

**MIGRATION ECOLOGY OF NEOTROPICAL MIGRANT SONGBIRDS EN ROUTE
THROUGH THE DARIÉN REGION OF COLOMBIA**

*A Thesis Submitted to the College of
Graduate and Postdoctoral Studies
In Partial Fulfillment of the Requirements
For the Degree of Master in Biology
In the Department of Biology
University of Saskatchewan
Saskatoon*

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ABSTRACT

Neotropical migrant songbirds have experienced severe and ongoing population declines. The lack of knowledge about migration outside North America inspired me to study the ecology of migration of a group of 11 species to determine: 1) breeding origins and patterns of migration, 2) how breeding origins, age, sex, El Niño–Southern Oscillation (*ENSO*), body size and route of migration affect body condition and phenology. I also described migration in detail for Canada Warbler due to its status as a species of concern. Constant-effort mist netting data and samples were collected for stable isotope ($\delta^2\text{H}$) analyses to determine breeding origin. For the 11 study species, we found populations derived from across their breeding range in 55% of species, while 27% had more westerly origins and 18% from eastern portions of their breeding range. The peak of migration for all species, except Yellow Warbler (late September), occurred in October. I found evidence for chain migration in 36% of species (Red eyed vireo, Yellow Warbler, Northern Waterthrush and Mourning Warbler) and leapfrog migration in 18% (Swainson's thrush and Gray-cheeked Thrush). Body condition was little affected by factors such as breeding origin, the *ENSO*, age and sex and route of migration. In contrast, body size affected almost half of the species (Veery, Swainson's Thrush, Gray-cheeked Thrush, Scarlett Tanager and Summer Tanager). For Canada Warbler, migration through Central America rather than across the Caribbean Sea was most probable and the study site was more frequently used by hatch-year birds (91% vs. 9% after hatch-year birds), and females (67% vs. 33% males). Most Canada Warblers (89%) arrived with low fuel reserves. These results combined with estimated flight ranges revealed that 46% of Canada Warblers captured in the Darién likely needed to

refuel to continue migrating. The large concentration of Neotropical migrants from across North America stopping in the Darién site confirms the ecological function of the Darién where potentially a large proportion of the breeding population of several species refuels or rests before reaching their wintering sites in South America.

ACKNOWLEDGEMENTS

First, I want to express my deepest appreciation to my supervisor Dr. Keith A. Hobson. This was the most productive time of my life and I was honored to learn from you and have been part of your incredible lab. This opportunity definitively changed my life. Thanks for making true one of the dreams of my life!

Secondly, I want to thank Dr. Karen Wiebe and Dr. Catherine Soos for agreeing to be on my committee. It has been a privilege to be able to learn from all of you.

In addition, Dr. Nicholas Bayly, was a strong support during the field season and also during the writing phase of my thesis. Thanks for your patience, your unconditional help, support and dedication to make this thesis an important contribution in the field of bird migration research in the tropics. My thesis is a little branch of your project: “Crossing the Caribbean” in Colombia led by SELVA. I feel happy and honored for having the chance to make part of it, but especially learning from you.

I would like also to thank the members of my lab, Chantel Gryba, Geoff Koehler, Kevin Kardynal, and David Soto for your great help with my feather preparation and analyses. The analyses performed in this thesis would not have been possible without the guidance and support from my supervisor Dr. Keith A Hobson and Dr. Nicholas Bayly. However, I am indebted to Kevin Kardynal for being incredibly generous with his time, patience and R and statistics knowledge. I learned so much from you and I want to express my deepest admiration to you and your work as a scientist in our lab.

I feel thankful to my colleagues and friends for supporting me in the field in Colombia and who helped us to gain incredible data to analyze in this thesis: Camila Gomez, Marta Rubio, Valentina Gomez, Jeyson Sanabria, Hernan Arias, Ana Maria

Diaz, Daniel Giesbrecht and Angela Caguazango. Fabio Jimenez y Marta Rubio for their permission to work with Selva in the Tacarcuna Nature Reserve. Gabriel Colorado, for his incredible disposition to donate his Canada Warbler data to me, analyzed in the third chapter of this thesis.

