NONBREEDING ECOLOGY AND CONSERVATION OF MIGRATORY

LANDBIRDS WITH A FOCUS ON THE GOLDEN-WINGED WARBLER

(VERMIVORA CHRYSOPTERA)

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NONBREEDING ECOLOGY AND CONSERVATION OF MIGRATORY LANDBIRDS WITH A FOCUS ON THE GOLDEN-WINGED WARBLER (*VERMIVORA CHRYSOPTERA*)

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Conservation of long-distance migratory birds is complicated by an annual cycle that spans broad geographies. Although these populations are affected by events throughout the year, basic knowledge of nonbreeding habitat selection, habitat quality, and migratory connectivity is often lacking. Habitat conservation is further challenged by behaviors, such as intraspecific competition and niche specialization, that can lead males and females to occupy different nonbreeding regions and habitats. This dissertation aimed to fill knowledge gaps regarding habitat selection, quality, and connectivity, with a special focus on cases where males and females segregate spatially. Specifically, we examined (1) the prevalence of sexual segregation among migratory landbirds and the degree to which conservation plans considered the behavior; (2) patterns, drivers, and conservation implications of sexual segregation in declining population of the Golden-winged Warbler (*Vermivora chrysoptera*); and (3) migratory connectivity and migration strategies for the Golden-winged Warbler and the closely related Blue-winged Warbler (*Vermivora cyanoptera*). Our review of the published literature and conservation plans for 66 North American migratory landbirds

of concern revealed that sexual segregation is a relatively common phenomenon yet is systematically overlooked in conservation plans. Working across Central America and New York between 2014 and 2017, we surveyed male and female Golden-winged Warblers, modeled fall arrival and overwintering occupancy, assessed body condition, and deployed geolocators on select males. Results suggest that sexual segregation is driven primarily by male exclusion of females from high quality habitat in nonbreeding sites, which results in mid- to high-elevation evergreen broadleaf forests being male-biased and lower elevation habitat with less structural diversity being female-biased. The failure to explicitly consider sexual segregation in conservation plans resulted in focal areas that over-represented male-dominated areas, despite greater habitat loss in female-dominated areas. In addition, our data from geolocators showed that Golden-winged Warblers employed a migration strategy that minimized spring migration time and used a previous undescribed stopover region in Guatemala and Mexico – with connectivity and timing being distinct from the Blue-winged Warbler. Overall, our research elucidates the causes and consequences of sexual segregation, highlights the importance of considering nonbreeding ecology in conservation plans, and provides new information to guide Golden-winged Warbler conservation.

BIOGRAPHICAL SKETCH

Ruth came to Cornell after receiving BAs in History and Biology at Pacific Lutheran University and an MS in Applied Ecology at Michigan Technological University. Between undergraduate and graduate school, she worked across the western United States on a variety of field jobs that focused on native plant restoration, rangeland heath assessment, Sage Grouse winter habitat use, and roadkill mitigation. As tracking birds was way more fun than watching plants grow or counting roadkill, she took an ornithology course at Michigan Tech, learned to capture and handle small birds with Dr. Amber Roth, and joined the Peace Corps in Honduras with the goals of becoming fluent in Spanish and conducting research on birds. While at her Peace Corps post at the Universidad Nacional de Agricultura, she discovered a small population of female Golden-winged Warblers in a fragmented agricultural matrix and a small population of males up in the mountains. These populations would inspire her MS research and later her PhD research on sexual segregation in migratory landbirds. But as Honduras also has amazing resident birds, she took opportunities to invest in other projects studying the biology and conservation of Ocellated Quail, Red-throated Caracara, Three-wattled Bellbird, and Great Antshrikes with the Honduran Ornithological Association and the Honduran Conservation Coalition.

Coming to Cornell opened doors to gain a deeper foundation in ornithology, invest in conservation efforts, and pursue international research. During her first two years as a PhD student, she wrote the Golden-winged Warbler Nonbreeding Season Conservation Plan with the support of many US and Latin American partners. She conducted exploratory research in Colombian coffee plantations, but ultimately decided to focus on Central America and spent three field seasons chasing warblers

across Panama, Nicaragua, Honduras, Guatemala, and Belize. Of course, as no field seasons is complete without a good side-project or two, she also collaborated with the American Bird Conservancy to study the impact of agroforestry systems on migratory birds in Guatemala, led a museum collecting expedition in Honduras, and described a melanistic population of Green Herons in the Caribbean that she discovered while kayaking in mangroves with her field crew. After graduating from Cornell, Ruth will be a post-doctoral fellow at the Smithsonian Migratory Bird Center, where she will study certified and shade-grown cacao. Over the long term, she plans to continue studying and conserving birds, especially in tropical working landscapes.

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side projects, and for building the strong lab community that supported and challenged me over these years. Amanda, you were the best advisor I could have hoped for and are an inspiring example of what one can accomplish with dedication, hard work, and a bit of humor.

Working across Central American countries was a joy and challenge made possible by numerous partner groups and institutions. A special thanks to the Golden-winged Warbler Working Group, Alianza Alas Doradas, FUNDAECO, Scarlet-Six Macaw, Reserva El Jaguar, Universidad Nacional de Agricultura, Escuela El Sembrador, Finca Las Orquidias, Mesoamerican Development Institute, COMISUYL coffee cooperative, and Canopy Tower. Additional thanks to the people who were instrumental in facilitating logistics and contacts within Central America: Josue David Matute, Blanca Elena Moradel, Germanico Barrios, Roni Martinez, Jose Mendoza, and Liliana Chavarria. Finally, a huge thank you to the incredible team who gathered data in the field, often in tick, chigger, and mosquito filled areas: Mayron McKewy Mejia, Jacob Drucker, Angel Fong, Esdras Mejia Lopez, Isidro Zuniga, Olbin Benharano, Tania Palacios, Stephany Flores, Denis Mendoza, Olvin Calixto Ordonez, Lila Fried, DJ McNeil, Andrew Dreelin, Forrest Howk, Jack Hruska, John Cahill, Daniel Aldena, David Murillo, Miguel Ramirez, Samael Santamaria, Moises Siles, Georges Duriaux, and others.

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Ritwick, Samar, Abby, and Pepe: may the Bandwagon crew live forever.

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CHAPTER 1

INTRODUCTION

Background

The study and conservation of long-distance migratory landbirds are complicated by a lifecycle that includes annual migrations between ecologically and geographically distinct breeding and nonbreeding areas (Rappole and McDonald 1994, Faaborg et al. 2010a, Norris and Marra 2010). The annual cycle includes a breeding season and three nonbreeding periods – fall migration, overwintering (i.e. stationary period corresponding with Boreal winter; Bayly et al. 2018), and spring migration. Not only do migratory birds require distinct habitats at different stages of their annual cycle, but the impact of seasonal events and habitat quality can carry over to affect individual performance in subsequent stages (Sillett and Holmes 2002, Norris et al. 2004). Although the potential for these carryover effects underscores the importance of understanding the full annual cycle, most investigations focus on the few months in which a bird species breeds (Faaborg et al. 2010b). Recently, knowledge of nonbreeding periods has improved through research using new technologies that track birds throughout their migrations and through monitoring of demographics and habitat selection and quality in the overwintering period (Holmes 2007, Stutchbury et al. 2009). With this new knowledge, conservation efforts can now begin to identify and prioritize nonbreeding habitats of high value to declining species (Faaborg et al. 2010a).

Despite recent conservation successes, populations of many North American migrants continue to decline (Sauer 2017). Migrants that overwinter in tropical broadleaf forests are particularly threatened, yet detailed information about habitat requirements and population limitation during nonbreeding periods exists for only a few species (Faaborg et al. 2010a, Sauer 2017). Evidence from well-studied systems suggests that direct mortality is often greatest during spring migration and that loss or degradation of overwintering habitat can cause population declines (Sillett and Holmes 2002, Norris and Marra 2007, Rushing et al. 2016). As such, research that elucidates population-level migration strategies and describes the characteristics and threats to high-quality overwintering habitat can help focus conservation efforts on the time periods and locations of greatest importance for population persistence.

Nevertheless, identification of high-quality habitat can be complicated by sexual segregation during nonbreeding periods (Ornat and Greenberg 1990, Komar et al. 2005). Sexual segregation is a common phenomenon in vertebrates in which males occur in spatially distinct areas from females for portions of the annual cycle (Conradt 2005). For small-bodied migratory landbirds, sexual segregation typically follows two patterns: 1) males occur farther north than females during the overwintering period, and 2) males occupy habitat that is more humid and less disturbed than females (Catry et al. 2006). Understanding patterns of sexual segregation is especially important for threatened or declining species because segregation may differentially expose the sexes to predation, disease, or habitat loss (Bowyer 2004). The population-level consequences of this sexual segregation can be profound, even affecting species persistence in some cases (Schroeder et al. 2010). Human disturbance also can modify

exposure to risks and affect access to resources in ways that can impact—and potentially exacerbate differences in—sex-specific survival rates (Burger and Lynch 1995). This possibility is worrisome as the biased adult sex ratios that result can impact population growth rate, reduce effective population size, and contribute to population declines (Lande and Barrowclough 1987, Rubin and Bleich 2005, Catry et al. 2006). Indeed populations with skewed adult sex ratios—usually a male bias—are more common among threatened and endangered birds than among species with stable populations (Donald 2007).

Of all periods of the annual cycle, migration is the most difficult to study and often the least understood. Despite research challenges, ornithologists have built a considerable body of literature describing the endogenous controls, individual decisions, population-level constraints, and broad strategies that govern bird migration (Alerstam and Lindström 1990, Newton 2004, Moore 2018). As radar and individual tracking technologies continue to advance, we have improved ability to connect breeding and wintering populations, describe migratory pathways and phenology, and understand how migration is constrained for populations (Stutchbury et al. 2009, Bridge et al. 2013, Hallworth et al. 2013). Data from new technologies indicate that both landbirds and shorebirds commonly utilize a migration strategy of rapid passage between stopover sites, where birds rest and refuel for multiple days (Atkinson et al. 2007, Bayly et al. 2018). These stopover sites play a critical role in a bird's ability to cross major geographical barriers and successfully complete migration (Gómez et al. 2017). However, stopover site locations and usage patterns, especially south of the U.S., remain unknown for most species.

Migration strategies are typically discussed within an optimality framework, in which the pace of migration, pathways, and refueling stopovers reflects an optimal balance of energy expended, the amount of time spent migrating, and risk of predation or starvation (Clark and Butler 1999, Alerstam 2011). In this context, optimal strategies may differ between species and seasons. For example, passage time in most species is substantially shorter in spring than fall, which is consistent with a spring migration strategy that minimizes time and is driven by selective pressure to establish breeding territories as early as possible (reviewed in Nilsson et al. 2013). Conversely, migration strategies may prioritize low energy expenditure, and these migrants would accordingly travel at a slower pace, refuel more frequently, and carry less fuel reserves (Alerstam 2011, Nilsson et al. 2013). In theory, a time-minimizing strategy should be riskier than an energy-minimizing strategy, as time-minimizing individuals have decreased ability to detect and escape predators and may run the risk of depleting fuel reserves and starving before arriving at the next appropriate stopover (Newton 2004, Gómez et al. 2017).

Within a population, the migratory movement behaviors of individuals—including timing, duration, pathway, and use of stopover sites—reflect individual approaches to an optimal migration strategy. The range of variation among individual behavior—potentially mediated by morphology and prior experience—should furthermore influence the flexibility of a population to respond to locally changing conditions during the migratory period (Charmantier and Gienapp 2014). Quantifying movement behaviors of individuals within a population is therefore critical to identify possible constraints on migration and develop appropriate conservation strategies for

declining or threatened species.

Our research addresses the patterns, processes, and impacts of sexual segregation and migration strategies on migratory landbirds of conservation concern. We use the Nearctic-Neotropical migratory Golden-winged Warbler (*Vermivora chyrsoptera*) as a focal species to investigate these important aspects of bird ecology and conservation. Since the 1960's, the Golden-winged Warbler has lost over 66% percent of its population, and the observed loss of nonbreeding habitat is hypothesized to be one of the primary drivers of the population decline (Rosenberg et al. 2016, Kramer et al. 2018). However, current lack of knowledge precludes an assessment of threats and constraints on the population during the migratory and overwintering periods.

Evidence suggests the sexes may segregate habitats during the nonbreeding season (Bennett 2012, Chandler et al. 2016), but previous conservation research has been restricted to male-dominated overwintering habitats within mid- to high-elevation humid broadleaf forests of Central America and the northern Andes of South America (Chandler and King 2011, Chandler et al. 2016, Rosenberg et al. 2016).The fall and spring migration patterns of the Golden-winged Warbler have also been the subject of recent research. Field studies point to the possibility of a migratory divide between the Appalachian breeding population that overwinters in the northern Andes of South America and the Great Lakes breeding population that overwinters in Central America (Larkin et al. 2017, Kramer et al. 2018). However, important stopover areas, general migration strategies, female distribution, and habitat quality have yet to be rigorously investigated.

Dissertation organization

This dissertation is organized starting with Chapter 1, which overviews the nonbreeding ecology and conservation of long distance migratory birds and summarizes our research objectives. Subsequent chapters are written as manuscripts for publication in scientific journals, with Chapter 5 already being published (Bennett et al. 2017). As such, some introductory material is redundant among chapters. In Chapter 2, we investigate how conservation efforts account for sexual segregation in a group of 66 migratory landbird species of conservation concern. We also model the occupancy of male and female Golden-winged Warblers across Central America to assess if conservation plans reflect the needs of both sexes and different threats they may face. In Chapter 3, we study the patterns and mechanisms of Golden-winged Warbler sexual segregation in a mid-elevation evergreen broadleaf forest and a lower-elevation semi-deciduous forest in central Honduras. To accomplish this, we examined arrival patterns, overwintering occupancy, and body condition over three nonbreeding seasons. Chapter 4 explores the migration strategies and constraints in the Central America-Great Lakes linked population of Golden-winged Warblers using data from light-level geolocators. Finally, Chapter 5 compares the migratory connectivity and phenology of a sympatric-breeding population of Golden-winged Warbler and the closely related Blue-winged Warbler (*Vermivora chyrsoptera*). Given extreme genetic similarity between the two species (Toews et al. 2016), we predicted that the two species would exhibit similar migration patterns, including direction, distance, and timing.

Significance

This research provides important insights into the nonbreeding ecology of Golden-winged Warblers and their implications for the conservation of migratory landbirds. We show that male Golden-winged Warblers occupy different habitats than females during the overwintering season, such that broad landscapes can be biased towards male or female occupancy. While sexual segregation appears to be driven by males competitively excluding females from high quality habitat, we found no evidence that females suffered a decrease in body condition within female-dominated habitat. This highlights the importance of conserving both habitats. We also show that conservation plans for migratory landbirds systematically overlooked the impacts of sexual segregation, and our findings highlight the need to explicitly consider the distributions, habitat associations, and threats for both males and females. Finally, our demonstration of different migratory pathways and stopover locations provides justification for managing Golden-winged Warbler independently from its sister species, the Blue-winged Warbler. Collectively, the research included in this dissertation points to the urgency of incorporating nonbreeding ecology and sexual segregation into conservation plans for migratory landbirds and provides new information to guide the conservation of the declining Golden-winged Warbler.

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CHAPTER 2

FAILURE TO ADDRESS SEXUAL SEGREGATION LEADS TO BIASED
CONSERVATION RECOMMENDATIONS FOR MIGRATORY LANDBIRDS

Abstract

Many conservation efforts fail to consider the possibility that male and female animals spatially segregate among habitats or landscapes, a pattern that is common in vertebrates. When resources or threats vary spatially, sexual segregation can profoundly affect sex-specific survival rates to the point of influencing population persistence. We reviewed how sexual segregation is addressed in conservation plans for 66 North American migratory birds of conservation concern and found that plans considered segregation for just 7% of species, despite evidence of sexual segregation in one-third of these species and in two-thirds of those with reported nonbreeding sex ratios. Using the declining Golden-winged Warbler (*Vermivora chrysoptera*) as a case study, we showed that females lost twice as much nonbreeding habitat as males from 2000-2016, yet existing conservation focal areas remain heavily biased towards male-occupied landscapes. Our work shows that failure to explicitly address sexual segregation severely handicaps conservation efforts for migratory birds.

Introduction

Effective conservation planning requires identification of the geographies and habitats that are most important to a species. Because incomplete knowledge can severely

constrain conservation, we are challenged to identify or anticipate information gaps and explicitly address uncertainty during the planning process. Overlooked or unrecognized ecological patterns in distribution and habitat use may bias conservation recommendations and reduce the likelihood that a species will be sufficiently protected.

Sexual habitat segregation, where males and females occupy different landscapes or habitats during portions of their lifecycles, is one example of an underappreciated phenomenon with potentially important implications for conservation. Sexual segregation is widespread in vertebrates and has been documented in many species of mammals, fish, herpetofauna, and birds (Ruckstuhl et al. 2005). Irrespective of the underlying mechanisms that drive segregation across taxa and life-history strategies, the population-level consequences can be profound, even affecting species persistence in some cases (Schroeder et al. 2010).

Understanding patterns of sexual segregation is especially important for threatened or declining species, as segregation may differentially expose the sexes to predation, disease, or habitat loss (Bowyer 2004). Human disturbance also can modify exposure to risks and affect access to resources in ways that can impact—and potentially exacerbate differences in—sex-specific survival rates (Burger and Lynch 1995). Such differential survival can lead to biased sex ratios, which can impact population growth rate (Lande and Barrowclough 1987), reduce effective population size, and contribute to population declines (Catry et al. 2006). Indeed populations with skewed adult sex ratios—usually a male bias—are more common among threatened and endangered birds than in species with stable populations (Donald 2007).

Growing awareness of the implications of sexual segregation has prompted calls to explicitly consider the phenomenon in conservation research and policy (Bowyer 2004, Rubin and Bleich 2005, Catry et al. 2006, Wearmouth and Sims 2008). In response, conservation plans for many terrestrial mammals and long-lived marine species now incorporate sex-based differences in space use and threats (Mucientes et al. 2009, Whiting et al. 2010, Jacoby et al. 2012). Nevertheless, sexual segregation is rarely considered in conservation planning processes for many groups of species, including migratory landbirds (e.g. Kirby et al. 2008, Faaborg et al. 2010). Amid growing concerns over migratory bird population declines (Rosenberg et al. 2016a), full annual-cycle conservation strategies can be constrained, or even compromised, by the extent to which they consider needs of both sexes (Catry et al. 2006).

Here we provide the first systematic review of how well contemporary conservation planning and practice address the phenomenon of sexual segregation outside of the breeding season for North American migratory landbirds. To do this, we first reviewed published literature and conservation plans to assess the degree to which sexual segregation was investigated and addressed in conservation recommendations and plans for 66 species identified as high conservation priority. Next, we used our own data on the declining Golden-winged Warbler (*Vermivora chyrsoptera*) as a case study to investigate how conservation recommendations and prioritization of focal areas might be affected by patterns of sexual segregation. Specifically, we conducted field surveys to model nonbreeding distributions of both males and females and evaluated rates of recent habitat loss within the core male and female ranges to test for sex bias in the amount of male and female habitat prioritized by current conservation

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planning efforts.

Methods

Literature review

To investigate the extent to which conservation planning considers spatial segregation
of sexes, we reviewed the gray and published literature focused on nonbreeding
ecology and conservation for North American migratory landbirds, which have been
monitored through standardized breeding surveys since 1966 (Sauer et al. 2017).
Drawing upon Partners in Flight's standardized assessment process to prioritize
species for conservation (Carter et al. 2000), we restricted our review to the 66 species
of conservation concern that Partners in Flight designated as *Red* or *Yellow Watch List*
species (n=45) or *Common Birds in Steep Decline* (n=21; Rosenberg et al. 2016a). For
each species, we reviewed both the published evidence for sexual segregation and
efforts to study it during nonbreeding periods and then evaluated whether and how
conservation plans accounted for such segregation. We searched for published articles
and conservation plans using the databases Google Scholar, Google, the Birds of
North America online, Partners in Flight online resources
(https://www.partnersinflight.org/resources/), U.S. Fish and Wildlife Service
Environmental Conservation Online System (ECOS), and the Committee on the Status
of Endangered Wildlife in Canada (COSWEIC) species reports. Searches included the
English and scientific name of each species along with each of the keywords:
"nonbreeding, winter, sex, male, female, conservation, plan, management,
prioritization, and distribution model."

Within each relevant article or conservation document, we searched for other articles (cited or citing) referencing any of our keywords. We noted any evidence for nonbreeding sexual segregation at a habitat or landscape scale. We considered sexual segregation to be present if the male:female ratio differed significantly among overwintering habitats, within migration pathways, or in extremities of the overwintering range. We recorded sexual segregation as unknown if no study reported a nonbreeding sex ratio or sex-specific habitat associations. Evidence was considered inconclusive if sex ratios were reported in a study with fewer than 20 individuals, if a skew in nonbreeding sex ratio reflected biased sex ratios in the population at large, or if sex ratios were reported from small geographic area representing <10% of the overwinter range (as delineated in the Birds of North America online database). We restricted our review to spatial segregation, as temporal segregation by sex has been extensively reviewed during migration periods (Morbey and Ydenberg 2001). We also noted if a published species distribution model (SDM) existed for the nonbreeding season and accounted for differences in detection probability, distribution, or habitat use by sex. We considered any occupancy, abundance, or MaxEnt model documenting the full nonbreeding distribution to be a SDM. Finally, we recorded if nonbreeding conservation recommendations (i.e. management action and geographic or habitat prioritization) had been published for a species and whether those recommendations accounted for nonbreeding sexual segregation.

Case Study: Golden-winged Warbler

We evaluated how explicit consideration of sexual segregation may affect conservation prioritization with a case study of the declining Golden-winged Warbler.

Prior field surveys suggested that male and female Golden-winged Warblers segregate during the nonbreeding season (Chandler et al. 2016, Rosenberg et al. 2016b), yet the most recent nonbreeding season conservation plan for Golden-winged Warbler prioritized focal areas based primarily on male distributions, given a paucity of data on females (Bennett et al. 2016). We modeled the distribution of both sexes using data from point-count surveys at 1,177 locations in Belize, Guatemala, Honduras, Nicaragua, and Panama between 2014 and 2017. Survey locations were separated by >400 m across broad gradients of elevation (7–3171 m; mean 736 $\pm$ 609 SD) and precipitation (0.9–5.4 m of annual rainfall; mean 2.2 $\pm$ 0.9 SD) representative of Central American biomes (Corrales et al. 2015). Each point was surveyed one (5%), two (12%), or three (82%) times during a single nonbreeding season (Nov 15–March 15).

To improve detection probability of both sexes, we broadcast a five-minute recording of Golden-winged Warbler male songs and female chip notes (Chandler and King 2011) followed by a five-minute recording of Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) and Eastern Screech-Owl (*Megascops asio*) and alarm and mobbing calls of ten common migratory songbirds (Bennett et al. in review). Vocalizations were broadcast at maximum volume with an EasyAcc Mini Portable Speaker (Model # MODB00JK6MQEI). We visually observed that individual Golden-winged Warblers and flocks of small birds stopped foraging and approached the speaker from a maximum distance of 50 meters. During each survey, we recorded the sex of any Golden-winged Warbler detected within a 50 m radius of the point-count center along with time of day, a wind index (1–no wind to 5–trunks moving), and a

precipitation index (1–no precipitation to 5–heavy rain). We did not conduct surveys

during periods of high wind or rain. Latitude, longitude, and elevation of each survey

location were recorded with a Garmin eTrex 10 handheld GPS unit.

Separate detection histories were created for males and females during each

survey period, and single-season occupancy models were fit using the 'unmarked'

package in program R (Fiske and Chandler 2017, MacKenzie et al. 2017, R Core

Team 2017) to account for imperfect detection probability during the survey periods.

We considered four detection covariates: 1) time of day; 2) the wind index; 3) the

precipitation index; and 4) an observer skill index (less than or greater than one year of

experience surveying overwintering GWWA). Five occupancy covariates were

modeled: 1) longitude; 2) latitude; 3) elevation; 4) mean annual precipitation (Fick and

Hijmans 2017); and 5) mean composites of March NDVI from 2015 to 2017

(Normalized Difference Vegetation Index,

https://earlywarning.usgs.gov/fews/product/445).

Occupancy covariates were selected based on indications from other studies

that nonbreeding sexual segregation correlates with geographic distance (i.e. latitude

and longitude; Cristol et al. 1999), precipitation (Conway et al. 1995), and elevation

(Smith et al. 1993). The March NDVI covariate provided a proxy for habitat humidity

prior to migration, which also predicts patterns of sexual segregation in some species

(Parrish and Sherry 1994, McKinnon et al. 2015). Continuous covariates were scaled

prior to analysis. A correlation analysis indicated that latitude and longitude were

correlated (r=0.89; others r<0.3), and therefore we compared global models for males

and females that included latitude or longitude. The model with latitude was not

supported (delta AICc >30), so we retained longitude as the spatial covariate for occupancy models. We included all occupancy covariates as both linear and quadratic terms given the likelihood that occupancy peaks at intermediate covariate values (Chandler and King 2011). Prior to running final models, we fit all possible subsets of the detection covariates with the global occupancy model and retained only detection covariates that were supported in a model with delta AICc of 2 from the best model (Anderson 2002, Murtaugh 2009). We tested the goodness of fit of the global male and female models with 1,000 parametric bootstrap simulations of model fit using a chi-squared statistic as described by (MacKenzie and Bailey 2004) for single-season occupancy models. We failed to reject the null hypothesis that our models adequately described our data for the global male model (p=0.885) and the global female model (p=0.010), indicating reasonable model fit for both sexes. Using the retained detection parameters, we evaluated all possible models (N=648 for males and females) with package 'MuMin' (Barton 2016).

