a predation risk, demonstrating that migrants are indeed relying on vegetation as protection and perceive increased cover as increased protection. Additional behavioral studies are needed to determine the precise behavioral mechanisms responsible for the patch associations presented here.

Across all sites, capture rates were higher at sites with greater raptor abundances. Aborn (1994) also found a positive correlation between raptor and landbird abundances during spring migration along the Gulf of Mexico coastline. Correlations in abundances may be due to migratory behaviors that are similar across both avian groups, to predator movements tracking prey resources, or both. Beneficial weather patterns for migrating raptors are also advantageous for migrating landbirds (Aborn 1994, Moore and Kerlinger 1987, Woltmann and Cimprich 2003); neither group prefers to fly into a headwind or heavy precipitation. Also, landbird abundance along the Gulf of Maine is directly proportional to the amount of vegetated land available for stopover at the scale of a few kilometers (McCabe and Olsen 2015). It is reasonable to assume that similar behavioral processes are at work among raptor species. Since landbirds are an important food source for migrating raptors (Ydenberg, Butler, and Lank 2007, Aborn 1994), raptor movements might also track the abundance of their prey. For these reasons we hypothesize that increased landbird captures at high raptor sites is not related to landbird movements in response to raptor abundances. If, however, landbirds are unable to avoid sites with high raptor abundances due to these mechanisms, avoiding sites with a trade-off between cover and food might be the adaptive solution to a predatory constraint.

3.5.1. Conclusion

Migration is a critical event in the life cycle of most North American landbirds. With increases in both predation risk and energetic demand relative to stationary periods of the annual cycle, migration is inherently costly (Moore et al. 1995). Balancing predator avoidance with foraging is critical because of direct mortality risk and the costs of arriving late to either non-breeding or breeding grounds (Moore 1994). We suggest that migrating landbirds universally prioritize habitat patches with high cover but avoid sites where this cover is not correlated with the presence of food resources. Further, increased energetic demand (as indicated by migration distance) is associated with increased use of patches with abundant food resources regardless of cover. Our community-scale results thus corroborate past single-species behavioral research demonstrating that migrants prioritize foraging when energetic demand is high (Metcalfe and Furness 1984, Hebblewhite and Merrill 2009, Yasué, Quinn, and Cresswell 2003).

Important stopover habitat for the entire migratory community may be difficult to define (Hutto 2000). In this study, however, we found that when given the opportunity migrants prefer habitats with both high vegetative protection and high fruit resources. Both resources are typically found in edge-dominated, early successional habitats, which are not considered high quality breeding habitats for many of the species we studied here (Rodewald and Brittingham 2007, Suomala et al. 2010, Vitz and Rodewald 2007). Thus, landbird conservation efforts should consider not only prime breeding habitats, but also habitats where migrants can find protection from aerial predators while efficiently and safely refueling. Additionally, habitats with fruit resources that occur during the migration seasons may be particularly important. More study is needed to quantify the costs to bird condition and survival in sites that lack these resources.

CHAPTER 4: WIND PATTERNS AS A POTENTIAL DRIVER IN THE EVOLUTION AND MAINTENANCE OF A NORTH AMERICAN MIGRATORY SUTURE ZONE

4.1. Summary

Suture zones are areas where range contact zones and hybrid zones of multiple taxa are clustered. Such zones have been regarded as strong evidence for allopatric divergence. Migratory divides, contact zones between divergent populations that breed adjacent to one another but use different migratory routes, are a particular case of suture zones seen in many North American migratory songbirds. One major divide is along the eastern flank of the Canadian Rocky Mountains. The factors responsible for migratory divides, however, are not well understood. Hypotheses include geographic barriers, Late Pleistocene habitat expansions, and meteorological factors, specifically wind. We tested for the ability of wind alone to explain the evolution and maintenance of the Canadian Rocky Mountain migratory divide using individual-based models. Specifically, we examined the effects of atmospheric winds on populations of birds with breeding range boundaries on either side of the divide, by modeling their autumn migratory flight paths. Empirical observations of eastern birds suggest a circuitous migratory route, where birds cross Canada before heading south along the Atlantic coast. Western breeders, however, travel more directly south along the Pacific coast to their wintering grounds. We modeled bird flights by allowing them to float at elevation during the fall using modeled wind data from the European Center for Medium-range Weather Forecast, over ten random years between 1979-2012. Modeled eastern birds had mean trajectories toward the east while western breeders showed a mean orientation significantly more to the south. We also

determined that a mean bird airspeed of 18.5 m s^{-1} would be necessary to eliminate this difference in trajectory, resulting in the breakdown of the migratory divide. This airspeed is achieved only by the larger and stronger migratory bird species, such as shorebirds and waterfowl, species that do not show a migratory divide in this region. These results lend support for the importance of wind as a dominant influence on the maintenance of migratory divides in North America for songbirds.

4.2. Introduction

Hybrid zones and areas of contact between sister taxa often overlap across multiple, unrelated phylogenetic pairs (e.g. birds, trees, and mammals) across the world (Remington, Charles 1968, Hewitt 1996, Swenson and Howard 2005, Godfrey M Hewitt 1999, Swenson and Howard 2004). Using only spatially coincident hybrid zones, Remington (1968) proposed that there are 13 of these so-called suture zones in North America. Swenson and Howard's (2005) more recent work included both hybrid zones and contact zones between closely related taxa in their definition of suture zones and found support for these zones across North America. Multiple hypotheses for the formation and locations of suture zones have been proposed, including biotic range expansions out of shared glacial refugia (Remington, Charles 1968, Swenson and Howard 2005, Anderson 1948) and proximity to geographic barriers (Remington, Charles 1968, Swenson and Howard 2005).

Migratory divides are a special case of suture zones where the proximate cause of divergence is known, namely the distinct migratory routes of each population (Helbig 1996, Bensch, Andersson, and Akesson 1999, Delmore, Fox, and Irwin 2012, Ruegg and

Smith 2002, Rohwer and Irwin 2011, Møller et al. 2011). The ultimate cause of a migratory divide, however, must be a mechanism that maintains migratory route divergence in the face of parapatry (or sympatry in some extreme cases) and potential gene flow. A similar problem is presented by attempts to explain any suture zone, but in the case of migratory divides, the explanation must explain divergence among populations where individuals possess significant dispersal abilities. Mere geographic isolation is unlikely the ultimate cause. An understanding of migratory divides, therefore, provides a window into the mechanisms producing not only suture zones but also parapatric divergence more broadly.

Migratory divides have been identified for Passerine songbirds across the world. The most well studied is the Central European divide, where populations migrate either southwest or southeast of the Mediterranean Sea on their way to their wintering grounds in Africa (Helbig 1991, Helbig 1992, Helbig 1996, Berthold and Helbig 1992, Berthold and Terrill 1988). Irwin and Irwin (2005) noted a Siberian divide north of the Tibetan Plateau where 85% of breeding species either migrate east or west around the plateau. Of the species that utilized both eastern and western routes, about half showed subspecific divergence that aligned with migratory route (Irwin and Irwin 2005).

The Canadian Rockies in North America also possess a divide where eastern and western taxa breed parapatrically or sympatrically and exhibit different migration routes and wintering grounds (Ruegg 2008, Ruegg and Smith 2002, Delmore, Fox, and Irwin 2012, Kelly and Hutto 2005, Toews, Brelsford, and Irwin 2011, Rohwer and Irwin 2011). Empirical observations of diverse eastern migrants suggest a circuitous migratory route, where birds fly even further east before heading south. Western breeders, however, travel more directly south. For example, Kelly and Hutto (2005) found that of the 51 North American wood warblers, 41 have distinct eastern and western routes, eight have distinct eastern and western haplotypes, and only two, American redstart (*Setophaga ruticilla*) and black-and-white warbler (*Mniotilta varia*), have ranges that span the divide. Using geolocators, Delmore et al. (2012) were able to confirm a Canadian Rocky Mountain migratory divide between eastern and western subspecies of Swainson's thrushes (*Catharus ustulatus*). For a compiled species list associated with this divide and their related references see Tables 1 and 2 in Rohwer and Irwin (2011).

Selection pressures that maintain differential migratory behaviors in the face of gene flow could be the result of differential costs of migration in terms of time, energy, or survival (Helbig 1996). Natural selection often optimizes migratory behaviors to minimize time spent traveling or total energy expended on migration (Alerstam and Lindstrom 1990). Both ecological barriers (Rappole et al. 1979, Alerstam 1979, Gauthreaux 1980, Moore et al. 1995, Gauthreaux et al. 2005) and meteorological factors (e.g., wind) (Richardson 1978a, Alerstam 1979, Gauthreaux 1980a, Moore et al. 1995, Liechti and Bruderer 1998, Chapman et al. 2011) simultaneously affect the timing and energy expenditures of migrants, in turn influencing the evolution and maintenance of migratory routes (Irwin and Irwin 2005). As such, divergence in these factors is a logical hypothesis for the evolution and maintenance of migratory divides.

While no single hypothesis for the maintenance of migratory divides is mutually exclusive, there has been no direct test of the importance of wind or water currents. This mechanism, however, would be widely applicable to the maintenance of population structure and parapatric divergence for any organism that relies on the movement of a fluid for dispersal. In this study we created an individual-based model to simulate the autumn migration of bird populations from either side of the Canadian Rocky Mountain divide. We used this model for two objectives: first, we tested for a wind divergence along the migratory divide by modeling the movement of birds with no flight trajectory (i.e., “floating”); second, we solved for the airspeed necessary for a bird’s vector (magnitude and direction) to overpower any wind divergence along the divide and cause the migratory divide to collapse. These tests will determine whether wind divergence alone is an adequate mechanism for maintaining distinct migratory directions and to predict which taxa fly at sufficiently slow speeds to experience differential selection on migratory orientation.

4.3. Methods

4.3.1. Individual-based model

We developed a spatially explicit, individual-based model in MATLAB (Mathworks 2012), simulating avian migration from populations located on either side of the Canadian Rocky Mountain migratory divide. The model’s domain encompasses most of North America from eastern Alaska, USA to western Labrador, Canada (Figure 4.1) during fall migration (September – October) over 33 years (1979-2012).

In the model birds are given an elevation (via air pressure) and an explicit starting location and time (local sunset) and are then allowed to interact with the modeled wind data for a migratory flight each night (6 hours), followed by a stopover period during the following day. Using values from the literature we defined the time of flight start, length of migratory flights, and air pressure of flight elevation.

We modeled bird migration starting from explicit locations on either side of the migratory divide. We subsampled the two sides by randomly choosing 12 starting locations within a 15,082 km^2 area on either side of the suture zone represented by the breeding range margins of 25 phylogenetic pairs of avian taxa (Figure 4.1; Tables 1 & 2 in Rohwer and Irwin 2011).

We modeled bird movement at each location starting at sunset and continuing for six hours nightly, because nearly all North American songbirds are nocturnal migrants (Able 1973). Observational and radar studies indicate that nightly migration begins near sunset and ends before sunrise, with a peak near midnight (Drury and Keith 1962, Gauthreaux 1971, Able 1973, Alerstam 1976, Richardson 1978, Kerlinger and Moore 1989).

We modeled bird flights in the wind stream at three isobaric levels, 925 mb, 850 mb, and 750 mb, corresponding to altitudes of approximately 750 - 2,500 m above sea level. We chose these three isobaric levels both to encompass the altitudinal range with the highest densities of migrants in studies from both North America and Asia (Kerlinger and Moore 1989, Liechti et al. 2000, Gauthreaux et al. 2005) and also to test the sensitivity of our results to changes in flight altitude, about which little is known.

Autumn (September – October) atmospheric horizontal wind components were obtained from the European Center for Medium-Range Weather Forecast (Dee et al. 2011) for ten randomly selected years between 1979-2012 at a spatial resolution of 0.85º latitude and longitude. This selection of years maximized data quality and consistency. Since global circulation patterns have remained moderately steady from glacial times to the present (Williams and Webb 1996, Preusser et al. 2002, Gauthreaux et al. 2005), however, the last 30 years of wind patterns should adequately represent circulation patterns from as far back as 10,000 years ago. Wind data were linearly interpolated in time from the original 6-hour resolution to predict hourly conditions and bilinearly interpolated in space for a finer spatial resolution.

4.3.2. Testing for the effects of wind

First, we simulated the effect of wind on the headings of the eastern and western populations by allowing them to float passively at each of the three isobaric levels. A drag force, or air resistance component was not considered in the model. The model recorded the heading of each individual bird as they crossed a radius of 500 km from their starting location, a distance corresponding to a flight of at least one complete night (Hedenström and Pettersson 1987, Bensch, Andersson, and Akesson 1999) beyond the starting location. If a bird did not reach 500 km after one night's flight (6 hours), the model omitted the daytime hours and began again at sunset the next night, and so on until the birds reached 500 km. We than tested for significant differences between the headings of the two populations and the time it took to reach 500 km at each air pressure level. We were interested in any differences in time as faster times equate to shorter migration lengths and more efficient energetic expenditure during migration. Any differences in time could therefore suggest how wind currents apply selection to the evolution of migrant behavior.

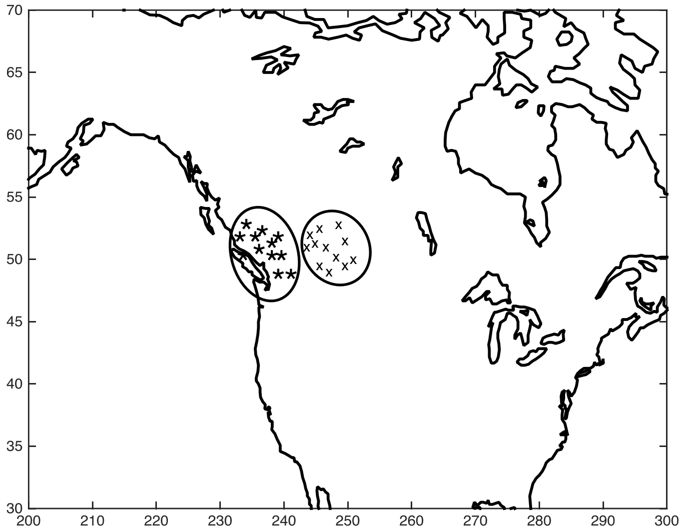


Figure 4.1. Map illustrating model starting locations representing the migratory divide among many North American sister species and subspecies. Western migrant's starting locations (n= 12) are denoted as stars, while eastern migrants (n = 12) are x's.

Second, we calculated the bird airspeed necessary to eliminate any differences between the headings of the two modeled populations (and thus the airspeed necessary to prevent a migratory divide). Typical airspeeds of migrating songbirds range from 10-15 m s^{-1} (Bloch and Bruderer 1982, Bruderer and Boldt 2001), although other groups like shorebirds and waterfowl migrate at faster speeds (mean 20 m s^{-1}: Williams 1985, Bruderer and Boldt 2001). We ran the model again from the same starting locations and times of the previous "floating" test, giving each bird a heading equal to the midpoint between the two population headings from the first analysis (102.5°).

We tested airspeeds of 0-30 m s^{-1} in intervals of 0.5 m s^{-1} at the median altitude of 850 mb. Due to the minimal variation between model results at the three isobaric levels (see results) we used only 850 mb for this second simulation. We chose 850 mb over the other altitudes for two specific reasons. First, many migration modeling studies use similar isobaric levels (McLaren, Shamoun-Baranes, and Bouten 2012, Erni, Liechi, and

Bruderer 2005). Second, the atmosphere within altitudes close to the surface is exposed to topographic distortion by the Rocky Mountains, while 850 mb is typically found above the planetary boundary layer in the lower troposphere, where the effects of surface friction are negligible. This is important because we were interested in isolating the effect of wind from geography.

We introduced random stochasticity into the birds' headings at the start of every nightly flight based on variation observed in previous field studies. We selected a random heading from a wrapped normal distribution with a mean equal to 102.5^{o} and an angular deviation of 38^{o} (Erni, Liechi, and Bruderer 2005, Moore 1984), corresponding to a mean vector length, r, of 0.803 (Batschelet 1981, Fisher 1993). We ran the model ten times to incorporate sampling error and averaged the results to determine the speed at which the migratory divide would collapse. Thus, in the first model birds were influenced only by the wind, while birds in the second simulation were influenced by their own airspeed, endogenous orientation, random stochasticity, and wind currents.

4.3.3. Statistical analysis

We used the Rayleigh test of uniformity (Batschelet 1981) to calculate whether the mean angle of orientation differed from a random distribution for each group of modeled floating birds. The difference in mean angle of orientation between the two populations was analyzed at each flight altitude using the Watson's U^2 test (Batschelet 1981, Agostinelli and Lund 2013). We also tested for significant differences in the variance of the headings for both eastern and western populations. This was done by first rotating the distributions so the mean vectors coincided (allowing any differences in the distribution to be due to scatter) and then running a Watson's U^2 test on the rotated distributions.

We used a nonparametric Levene's test (Levene 1960) to test whether the length of time the two groups of modeled birds took to reach 500 km by floating in the wind differed from each other at each of the three isobaric levels. As our simulations involved a large number of modeled birds (n=1200 for each population), we have an increased risk of type 1 statistical error and the detection of differences that are not biologically relevant. To prevent this bias, we tested for significance in population mean headings and the time it takes to reach 500 km in ten subsets (n = 100 per population) of our full dataset, at each isobaric level.

To determine at what speed the migratory divide collapses in our second simulation, we found the speed at which the eastern and western populations no longer showed significantly different mean migratory headings for each of the ten model runs. We considered the mean headings to be similar when the 95% confidence intervals around the difference between the eastern and western populations mean headings included zero. We then averaged, across the ten model runs, the speeds where the confidence intervals first overlapped zero to estimate the airspeed of migratory divide collapse.

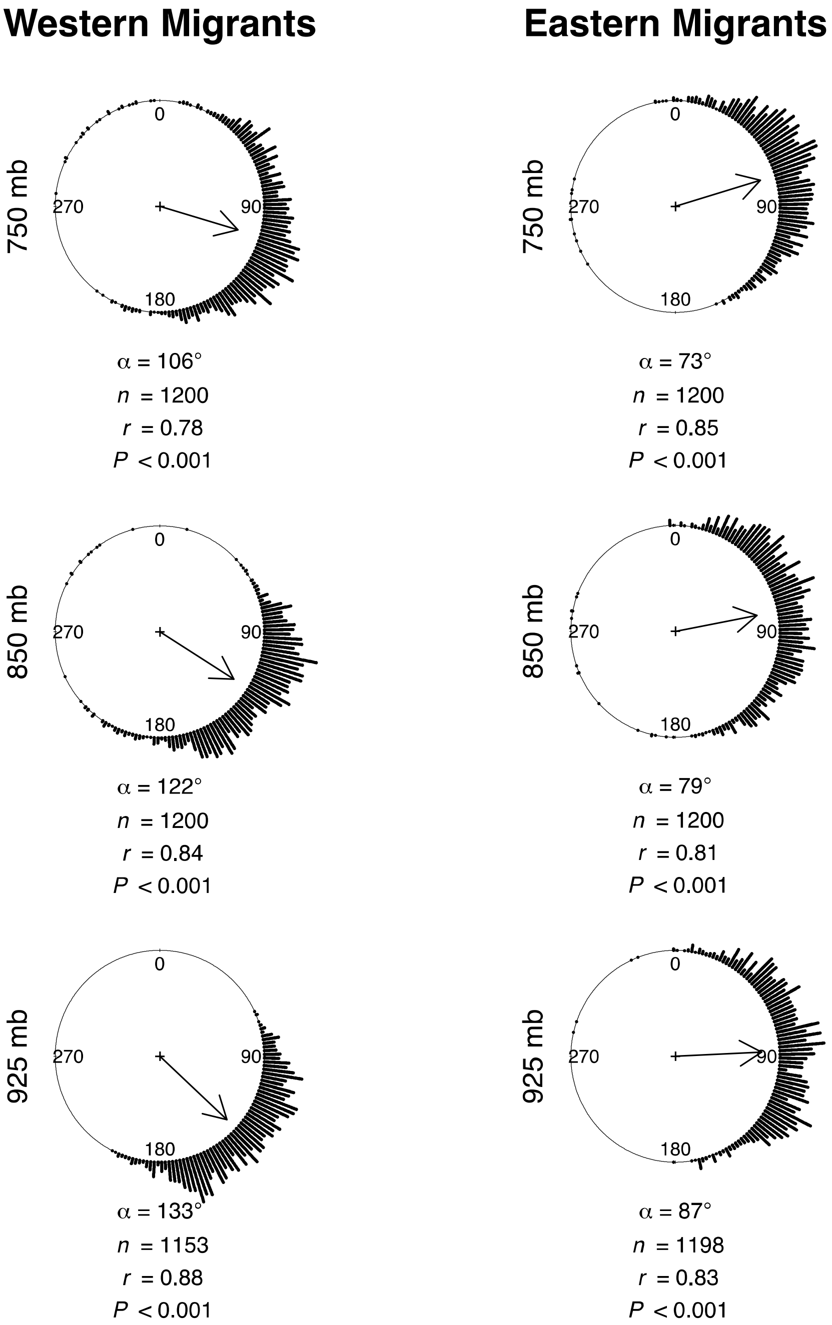
4.4. Results

4.4.1. Wind divergence across a migratory divide

We found a statistically significant difference at all three isobaric levels between the mean heading of populations on either side of the migratory divide after a migratory flight with a Euclidean distance of 500 km (Table 4.1 and Figure 4.2), indicating a wind divergence along the migratory divide. The mean direction of floating heading for eastern migrants differed from that of western migrants at 750 mb (east = 73^o, west = 107^o; Watson's U^2 = 8.5, $P < 0.001$), 850 mb (east = 79^o, west = 126^o; Watson's U^2 = 12.4, $P < 0.001$), and 925 mb (east = 87^o, west = 139^o; Watson's U^2 = 15.3, $P < 0.001$) (Table 4.1 & Figure 4.2). Eastern birds moved more directly east while western birds showed a mean orientation significantly more to the south (Table 4.1 & Figure 4.2). All ten subset datasets resulted in significantly divergent headings (Table 4.1). At the two lower elevations (the two higher air pressure levels: 850 & 925 mb), the variance in the heading of the eastern birds was significantly greater than at 750 mb (925 mb: Watson's U^2 = 0.6, $P < 0.001$ & 850 mb: Watson's U^2 = 1.2, $P < 0.001$), while the reverse was true for the western birds (925 mb: Watson's U^2 = 1.2, $P < 0.001$ & 850 mb: Watson's U^2 = 1.5, $P < 0.001$) (Table 4.1 & Figure 4.2).