I am also incredibly grateful to my family for being my unconditional emotional support. Even at distance, you were always with me helping me to be a strong and positive woman during the difficult times.

I want to thank my friends in Saskatoon, Ana Maria Diaz, Marta Bonilla, Andres Posso, Ana Rita Krause and Xiomara Mora Alvarez for helping me to adjust to this city and for their academic and life advice, but mostly for their friendship that kept me happy during the academic life.

This research was supported by an operating grant from Environment and Climate Change Canada and an NSERC Discovery grant to Keith A. Hobson. Further financial support was provided by a grant to Nicholas Bayly from the Rufford Small Grants Foundation. Field work and exportation of feathers were conducted under permits issued by the Autoridad Nacional de Licencias Ambientales (ANLA) in Colombia.

Finally, I have to thank the University of Saskatchewan for providing me with two scholar travel awards to attend two international ornithology conferences through my academic years. Also the Smithsonian Institution and the migratory bird center provided me a scholarship to attend one of my credit courses.

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CHAPTER 1. THE IMPORTANCE OF UNDERSTANDING MIGRATION ECOLOGY OF NEOTROPICAL MIGRANTS

1.1 INTRODUCTION

Neotropical migrant birds are an important biological resource shared between temperate and tropical latitudes in the Nearctic Neotropical migration system.

Approximately six billion birds migrate from the breeding grounds in North America to spend the winter in the tropics of the Caribbean, Central America and South America (Faaborg et al. 2010). Understanding the physical and demographic linkages between areas used by migratory birds is important, especially those used on migration, as most annual mortality occurs during the migratory period (Sillett and Holmes, 2002).

However, while most attention has been directed at causes occurring at breeding and wintering sites (Norris et al. 2004; Faaborg et al. 2010), the importance of events occurring during migration and at stopover sites on the Caribbean coast of Central and South America are largely understudied (Faaborg et al. 2010, 2013). In this study, I used the definition of stopover site as an area with the combination of resources (i.e. food, cover, water) and environmental conditions that promotes occupancy by individuals of a given species (or population) that allows those individuals to survive during passage (Morrison et al. 1992; Moore et al. 1995).

Little is known about the geographical origins of the Neotropical migratory species that migrate to South America and less about the factors influencing their arrival time and body condition.

Studies using long-term census data for several species of landbirds that migrate to the tropics have revealed considerable population declines during the last three decades (Faaborg et al. 2010). Habitat degradation along migratory routes together with long-term changes in climate or local weather conditions will influence the costs of migration and survival rates (Yong and Moore 1997a). Therefore, it is important to invest in studying Neotropical migratory birds in areas such as the Darién in Colombia, which acts as a funnel for migratory birds during migration (Bayly et al. 2014; Gómez et al. 2014), especially considering the increasing rates of deforestation and habitat loss in this region (Cardenas-Ortiz et al. 2017)

Despite decades of research and banding efforts, we have only a rudimentary understanding of where birds that breed in North America reside during the winter (Faaborg et al. 2010). “Migratory connectivity” is a term that explains the degree to which individuals from the same breeding grounds migrate to the same wintering areas (Trierweiler et al. 2014). It is important to establish patterns of migratory connectivity at the population level, linking not only breeding and wintering grounds, but also linking these sites with migratory stopover sites (Hobson et al. 2014). This kind of information is especially important, in order to protect species facing population declines.

Recently, several types of technology have been used to track bird migration in order to establish wintering or stopover sites. For example, satellite tracking or weather radar has been used to follow migrants or identify areas of migratory concentrations and stopover (Dokter et al. 2013), and, more recently, archival light-sensitive geolocators or Global Positioning System (GPS) tags have been miniaturized enough to be deployed on small birds (>10g) (Bächler et al. 2010; DeLuca et al. 2015; Stutchbury et al. 2009).

In addition, the creation of receiver tower arrays like the MOTUS system in North America will provide important new information on movements of small passerines fitted with radio-transmitters (Rowlands 2015; Gómez et al. 2017). However, such exogenous markers suffer from a number of problems. They are typically expensive, need to be recovered (or detected) from marked individuals and can only feasibly be applied at a relatively small scale and are biased to the choice of sampling sites (typically on the breeding grounds).