To predict occupancy, we used the model averaged coefficients to create a a 1-km^2 raster covering the spatial extent of our sampling area (Belize and Guatemala to Panama). In order to standardize and compare female and male occupancy predictions, we binned the 95th, 90th, 85th, 80th, and 75th predicted occupancy quantiles for both sexes. The 75th occupancy quantile for both sexes covered most of the nonbreeding distribution in Central America, so we did not consider lower occupancy values. Within each occupancy quantile polygon, we calculated percent tree cover in the year 2000 and the percent forest loss between 2000 and 2016 with University of Maryland global forest change dataset (Hansen et al. 2013). We considered the 30-m pixels with

less than 30% forest to be nonhabitat, given evidence that Golden-winged Warblers forage predominantly in the forest canopy and mid-story vine tangles (Chandler et al. 2016).

To quantify differences in male and female distributions, we created a raster of differences in male and female occupancy quantiles by assigning each quantile a rank of 1 to 5 (1 = 75th; 5 = 95th) and then subtracted ranked female quantiles from those of males in ArcGIS 10.5. We considered pixels with value of -1 to -5 to be female-biased (i.e. greater female than male occupancy), 0 to be sex-neutral, and 1 to 5 to be male-biased. Potential sex-bias in Golden-winged Warbler conservation planning efforts was evaluated by extracting the occupancy difference raster values within the Central American Golden-winged Warbler focal area polygons delineated in Bennett et al. (2016) and reported as the percent of pixels biased towards males or females across all focal areas.

Results

Prevalence of sexual segregation in nonbreeding season
We found 196 documents that addressed nonbreeding conservation and/or sexual segregation for the 66 North American migratory bird species of conservation concern (Appendix 2.1). Among these, evidence of sexual segregation in nonbreeding distribution or habitat use existed for 19 species (29% of focal species; 68% of focal species with reported sex ratios), whereas only one species, the Kirtland's Warbler (*Setophaga kirtlandii*), had confirmed absence of sex segregation (Figure 2.1;

Wunderle Jr et al. 2014). Nonbreeding sex ratios were reported for eight additional species, but we considered the evidence inconclusive due to low sample size or small geographic area sampled. Segregation was unstudied or unreported in 58% of focal species (Figure 2.1). Species with plumage dimorphism were more likely to have sexual segregation investigated and described ($X^2_{(2, N=66)}$=9.424, P=0.002), but four monomorphic species were also reported to segregate during the nonbreeding season (Figure 2.1A). A higher proportion of Red Watch List species were reported to segregate than species of lower concern, though the disparity was proportional to the number of studies considering sexual segregation (Figure 2.1B).

We found nonbreeding conservation recommendations and SDMs for 38 and 35 species, respectively. Quality and resolution of SDMs varied widely, but only one Bicknell's Thrush (*Catharus bicknelli*) model explicitly accounted for difference in distribution between the sexes (Figure 2.2; McFarland et al. 2018). Differences in detection probabilities for females and males were only investigated for two species: Wood Thrush (*Hylocichla mustelina*) and Golden-winged Warbler (Chin et al. 2014, Rosenberg et al. 2016b). Conservation plans and recommendations discuss sex-based differences in nonbreeding habitat selection or distribution for only three species: Bicknell's Thrush, Black-capped Vireo (*Vireo atricapilla*), and Golden-winged Warbler (Figure 2.2). Of these, the Bicknell's Thrush conservation plan was alone in specifically addressing how threats differed for male and female habitat and how loss of female habitat may affect the overall population (IBTCG and BCPWG 2011).

Golden-winged Warbler Case Study

Between 2014 and 2017, we detected 122 female Golden-winged Warblers at

96 sites and detected 200 males at 135 sites. Under ideal conditions, detection probability was 34% (10% SE) for females and 46% (2% SE) for males, with detectability declining with increasing wind and precipitation. Female detection probability improved with observer experience, and males were more detectible early in the day (Table 2.1 and 2.2). For both males and females, longitude and elevation best explained occupancy and were included in all supported models (Table 2.1 and 2.2). Occupancy peaked around the same longitude for both sexes, but females occurred at lower elevations than males (Figure 2.3). Intermediate annual precipitation explained female occupancy but was unrelated to male occupancy. Neither male nor female occupancy had a strong relationship with March NDVI (Figure 2.3).

Across Central America, predicted occupancy for females was greatest at mid-elevations (300–1300 m) of the Caribbean slope of Honduras and Nicaragua and on the Pacific slope of Costa Rica and Panama (Figure 2.4A), whereas male occupancy peaked throughout the central highlands from Honduras to Panama (800–1800 m; Figure 2.4B). These differences resulted in regions with sex-bias in predicted occupancy (Figure 2.4C). Little overlap occurred in the predicted distributions for the 85th to 95th occupancy quantiles for males and females, though the sexes overlapped in the 75th to 80th quantiles at 800–1300 m from central Honduras to Panama (Figure 2.4A, B, C). Our models predicted male bias in the central and western highlands of Honduras and Nicaragua and female bias at mid-elevations in eastern Honduras and Nicaragua. Similarly, Costa Rica and Panama have predicted male bias at high elevations and female bias in patches of suitable habitat at mid-elevations (Figure 2.4C).

Percent forest coverage in the year 2000 was comparable for males and

females within the 75th and higher occupancy quantiles (75.3% and 74.8% for females

and males respectively). However, rate of deforestation between 2000 and 2016 was

more than double in female- than male-occupied areas (Figure 2.4D). Within their

highest occupancy quantile, females have lost 8.5% of remaining forest since the year

2000 versus 4.1% for males. Similarly, we found a strong sex bias in predicted

occupancy across the 65 conservation focal areas covering 11,000 km^2 of Central

America (excluding Guatemala where predicted occupancy was low; Figure 2.4E;

Bennett et al. 2016). More than half of the total area (54.5%) exhibited male-biased

occupancy, while 11.6 % had female-bias and 33.9% was sex-neutral (Figure 2.4F).

Discussion

Our findings show that conservation planning for North America's most vulnerable

migratory landbirds largely ignores the implications of sexual segregation, despite

evidence that one-third of these species and two-thirds of those with sex ratios

reported from nonbreeding sites are known to segregate spatially. The tendency for

sexual segregation to be better documented in species that were either sexually

dimorphic or of greater conservation priority most likely resulted from a bias in the

focus of investigations rather than greater prevalence of the phenomenon in those

species. Our review indicates that sexual segregation is common across migratory

landbirds and requires greater attention from the conservation community.

Our case study with the Golden-winged Warbler further illustrates how a

failure to account for sexual segregation can lead to sex-bias in conservation planning,

such that far more male than female habitat was prioritized for conservation during the nonbreeding season (Bennett et al. 2016). Loss of nonbreeding habitat is widely considered to be a serious threat to migratory landbirds (Faaborg et al. 2010). As such, habitat protection that favors males may have serious implications for population recovery, especially given that female habitat is subject to disproportionately higher rates of deforestation. In light of this, our findings highlight how threats to migratory birds may manifest differently for the sexes and show that failure to account for sexual segregation represents a serious shortfall of current conservation research and planning.

We suggest that long-held assumptions about habitat quality partly explain why sexual segregation is not routinely considered in conservation planning. One of the dominant narratives explaining sexual segregation in migratory landbirds is that male-dominated habitat is better quality than female-dominated habitat and, therefore, should be preferentially conserved (Sherry and Holmes 1996, Johnson 2007). This narrative is primarily borne from evidence of males excluding females from the highest quality and preferred habitat in a single overwintering population of American Redstarts (*Setophaga ruticilla*; Marra and Holmes 2001), but this conclusion may not apply to all species and geographies. For example, males and females of at least one species within the same family (Parulidae) select different habitats irrespective of intraspecific dominance hierarchies (Morton 1990) and would therefore not respond to conservation of male-dominated habitat. Consequently, we caution against generalizing insights from the American Redstart system in ways that diminish the perceived value of female-dominated habitats and landscapes. As we showed with

Golden-winged Warblers, female- and male-dominated landscapes may differ in terms of threats, including rates of land conversion, and therefore require different conservation actions.

For many Neotropical migratory birds, male occupy higher elevations and wetter habitats than females in the nonbreeding season (Catry et al. 2006). This pattern corresponds with general trends in land use change that are likely to differentially affect the sexes. In the tropics, dry and low-elevation forest have experienced greater rates of land use change than montane and humid forest (Helmer 2000, Hoekstra et al. 2005), signifying more female than male habitat is likely being lost across multiple species. An extreme case of female-dominated habitat loss has been reported for Bicknell's Thrush, which is the only species we found with conservation recommendations that account for sexual segregation of habitats (Townsend et al. 2012). Most of the low- to mid-elevation humid forest preferred by females has been lost due to human activities, whereas the cloud forests used by males have been conserved at a higher rate. Loss of female habitat is hypothesized to have created or exacerbated an 8:1 adult male:female skew in Bicknell's Thrush, motivating current conservation plans to prioritize protection of the rare and declining habitat for female (McFarland et al. 2018). The cases of Bicknell's Thrush and Golden-winged Warbler highlight the importance of understanding and prioritizing female habitat and the implications of overlooking sexual segregation in migratory landbirds.

Sexual segregation is not an obscure or uncommon behavior among animals (Ruckstuhl et al. 2005). Because sufficient knowledge is the necessary foundation for effective conservation recommendations, we recommend that scientists and

conservation practitioners alike make greater efforts to investigate and account for sexual segregation in research and conservation planning. Our study illustrates how sexual segregation is one important lens through which we should evaluate threats, develop conservation strategies, and delineate priority landscapes and habitats for migratory landbirds.

Acknowledgments

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Figures and Tables

Table 2.1: Female Golden-winged Warbler occupancy model-averaged results from 648 models with all possible subsets of covariates. Parameter estimates are presented on logit scale. All covariates except detection indices are scaled.

	Covariate	Estimate	SE	Z
Detection	Intercept	0.193	0.561	0.343
	Precip	-0.578	0.255	2.267
	Wind	-0.335	0.153	2.188
	Observer Skill	0.039	0.167	0.233
Occupancy	Intercept	-2.340	0.243	9.632
	X	0.372	0.200	1.861
	X^2	-0.942	0.189	4.975
	Annual Precip	-0.244	0.194	1.256
	Annual Precip^2	-1.124	0.581	1.933
	Elevation	-0.086	0.176	0.488
	Elevation^2	-0.912	0.314	2.904
	March NDVI	-0.052	0.158	0.330
	March NDVI^2	-0.170	0.255	0.666

Table 2.2: Male Golden-winged Warbler occupancy model-averaged results from 648 models with all possible subsets of covariates. Parameter estimates are presented on logit scale. All covariates except detection indices are scaled.

	Detection	Estimate	SE	Z
Detection	Intercept	0.202	0.571	0.354
	Precip	-0.088	0.134	0.656
	Wind	0.004	0.061	0.058
	Time of Day	-1.248	1.153	1.083
Occupancy	Intercept	-2.139	0.153	13.954
	X	0.282	0.153	1.836
	X^2	-0.872	0.161	5.404
	Annual Precip	0.049	0.127	0.386
	Annual Precip^2	-0.095	0.191	0.500
	Elevation	0.859	0.161	5.347
	Elevation^2	-0.602	0.160	3.766
	March NDVI	0.041	0.095	0.436
	March NDVI^2	0.006	0.054	0.110
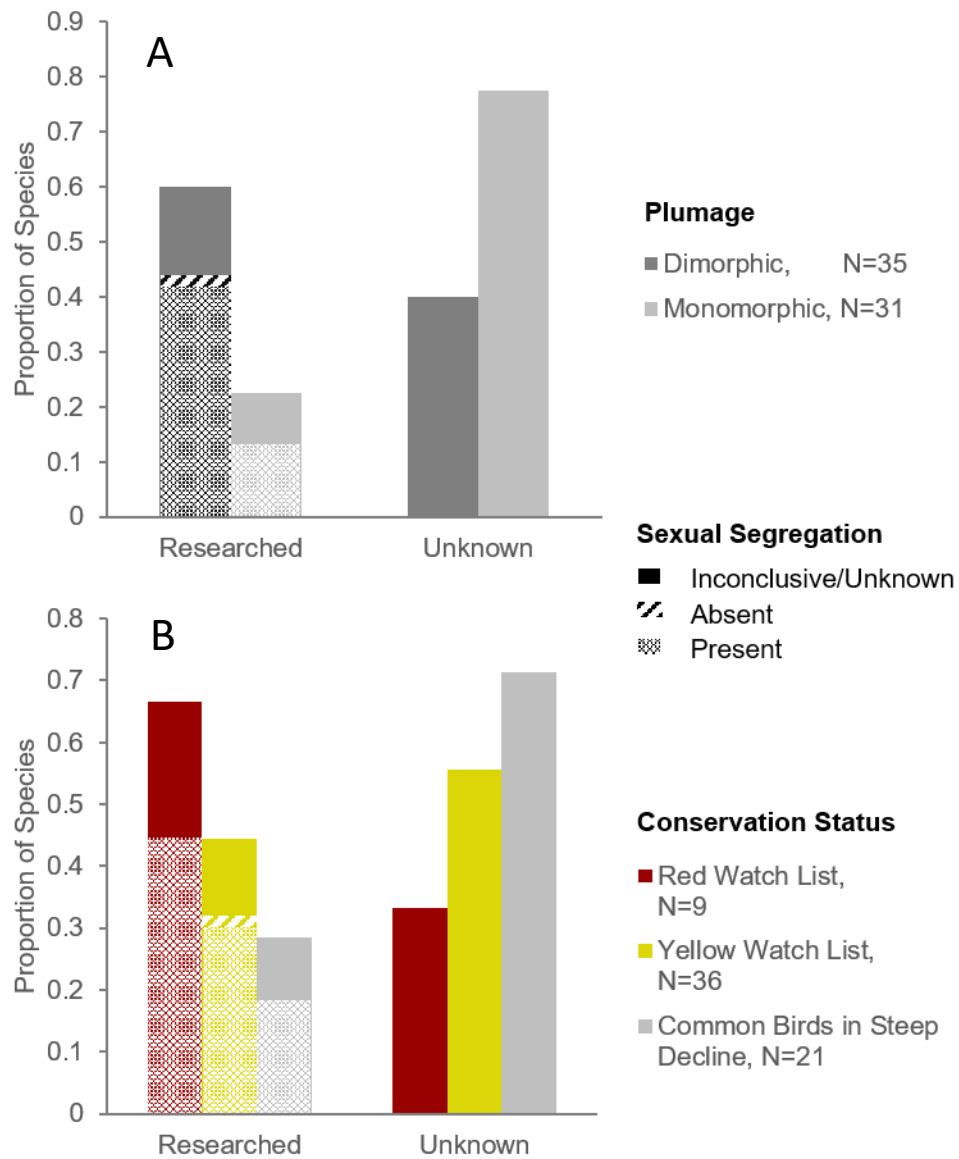
Figure 2.1. Evidence of nonbreeding sexual segregation in North American migratory birds of conservation concern based on A) sexual dimorphism in plumage and B) Partners in Flight Conservation Status
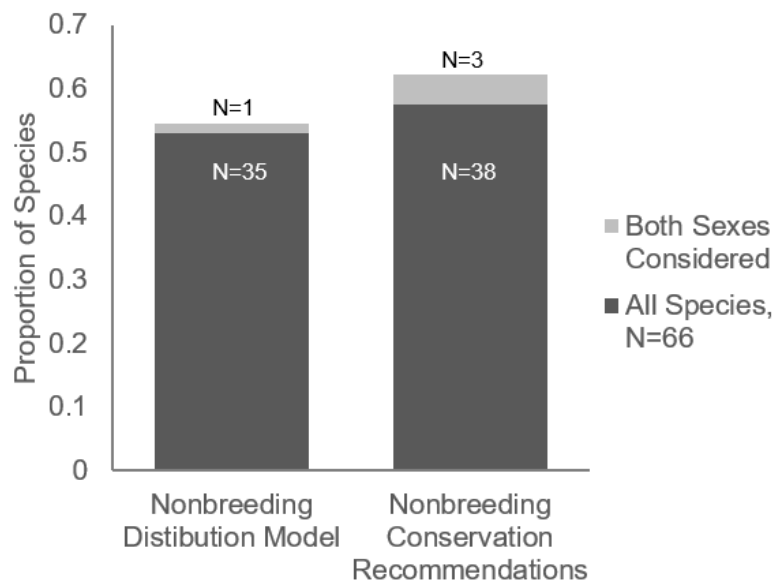
Figure 2.2. Proportion of North American migratory birds of conservation concern with published nonbreeding distribution models or conservation recommendations that account for differences in distribution or habitat requirements between males and females.
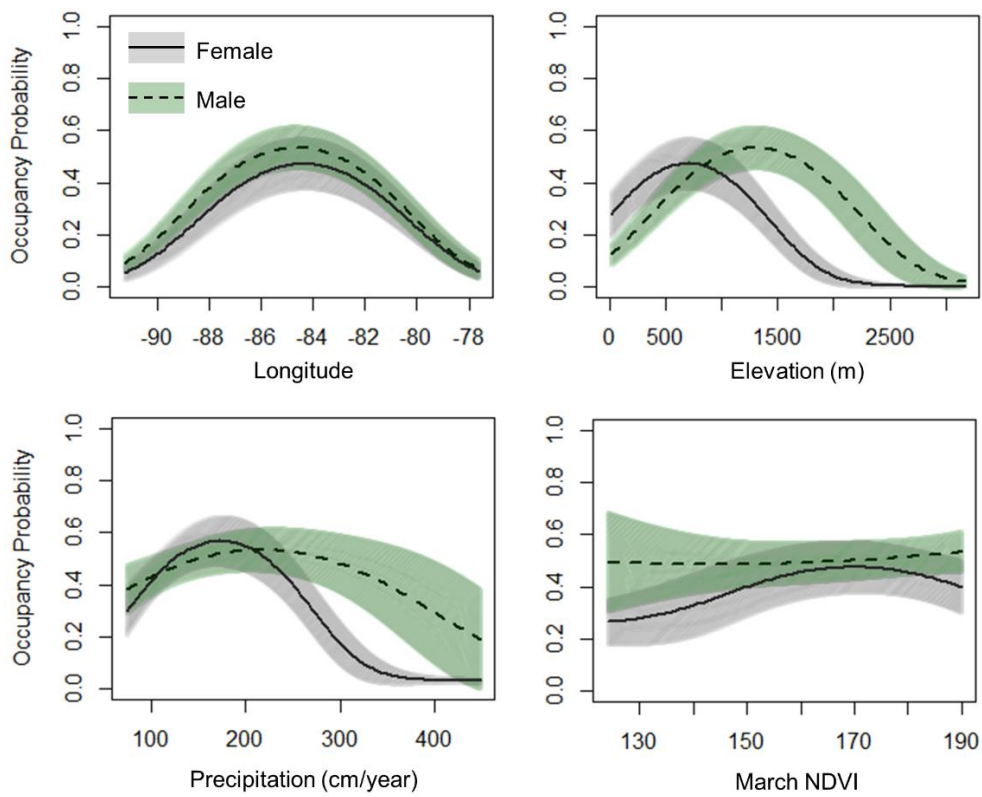
Figure 2.3. Differences in male and female predicted occupancy based on model averaged results the four occupancy covariates. Shaded lines show the standard error around the estimate.
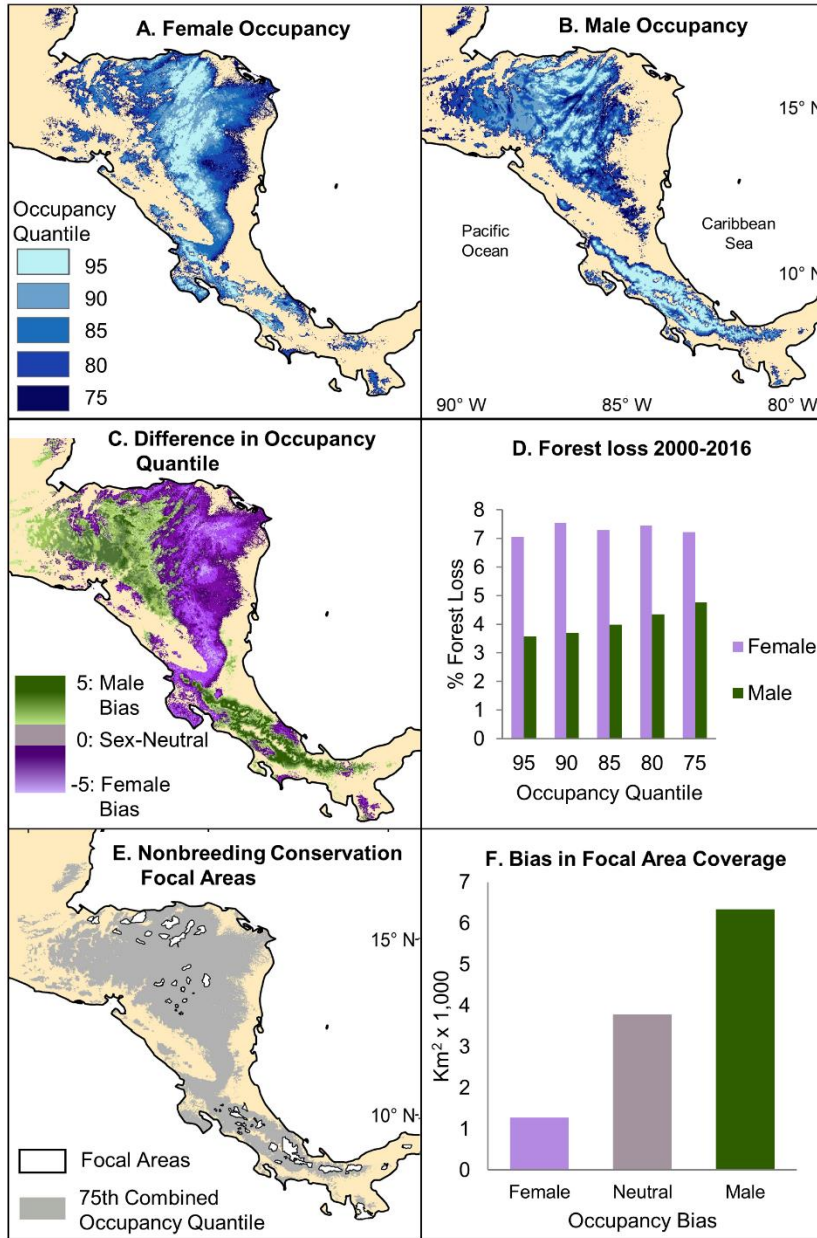
Figure 2.4. Predicted occupancy distributions of male (A) and female (B) Golden-winged Warblers in Central America during the nonbreeding season. Difference between male- and female-occupancy distributions (C) reveals sex biased landscapes within the nonbreeding range, which is associated with differing amounts of forest lost since between 2000 and 2016 (D). The locations of conservation focal areas for Golden-winged Warblers during the nonbreeding season (E), adapted from Bennett et al. (2016) show bias towards male occupied areas (F) when considering the total amount of cumulative land area within conservation focal areas exhibiting a sex bias in predicted occupancy.

CHAPTER 3

SEXUAL SEGREGATION OF OVERWINTERING HABITAT IN A DECLINING

MIGRATORY SONGBIRD

Abstract

Sexual segregation of habitats is a common phenomenon for vertebrates that can complicate conservation when habitats differ in availability and quality between sexes. Understanding the mechanisms that drive segregation is important, especially as effective conservation strategies will differ for systems where a dominant sex excludes a subordinate sex from high-quality habitat versus systems where both sexes specialize in different habitats. Here we investigate how habitat selection, occupancy, and quality differed between two habitat types for males and female of the declining migratory songbird, Golden-winged Warbler (*Vermivora chrysoptera*), during three nonbreeding seasons in Honduras. We conducted point-count surveys and modeled occupancy across arrival and overwintering periods in mid-elevation evergreen forest and low-elevation semi-deciduous habitat while accounting for differences in male and female detection probability. Habitat quality was assessed for 22 females and 84 males via three metrics of body condition—size-adjusted weight, pectoral muscle protrusion, and subcutaneous fat. We found that males preferentially selected, occupied, and maintained better body condition in evergreen forest, whereas females selected and maintained equal body condition in both habitats. In the final week of arrival, female occupancy declined relative to males in both habitats, and at a greater rate in evergreen

forest, suggesting males mediate female access to habitat through dominance. Age

ratios did not vary between habitats for either sex, indicating sex is a stronger

determinant of dominance than age for this species. Arrival patterns ultimately

resulted in a male occupancy bias in evergreen forest and a female bias in semi-

deciduous forest that was stable across overwintering seasons. Our results validate the

prioritization of male-dominated evergreen broadleaf forests for the conservation of

this species, given its higher quality for males and partial selection by females.

However, as female-dominated, semi-deciduous forests face high rates of conversion

and were of equal quality for females, we recommend that conservation plans also

promote the protection or sustainably use of that habitat. Ultimately, we show that

segregation mechanisms can be elucidated through field study and interpreted to

increase conservation efficacy for a declining species.

Introduction

Effective conservation of long-distance migratory birds is complicated by an annual

cycle that spans widely separated geographies. Migratory birds require multiple

habitats throughout their annual cycle, and the impact of habitat quality in any season

can carry over to affect individual performance in subsequent seasons (Norris et al.

2004, Rockwell et al. 2017). Although populations can be limited by events across the

annual cycle, a robust understanding of ecology and demography is often restricted to

the few months in which a species breeds (Faaborg et al. 2010b). As research fills

knowledge gaps from the migratory and overwintering periods, conservation efforts

are increasingly able to identify and protect critical nonbreeding habitats (Faaborg et al. 2010a). However, conservation efforts can be complicated by sexual segregation of habitats and intraspecific that mediate access to high quality nonbreeding habitat (Marra et al. 1993, Marra and Holmes 2001).