Table 4.1. Mean headings (mean resultant vector with bootstrapped 95% confidence intervals) of simulated birds from two populations (n=1200 birds per population). The length of the arrow (r), as calculated using the Rayleigh test, is proportional to the strength in which the mean represents the sample (Batchelet 1981). Differences between the two population mean headings at each isobaric level were tested with the Watson's U^2 test, and the asterisk indicates that the heading difference was also statistically significant with 10 subset datasets (n = 100/population).

Isobaric level (mb)	*Population*	*Mean heading (º)*	*95% CI (º)*	*r*	*Difference in mean heading (º)*	*Watson's U^2 p value*
750	Eastern	73	(75, 71)	0.85	34	< 0.001 *
	Western	107	(109, 104)	0.72		
850	Eastern	79	(81, 77)	0.80	47	< 0.001 *
	Western	126	(128, 124)	0.81		
925	Eastern	87	(89, 85)	0.83	52	< 0.001 *
	Western	139	(142, 138)	0.86		



$\alpha = 106°$
$n = 1200$
$r = 0.78$
$P < 0.001$

$\alpha = 73°$
$n = 1200$
$r = 0.85$
$P < 0.001$

$\alpha = 122°$
$n = 1200$
$r = 0.84$
$P < 0.001$

$\alpha = 79°$
$n = 1200$
$r = 0.81$
$P < 0.001$

$\alpha = 133°$
$n = 1153$
$r = 0.88$
$P < 0.001$

$\alpha = 87°$
$n = 1198$
$r = 0.83$
$P < 0.001$

Figure 4.2. Bird headings (solid dots, in relation to geographic north) of modeled birds, from two populations on either side of a migratory divide, as they crossed a 500 km distance from their starting location. The mean direction (α) is represented by the arrow. The length of the arrow, *r* (the mean resultant vector length), was calculated using the Rayleigh test and is proportional to the strength in which the mean represents the sample (Batchelet 1981), the sample size (*n*), and the *P* value obtained from the Rayleigh test. The 95 % confidence intervals around the means can be found in Table 4.1.

As seen in Table 4.1 and Figure 4.2, the difference between the mean headings of the two populations was similar among isobaric levels. The smallest difference was seen at 750 mb (34º ± 0.02º), which corresponds to the highest elevation, and the greatest difference was found at 925 mb (52º ± 0.01º).

4.4.2. Floating time

Modeled eastern birds reached 500 km significantly faster than the western birds at all isobaric levels (Table 4.2).

Table 4.2. Mean number of hourly times steps, standard deviation (sd), and mean number of nights taken to travel. The F-value and P-values were obtained from the Levene's test of the difference between the two populations at each of three isobaric levels and the asterisk indicates that the heading difference was also statistically significant with 10 subset datasets (n = 100/population)

Isobaric level (mb)	***Population***	***Mean # of time steps***	***sd***	***Mean # of nights***	***F - value***	***p - value***
750	Eastern	28.58	19.93	4.76	55.06	< 0.001 *
	Western	36.29	27.26	6.05		
850	Eastern	58.64	47.67	9.77	10.04	0.002
	Western	77.81	48.87	12.97		
925	Eastern	95.88	59.5	15.98	174.82	< 0.001 *
	Western	138.72	80.92	23.12		

4.4.3. Divergence maintained under moderate airspeeds

At an average airspeed of 18.5 m s^{-1}, birds with an orientation of 102.5° were able to overcome the wind currents and eliminate any difference in the headings due to starting location (Figure 4.3).

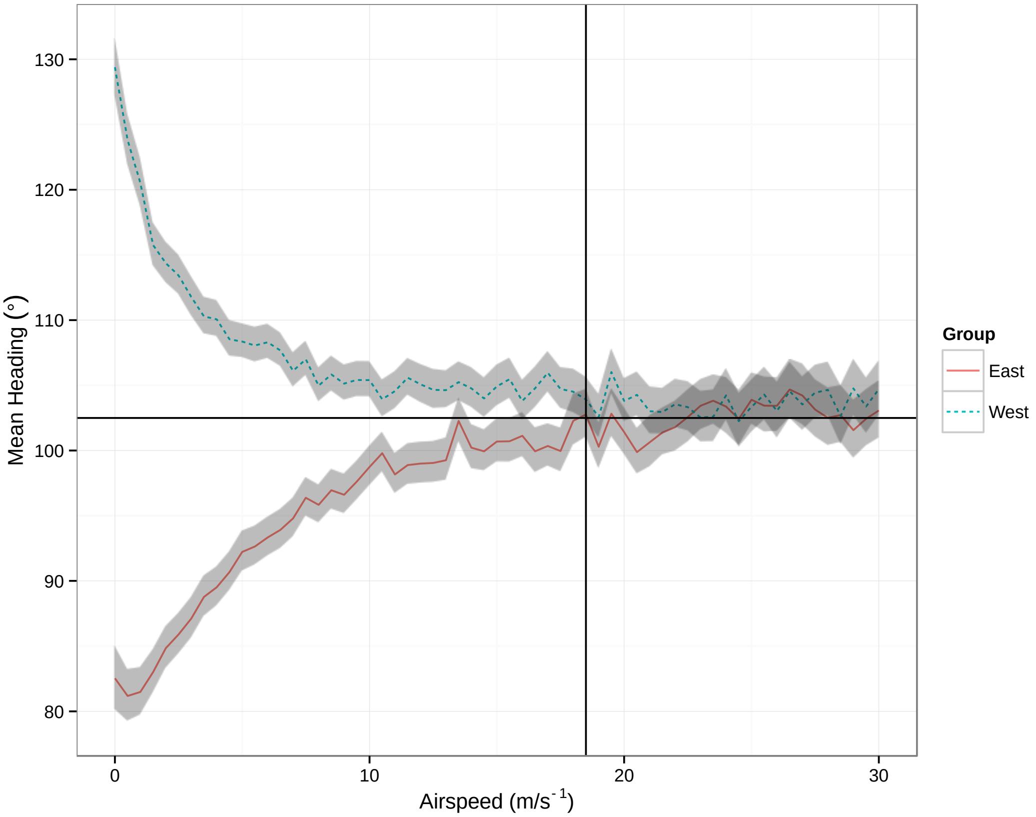


Figure 4.3. Modeled mean headings (± 95% CI) of migrants from either side of a migratory divide for airspeeds ranging from 0 to 30 m s^{-1} and an orientation direction of 102.5° (indicated with horizontal black line). The vertical black line indicates the speed (18.5 m s^{-1}) at which the populations no longer differ by their heading (i.e., migratory divide collapses).

4.5. Discussion

Results from this modeling exercise support wind as a driver in the evolution and maintenance of the Canadian Rocky Mountain divide for songbird species. Our first test revealed that the wind divergence was present at all three isobaric levels tested (Figure 4.1 & Table 4.1) and ranged from a 34º-52º difference between sites to the east and west of the divide. Similar differences in the migratory orientation directions of songbirds have been reported from wild populations that straddle a European migratory divide (39º: Bensch et al. 1999). Our second analysis tested what airspeed, with a given heading of 102.5°, would cause the migratory divide to collapse. We found that birds with airspeeds at or exceeding 18.5 m s^{-1} could overcome the wind vector and should therefore not exhibit a migratory divide on the eastern flank of the Canadian Rocky Mountains (Figure 4.3). The averaged speed, 18.5 m s^{-1}, is within the migration speed of both waterfowl (Bellrose and Crompton 1981, Meinertzhagen 1955) and shorebird species (Williams 1985), but above the flight speeds of songbird species who migrate below 15 m s^{-1} (Videler 2005, Bruno Bruderer and Boldt 2001). To our knowledge North American migratory waterfowl and shorebird breeding ranges do not demonstrate the same east – west pattern as we see with songbirds. We cannot confirm that the ability to overcome the wind is the mechanism behind the lack of a suture zone among these species, but the evidence does support that hypothesis. Our findings do not discount ancestral habitat expansion following deglaciation or geographical barriers as contributing factors in the formation and maintenance of this North American migratory divide; they merely provide strong support for wind as an influencing factor.

Across the northern hemisphere, there is ample evidence supporting the divergence of plant and animal species in isolated refugia during the Late Pleistocene (Pielou 1991, Ruegg and Smith 2002, Weir and Schluter 2004). Divergence in habitat preferences during these periods of refugia has been hypothesized to prevent populations from interbreeding freely upon secondary contact. Along the Rocky Mountain suture zone we investigated here, habitat is transitional between mixed-wood boreal forest east of the divide and conifer-dominated cordilleran forests to the west (Ruegg 2008, Toews, Brelsford, and Irwin 2011). Habitat preference differences have been shown across this divide in many warbler species complexes (Kelly and Hutto 2005, Toews, Brelsford, and Irwin 2011) and Swainson's thrush subspecies (Delmore et al. 2012). Hybrids between these two populations are presumed to exhibit intermediate habitat preferences that are not successful in either forest type (Toews, Brelsford, and Irwin 2011), thereby ecologically isolating the sympatric or parapatric breeding populations. Habitat preference divergence, however, cannot be the sole explanation in maintaining the divide, since the avifaunal suture zone is only present for migratory species. Year-round resident taxa in many taxonomic families (e.g. corvidae and picidae) do not show structure at the level of species or subspecies across the divide, while migratory taxa do. Further, only migratory taxa with flight speeds below 18.5 m s^{-1} align with the suture zone. Divergent habitat preferences cannot explain the taxonomic differences in alignment with the suture zone. Toews et al. (2011) also refuted habitat as the only driver of divergence at the hybrid zone between migratory Townsend's warblers (*Setophaga townsendi*) and black-throated green warblers (*Setophaga virens*), reporting that the two species defend territories next to each other and implying that pre-mating isolation based on habitat alone is unlikely.

Migratory divides are also thought to form when there is more than one optimal route around an ecological barrier (Irwin and Irwin 2005, Helbig 1992). Irwin and Irwin (2005) report two adjacent populations of the greenish warbler (*Phylloscopus trochiloides*) breeding in the northern forests of central Siberia that migrate to either side of the Tibetan Plateau. Hybrids are presumed to possess intermediate migratory directions over the Tibetan Plateau (Irwin and Irwin 2005), where survival would be dramatically reduced.

Birds breeding on either side of the Canadian Rocky Mountain divide may face similar restrictions on intermediate migratory directions, which would cause some species to travel over the Rocky Mountains and the deserts of the southwestern United States. Inland breeding populations of Swainson's thrushes from Alaska and British Columbia, however, appear to migrate over equally large mountain ranges as they migrate east (Ruegg and Smith 2002), making it unclear how a similar barrier would cause a migratory divide in one location and not another for the same species. Further, many songbirds take direct routes across habitat barriers that are larger and more inhospitable than the southwestern American deserts, such as the Gulf of Mexico (Moore and Kerlinger 1987, Yong and Moore 1993, Simons et al. 2000) and the Sahara desert (Biebach, Friedrich, and Heine 1986).

Wind, however, remains a strong candidate driver of the Rocky Mountain migratory divide. It explains which taxa are members of the suture zone and which are not; it has likely been a consistently operating force on the continent since deglaciation;

and optimality migration theory can explain why hybridization between taxa on either side of the divide is selected against. Birds should modify their behavior to minimize the expenditures of three main currencies: total migration time, total energy spent on migration, and predation risk (Alerstam and Lindstrom 1990, Chernetsov 2012). Assistance from wind can aid in both reducing energy expenditures and total time spent on migration (Richardson 1978b, Gauthreaux 1980b, Liechti and Bruderer 1998, Dänhardt and Lindström 2001, Liechti 2006). Our model does not calculate energy expended or saved, but we show clearly that the average tail winds would differ on either side of the migratory divide. In modeling and empirical studies in Europe, it is clear that flying downwind can net migratory songbirds large energetic gains relative to goal-oriented navigation (McLaren, Shamoun-Baranes, and Bouten 2012, McLaren et al. 2014, Shamoun-Baranes and van Gasteren 2011). We thus hypothesize that birds that align their orientation to the prevailing tailwinds of their starting location will net both faster and more energetically efficient migration, and that hybrids would perform worse than either parental population.

The preliminary descriptions of migration length we present here support this hypothesis by providing a possible explanation for the circuitous migration of the suite of species found on the eastern side of the migratory divide (Delmore, Fox, and Irwin 2012). Eastern birds in our model moved 500 km in significantly less time than their western counterparts (Table 4.2). Further, our calculated heading for the eastern population was very similar to empirical measurements of birds as they travel across the Canadian boreal forest (Ruegg and Smith 2002). Higher wind assistance would explain a circuitous route in eastern birds over a more geographically direct route south to their non-breeding grounds. While total distances are higher for eastern migrants using the circuitous route, they nonetheless arrive at their wintering grounds in comparable times to the western birds (Delmore et al. 2012). Our results provide a mechanism for this empirical observation.

We did find, however, some support for a combination of wind and geographic barriers in the maintenance of the Rocky Mountain migratory divide. Birds floating at 925 mb showed greater divergence in mean heading than birds modeled at our two higher isobaric levels (850 & 750 mb). The most divergent migration movements were thus made by birds migrating within the planetary boundary layer, where wind currents are affected by the earth’s topography. Birds from pressure levels chosen to represent altitudes not affected by the earth’s surface showed less of a difference in mean heading (Table 4.1 & Figure 4.1). This suggests that interactions between local geography and wind currents may be a factor in maintaining the migratory divide. Wind alone, however, was also adequate to maintain the divide.

4.5.1. Climate change and migratory divide

The prevailing westerly winds in North America are projected to slow by 1.0 to 3.2% and 1.4 to 4.5% over the next 50 and 100 years respectively (Breslow and Sailor 2002). If the prevailing winds decrease substantially, the migratory divide could collapse under a much lower airspeed, perhaps even for the slowest passerine species. As one example, the wind assistance given to the migrants on the eastern side of the divide may no longer be sufficient to maintain this route as optimal relative to more direct routes south. Genetic analysis of orientation vectors have shown that populations can shift their migratory direction in only a few generations (Berthold 1990, Helbig 1991, Irwin 2009) when a new strategy increases fitness relative to historical strategies (Bearhop et al. 2005). Without the migratory divide in place, we would expect to see an increase in the genetic mixing of the populations, in turn impacting North America's avifaunal biodiversity and the current trajectory of ongoing speciation events.

4.5.2. Currents and population structure

Fluids, such as wind and water currents, can impact genetic structure through migration and dispersal (Newton 2008, Shi, Kercelhue, and Ye 2005, Bohrer, Nathan, and Volis 2005, White et al. 2010, Szövényi et al. 2008). White et al. (2010) found that popular population genetics models (Kimura and Weiss 1964) that assume decreases in genetic dispersal probability with distance did not explain the complex genetic patterns found in marine systems. After accounting for currents by transforming distance into "oceanographic" distance, they found distance explained 50% of the variance in population genetics of an empirical snail larva (*K. kellettii)*. Additionally, a simulation study of Aleppo pine (*Pinus halpensis*) dispersal confirmed that long-distance dispersal through strong winds enhances metapopulation survival and slows the rate of genetic variability loss. In our study we show that currents may also provide isolating barriers and be sources of divergence. Given enough time, currents are likely important mechanisms both for creating and maintaining genetic teleconnections among populations and for parapatric or ecological speciation at areas where currents diverge. Consequently, including fluid dynamics into ecological and biological research will assist in explaining the earth's biodiversity.

CHAPTER 5: THE INFLUENCE OF WIND SELECTIVITY ON MIGRATORY BEHAVIORAL STRATEGIES

5.1. Summary

Weather impacts a migratory animal's decision to initiate migration. Although many factors influence an animal's choice to depart, currents are generally accepted as being one of the most significant. Currents have a very strong effect on the timing and energy expenditures of animals and therefore selection of favorable currents for departure is of foremost importance for optimal migratory performance. However, there is also a cost of waiting for favorable currents. The degree to which departure selectivity by nocturnal migrants influences the ultimate migratory strategies observed in wild flying birds remains uncertain. Here we conduct an optimality analysis to determine how wind selectivity affects three optimized migratory behaviors: time (total migration time), energy (total time spent in flight), and risk (whether or not migration was completed). To describe variation in these metrics under varying degrees of wind selectivity, we constructed an individual-based model (IBM) to simulate fall migration of small passerines across northeastern North America using different thresholds of wind profit, the distance per second the wind carries the bird towards its intended goal. A gradient of wind profit values were tested, from initiating flights only on nights when winds were directed in their preferred migratory direction (highly selective), to flying under most wind conditions (low selectivity). Our analysis indicated that relative mortality risk was lowest at intermediate selectivity and increased at both high and low threshold wind-profit values. Birds with increasing selectivity used less energy for migratory flight; however, there was an upper threshold beyond which no wind conditions ever met the

criteria for take off. Of those who successfully completed migration, those with the lowest selectivity spent less time on migration. By optimizing risk, time, and energy, we solved for an optimal range of wind selectivity for autumn migrants in northeast North America that agrees well with empirical values. Overall, we show that variation in wind selectivity at departure can produce migratory behaviors that mimic the classic "time-minimizer" and "energy-minimizer" strategies developed from measurements of wild birds.