However, endogenous markers like the measurement of naturally occurring ratios of stable isotopes in avian tissues, have been shown to be a useful alternative to exogenous markers because it is relatively inexpensive, not biased to original sampling location and requires only a single capture (Hobson and Wassenaar 2008). The technique is based on the fact that stable isotope values in animal tissues reflect those of local food webs which vary spatially, often in predictable ways (Hobson & Clark, 1992; Hobson & Wassenaar, 2008). Animals that move across regions or isoscapes, where food web isotope signatures vary, can retain information in their tissues about their prior location/s. The most useful isotope measurements to date for tracking long-distance migrant birds are those of hydrogen ($\delta^2\text{H}$), which are strongly influenced by continent-wide patterns of amount-weighted $\delta^2\text{H}$ in precipitation (Hobson and Wassenaar 2008). In North America, most Neotropical migrants grow flight feathers on their breeding grounds prior to fall migration. Isotopic signals of origin are then locked into these feathers and they can be sampled at other locations to infer origins (Hobson 2011). Nevertheless, little is known about the breeding origins of long-distance migrants passing through most stopover sites like the Darién region of Colombia and only a few

studies have collected feather samples at stopover sites to address this knowledge gap (González-Prieto et al. 2011).

Other knowledge gaps that inhibit our ability to design effective conservation strategies for Neotropical migrants in Colombia and elsewhere, is that the factors affecting the timing of migration of Neotropical migratory species through stopover sites are largely unknown. This makes it impossible to predict the effects of anthropogenic change on the movements of migrants. At my study site in the Darién region of Colombia, several factors such as geographical breeding origin, age/sex and weather conditions, which are likely to be influenced at broad scales by the El Niño–Southern Oscillation (*ENSO*), could affect the arrival time and body condition of migrant birds and have a subsequent carry over effect in their breeding or wintering areas.

To address these knowledge gaps, I collected data at a constant-effort monitoring station established in the Darién (Tacarcuna Reserve, Sapzurro). I selected a group of 11 long-distance migrant species captured during fall migration (September to November). The group was selected from a considerable diversity of Neotropical migrants in the area and covers a variety of genera, trophic groups, body sizes, and configurations of breeding distribution. The study was carried out at the Tacarcuna reserve in Sapzurro, Colombia, between 2011 and 2015. The group of species includes: Red-eyed Vireo (*Vireo olivaceus*), Veery (*Catharus fuscescens*), Swainson's thrush (*Catharus ustulatus*), Gray-cheeked Thrush (*Catharus minimus*), Yellow Warbler (*Setophaga petechia*), Mourning Warbler (*Geothlypis philadelphia*), Northern Waterthrush (*Parkesia noveboracensis*), Canada Warbler (*Cardellina canadensis*), Prothonotary Warbler (*Protonotaria citrea*), Scarlet Tanager (*Piranga olivacea*) and

Summer Tanager (*Piranga rubra*). In this study, I used stable isotope analyses of feathers to determine breeding origins, connectivity patterns, arrival dates and phenology of migration, patterns of migration, besides examining how factors such as breeding origins, can affect the arrival date and also other factors affecting body condition of birds at the Darién.

1.2 LIGHT STABLE ISOTOPES

Stable isotopes are forms of an element that contain the same number of protons but differ in the numbers of neutrons (Fry 2006). Within applied ecology, researchers have focused mainly on using stable isotope measurements of the light elements C, N, H, O, and S, because they form the principal components of animal tissues, and vary isotopically in nature at different environmental scales and due to various biogeochemical processes (Hobson and Wassenaar 2008). Each of these light elements has an abundant light isotope (e.g., ^{12}C ; 98.894%) and one or more “heavier” rare isotopes of interest (e.g., ^{13}C ; 1.1056%) (Hoefs, 2004).