Segregation of habitats by sex and age is a widespread phenomenon in migratory birds during nonbreeding periods with potential population-level consequences (Catry et al. 2006). Two main hypotheses have been proposed to explain why birds segregate by sex. The dominance-mediated exclusion hypothesis states that dominant birds—typically adult males in migratory passerines—exclude subordinate birds from their preferred habitat, which results in habitats with different age structures and sex ratios. For example, adult male American Redstarts (*Setophaga ruticila*) exclude females and first year birds from high-quality mangrove habitat in Jamaica, driving high female and juvenile occupancy of a suboptimal habitat (Marra 2000, Marra and Holmes 2001). In contrast, the ecological specialization hypothesis posits that differences in morphology or physiological requirements lead the sexes to specialize in different habitats such that each sex should experience the greatest fitness within the habitat that their sex predominates. Consistent with the ecological specialization hypothesis, sexual segregation of overwintering habitats is thought to reflect innate differences in habitat preference for Hooded Warblers (*Setophaga citrina*; Morton et al. 1987, Morton 1990, Morton et al. 1993) and specialization of male and female foraging niches for multiple species of albatross (Phillips et al. 2004). Both mechanisms can cause sexual segregation at different spatial scales depending on whether species range widely, maintain individual territories, or participate in

conspecific flocks (Desrochers 1989, Hogstad 1989, Wunderle Jr 1995, González-Solís et al. 2000, Marra 2000).

Understanding both the patterns and mechanisms of sexual segregation is especially important for species threatened by loss of habitat, as the two proposed mechanisms have different implications for population-level responses to habitat change. Under dominance-mediated exclusion, the greatest fitness is achieved in a single preferred habitat, irrespective of sex or age, and populations are regulated by access (Marra and Holmes 2001). Under this mechanism, conservation of the preferred habitat type is most essential for population persistence, though conservation of suboptimal habitats may serve to buffer the population (Norris 2005, Norris and Marra 2007). However, if segregation stems from ecological specialization, females and males will prefer and thrive in different habitats, and each would need to be conserved to avoid creating or exacerbating sex ratio biases that reduce effective population size (Lande and Barrowclough 1987, Catry et al. 2006).

Here we study sexual habitat segregation in a declining Neotropical migratory songbird, the Golden-winged Warbler. Since the 1960's the Golden-winged Warbler has lost over 66% percent of its population, and loss of nonbreeding habitat is hypothesized to be one of the primary drivers of the population decline (Rosenberg et al. 2016, Kramer et al. 2018). Some studies suggest that males and females occupy different habitats during the nonbreeding season (Bennett 2012, Chandler et al. 2016), but female-dominated habitats are still undescribed. Previous work on the habitat requirements of nonbreeding individuals has only occurred in male-dominated habitats (Chandler and King 2011, Chandler et al. 2016) within mid- to high-elevation humid

broadleaf forests of Central America and the northern Andes of South America (Rosenberg et al. 2016). This lack knowledge impedes conservation by precluding an assessment of nonbreeding habitat quality for the species in general and specifically for females (Bennett et al. 2016).

The quality of nonbreeding habitats is difficult to assess in long-distance migratory birds. Although habitat quality is most directly assessed by honest metrics of fitness such as lifetime reproductive success (Newton 1998, 2004), individual body condition can serve as a useful proxy for nonbreeding habitat quality (Brown 1996, Johnson 2007). For this system, we use three estimates of body condition—size-adjusted mass, pectoral muscle protrusion, and amount of subcutaneous body fat—to assess habitat quality. Both size adjusted mass and pectoral muscle are expected to be greatest in high-quality habitats (Latta and Faaborg 2002). Subcutaneous fat, however, should show the opposite pattern in non-migratory periods, because extra weight can impair flight ability and increase predation risk. Consequently, birds often maintain little to no body fat in habitats with predictable food resources compared to more fat in habitats with less predictable food resources (Clark and Ekman 1995, Rogers 2005).

In order to address the mechanisms and consequences of sexual segregation for the Golden-winged Warbler, we investigated how overwintering habitat selection, occupancy, and quality of differed for males and females in two forested habitat types in Honduras. Each hypothesized mechanism predicts a different pattern of arrival and settlement (described by Marra 2000). Briefly, the ecological specialization hypothesis predicts that both sexes will settle their preferred habitat earlier and at a greater rate than the nonpreferred habitat, whereas the dominance meditated exclusion hypothesis

predicts both sexes will preferentially select the same habitat during arrival, but the subordinate sex will eventually be displaced into the nonpreferred habitat type (Figure 3.1). After the territory establishment period ended, we described patterns of male and female overwintering occupancy and assessed how body condition varied between sexes and habitats.

Methods

Study Area and Habitat

We studied the nonbreeding ecology of Golden-winged Warblers in the Sierra de Agalta mountains and surrounding lowlands in Department of Olancho, Honduras during three nonbreeding seasons between 2012 and 2017. The region is a conservation focal area where the species is abundant during the nonbreeding season (Bennett et al. 2016, Rosenberg et al. 2016). The study area ranged from 300 m to 2340 m above sea level and included both slopes of the mountain range and the lowland valleys to the north and south of the range. Rainfall in Sierra de Agalta increases with elevation, ranging from 1.1 m per year in the lowland valleys to the north and south of the range to 2.0 m per year on the peaks (Fick and Hijmans 2017).

We conducted fieldwork in two habitat types: humid evergreen broadleaf forest above 700 m (hereafter evergreen forest) and semi-deciduous broadleaf forest below 700 m above sea level (hereafter semi-deciduous forest). Both habitat types occur within a working landscape, meaning successional stage, disturbance, and fragmentation are variable. To characterize the habitat types, we conducted vegetation surveys at 78 points in evergreen forest and 80 points in semi-deciduous forest. At

each point, we recorded latitude, longitude, tree basal area with a 10-factor prism, slope with a clinometer, and presence of an edge within 150 m (either a change in land use or a natural disturbance that disrupted the vegetation across all vertical strata, such as a river or landslide). Using a pole and an ocular tube, we measured habitat structure within 50 m of each point by noting the presence or absence of woody vegetation in the following height intervals: 0-.0.5m, 0.6-2.5m, 2.6-5m, 5.1-10m, 10.1-15m, 15.1-20m, 20.1-30m, and 30+ m. Vertical structure was measured at 0, 10, 20, 30, 40, and 50 m from the plot center in each of the cardinal directions (n=21 points) and then summed (max = 168 per point) for a single metric of vertical structural diversity following McDermott and Rodewald (2014). At each point, we also extracted the mean annual precipitation (Fick and Hijmans 2017) and average March NDVI from 2015-2017 (https://earlywarning.usgs.gov/fews/product/445) with ArcGIS 10.5. The distribution of surveys for each habitat type did not differ with respect to latitude or longitude and covered a spatial extent of 23 km x 30 km.

Arrival Surveys

In two successive years, 2015 and 2016, we surveyed Golden-winged Warblers as they arrived in Sierra de Agalta from fall migration between 26 Sept and 30 Oct. We conducted surveys at 261 unique points, located at least 250 m from all other points. Points were surveyed once during arrival weeks 3, 4 and 5 in 2015, and once during each of the following arrival weeks in 2016: week 1 (26 Sept-2 Oct), week 2 (3 Oct-9 Oct), week 3 (10 Oct-16 Oct), week 4 (17 Oct-23 Oct), and week 5 (24 Oct-30 Oct). Points were split between evergreen forest (N=13 in 2015, N=115 in 2016) and semi-deciduous forest (N=49 in 2015, N=146 in 2016). To improve detection probability,

we broadcast a five-minute Golden-winged Warbler recording consisting of male songs and female chip notes (Chandler and King 2011) followed by a five-minute mobbing recording of alarm calls of ten common migratory songbirds and the songs of Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) and Eastern Screech-Owl (*Megascops asio*). Vocalizations were broadcast at maximum volume with an EasyAcc Mini Portable Speaker (Model # MODB00JK6MQEI) and followed by one minute of passive observation. During each survey, we recorded the sex of any Golden-winged Warbler detected within a 50 m radius of the point-count center, time of day, a wind index (1—no wind to 5—trunks moving), and a precipitation index (1—no precipitation to 5—heavy rain). We did not conduct surveys during periods of high wind or rain. Latitude, longitude, and elevation of each survey location were recorded with a Garmin eTrex 10 handheld GPS unit. Surveys were conducted by six trained observers who we classified as 1: inexperienced with one or fewer years detecting overwintering Golden-winged Warblers or 2: more than one year of experience.

Overwintering Surveys

We surveyed Golden-winged Warblers during three overwintering seasons (1 Nov to 15 March in 2012-2013, 2015-2016, and 2016-2017; hereafter Year 1, Year 2, and Year 3) at 78 points in evergreen forest (N=11 Year 1, N=59 Year 2, N=76 Year 3) and 80 points in semi-deciduous forest (N=31 Year 1, N=38 Year 2, N=80 Year 3). Based on the large overwintering home ranges reported for the species (Chandler et al. 2016), we separated points by least 400 m (and typically 500 m) to maintain independence. Within an overwintering season, points were surveyed once (1%), twice

(14%), or three times (85%) using the same point-count method as described for the arrival surveys above.

Body condition captures

Between 2011 and 2017, we conducted targeted captures of Golden-winged Warblers in both habitats during the overwintering season. Birds were captured using a 30-mm mist net and attracted with conspecific playback. Each captured individual was marked with a unique combination of color bands, and we recorded sex, wing chord, weight, body fat on a 0-5 scale (Holmes et al. 1989), and pectoral muscle protrusion on a 0-3 scale (Gosler 1991). Age was recorded as hatch year (HY, less than one year old) or after hatch year (AHY, greater than one year old; Pyle et al. 1987). Pectoral muscle was not recorded in 2011-2013.

Data analysis

We analyzed overwintering and arrival surveys in an occupancy framework using the 'unmarked' package in program R (Fiske and Chandler 2017, MacKenzie et al. 2017, R Core Team 2017) which accounts for imperfect detection probability during each survey. For overwintering surveys, we created detection histories for males and females at each point and fit single-season occupancy models. We considered two categorical occupancy covariates—habitat type and year—and four detection covariates: 1) time of day; 2) the wind index; 3) the precipitation index; 4) and the observer skill index. Time of day was scaled from 0 (12:00 AM) to 1 (11:59 PM). We tested the goodness of fit of global models with 1,000 parametric bootstrap simulations of model fit using a chi-squared statistic as described by MacKenzie and Bailey (2004) for single-season occupancy models. We failed to reject the null

hypothesis that our models adequately described data for the global male (P=0.914) and female models (P=0.326), indicating reasonably good fit for both sexes. We then fit all possible subsets of the detection covariates with both occupancy covariates and retained the detection covariates from the model with the lowest AICc (Murtaugh 2009). Using the retained detection parameters, we evaluated four combinations of the occupancy parameters 1) Habitat only, 2) Year only, 3) Habitat*Year, and 4) a null model. We compared models with AICc and considered models competitive at AICc < 2 (Anderson 2002).

For each arrival survey, we estimated probability of detecting males and females using the detection coefficients from the best male and female overwintering models. We used the 'predict' function in package 'unmarked' to predict detection probability and SE for the combination of detection covariates recorded during each arrival survey. This technique assumes the detection probability was the same during the arrival period as during the stationary overwintering period (MacKenzie et al. 2002). We observed males and, to a lesser extent, females aggressively respond to intraspecific playback during the arrival period, often singing or chipping in response and approaching the speaker. This response continued throughout the overwintering period, suggesting detectability was similar in both periods. For each arrival survey, occupancy was 1 if we detected a Golden-winged Warbler. If no individual was detected, we estimated occupancy as the average study area occupancy probability multiplied by the probability that we did not detect a present individual (one minus survey detection probability; MacKenzie et al. 2002). We estimated the study area occupancy probability for males and females for each arrival week by multiplying the

proportion of sites known to be occupied by one minus the average detection

probability from all points during that week (MacKenzie et al. 2002). We averaged

occupancy values and 95% CI from each point to create a metric of average proportion

of sites occupied for each sex in each habitat during each arrival week. We combined

data across years because the Habitat*Year model was not supported for either sex

(described in Results) indicating that relative occupancy of habitats did not vary

significantly between years.

Three metrics of body condition were compared between habitats using simple

linear regression: 1) Time and size adjusted mass, 2) Pectoral muscle index, and 3) Fat

Index. Because bird body mass typically increases throughout the day (McNamara et

al. 1994), we adjusted weight by time of day by using the residuals of a linear

regression of the two variables for each sex. We then adjusted mass for body size by

taking the residuals of a linear regression of time adjusted mass and wing chord. Wing

chord and body mass for each sex were scaled around their means prior to analysis.

We compared age between habitat types for each sex with Chi-squared tests. Finally,

we scaled all continuous habitat variables and compared them in a logistic regression

with habitat type as the response variable. Habitat covariates were not correlated (r <

0.45).

Results

Habitat Differences

Habitats differed structurally (Table 3.1), with semi-deciduous forest having more

edge and less structural complexity and slope. Semi-deciduous forest was significantly

drier than evergreen forest at the end of the overwintering period across years and received less annual precipitation.

Arrival Occupancy Patterns

Across years, we detected 136 males (N = 6, 12, 32, 42, 44 for each respective week) and 114 females (N = 3, 4, 29, 43, 35 for each week) during the arrival period, with different detection probabilities between sexes (female mean = 30.7%, SE = 6.9; male mean = 50.3%, SE = 5.2). For both sexes, peak arrival (i.e., most rapid accumulation of birds) occurred between weeks 2 and 3. Between the final two arrival weeks, male occupancy was stable, but female occupancy declined in both habitats. Male occupancy was greater and increased more rapidly in evergreen forest than semi-deciduous forest across weeks (Figure 3.3A), while female occupancy was greater in semi-deciduous forest than evergreen forest only during weeks 4 and 5 (Figure 3.3B). Habitats differed in the rate at which they were occupied, with evergreen forest being settled at the greatest rate between weeks 2 and 3, while semi-deciduous forest continued to be settled at the same rate between through week 4 for both sexes (Figure 3.3C, D).

Overwintering Occupancy

Combining across years, we detected 93 overwintering females at 69 points and 149 males at 95 points. Time of day and observer skill influenced detection of males and females, the latter of which also was affected by precipitation and wind (Table 3.4). Detectability of females (range 1.6% to 52.2%; mean = 26.0%, SE = 6.0) was lower than for males (18.6% to 69.0%; mean = 42.1%, SE = 5.5). Male occupancy was significantly higher in evergreen forest than semi-deciduous forest (Table 3.2 and 3.3,

Figure 3.2). Female occupancy was greatest in year 3 (Table 3.3), but habitat, year, and null models all received support (Table 3.2), and none provided evidence that female occupancy varied significantly between habitat types (Table 3.3, Figure 3.1).

Body condition

We captured 11 females and 63 males in evergreen forest and 11 females and 21 males in semi-deciduous forest. Overall, we captured more AHY than HY individuals (54% of females and 62% of males = AHY), and age structure did not vary between habitat types for females ($X^2_{(2, N=22)}$=0.733, P=0.393) or males ($X^2_{(2, N=84)}$=0.000, P=1.000). Males had greater adjusted weight and pectoral muscle and had less body fat in evergreen forest, whereas female size and condition were similar between habitat types (Table 3.5, Figure 3.4).

Discussion

Our results show that habitat selection, occupancy, and quality of overwintering habitats differ for male and female Golden-winged Warblers. During arrival and overwintering periods, males preferentially selected and occupied evergreen forest, where they also maintained better body condition and less subcutaneous fat. These results indicate that evergreen forest was better quality for males (Rogers 2005, Johnson 2007). Females, in contrast, appeared to show no habitat preference and occupied both habitats equally during peak arrival and the overwintering period. Female size-adjusted weight, pectoral muscle, and body fat was similar in both habitats, suggesting they provided similar quality to females during this study. However, we cannot exclude the possibility that other factors, such as antagonism

from males in evergreen forest, affected the condition of females.

Despite lack of evidence that the female-dominated habitat was poor quality for females, arrival patterns are consistent with the predictions for dominance-mediated segregation. Males showed a clear preference for evergreen forest during arrival, whereas female occupancy increased in semi-deciduous forest while occupancy leveled-off in evergreen forest. This is consistent with evergreen forest becoming saturated before semi-deciduous forest and also follows the settlement predictions of the Ideal Despotic Distribution (IDD) (Fretwell 1972, Parker and Sutherland 1986). Under IDD, strong competitors pack into the highest quality habitat and exclude individuals with lower competitive ability. Accordingly, the poor condition of males in semi-deciduous forest may reflect a low competitive ability as well as lower intrinsic habitat quality (Johnson 2007). The fact that female occupancy in evergreen forest only declined relative to males in the final arrival week when male occupancy stabilized is consistent with females being excluded after saturation with dominant males (Marra 2000, Johnson 2007). Surprisingly, female occupancy even declined relative to males in semi-deciduous forest, which we showed is suboptimal habitat for males, during the final arrival week. To our knowledge, this pattern has not been described in a female-dominated overwintering habitat and suggests that females are subject to displacement by males across habitat types and across a gradient of sex-ratio bias. Furthermore, this occupancy decline suggests females with low-competitive ability may be relegated to an undescribed, low-quality habitat type outside of our study area. However, no evidence of latitudinal segregation exists for this species (Bennett et al. in review), and we searched the landscapes around our study area

without discovering additional females. We therefore expect that excluded females either cryptically float within our study area or diffusely occupy other landscapes in low numbers (Brown and Long 2007).

Although dominance-mediated segregation is supported by these arrival and settlement patterns, the similar body condition of females in both habitats precludes us from dismissing that either (a) females in evergreen forest were negatively impacted by antagonistic behavior or competition from males or (b) females are more flexible in their habitat needs and therefore able to occupy semi-deciduous forest without bearing fitness costs. In the classic Hooded Warbler example of ecological specialization, authors posited that sexual differences in habitat preference may have evolved to limit competition between the sexes during the overwintering period (Morton 1990). Similarly, researchers have proposed that the extreme size dimorphism that facilitates niche divergence in albatrosses originally evolved to limit intraspecific competition between sexes (Phillips et al. 2004). Other migratory species that sexually segregate, such as the Black-throated Blue Warbler (*Setophaga caerulescens*) and Eurasian Oystercatcher (*Haematopus ostralegus*) have evidence that simultaneously correspond to predictions from both dominance-mediated segregation and ecological specialization (Wunderle Jr 1995, Durell et al. 2001), suggesting the mechanisms are not mutually exclusive. In this context, the Golden-winged Warbler's sexual dimorphism in wing length and shape, with females possessing smaller and rounder wings (Pyle et al. 1987), raises the possibility that females better exploit food resources within semi-deciduous forest compared to males. Shorter and rounder wings are associated with hovering maneuvers and foraging at lower heights (Marchetti et al.

1995). Though we show that habitats differed in several structural components, further study of foraging behavior is required to determine if the sexes differ in foraging success within these habitat types.

Contrary to our expectations, age-ratios for both males and females were similar across habitats with almost 50% of captures being HY individuals. In most avian dominance hierarchies, HY birds are subordinate to AHY birds (Piper 1997) and thus more likely to occupy suboptimal habitats, as seen with overwintering American Redstarts (Marra 2000). However, Golden-winged Warblers are unusual among dimorphic migratory warblers in that HY birds obtain adult plumage prior to fall migration (Pyle et al. 1987). The lack of an age-related plumage signal may mediate aggressive territorial encounters (Rohwer 1975, Balph et al. 1979). Indeed, male and female Golden-winged Warblers arrivals followed the patterns described for AHY male and HY female American Redstarts (the most dominant and subordinate classes) in high and low quality overwintering habitat, further suggesting a lack of an age effect in this system (Marra 2000). As a caveat, numbers of AHY birds in low-quality habitats may be inflated in some years due to high interannual site fidelity (i.e. up to 50% return rates of males in Costa Rica; Chandler 2011b). Still, the absence of age structure and arrival patterns suggest that sex, rather than age, drives the dominance hierarchy in this system.

Overall, our study makes two important contributions to ecological and conservation literature. First, we showed that explicitly accounting for sex-related differences in detection probability is important, despite not being regularly considered in nonbreeding studies of migratory landbirds (but see Wunderle Jr 1995,

Chin et al. 2014). Second, our finding that mid-elevation broadleaf forest was high

quality for males and selected and occupied by nearly 50% of females indicates that

conserving male-dominated habitat should remain a priority. At the same time, we

also recommend that conservation plans promote the protection or sustainable use of

drier and lower elevation forests, because they support females and are subject to high

rates of conversion (Bennett et al. *in review*). Sexual segregation of habitats is cited as

a complication to conservation efforts (Faaborg et al. 2010), but we ultimately showed

that segregation mechanisms can be elucidated through field study and interpreted for

more effective conservation of a declining species.

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Tables and Figures

Table 3.1. Model coefficients from logistic regression comparing evergreen forest and semi-deciduous forest. Habitat covariates are significant at *P < 0.05, **P < 0.01, and ***P < 0.001.

Habitat Metric	Coefficient	SE	P	
Intercept	-1.65	0.76	0.030	
Latitude	0.44	0.40	0.269	
Longitude	-0.42	0.32	0.192	
Edge	1.81	0.67	0.007	**
Basal Area	0.17	0.33	0.604	
Slope	-1.12	0.35	0.001	**
Structural Complexity	-1.99	0.57	<0.001	***
March NDVI	-2.63	0.65	<0.001	***
Annual Precipitation	-4.63	1.05	<0.001	***

Table 3.2 Model section for female and male overwintering occupancy. Models are considered competitive at delta AICc <2.0. Detection covariates are indices described in Methods.

Model	Detection covariates	Occupancy covariates	AICc	Delta AICc
Female 1	precip+wind+time+observer	Year	545.14	0.00
Female Null	precip+wind+time+observer	1	546.31	1.17
Female 2	precip+wind+time+observer	Habitat	546.91	1.77
Female 3	precip+wind+time+observer	Habitat*Year	548.75	3.61
Male 1	time+observer	Habitat	672.19	0.00
Male 2	time+observer	Habitat*Year	687.45	15.26
Male Null	time+observer	1	712.69	40.50
Male 3	time+observer	Year	716.44	44.25

Table 3.3 Occupancy coefficients from competitive overwintering occupancy models. Occupancy covariates are significant at *P < 0.05, **P < 0.01, and ***P < 0.001.

Model	Occupancy covariates	Estimate	SE	Z	P	
Female 1	Intercept	-1.11	0.48	-2.32	0.020	
	Year2	0.67	0.57	1.16	0.250	
	Year3	1.16	0.54	2.12	0.030	*
Female 2	Intercept	-0.594	0.321	-1.85	0.064	
	Low Dry Habitat	0.429	0.362	1.18	0.236	
Female Null	Intercept	-0.34	0.25	-1.34	0.180	
Male 1	Intercept	0.686	0.302	2.27	0.023	
	Low Dry Habitat	-2.057	0.362	-5.68	<0.001	***

Table 3.4. Detection coefficients from top female and male overwintering occupancy models. Detection covariates Detection covariates are indices described in Methods and are significant at *P < 0.05, **P < 0.01, and ***P < 0.001.

Model	Detection covariates	Estimate	SE	Z	P	
Female1	Intercept	-0.193	0.971	-0.199	0.842	
	precip	-0.482	0.310	-1.556	0.120	
	wind	-0.308	0.182	-1.691	0.091	
	time of day	-2.687	1.360	-1.975	0.048	*
	observer	0.873	0.327	2.667	0.008	**
Male1	Intercept	-0.804	0.699	-1.150	0.250	
	time of day	0.873	0.283	3.090	0.002	**
	observer	-2.08	1.149	-1.810	0.070	*

Table 3.5. Results for six linear models comparing size and body condition metrics to habitat type for males and females. Models are significant at *P < 0.05, **P < 0.01, and ***P < 0.001.