5.2. Introduction

Air and water currents can be strong selective forces on the movements of migratory animals (Kemp et al. 2012, Richardson 1990, Chapman et al. 2010, Melià et al. 2013, Xue et al. 2008, Incze et al. 2010, Alerstam et al. 2011, Srygley and Dudley 2007). For instance, wind currents affect migration speed (Weber and Hedenström 2000, Alerstam et al. 2011), energy expenditure (Liechti 1995), resting (hereafter "stopover") behavior (Åkesson and Hedenström 2000, McLaren, Shamoun-Baranes, and Bouten 2012), and migration intensity (Van Belle et al. 2007, Erni, Liechti, and Bruderer 2002, Kemp et al. 2012, Åkesson and Hedenström 2000). Animals that engage in goal-orientated movements, such as migration, can therefore be expected to have evolved behavioral mechanisms for identifying and exploiting favorably directed flows (Chapman et al. 2011). Further, many taxa spend a considerable part of their annual cycle on migration, and it is therefore likely that populations experience significant selection pressures to optimize time, energy, and risk during migration (Dingle 1996, Thomas Alerstam and Lindstrom 1990, Weber and Hedenström 2000, Hedenström 2003, Hedenström 2009, Srygley and Dudley 2007). The ultimate result of these optimization pressures has been hypothesized as a gradient of stable behavioral strategies (Alerstam and Lindstrom 1990) that optimize different combinations of the three currencies (Alerstam 1991, Mateos-Rodriguez and Liechti 2011). Here we model the consequences for these three currencies as a result of variation in one migratory behavior, the degree of selectivity of wind currents, and suggest alternate phenotypes that solve the behavioral tradeoff for passerine songbirds during fall migration in eastern North America.

The most studied strategy empirically is one that prioritizes minimization of time spent on migration (Dänhardt and Lindström 2001). The advantage of a time-minimizing strategy may be to arrive earlier than competitors to a breeding or wintering site and to decrease the amount of time spent in unknown stopover sites (Dänhardt and Lindström 2001, Weber and Hedenström 2000). Alternatively, a different suite of behaviors can minimize energy spent in flight and on stopover (Hedenstrom and Alerstam 1997, Liechti 1995). A energy-minimizing strategy has advantages for animals attempting shorter distance migrations that can afford to take shorter movements, stopover more frequently, and carry smaller, more efficient fuel loads (Alerstam 2011). Lastly, an animal's optimal strategy may be to prioritize risk minimization. Many optimal migration analyses define risk specifically as predation risk (Alerstam and Lindstrom 1990, Alerstam 1990; Schmaljohann and Dierschke 2004). However, defining risk more broadly as migratory survival (i.e., does a bird complete migration or not) would better reflect classically supported life-history tradeoffs (Stearns 1992, Martin 1995) and capture the suite of correlated behaviors that minimize risk from all mortality factors (e.g. weather, food availability, predation, stopover site selection).

The timing, magnitude, and direction of local currents can change the optimal solution along all three migration-strategy axes. For example, the presence of currents flowing in the animals preferred direction will decrease both the time and energy expended on migration, therefore decreasing the costs to these two currencies by further minimizing risk (Åkesson and Hedenström 2000). However, the magnitude and timing of preferred flow also has the potential to affect each axes differently. If the preferred flow is relatively light, compared to the speed of the animal, total migration time may decrease while energy spent on migration may not because the animal will have to compensate for the lack of current assistance. If preferred flows are few and far between, migration risk becomes greater because optimal conditions may not come often enough to complete migration (Weber and Hedenström 2000). Conversely, if preferred flows are generally available, then risk inherent in waiting becomes less.

In many migratory taxa, behavioral plasticity in relation to flow conditions, (i.e. current selectivity), may strongly influence the optimality of migration (Liechti and Bruderer 1998, McLaren et al. 2014, Schmaljohann and Naef-Daenzer 2011, Jansen et al. 2007). Migratory success should be significantly increased for flying and swimming animals that possess the ability to adapt to flow conditions compared to those who cannot (Kemp, Gessel, and Williams 2005, Gaspar et al. 2006, McLaren, Shamoun-Baranes, and Bouten 2012, Scholtyssek et al. 2014).

For birds in particular, winds have significant influence on timing and energy expenditures, and therefore the selection of favorable winds at departure is critical for optimal migration performance (Alerstam 2011, Alerstam 1979a). Wind assistance can increase flight speed by 30% (Bruderer and Liechti 1998). Thus, by responding adaptively to wind patterns, individuals can significantly increase flight speed and save nearly half the amount of energy required for migration (Liechti and Bruderer 1998). Given the transitory nature of winds, it is reasonable to hypothesize that migrants would benefit from some flexibility in their responses to winds at departure (McLaren, Shamoun-Baranes, and Bouten 2012, McLaren et al. 2014). These responses should be dependent upon which migratory behavioral strategy they employ. For instance, to minimize energetic expenditure on migratory flights, a bird should migrate only in the most favorable winds. Selectivity, however, restricts departure opportunities, potentially increasing risk associated with stopover and overall time spent on migration (Alerstam 2011, Bruderer, Underhill, and Liechti 1995, McLaren, Shamoun-Baranes, and Bouten 2012).

The degree to which departure wind selectivity influences the ultimate migratory strategies of wild nocturnal migrants remains unclear. The aim of this study was to evaluate the consequences of departure wind selectivity on three migratory currencies, 1) risk, 2) time, and 3) energy and to determine an optimal range of wind selectivity for autumnal passerine migrants in northeastern North America. We simulated fall migration along the Atlantic flyway using a spatially explicit individual-based model (IBM) and six years of wind data. In our analysis, we used a gradient of wind selectivity from initiating flights only when winds were flowing in their preferred direction (highly selective), to flying under most wind conditions (low selectivity).

5.3. Methods

5.3.1. Model creation

The environment was modeled as a two-dimensional grid map with a 10 km by 10 km resolution, defined between 57^{o} N to 21^{o} N and 115^{o} W to 42^{o} W (Figure 5.1). The model grid contains five layers: topography, endogenous direction, wind vectors, precipitation, and mean sea-level pressure. The first layer formed the topographical map. Each grid cell of the map was assigned a feature (land, fresh water, or ocean) that altered flight behavior (see below).

The second layer was the endogenous or preferred migratory direction layer. Flight direction, for many songbirds, especially juveniles departing on their first migration, is thought to be primarily controlled by an endogenous genetic program that may be modified by experience (Pulido 2007, Berthold 1990, Mitchell et al. 2015). Many North American migration studies have shown that western breeding birds migrating east along the boreal forest (Holberton et al. 2015, Dunn et al. 2006, Williams et al. 1977) until reaching the Atlantic coast, after which they alter their heading south following the coastline (Buler and Dawson 2014). Ancestral range expansions post deglaciation (Ruegg 2007, Ruegg and Smith 2002) and/or the prevailing westerly winds in autumn (Figure 5.2; McCabe et al. in prep) are two potential reasons for why some birds take this circuitous eastern route during autumn. Migration routes can also follow the morphology of geological features such as coastlines. Coastlines are known to concentrate migrant landbirds (Gauthreaux, 1971, Williams et al., 1977, Moore et al., 1995), specifically birds born that year that may rely on coastlines to navigate on their first migration (Ralph 1971). Hence, in our model we gave birds within grid cells over the continent a preferred bearing of 135^{o} and birds within cells along the coast (500 km buffer around the coastline: Figure 5.1) an endogenous bearing parallel to the eastern coast at 225^{o}.

We introduced random stocasticity into the birds heading at the start of every flight by randomly choosing a heading from a wrapped normal distribution with an angular deviation of 30^{o}, corresponding to a mean vector length, *r*, of 0.863 (Erni, Liechi, and Bruderer 2005) and a mean bearing equal to the endogenous direction.

The third, forth, and fifth layers comprised the weather variables: mean sea-level pressure (MSLP), precipitation, and wind vector data. All weather data is Climate Forecast System Reanalysis (CFSR) 3-hourly data from the National Center for Atmospheric Research (NCAR). We used weather data during autumn migration (Aug – Nov) 2008-2013. The CFSR data has a 0.5 degree resolution on a cylindrical equidistant projection. We bilinearly interpolated the weather data to produce a 10 km resolution layer with a Lambert Conformal projection using NCAR command Language. Weather data was also linearly interpolated in time from the original 3-hourly resolution to a 1-hourly resolution, using Matlab (Mathworks 2012).

We used wind profit selectivity as a simple proxy for wind selectivity. Wind profit is defined as the distance per second the wind carries the bird towards its intended goal (Erni, Liechti, and Bruderer 2002, Erni, Liechi, and Bruderer 2005). Winds with negative profit values would carry a motionless bird away from its goal, while positive values would carry the bird towards its goal. At the start of each night, we set a variety of wind profit thresholds at the surface, such that the bird migrates only if the wind profit was above the threshold. Once airborne, the birds remained in the 850 mb isobaric pressure level for the remainder of the flight. We chose 850 mb because it lies within the range of passerine migratory flight altitudes (Gauthreaux et al. 2005, Liechti 2006), and many migration simulation studies have used similar pressure levels successfully (Erni, Liechi, and Bruderer 2005, McLaren, Shamoun-Baranes, and Bouten 2012, Kemp et al. 2010).

Mean sea-level pressure change was used as a proxy for the passage of a cold front. Rapidly decreasing pressure often signifies stormy weather (i.e. significant rain and winds) and winds from the south in northern latitudes, typically requiring autumn migrants to expend more energy (Gauthreaux 1971, Erni et al. 2002b, Gauthreaux et al. 2005) or stay grounded. As weather passes, pressure rises, and winds begin to come from the north, fall migration intensity often increases (Erni et al. 2002, Richardson 1978a). To indicate stormy weather at the location of take off, we regressed MSLP at the time of take off to the pressure value from six hours prior to departure. Thus, birds did not take off when MSLP was low (<= 1009 mb) and the slope of the regression line was steeply declining (< -1.0 mb hr^{-1}), indicating rapidly falling pressure. We also prevented birds from taking off when hourly precipitation accumulation values were higher than 2 mm. Since our objective was to understand the affects of wind selectivity, and not precipitation and pressure change, on departure behavior, we held the pressure and precipitation rules constant though all simulations, only varying wind profit thresholds. Therefore, all results presented are due to changes in wind selectivity.

Birds airspeed was set to 10.5 m s^{-1} for all trials, which is well within the range of values observed for small passerine birds (Erni, Liechi, and Bruderer 2005, Bloch and Bruderer 1982, Bruderer and Boldt 2001, Videler 2005). Because we are modeling autumn migration, which is dominated by first-time migrants, birds are subjected to full wind drift and we do not consider rules for in-flight wind compensation. All migratory flights began at local sunset to mimic songbird behavior (Fitzgerald and Taylor 2008). Flight duration followed a series of systematic rules. Flight time per night was set to 6 hours while over land, and if after that time the bird was over the ocean, flight continued for an additional 4 hours. At this point, if birds are over land, they rest until nightfall, if not, they continue flying but change their heading directly to the west (270^o) in search of land. If the birds are unable to find land after 24 hours of continuous flying, they perish.

The IBM was created in C. In our simulation birds will initiate migratory flight if, 1) the wind profit is at or below the selectivity threshold, 2) precipitation is below 2 mm at the hour of take off, and 3) the MSLP has not declined sharply (< -1.0 mb hr^{-1}) over the past 6 hours. Stopover strategies were not considered in this model, birds only stopped over longer than a day if the above rules were met. We did not consider such strategies for two reasons. First, there is not enough empirical evidence as to how long birds stopover in our study region, and the variation in stopover length is most likely species dependent. Second, this approach allows us to quantify variation in stopover length due entirely to the effect of wind selectivity, which is difficult to quantify in the wild.

5.3.2. IBM simulations

For all simulations the birds started from locations within an area of 8,000 km^2 east of the Hudson Bay and west of Newfoundland and Labrador. Breeding birds in this area represent potential migrants heading south during autumn migration within the Atlantic Flyway. To select the starting points we first created a grid of points within the 8,000 km^2 area (Figure 5.1), one point every 100 km. We then removed all points that fell within the Hudson Bay or large lakes, and then randomly chose 50 points from the remaining points. Lastly, we removed five points that were not located in breeding habitats (i.e., boreal forest habitat types), leaving 45 starting locations. Each starting location was given a random calendar date between Aug 15th – Sept 15th on a random year between 2008-2013.

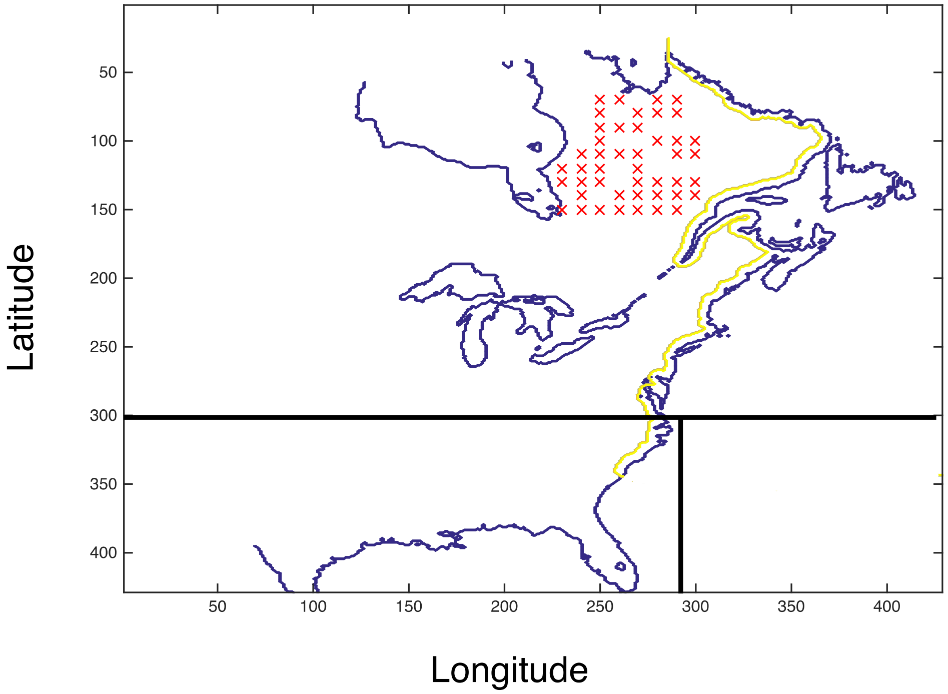


Figure 5.1. Map of the eastern United States and Canada illustrating model extent and random starting locations. Staring locations are indicated with red X's (i.e., breeding locations of potential migrants). The yellow line indicates a 500 km buffer around the coastline. Endogenous migratory bearing was set to 135° for all areas west of the yellow line and 225° within the area between the yellow line and the coast, based on empirical observations. Migratory success and the time spent during migration was calculated when birds passed the horizontal black line and were to the west of the vertical black line.

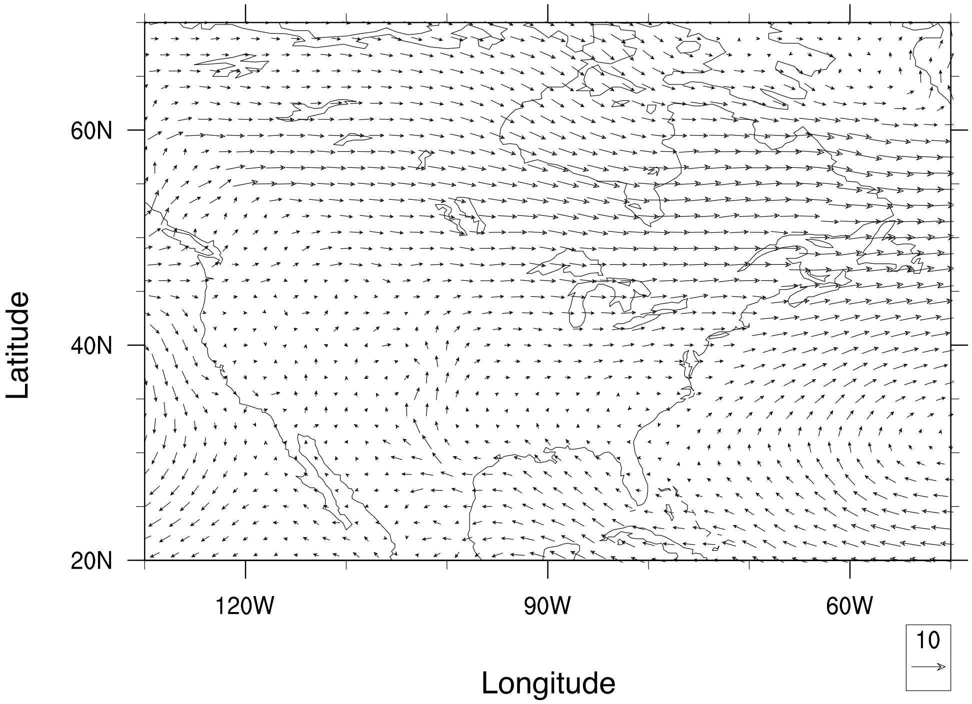


Figure 5.2. Monthly mean vector plots of winds at 850 mb pressure level for September 2008-2013 using Climate Forecast System Reanalysis (CFSR) data from the National Center for Atmospheric Research (NCAR). Vector arrows display wind direction (as angle) and magnitude (as length). The length of the reference arrow represents 10 m s^{-1}.

5.3.3. Statistical analysis

To understand how wind selectivity at departure may affect migratory behavior, we evaluated three variables as proxies of risk, time, and energy for wind profit values between -20 and 10 m s^{-1}. We conducted 1,395 simulations, one per wind profit value at each of the 45 random starting locations. As a proxy of risk, we counted how many of the 45 simulations failed for each wind profit threshold. We considered a migration to have failed if the bird did not make it past 38^o 53’N latitude (horizontal black line in Figure 5.1) by December 1st, or was far out to sea when it crossed the latitude (further east than 73^o32’W: vertical line in Figure 5.1), and if they were out to sea over 24 hours. As a proxy of time investment, we used total number of days spent on migration, which is consistent with optimal migration theory (Alerstam and Lindstrom 1990). For a proxy of energetic investment, we counted the number of days spent flying. However, energy expended on migration is often considered as the summation of energy spent in flight and during stopover. In empirical migration studies, proxies for energy typically capture a refueling rate during stopover; a physiological proxy for energy expended because time spent in-flight is a difficult and expensive metric to acquire. Here we measure energy at a courser level, but with a proxy that is more tightly tied to energetic expenditure in-flight than is typically achieved with empirical measures. Mitchell et al. (2015), after controlling for tailwind component, failed to find a difference in airspeed or ground speed among age groups of migrating savannah sparrows (*Passerculus sandwichensis*), which suggests that differences in flight speed are unrelated to differences in frequency or intensity of muscular contraction. If these results are generalizable across passerine songbirds, differences in flight duration can thus act as a reliable proxy for energy expended while in flight. Both time and energy metrics were only calculated for birds that completed migration.

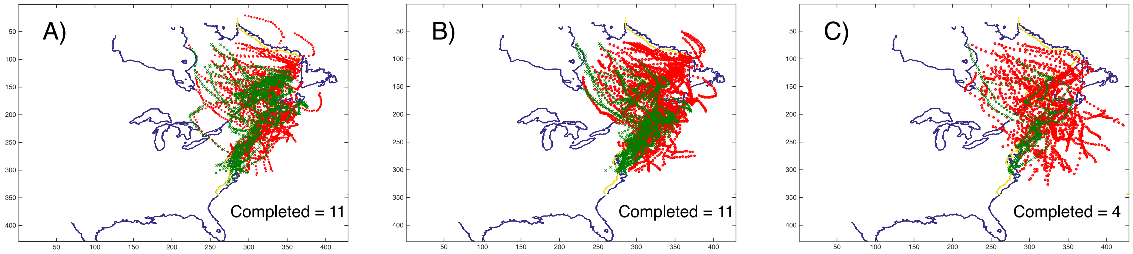
To explore the effects of wind selectivity on our three migration currencies, we fit three general linear models in Program R (R Development Core Team 2012) using each currency as a dependent variable and the wind profit threshold (replicated across starting location and date) as an independent variable. A natural log transformation was used on time to meet linear assumptions. The relationships between wind profit and the migration variables were non-linear; consequently we added a quadratic term for wind profit in all three models.

To determine the optimum value for risk, time, and energy, we solved for the minimum of the polynomial relationship between wind profit and each migration variable. We then standardized all migration variables by subtracting the mean and dividing by the standard deviation. We can thus directly compare the relationships between each variable and wind profit. We then combined the three optimal migration values to create an optimal range of wind selectivity for autumn migrants in northeastern North America.