Stable isotope values are depicted in δ -notation by the formula $\delta^{\text{H}}\text{X} (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] * 1000$ where X is the element of interest (e.g. H, C, N, O or S), the superscript H gives the heavy isotope mass of that element (e.g. ^2H , ^{13}C , ^{15}N , ^{18}O , ^{34}S), and R is the ratio of the heavy isotope to the light isotope for the element, (e.g. $^2\text{H}/^1\text{H}$, $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, $^{18}\text{O}/^{16}\text{O}$, or $^{34}\text{S}/^{32}\text{S}$). A small difference of one percent in relative abundance of the heavy isotope in a sample compared to a standard becomes a 10 per mil (‰) difference in δ units (Fry, 2006).

1.2.1 The use of Hydrogen stable isotopes ($\delta^2\text{H}$) to track bird migration

Over half of temperate-breeding species in the Americas migrate to the tropics during the winter to spend their stationary nonbreeding season there (Newton 2008; Faaborg et al. 2010). There is increasing interest among scientists and conservationists in Latin America to contribute to the development of our knowledge of migratory connectivity and the use of isotopic methods will greatly enhance this field.

Stable hydrogen isotopes are a particularly useful tool to track bird migration in the New World. The weighted mean annual or growing season $\delta^2\text{H}$ in precipitation ($\delta^2\text{H}_p$) show continent-wide patterns (Taylor 1974) with a general trend of decreasing $\delta^2\text{H}_p$ values in precipitation toward northern latitudes. This is most pronounced in North America with systematic declines in $\delta^2\text{H}_p$ values from the Gulf of Mexico across the North American continent to higher latitudes in a northwesterly direction (Hobson and Wassenaar 1997). Values of $\delta^2\text{H}_p$ are fixed in plants, and therefore, passed on to higher trophic-level consumers like birds, insects or other vertebrates (Cormie et al. 1994). In the case of migrant songbirds, the isotopic composition of feathers reflects diet exclusively during the period of growth (Hobson and Clark 1992) as it is assumed no endogenous stores are used (Fox et al. 2009). Taking into account that migrant songbirds breeding in North America grow feathers on or close to their natal grounds before migration (Pyle 1997), the $\delta^2\text{H}$ values of their feathers ($\delta^2\text{H}_f$) are strongly correlated with $\delta^2\text{H}_p$ values during the growing season at the breeding site (Hobson and Wassenaar 1997; Bayly et al. 2012; Hobson et al. 2014). Based on this correlation, it is possible to approximate breeding or natal origins, especially latitude in long-distance migrants by sampling feathers at tropical wintering and stopover sites (González-Prieto et al. 2011; Hobson et al. 2016).

Since the nineties, researchers have sampled feathers of songbirds on their Neotropical wintering grounds with the aim of determining the location of breeding areas and to link them with winter grounds. Hobson and Wassenaar (1997) first demonstrated the broad potential of feather $\delta^2\text{H}$ values by examining several Neotropical migrants at a wintering site in Guatemala and Chamberlain et al. (1997) similarly demonstrated how $\delta^2\text{H}$ values of feathers from Black-throated Blue Warblers (*Setophaga caerulescens*) were correlated with the expected $\delta^2\text{H}$ based on rainfall in the areas where the birds were sampled.

Other investigators like Kelly et al. (2002) used $\delta^2\text{H}_f$ values from Wilson's Warbler (*Cardellina pusilla*) feathers, not only to track breeding origins, but also to describe migration patterns. Migrants sampled in the southernmost region of their winter range had the lowest $\delta^2\text{H}_f$ values, whereas those with the highest values wintered the farthest north, demonstrating a leapfrog migration pattern. This pattern occurs when a more northerly group of birds migrates beyond their southern counterparts to become the more southerly group during winter (Welty 1982). An example of a different pattern, chain migration, identified using stable isotope measurements was provided by researchers in Colombia. González-Prieto et al. (2011) found that individuals of Veery (*Catharus fuscescens*) from southern breeding latitudes arrived at a stopover site on the Caribbean coast of Colombia before those from the northern breeding latitudes.