Sex	Predictor	df	F	P	
Male	Time and size adjusted weight	82	5.613	0.020	*
Male	Pectoral muscle index	71	6.848	0.011	*
Male	Body Fat	81	16.080	<0.001	***
Female	Time and size adjusted weight	20	0.610	0.444	
Female	Pectoral muscle index	20	0.993	0.348	
Female	Body Fat	20	1.622	0.217	

Figure 3.1. Predicted arrival patters under the (A) ecological specialization hypothesis and (B) dominance-mediated segregation hypothesis. Occupancy values are arbitrary.
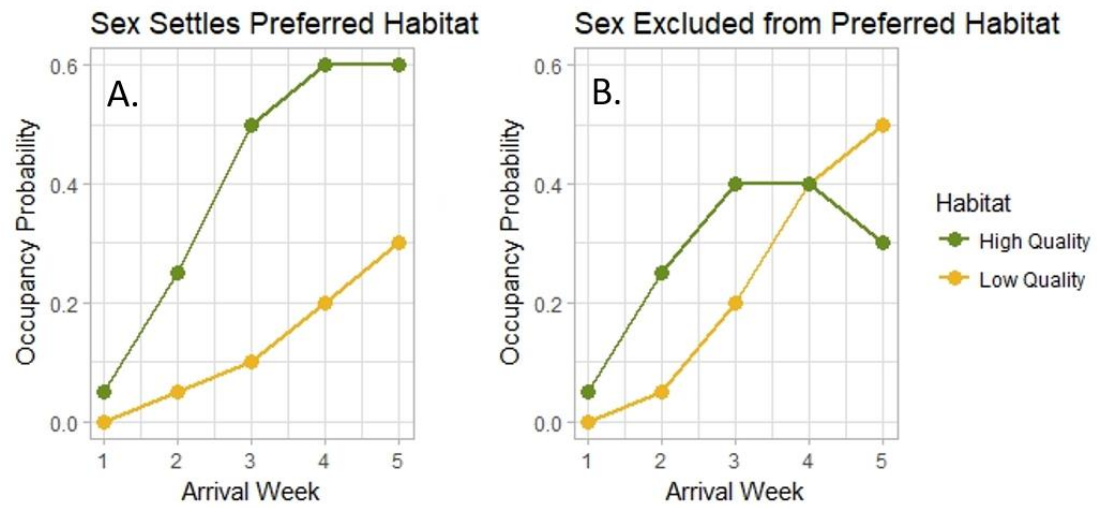
Figure 3.2. Overwintering occupancy estimations for male and female Golden-winged Warblers over three seasons for all supported occupancy models with predictions between mid-elevation evergreen broadleaf forest and low-elevation semi-deciduous forest.
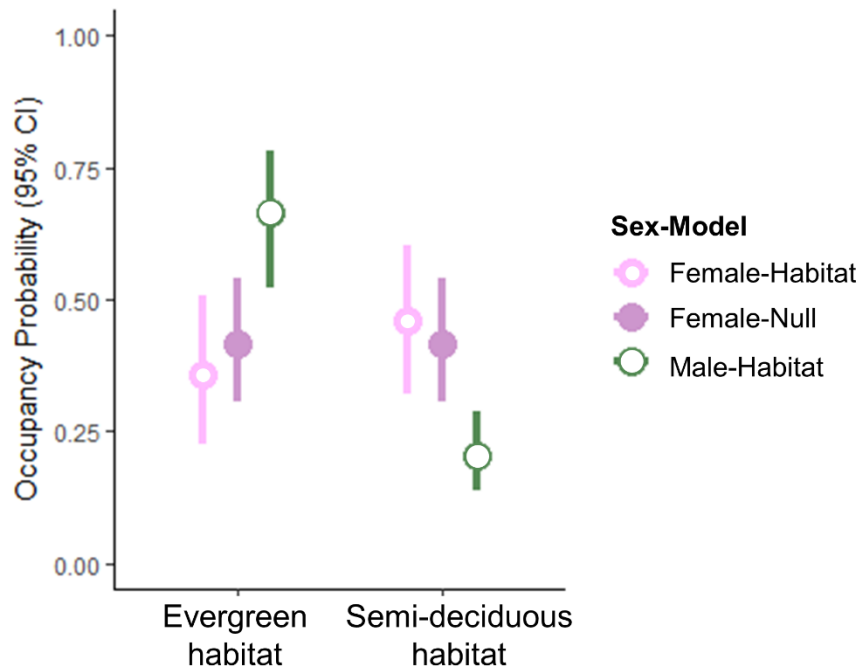
Figure 3.3. Pattern of occupancy across five arrival weeks from September 26 to October 30 in 2015 and 2016 for (A) males and (B) females by habitat type and for (C) evergreen forest and (D) semi-deciduous forest by sex.
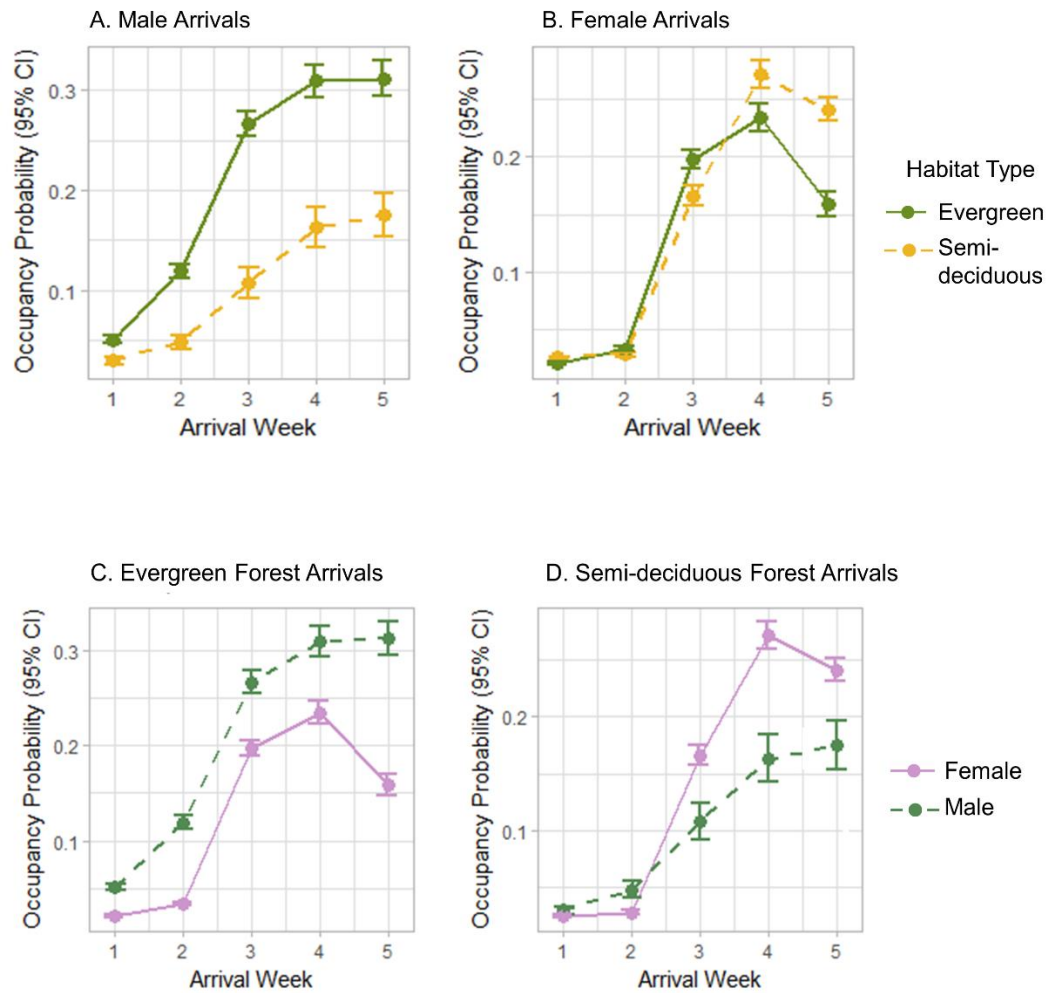
Figure 3.4. Three metrics of body condition for overwintering male and female Golden-winged Warblers in evergreen forest semi-deciduous forest: (A) weight adjusted for wing chord and time of day, (B) pectoral muscle index, and (C) body fat index. Whiskers correspond to 1.5 times the interquartile range.
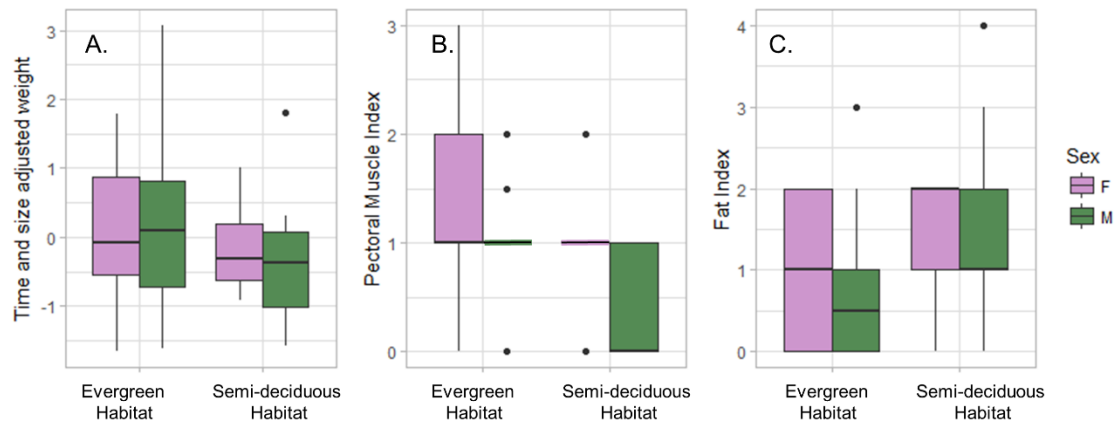
CHAPTER 4

OPTIMAL MIGRATION STRATEGIES REVEALED THROUGH INDIVIDUAL

VARIATION IN BEHAVIORS AND TRAITS IN A DECLINING SONGBIRD

Abstract

Understanding migration strategies is critical for conserving long distance migratory

birds given evidence that populations are limited during migratory periods. We used

optimal migration theory, which predicts tradeoffs between minimizing passage time,

energy expenditure, and mortality risk, to assess the degree to which spatial and

temporal patterns of migration vary among individuals, seasons, and years for a

declining migratory songbird, the Golden-winged Warbler (*Vermivora chrysoptera*).

We analyzed data from 37 light-level geolocators deployed over four years in the

linked Great Lakes-Central America population. In spring migration, we found most

birds (69%) employed a multi-day refueling stop (hereafter stopover) before crossing

the Gulf of Mexico followed by a stopover in the central United States, while fewer

birds (23%) crossed the Gulf of Mexico without refueling followed by a stopover near

the U.S. Gulf coast. Only experienced individuals (undertaking ≥ 2nd spring

migration) employed the second strategy, migrating 7 days (2 SD) faster than other

birds. The difference in stopover regions following the trans-Gulf flight suggests that

experienced individuals trade off total migration time with fuel loading before

crossing a major geographic barrier. Wing length positively predicted total distance

and duration of migration in both spring and fall, providing the first indication that that

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intraspecific variation in morphology influences migration range within a long-distance migratory population. Timing and duration of spring migration were similar among years and nearly twice as fast as fall migration, which varied among years. Overall, these results are consistent with a population-level migration strategy that minimizes migration time in the spring and relaxes that pressure in the fall. As such, spring migrants are likely to rely on fewer stopover sites and face greater energetic risks than fall migrants.

Introduction

Each year, millions of birds migrate between temperate northern latitudes and the tropics in a fascinating process that impacts global ecological networks (Keast and Morton 1980, Bauer and Hoye 2014). Long-distance migratory species are impacted by events in multiple geographies across their annual cycle, and effective conservation requires understanding where and how populations may be limited (Sherry and Holmes 1996, Norris and Marra 2007). In many parts of the world, migratory bird populations are declining (Sanderson et al. 2006, Sauer 2017), and survival is often lowest during migratory periods (Sillett and Holmes 2002, Rushing et al. 2016, Rockwell et al. 2017). It is therefore of critical importance to elucidate how these populations migrate and are constrained.

Birds are one of the best studied migratory taxa, with a rich literature that provides insights into the innate cues, optimality constraints, and individual decisions that govern their migrations (Berthold 2001). Date of migration initiation has been

shown to be under endogenous control in long-distance migrants, with little to no individual plasticity in most species (Gwinner and Helm 2003, Gill et al. 2014). In contrast, migration pathways and speed are thought to be relatively flexible at both the individual and population level (Stanley et al. 2012, Cohen et al. 2014, La Sorte and Fink 2017). Constraints on migration are typically discussed within an optimality framework in which migration routes and refueling stopovers balance energy expended, the amount of time spent migrating, and risk of predation or starvation (Clark and Butler 1999, Alerstam 2011). Optimal strategies may differ between species, seasons, and sexes. For example, passage time is substantially shorter in spring than fall for most species, which is consistent with a time-minimizing spring migration strategy driven by a stronger selective pressure to establish breeding territories than overwinter territories (reviewed in Nilsson et al. 2013). Conversely, migration strategies may prioritize low energy expenditure, and these migrants would accordingly travel at a slower pace, refuel more frequently, and carry smaller fuel reserves (Alerstam 2011, Nilsson et al. 2013). In theory, a time-minimizing strategy should be riskier than an energy-minimizing strategy, as time-minimizing individuals have a decreased ability to detect and escape predators at a stopover and may run the risk of depleting fuel reserves and starving between stopovers (Newton 2004, Gómez et al. 2017). The extent to which selection for passage-time minimization mediates mortality risk is unknown, but recent demographic work shows that survival is often lowest during spring migration (Klaassen et al. 2014, Lok et al. 2015, Rushing et al. 2017) suggesting spring time-minimization may carry a survival cost.

Within a population, the migratory movement behaviors of individuals—

including timing, duration, pathway, and use of stopover sites—reflect individual approaches to an optimal migration strategy. Our understanding of these behaviors has advanced with the development of small tracking technologies that can follow individuals across the annual cycle (Stutchbury et al. 2009). For example, we now know that both landbirds and shorebirds commonly utilize a migration strategy of rapid passage between only a few stopover sites (Atkinson et al. 2007, Bayly et al. 2018). These stopover sites play a critical role in a bird's ability to sufficiently refuel, cross major geographical barriers, and successfully complete migration (Gómez et al. 2017, Moore 2018), but stopover locations and usage patterns are still unknown for most species. Movement behaviors may also be influenced by variation in morphology, such as wing shape (Arizaga et al. 2006), as well as by prior migration experience (McKinnon et al. 2014). The range of variation within individual migration behaviors and morphology should furthermore impact the flexibility of a population to respond to locally changing conditions (Charmantier and Gienapp 2014). Quantifying the variation in individual movement behaviors, and how morphology and experience impact those behaviors, is necessary to understand constraints on migration and develop appropriate conservation strategies for declining or threatened species.

In this paper, we investigate the seasonal migration strategies of an imperiled Nearctic-Neotropical migratory songbird, the Golden-winged Warbler (*Vermivora chrysoptera*). Specifically, we evaluated the degree to which the spatial and temporal structure of migration vary among years, seasons, and individuals within a linked population that breeds in the Great Lakes region of U.S. and Canada and overwinters in Central America (Bennett et al. 2017, Larkin et al. 2017, Kramer et al. 2018). By

assessing the observed patterns of movement and stopover behaviors and their association with morphology and migration experience, we evaluate how and when their migration strategy optimizes times and energy minimization. Our study is the first to integrate geolocators deployed at both breeding and overwintering sites over multiple years and thereby elucidate individual variation within the migration strategy of a linked population.

Methods

Data collection

During the overwintering season of 2015-2016 (15 Nov to 15 March) we deployed geolocators on 123 Golden-winged Warblers at eight sites in Central America (Table 4.1). While migration strategies may differ between sexes (Dierschke et al. 2005), we restricted this study to males, due to low capture rates and small body size of females. Golden-winged Warblers were captured with a 30mm mist net and fitted with a Lotek ML6040 stalkless geolocator attached to the leg-loop harness described by Streby et al. (2015). We recorded age (Pyle et al. 1987), wing chord (mm), and weight (g) of all captured birds, and affixed a single color-band to aid in resighting. We recovered geolocators during the following nonbreeding season, beginning on October 15, 2016, and performed at least 3 area searches within a 500 m radius of each initial deployment location using GWWA male broadcast vocalizations to increase probability of resighting individuals (Chandler and King 2011). We resighted 26 of 123 Golden-winged Warblers and successfully recaptured 22 in mist nets. Because two geolocators failed within their first day of activation, we included only 20 units from this field effort in the analysis.

We supplemented our sample size with published geolocator data from 6 Golden-winged Warblers tagged during January and February 2015 at El Jaguar, Nicaragua (Larkin et al. 2017), and 11 individuals tagged between May 2013 and June 2014 at Rice Lake National Wildlife Refuge, MN described by Kramer et al. (2016, 2017) (Table 4.1). We excluded one geolocator that was part of the Rice Lake dataset (RL3) because light data were significantly distorted by mud caked on the light sensor (Kramer et al. 2016). For Nicaragua birds, we also acquired associated morphological data for all individuals that returned with a geolocator (Larkin et al. 2017).

Geolocator analysis

We analyzed 37 geolocators carried by male Golden-winged Warblers, first unpacking data with BASTrack software and then refining position estimates in a Baysian framework with package 'SGAT' version 3.3.0 (Wootherspoon et al. 2016) in program R (R Core Team 2017). All geolocators recorded light on the same arbitrary 0-64 scale. To create starting locations for the Baysian models, we defined sunrise and sunset times using a threshold value of 1.25 on the arbitrary 0-64 light scale with the 'preprocessLight' function in package 'SGAT.' We did not alter any of the defined sunrise and sunset values as the modeling process corrects data outliers. For geolocators deployed at overwintering sites, we calculated average solar zenith and defined a log-normal density distribution of error in sunrise and sunset values between deployment and 15 March, as Golden-winged Warblers are known to remain on winter territories until late March or the beginning of April (Rosenberg et al. 2016). For three geolocators deployed after 10 March, we extended the calibration period to 1 April after checking raw light data for evidence that no obvious migratory movement

occurred before that date. For geolocators deployed in MN on the breeding grounds, we calculated average solar zenith and a log-normal error distribution between deployment and 25 June. We incorporated a behavioral model that assumes birds are usually stationary but capable of moving long distances during migration (gamma distribution with shape = 0.7 and scale = 0.08). We created a spatial mask in ArcGIS 10.5 to constrain locations during the spring and fall equinoxes, when latitude is impossible to estimate. The mask was bounded by the 7° latitude at the south, because all birds overwintered in Central America, and by a 250 km buffer above the northern edge of the Golden-winged Warbler breeding range, which we delineated with a polygon around the northern edge of all eBird.com records from the months of June and July over the past ten years. We did not constrain locations to occur over land, as land masks have been shown to bias the predicted location of birds that occur on islands or near large bodies of water (Cooper et al. 2017). Using these priors, we refined location estimates with a the 'estellemetropolis' algorithm in package 'SGAT.' We ran three independent chains each with 50,000 iterations for burn-in and tuning, drew 5000 iterations per chain for posterior analysis, and visually inspected convergence.

Solar zenith angle analysis and adjustments

The solar zenith angle recorded by a geolocator is known to vary among habitat types and life-stages, which can have a profound effect on location estimates (McKinnon et al. 2013, McKinnon et al. 2015). We were able to test and account for differences in solar zeniths between season and habitats by comparing the mean calibration zeniths of the geolocators deployed at breeding sites (mean z=92.6 and 95th

quantile=94.6) and overwintering sites (mean z=90.9 and 95th quantile=93.4). These mean zeniths and 95th quantile values were used as priors for the unknown breeding or overwintering locations estimated by each geolocator. For migratory periods, we averaged the calibration zenith with the mean zenith for breeding or overwintering periods following Cooper et al. (2017).

Five of the 12 geolocators from MN had overwintering centroids that failed to converge over a landmass. For those individuals, we reduced their overwintering zenith to the minimum recorded overwinter calibration zenith (mean z=88.8 and 95th quantile =92.3), reran models, and relocated any centroids still over open ocean to the nearest landmass (max 150 km). We did not include centroid locations that failed to converge over land in calculations of distance between breeding and overwintering areas (n=3).

During the breeding season, 34 of 37 geolocator tracks showed substantial movements southward between their June centroids and July centroids. Although Golden-winged Warblers do not begin southward migration movements until August (Rosenberg et al. 2016), they do shift habitat in ways that may bias position estimates due to shading during that period. Specifically, males in this population leave their unshaded song perches to provision young and move their fledglings from open-canopy habitat into closed-canopy forest during the post-fledgling period (Streby et al. 2016). To address this, we compared the average solar zenith in the breeding calibration period to the average solar zenith between July 7th (mean date of southward drift) and July 31st (a conservative estimate of the end of the post-fledgling period) for all geolocators deployed on the breeding grounds. The mean July zenith shifted by

over one degree during these two time periods (7 July-31 July mean z=91.4, 95th quantile=93.5), so for the 34 birds with southward movement, we used the mean July zenith between the date their locations started to drift south and their fall migration departure date. This corrected the southward drift in almost all birds.

Given the strong seasonality of precipitation in Central America, we also suspected solar zeniths might differ at overwintering sites in response to changes in vegetation coverage between the dry season (March-April) when most birds depart for spring migration and the wet season (October-November) when most birds arrive from fall migration. For geolocators deployed at overwintering sites (N=26), we compared the mean calibration zenith (which either included or entirely described the dry season) with a wet-season zenith defined as the mean zenith between the subsequent overwinter arrival and 1 December. The wet season zenith was substantially lower for most birds (mean=89.9 and 95th quantile=93.0) but varied between individuals. We therefore adjusted the post-fall arrival zenith to the mean wet season zenith for individuals with location differences between years. We reran all models with these redefined zeniths and recalculated breeding, overwintering, and migration dates and locations.

Migration timing definition

We defined breeding location for each bird as the centroid location between the breeding grounds arrival date and 25 June and overwintering location as the centroid between winter grounds arrival date and 10 February to avoid incorporating any latitudinal skew from the equinox or from light level changes during post-fledgling habitat shifts. We defined migration departure as the date the mean location pathway

moved away from the centroid location without returning during the time periods when spring and fall migration are possible. Migration arrival was defined as the date at which daily movements in the mean pathway stopped advancing in a single direction and the mean pathway was within the breeding or wintering range. The spring landfall date after trans-gulf migration was calculated as the date the mean pathway entered the continental United States along the Texas or Louisiana Gulf Coast. Stopover duration was estimated for spring migration with time-spent maps created with the 'slice' function in package SGAT. We present stopover information for groups of individuals with averaged time-spent rasters created with the 'slice' function in package 'SGAT.'

Statistical analysis

We calculated rhumbline direction and great circle distance between breeding and overwintering centroids with package 'Geosphere' in program R (Hijmans et al. 2017). Using Pearson's correlations, we compared breeding and wintering latitudes and longitudes to examine structure in migratory connectivity at the population level. We used simple linear regression to compare wing chord with the duration and total distance of migration. The relationships between total migration distance, body mass, and all metrics of migratory timing including spring departure date, spring arrival date, fall departure date, fall arrival date, and duration of fall and spring migration were compared with Pearson's correlations. We used one-way ANOVAs to test for variation in mean spring migration initiation date, trans-gulf migration landfall date, and spring arrival date between yearling (birds hatched the previous summer and undertaking their first spring migration) and adult (after hatch year) individuals.

Finally, we tested for differences in seasonal timing of migration between years with one-way ANOVAs.

Results

Breeding and nonbreeding ranges

All 37 Golden-winged Warblers that we sampled overwintered in Central America and spent the breeding season in the western portion of the Great Lakes region, as expected for members of this linked population. Individuals captured at overwintering sites from Guatemala to northern Costa Rica occupied breeding areas throughout Minnesota, Wisconsin, and southern Ontario (Figure 4.1). Similarly, individuals originating from the breeding site at Rice Lake, Minnesota occupied overwintering sites from the Yucatan Peninsula, Mexico to southern Nicaragua as previously described by Kramer et al. (2017). Great-circle distance and direction between individual overwintering and breeding centroids were normally distributed with a mean distance of 3,472 km (293 km SD) and a mean direction of 351° (3.6° SD). Breeding latitude and longitude were not correlated with overwintering latitude (r=0.29, p=0.14) or longitude (r=0.22, p=0.29) respectively.

Migration pathways and stopovers

Of the 37 geolocators we analyzed, 35 recorded spring migration and 36 recorded fall migration. Individuals migrated south and crossed the Gulf of Mexico along a more easterly route in fall and migrated north along a more westerly route in spring (Figure 4.2). Overlap existed in fall and spring migration routes throughout the Mississippi River Valley and along the Louisiana and Alabama coasts. However, birds traveled

over Florida and Cuba exclusively during fall migration, while the western Gulf of Mexico was only used during spring migration. All birds crossed the Gulf of Mexico during fall migration. Of the 35 birds with recorded spring migrations, three individuals migrated along the eastern Mexico coastline with mean pathways occurring near or over land (Figure 4.3A), and 32 flew across the Gulf of Mexico (Figure 4.3B, C).

During spring migration, 69% of individuals made at least one prolonged stopover in Central America or southern Mexico before crossing the Gulf of Mexico. Duration of pre-Gulf stopovers varied from 3 to 12 days (mean 5 days, 2 SD). Pre-Gulf stopovers occurred to the west or northwest of individual overwintering sites, primarily in the region encompassing Guatemala and the states of Campeche and Chiapas, Mexico (Figure 4.3A, C). Twenty-three percent of individuals moved from overwintering sites to the Yucatan Peninsula and crossed the Gulf of Mexico without a multi-day refueling stopover (Figure 4.3B). These 'direct fliers' took on average 7 fewer days (mean 21 days, 4 SD) to reach the breeding grounds than individuals that did stop over south of the Gulf of Mexico (mean 28 days, 5 SD). All seven direct fliers overwintered in the northern and western half of the study region (Mexico, Guatemala, and western Honduras; Figure 4.3B). No birds that overwintered in eastern Honduras, Nicaragua, or Costa Rica crossed the Gulf of Mexico without a multi-day, pre-Gulf stopover (Figure 4.3C). Notably, only individuals with prior spring migration experience (i.e. after-hatch-year adults) crossed the Gulf of Mexico without undertaking a multi-day stopover.

After crossing or circumventing the Gulf of Mexico during spring migration,

all birds employed one or more additional multi-day stopovers within the United States. Stopovers occurred throughout the spring-migration pathway in the United States, which is closely aligned with the Mississippi Valley. However, birds that did not stop to refuel in Central America were more likely to stop over farther south, closer to the Gulf Coast (Figure 4.3B), whereas birds that made a multi-day stop in Guatemala and Mexico were more likely to continue to the central United States before stopping over again (Figure 4.3C). Due to uncertainty in latitudinal positions around the fall equinox, we did not attempt to define specific stopover locations during the fall migration.

Migration timing

Across years, mean departure from overwintering sites occurred on April 19 (6-day SD; range April 7 – May 5), with spring migration lasting an average of 27 days (6 SD; range = 16-39). Arrival at breeding sites ranged from May 6 to 26, averaging May 16 (5-day SD). In contrast, fall migration, which took an average of 49 days (10 SD), was nearly twice as long as spring and was more variable among individuals in duration (range 30 to 78 days). Across individuals, mean fall departure from breeding sites occurred on September 4 (9-day SD; range Aug 15 – Sept 15) and mean arrival at overwintering sites on October 23 (7-day SD; range Oct 7 – Nov 4). Spring departure date from overwintering sites was significantly correlated with arrival date on breeding grounds (r=0.56, P=0.003), but fall departure date from breeding sites did not correlate with arrival date on wintering grounds (r=0.25, P=0.219). Neither spring and fall departure dates (r=0.20, p=0.344) nor length of fall and spring migration (r=0.27,

p=0.194) were correlated between individuals. Spring migration length, departure

date, and arrival date of individuals were consistent between years, although the date

on which birds crossed the Gulf of Mexico varied significantly between years (Table

4.2). Conversely, all metrics describing the timing of fall migration varied

significantly among years and were highly variable among individuals in any given

year (Table 4.2).