5.4. Results

5.4.1. IBM simulation

We ran the migration model at each wind profit value from 45 starting locations for a total of 1,395 migratory tracks. Of the 1,395 tracks, 87% failed to reach the finish latitude/longitude or were over the open ocean for more than 24 hours (Table 5.1 & Figure 5.3). At wind profits larger than 4.0 m s^{-1}, no bird completed a migration in the time allotted (Table 5.1). Although the minimum and median wind profits investigated both include 11 completed and 44 failed migration tracks, the completed tracks show different patterns (Figure 5.3 A & B). The completed tracks from -20.0 m s^{-1} wind profit show a bunching along eastern Quebec and the Saint Lawrence River before heading to the coast, while the -8.0 m s^{-1} tracks show migration route that are more direct to the coast (Figure 5.3 C), resulting in the less selective birds expending more energy in flight and more time spent on migration overall (Figure 5.4 B & C). All tracks from the highest selectivity simulation follow the preferred direction more directly over land than over the ocean. While the lower selectivity tracks show more scatter, as seen in the tracks flying opposite the preferred direction (to the northwest) (Figure 5.3).



Wind Profit -20

Wind Profit -8

Wind Profit 4

Figure 5.3. Output from three simulations for the maximum, median, and the minimum wind profit thresholds investigated. Red tracks are birds that did not complete the migration due to either not crossing the benchmark latitude or longitude before 1 December, or due to more than 24 hours spent out at sea. Green tracks indicate birds that successfully completed their migration.

Our general linear models demonstrating the quadratic relationships between wind profit and risk ($r^2 = 0.13$), time ($r^2 = 0.88$), and energy ($r^2 = 0.61$) demonstrated adequate fit. Wind profit had a significant effect on all three variables (Table 5.2). Our analysis indicated that relative risk was lowest at intermediate selectivity and increased at both high and low wind-profit values. Of the tracks that successfully completed migration, those with the lowest selectivity spent less overall time on migration but expended more energy (Figure 5.4 B & C), while those with the highest selectivity expended the least amount of energy in flight but spent significantly more time on migration overall (Figure 5.4 B & C). Of the three relationships with wind profit, risk showed the highest variance (Figure 5.4 A). Variance in energy and time was highest at the lower wind profit values and low at the highest wind profits (Figure 5.4 B & C).

The minimum wind profit for our risk variable was -8 m s^{-1} (Figure 5.5). For birds that completed migration, the minimum wind profit value for time was -13.8 m s^{-1} and 4 m s^{-1} for energy (Figure 5.5). The energy minimum is not the inflection point like the minimum for time and risk, rather is represents the minimum number of days in flight before no birds are able to complete the migration. By combining the optimal strategies we came up with an optimal range of wind selectivity for autumn migrants in northeast North America, -13.8 to 4.0 m s^{-1} (Figure 5.5).

Table 5.1: Output of migration simulations for each variable. Model was run 45 times at different randomly selected starting locations for each wind profit threshold. The means and standard deviation (SD) are shown for both time and energy and were calculated from only the completed migrations for each wind profit value.

Wind Profit Value (m s^{-1})	***Risk*: % failed**	***Time:* # of migration days**		***Energy:* # of days in flight**	
		mean	***SD***	***mean***	***SD***
-20	76	14.64	6.17	13.82	6.11
-19	80	11.56	4.82	11.00	4.77
-18	84	9.14	2.54	8.29	2.43
-17	89	16.40	5.27	15.40	5.27
-16	98	7.00		6.00	
-15	91	9.00	2.16	8.00	2.16
-14	87	13.00	5.55	12.33	5.47
-13	89	8.20	1.92	7.40	1.95
-12	82	11.38	4.34	10.50	4.13
-11	91	9.75	3.40	9.25	3.30
-10	80	13.22	6.28	12.44	5.77
-9	84	9.29	1.50	8.14	1.35
-8	76	10.27	2.37	9.45	2.46
-7	89	11.20	3.19	9.80	2.68
-6	87	10.17	2.40	8.50	1.64
-5	87	14.00	4.47	10.83	5.12
-4	75	12.82	4.07	8.55	1.44
-3	84	15.86	60.7	9.71	2.56
-2	78	15.90	6.57	8.40	3.10
-1	78	20.00	9.08	7.50	2.12
0	76	20.45	4.34	6.45	1.57
1	71	35.31	14.68	7.69	1.65
2	87	35.33	10.52	6.83	1.17
3	87	54.33	21.07	6.50	1.97
4	91	76.50	8.27	5.75	1.71
5	100	na	na	na	na
6	100	na	na	na	na
7	100	na	na	na	na
8	100	na	na	na	na
9	100	na	na	na	na
10	100	na	na	na	na

Table 5.2. Parameter estimates, standard errors (SE), and p-values for three models explaining the linear and quadratic relationships of wind profit on risk, time, and energy.

Model	***Wind Profit Variable***	***Parameter Estimate (SE)***	***p-value***
Risk	linear	0.399 (0.161)	0.02
	quadratic	0.024 (0.011)	0.04
Time	linear	0.177 (0.015)	< 0.0001
	quadratic	0.007 (0.001)	< 0.0001
Energy	linear	-0.600 (0.111)	< 0.0001
	quadratic	-0.021 (0.007)	0.009

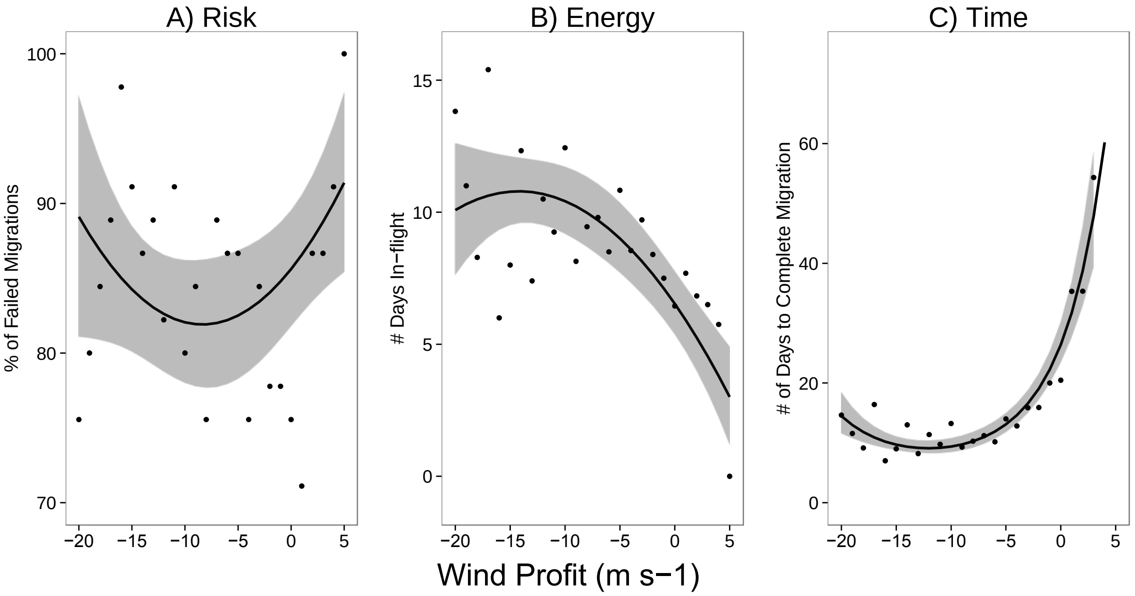


Figure 5.4. The quadratic relationships (± 95% confidence intervals shown in gray) between wind profit on A) risk (% failed migrations), B) energy (# of days inflight), and C) time (# of days to complete migration). The dots represent the mean model outputs across all 45 staring locations.

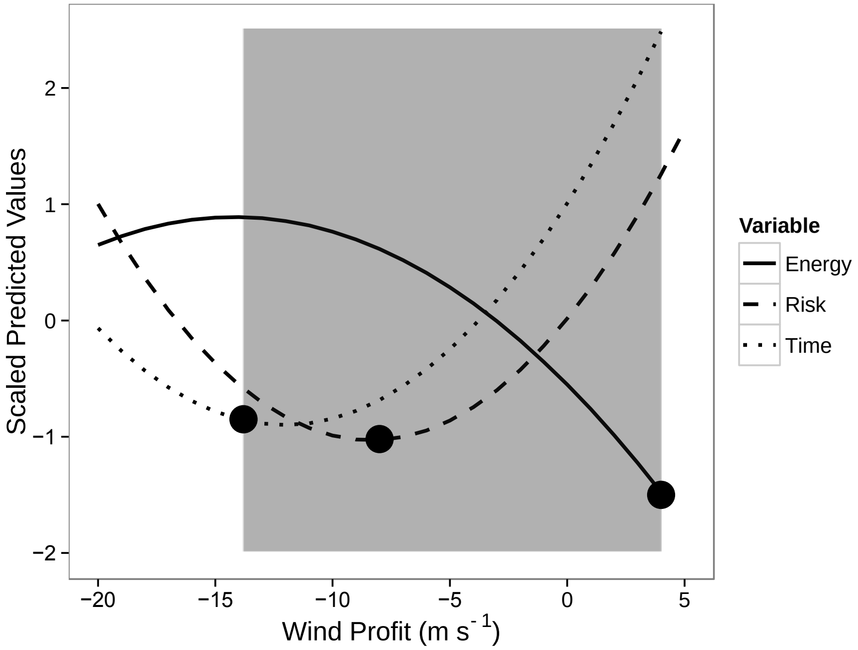


Figure 5.5. Scaled predicted values for models explaining the effect of wind profit thresholds (m s^{-1}) on three migratory variables. Black dots represent the optimal wind profit value for each migratory currency. If optimizing only energy, birds should fly at wind profits of 4.0 m s^{-1}. Time optimizers should fly at wind profits of -13.8 m s^{-1} and to optimize solely for risk, birds should migrate with a wind profit threshold of -8.0 m s^{-1}. The gray rectangle is the range of optimum migratory selectivity if multiple strategies are being used.

5.5. Discussion

Wind is thought to be one of the most important factors affecting bird migration timing, orientation, energy expended, and flight speed (Alerstam and Lindstrom 1990, Erni et al. 2002, McLaren, Shamoun-Baranes, and Bouten 2012). How selective birds are at departure can thus have large fitness implications, but the degree of selectivity should depend on their particular behavioral strategy (Alerstam 1979a). Our optimality analysis indicated a range of wind profits that would variously minimize time spent on migration, energy expended in flight, or the risk of failure to complete migration. Further, variation in wind selectivity alone was able to simulate migratory behaviors that align with the classic “time-minimizer” and “energy-minimizer” movements described in wild bird populations.

We found that birds with less wind selectivity flew on more nights and behaved more like time-minimzers, while simulated birds with the lowest energy expended in flight were the most selective. The degree of wind selectivity that produced the greatest proportion of birds that finished migration (i.e., lowest risk) was intermediate to the selectivity values that optimized time and energy (Figure 5.4 & 5.5). Alerstam (2011) found similar behavior with long-distance migrants in Europe. He found that these birds, which are generally described as time-minimzers, were less selective than originally predicted, relaying on self-powered flight in their preferred direction, often with little or no wind tailwind assistance, emphasizing how time constraints within the annual routine can necessitate tolerance of nonsuportive winds (McLaren, Shamoun-Baranes, and Bouten 2012).

The optimization curve for risk was a convex parabola with optimal wind selectivity at the intermediate wind profit values (Figure 5.4 & 5.5). Because birds can fail for multiple reasons, risk increases at either end of the selectivity range. If they are too choosy, they were more likely to wait too long to complete migration in the time allotted (before 1 December). If birds aren’t choosy enough, they risk being blown in directions other than their preferred bearing. To optimize for overall migration risk, birds should be moderately choosy at departure and migrate at a wind profit of -8.0 m s^{-1}. This result agrees well with empirical values from Erni et al. (2002b), a radar study in central Europe that found that migratory intensity increased at wind profits of -7.0 m s^{-1} and greater.

Unlike risk, time showed a rapidly increasing curve, where the number of days needed to complete migration quickly accumulated for wind profits greater than -13.8 m s^{-1} (Figure 5.4 & 5.5). For our fitted quadratic curve, time-minimizers should migrate using a wind profit threshold of -13.8 m s^{-1} (Figure 5.5). Although a quadratic polynomial fit the data well (Table 5.2 & Figure 5.4), the total number of days to complete a migration may reach a bottom threshold once birds are migrating every day (Figure 5.4). If such a threshold exists, time-minimizers would net no decrease in time spent on migration for being less selective than -13.8 m s^{-1}, and thus any wind profit selectivity at or lower than -13.8 m s^{-1} would produce similar departure behaviors and be equally optimal for time expenditure.

The energy curve resembles an inverted time curve. Birds with low selectivity experienced the greatest number of days in flight and flight energetic expenditure decreased considerably with increasing selectivity (among those birds that successfully completed migration) until the line reaches the global minimum at a wind profit of 4 m s^{-1} (Figure 5.4 & 5.5). For wind profit thresholds that are more selective than this, no birds completed migration (Table 5.1). To optimize energy expenditure, birds should migrate at the global minimum. If the relationship is truly quadratic, energy expenditure may decrease as wind profit thresholds become more negative than the range we show here, producing a second minimum wind profit value. There is good reason to suspect, however, that energy expenditure reaches some maximum threshold once birds are flying every night (among the subset that can still complete migration).

Variance in each of the three model outputs differed as well. For risk, the variance was relatively high compared to the other two currencies at all wind profit values (Figure

5.4), most likely due to the multiple ways birds failed to complete migration and the inherent variability in winds across all starting dates and locations. Less selective birds were more likely to fail overall because of inadequate time, and more selective birds were more likely to fail because exceptionally strong winds pushed them out to sea (Figure 5.3). However, we are unsure as to what is contributing to the scatter below the line (Figure 5.4 A). For both energy and time the variance is highest at lower wind profits. The variance could be attributed to flight dates coinciding with highly profitable winds and in orientation errors dues to the random stocasticity around the endogenous heading compounding throughout migration. Also, since we only calculated time spent in flight and the duration of migration among birds that successfully completed migration, the values for extreme wind profit thresholds, which exhibited lower proportions of success, are calculated across fewer model trials, inflating variance.

By optimizing risk, time, and energy, we derived an optimal range of wind selectivity, -13.8 to 4.0 m s^{-1}, for autumn migrants in northeast North America (Figure 5.5). Birds selecting departure winds higher than 4.0 m s^{-1} will not complete migration because winds with ample assistance do not exist in the region frequently enough, reducing the number of completed migrations to zero. Conversely, birds departing at wind profits lower than -13.8 m s^{-1} will spend too many nights being carried away from their destination to complete migration before the end of the season. Risk optimization has little effect on the optimal selectivity range; the optimal wind profit value is approximately halfway between the time- and energy-optima (Figure 5.5). Those birds compromising between time and energy optima, therefore, will show similar departure wind selectivity to those optimizing exclusively for risk. If these results are generalizable, this could explain why empirical evidence for time-minimizing strategies (Lindstrom and Alerstam 1992), energy minimizing strategies (Dänhardt and Lindström 2001), and compromises between the two strategies (Alerstam and Lindstrom 1990) have been reported, while there are no recorded species suggested to follow a purely risk-minimizing strategy. One potential example of risk-minimization, however, has been reported recently in juvenile savannah sparrows, which are less selective than their adult counterparts (Mitchell et al. 2015). The authors suggested that the choosiness of juveniles relative to adults could be an adaptation to higher predation risk in the younger age class. Our results would predict the same difference in selectivity under these conditions.

Our model includes a few assumptions that warrant discussion. First, our estimates of risk are biased high because of the way we defined migration failure. We consider birds to have failed if they did not reach 38°53’N latitude by Dec 1st, if they crossed the latitude in time but were far out to sea, or if they spent over 24 hours out to sea. Our definitions of failure due to excessive time or distance at sea may not imitate how live birds migrate over the open ocean in many circumstances. For instance, Deluca et al. (2015) found that four blackpolls fitted with geolocators made nonstop flights over the Atlantic Ocean lasting between 49 and 73 hours. Other studies in North America and in Europe have shown successful long distance flights over ecological barriers (Williams et al. 1977, Bairlein 1988), indicating the potential for long continuous flights. As advances in tracking technology allow for better measurements of small passerines, we may find that transoceanic flights are more common then we have previously thought. For instance, our simulations show that birds with high selectivity commonly exhibit migratory paths far out to sea, even with an endogenous bearing parallel to the coast (Figure 5.3). Assuming that some species orient downwind under such circumstances (McLaren et al. 2014), considerable assistance from tailwinds could be common for highly selective species. Indeed, our model assumption that birds reorient directly to shore (270º bearing) if they are over water after daybreak is certainly incorrect for species making purposeful flights over the ocean. We maintain, however, that it is a realistic assumption for the set of migratory songbirds for which this is not true. Further, our endogenous direction choice over land may have been an over-simplification. These bearings are based on ample empirical observations (see methods), however, and our inclusion of stochasticity into the direction should prevent results that would be sensitive to small changes in our assumed orientation. Similarly, we assumed that birds would shift migratory orientation to a “coastal” paradigm (225º bearing) over lands within 500 km of the Atlantic Ocean and the mouth of the St. Lawrence River (see Figure 5.1). However, we have no empirical evidence to support or deny birds perception of what constitutes the coast.

Certainly migratory departure is not only governed by wind conditions but also by refueling rates and other environmental conditions. Probably, there is a balance between several endogenous and exogenous factors that together determine departure. Lietchi and Bruderer (1998), however, suggested that in situations with highly variable winds the relationship between fuel deposition rate and fuel load at departure is unreliable as a cue for understanding migratory strategies. The importance of wind selectivity could also be decreased by altitudinal adjustments, which have been shown to offset some suboptimal wind conditions (Stoddard et al. 1983, Gauthreaux 1991, Bruderer et al. 1995, Liechti

2006, Mateos-Rodriguez and Liechti 2011, Kemp et al. 2013). Further, many studies have found evidence that migrating birds evaluate wind conditions while climbing through the air column and choose altitudes based on favorable winds (Mateos-Rodriguez and Liechti 2011, Richardson 1978a). Shamoun-Baranes and van Gasteren (2011), however, found that pressure level (i.e. altitude) only had a minor effect on the proportion of successful trajectories in a modeling study. Additional endogenous and environmental factors such as these should allow for a wider range of optimal selectivity than our model predicts, although it is unclear exactly how important other factors may actually be.

Despite the lack of support for some of our model assumptions and an understanding that reality is undoubtedly more complicated than what we have modeled here, we were able to mimic time and energy minimization behaviors using only variation in wind selectivity, lending support for the potential importance of wind selectivity as a significant driving force in migratory behavioral strategies. While improvements in our modeled endogenous direction, the behavior of birds over open water, and the inclusion of other factors involved in migratory departure would undoubtedly improve the predictions of our simulation, the results concerning the effect of selectivity on tradeoffs among time, energy, and risk optimization would likely be similar. Of the three currencies, the risk optimum is most likely to change with an improved model, as it relies more heavily on appropriate modeling of over-water behavior. This optimum, however, did not affect the range of optimal wind selectivity we report here, and if an improved model maintained the relative positions of the three optima, our general results would not change.

In general, we expect birds to adapt their wind selectivity to account for total migration time, energy expenditure, and mortality risk during migration, yet the relative importance of these pressures should vary among species, regions, seasons, and phases of migration (Kemp et al. 2013). In our study region, birds exhibiting optimal degrees of wind selectivity at departure behaviorally mimic the classic optimal migratory behavioral strategies of time and energy minimization. Our findings indicate that wind selectivity is important to departure behavior and should continue to be incorporated into optimality migration analysis. These results should be generalizable to any species where the efficacy of movement is affected by currents. To expand our understanding of migratory behaviors more broadly, further research should combine simulations, empirical measurements across multiple spatial and temporal scales, and experiments that allow researchers to consider multiple trade-offs simultaneously.

CHAPTER 6: CONCLUSION

Optimal migration analysis has evolved tremendously since its inception by Alerstam and Lindstrom (1990). The use of optimality assessments is now considered an essential way to understand behavioral adaptation and the variability in behavioral strategies within and among migrating bird taxa (Alerstam 2011). The overall aim of my dissertation was to use novel methods to better understand behaviors utilized by autumn migrating birds to balance three currencies (time, energy, and risk) during stopover (chapters 2-4 & 5) and in flight (chapters 4 & 5).