Knowledge of migratory connectivity is important for identifying key wintering areas and also to predict how conservation measures in one season will influence populations in the following season. For example, Norris et al. (2006) found two different wintering regions for individuals of American Redstart. Stable hydrogen isotopic

compositions from feathers sampled on the wintering grounds were highly correlated with the longitude of sampling location. Redstarts wintering in Central America were most likely to have originated from the northwest and Midwest breeding regions, whereas individuals from the Caribbean were most likely to have bred in northeast, central-east, and southeast regions. Subsequently, Martin et al. (2007) demonstrated the relative value of conservation efforts on the non-breeding grounds for American Redstart (*Setophaga ruticilla*) based on rate of habitat loss, density, and land costs. The analysis, based on stable isotope data, predicted almost complete extinction of one breeding region because the criteria for establishing non-breeding areas for conservation did not include the habitat where individuals were spending the winter in the tropics. Consideration of how populations are connected can, therefore, result in radically different decisions on how to allocate resources for conserving species.

Taking into account that wintering areas for Neotropical migrant birds like Mexico, Guatemala, Cuba, Puerto Rico, Venezuela and Colombia have been poorly studied, Hobson et al., (2014) demonstrated how the isotope approach using $\delta^2\text{H}_f$ measurements can be effectively used to provide a rapid evaluation of migratory connectivity with the aim to protect bird populations in these wintering areas. However, while an increasing number of studies have investigated connectivity between breeding and wintering grounds, there are still very few studies determining the degree of population mixing at stopover sites, in spite of events on migration being responsible for the majority of annual mortality (Faaborg et al. 2010).

1.3 PHENOLOGY OF MIGRATION

The phenology of migration can be influenced by internal physiological rhythms, and also by extrinsic weather conditions (Gill 2007). For migrant birds, the timing of their arrival on the breeding grounds is an important determinant of reproductive success and fitness (Both & Visser; 2001; Marra et al. 1998). Among migratory species, early arrival may allow priority of access to the highest quality territories (Bensch and Hasselquist 1991; Aebischer et al. 2015; Lozano et al. 2015). This presumed advantage is often cited as an explanation for the territorial sex preceding the non-territorial sex during migration and arrival (Francis & Cooke, 1986; Stewart et al. 2012).

The arrival time of a migrant bird depends on events that occur between the place where the bird departs, its destination and its departure time. These events are: (1) the speed of progression through passage areas, and (2) the total time spent at stopovers (Gordo 2007).

Despite the importance of the phenology of migration to the ultimate conservation of migratory birds, most information on migration phenology centers on the spring and autumn period in North America (Jenni and Kéry 2003). However, basic data for most species in Central and South America remains poorly documented and only few studies in the Caribbean have contributed to fill this knowledge gap (Bayly and Gomez 2011; Cardenas-Ortiz et al. 2017).

1.4 EFFECTS OF THE EL NIÑO–SOUTHERN OSCILLATION (ENSO)

Studies of the relationship between weather and bird migration have been conducted almost entirely within the temperate areas of Europe and North America (Alerstam 1990). Most studies have investigated the role of weather conditions on departure

decisions, and passerines usually select weather conditions that provide tail-wind assistance, but avoid rain or cloud cover (Åkesson and Hedenström 2000; Dänhardt and Lindström 2001).

One of the commonest relationships reported on the effects of weather on migration is that between arrival at a certain place and climate conditions (Huin & Sparks, 1998, Ahola et al. 2004; Sparks et al. 2007). Although there are some studies investigating arrival dates at stopover sites in the tropics (Bayly and Gomez 2011) and at wintering grounds (Kok et al. 1991; Gordo and Sanz 2005), only a few researchers have studied the effects of climatic patterns on migration at stopover sites in Central America (Wolfe and Ralph 2009). Filling this gap is important, considering the increasing evidence that variation in climate during the non-breeding season.

Migratory birds depart from their breeding sites at 100s or 1000s of kilometers away from their final destinations (e.g. wintering grounds in the tropics), and therefore it is unlikely that they can accurately assess the *en route* climate conditions. The variation in climate conditions as a result of the combination of La Niña and El Niño, collectively referred as El Niño–Southern Oscillation (ENSO) cycle, can affect the body condition of Neotropical birds during migration through its influence on habitat condition at stopover sites. Climatic variability and ENSO may strongly affect the availability of resources necessary for a successful completion of migration (Wolfe and Ralph 2009). At the two extremes of the cycle, ENSO causes strong and persistent deviations away from normal conditions along the entire length of major flyways in Central America, the Caribbean and northern South America. Conditions during El Niño year are drier than in a normal year. Researchers in the Caribbean have found that the drier conditions induced by El

Niño negatively affects the overwintering survivorship of species like Black-throated Blue Warblers, as a result of reduced food availability (Fraser et al. 2012). Therefore, El Niño years, birds are likely to encounter reduced habitat quality at all stopover sites along their route.