Effect of morphology and experience on migration

Wing chord was strongly associated with the timing and duration of migration. Birds

with longer wings departed earlier from wintering areas, spent more days during

spring migration, and traveled longer distances than shorter-winged birds (Figure 4.5).

Without accounting for morphology, migration distance and duration were not

correlated (r=-0.08, p=0.687 in fall; r=0.28, p=0.158 in spring). Wing chord was not

correlated with weight of birds at time of capture (r=0.04, p=0.840), and weight was

not correlated with spring departure date (r=-0.06, p=0.753) or distance travelled

(r=0.18, p=0.378). Half of the 26 birds for whom we had age data were hatch-year

(HY) birds undertaking their first spring migration, and half were after hatch-year

(AHY) that had already completed at least one annual migration. Age was not

significantly related to spring departure date ($F_{(24)}$=0.146, P=0.706), post-gulf landfall

date ($F_{(24)}$=2.624, P=0.119), or spring arrival date ($F_{(24)}$=0.146, P=0.706; one-way

ANOVA); however, adults were significantly more likely to cross the Gulf of Mexico

without a multi-day stopover.

Discussion

The patterns of variation we found in migration timing among years, seasons, and individuals for male Golden-winged Warblers is consistent with intense selection for time-minimization during spring migration and reduced selection in the fall. Across three spring migrations, individuals departed Central America and arrived on the breeding grounds on approximately the same dates, though migratory pathway and stopover behavior varied among individuals. Surprisingly, birds crossing the Gulf of Mexico with or without a prior stopover and birds circumventing the Gulf through eastern Mexico all showed remarkable consistency in arrival time at breeding sites, suggesting that individuals compensated for varying conditions to ensure on-time arrival. Spring migration also proceeded at nearly twice the pace as fall migration and showed less individual variation in duration than in the fall. These patterns are consistent with those of a species under strong selection to arrive on the breeding grounds on an optimal date (Alerstam 2011). The strong relationship between departure and arrival date furthermore suggests that individuals travel at or near their physiological limit (McWilliams et al. 2004). Fall migration conversely showed no consistency in timing between years and no relationship between arrival and departure date, which suggests that the timing of overwinter territory establishment does not constrain fall migration. Optimal migration theory predicts that the population should have greater flexibility to minimize energy costs and avoid risks in the absence of time-minimization selection (Hedenström and Alerstam 1997, Alerstam 2011). As such, spring migration is likely to be more energetically costly and expose migrants to greater risk from starvation and predation than fall migration.

Our analysis of spring migration pathways revealed three patterns of movement and stopover behaviors employed by this linked population of Golden-winged Warblers. The pathway used by most individuals included a 3- to 12-day stopover in Guatemala or southern Mexico prior to crossing the Gulf of Mexico, followed by an additional stopover in the central United States. The importance of this previously unknown, pre-Gulf stopover is underscored by its adoption by all first-year birds and all individuals originating from the southern and eastern portions of the overwintering distribution. Furthermore, the fact that most individuals employing this migration pattern continued to the central United States before making a subsequent stopover suggests that individuals amassed more fuel at the pre-Gulf stopover than was needed to simply cross the geographic barrier. Optimal migration theory predicts that if selective pressures favor time minimization, then individuals should maximize fuel deposition at stopovers in accordance with the quality and availability of food (Hedenström and Alerstam 1997). The quality and availability of food in this stopover region should therefore directly impact the subsequent pace of migration for individuals, as was recently shown for another long-distance Neotropical migrant with similar migration constraints (Gómez et al. 2017).

Nearly one-quarter of individuals in our study were able to forgo a stopover prior to crossing the Gulf of Mexico, after moving directly to the Yucatan Coast from overwintering sites in northern Central America. Birds employing this behavior migrated on average seven days faster than birds that stopped before crossing the Gulf of Mexico, which may give them a competitive advantage in a time-minimizing migration system. As this strategy was only detected for birds that overwintered in the

northernmost extent of the winter range (Mexico, Guatemala, and Honduras), it is likely that birds overwintering further south are not physically capable of amassing sufficient fuel to both migrate to and cross the Gulf of Mexico. These direct fliers may have amassed greater fuel reserves at or near overwintering sites prior to departing on migration than individuals undertaking a pre-Gulf stopover. Because geolocators cannot detect changes in behavior associated with pre-migratory fuel accumulation if a bird remains relatively stationary, on-the-ground field studies will be necessary to understand in more detail how pre-migratory fuel deposition impacts subsequent stopover decisions (Bayly et al. 2018). As only after-hatch-year individuals employed this strategy, this decision or ability to forego a pre-Gulf stopover is likely linked to experience from previous migrations. The fact these individuals were more likely to stopover closer to the US Gulf Coast also suggests that they migrate across the Gulf with fewer fuel reserves than birds making a pre-Gulf stopover. This pattern further supports a time-minimizing spring migration strategy in which experienced individuals optimize speed at the expense of energetic safety while crossing a major geographic barrier.

Over the three years of our study, only three individuals migrated overland or along the coastline of the western Gulf of Mexico rather than flying directly across the Gulf. Given how rarely the overland/coastal strategy was used, we presume that trans-gulf migration is the optimal strategy for this population. Nevertheless, individuals taking a longer route around the western Gulf of Mexico arrived within the range of arrival dates for trans-Gulf migrants, suggesting that birds can compensate for varying conditions experienced in the southern part of their migration route. The demonstrated

variability in migratory pathway and stopover site selection within this population should increase resilience to climate change and habitat loss relative to populations where all individuals use a single stopover area or a single migration pathway (Charmantier and Gienapp 2014).

Although nearly all individuals crossed the Gulf of Mexico in spring migration, our data indicate strong annual variation in the dates on which birds crossed the Gulf of Mexico, despite high year-to-year consistency in spring departure and arrival dates. Migratory birds from Central America and the Caribbean are known to delay flights across the Gulf of Mexico by 2-3 days when spring conditions are dry (Cohen et al. 2015) or when weather conditions are unfavorable for sustained flight (Richardson 1990). Anecdotally, we noticed extremely dry conditions in the springs of both 2015 and 2016 related to the El Niño phenomenon, and in both years Golden-winged Warblers crossed the Gulf later than in 2014. Declines in rainfall at the end of the winter season can also affect both the departure date and annual survival of insectivorous migratory warblers (Faaborg et al. 1984, Rockwell et al. 2017), and migrants are known to make landfall after crossing the Gulf of Mexico with extremely depleted fat and muscle reserves in El Niño years (Paxton et al. 2014). Thus, weather conditions likely contributed to this intra-migratory route variation in spring migration. Interestingly, Golden-winged Warbler spring migration timing did not vary between HY and AHY individuals, despite differences in stopover behavior. This pattern contrasts to that of migrating Wood Thrush (*Hylocichla mustelina*), where HY individuals cross the Gulf of Mexico and arrive on the breeding grounds later than AHYs (McKinnon et al. 2014). We therefore suggest that the presence of age-structure

in migratory timing varies among Neotropical migratory landbird species.

Migratory behavior in many species is related to intraspecific variation in wing shape and length; long and pointed wings generally correspond to better energy efficiency in long-distance flights (Norberg 1995). Intraspecific variation in wing size predicts migration distance among populations for many species, in which long distance migratory populations have longer and more pointed wings than sedentary and short-distance migratory populations (Fitzpatrick 1998, Pérez-Tris and Tellería 2001, Arizaga et al. 2006). However, we know of no other study that demonstrates a relationship between wing length and migration distance within a single migratory population (but see Peiró 2003). Indeed, the strong relationship we found between male Golden-winged Warbler wing length and their migratory duration and distance is surprising given that we detected relatively little variation in total migration distance in this linked population. As only wing length predicted migratory distance, we suggest the range of possible migration distances depends on the amount of intraspecific variation in wing size within the population. However, it is necessary to emphasize that our entire sample was comprised of male individuals, which have longer wings than females (Pyle et al. 1987), and likely face greater pressure to arrive early on the breeding grounds (Cristol et al. 1999, Dierschke et al. 2005).

Ultimately, our findings call for focused conservation and further research of spring migration stopover regions for the Golden-winged Warbler. Within Mesoamerica, where the majority of Golden-winged Warblers overwinter (Rosenberg et al. 2016), additional conservation efforts should focus on the key, pre-Gulf stopover region we identified in southeastern Mexico and Guatemala. We recommend future,

on-the-ground research within that stopover region to add habitat-specific resolution to our knowledge of migratory resource requirements. Conserving stopover habitats within the United States may be less important, given that birds moved across wider geographic areas and showed more variability in stopover locations. However, habitat alteration and forest conversion are occurring at a landscape scale both in Central America and in the central United States (Hansen et al. 2013), and quality of migratory stopover habitat is likely to decline at that same scale. Broad approaches are therefore warranted to conserve suitable stopover habitat across these landscapes.

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Tables and Figures

Table 4.1. Number of light-level geolocators deployed on male Golden-winged Warblers, with deployment locations and the years in which data were recorded.

Site	Latitude	Longitude	Year Deployed	# Deployed	# in analysis
Cerro de La Muerte, Costa Rica	9.56	-83.79	2016	2	0
Monteverde, Costa Rica	10.26	-84.69	2016	20	1
Finca Esperanza Verde, Nicaragua	12.94	-85.78	2016	21	4
El Jaguar, Nicaragua	13.24	-86.05	2016	9	4
Catacamas, Honduras	13.78	-86.03	2016	27	5
Pico Pijol, Honduras	15.14	-87.44	2016	27	2
Sierra Caral, Guatemala	15.37	-88.67	2016	20	4
Mountain Pine Ridge, Belize	16.95	-88.82	2016	2	0
El Jaguar, Nicaragua[1]	13.24	-86.05	2015	NA	6
Rice Lake, Minnesota[2]	46.5	-93.33	2014	NA	3
Rice Lake, Minnesota[2]	46.5	-93.33	2013	NA	8

[1]Data from Larkin et al. 2017

[2]Data from Kramer et al. 2017

Table 4.2. Timing and duration of spring and fall migration among years.

	Spring Migration Year			
	2014 (n=9)	2015 (n=8)	2016 (n=20)	P
Spring Departure Date[1]	10 (6)	12 (6)	13 (7)	0.547
Trans Gulf Landfall Date[1]	20 (4)	27 (5)	24 (6)	0.041*
Spring Arrival Date[1]	38 (4)	39 (6)	40 (5)	0.635
Spring Migration Days	28 (9)	27 (5)	27 (5)	0.920

	Fall Migration Year				
	2013 (n=9)	2014 (n=2)	2015 (n=6)	2016 (n=20)	P
Fall Departure Date[2]	27 (5)	15 (21)	13 (11)	20 (6)	0.008*
Fall Arrival Date[2]	71 (7)	79 (1)	69 (6)	66 (7)	0.022*
Fall Migration Length[2]	44 (6)	64 (20)	56 (11)	46 (7)	0.004*

[1]Spring Dates presented as the mean (SD) number of days after first spring departure date, April 7th

[2]Fall dates presented as the mean (SD) number of days after first fall departure date, August 16th

*P significant at <0.05 in a one-way ANOVA test for difference across years.
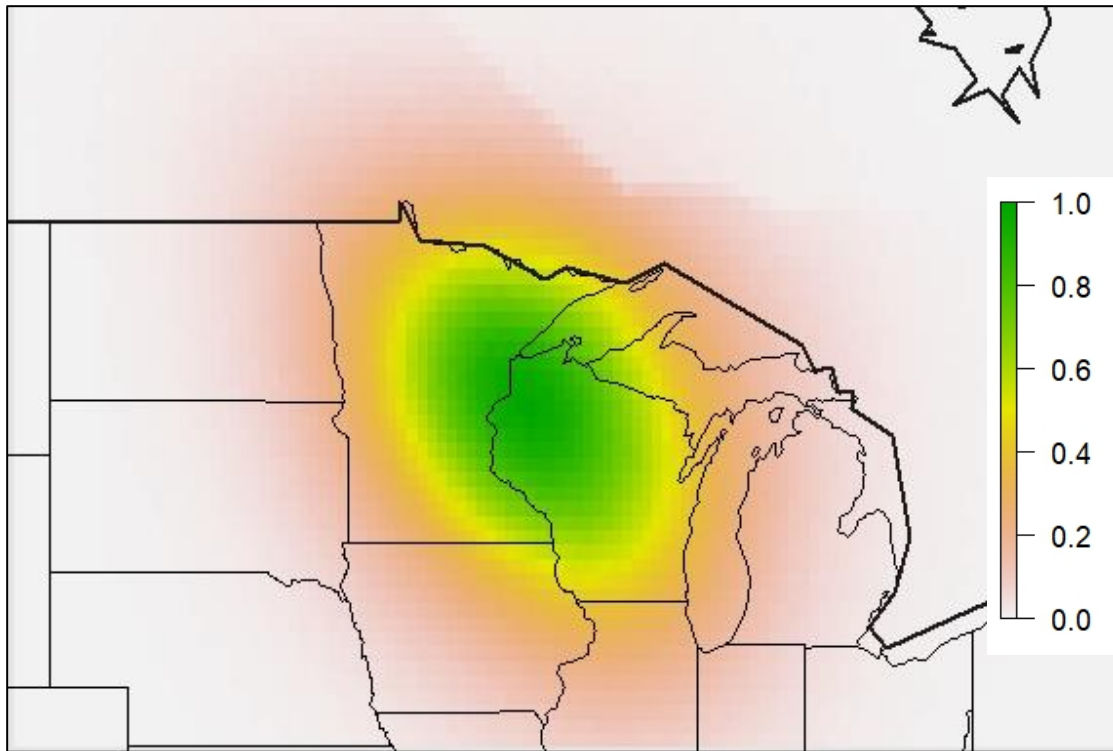
Figure 4.1. Average breeding site probability density distribution for 26 Golden-winged Warblers captured during the overwintering season in Central America.
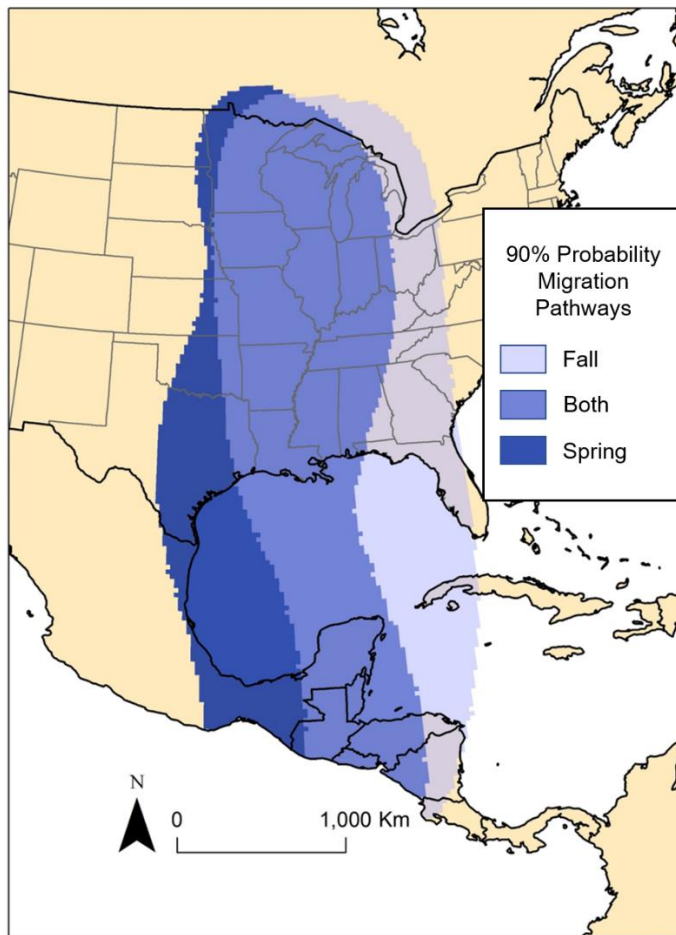
Figure 4.2. Averaged fall and spring migration pathways for 37 Golden-winged Warblers in the linked Great Lakes-Central America populations. Map projected in USA Contiguous Albers Equal Area Conic.
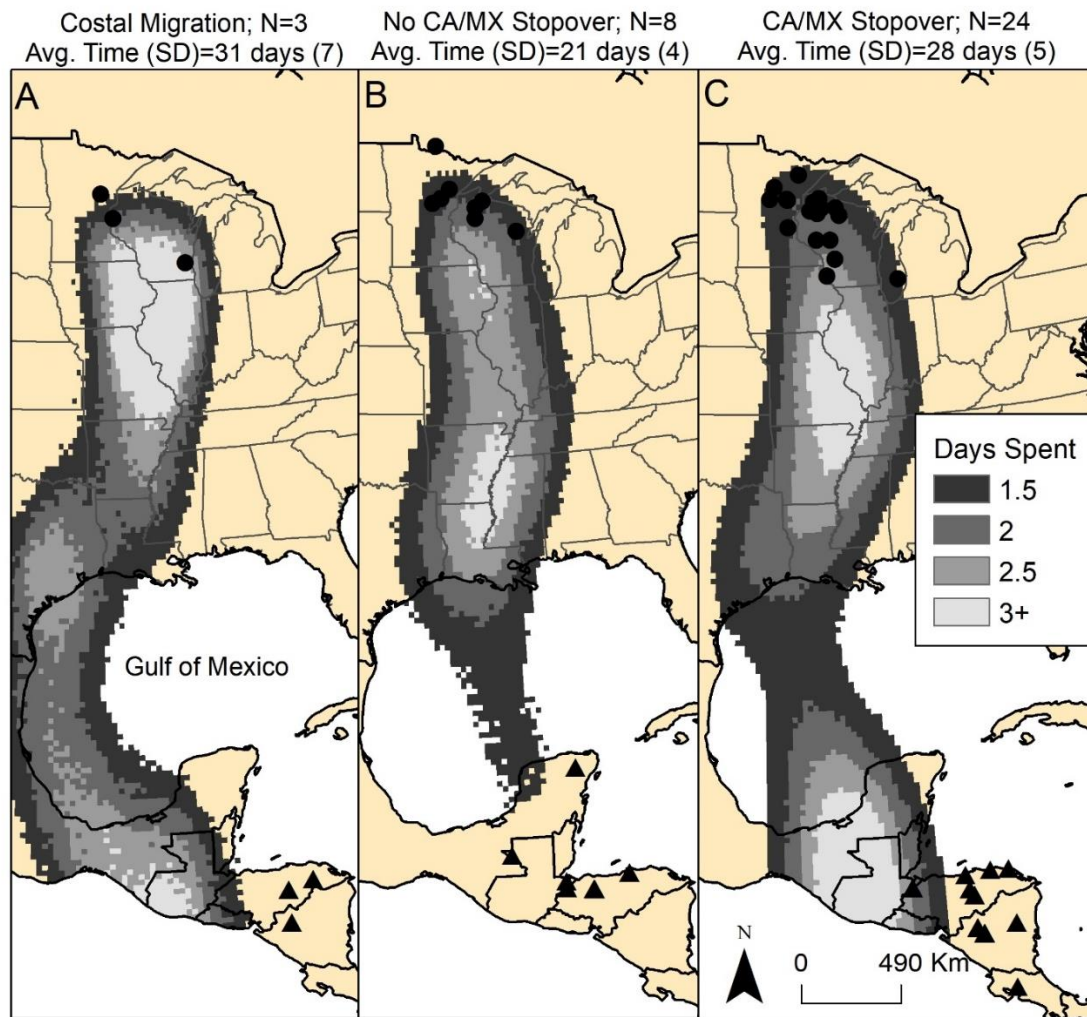
Figure 4.3. Patterns of spring stopover and movement behaviors exhibited by 35 individual Golden-winged Warblers after departing from overwintering sites in Central America. Migration pathways show the average number of days spent within the spring migration pathway for all individuals in the subgroup. A) 3 individuals traveled along the coastline of the western Gulf of Mexico after conducting a stopover in southern Mexico/Guatemala; B) 8 individuals crossed the Gulf of Mexico without conducting a stopover in Central America or Mexico; C) 24 individuals conducted a multi-day stopover in the region encompassing southern Mexico and Guatemala before flying across the Gulf of Mexico. Winter deployment or centroid locations shown as black triangles, and breeding deployment or centroid locations shown as black dots. Values below 1 day spent were truncated. Maps projected in USA Contiguous Albers Equal Area Conic.
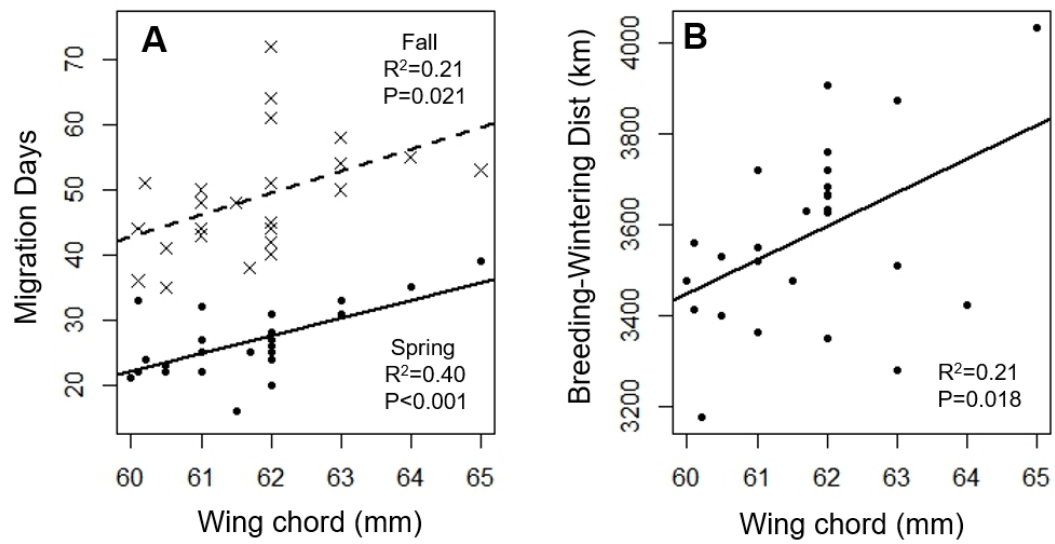
Figure 4.4. Linear models showing least-squares regression lines between wing chord and (A) number of days spent in fall migration (xs and dashed regression line) and spring migration (dots and solid line) and (B) great circle distance between breeding and wintering centroids.

CHAPTER 5

EXTREME GENETIC SIMILARITY DOES NOT PREDICT NONBREEDING

DISTRIBUTION OF TWO CLOSELY RELATED WARBLERS[1]

Abstract

Detailed knowledge of migratory connectivity can facilitate effective conservation of

Neotropical migratory birds by helping biologists understand where and when

populations may be most limited. We studied similarity in migratory behavior and

non-breeding distribution for two closely related migratory species of conservation

concern, the Golden-winged Warbler (*Vermivora chrysoptera*) and Blue-winged

Warbler (*V. cyanoptera*). While both species have undergone dynamic range shifts and

population changes attributed to habitat loss and social interactions promoting

competition and hybridization, full lifecycle conservation planning has been limited by

a lack of knowledge about their non-breeding ecology. Because recent work has

demonstrated the two species to be nearly identical genetically, we predicted that

individuals from a single breeding population would migrate and overwinter in similar

areas. In 2015, we placed light-level geolocators on 25 males of both species and

hybrids in an area of breeding sympatry at the Fort Drum Military Installation in

Jefferson and Lewis counties, New York. Despite extreme genetic similarity, returned

individuals differed in non-breeding location and duration of migration in accordance

with their genotype. Golden-winged Warblers (n=2) overwintered > 1900 km

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[1] This chapter is published in the Journal of Field Ornithology (Bennett. et al. 2017).

southeast of the nearest Blue-winged Warbler (n=3) and spent nearly twice as many days in migration, whereas hybrids (n=2) showed intermediate distributions and migratory timing. Spring migration departures were staggered based on distance from the breeding grounds, and all birds arrived at the breeding site within eight days of each other. Our results show that Golden-winged Warblers and Blue-winged Warblers from this mixed population retain species-specific non-breeding locations despite extreme genetic similarity, and suggest that non-breeding location and migratory timing vary along a genetic gradient. The threats to non-breeding habitat likely differ between the two species, and Golden-winged Warblers from this population may be inherently more vulnerable due to their longer migration.

Introduction

The study and conservation of Neotropical migratory landbirds are complicated by a lifecycle that includes annual migrations between ecologically and geographically distinct breeding and non-breeding areas (Rappole and McDonald 1994, Faaborg et al. 2010, Norris and Marra 2010). Our understanding of long-distance migratory birds throughout their full annual cycles has been impeded by technological limitations associated with tracking small birds over long distances. The recent advent of light-level geolocators allows researchers to map the annual movements of these migratory birds with greater precision than stable isotope analysis and for a greater number of individuals than traditional band-recovery studies (Stutchbury et al. 2009, Bridge et al. 2013, Hallworth et al. 2013). Additionally, geolocators can provide data about migration timing and pathways, allowing comparisons of the migratory strategies

within and across species. Understanding linkages between breeding and non-breeding populations is key to conservation efforts for long-distance migrants, given that populations may be limited in multiple, interacting phases of annual lifecycles (Rappole and McDonald 1994, Webster and Marra 2005, Faaborg et al. 2010).