Generally, studies exploring the trade-offs between the above currencies have been single-species analyses, using small-scale behavioral experiments or, more recently, the description of individual movements using GPS receivers or geolocators. These studies can be expensive, time-consuming, and suffer from small statistical sample sizes. Here I have attempted to use data that is already widely collected and therefore implementable in other regions. While individual behavioral and tracking studies continue to have wide applicability, migration monitoring banding data and associated habitat data is collected by hundreds of groups around the country, and very little of it is actually analyzed due to analytical constraints, despite the advantages in temporal and spatial scale this data resource presents. Moreover, migration monitoring-station data presents an opportunity to understand the response of the entire avian community to variation in geographic and environmental settings. The biological scale presented by these data matches that needed by management and conservation agencies faced with the preservation of biodiversity at large spatial and taxonomic scales. I have attempted to increase our understanding of behavioral processes at this scale to inform the actions of these agencies, information that is generally lacking from investigations of individual species.

With the first half of my dissertation (Chapters 2 & 3) I investigated the behavioral strategies utilized by the entire migratory community in regards to stopover habitat selection at the regional and habitat patch scale. At the regional spatial scale I found that the migratory community behaved similarly to predictions of both time- and energy- minimization strategies. Short to medium distance migrants selected stopover habitat based on the availability of vegetated lands. “Habitat islands” thus concentrated these shorter distance migrants, but the same was not true for longer distance migrants (i.e., time-minimizers), which should carry more fuel, make longer flights, and stop less often.

When exploring the trade-off between risk avoidance and energetic gain (Chapter 3), I again found evidence consistent with time and energy minimization strategies. When selecting habitat patches on stopover, long-distance species chose patches with higher food resources regardless of the relative risk associated with the patch. Such time-minimization behavior should reduce the time spent on stopover, in turn shortening total migratory passage time. Short-distance migrants did not prioritize patches with food; instead they choose patches that lessened predation risk at a cost to migration time. Interestingly, my community-scale investigations found analogous results to many single-species studies (Cimprich and Moore 1999, Moore 1994).

Secondly, I was interested in determining if computer-simulated data with simplified behavioral rules could mimic migratory bird behavioral strategies. In the second half of my dissertation (Chapters 4 & 5), I successfully modeled the influence of wind patterns on migratory behavioral strategies. Optimal migration analysis has been incorporating wind into its equations for quite some time (Alerstam 2011). However, many of the studies, including modeling, theoretical, and empirical efforts, have taken place in Europe (Erni, Liechi, and Bruderer 2005, McLaren, Shamoun-Baranes, and Bouten 2012, McLaren et al. 2014, Erni, Liechti, and Bruderer 2003, Mateos-Rodriguez and Liechti 2011). Studies of the effect of wind on migration conducted in North America have generally been correlative studies, associating wind patterns with observations of birds in the air (Gauthreaux 1991, Buler and Diehl 2009).

Using individual-based models (IBM), I validated the ability of wind assistance to influence the evolution of migratory routes and stopover departure behaviors in North America. By modeling birds floating in the wind along the Rocky Mountain migratory divide, I was able to isolate the effect of wind and show that wind is in fact a strong candidate driver for the creation of this migratory divide. Further, my analysis indicated the range of wind profits that would variously minimize time spent on migration, energy expended in flight, and the risk of failure to complete migration. Variations in departure wind selectivity alone were able to simulate migratory behaviors that align with the classic “time-minimizer” and “energy-minimizer” strategies.

The work presented here demonstrates the extensive ability to test migratory theory using IBMs and atmospheric wind data. As I state in the discussion of chapter 5, migratory departure is not only governed by wind conditions but is likely modified by several endogenous and exogenous factors that together determine departure. In the future, I hope to add additional behaviors to the IBM allowing us to test other factors associated with migratory decisions. Specifically, I would like to create a threedimensional model environment by incorporating the entire range of landbird migratory flight altitudes and incorporate a range of individual energetic condition (e.g., refueling rates and energy expended in flight).

For example, altitudinal adjustments in flights could dramatically alter the range of conditions that would be optimal for migration. Not only are birds selecting stopover habitat while on the ground, but they are also likely choosing atmospheric habitat while aloft. My efforts here have raised numerous questions about avian abilities to sense and adjust to changing wind patterns. What is the cost of vertical movements within the air column for various sized birds? Are birds constantly adjusting their altitude throughout the flight or is there a threshold after which adjustments become too costly? Do vertical adjustments differ between age groups, migratory strategies, or region? To begin to answer these questions, we also need to include a formula for energy expended in flight using wind loading and energy equations that is validated by radar and wind tunnel data. With both refueling rates during stopover and in-flight energy expenditures, we will be able to more accurately model birds ability to balance time, energy, and risk across the entirety of migration.

Eventually, my hope for the IBM is to model future migration distributions under various climate change scenarios. My intention was to create something that researchers and land managers can use to both identify important contemporary stopover sites and to forecast changes in the timing and spatial distribution of migrants. The most pressing next step of the work I present here is to validate the model with empirical data. Radar data (density of birds in the air at a given location) and crowd-sourced survey data (e.g., “eBird”) both offer strengths and weaknesses in this regard. Radar data is the most accurate; unfortunately, there is no collaboration between Canadian and US radar programmers that allows for systematic and comprehensive approaches to bird movement across the continent. Crowd-sourced data does not suffer from this weakness and covers the entire spatial extent of our study, but suffers from greater variation in data accuracy and heterogeneity in spatial grain and temporal resolution.

In conclusion, as the process of global change accelerates, the latest tracking techniques producing new information about routes, timing and habitats of migrating individuals that can be used to test predictions about migratory strategies, and undetected tradeoffs in migration become identified that optimization is an essential approach for understanding the ever changing field of migration. I hope that with my research I was able to demonstrate optimal analyses that are adaptable to the changing times, ones where commonly collected and novel forms of data can be used to comprehensively understand bird migration.

BIBLIOGRAPHY

Able, Kenneth P. 1973. “The Role of Weather Variables and Flight Direction in Determining the Magnitude of Nocturnal Bird Migration.” *Ecology* 54 (5): 1031–1041.

Aborn, David A. 1994. “Correlation between Raptor and Songbird Numbers at a Migratory Stopover Site.” *The Wilson Bulletin* 106 (1): 150–154.

Adams, Evan M. 2014. “Using Migration Monitoring Data to Assess Bird Population Status and Behavior in a Changing Environment.” The University of Maine.

Åkesson, S., and a. Hedenström. 2000. “Wind Selectivity of Migratory Flight Departures in Birds.” *Behavioral Ecology and Sociobiology* 47 (3) (February 1): 140–144. doi:10.1007/s002650050004. http://link.springer.com/10.1007/s002650050004.

Alerstam, T., J. W. Chapman, J. Backman, a. D. Smith, H. Karlsson, C. Nilsson, D. R. Reynolds, R. H. G. Klaassen, and J. K. Hill. 2011. “Convergent Patterns of Long-Distance Nocturnal Migration in Noctuid Moths and Passerine Birds.” *Proceedings of the Royal Society B: Biological Sciences* 278 (1721): 3074–3080. doi:10.1098/rspb.2011.0058. http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2011.0058.

Alerstam, Thomas. 1976. “Nocturnal of Thrushes Migration (Turdus Spp.) in Southern Sweden.” *Oikos* 27 (1976): 457–475.

Alerstam, Thomas. 1979a. “Wind as Selective Agent in Bird Migration.” *Ornis Scandinavica* 10 (1): 76–93.

Alerstam, Thomas. 1979b. “Optimal Use of Wind by Migrating Birds: Combined Drift and Overcompensation.” *Journal of Theoretical Biology* 79 (3) (August 7): 341–53. http://www.ncbi.nlm.nih.gov/pubmed/522498.

Alerstam, Thomas. 1990. *Bird Migration*. Cambridge: Cambridge University Press.

Alerstam, Thomas. 1991. “Ecological Causes and Consequences of Bird Orientation.” In *Orientation in Birds*, edited by Peter Berthold, 202–225. Birkhauser Basel.

Alerstam, Thomas. 2011. “Optimal Bird Migration Revisited.” *Journal of Ornithology* 152 (S1) (May 15): 5–23. doi:10.1007/s10336-011-0694-1. http://link.springer.com/10.1007/s10336-011-0694-1.

Alerstam, Thomas, and A. Lindstrom. 1990. “Optimal Bird Migration: The Relative Importance of Time, Energy, and Safety.” In *Bird Migration*, edited by E. Gwinner, 331–351. Berlin Heidelberg: Springer.

Alerstam, Thomas, and S Pettersson. 1977. "Why Do Migrating Birds Fly Along Coastlines?" *Journal of Theoretical Biology* 65 (4) (April 21): 699–712. http://www.ncbi.nlm.nih.gov/pubmed/875399.

Anderson, Edgar. 1948. "Hybridization of the Habitat." *Evolution* 2 (1): 1–9.

Andrews, Chandler B, Stuart A. Mackenzie, and T. Ryan Gregory. 2009. "Genome Size and Wing Parameters in Passerine Birds." *Proceedings. Biological Sciences / The Royal Society* 276 (1654) (January 7): 55–61. doi:10.1098/rspb.2008.1012. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2614259&tool=pmcentrez&rendertype=abstract.

Bagg, Aaron C. 1923. "The Connecticut Valley: A Highway for Bird Migration." *The Auk* 40 (2): 256–275.

Bairlein, F. 1988. "How Do Migratory Songbirds Cross the Sahara?" *Trends in Ecology & Evolution* 3 (8) (August): 191–4. doi:10.1016/0169-5347(88)90005-5. http://www.ncbi.nlm.nih.gov/pubmed/21227199.

Bairlein, F, and E Gwinner. 1994. "Nutritional Mechanisms and Temporal Control of Migratory Energy Accumulation in Birds." *Annual Review of Nutrition* 14: 187–215. doi:10.1146/annurev.nutr.14.1.187.

Bairlein, Franz. 1998. "The Effect of Diet Composition on Migratory Fuelling in Garden Warblers Sylvia Borin." *Oikos* 29 (4): 546–551.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. "lme4: Linear Mixed-Effects Moels Using Eigen and S4." http://cran.r-project.org/package=lme4.

Batschelet, Edward. 1981. *Circular Statistics in Biology*. London: Academic Press.

Bearhop, Stuart, Wolfgang Fiedler, Robert W Furness, Stephen C Votier, Susan Waldron, Jason Newton, Gabriel J Bowen, Peter Berthold, and Keith Farnsworth. 2005. "Assortative Mating as a Mechanism for Rapid Evolution of a Migratory Divide." *Science* 310 (October 21): 502–4. doi:10.1126/science.1115661. http://www.ncbi.nlm.nih.gov/pubmed/16239479.

Bellrose, Frank C, and Robert C . Crompton. 1981. "Migration Speeds of Three Waterfowl Species." *The Willson Bulletin* 93 (1): 121–124.

Bensch, Staffan, Tord Andersson, and Susanne Akesson. 1999. "Morphological and Molecular Variation across a Migratory Divide in Willow Warblers, Phylloscopus Trochilus." *Evolution* 53 (6): 1925–1935. doi:10.2307/2640451. http://www.jstor.org/stable/2640451.

Berthold, Peter. 1990. “Genetics of Migration.” In *Bird Migration: Physiology and Ecophysiology*, edited by Peter Berthold, Eberhard Gwinner, and Edith Sonnenschein, 269–283. Berlin: Springer.

Berthold, Peter, and Andreas Helbig. 1992. “The Genetics of Bird Migration: Stimulus, Timing, and Direction.” *Ibis* 134: 35–40. doi:10.1111/j.1474-919X.1992.tb04731.x.

Berthold, Peter, and Scott B. Terrill. 1988. “Migratory Behaviour and Population Growth of Blackcaps Wintering in Britain and Ireland: Some Hypotheses.” *Ringing & Migration* 9 (3): 153–159. doi:10.1080/03078698.1988.9673939.

Biebach, H., W. Friedrich, and G.le Heine. 1986. “Interaction of Bodymass, Fat, Foraging and Stopover Period in Trans-Sahara Migrating Passerine Birds.” *Oecologia* 69 (3): 370–379. doi:10.1007/S00442-004-V.

Blake, J.G., and James R. Karr. 1987. “Breeding Birds of Isolated Woodlots: Area and Habitat Relationships.” *Ecology* 68 (6): 1724–1734.

Bloch, Raymond, and Bruno Bruderer. 1982. “The Air Speed of Migrating Birds and Its Relationship to the Wind.” *Behavioral Ecology: Official Journal of the International Society for Behavioral Ecology* 11 (1): 19–24.

Bohrer, Gil, Ran Nathan, and Sergei Volis. 2005. “Effects of Long-Distance Dispersal for Metapopulation Survival and Genetic Structure at Ecological Time and Spatial Scales.” *Journal of Ecology* 93 (5): 1029–1040. doi:10.1111/j.1365-2745.2005.01048.x.

Bonter, David N, Sidney A. Gauthreaux Jr, and Therese M Donovan. 2008. “Characteristics of Important Stopover Locations for Migrating Birds: Remote Sensing with Radar in the Great Lakes Basin.” *Conservation Biology : The Journal of the Society for Conservation Biology* 23 (2) (May): 440–8. doi:10.1111/j.1523-1739.2008.01085.x. http://www.ncbi.nlm.nih.gov/pubmed/18983598.

Borgmann, Kathi L, Scott F Pearson, Douglas J Levey, and Cathryn H Greenberg. 2004. “Wintering Yellow-Rumped Warblers (Dendroica Coronata) Track Manipulated Abundance of Myrica Cerifera Fruits.” *The Auk* 121 (1): 74–87.

Breslow, Paul B., and David J. Sailor. 2002. “Vulnerability of Wind Power Resources to Climate Change in the Continental United States.” *Renewable Energy* 27 (4) (December): 585–598. doi:10.1016/S0960-1481(01)00110-0. http://linkinghub.elsevier.com/retrieve/pii/S0960148101001100.

Brown, Joel S., and Burt P. Kotler. 2004. “Hazardous Duty Pay and the Foraging Cost of Predation.” *Ecology Letters* 7 (10) (September 15): 999–1014. doi:10.1111/j.1461-0248.2004.00661.x. http://doi.wiley.com/10.1111/j.1461-0248.2004.00661.x.

Brown, J.S., Laundre, J. W., and Gurung, M. 1999. “The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Ineractions.” *Journal of Mammalogy* 80 (2): 385–399.

Bruderer, B., L. G. Underhill, and F. Liechti. 1995. “Altitude Choice by Night Migrants in a Desert Area Predicted by Meteriological Factors.” *Ibis* 137 (1): 44–55.

Bruderer, Bruno, and Andreas Boldt. 2001. “Flight Characteristics of Birds: I . Radar Measurements of Speeds.” *Ibis* (1985): 178–204.

Bruderer, Bruno, and Felix Liechti. 1998. “Flight Behaviour of Nocturnally Migrating Birds in Coastal Areas - Crossing or Coasting.” *Journal of Avian Biology* 29 (4): 499–507.

Buler, J.J., and R.H. Diehl. 2009. “Quantifying Bird Density During Migratory Stopover Using Weather Surveillance Radar.” *IEEE Transactions on Geoscience and Remote Sensing* 47 (8) (August): 2741–2751. doi:10.1109/TGRS.2009.2014463. http://ieeexplore.ieee.org/lpdocs/epic03/wrapper.htm?arnumber=4813234.

Buler, Jeffrey J, Frank R Moore, and Stefan Woltmann. 2007. “A Multi-Scale Examination of Stopover Habitat Use by Birds.” *Ecology* 88 (7) (July): 1789–802. http://www.ncbi.nlm.nih.gov/pubmed/17645025.

Buler, Jeffrey J., and Deanna K. Dawson. 2014. “Radar Analysis of Fall Bird Migration Stopover Sites in the Northeastern U.S.” *The Condor* 116 (3): 357–370. doi:10.1650/CONDOR-13-162.1. http://www.bioone.org/doi/abs/10.1650/CONDOR-13-162.1.

Buler, Jeffrey J., and Frank R. Moore. 2011. “Migrant–habitat Relationships during Stopover along an Ecological Barrier: Extrinsic Constraints and Conservation Implications.” *Journal of Ornithology* 152 (S1) (January 5): 101–112. doi:10.1007/s10336-010-0640-7. http://www.springerlink.com/index/10.1007/s10336-010-0640-7.

Burnham, Kenneth P, and David R Anderson. 2004. “Multimodel Inference: Understanding AIC and BIC in Model Selection.” *Sociological Methods & Research* 33 (2) (November 1): 261–304. doi:10.1177/0049124104268644. http://smr.sagepub.com/cgi/doi/10.1177/0049124104268644.

Burnham, Kenneth P., and David R Anderson. 2002. *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Springer.

Carlisle, Jay D, Sarah L Stock, Gregory S Kaltenecker, and David L Swanson. 2004. “Habitat Associations, Relative Abundance, and Species Richness of Autumn Landbird Migrants in Southwestern Idaho.” *Condor* 106 (3): 549–566.

Chapman, Jason W, Rebecca L Nesbit, Laura E Burgin, and Don R Reynolds. 2010. "Flight Orientation Behaviors Promote Optimal Migration Trajectories in High-Flying Insects." *Science* 327 (February): 682–685.

Chapman, Jason W., Raymond H G Klaassen, V. Alistair Drake, Sabrina Fossette, Graeme C. Hays, Julian D. Metcalfe, Andrew M. Reynolds, Don R. Reynolds, and Thomas Alerstam. 2011. "Animal Orientation Strategies for Movement in Flows." *Current Biology* 21 (20): R861–R870. doi:10.1016/j.cub.2011.08.014. http://dx.doi.org/10.1016/j.cub.2011.08.014.

Chernetsov, Nikita. 2012. *Passerine Migration: Stopover and Flight*. Springer.

Chernetsov, Nikita, Victor N. Bulyuk, and Pavel Ktitorov. 2007. "Migratory Stopovers of Passerines in an Oasis at the Crossroads of the African and Indian Flyways." *Ringing & Migration* 23 (4) (January): 243–251. doi:10.1080/03078698.2007.9674372. http://www.tandfonline.com/doi/abs/10.1080/03078698.2007.9674372.

Cimprich, David A., and Frank R. Moore. 1999. "Energetic Condtraints and Predation Pressure during Stopover." In *Proc. 22 Int. Ornithological. Congr.*, edited by N. J. Adams and R. H. Slowtow, 1–12. Durban: 834-846. Johannesburg: BirdLife South Africa.

Cimprich, David a., and Frank R. Moore. 2006. "Fat Affects Predator-Avoidance Behavior in Gray Catbirds (Dumetella Carolinensis) during Migratory Stopover." *The Auk* 123 (4): 1069. doi:10.1642/0004-8038(2006)123[1069:FAPBIG]2.0.CO;2. http://www.bioone.org/perlserv/?request=get-abstract&doi=10.1642%2F0004-8038(2006)123%5B1069%3AFAPBIG%5D2.0.CO%3B2.

Cimprich, David A., Mark S. Woodrey, and Frank R. Moore. 2005. "Passerine Migrants Respond to Variation in Predation Risk during Stopover." *Animal Behaviour* 69 (5) (May): 1173–1179. doi:10.1016/j.anbehav.2004.07.021. http://linkinghub.elsevier.com/retrieve/pii/S000334720500031X.

Cohen, Emily B, Scott M Pearson, and Frank R Moore. 2014. "Effects of Landscape Composition and Configuration on Migrating Songbirds: Inference from an Individual-Based Model." *Ecological Applications* 24 (1) (January): 169–80. http://www.ncbi.nlm.nih.gov/pubmed/24640542.

Cowlishaw, Guy. 1997. "Trade-Offs between Foraging and Predation Risk Determine Habitat Use." *Animal Behavior* 53: 667–686.

Cutler, D Richard, Thomas C Edwards, Karen H Beard, Adele Cutler, T Kyle, Jacob Gibson, Joshua J Lawler, H Beard, and T Hess. 2007. "Random Forests for Classification in Ecology." *Ecology* 88 (11): 2783–2792.