The relative impact of ENSO cycles may depend on diet. Migrants that depend on insects for refueling during stopover may not be as strongly affected by El Niño, because in the tropics, insects are relatively abundant year-round (Levey and Stiles 1992). In contrast, migrants that depend on fruit resources for refueling may be especially affected by El Niño if fruit becomes scarce, due to the dry conditions. For instance, Wolfe and Ralph (2009) found a positive correlation between migrant condition and ENSO during spring migration in Costa Rica. At their field study site, Traill's Flycatchers and Swainson's Thrushes had lower body condition indices during El Niño years (dry conditions) and higher body condition indices during La Niña years (wet conditions), when fruit is an abundant resource.

Regarding weather conditions encountered by Neotropical migrants while they fly through regions north of the Darién, it is known that individuals from the eastern coast of North America typically migrate over the western Atlantic ocean or the Gulf of Mexico avoiding periods of unfavorable conditions and large scale movements coincide with good weather conditions (Alerstam and Lindström 1990; Moore et al. 1995). However, they also have a high probability of encountering unfavorable conditions while flying over water e.g. they may leave the US with good conditions but encounter a tropical storm or worse a hurricane over the southern Gulf. In contrast, species from the western coast of North America typically migrate over land through Mexico and Central America

(Moore et al. 1995). Therefore, they can presumably stop if weather conditions deteriorate. In contrast, many birds succumb during unfavorable weather while attempting to cross parts of the Atlantic Ocean (Alerstam 1990) and the Gulf of Mexico (Lowery 1946). As a consequence, the abundance of Neotropical migrants from eastern North America might be affected more strongly by the frequency of unfavorable weather conditions during migration than would the abundance of songbirds from western North America, because the latter group does not have to migrate over the ocean (Butler 2000).

In conclusion, the effect of Climate conditions on *en route* migration is a field still unexplored especially in the tropics at stopover sites. This topic deserves the attention of researchers in order to detect new factors that negatively affect bird migration and therefore survivorship of Neotropical migrants during the migration season in South America.

1.5 OVERALL OBJECTIVE AND HYPOTHESIS

The objective of this thesis is to investigate factors influencing fall migration of a group of Neotropical migrants arriving to a stopover site in the Darién region of Colombia. The following is an outline of each chapter:

1.5.1 Chapter II

This chapter describes the origins and degree of population mixing in the Darién region. I used $\delta^2\text{H}$ measurements of feathers grown in the breeding or natal sites and used Bayesian assignment techniques to evaluate approximate origins of these birds (Hobson et al. 2014). This allowed me to evaluate to what degree the Darién region is

acting as an important geographical focal point to concentrate species or birds moving from their entire breeding region during fall migration, or whether there is more structure in the connectivity and movement of birds through this point of contact with the northern Hemisphere. These analyses also allowed me to test how breeding or natal origin determines arrival time and phenology of migration. The following questions were investigated:

1. Is the Darién region acting as an important geographical area concentrating migratory birds from different breeding latitudes and longitudes?
2. Do birds from more northern origins (i.e. longest distance migrants) arrive to the Darién later than those from more southern origins based on the distance that they have to migrate? (i.e. chain migration).

1.5.2 Chapter III

Changes in body condition reflect changes in the energy reserves available to birds to migrate. Therefore, it is important to evaluate different factors such as breeding origin, age, sex, body size, route of migration and climatic cycles as possible factors affecting energy reserves during fall migration in the Darién region of Colombia.

The following hypotheses were tested.