Golden-winged Warblers (*Vermivora chrysoptera*) and closely related Blue-winged Warblers (*Vermivora cyanoptera*) are two long-distance, migratory species for which interspecific interactions and habitat loss, both in breeding and non-breeding areas, have resulted in dynamic range shifts and population changes (Rosenberg et al. 2016). Golden-winged Warblers have experienced a range-wide population decline of 2.65% per year since 1966, making it one of the most rapidly declining passerine species in North America (Sauer et al. 2014). Population trajectories vary regionally, with the most severe declines occurring in the Appalachians and northeastern United States, although the population appears to be stable in the northwestern part of the breeding range (Sauer et al. 2014, Rosenberg et al. 2016). Over the same time period, Blue-winged Warbler populations expanded into areas previously occupied by Golden-winged Warblers, although some populations have subsequently declined (Confer and Tupper 2000, Sauer et al. 2014). Declining populations of Golden-winged Warblers have been partially attributed to competition and hybridization with Blue-winged Warblers, especially in regions where the two species now have extensive range overlap and share similar habitats (Murray and Gill 1976, Confer and Larkin 1998, Gill 2004, Wood et al. 2016). The distributional changes have created a complex and dynamic mosaic, with some breeding populations remaining allopatric, others transitioning to sympatry, and hybridization and genetic introgression occurring in

sympatric breeding areas (Shapiro et al. 2004, Rosenberg et al. 2016). In many areas of breeding sympatry, abundance of Blue-winged Warblers has increased over time while Golden-winged Warblers have declined or reached extirpation (Confer et al. 1991, Gill et al. 2001, Cadman et al. 2007, Patton et al. 2010). This shift from occupancy by Golden-winged Warblers to Blue-winged Warblers in many sympatric breeding populations corresponds with a northward shift in the breeding ranges of both species (Rosenberg et al. 2016).

Golden-winged Warblers exhibit structure in their migratory connectivity (Hobson et al. 2016, Kramar et al. 2017) and maintain stationary, non-overlapping territories between ~1 November and 15 March (hereafter, the overwintering period), primarily in mid-elevation, humid ecosystems from Guatemala to Colombia and Venezuela (Chandler 2011, Rosenberg et al. 2016). Blue-winged Warblers overwinter primarily in southern Mexico and the Caribbean lowlands of northern Central America (Gill et al. 2001a). Overwintering sympatry occurs from southern Mexico to Panama, although Golden-winged Warblers become rare in northern Guatemala, the Yucatan, and Belize whereas Blue-winged Warblers become rare in southern Nicaragua, Costa Rica, and Panama (Gill et al. 2001, Rosenberg et al. 2016). Rosenberg et al. (2016) hypothesized that as the breeding range of Golden-winged Warblers shifts northward, the non-breeding range is simultaneously shifting northward, potentially increasing the range overlap with non-breeding Blue-winged Warblers and facilitating interspecific interactions. Identifying the linkages of both species between their breeding and non-breeding ranges is critical to untangling these potential interactions.

The conservation implications of these population changes are complicated by

an unusually close genetic relationship between the two currently recognized species (American Ornithologist's Union, 1998). Toews et al. (2016) found that the two species differ across a mere six regions of the nuclear genome, corresponding primarily to plumage traits, and suggesting high levels of gene flow and a long history of admixture. Current conservation efforts focused on Golden-winged Warblers will depend on a greater understanding of the biology of both species, particularly factors that might be important in maintaining species-specific differences or promoting hybridization (Vallender et. al 2016).

We used light-level geolocators to compare migration strategies and overwintering locations of male Golden-winged Warblers, Blue-winged Warblers, and their hybrids in an area of sympatry and active hybridization at the northeastern edge of their breeding distribution. Specifically, we sought to determine whether close sympatry and genetic mixing on the breeding grounds results in strong migratory connectivity across a mixed population, or whether birds exhibiting phenotypic and genetic characteristics of Golden-winged and Blue-winged warblers would show species-specific non-breeding behavior. Given their extreme genetic similarity and documented similarities in breeding and overwintering ecology (Bennett 2012, Wood et al. 2016), we predicted that Golden-winged and Blue-winged warblers originating from a single breeding location would have similar migratory timing and overwintering locations.

Methods

Our research was conducted at the 43,400-ha Fort Drum Military Installation in Jefferson and Lewis counties, New York (-75.7115, 44.0701, Fig. 1). Fort Drum is

located within the active contact zone between Golden-winged and Blue-winged

Warblers and is the site of recent habitat (Wood et al. 2016) and genetic (Toews et al.

2016) studies for both species. Anecdotal evidence suggests Golden-winged Warblers

established a population in the area around Fort Drum between 1960 and 1980

whereas Blue-winged Warblers arrived in the late 1980s (McGowan and Corwin 2008,

Rosenberg et al. 2016). Fort Drum biologists have conducted standardized point-count

surveys since 2008 for Golden-winged and Blue-winged warblers, documenting a

consistent increase in Blue-winged Warbler abundance relative to Golden-winged

Warblers and a continuous presence of phenotypic hybrids (Fig. 1, Bolsinger, unpubl.

data).

Field methods

We attached stalkless geolocators (ML6040, BioTrack, Wareham, UK) to 10 male

Golden-winged Warblers, 10 male Blue-winged Warblers, and five male phenotypic

hybrids during May and June 2015. All birds were captured in a 14 x 7.5 km area at

the Fort Drum Military Installation. Birds were selected for capture where a Golden-

winged and Blue-winged warbler and sometimes a hybrid occupied territories within

200 m of each other to minimize any potential impact of habitat on the comparison of

migratory movements. We captured birds using mist nets and call broadcasts and fitted

them with a U. S. Geological Survey aluminum band and a color band to aid in re-

sighting. We used the modified Rappole and Tipton (1970) leg-loop harness described

in Streby et al. (2015) to attach geolocators. Previous studies have revealed no

negative consequences of this particular attachment method and unit weight on annual

survival of Golden-winged Warblers (Peterson et al. 2015). Geolocators sampled

available ambient light on an arbitrary 0-64 scale every minute and recorded

maximum light every 2 min either for the life of the unit or until we downloaded the

data. In May and June 2016, we conducted an intensive search of the study area to

locate birds with geolocators that had returned to their former breeding territories. All

territories and areas within a 500-m radius of initial capture locations were searched at

least three times. We collected ~10 μL of blood from the brachial artery of each

recaptured bird and immediately transferred samples to a lysis-buffer tube to preserve

it for genetic analysis.

Geolocator analysis

Light-level data from the geolocators were downloaded and decompressed using

BASTrack software and processed in a Baysian framework with package 'SGAT'

version 3.3.0 (Wootherspoon et al. 2016) in program R (R Core Team 2016). We used

a light-level threshold of 1.5 to define twilight transition times and performed minimal

editing of twilight values (<4 alterations per unit) to fix extreme outliers and days

without a defined twilight. We calibrated each geolocator for the time period between

deployment and 31 July 2015 (34-39 days), conservatively estimating the known

stationary breeding period of Golden-winged and Blue-winged warblers. Following

the methods of Yamaura et al. (2016), we calculated the average solar zenith angle at

twilight and a log-normal density distribution of twilight errors during the calibration

period. Because the solar angle recorded by geolocators has been found to vary among

habitat types and between breeding and non-breeding areas (Stutchbury 2013,

McKinnon et al. 2015), we compared our average calibration zenith angle to the angle

recorded on five ML6040 geolocators placed on overwintering Golden-winged

Warblers in Jinotega, Nicaragua, in January 2015. The mean calibration zenith angle of the five Nicaragua geolocators was only 0.5° greater than the mean calibration angle of our geolocators and fell within the range of the individual calibration zeniths. We therefore found no justification to alter the zenith angle by season and used the breeding area calibration zenith to approximate latitude and longitude positions for the entire recording period. With the 'estellemetroplis' function that uses Baysian Markov Chain Monte Carlo (MCMC) in package 'SGAT,' we refined the location data for each unit with simulations that used a twilight model incorporating the calibration twilight error distribution and a movement parameter that assumes birds are normally stationary but move large distances when they do move (gamma distribution with shape = 0.7 and scale = 0.08). These warblers may cross the Gulf of Mexico during fall and spring migration, but only occur on land during the rest of their annual cycle, so we constrained the models with a land mask for all birds overwintering on the mainland of Central and South America in which probability of locations occurring on land was four times greater than over water. We chose unconstrained models for two birds that wintered in the Caribbean region because land mask models failed to provide biologically feasible overwinter locations for birds wintering on islands (i.e., modeled locations move between adjacent islands and mainland features over large water distances). To refine location estimates from each geolocator, we ran one chain with 70,000 iterations with a burn-in of 20,000. We drew three chains of the final 5000 iterations for analysis and visually inspected model convergence by plotting the mean value of each chain against the 2.5% and 97.5% CI for each day. Model convergence was high for all days outside the equinox periods. For all birds, we define

overwintering locations as the location with highest probability of occurrence between 1 November 2015 and 15 March 2016, calculated using the 'slice' function in 'SGAT'. The posterior probability distribution of one model placed the overwintering location of a Blue-winged Warbler in the Gulf of Mexico, 240 km north of Cuba. We assigned the overwinter location for that individual to the landmass closest to the modeled location, given the biological impossibility of overwintering over open water, and as a southward movement of this location does not change any of our central results. We calculated all distances presented in this paper using great circle distance on a WGS84 spheroid.

Dates of migration were determined by plotting a local regression (LOESS) of the modeled latitude and longitude by day with a smoothing parameter (1/20) that captured all major fluctuations in the location data. We then plotted the absolute value of the slope of the LOESS to identify movement peaks. Background variation in the slope values during known stationary periods reached a maximum of 0.27 for longitude and 0.4 for latitude (excluding outliers and the equinox periods), which we used as the threshold values to determine migration movements. Arrival and departure dates were first determined using the longitude data, which are precise even around equinox periods. We assigned fall and spring departure date to the first date with a slope value ≥ 0.27 followed by a movement peak, defined as a ten day minimum period with a mean slope of ≥ 0.27. We assigned arrival date to the last date of a movement peak with a slope value ≥ 0.27 followed by a 10-day period with a mean slope ≤ 0.27. These dates were then compared to the slopes of the latitude data for dates not within 15 days of an equinox and adjusted to include additional migration

dates using the same method described for longitude, but with a threshold value of 0.4.

All birds migrated during the fall equinox, so only longitude was used to estimate

arrival and departure dates for fall migration, which may underreport the number of

migration dates for birds that migrated straight south or north. Both latitude and

longitude were used to determine spring arrival and departure dates. The

'changeLight' function in package 'GeoLight' has been used in other studies to

determine movement periods (Lisovski et al. 2012, Yamaura et al. 2016), but failed to

differentiate obvious migration movements from known stationary periods with our

data.

Genetic analysis

The Fuller Evolutionary Biology Lab at Cornell University conducted restriction

fragment length polymorphism (RFLP) assays for the six loci identified by Toews et

al. (2016) to have strong differentiation between Golden-winged and Blue-winged

Warblers. They used the primers and enzyme digests developed and fully described in

Toews et al. (2016, Supplemental Information p. 17), visualized the results in a 2%

agarose gel, and recorded the number of Blue-winged Warbler alleles at each of the

six loci (0 for homozygous Golden-winged Warbler to 12 for homozygous Blue-

winged Warbler). The same study showed that nearly all phenotypically pure warblers

have ≤3 alleles of the other species. We therefore consider all birds with Blue-winged

Warbler alleles at 4/12 (0.34) to 8/12 (0.67) loci to be genetic hybrids. Not all alleles

are linked to known phenotypic traits, and we therefore do not attempt to link

phenotype and genotype in this paper. Proportion of Blue-winged Warbler alleles was

compared to overwintering location and number of days spent in migration using

linear regression in R (R Core Team 2016). Values are presented as means ± 1 SD.

Results

During May-June 2016, we recovered geolocators from eight of 25 warblers (32%) captured the previous year of which seven contained useable data (two Golden-wing Warblers, four Blue-winged Warblers, and one Blue-winged Warbler with yellow wing bars suggesting an introgressed hybrid). Genetic scores indicated that the two Golden-winged Warblers and three of the four Blue-winged Warblers were genetically pure individuals, with > 80% genetic similarity to homozygous genotypes, whereas one phenotypic Blue-winged Warbler and the introgressed hybrid had a mixture of alleles (50-67% Blue-winged Warbler) from both species (Table 1). We classify both of these birds as genetic hybrids for the remainder of the results and discussion.

Winter locations

Both Golden-winged Warblers overwintered in northern Colombia, near the southern limit of their known non-breeding range, and well outside of the non-breeding range of Blue-winged Warblers (Fig. 2). The Blue-winged Warblers overwintered in the Yucatan Peninsula of Mexico and the western tip of Cuba, and the genetic hybrids overwintered in the western tip of Cuba and north-central Nicaragua. The smallest great-circle distance between overwintering locations of Blue-winged and Golden-winged Warblers was 1968 km as measured from the centroids of the 80% probability polygons for both species. Latitude and longitude of overwinter location was significantly correlated with genetic composition at the six differentiated loci (Fig. 3C, D), with an increasing proportion of Blue-winged Warbler alleles predicting more

northerly and westerly overwintering locations.

Migration strategies

The two Golden-winged Warblers spent nearly twice as much time migrating both in fall ($\bar{x} = 57 \pm 12$ days) and spring ($\bar{x} = 54 \pm 1$ days) as the Blue-winged Warblers ($\bar{x} = 33 \pm 5$ days fall, $\bar{x} = 33 \pm 10$ days spring) and genetic hybrids ($\bar{x} = 30 \pm 21$ days fall, $\bar{x} = 32 \pm 1$ days spring). Individuals varied in the duration of migration, with a range of 46 to 119 days spent in both fall and spring migrations. Despite this variation, all birds arrived on the breeding grounds within an eight-day period (Fig. 4A). The consistency in arrival dates to the breeding grounds can be attributed to staggered departures from winter locations, with the most distant Golden-winged Warblers in Colombia departing on average of 19 ± 11 days earlier than the Blue-winged Warblers and hybrids that wintered in Mesoamerica. The number of days spent in spring migration correlates significantly with the genetic composition of birds, whereas the number of days spent in fall migration showed a similar, but non-significant, trend (Fig. 3A, B). All birds migrated south during the fall equinox, when latitude cannot reliably be estimated. However, longitudinal data show that all but one bird crossed the Gulf of Mexico along a more easterly route in the fall and a more westerly route in the spring (Fig. 4B).

Discussion

Our results show that individual Golden-winged Warblers, Blue-winged Warblers, and hybrids from a sympatric and hybridizing breeding population differed in overwintering locations and migratory durations consistent with their genotypes. The

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two Golden-winged Warblers migrated to areas well outside the overwintering range of Blue-winged Warblers, whereas the three Blue-winged Warblers migrated to areas where Golden-winged Warblers are rare or absent during the overwintering period (Fig. 2). All locations except Cuba fell within the expected overwintering distributions of each species. Blue-winged Warblers have previously been described as rare winter migrants in Cuba, though the western part of Cuba is data poor and multiple overwintering Blue-winged Warblers have been documented recently in the region through eBird, while Golden-winged Warblers are not known to overwinter there (Gill et al. 2001, Raffaele et al. 2003, eBird 2016). The observed pattern of more eastward fall migration and more westward spring migration is consistent with the loop migration that has been documented to occur regularly in many species of trans-gulf Neotropical migrants, following seasonal changes in prevailing winds (La Sorte et al. 2014).

The tight correlation between longitude and genetic composition is consistent with studies showing that migratory behavior, including orientation and distance, is heritable in passerines (Helbig 1996, Pulido and Berthold 2003, Winger et al. 2011, Delmore et al. 2016). These results are fascinating in light of the recent studies showing that Golden-winged and Blue-winged warblers share 99.55% of the nuclear genome, with only six regions of differentiation that correspond primarily to plumage traits (Toews et al. 2016). If the genetic differences between the two species only corresponded to plumage traits (sensu Toews et al. 2016), convergent migratory behavior of individuals that breed sympatrically would be expected, given the heritability of migratory orientation and pathways (Helbig 1996, Delmore et al. 2016).

Our results, although based on a small sample size, suggest the opposite, i.e., that the direction and duration of migration of the two species in our study population, especially longitudinal orientation, is structured along a genetic gradient.

Understanding the migratory connectivity of the *Vermivora* species complex is critical to understanding how non-breeding forces, such as directional interspecific competition or the loss of non-breeding habitat, may contribute to the population trajectories of both species. A recent stable isotope analysis showed that Golden-winged Warblers maintain considerable structure in their migratory connectivity, with breeding origins differing significantly among populations overwintering in western Honduras, eastern Honduras, Nicaragua and Costa Rica, and Colombia and Venezuela (Hobson et al. 2016). Using geolocators, Kramer et al. (2017) confirmed strong migratory connectivity for Golden-winged Warblers, with no overlap in overwinter location between birds originating from isolated breeding populations. The maximum distance reported between overwintering Golden-winged Warblers originating from a single breeding population was ~1000 km ($N = 12$ individuals from the breeding population, Kramer et al. 2017). Central Costa Rica, located 1000 km from the overwintering locations of Golden-winged Warblers in our study, is at the southeastern edge of the overwintering range of Blue-winged Warblers and where Blue-winged Warblers are documented to be rare (Stiles and Skutch 1989). This suggests that overwintering individuals of Blue-winged Warblers from our Fort Drum population would be unlikely to encounter overwintering Golden-winged Warblers from the same population, with both likely maintaining allopatric non-breeding distributions.

Allopatric non-breeding distributions and migratory pathways are common for subspecies of birds separated on the breeding grounds by narrow geographic divides, formed by refugia populations that expanded northward after the last glacial retreat (Møller et al. 2011, Delmore et al. 2102). Although Blue-winged and Golden-winged warblers in the Fort Drum population are no longer separated geographically, the probable retention of allopatric overwintering locations and migratory duration is reminiscent of the migratory divides documented for subspecies of Swainson's Thrushes (*Catharus ustulatus*) and Blackcaps (*Sylvia atricapilla*). These species have narrowly separated populations with unique migratory distances and directions and narrow zones of hybridization. For both species, hybrids exhibit intermediate migratory orientation, and hybrid Swainson's Thrushes migrate through intermediate pathways to intermediate overwintering locations (Helbig 1996, Delmore and Irwin 2014). Although our sample size is small, our results suggest that Golden-winged Warbler and Blue-winged Warbler hybrids have intermediate overwintering locations, spring departure dates, and durations of spring migration. This type of variation in non-breeding ecology of these two species and hybrids, which also includes subtle differences in timing and extent of molt (Dunn and Garrett 1997, Gill et al. 2001, Confer et al. 2011), may reflect retained genetic differences despite the remarkably similar genomes of Golden-winged and Blue-winged warblers in the Fort Drum breeding population.

Given the demonstrated effects of non-breeding events and habitat quality on survivorship and future reproductive success, differences in overwintering locations and migration duration can potentially impact Golden-winged and Blue-winged

warblers from this population in different ways (Marra and Holmes 2001, Newton 2004, Norris 2005). Loss of the non-breeding habitat of Golden-winged Warblers due to land-use conversion is an ongoing threat throughout their non-breeding range (Bennett et al. 2016, King et al. 2016). Golden-winged Warblers overwintering in Colombia likely experience different threats and land-use changes than Blue-winged Warblers and hybrids overwintering in Mesoamerica. The difference between the two species in the duration of migration could also impact this population in a species-specific manner because migration can be a limiting factor during the full annual cycle of a migratory species (Sillett and Holmes 2002, Newton 2006). If the migratory period is limiting for these species, Golden-winged Warblers from the Fort Drum population may be more vulnerable to population declines than Blue-winged Warblers, because they spend almost twice as many days migrating. We recommend future work to increase the sample size of both species and hybrids from other sympatric breeding populations to test the generalizability of our results. Additionally, full, annual life-cycle models and detailed habitat and demographic studies on the winter range are needed to determine how and when non-breeding events impact each species (Hostetler et al. 2015). Conserving both Golden-winged and Blue-winged warblers, as well as their ongoing dynamic evolutionary process, will require a greater understanding of the year-round dynamics and behavioral interactions of individuals from both sympatric and allopatric populations throughout their annual cycles.

Acknowledgments

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Tables and Figures

Table 5.1. Proportion of Blue-winged Warbler (BWWA) alleles at the six loci with species-specific differences and overwintering location for all birds with recovered geolocator data.