Dänhardt, Juliana, and Åke Lindström. 2001. “Optimal Departure Decisions of Songbirds from an Experimental Stopover Site and the Significance of Weather.” *Animal Behaviour* 62 (2) (August): 235–243. doi:10.1006/anbe.2001.1749. http://linkinghub.elsevier.com/retrieve/pii/S000334720191749X.

Dee, D. P., S. M. Uppala, a. J. Simmons, P. Berrisford, P. Poli, S. Kobayashi, U. Andrae, et al. 2011. “The ERA-Interim Reanalysis: Configuration and Performance of the Data Assimilation System.” *Quarterly Journal of the Royal Meteorological Society* 137 (656) (April 28): 553–597. doi:10.1002/qj.828. http://doi.wiley.com/10.1002/qj.828.

Delmore, Kira E, James W Fox, and Darren E Irwin. 2012. “Dramatic Intraspecific Differences in Migratory Routes, Stopover Sites and Wintering Areas, Revealed Using Light-Level Geolocators.” *Proceedings. Biological Sciences / The Royal Society* 279 (1747) (November 22): 4582–9. doi:10.1098/rspb.2012.1229. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3479719&tool=pmcentrez&rendertype=abstract.

Deluca, William V, Bradley K Woodworth, Christopher C Rimmer, Peter P Marra, Philip D Taylor, Kent P Mcfarland, Stuart A Mackenzie, and D Ryan Norris. 2015. “Transoceanic Migration by a 12 G Songbird.” *Biology Letters* 11: 1–4.

Deppe, Jill, L., and John T Rotenberry. 2008. “Scale-Dependent Habitat Use by Fall Migratory Birds: Vegetation Structure, Floristics, and Geographyogy.” *Ecological Monographs* 78 (3): 461–487.

DeSorbo, Chris, R., K. G. Wright, I. Johnson, and R. Gray. 2012. “Bird Migration Stopover Sites: Ecology of Nocturnal and Diurnal Raptors at Monhegan Island.”

Dingle, Hugh. 1996. *Migration: The Biology of Life on the Move*. Oxford: Oxford University Press.

Drury, W.H., and J.A. Keith. 1962. “Radar Studies of Songbird Migration in Coastal New England.” *Ibis* 104 (4): 449–498.

Dunn, Erica H, Keith A Hobson, Len I Wassenaar, David J T Hussell, and Martha L Allen. 2006. “Identification of Summer Origins of Songbirds Migrating through Southern Canada in Autumn Détermination de L’aire Estivale Des Oiseaux Chanteurs Qui Migrent Par Le Sud Du Canada En Automne.” *Avian Conservation and Ecology* 1: 4.

Ellegren, Hans. 1993. “Speed of Migration and Migratory Flight Lengths of Passerine Birds Ringed during Autumn during Autumn Migration in Sweeden.” *Ornis Scandinavica* 24 (3): 220–228.

Environmental Systems Research Institute. 2011. “ArcGIS Desktop: Release 10.” Redlands, CA.

Erickson L., McGowan K., Powell H., Savoca M., Sedgwick C. 2011. “All About the Birds.” *Cornell University*. www.allaboutbirds.org.

Erni, Birgit, Felix Liechti, and Bruno Bruderer. 2002. “Stopover Strategies in Passerine Bird Migration: A Simulation Study.” *Journal of Theoretical Biology* 219: 479–493. doi:10.1006/yjtbi.3138.

Erni, Birgit. 2003. “How Does a First Year Passerine Migrant Find Its Way? Simulating Migration Mechanisms and Behavioural Adaptations.” *Oikos* 2 (December 2002): 333–340.

Erni, Birgit, Felix Liechti, L.G. Underhillz, and Bruno Bruderer. 2002. “Wind and Rain Govern the Intensity of Nocturnal Bird Migration in Central Europe: A Log-Linear Regression Analysis.” *Ardea* 90 (1): 155–166.

Erni, Birgit, Felix Liechi, and Bruno Bruderer. 2005. “The Role of Wind in Passerine Autumn Migration between Europe and Africa.” *Behavioral Ecology* 16 (4) (February 9): 732–740. doi:10.1093/beheco/ari046. http://www.beheco.oupjournals.org/cgi/doi/10.1093/beheco/ari046.

Farmer, Adrian H, and John A Wiens. 1998. “Optimal Migration Schedules Depend on the Landscape and the Physical Environment: A Dynamic Modeling View.” *Journal of Avian Biology* 29: 405–415.

Fisher, N.I. 1993. *Statistical Analysis of Circular Data*. Cambridge: Cambridge University Press.

Fitzgerald, Trina M., and Philip D. Taylor. 2008. “Migratory Orientation of Juvenile Yellow-Rumped Warblers (Dendroica Coronata) Following Stopover: Sources of Variation and the Importance of Geographic Origins.” *Behavioral Ecology and Sociobiology* 62 (9) (March 27): 1499–1508. doi:10.1007/s00265-008-0579-3. http://link.springer.com/10.1007/s00265-008-0579-3.

Fransson, Thord, and Thomas P. Weber. 1997. “Migratory Fuelling in Blackcaps (Sylvia Atricapilla) under Perceived Risk of Predation.” *Behavioral Ecology and Sociobiology* 41 (2) (August 6): 75–80. doi:10.1007/s002650050366. http://link.springer.com/10.1007/s002650050366.

Freemark, Kathryn E., and H. G. Merriam. 1986. “Importance of Area and Habitat Heterogeneity to Bird Assemblages in Temperate Forest Fragments.” *Biological Conservation* 36 (2) (January): 115–141. doi:10.1016/0006-3207(86)90002-9. http://linkinghub.elsevier.com/retrieve/pii/0006320786900029.

Gaspar, Philippe, Jean-Yves Georges, Sabrina Fossette, Arnaud Lenoble, Sandra Ferraroli, and Yvon Le Maho. 2006. "Marine Animal Behaviour: Neglecting Ocean Currents Can Lead Us up the Wrong Track." *Proceedings. Biological Sciences / The Royal Society* 273 (1602): 2697–2702. doi:10.1098/rspb.2006.3623.

Gauthreaux Jr, Sidney A. 1971a. "A Radar and Direct Visual Study of Passerine Spring Migration in Southern Louisiana." *The Auk* 88 (2): 343–365.

Gauthreaux Jr, Sidney A. 1971b. "A Radar and Direct Visual Study of Passerine Spring Migration in Southern Louisiana." *The Auk* 88 (2): 343–365.

Gauthreaux Jr, Sidney A. 1980. "The Influence of Global Climatological Factors on the Evolution of Bird Migration Pathways." In *Symposium on Patterns of Migration. International Ornithological Congress Proceedings*, 517–625.

Gauthreaux Jr, Sidney A. 1991. "The Flight Behavior of Migrating Birds in Changing Wind Fields: Radar and Visual Analyses." *American Zoologist* 31 (1): 187–204.

Gauthreaux Jr, Sindey A. 1980. "The Influnce of Global Climatological Factors on the Evolution of Bird Migration Pathways." *Acta XVII International Ornithological Congress*: 517–525.

Gauthreaux Jr, Sidney, A., J. E. Michi, and C. G. Beiser. 2005. "The Temporal and Spatial Structure of the Atmosphere and Its Influence on Bird Migration Stratagies." In *Birds of Two Worlds: The Ecology and Evolution of Migration*, 182–193. Baltimore, MD: John Hopkins University Press.

Gotceitas, Vytenis. 1990. "Foraging and Predator Avoidance : A Test of a Patch Choice Model with Juvenile Bluegill Sunfish." *Oecologia* 83 (3): 346–351.

Hebblewhite, Mark, and Evelyn H Merrill. 2009. "Trade-Offs between Predation Risk and Forage Differ between Migrant Strategies in a Migratory Ungulate." *Ecology* 90 (12) (December): 3445–54. http://www.ncbi.nlm.nih.gov/pubmed/20120812.

Hedenstrom, A, and Thomas Alerstam. 1997. "Optimum Fuel Loads in Migratory Birds: Distinguishing between Time and Energy Minimization." *Journal of Theoretical Biology* 189 (3) (December 7): 227–34. doi:10.1006/jtbi.1997.0505. http://www.ncbi.nlm.nih.gov/pubmed/9441816.

Hedenström, Anders. 1992. "Flight Performance in Relation to Fuel Load in Birds." *Journal of Theoretical Biology* 158: 535–537. doi:10.1016/S0022-5193(05)80714-3.

Hedenström, Anders. 2003. "Optimal Migration Strategies in Animals That Run: A Range Equation and Its Consequences." *Animal Behaviour* 66 (4): 631–636. doi:10.1006/anbe.2003.2234. http://linkinghub.elsevier.com/retrieve/pii/S0003347203922342.

Hedenström, Anders. 2009. “Optimal Migration Strategies in Bats.” *Journal of Mammalogy* 90 (6): 1298–1309. doi:10.1644/09-MAMM-S-075R2.1.

Hedenström, Anders, and Jan Pettersson. 1987. “Migration Routes and Wintering Areas of Willow Warblers Phylloscopus Trochilus (L.) Ringed in Fennoscandia.” *Ornis Fennica* 64: 137–143.

Helbig, A J. 1996. “Genetic Basis, Mode of Inheritance and Evolutionary Changes of Migratory Directions in Palearctic Warblers (Aves: Sylviidae).” *The Journal of Experimental Bology* 55: 49–55.

Helbig, Andreas J. 1991. “Inheritance of Migratory Direction in a Bird Species: A Cross-Breeding Experiment with SE- and SW-Migrating Blackcaps (Sylvia Atricapilla).” *Behavioral Ecology and Sociobiology* 28 (1): 9–12.

Helbig, Andreas J. 1992. “Population Differentiation of Migratory Directions in Birds: Comparison between Ringing Results and Orientation Behaviour of Hand-Raised Migrants.” *Oecologia* 90 (4): 483–488.

Hewitt, G M. 1996. “Some Genetic Consequences of Ice Ages, and Their Role, in Divergence and Speciation.” *Biological Journal of the Linnean Society* 58 (September 1994): 247–276. doi:10.1006/bijl.1996.0035.

Hewitt, Godfrey M. 1999. “Post-Glacial Re-Colonization of European Biota.” *Biological Journal of the Linnean Society* 68 (1-2): 87–112. doi:10.1111/j.1095-8312.1999.tb01160.x. http://dx.doi.org/10.1111/j.1095-8312.1999.tb01160.x.

Holberton, Rebecca L., Steven L. Van Wilgenburg, Adrienne J. Leppold, and Keith a. Hobson. 2015. “Isotopic ($\delta^{2}H_{f}$) Evidence of ‘loop Migration’ and Use of the Gulf of Maine Flyway by Both Western and Eastern Breeding Populations of Blackpoll Warblers.” *Journal of Field Ornithology* 86 (3): 213–228. doi:10.1111/jofo.12112. http://doi.wiley.com/10.1111/jofo.12112.

Houston, A. I., J. M. McNamara, and J. M. C. Hutchinson. 1993. “General Results Concerning the Trade-Off between Gaining Energy and Avoiding Predation.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 341 (1298) (September 29): 375–397. doi:10.1098/rstb.1993.0123. http://rstb.royalsocietypublishing.org/cgi/doi/10.1098/rstb.1993.0123.

Hutto, R.L. 1985. “Habitat Selection by Nonbreeding, Migratory Land Birds.” In *Habitat Selection in Birds*, edited by M. Cody, 455–476. Academic Press.

Hutto, Richard L. 1998. “On Th Eimportance of Stopover Sites to Migrating Birds.” *The Auk* 115 (4): 823–825.

Hutto, Richard L. 2000. “On the Importance of En Route Periods to the Conservation of Migratory Landbirds.” *Studies in Avian Biology* 20: 109–114.

Incze, Lewis, Huijie Xue, Nicholas Wolff, Danya Xu, Carl Wilson, Robert Steneck, Richard Wahle, Peter Lawton, Neal Pettigrew, and Yong Chen. 2010. “Connectivity of Lobster (Homarus Americanus) Populations in the Coastal Gulf of Maine: Part II. Coupled Biophysical Dynamics.” *Fisheries Oceanography* 19 (1) (January): 1–20. doi:10.1111/j.1365-2419.2009.00522.x. http://doi.wiley.com/10.1111/j.1365-2419.2009.00522.x.

Irwin, Darren E. 2009. “Speciation: New Migratory Direction Provides Route toward Divergence.” *Current Biology* 19 (24): R1111–R1113. doi:10.1016/j.cub.2009.11.011. http://dx.doi.org/10.1016/j.cub.2009.11.011.

Irwin, Darren E., and Jessica H. Irwin. 2005. “Siberian Migratory Divides.” In *Birds of Two Worlds: The Ecology and Evolution of Migration,* 27–40. Baltimore, MD: John Hopkins University Press.

Jansen, Henrice M., Hendrik V. Winter, M. C M Bruijs, and H. J G Polman. 2007. “Just Go with the Flow? Route Selection and Mortality during Downstream Migration of Silver Eels in Relation to River Discharge.” *ICES Journal of Marine Science* 64 (7): 1437–1443. doi:10.1093/icesjms/fsm132.

Johnson, D. H. 1980. “The Comparison of Usage and Availability Measurements for Evaluating Resource Preference.” *Ecology* 61 (1): 65–71.

Kelly, Jeffrey F, and Richard L Hutto. 2005. “An East-West Comparison of Migration in North American Wood Warblers.” *The Condor* 107 (2): 197–211.

Kemp, Michael U., Judy Shamoun-Baranes, Adriaan M. Dokter, Emiel van Loon, and Willem Bouten. 2013. “The Influence of Weather on the Flight Altitude of Nocturnal Migrants in Mid-Latitudes.” Edited by Ryan Norris. *Ibis* (July 27): n/a–n/a. doi:10.1111/ibi.12064. http://doi.wiley.com/10.1111/ibi.12064.

Kemp, Michael U., Judy Shamoun-Baranes, Hans Van Gasteren, Willem Bouten, and E. Emiel Van Loon. 2010. “Can Wind Help Explain Seasonal Differences in Avian Migration Speed?” *Journal of Avian Biology* 41 (6) (November 1): 672–677. doi:10.1111/j.1600-048X.2010.05053.x. http://doi.wiley.com/10.1111/j.1600-048X.2010.05053.x.

Kemp, Michael U., Judy Shamoun-Baranes, E. Emiel van Loon, James D. McLaren, Adriaan M. Dokter, and Willem Bouten. 2012. “Quantifying Flow-Assistance and Implications for Movement Research.” *Journal of Theoretical Biology* 308: 56–67. doi:10.1016/j.jtbi.2012.05.026. http://dx.doi.org/10.1016/j.jtbi.2012.05.026.

Kemp, Paul S., Mike H. Gessel, and John G. Williams. 2005. “Fine-Scale Behavioral Responses of Pacific Salmonid Smolts as They Encounter Divergence and Acceleration of Flow.” *Transactions of the American Fisheries Society* 134 (2): 390–398. doi:10.1577/T04-039.1. http://www.tandfonline.com/doi/abs/10.1577/T04-039.1.

Kerlinger, Paul, and Frank R Moore. 1989. “Atmospheric Structure and Avian Migration.” *Current Ornithology* 6: 109–142.

Kimura, M, and G H Weiss. 1964. “The Stepping Stone Model of Population Structure and the Decrease of Genetic Correlation with Distance.” *Genetics* 49 (4): 561–576. doi:10.1093/oxfordjournals.molbev.a025590.

Knutson, Melinda G., Nick P. Danz, Todd W. Sutherland, and Brian R. Gray. 2008. “Landbird Monitoring Protocol for the US Fish and Wildlife Service, Midwest and Northeast Regions, Version 1.” *Biological Mornitoring Team Technical Report BTM-2008-01. US Fish and Wildife Service, La Crosse, WI 25.*

Koenker, Roger. 2013. “Quantreg: Quantile Regression.” http://cran.r-project.org/package=quantreg.

Koivula, Karl, Seppo Rytkonen, and Markku Orell. 1995. “Hunger-Dependency of Hiding Behaviour after a Predator Attack in Dominant and Subordinate Willow Tits.” *Ardea* 83: 397–404.

Krebs, J. R. 1980. “Optimal Foraging, Predation Risk and Territory Defense.” *Ardea* 68: 83–90.

Ktitorov, Pavel, Franz Bairlein, and Maxim Dubinin. 2008. “The Importance of Landscape Context for Songbirds on Migration: Body Mass Gain Is Related to Habitat Cover.” *Landscape Ecology* 23 (2) (December 6): 169–179. doi:10.1007/s10980-007-9177-4. http://www.springerlink.com/index/10.1007/s10980-007-9177-4.

Kuenzi, Amy, J., Moore, F. R., and T. R. Simons. 1991. “Stopover of Neotropical Landbird Migrants on East Ship Island Following Trans-Gulf Migration.” *Condor* 93 (4): 869–883.

Kullberg, Cecilia, Third Fransson, and Sven Jakobsson. 1996. “Impaired Predator Evasion in Fat Blackcaps (Sylvia Atricapilla).” *Proceedings: Biological Sciences* 263 (1377): 1671–1675.

Larkin, Ronald P. 1991. “Flight Speeds Observed with Radar, a Correction: Slow ‘ Birds ’ Are Insects.” *Behavioral Ecology and Sociobiology* 29 (3): 221–224.

Lehnen, Sarah E, and David G Krementz. 2005. “Turnover Rate of Fall-Migrating Pectoral Sandpipers in the Lower Mississippi Alluvial Valley.” *Journal of Wildlife Management* 69 (2): 671–680.

Levene, H. 1960. “Robust Tests for Equality of Variance.” In *Contributions to Probability and Statistics,* edited by I. Olkin, S. G. Ghurye, W. Hoeffding, W. G. Madow, and H. B. Mann, 278–292. Stanford, CA: Stanford University Press.

Liaw, A., and M. Wiener. 2002. “Classification and Regression by randomForest.” *R News* 2 (3): 18–22.

Liechti, Felix. 1995. “Modelling Optimal Heading and Airspeed of Migrating Birds in and Wind Influence Relation to Energy Expenditure.” *Journal of Avian Biology* 26 (4): 330–336.

Liechti, Felix. 2006. “Birds: Blowin’ by the Wind?” *Journal of Ornithology* 147 (2) (March 21): 202–211. doi:10.1007/s10336-006-0061-9. http://www.springerlink.com/index/10.1007/s10336-006-0061-9.

Liechti, Felix, and Bruno Bruderer. 1998. “The Relevance of Wind for Optimal Migration Theory.” *Journal of Avian Biology* 29 (4): 561–568.

Liechti, Felix, Marcel Klaassen, and Bruno Bruderer. 2000. “Predicting Migratory Flight Altitudes by Physiological Migration Models.” *The Auk* 117 (1): 205–214.

Lima, Steven L. 1988. “Vigilance during the Initiation of Daily Feeding in Dark-Eyed Juncos.” *Oikos* 53: 12–16.

Lima, Steven L., and Lawrence M. Dill. 1990. “Behavioral Decisions Made under the Risk of Predation: A Review and Prospectus.” *Canadian Journal of Zoology* 68 (4) (April): 619–640. doi:10.1139/z90-092. http://www.nrcresearchpress.com/doi/abs/10.1139/z90-092.

Lindström, Åke. 1989. “Finch Flock Size and Risk of Hawk Predation at a Migratory Stopover Site.” *The Auk* 106 (2): 225–232.

Lindström, Åke. 1990. “The Role of Predation Risk in Stopover Habitat Selection in Migrating Bramblings, Fringilla Montifringilla.” *Behavioral Ecology* 1 (2): 102–106.

Lindström, Åke, and Thomas Alerstam. 1992. “Optimal Fat Loads in Migrating Birds: A Test of the Time-Minimization Hypothesis.” *The American Naturalist* 140 (3): 477–491.

Long, Jennifer A, and Philip C Stouffer. 2003. "Diet and Preparation for Spring Migration in Captive Hermit Thrushes (Catharus Guttatus)." *The Auk* 120 (2): 323–330.