1. Birds from northern origins arrive to the Darién in poorer body condition than those from southern origins. This is expected because birds from northern populations must migrate longer distances than those from southern populations.
2. Between species, individuals with relatively larger body size will arrive in better body condition than those of smaller body size, particularly among species known to make over-water crossings. This is based on the fact that longer wing length measures as an estimate of body size may produce better flight

performance and therefore better body condition than shorter wing length measures.

3. Species for which part of the population is known to migrate mostly over water, crossing the Gulf of Mexico and/or the Caribbean Sea (those primarily from eastern North America), will arrive in lower body condition relative to those that migrate mostly overland, because they are unable to top-up their energy reserves while migrating over water.

4. Migrants are affected by the ENSO cycle, such that El Niño years lead to poorer body condition on arrival relative to La Niña years. This is expected because during El Niño years, the conditions are dryer than during La Niña years, during which the food resources are expected to be more abundant.

1.5.3 Chapter IV

In this chapter I analyzed banding data from Canada Warblers captured over three years at two sites located on Colombia's Caribbean coast during fall migration: the Darién and the Sierra Nevada de Santa Marta.

My objectives were to determine:

1. The breeding origins of migrating Canada Warbler.
2. The relative importance of the two migration pathways (trans-Caribbean and Central American).
3. The phenology of migration at each site.
4. Whether there are differences in the age and sex composition of Canada Warblers at the two sites.
5. The body condition of Canada Warblers at the time of arrival in Colombia.

6. Does Canada Warbler use our study sites for refueling during multi-day stopovers?

1.6 THESIS STRUCTURE

This document was formatted according to the guidelines set forth by the College of Graduate Studies and Research at the University of Saskatchewan. It has been divided into five chapters. Over the first chapter, I introduce the topic of the importance of studying the ecology of migration using stable isotope ratios in feathers of Neotropical migrants during *en route* migration and outline my thesis objectives. Chapters 2, 3 and 4 are data chapters and Chapter 5 represents the conclusion of this thesis in which I briefly summarize the results of my work and discuss its relevance.

CHAPTER 2. BREEDING ORIGINS, TIMING AND MIGRATION PATTERNS OF NEOTROPICAL MIGRANTS THROUGH THE DARIÉN REGION OF COLOMBIA

2.1 INTRODUCTION

Successful completion of the migratory route is one of the most demanding activities in the annual cycle of migratory birds (Cohen et al., 2014, Weber & Stilianakis, 2007).

Many species breeding in North America undergo long-distance migrations covering thousands of kilometers between their breeding sites and over-wintering sites in Central America, the Caribbean and South America. These Neotropical migrants typically stop at several sites *en route* where they may either rest, ride out unfavorable conditions at emergency stops or undergo refueling (Bayly et al., 2012; Mehlman et al., 2005; Yong & Moore, 1997). However, little is known about the location and use of such sites during fall migration in the Neotropics and even fewer studies have addressed our lack of knowledge of basic connectivity patterns between breeding and stopover sites, despite the importance of such information for the conservation of migratory birds (Faaborg et al., 2010; González-Prieto et al., 2011; Hobson et al., 2015; Trierweiler et al., 2014).

Stopover sites that concentrate migrants during their fall migrations are particularly valuable for conservation because they can involve birds from potentially diverse origins at continental scales (Hobson et al., 2014). The Darién region of Colombia, located at the international border with Panama, marks the end of the Mesoamerican landmass, an important corridor of land that connects North and South America and acts as a major flyway for birds migrating between the two continents. The region is known to be important, not only for diurnal and nocturnal migrants (Bayly et al.

2014) but also as a stopover site for species groups such as the *Catharus* thrushes (Gómez et al., 2014). However, despite the demonstrated strategic importance of the region for a few species, it is still unclear the degree to which the Darién region is important to species with broad breeding origins in North America and which can presumably reach South America by several alternate routes. The greater the proportion of the breeding population using the Darién during migration, the greater its relative importance from a conservation perspective. Further, the determination of breeding origins of those species using the Darién during fall will assist in understanding the full annual cycle and ecology of these migrants (Gómez et al. 2014; Hostetler et al. 2015).