Phenotype	Proportion BWWA alleles	Overwinter Location
BWWA	0.92	Mexico
BWWA	0.92	Cuba
BWWA	0.83	Mexico
BWWA	0.67	Nicaragua
Introgressed BWWA	0.50	Cuba
GWWA	0.17	Colombia
GWWA	0.08	Colombia
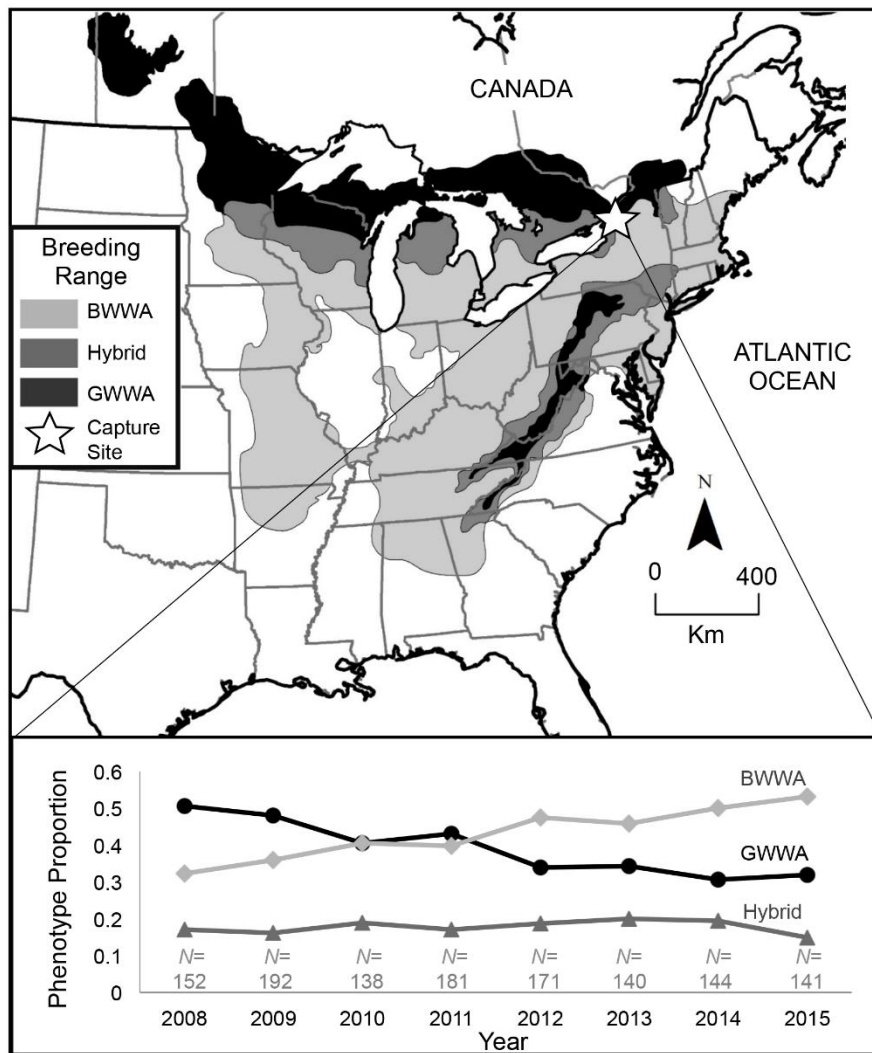
Figure 5.1. Location of capture site at Fort Drum Military Instillation in New York showing a consistent increase of the Blue-winged Warbler (BWWA) phenotype at that site since the year 2008, with the total number of these two species and hybrids observed each year in gray. Base map shows the breeding ranges of Golden-winged Warblers (GWWA) and BWWA, including zones where they regularly hybridize (derived from Toews et al. 2016). Map projected in USA Contiguous Albers Equal Area Conic.
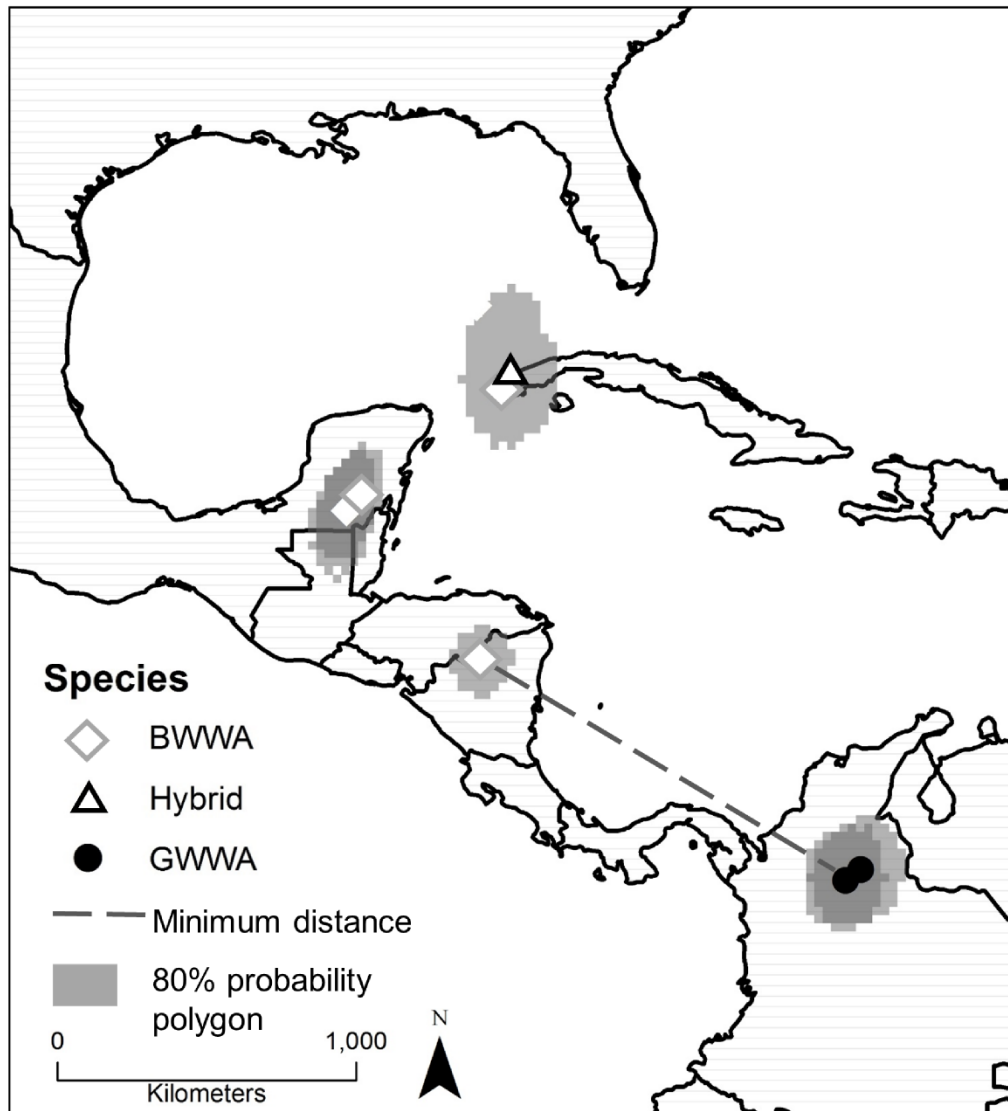
Figure 5.2. Locations for all recovered Golden-winged Warblers (GWWA), Blue-winged Warblers (BWWA), and genetic hybrids between 1 November 2015 and 15 March 2016 with 80% probability polygons around all locations except for the BWWA on the western tip of Cuba, whose location was estimated as the closest landmass to the highest probability location. Base map shows the wintering ranges of Blue-winged Warblers (derived from Gill et al. 2001) and Golden-winged Warblers (derived from Rosenberg et al. 2016). Map projected in USA Contiguous Albers Equal Area Conic.
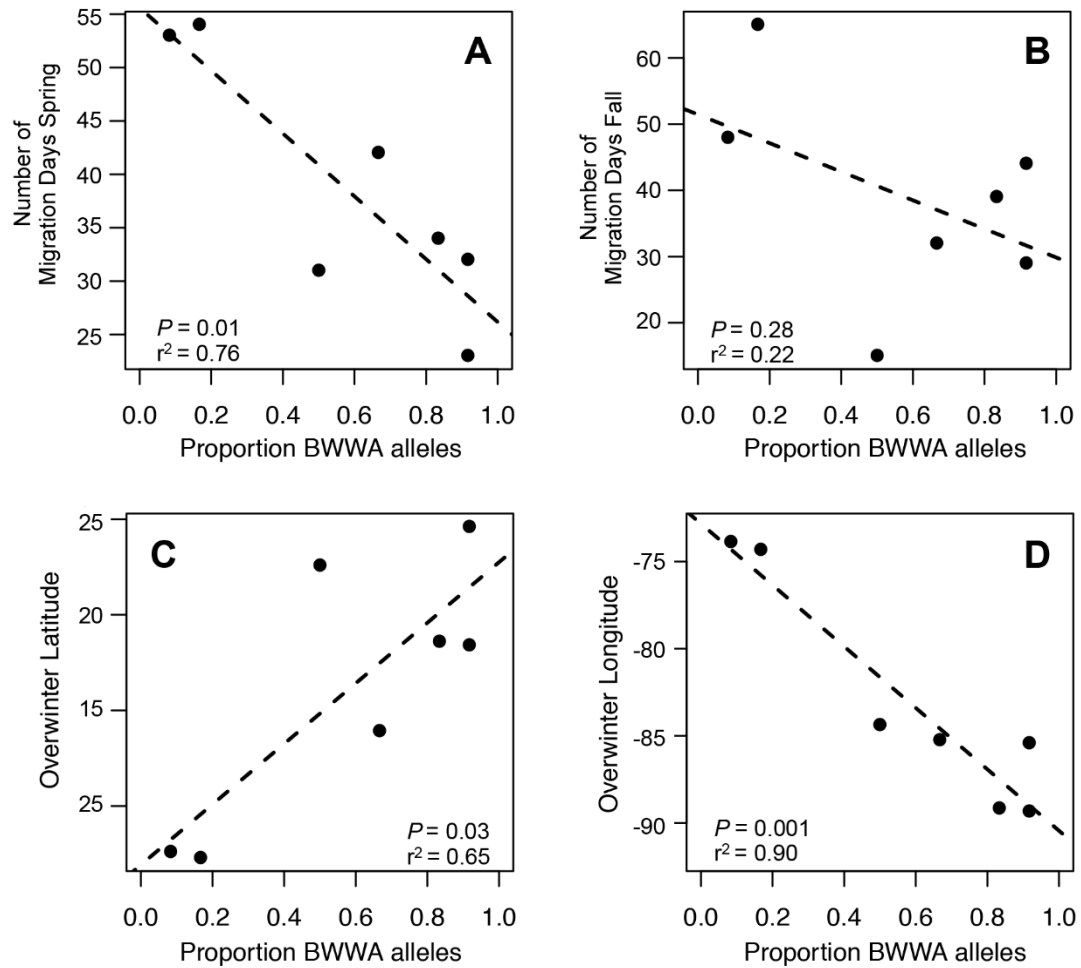
Figure 5.3. Linear models showing least squares regression line comparing the proportion of Blue-winged Warbler (BWWA) alleles at six species-differentiated loci with the number of days spent in spring (A) and fall (B) migration and the latitude (C) and longitude (D) of the overwinter location of all returned birds.
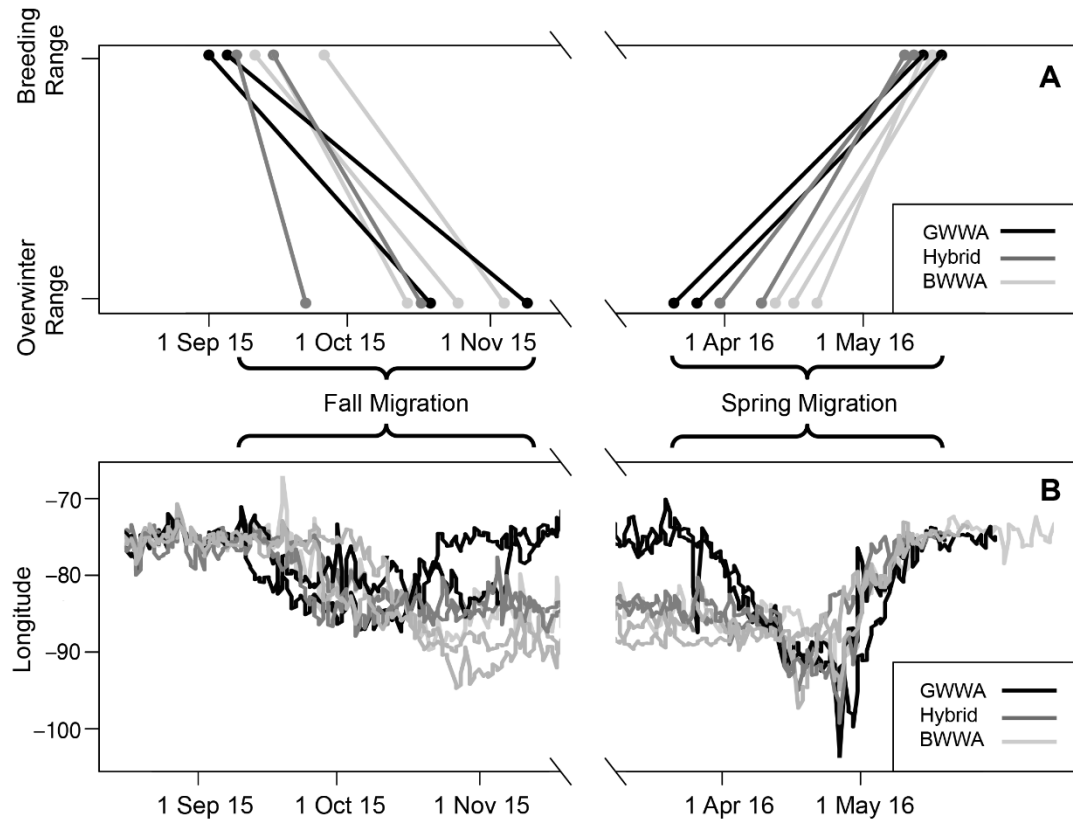
Figure 5.4. Migration duration with arrival and departure dates (A) and longitude (B) during fall and spring migration of all returned birds (GWWA, Golden-winged Warbler; BWWA, Blue-winged Warbler).

CHAPTER 2 APPENDIX

This appendix contains a summary of the data that was analyzed in Chapter 2 with the following elements:

- Table 2A: Review of nonbreeding conservation planning efforts and sexual segregation in 66 North American migratory bird species of conservation concern

- References for Table 2A

- Table 2B: Male and female detections by region

- Table 2C: Summary statistics of habitat covariates by region

- Figure 2A: Map of all points surveyed by region

Table 2A. Review of nonbreeding conservation planning efforts and sexual segregation in 66 North American migratory bird species of conservation concern

Species	Partner's in Flight Status	Plumage Dimorphism	Nonbreeding Sex Segregation	Nonbreeding SDM	Sex-specific SDM	Nonbreeding conservation recommendations	Sex specific conservation recommendations	References
American Tree Sparrow *Spizella arborea*	CSD	N	U	Y	N	Y	N	National Audubon Society 2010, Hovick et al. 2014, Naugler et al 2017, Tanner et al. 2017
Bachman's Sparrow *Peucaea aestivalis*	R	N	U	Y	N	Y	N	Liu et al. 1995, National Audubon Society 2010, Brooks and Stouffer 2011, Korosy et al. 2013, Taillie et al. 2015
Baird's Sparrow *Ammodramus bairdii*	Y	N	I	Y	N	Y	N	Gordon 2000a, Gordon 2000b, Merola-Zwartjes 2005, Wiggins 2006, Martínez-Guerrero et al. 2011
Band-tailed Pigeon *Patagioenas fasciata*	Y	N	U	N	N	Y	N	Marcot 1984, Keppie and Braun 2000
Bank Swallow *Riparia riparia*	CSD	N	U	N	N	N	N	Garrison 1998, Garrison 1999
Bendire's Thrasher *Toxostoma bendirei*	R	N	U	N	N	N	N	England and Laudenslayer 1993
Bicknell's Thrush *Catharus bicknelli*	R	N	Y	Y	N	Y	Y	IBTCG 2010, IBTCG and BCPWG 2011, Townsend et al 2011, Timyan et al. 2012, Townsend et al. 2012, McFarland et al. 2013, McFarland et al. 2018
Black Rosy Finch *Leucosticte atrata*	R	Y	I	N	N	Y	N	French 1959, King and Wales 1964, GBBO 2010
Black Swift *Cypseloides niger*	Y	N	U	N	N	N	N	Lowther and Collins 2002
Black-billed Cuckoo *Coccyzus erythropthalmus*	Y	N	U	N	N	N	N	Hughes 2018
Black-capped Vireo *Vireo atricapilla*	R	Y	Y/I	Y	N	Y	Y	USFWS 1991, USFWS 2007b, Wilkins et al. 2006, USFWS 2018, Rivera et al. 2011, Powell 2013, Colon et al. 2015,
Blackpoll Warbler *Setophaga striata*	CSD	Y	U	N	N	N	N	DeLuca et al. 2013

Species								References
Bobolink *Dolichonyx oryzivorus*	Y	Y	U	N	N	Y	N	Bollinger and Gavin 1989, Di Giacomo et al. 2002, Lopez-Lanus et al. 2007, Renfrew and Saavedra 2007
Brewer's Blackbird *Euphagus cyanocephalus*	CSD	Y	U	N	N	N	N	Martin 2002
Brown-capped Rosy Finch *Leucosticte australis*	R	Y	I	N	N	N	N	King and Wales 1964, National Audubon Society 2010
Canada Warbler *Cardellina canadensis*	Y	Y	Y	Y	N	Y	N	COSEWIC 2008, McDermott and Rodewald 2014, Bayly and Gonzales 2015, Environment Canada 2016a, eBird 2017
Cape May Warbler *Setophaga tigrina*	Y	Y	Y	N	N	N	N	Russell 1981, Latta and Faaborg 2002, Cooper and Beauchesne 2004
Cassin's Finch *Haemorhous cassinii*	Y	Y	Y	Y	N	N	N	Samson 1977, Hahn 1996, National Audubon Society 2010
Cerulean Warbler *Setophaga cerulea*	Y	Y	I	Y	N	Y	N	Hamel 2000, USFWS 2007a, Colorado et al 2008, Bakermans et al. 2009, COSEWIC 2010, Fundacion ProAves 2010, Colorado et al. 2012, Dawson et al. 2012, Muñoz and Colorado 2012, Skolnik et al. 2012
Chestnut-collared Longspur *Calcarius ornatus*	Y	Y	U	Y	N	Y	N	Sedgwick 2004
Chimeny Swift *Chaetura pelagica*	CSD	N	U	N	N	N	N	COSEWIC 2007a, Steeves et al. 2014
Chuck-wills-widow *Antrostomus carolinensis*	CSD	Y	U	N	N	N	N	Straight and Cooper 2012
Colima Warbler *Oreothlypis crissalis*	Y	N	U	N	N	N	N	Lanning et al. 1990, Beason and Wauer 2013
Common Grackle *Quiscalus quiscula*	CSD	Y	Y	Y	N	N	N	Dolbeer et al. 1978, Dolbeer 1982, Peer and Bollinger 1997, National Audubon Society 2010
Common Nighthawk *Chordeiles minor*	CSD	N	U	N	N	Y	N	COSEWIC 2007b, Brigham et al. 2011, Environment Canada 2016b
Connecticut Warbler *Oporornis agilis*	Y	Y	U	N	N	N	N	Pitocchelli et al. 2012
Eastern Meadowlark *Sturnella magna*	CSD	N	U	N	N	Y	N	Baker and Guthery 1990, Bock and Bock 1999, Igl and Ballard 1999

Eastern Whip-poor-will *Caprimulgus vociferus*	Y	Y	U	N	N	N	N	Environment Canada 2015, Cink et al. 2017
Evening Grosbeak *Coccothraustes vespertinus*	Y	Y	Y	Y	N	N	N	Prescott 1991, Prescott 1992, Bonter and Harvey 2008
Field Sparrow *Spizella pusilla*	CSD	N	U	Y	N	N	N	Carey et al. 2008, Monahan and Hijmans 2008
Flammulated Owl *Psiloscops flammeolus*	Y	N	U	N	N	N	N	Linkart and McCallum 2013
Golden-cheeked Warbler *Setophaga chrysoparia*	R	Y	Y/I	Y	N	Y	N	USFWS 1992, Vidal et al. 1994, Rappole et al. 1999, 2000, 2003, Alianza 2008, Groce et al. 2010, Komar et al. 2011, Texas A&M IRNR 2015
Golden-winged Warbler *Vermivora chrysoptera*	R	Y	Y	Y	N	Y	Y	Bennett 2012, Chandler and King 2011, Bennett et al. 2016, Chandler et al. 2016, King et al. 2016
Grasshopper Sparrow *Ammodramus savannarum*	CSD	N	U	Y	N	Y	N	Pool et al. 2012, Ruth et al. 2014, Macías-Duarte et al. 2017
Gray Vireo *Vireo vicinior*	Y	N	I	N	N	N	N	Bates 1992a&b, Barlow 1999
Harris's Sparrow *Zonotrichia querula*	Y	Y	U	Y	N	N	N	Rohwer et al. 1981, Watt 1986, National Audubon Society 2010, Norment et al. 2016
Henslow Sparrow *Ammodramus henslowii*	Y	N	Y/I	N	N	Y	N	Burhans 2002, Bechtoldt and Stouffer 2005, Palasz 2008, Johnson et al. 2009 & 2011, Cooper 2012
Horned Lark *Eremophila alpestris*	CSD	Y	I	Y	N	Y	N	Desmond 2004, Merola-Zwartjes 2005, Pearson and Altman 2005, Camfield 2008, Cascadia Prairie Oak Partnership 2016
Kentucky Warbler *Geothlypis formosa*	Y	Y	Y/I	Y	N	Y	N	Ornat and Greenberg 1990, Conway et al. 1995, McDonald 2013, eBird 2017
Kirtland's Warbler *Setophaga kirtlandii*	Y	Y	N	Y	N	Y	N	USFWS 1985, USFWS 2012, Bocetti et al. 2012, Wunderle Jr et al. 2014
Lark Bunting *Calamospiza melanocorys*	CSD	Y	U	Y	N	Y	N	Merola-Swartjes 2005, Pool et al. 2012
LeConte's Sparrow *Ammodramus leconteii*	Y	N	U	Y	N	Y	N	Grzybowski 1983, Igl and Ballard 1999, Baldwin et al. 2010, National Audubon Society 2010, Hovick et al. 2014

Species								References
Least Flycatcher *Empidonax minimus*	CSD	N	I	N	N	N	N	Komar et al. 2005, Tarof and Briskie 2008
Lewis' Woodpecker *Melanerpes lewis*	Y	N	U	Y	N	Y	N	Abele et al. 2004, GBBO 2010, National Audubon Society 2010, Environment Canada 2011a, Vierling et al. 2013, Environment and Climate Change Canada 2017
Loggerhead Shrike *Lanius ludovicianus*	CSD	N	U	Y	N	Y	N	Brooks and Temple 1990, Chavez-Ramirez et al. 1994, Cade and Woods 1997, Merola-Swartjes 2005, National Audubon Society 2010, Pool et al. 2012
Lucifer Hummingbird *Calothorax lucifer*	Y	Y	U	N	N	N	N	Scott 1994
McCown's Longspur *Rhynchophanes mccownii*	Y	Y	U	Y	N	Y	N	Sedgwick 2004, With 2010, Environment Canada 2014
McKay's Bunting *Plectrophenax hyperboreus*	Y	Y	U	N	N	N	N	Montgomerie and Lyon 2011
Nelson's Sparrow *Ammodramus nelsoni*	Y	N	U	N	N	Y	N	Shriver et al. 2011, Watts and Smith 2015
Olive-sided Flycatcher *Contopus cooperi*	Y	N	U	N	N	Y	N	Marshall 1988, Willis et al. 1993, Kotliar 2007, Environment Canada 2016c.
Pine Siskin *Spinus pinus*	CSD	Y	U	Y	N	Y	N	Tilghman 1987, National Audubon Society 2010, Dawson 2014
Prairie Warbler *Setophaga discolor*	Y	Y	Y/I	N	N	N	N	Murphy et al. 2001, Southwell 2001, Latta et al. 2003
Prothonotary Warbler *Protonotaria citrea*	Y	Y	Y/I	N	N	Y	N	Ornat and Greenberg 1990, Lefebvre et al. 1992, Warkentin and Morton 2000, Environment Canada 2011b, COSEWIC 2016
Red-headed Woodpecker *Melanerpes erythrocephalus*	Y	N	I	Y	N	Y	N	Smith and Scarlett 1987, National Audubon Society 2010, Vukovich and Kilgo 2013, Frei et al. 2017
Rufous Hummingbird *Selasphorus rufus*	Y	Y	Y	N	N	Y	N	Kodric-Brown and Brown 1978, Carpenter et al. 1993, Temeles and Roberts 1993, Hill et al. 1998, Moran et al. 2013, Arizona-Sonora Desert Museum 2014

Species								References
Rusty Blackbird *Euphagus carolinus*	CSD	Y	Y/I	Y	N	Y	Y	Rogers 2005, Turcotte and Desrochers 2008, DeLeon 2012, Newell 2013, Borchert 2015, Environment Canada 2015, Mettke-Hofmann et al. 2015, Evans 2016
Saltmarsh Sparrow *Ammodramus caudacutus*	R	N	U	N	N	Y	N	Watts and Smith 2015
Seaside Sparrow *Ammodramus maritimus*	Y	N	U	N	N	Y	N	Slater et al. 2014
Short-eared Owl *Asio flammeus*	CSD	N	U	Y	N	Y	N	Clark 1975, Wiggins 2004, National Audubon Society 2010, Booms et al. 2014
Snowy Owl *Bubo scandiacus*	Y	Y	Y	N	N	N	N	Boxall and Lein 1982, Kerlinger and Lein 1986, Chang and Wiebe 2018
Sprauge's Pipit *Anthus spragueii*	Y	N	U	Y	N	Y	N	Merola-Swartjes 2005, Environment Canada 2008, Jones 2010, Pool et al. 2012
Varied Thrush *Ixoreus naevius*	CSD	Y	I	Y	N	N	N	Martin 1970, George 2000, National Audubon Society 2010
Virginia's Warbler *Leiothlypis virginiae*	Y	Y	U	N	N	N	N	Olson and Martin 1999
Wilson's Warbler *Cardellina pusilla*	CSD	Y	Y	N	N	Y	N	Greenberg et al. 2000, Komar et al. 2005, Johnson and Anderson 2003, Ruiz-Sánchez et al. 2017
Wood Thrush *Hylocichla mustelina*	Y	N	Y/I	Y	N	Y	N	Roberts 2007, Chin et al. 2014, McKinnon et al. 2015, Stanley et al. 2015, Rushing et al. 2016, Taylor and Stutchbury 2016, eBird 2017
Yellow-billed Cuckoo *Coccyzus americanus*	CSD	N	U	N	N	N	N	Hughes 2015

Table 2A References

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Table 2B: Male and female detections by region

Region	Name	# points	# points w/male	# males detected	# points w/female	# females detected
1	Eastern Panama	122	0	0	3	4
2	Central Panama	206	17	24	12	15
3	Western Panama	116	18	24	14	15
4	Western Nicaragua	52	1	1	4	6
5	Eastern Honduras and Nicaragua	168	54	93	44	62
6	Central Honduras	79	16	23	1	1
7	Caribbean lowlands, Guatemala	142	13	16	8	9
8	Petén and Belize	125	3	3	4	5
9	Central highlands, Guatemala	167	13	16	5	6

Table 2C: Summary statistics of habitat covariates by region

Region	Precipitation (cm/yr)				March NDVI				Elevation (masl)				Longitude				Latitude			
	mean	min	max	sd	mean	min	max	sd	mean	min	max	sd	mean	min	max	sd	mean	min	max	sd
1	2027	1824	2555	182	163	138	179	8	93	7	683	127	-77.75	-77.88	-77.62	0.07	8.19	8.00	8.39	0.13
2	2750	1781	3561	477	171	124	188	13	460	10	939	291	-79.62	-80.24	-78.96	0.41	9.00	8.59	9.39	0.28
3	2756	2208	3561	363	173	132	190	12	1112	87	3171	782	-82.07	-82.58	-80.75	0.66	8.51	7.33	9.27	0.60
4	1537	1250	1899	215	174	150	188	10	713	374	1206	249	-86.16	-86.28	-85.97	0.12	11.93	11.83	12.06	0.09
5	596	0	2535	867	171	143	188	11	781	53	2362	481	-85.75	-86.04	-84.02	0.52	14.86	14.37	15.07	0.17
6	1256	884	1725	193	176	147	186	9	1488	629	2109	313	-87.17	-87.33	-86.98	0.11	14.26	14.14	14.35	0.07
7	2802	1916	3477	500	180	164	187	4	485	11	1652	528	-89.05	-89.38	-88.68	0.26	15.54	15.18	15.84	0.24
8	1559	1220	2574	438	182	172	188	3	304	56	653	184	-89.36	-89.71	-88.37	0.42	17.18	16.73	17.44	0.26
9	2935	1588	5375	1247	169	139	184	10	1430	755	2289	275	-90.67	-91.28	-90.16	0.45	15.34	14.51	15.88	0.41
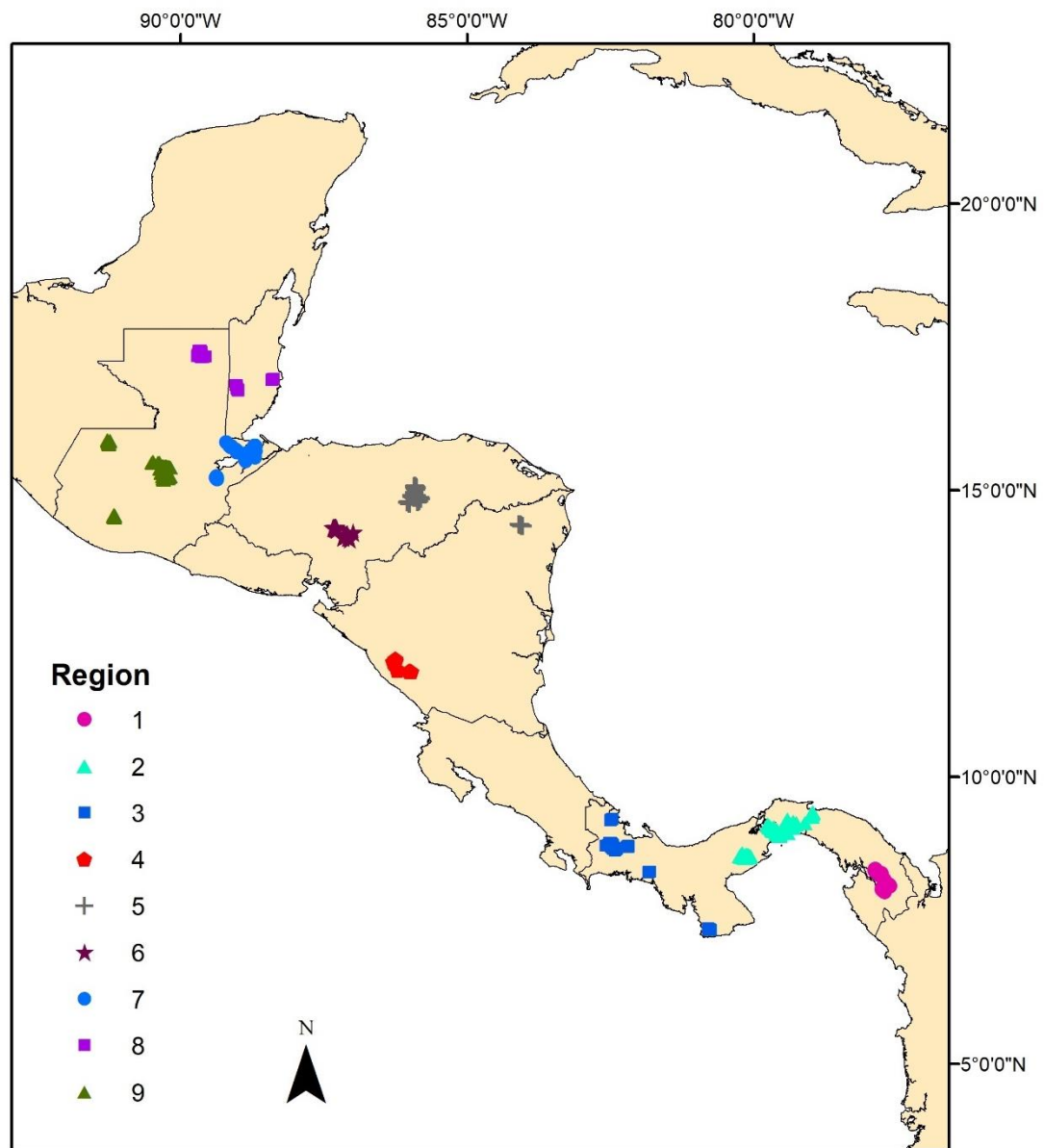
Figure 2A: Map of all points surveyed with by region

CHAPTER 3 APPENDIX

This appendix contains a summary of the data that was analyzed in Chapter 3 with the following elements:

- Table 3A: Banding data from all captures for evergreen broadleaf forest and semi-deciduous forest.