Martell, Mark S, Charles J Henny, Peter E Nye, and Matthew J Solensky. 2001. "Fall Migration Routes, Timing, and Wintering Sites of North American Ospreys as Determind by Satellite Telemetry." *The Condor* 103 (4): 715–724.

Martin, Thomas E. 1980. "Diversity and Abundance of Spring Migratory Birds Using Habitat Islands on the Great Plains." *Condor* 82 (4): 430–439.

Martin, Thomas E. 1995. "Avian Life History Evolution in Relation to Nest Sites, Nest Predation, and Food." *Ecological Monographs* 65 (1): 101–127.

Martin, Thomas E, and James R Karr. 1986. "Patch Utilization by Migrating Birds: Resource Oriented?" *Ornis Scandinavica* 17 (2): 165–174.

Mateos-Rodriguez, M., and F. Liechti. 2011. "How Do Diurnal Long-Distance Migrants Select Flight Altitude in Relation to Wind?" *Behavioral Ecology* 23 (2) (November 28): 403–409. doi:10.1093/beheco/arr204. http://www.beheco.oxfordjournals.org/cgi/doi/10.1093/beheco/arr204.

Mathworks, Inc. 2012. "MATLAB and Statistics Toolbox Release 2012b." Natick, Massachusetts.

Matthews, Stephen N., and Paul G. Rodewald. 2010. "Urban Forest Patches and Stopover Duration of Migratory Swainson's Thrushes." *The Condor* 112 (1) (February): 96–104. doi:10.1525/cond.2010.090049. http://www.jstor.org/stable/10.1525/cond.2010.090049.

McCabe, Jennifer D., and Brian J. Olsen. 2015. "Landscape-Scale Habitat Availability, and Not Local Geography, Predicts Migratory Landbird Stopover across the Gulf of Maine." *Journal of Avian Biology* (February): n/a–n/a. doi:10.1111/jav.00598. http://doi.wiley.com/10.1111/jav.00598.

McCann, J. M., S.E. Maybey, L. J. Niles, C. Bartlett, and P. Kerlinger. 1993. "A Regional Study of Coastal Migratory Stopover Habitat for Neotropical Migrant Songbirds: Land Management Implications." *Transactions of the North American Wildlife and Natural Resources Conference* 58: 398–407.

McDonald, Lyman L., J. R. Alldredge, Mark S. Boyce, and Wallace P. Erickson. 2005. "Measuring Availability and Vertebrate Use of Terrestrial Habitats and Foods." *The Wildlife Society: Bethesda*: 465–488.

McGarigal, K., S.A. Cushman, and E. Ene. 2012. “FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps.” University of Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html.

McLaren, James D, Judy Shamoun-Baranes, Adriaan M Dokter, Raymond H G Klaassen, and Willem Bouten. 2014. “Optimal Orientation in Flows: Providing a Benchmark for Animal Movement Strategies.” *Journal of the Royal Society, Interface* 11 (99): 20140588–. doi:10.1098/rsif.2014.0588. http://rsif.royalsocietypublishing.org/content/11/99/20140588.abstract?etoc.

McLaren, James D., Judy Shamoun-Baranes, and Willem Bouten. 2012. “Wind Selectivity and Partial Compensation for Wind Drift among Nocturnally Migrating Passerines.” *Behavioral Ecology* 23 (5): 1089–1101. doi:10.1093/beheco/ars078.

Meinertzhagen, Richard. 1955. “The Speed and Altitude of Bird Flight (with Notes on Other Aniumals).” *Ibis* 97 (1): 81–117.

Melià, P, M Schiavina, M Gatto, L Bonaventura, S Masina, and R Casagrandi. 2013. “Integrating Field Data into Individual-Based Models of the Migration of European Eel Larvae.” *Marine Ecology Progress Series* 487 (July 30): 135–149. doi:10.3354/meps10368. http://www.int-res.com/abstracts/meps/v487/p135-149/.

Metcalfe, N. B., and R. W. Furness. 1984. “Changing Priorities: The Effect of Pre-Migratory Fattening on the Trade-off between Foraging and Vigilance.” *Behavioral Ecology and Sociobiology* 15 (3) (August): 203–206. doi:10.1007/BF00292976. http://link.springer.com/10.1007/BF00292976.

Mills, Alexander M., Bethany G. Thurber, Stuart a. Mackenzie, and Philip D. Taylor. 2011. “Passerines Use Nocturnal Flights for Landscape-Scale Movements during Migration Stopover.” *The Condor* 113 (3) (August): 597–607. doi:10.1525/cond.2011.100186. http://www.jstor.org/stable/info/10.1525/cond.2011.100186.

Mitchell, Greg W, Bradley K Woodworth, Philip D Taylor, and D Ryan Norris. 2015. “Automated Telemetry Reveals Age Specific Differences in Flight Duration and Speed Are Driven by Wind Conditions in a Migratory Songbird.” *Movement Ecology* 3 (1): 19. doi:10.1186/s40462-015-0046-5. http://www.movementecologyjournal.com/content/3/1/19.

Møller, A. P, L. Z Garamszegi, J. M Peralta-Sánchez, and J. J Soler. 2011. “Migratory Divides and Their Consequences for Dispersal, Population Size and Parasite-Host Interactions.” *Journal of Evolutionary Biology* 24 (8) (August): 1744–55. doi:10.1111/j.1420-9101.2011.02302.x. http://www.ncbi.nlm.nih.gov/pubmed/21599774.

Moore, F. R., Sidney A. Gauthreaux Jr, Paul Kerlinger, and T. R. Simons. 1995. “Habitat Requirements during Migration: Important Link in Conservation.” In *Ecology and Management of Neotropical Migratory Birds, a Synthesis and Review of Critical Issues*, edited by T. E. Martin and D. M. Finch, 121–144. Oxford University Pres, New York.

Moore, Frank, and Paul Kerlinger. 1987. “Stopover and Fat Deposition by North American Wood-Warblers (Parulinae) Following Spring Migration over the Gulf of Mexico.” *Oecologia* 74 (1): 47–54. doi:10.1007/S00442-004-V.

Moore, Frank R. 1984. “Age-Dependent Variability in the Migratory Orientation of the Savannah Sparrow (Passerculus Sandwichensis).” *The Auk* 101 (4): 875–880.

Moore, Frank R, Mark S Woodrey, Jeffrey J Buler, Stefan Woltmann, and Ted R Simons. 2005. “Understanding the Stopover of Migratory Birds: A Scale Dependent Approach.” In *Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference*, edited by CJ Ralph and Terry Rich, 684–689.

Moore, Frank R. 1990. “Evidence for Redetermination of Migratory Direction Following Wind Displacement.” *The Auk* 107 (2): 425–428.

Moore, Frank R. 1994. “Resumption of Feeding under Risk of Predation: Effect of Migratory Condition.” *Animal Behavior* 48: 975–977.

Moore, Frank R., and David A. Aborn. 2000. “Mechanisms of En Route Habitat Selection.” *Studies in Avian Biology*: 34–42.

Moore, Frank R. and Kerlinger, P. 1987. “International Association for Ecology Stopover and Fat Deposition by North American Wood-Warblers (Parulinae) Following Spring Migration over the Gulf of Mexico.” *Oecologia* 74 (1): 47–54.

Moore, Frank R., Kerlinger, P., and Simons, T. 1990. “Stopover on a Gulf Coast Barrier Island by Spring Migrants.” *Willson Bulletin* 102 (3): 487–500.

Newton, Ian. 2008. *The Migration Ecology of Birds*. London: Academic Press.

Niles, Lawrence J, Joanna Burger, and Kathleen E. Clark. 1996. “The Influence of Weather, Geography, and Habitat on Migrating Raptors on Cape May Peninsula.” *The Condor* 98 (2) (May): 382. doi:10.2307/1369156. http://links.jstor.org/sici?sici=0010-5422(199605)98:2<382:TIOWGA>2.0.CO;2-N&origin=crossref.

Nisbet, Ian C T. 1970. “Autumn Migration of the Blackpoll Warbler: Evidence for Long Flight Provided by Regional Survey.” *Bird-Banding* 41 (3): 207–240.

Olsen, Brian J, Jennifer D. McCabe, Evan M. Adams, P. Grunzel, David, and Adrienne J. Leppold. 2015. “Matching Ephemeral Resources on Autumnal Stopover and the Potential for Mismatch.” *Phenological Synchrony and Bird Migration: Changing Climate and Seasonal Resources in North America*.

Parrish, J. D. 2000. “Behavioral, Energetic, and Conservation Implications of Foraging Plasticity during Migration.” *Studies in Avian Biology* 20: 53–70. http://cat.inist.fr/?aModele=afficheN&cpsidt=1176943.

Parrish, Jeffrey D. 1997. “Patterns of Frugivory and Energetic Condition in Nearctic Landbirds during Autumn Migration.” *The Condor* 99 (3) (August): 681–697. doi:10.2307/1370480. http://www.jstor.org/stable/1370480?origin=crossref.

Pennycuick, Colin J. 1969. “The Mechanics of Bird Migration.” *Ibis* 111 (4): 525–556.

Petit, D.R. 2000. “Habitat Use by Landbirds along Nearctic-Neotropical Migration Routes; Implications for Conservation of Stopover Habitat.” *Studies in Avian Biology* 20: 15–33.

Pielou, E. C. 1991. *After the Ice Age: The Return of Life to Glaciated North America, Part II*. The University of Chicago Press.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Devlopment Core Team. 2012. “Nlme: Linear and Nonlinear Mixed Effects Models.”

Place, Allen R, and Edmund W Stiles. 1992. “Living off the Wax of the Land: Bayberries and Yellow-Rumped Warblers.” *Th Auk* 109 (2): 334–345.

Pomeroy, A. C., R. W. Butler, and R. C. Ydenberg. 2006. “Experimental Evidence That Migrants Adjust Usage at a Stopover Site to Trade off Food and Danger.” *Behavioral Ecology* 17 (6) (September 6): 1041–1045. doi:10.1093/beheco/arl043. http://www.beheco.oxfordjournals.org/cgi/doi/10.1093/beheco/arl043.

Pomeroy, Andrea C., Dana A. Acevedo Seaman, Robert W. Butler, Robert W. Elner, Tony D. Williams, and Ronald C. Ydenberg. 2008. “Feeding–danger Trade-Offs Underlie Stopover Site Selection by Migrants.” *Avian Conservation and Ecology-Écologie et Conservation Des Oiseaux* 3 (1): 7. http://www.sfu.ca/biology/wildberg/papers/PomeroyetalACEECO08.pdf\npapers2://publication/uuid/8FD75E0B-D0B6-4039-9CE3-B43E2449CE95.

Press, California, and American Ornithologists. 1971. “A Radar and Direct Visual Study of Passerine Spring Migration in Southern Louisiana Author (S): Sidney A . Gauthreaux , Jr . Reviewed Work (S): Published by : University of California Press on Behalf of the American Ornithologists ’ Union Stable URL :” *The Auk* 88 (2): 343–365.

Preusser, Frank, Dirk Radies, and Albert Matter. 2002. “A 160,000-Year Record of Dune Development and Atmospheric Circulation in Southern Arabia.” *Science (New York, N.Y.)* 296 (5575): 2018–2020. doi:10.1126/science.1069875.

Pulido, Francisco. 2007. “The Genetics and Evolution of Avian Migration.” *BioScience* 57 (2): 165. doi:10.1641/B570211.

R Development Core Team. 2012. “R: A Language and Environment for Statistical Computing.” Vienna, Austia: R Foundation for Statistical Computing. http://www.r-project.org.

Raim, A., William W. Cochran, and R. D. Applegate. 1989. “Activities of a Migrant Merlin during an Island Stopover.” *Journal of Raptor Research* 23: 49–52.

Ralph, C John. 1981. “Age Ratios and Their Possible Use in Determining Autumn Routes of Passerine Migrants.” *Wilson Bulletin* 93 (2): 164–188.

Ralph, C.J. 1971. “An Age Differential of Migrants in Coastal California.” *The Condor* 73 (2): 243–246.

Ralph, John C, Geoffrey R Geupel, Peter Pyle, Thomas E Martin, and David F DeSante. 1993. “Handbook of Field Methods for Monitoring Landbirds.” *USDA Forest Service/UNL Factulty Publications*.

Rappole, John H., Mario A. Ramos, Richard J. Oehlenschlager, Dwain W. Warner, and Christopher P. Barkan. 1979. “Timing of Migration and Route Selection in North American Songbirds.” In *Proceedings of the First Welder Wildife Foundation Symposium*, 199–214. Sinton, TX: Welder Wildlife Foundation.

Remington, Charles, L. 1968. “Suture-Zones of Hybrid Interaction between Recently Joined Biotas.” In *Evolutionary Biology*, 321–428. US: Springer.

Richardson, John W. 1976. “Autumn Migration over Puerto Rico and the Western Atlantic: A Radar Study.” *Ibis* 118: 309–332.

Richardson, John W. 1978a. “Timing and Amount of Bird Migration in Relation to Weather: A Review.” *Oikos* 30 (2): 224. doi:10.2307/3543482. http://www.jstor.org/stable/3543482?origin=crossref.

Richardson, John W. 1978b. “Reorientation of Nocternal Landbird Migrants over the Atlantic Ocean near Nova Scotia in Autumn.” *The Auk* 95 (4): 717–732.

Richardson, John W. 1990. “Wind and Orientation of Migrating Birds: A Review.” *Experienta* 46 (416-428).

Rodewald, Paul G, and Margaret C Brittingham. 2002. “Habitat Use and Behavior of Mixed Species Landbird Flocks during Fall Migration.” *The Wilson Bulletin* 114 (1): 87–98.

Rodewald, Paul G. 2004. “Stopover Habitat of Landbirds during Fall: Use of Edge-Dominated and Early-Successional Forests.” *The Auk* 121 (4): 1040–1055.

Rodewald, Paul G., and Margaret C. Brittingham. 2007. “Stopover Habitat Use by Spring Migrants Landbirds: The Roles of Habitat Structure, Leaf Development, and Food Availability.” *The Auk* 124 (3): 1063–1074. doi:10.1642/0004-8038(2007)124[1063:SHUBSM]2.0.CO;2. http://www.bioone.org/perlserv/?request=get-abstract&doi=10.1642/0004-8038(2007)124[1063:SHUBSM]2.0.CO;2.

Rohwer, Sievert, and Darren E. Irwin. 2011. “Molt, Orientation, and Avian Speciation.” *The Auk* 128 (2): 419–425.

Ruegg, Kristen C. 2007. “Divergence between Subspecies Groups of Swainson’s Thrush (Catharus Ustulatus Ustulatus and C. U. Swainsoni).” *Ornithological Monographs* 63 (1): 67. doi:10.1642/0078-6594(2007)63[67:DBSGOS]2.0.CO;2. http://www.bioone.org/perlserv/?request=get-abstract&doi=10.1642%2F0078-6594(2007)63%5B67%3ADBSGOS%5D2.0.CO%3B2.

Ruegg, Kristen C. 2008. “Genetic, Morphological, and Ecological Characterization of a Hybrid Zone That Spans a Migratory Divide.” *Evolution* 62 (2) (March): 452–66. doi:10.1111/j.1558-5646.2007.00263.x. http://www.ncbi.nlm.nih.gov/pubmed/18039327.

Ruegg, Kristen C, and Thomas B Smith. 2002. “Not as the Crow Flies: A Historical Explanation for Circuitous Migration in Swainson’s Thrush (Catharus Ustulatus).” *Proceedings. Biological Sciences / The Royal Society* 269 (1498) (July 7): 1375–81. doi:10.1098/rspb.2002.2032. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1691041&tool=pmcentrez&rendertype=abstract.

Sapir, Nir, Zvika Abramsky, Eyal Shochat, and Ido Izhaki. 2004. “Scale-Dependent Habitat Selection in Migratory Frugivorous Passerines.” *Die Naturwissenschaften* 91 (11) (November): 544–7. doi:10.1007/s00114-004-0564-2. http://www.ncbi.nlm.nih.gov/pubmed/15455207.

Savino, Jacqueline F., and Roy a. Stein. 1989. “Behavior of Fish Predators and Their Prey: Habitat Choice between Open Water and Dense Vegetation.” *Environmental Biology of Fishes* 24 (4) (April): 287–293. doi:10.1007/BF00001402. http://link.springer.com/10.1007/BF00001402.

Schmaljohann, Heiko, and Volker Dierschke. 2004. “Optimal Bird Migration and Predation Risk: A Field Experiment with Northern Wheatears Oenanthe Oenanthe.” *Journal of Animal Ecology* 74 (1) (December 6): 131–138. doi:10.1111/j.1365-2656.2004.00905.x. http://doi.wiley.com/10.1111/j.1365-2656.2004.00905.x.

Schmaljohann, Heiko, and Beat Naef-Daenzer. 2011. “Body Condition and Wind Support Initiate the Shift of Migratory Direction and Timing of Nocturnal Departure in a Songbird.” *Journal of Animal Ecology* 80 (6): 1115–1122. doi:10.1111/j.1365-2656.2011.01867.x.

Scholtyssek, Christine, Marie Dacke, Ronald Kröger, and Emily Baird. 2014. “Control of Self-Motion in Dynamic Fluids: Fish Do It Differently from Bees.” *Biology Letters* 10 (May): 20140279. doi:10.1098/rsbl.2014.0279. http://rsbl.royalsocietypublishing.org/content/10/5/20140279.abstract.

Seewagen, Chad L, and Eric J Slayton. 2008. “Mass Changes of Migratory Landbirds during Stopovers in a New York City Park.” *Wilson Journal of Ornithology* 120 (2): 296–303.

Seewagen, Chad L., and Christopher G. Guglielmo. 2010. “Effects of Fat and Lean Body Mass on Migatory Landbird Stopover Duration.” *The Wilson Journal of Ornithology* 122 (1) (March): 82–87. doi:10.1676/09-088.1. http://www.bioone.org/doi/abs/10.1676/09-088.1.

Shamoun-Baranes, Judy, and Hans van Gasteren. 2011. “Atmospheric Conditions Facilitate Mass Migration Events across the North Sea.” *Animal Behaviour* 81 (4) (April): 691–704. doi:10.1016/j.anbehav.2011.01.003. http://linkinghub.elsevier.com/retrieve/pii/S0003347211000042.

Sherry, T.W., and R.T. Holmes. 1985. “Dispersion Patterns and Habitat Responses of Birds in Northern Hardwood Forests.” In *Habitat Selection in Birds*, edited by M. Cody, 283–309. Academic Press.

Shi, Wei, Carole Kercelhue, and Hui Ye. 2005. “Population Genetics of the Oriental Fruit Fly , Bactrocera Dorsalis (Diptera: Tephritidae), in Yunnan (China) Based on Mitochondrial DNA Sequences.” *Molecular Biology and Evolution* (Ye 2001): 977–983.

Sih, Andrew. 1992. “Prey Uncertainty and the Balancing of Antipredator and Feeding Needs.” *The American Nauralist* 139 (5): 1052–1069.

Sillett, T. Scott, and Richard T Holmes. 2002. “Variation in Survivorship of a Migratory Songbird throughout Its Annual Cycle.” *Journal of Animal Ecology* 71 (2): 296–308.

Simons, T. R., S. M. Pearson, and F. R. Moore. 2000. “Application of Spatial Models to the Stopover Ecology of Trans-Gulf Migrants.” *Studies in Avian Biology* 20: 4–14.

Skagen, Susan K, Cynthia P Melcher, William H Howe, and Fritz L Knopf. 1998. “Comparative Use of Riparian Corridors and Oases by Migrating Birds in Southeast Arizona.” *Conservation Biology* 12 (4): 896–909.

Smith, Adam D., and Scott R McWilliams. 2009. “Protocol for the Rapid Assessment of Fruit Abundance on New England Wildlife Refuges.” Kingston, RI: University of Rhode Island.

Srygley, R. B., and R. Dudley. 2007. “Optimal Strategies for Insects Migrating in the Flight Boundary Layer: Mechanisms and Consequences.” *Integrative and Comparative Biology* 48 (1): 119–133. doi:10.1093/icb/icn011. http://icb.oxfordjournals.org/cgi/doi/10.1093/icb/icn011.

Stearns, Stephen C. 1992. *The Evolution of Life-Histories*. Vol. 249. Oxford: Oxford University Press.

Stewart, R.M., Mewaldt, L.R., and Kaiser, S. 1974. “Age Ratios of Coastal and Inland Fall Migrant Passerines in Central California.” *Bird-Banding* 45 (1): 46–57.

Stoddard, Philip K., J. Ellen Marsden, and Timothy C. Williams. 1983. “Computer Simulations of Autumnal Bird Migration over the Western North Atlantic.” *Animal Behavior* 31: 173–180.

Suomala, Rebecca W, Sara R Morris, Kimberly J Babbitt, D Thomas, and Thomas D Lee. 2010. “Migrant Songbird Species Distribution and Habitat Use during Stopover on Two Islands in the Gulf of Maine.” *The Wilson Journal of Ornithology* 122 (4): 725–737.

Suthers, Hannah B, Jean M Bickal, and Paul G Rodewald. 2000. “Use of Successional Habitat and Fruit Resources by Songbirds during Autumn Migration in Central New Jersey.” *The Wilson Bulletin* 112 (2): 249–260.

Swenson, Nathan G., and Daniel J Howard. 2004. “Do Suture Zones Exist?” *Evolution; International Journal of Organic Evolution* 58 (11): 2391–2397. doi:10.1554/04-239.

Swenson, Nathan G. 2005. “Clustering of Contact Zones, Hybrid Zones, and Phylogeographic Breaks in North America.” *The American Naturalist* 166 (5): 581–591. doi:10.1086/491688.

Szövényi, P., S. Terracciano, M. Ricca, S. Giordano, and a. J. Shaw. 2008. “Recent Divergence, Intercontinental Dispersal and Shared Polymorphism Are Shaping the

Genetic Structure of Amphi-Atlantic Peatmoss Populations.” *Molecular Ecology* 17 (24): 5364–5377. doi:10.1111/j.1365-294X.2008.04003.x.

Taylor, Philip D, Stuart A Mackenzie, Bethany G Thurber, Anna M Calvert, Alex M Mills, Liam P McGuire, and Christopher G Guglielmo. 2011. “Landscape Movements of Migratory Birds and Bats Reveal an Expanded Scale of Stopover.” *PloS One* 6 (11) (January): e27054. doi:10.1371/journal.pone.0027054. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3207824&tool=pmcentrez&rendertype=abstract.

Thaler, Jennifer S, Scott H McArt, and Ian Kaplan. 2012. “Compensatory Mechanisms for Ameliorating the Fundamental Trade-off between Predator Avoidance and Foraging.” *Proceedings of the National Academy of Sciences* 109 (30) (July 24): 12075–80. doi:10.1073/pnas.1208070109. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3409718&tool=pmcentrez&rendertype=abstract.

Toews, David P L, Alan Brelsford, and Darren E. Irwin. 2011. “Hybridization between Townsend’s Dendroica Townsendi and Black-Throated Green Warblers D. Virens in an Avian Suture Zone.” *Journal of Avian Biology* 42 (5): 434–446. doi:10.1111/j.1600-048X.2011.05360.x.

Valeix, Marion, Hervé Fritz, Andrew J. Loveridge, Zeke Davidson, Jane E. Hunt, Felix Murindagomo, and David W. Macdonald. 2009. “Does the Risk of Encountering Lions Influence African Herbivore Behaviour at Waterholes?” *Behavioral Ecology and Sociobiology* 63 (10) (March 31): 1483–1494. doi:10.1007/s00265-009-0760-3. http://link.springer.com/10.1007/s00265-009-0760-3.

Van Belle, J., J. Shamoun-Baranes, E. Van Loon, and W. Bouten. 2007. “An Operational Model Predicting Autumn Bird Migration Intensities for Flight Safety.” *Journal of Applied Ecology* 44 (4) (May 19): 864–874. doi:10.1111/j.1365-2664.2007.01322.x. http://doi.wiley.com/10.1111/j.1365-2664.2007.01322.x.

Videler, John J. 2005. *Avian Flight*. Oxford: University Press.

Vitz, A. C., and A. D. Rodewald. 2007. “Vegetative and Fruit Resources as Determinants of Habitat Use by Mature-Forest Birds during the Postbreeding Period.” *The Auk* 124 (2): 494–507.

Weber, T P, and A Hedenström. 2000. “Optimal Stopover Decisions under Wind Influence: The Effects of Correlated Winds.” *Journal of Theoretical Biology* 205 (1) (July 7): 95–104. doi:10.1006/jtbi.2000.2047. http://www.ncbi.nlm.nih.gov/pubmed/10860703.

Weir, Jason T, and Dolph Schluter. 2004. “Ice Sheets Promote Speciation in Boreal Birds.” *Proceedings. Biological Sciences / The Royal Society* 271 (1551): 1881–1887. doi:10.1098/rspb.2004.2803.

White, Crow, Kimberly a Selkoe, James Watson, David a Siegel, Danielle C Zacherl, and Robert J Toonen. 2010. “Ocean Currents Help Explain Population Genetic Structure.” *Proceedings. Biological Sciences / The Royal Society* 277 (1688): 1685–1694. doi:10.1098/rspb.2009.2214.

Wiens, John A, and John T Rotenberry. 1981. “Habitat Associations and Community of Birds in Shrubsteppe Environments.” *Ecological Monographs* 51 (1): 21–42.

Williams, Timothy C., J. M. Williams, L. C. Ireland, and J. M. Teal. 1977. “Autumnal Bird Migration over the Western North Atlantic.” *Atlantis* 31 (3): 251–267.

Williams, Timothy C. 1985. “Autumnal Bird Migration over the Windward Caribbean Islands.” *The Auk* 102 (1): 163–167.

Williams, Timothy C, Janet M Williams, Leonard C Ireland, and John M Teal. 1977. “Autumnal Bird Migration over the Western North Atlantic Ocean.” *American Birds* 31 (3): 251–267.

Williams, Timothy C., and Thompson Webb. 1996. “Neotropical Bird Migration during the Ice Ages: Orientation and Ecology.” *The Auk* 113 (1): 105–118. http://www.jstor.org/stable/10.2307/4088939\npapers2://publication/uuid/83B23DD4-5A57-42A6-A06E-8C3741CCFF9D.

Wilson, F. W., E. A. Porter, and R. S. Condit. 1982. “Avian Frugivore Activity in Relation to Forest Light Gaps.” *Caribbean Journal of Science* 18: 1–4.

Winker, Kevin, Dwain W Warner, and A R Weisbrod. 1992. “Migration of Woodland Birds at a Fragmented Inland Stopover Site.” *Wilson Bulletin* 104 (4): 580–598.

Woltmann, Stefan, and David Cimprich. 2003. “Effects of Weather on Autumn Hawk Movements at Fort Morgan, Alabama.” *Southeastern Naturalist* 2 (3) (September): 317–326. doi:10.1656/1528-7092(2003)002[0317:EOWOAH]2.0.CO;2. http://www.bioone.org/doi/abs/10.1656/1528-7092%282003%29002%5B0317%3AEOWOAH%5D2.0.CO%3B2.

Woodworth, Bradley K., Charles M. Francis, and Philip D. Taylor. 2014. “Inland Flights of Young Red-Eyed Vireos Vireo Olivaceus in Relation to Survival and Habitat in a Coastal Stopover Landscape.” *Journal of Avian Biology* 45 (4) (July 9): 387–395. doi:10.1111/jav.00276. http://doi.wiley.com/10.1111/jav.00276.

Xue, Huijie, Lewis Incze, Danya Xu, Nicholas Wolff, and Neal Pettigrew. 2008. “Connectivity of Lobster Populations in the Coastal Gulf of Maine.” *Ecological Modelling* 210 (1-2) (January): 193–211. doi:10.1016/j.ecolmodel.2007.07.024. http://linkinghub.elsevier.com/retrieve/pii/S0304380007004000.

Yasué, M, J L Quinn, and W Cresswell. 2003. “Multiple Effects of Weather on the Starvation and Predation Risk Trade-off in Choice of Feeding Location in Redshanks.” *Functional Ecology* 17: 727–736.

Ydenberg, Ronald C, Robert W Butler, David B Lank, Barry D Smith, and John Ireland. 2004. “Western Sandpipers Have Altered Migration Tactics as Peregrine Falcon Populations Have Recovered.” *Proceedings of the Royal Society B: Biological Sciences* 271 (1545) (June 22): 1263–9. doi:10.1098/rspb.2004.2713. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1691718&tool=pmcentrez&rendertype=abstract.

Ydenberg, Ronald C., Robert W. Butler, and David B. Lank. 2007. “Effects of Predator Landscapes on the Evolutionary Ecology of Routing, Timing and Molt by Long-Distance Migrants.” *Journal of Avian Biology* 38 (5) (September): 523–529. doi:10.1111/j.2007.0908-8857.04202.x. http://doi.wiley.com/10.1111/j.2007.0908-8857.04202.x.

Yong, Wang, Deborah M Finch, Frank R Moore, and Jeffrey F Kelly. 1998. “Stopover Ecology and Habitat Use of Migratory Wilson’s Warblers.” *The Auk* 115 (4): 829–842.

Yong, Wang, and Frank R Moore. 1993. “Relation between Migratory Activity and Energetic Condition among Thrushes (Turdinae) Following Passage across the Gulf of Mexico.” *Condor* 95 (4): 934–943. doi:10.2307/1369429.

APPENDIX – CHAPTER 7: FALL MIGRATORY STATION VEGETATION MONITORING

A.1. General Description

The following protocol was designed to quantify the vegetation of migration monitoring stations within the habitats sampled by A) mist-netting stations and B) daily fixed area censuses (both with an emphasis on vegetative structure and foraging resources).

The protocol consists of vegetative characterization on two time scales (weekly and once per season) at a small spatial scale that can be combined to assess larger spatial scales. The intent of this design is to allow for the assessment of local habitat covariates of net capture rates and fixed-area census results, as well as to allow for the characterization of the overall vegetation (or habitat zones within each site) that is being sampled by different groups at different sites.

A.2. General Design

We assume that the local sites are assessing bird habitat use through both mist-netting and daily surveys in areas outside of the established net lanes (Figure A.1). Modifications from this protocol that still allow for comparable data among monitoring stations are simple if only one of these approaches are being followed at any given site. Likewise, if local stations have stratified effort (by habitat type or any other factor of interest), this protocol is easily stratified as well to allow local stations to gather pertinent habitat data along local categories of interest while still providing net-lane, census area, and site level assessments that are directly comparable across multiple stations.

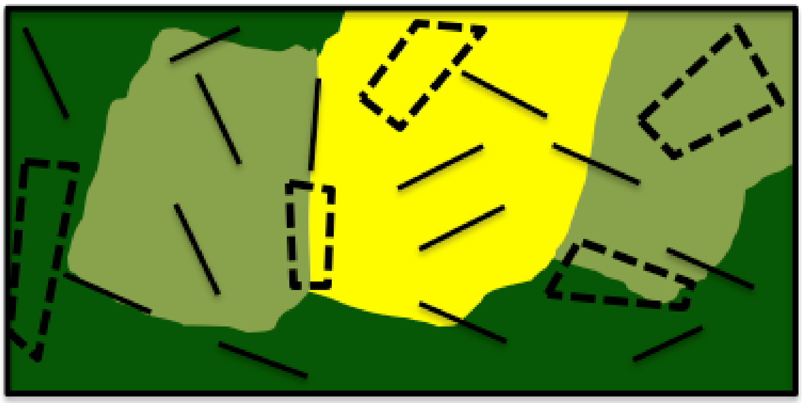


Figure A.1. The general assumed study design of a migratory monitoring station with net lanes (black lines) and fixed-area census area (dotted polygon outlines). The protocol allows for the two sampling methods to be stratified by any categorical treatment of interest (shown here in different colors, e.g. general habitat type, landscape history, land ownership, etc.), but this is not necessary.

We constructed the methods described largely by modifying those described in the *Handbook of Field Methods for Monitoring Landbirds* (Ralph et al. 1993), the US Fish and Wildlife Service's Landbird Monitoring Protocol (Knutson et al. 2008) and the USFWS *Protocol for the Rapid Assessment of Fruit Abundance on New England National Wildlife Refuges* (Smith and McWilliams 2009). Where possible, the methods for gathering data under this protocol have been described to match these previous protocols to allow for wider regional comparisons. However, we have modified these protocols when:

1. The methods from these protocols were inappropriate for censuses of populations in migration (the first two of the established protocols were designed to accompany standard breeding bird surveys),

2. The methods from these protocols were inappropriate for vegetative characterization during a time-period that includes leaf drop,
3. The methods from these protocols included sampling at a larger scale than that sampled by the migration station census or banding protocols
4. The methods from these protocols included the use of categorical indices that necessitated lengthy training of crews to ensure systematic application across technicians, crews, and sites (a feat that is difficult to maintain across multiple PI's, sites, and years).

A.3. Survey Placement

All of the surveys described below should occur in a series of belt transects that are 4-m wide and vary from 6 – 12 m in length (precise length can be varied by site, net size, or investigator interest, since all final measures will be transformed to a standard length – e.g. *per meter* – to allow for comparisons among stations). Two transects should be placed parallel to each net lane (one on each side of the net at a distance of 5m from the net) and two of a similar size should be placed randomly within the fixed-area census plots (Figure A.2). The transects that run along nets should be far enough away that the area disturbed by the cutting of the net lane is not being sampled. The two transects within the fixed area census plot should each begin at a random point and proceed in a random direction, so long as the two transects do not overlap and the entire transect is contained within the survey area. Flag the corners of each belt transect early in the season!

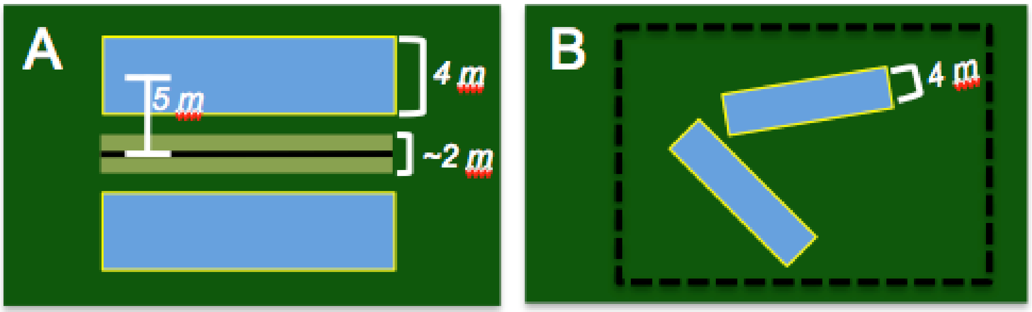


Figure A.2. Size and placement of the two belt transects (blue rectangles) for vegetative sampling; A) along each mist-net lane (shown in light green with black line to indicate net) and B) within each fixed area census plots (shown with dotted polygon outline that is not to scale).

A.3.2. Weekly Surveys

The belt transects described above should be sampled at least once per week throughout the monitoring period (the period of bird capture or census) to assess

- The timing and abundance of fruiting,
- The timing and degree of leaf drop

  (a similar protocol could be followed for leaf out during spring monitoring),
- The flux in water availability

These factors are highly dynamic within the monitoring period, likely impact bird habitat use and/or the detection of individuals, and would not be categorized well by more infrequent surveys.

A.3.2.1. Fruiting Surveys

During each weekly transect visit, researchers should note the species of fruiting plant, the state of fruit ripeness, and the rough abundance of fruit (by plant species). To assess “fruit state” for the transect, the rough percentage of fruit that falls into each of the following four categories should be noted:

1. Unripe
2. Ripe
3. Past Ripe (visual blight, wrinkling or drying)
4. Bare stems (on plants that still possess fruit in some state)

To assess fruit abundance, the number of individual fruits should be estimated for each species using the scale developed by Smith & McWilliams (2009)[*]:

1. <10
2. 11-25
3. 26-100
4. 101-250
5. 251-1000
6. 1001-3000
7. 3001-10000
8. >10000

---

[*] It should be noted that the original protocol developed by Smith and McWilliams (2009) for assessing fruiting notes the number of fruits *on each individual woody plant*. Here we have modified this protocol to estimate fruiting abundance category for the entire transect (to minimize survey time) and to include herbaceous fruit (as some fall berries can be very important for migrating songbirds). If individual sites want their numbers to be comparable to other FWS refuge fruit surveys, the numbers gathered under the standard Smith and McWilliams (2009) protocol can easily be summed to obtain the numbers under this protocol for woody plants as long as herbaceous fruiting species are still assessed for the full transect.

A.3.2.2. Leaf-drop Surveys

During each weekly visit, researchers should also assess the percentage of leaves in four broad categories:

1. Green Leaves (each leaf is > 90% green)
2. Turning/Turned Leaves (individual leaves are < 90% green and less than 50% brown)
3. Brown Leaves (individual leaves are > 50% brown)
4. Bare Stems (% of leaf drop)

These categories should be assessed for each of three vegetative "layers" for each transect:

- Tree layer (> 5 m)
- Shrub layer (woody vegetation < 5m)
- Herbaceous layer (non-woody vegetation)

A.3.2.3. Soil Drainage / Water Availability

Each week researchers should also note whether the surface soil within a transect is generally:

1. Dry
2. Moist but not saturated (no squishing)
3. Saturated (squishing)
4. Standing water present in low spots

7.3.3. Seasonal Surveys

Full transect characterizations will occur once over the season.

Within each belt transect, the researchers will record:

A.3.3.1. Species abundances by vegetation layer: each veg layer's abundance should total 100%

A) Abundance of each recorded species for the tree and shrub layers

Tree layer: woody vegetation >5m

- The diameter at breast height (dbh) of any tree with a circumference of >22cm

Shrub layer: woody vegetation <5m, this includes saplings and low woody vegetation such as blueberries.

B) Abundance of each group/category for the herbaceous and ground cover layers

Herbaceous: non-woody vegetation (ferns, forbs, grasses/sedges/rushes). Exception: even though they are woody, blackberry and raspberry vines are considered herbaceous because structurally they are more similar to forbs than shrubs.

C) Abundance of ground cover (bare ground, mosses, forest litter, woody debris, lichens, rocks)

- When the herbaceous layer is too thick to get a good view of the ground cover, push the vegetation aside in ten places as you move down the transect and use those ten looks to scale to percentages.

A.3.3.2. Presence of a district layer

The presence or absence of a "distinct" vegetative layer in each of the tree, shrub, herbaceous, or ground (<u>only moss or lichen</u>) zones. The layer should only be counted if it is continuous enough so an appropriately sized squirrel/monkey/wood nymph could move through the layer without touching the ground.

A.3.3.3. Percent cover of each vegetation layer

Record the % cover of each vegetation layer over the entire belt transect

- Percent cover can total more than 100%

A.3.3.4. Stem Count

Held at 0.5m above the ground, spread a meter tape down the center of each the transect

Along the tape:

A) Count the number of woody stems touching the meter stick at the first 30 cm of every other meter beginning at meter 1

B) Measure the “modal” height (height if you had to indicate a single height or average height) at a 0.5m circumference at every third meter interval (i.e. 0, 3, 6, 9, and 12m)

AND

C) Max height of each vegetation layer (tree, shrub, and herbaceous), at a 0.5m circumference at every third meter interval (i.e. 0, 3, 6, 9, and 12m)

D) Repeat the stem count with the meter tape held 1.5 m above the ground.

A.3.4. Naming Convention

Transect ID

Net lanes

Site_Net#_A or B

The ***north*** OR ***west*** side of the net, depending of which way the net is running, is side A.

The ***south*** OR ***east*** side is the side B.

BIOGRAPHY OF THE AUTHOR

Jennifer “Jenny” Dawn McCabe was born and raised in Ann Arbor, Michigan. She graduated from Greenhills High School in 1998. She attended The University of Vermont and earned her B. S. in Environmental Studies in 2003 after completing an honors undergraduate thesis. After graduating from undergrad, Jenny traveled around North America working as a biological technician, until she settled in Jackson, Wyoming in 2007. In Jackson, Jenny worked as Research Faculty at the Conservation Research Center of the Teton Science Schools managing their avian programs. She continued to work for the Science Schools throughout her graduate career. Jenny is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Science from the University of Maine in December 2015.