- Table 3B: Summary statistics for all habitat covariates in evergreen and semi-deciduous forest

- Table 3C: Summary of detections in arrival period for males and females in Habitat 1—evergreen forest and Habitat 2—semi-deciduous forest for each of the five arrivals weeks for the two years reported.

- Table 3D: Summary of male and female detections during overwintering period in Habitat 1—evergreen forest and Habitat 2—semi-deciduous forest for each of three survey repetitions over the three study years.

- Figure 3A: Map of all arrival survey points coded by color for habitat type

- Figure 3B: Map of all overwintering survey points coded by color for habitat type

Table 3A: Banding data from all captures. Habitat 1 is evergreen broadleaf forest and Habitat 2 is semi-deciduous broadleaf forest. Body fat and pectoral muscle indexes described in methods.

Sex	Age	Time	Body Fat	Wing Chord (mm)	Mass (g)	Pectoral Muscle	Date	Habitat
F	AHY	10:19	0	58	8	2	11/30/2015	1
F	AHY	8:38	0	60	8.75	1	10/29/2016	1
F	AHY	9:07	0	62	9	1	10/30/2016	1
F	AHY	11:45	0.5	60.5	7.85	0	2/23/2013	1
F	AHY	9:36	1	54	8.5	1	11/20/2015	1
F	AHY	16:04	2	61	9	1	11/24/2015	1
F	AHY	11:02	2	61	8.5	1	11/29/2015	1
F	HY	7:55	0	55	8	1	11/19/2015	1
F	HY	12:00	1	57.8	8	2	11/18/2015	1
F	HY	11:45	2	60	9.5	3	11/30/2016	1
F	HY	14:52	2	55.3	9.25	2	11/17/2015	1
M	AHM	13:55	2	61.5	8.9	1.5	10/30/2016	1
M	AHY	7:12	0	63	9	1	11/25/2015	1
M	AHY	7:26	0	62	9	1	11/27/2015	1
M	AHY	8:09	0	60	8.5	1	11/28/2015	1
M	AHY	13:12	0	62.2	9.25	1	12/14/2015	1
M	AHY	6:14	0	60	8.75	2	10/27/2016	1
M	AHY	6:28	0	64	8.5	1	10/28/2016	1
M	AHY	12:57	0	63	9.25	1	10/29/2016	1
M	AHY	11:31	0	61	9.5	1	10/30/2016	1
M	AHY	14:38	0	61	8.5	1	11/29/2016	1
M	AHY	8:38	0	63.5	8.75	2	1/12/2017	1
M	AHY	8:24	0	61.5	8.75	0	2/23/2013	1
M	AHY	12:57	0	62	8.5	0	2/24/2013	1
M	AHY	12:43	0.5	62	8.75	0	1/14/2013	1
M	AHY	10:33	0.5	61	8.45	0	2/26/2013	1
M	AHY	10:04	1	63.5	8.45	0	12/19/2012	1
M	AHY	8:24	1	61	8.45	0	12/18/2012	1
M	AHY	13:26	1	61	8.25	0	12/18/2012	1
M	AHY	9:21	1	61.7	10	1	11/19/2015	1
M	AHY	11:31	1	60	9	1	11/24/2015	1
M	AHY	8:24	1	62	9.5	1	11/25/2015	1
M	AHY	10:48	1	62	9.5	1	11/28/2015	1
M	AHY	12:00	1	63	9.5	1	11/28/2015	1
M	AHY	15:21	1	61	9	1	11/29/2015	1
M	AHY	13:55	1	63	9	2	11/30/2015	1
M	AHY	8:38	1	62	9.5	2	12/1/2015	1
M	AHY	14:24	1	63	8.8	2	10/27/2016	1
M	AHY	14:52	1	63	9.3	2	12/1/2016	1
M	AHY	12:57	1	62	8.25	1	1/11/2017	1
M	AHY	13:55	1	60	9.25	1	1/12/2017	1
M	AHY	10:04	1.5	65.5	8.75	0	12/18/2016	1
M	AHY	13:26	2	61.5	9.25	0	12/18/2016	1
M	AHY	14:52	2	62	9	2	11/24/2015	1
M	AHY	14:52	2	63	10.5	1	10/29/2016	1

Sex	Age	Time	Body Fat	Wing Chord	Mass	Pectoral Muscle	Date	Habitat
M	AHY	13:40	3	59.3	9	1	11/18/2015	1
M	AHY	14:24	3	62	9.75	2	10/26/2016	1
M	AHY	11:45	NA	61	8.5	NA	12/3/2016	1
M	AHY	10:19	0	62	9.5	1	12/3/2016	1
M	AHY	12:00	0.5	60	8.55	0	2/23/2013	1
M	HY	12:43	0	61	8.75	0	12/19/2012	1
M	HY	8:09	0	60.1	8.15	1	11/18/2015	1
M	HY	9:50	0	60	8.05	1	11/18/2015	1
M	HY	16:33	0	59.4	9	1	11/18/2015	1
M	HY	11:16	0	61	9.1	1	11/19/2015	1
M	HY	11:02	0	63.8	9.5	1	11/21/2015	1
M	HY	12:14	0	59	9	1	11/24/2015	1
M	HY	16:19	0	61	9.5	1	11/24/2015	1
M	HY	10:33	0	59	9.5	1	11/26/2015	1
M	HY	7:40	0	63	9	2	11/26/2015	1
M	HY	13:26	0	61	9	1	11/27/2015	1
M	HY	9:50	0	62	9.5	1	11/28/2015	1
M	HY	11:16	0	61	8.5	2	11/29/2015	1
M	HY	9:21	0	61	9.35	1	10/28/2016	1
M	HY	9:36	0	61.5	8.5	1	10/29/2016	1
M	HY	9:07	0.5	64	8.55	0	12/20/2012	1
M	HY	12:28	1	63	8.6	0	12/20/2012	1
M	HY	9:36	1	60	9	1	11/25/2015	1
M	HY	8:09	1	61	9.5	1	11/30/2015	1
M	HY	12:28	1	62	9.5	1	11/30/2015	1
M	HY	14:09	1	60	8.5	1	10/29/2016	1
M	HY	13:55	1	62	8.6	2	12/1/2016	1
M	HY	7:40	1	60	9	2	1/7/2017	1
M	HY	9:36	1	58	8.5	1	1/10/2017	1
F	AHY	8:38	2	58	8.75	NA	11/26/2011	2
F	AHY	7:55	2	61	8.25	1	11/27/2015	2
F	AHY	12:00	2	56.3	8.15	1	11/28/2015	2
F	AHY	8:38	2	58	8.1	2	11/28/2015	2
F	AHY	11:16	2	58.6	8.2	1	11/29/2015	2
F	HY	7:55	0	57	7.7	1	12/1/2015	2
F	HY	11:45	0	58.5	8.95	1	12/15/2016	2
F	HY	14:09	0	56	8.25	1	12/15/2016	2
F	HY	13:12	2	58	8.5	NA	12/6/2011	2
F	HY	14:09	2	57.7	9	0	11/24/2015	2
F	HY	10:19	2	59	8.3	1	11/29/2015	2
M	AHY	7:26	0	64.5	8.2	0	12/4/2012	2
M	AHY	13:40	1	61	9	0	12/3/2012	2
M	AHY	13:26	1	62.5	8.25	0	12/7/2012	2
M	AHY	12:43	1	59	8.25	NA	11/25/2011	2
M	AHY	9:36	1	62.5	8.5	NA	11/27/2011	2
M	AHY	7:12	1	61	8.5	NA	12/6/2011	2
M	AHY	8:52	1	63	8.7	0	12/5/2012	2
M	AHY	10:48	1	63	8.5	1	11/30/2015	2
M	AHY	13:26	1	61	9.8	1	12/17/2016	2
M	AHY	13:12	2	62	8.5	NA	11/22/2011	2

Sex	Age	Time	Body Fat	Wing Chord	Mass	Pectoral Muscle	Date	Habitat
M	AHY	9:50	4	61	8.15	1	11/27/2015	2
M	AHY	14:24	2	62.5	9	NA	12/4/2011	2
M	AHY	15:07	2	63.2	9	1	12/8/2015	2
M	HY	9:21	0	60	8.5	1	12/16/2016	2
M	HY	10:04	0.5	63.5	9	0	12/13/2012	2
M	HY	15:21	1	64	8.5	0	12/6/2012	2
M	HY	10:33	1.5	61.5	9	NA	11/29/2012	2
M	HY	10:04	2	63	9	NA	11/26/2011	2
M	HY	9:36	2	62	9	NA	12/3/2011	2
M	HY	11:31	3	64.5	9	NA	11/27/2011	2
M	HY	10:48	3	63	8.75	NA	12/6/2011	2

Table 3B: Summary statistics for all habitat covariates in evergreen and semi-deciduous forest

Habitat Covariate	mean	min	max	SD
Latitude°	14.91	14.78	15.06	0.08
Longitude°	-85.94	-86.04	-85.88	0.05
Elevation (masl)	1220	728	2350	302
Basal Area (10 factor)	68	6	150	33
Slope°	21	0	45	12
Vertical Complexity	63	18	98	15.5
NDVI	176	141	189	11
Annual Precip (cm/yr)	1486	1230	1990	165

Evergreen Forest

Habitat Covariate	mean	min	max	SD
Latitude°	14.88	14.76	15.07	0.06
Longitude°	-85.89	-86.02	-85.8	0.1
Elevation (masl)	460	325	700	126
Basal Area (10 factor)	57	0	140	26
Slope°	7	0	45	11
Vertical Complexity	41	5	84	19
NDVI	165	141	180	10
Annual Precip (cm/yr)	1326	1216	1410	43

Semi-deciduous Forest

Table 3C: Summary of detections in arrival period for males and females in Habitat 1—evergreen forest and Habitat 2—semi-deciduous forest for each of the five arrivals weeks for the two years reported.

Sex	Habitat	Year	# Points	Number of Detections per Week				
				Week 1	Week 2	Week 3	Week 4	Week 5
males	1	1	14	0	0	7	5	7
	1	2	114	4	10	19	24	22
	2	1	48	0	0	2	7	5
	2	2	147	2	2	4	6	10
females	1	1	14	0	0	4	3	0
	1	2	114	1	2	10	10	6
	2	1	48	0	0	5	11	13
	2	2	147	2	2	10	19	16

Table 3D: Summary of male and female detections during overwintering period in Habitat 1—evergreen forest and Habitat 2—semi-deciduous forest for each of three survey repetitions over the three study years.

Habitat	Year	# Points	Points with a Male			Points with a Female		
			Rep 1	Rep2	Rep3	Rep1	Rep2	Rep3
1	1	11	4	5	5	0	1	0
1	2	59	19	15	9	3	4	2
1	3	76	29	21	17	5	6	12
2	1	31	3	3	1	5	3	2
2	2	38	3	2	4	6	5	6
2	3	80	7	7	5	5	16	9

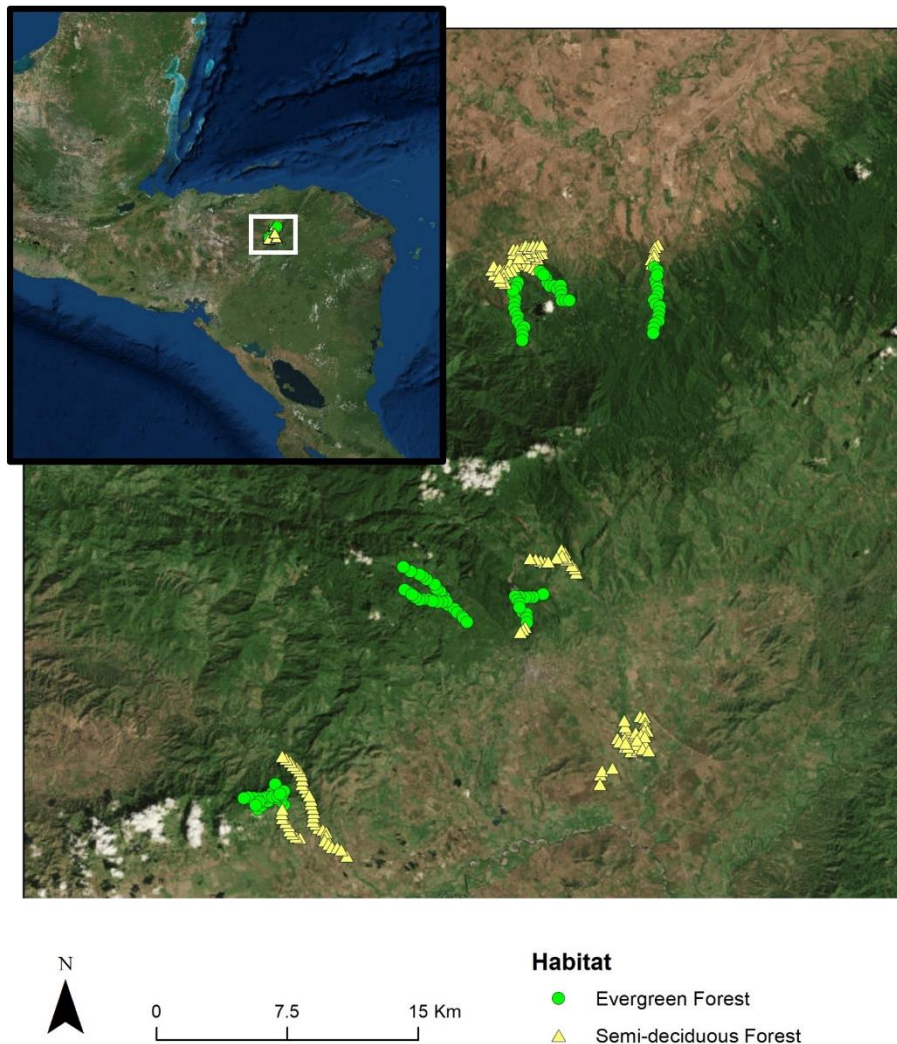Figure 3A: Map of all arrival survey points coded by color for habitat type
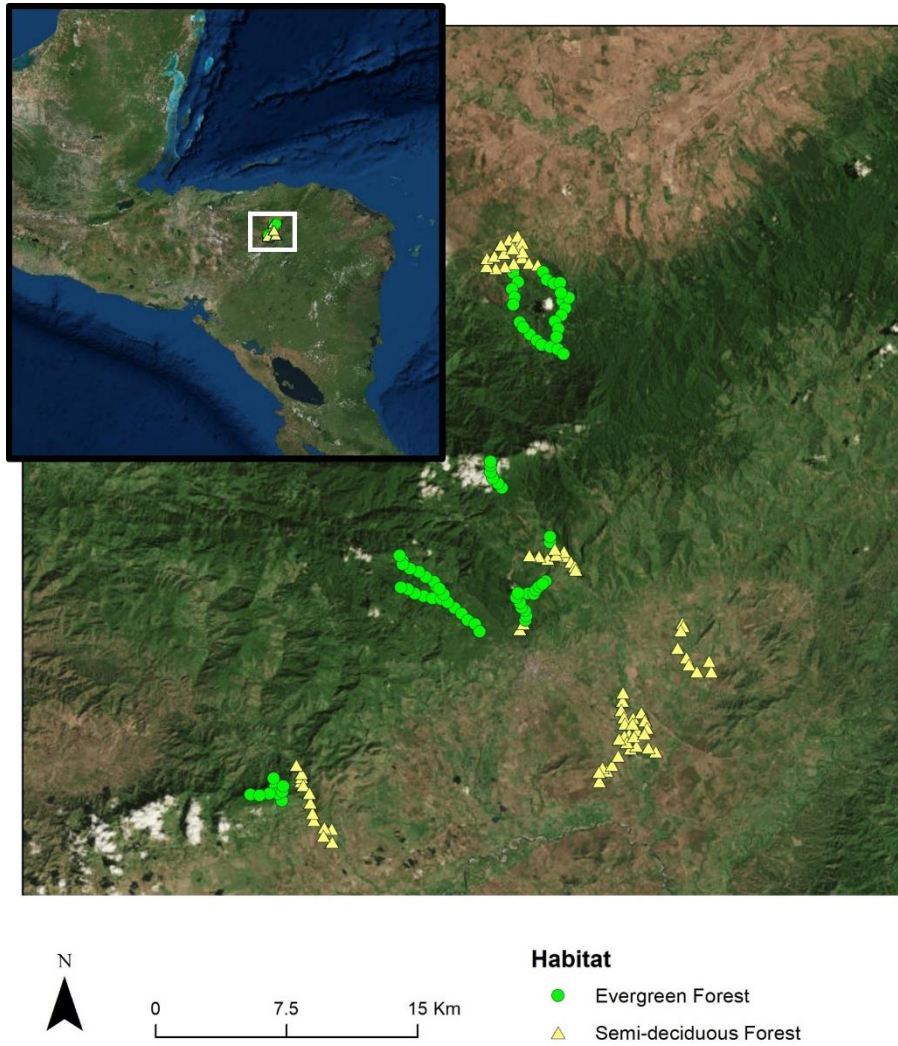
Figure 3B: Map of all overwintering survey points coded by color for habitat type

CHAPTER 4 APPENDIX

This appendix contains a summary of the data that was analyzed in Chapter 4 with the following elements:

- Table 4A. Centroid locations and migration timing for 37 recovered geolocators with wing chord, weight, and age at deployment

Table 4A. Centroid locations and migration timing for 37 recovered geolocators with wing chord, weight, and age at deployment

Deploy Site	Spring Year	Bree-ing N	Breed-ing W	Winter N	Winter W	Spring Depart	Pre-Gulf stop	Post-Gulf Landfall	Spring Arrive	Spring Days	Fall Depart	Fall Arrive	Fall Days	Age	Weight (g)	Wing (mm)
Costa Rica	2016	46.05	-91.17	10.22	-84.66	7-Apr	y	19-Apr	16-May	39	2-Sep	25-Oct	53	SY	8.7	65.0
Nicaragua	2016	47.57	-92.51	12.93	-85.78	18-Apr	y	1-May	14-May	26	3-Sep	24-Oct	51	ASY	9.5	62.0
Nicaragua	2016	46.05	-91.17	12.94	-85.78	25-Apr	y	11-May	23-May	28	3-Sep	24-Oct	51	SY	9.0	62.0
Nicaragua	2016	47.04	-94.11	12.94	-85.78	15-Apr	y	28-Apr	18-May	33	25-Aug	14-Oct	50	SY	8.7	63.0
Nicaragua	2016	45.69	-90.07	12.95	-85.78	25-Apr	y	10-May	20-May	25	13-Sep	27-Oct	44	ASY	8.5	62.0
Nicaragua	2015	43.76	-90.48	13.23	-86.06	13-Apr	y	6-May	18-May	35	31-Aug	25-Oct	57	ASY	8.0	64.0
Nicaragua	2016	46.46	-93.28	13.23	-86.05	17-Apr	y	30-Apr	13-May	26	7-Sep	17-Oct	40	SY	9.5	62.0
Nicaragua	2015	42.68	-86.75	13.23	-86.05	22-Apr	y	6-May	23-May	31	15-Aug	12-Oct	58	SY	9.0	63.0
Nicaragua	2015	43.03	-91.03	13.24	-86.05	25-Apr	y	8-May	19-May	24	25-Aug	28-Oct	64	ASY	8.0	62.0
Nicaragua	2015	45.82	-91.44	13.24	-86.05	23-Apr	y	9-May	19-May	26	18-Aug	29-Oct	72	ASY	8.5	62.0
Nicaragua	2016	44.89	-88.67	13.24	-86.05	21-Apr	y	27-Apr	14-May	23	3-Sep	8-Oct	35	SY	8.0	60.5
Nicaragua	2015	45.24	-93.31	13.24	-86.05	19-Apr	y	28-Apr	9-May	20	10-Sep	25-Oct	45	SY	8.6	62.0
Nicaragua	2016	45.40	-92.60	13.24	-86.05	25-Apr	n	NA	26-May	31	24-Aug	24-Oct	61	SY	8.6	62.0
Nicaragua	2015	45.96	-91.89	13.24	-86.05	19-Apr	y	6-May	16-May	27	11-Sep	23-Oct	42	ASY	8.6	62.0
Nicaragua	2016	44.62	-90.70	13.24	-86.05	18-Apr	y	1-May	15-May	27	6-Sep	24-Oct	48	ASY	9.2	61.0
MN	2015	46.51	-93.33	13.27	-84.36	7-Apr	y	26-Apr	6-May	29	15-Sep	4-Nov	50	NA	NA	NA
MN	2014	46.51	-93.33	14.34	-83.12	NA	NA	NA	NA	NA	21-Sep	27-Oct	36	NA	NA	NA
Honduras	2016	46.92	-92.76	14.78	-86.03	23-Apr	n	1-May	18-May	25	3-Sep	11-Oct	38	AHY	10.0	61.7
Honduras	2016	46.34	-91.63	14.79	-86.03	28-Apr	y	10-May	23-May	25	7-Sep	20-Oct	43	HY	9.5	61.0
Honduras	2016	44.65	-91.57	14.79	-86.03	17-Apr	y	2-May	19-May	32	5-Sep	25-Oct	50	AHY	9.0	61.0
Honduras	2016	46.48	-91.26	14.79	-86.02	15-Apr	y	27-Apr	18-May	33	1-Sep	7-Oct	36	HY	8.2	60.1
Honduras	2016	43.25	-88.28	14.79	-86.02	12-Apr	y	24-Apr	6-May	24	3-Sep	24-Oct	51	AHY	NA	60.2
MN	2014	46.51	-93.33	15.08	-86.22	19-Apr	y	28-Apr	19-May	30	12-Sep	15-Oct	33	NA	NA	NA
MN	2014	46.51	-93.33	15.17	-84.93	7-Apr	y	23-Apr	15-May	38	14-Sep	29-Oct	45	NA	NA	NA

Honduras	2016	45.57	-91.20	15.18	-87.48	26-Apr	n	1-May	18-May	22	13-Sep	24-Oct	41	SA	9.3	60.5
Honduras	2016	46.32	-90.69	15.21	-87.50	23-Apr	n	29-Apr	14-May	21	NA	NA	NA	ASY	8.5	60.0
Guatemala	2016	46.31	-93.87	15.36	-88.69	5-May	n	10-May	21-May	16	10-Sep	28-Oct	48	ASY	8.3	61.5
Guatemala	2016	46.52	-94.42	15.36	-88.68	10-Apr	y	25-Apr	11-May	31	28-Aug	21-Oct	54	SY	9.5	63.0
Guatemala	2016	46.02	-90.26	15.38	-88.70	21-Apr	y	30-Apr	13-May	22	12-Sep	26-Oct	44	SY	8.4	60.1
Guatemala	2016	48.86	-93.57	15.67	-88.68	25-Apr	n	2-May	17-May	22	13-Sep	27-Oct	44	ASY	8.5	61.0
MN	2014	46.51	-93.33	15.76	-86.34	11-Apr	y	25-Apr	20-May	39	12-Sep	25-Oct	43	NA	NA	NA
MN	2014	46.51	-93.33	15.81	-85.91	19-Apr	y	25-Apr	6-May	16	9-Sep	28-Oct	49	NA	NA	NA
MN	2014	46.51	-93.33	15.85	-84.45	20-Apr	y	6-May	16-May	26	10-Sep	30-Oct	50	NA	NA	NA
MN	2014	46.51	-93.33	17.04	-91.01	24-Apr	n	27-Apr	12-May	18	3-Sep	23-Oct	50	NA	NA	NA
MN	2015	46.51	-93.33	19.45	-85.23	22-Apr	y	5-May	17-May	25	16-Aug	2-Nov	78	NA	NA	NA
MN	2014	46.51	-93.33	19.90	-87.44	NA	NA	NA	NA	NA	18-Sep	4-Nov	47	NA	NA	NA
MN	2014	46.51	-93.33	20.90	-87.87	21-Apr	n	24-Apr	16-May	25	13-Sep	26-Oct	43	NA	NA	NA