Stable hydrogen isotope ($\delta^2\text{H}$) analyses have been used to approximate origins of birds in North America based on the fact that feather $\delta^2\text{H}$ values ($\delta^2\text{H}_f$) have been shown to be good indicators of moulting latitude. Most North American passerines molt following breeding and before migration (Pyle 1997). Isotopic information at these breeding locations is thus locked in and available for forensic analysis through subsequent feather sampling. Predictable continent-wide patterns of $\delta^2\text{H}$ in precipitation ($\delta^2\text{H}_p$) have been established which in turn structure the isotopic composition of foodwebs leading to birds (Hobson et al. 2012; Hobson & Wassenaar, 2008). Therefore, $\delta^2\text{H}_f$ values serve as a proxy for estimating primarily latitude of breeding origin and hence potential distance travelled prior to arrival at the sampling site. Thus, apart from predicting general latitude of origin for individuals and species, $\delta^2\text{H}_f$ measurements can also allow insight into patterns of migration.

Timing of migration of individuals through stopover sites is expected to be controlled, in part, by distance travelled from the breeding grounds and the speed of migration (Kelly et al., 2002; Wilson et al., 2008). Nonetheless, migratory species exhibit a diversity of movement patterns including chain and leapfrog migration (Fontaine et al., 2015; Newton, 2008) but the documentation of such population patterns is rare (Kelly, 2006). Chain migration involves birds from southern and northern breeding latitudes moving in sequence to their wintering grounds, with southerly birds moving through stopovers first (e.g. Sharp-shinned Hawks (*Accipiter striatus*), (Smith 2013). In contrast, leapfrog migration involves birds from more northern breeding latitudes overflying those from more southern populations, presumably to arrive at stopover sites first (e.g. Wilson's Warbler (*Wilsonia pusilla*), Kelly et al., 2002). Patterns of migration are important not only because they can affect individual fitness and population dynamics (Gow and Wiebe 2014), but also because they can be crucial to conserve species in decline like Neotropical migrants. When the majority of individuals of a breeding population winter or stopover in the same location and do not mix with other populations (i.e. strong connectivity), the impacts of environmental effects on both breeding and non-breeding grounds, such as habitat loss or disturbance, will be focused on that specific breeding population (Sheehy et al., 2010; Webster et al., 2002). In contrast, when individuals without strong connectivity overlap with other breeding populations at stopover sites or wintering sites, negative effects of changes to stopover, breeding and wintering sites may be less critical at the population level (Webster et al. 2002; Fraser et al. 2012).

My objectives were to: 1) Determine breeding origins of 11 long-distance Neotropical migrants captured during fall migration in the Tacarcuna Nature Reserve, Darién, Colombia using stable hydrogen isotope ($\delta^2\text{H}$) analyses of feathers; 2) Determine the timing of migration of the same group of species through the Darién; 3) Describe patterns of migration by combining isotopic breeding signatures with arrival dates. I reasoned that these data are fundamental to any understanding of the conservation value of this region to a broad spectrum of Neotropical migrants.

2.2 METHODS

2.2.1 Study sites

My field site was located in the Tacarcuna Nature Reserve (08°39'41.53"N, 77°22'06.74"W), near the village of Sapzurro and the international border of Colombia and Panama (Figure. 2.1). Habitat consisted of seasonal tropical humid forest interspersed with small clearings for agriculture and houses, approximately 100 m above sea level in close proximity to the Caribbean coast.

2.2.2 Data collection

I studied Red-eyed Vireo (*Vireo olivaceus*), Veery (*Catharus fuscescens*), Swainson's Thrush (*Catharus ustulatus*), Gray-cheeked Thrush (*Catharus minimus*), Yellow Warbler (*Setophaga petechia*), Northern Waterthrush (*Parkesia noveboracensis*), Mourning Warbler (*Geothlypis philadelphia*), Canada Warbler (*Cardellina canadensis*), Prothonotary Warbler (*Protonotaria citrea*), Scarlet Tanager (*Piranga olivacea*) and Summer Tanager (*Piranga rubra*). This group of species represents a diverse range of breeding origins across North America and all are long-distance Neotropical migrants.

The majority of these species have shown population declines over the last decades (Sauer et al. 2014).

I collected data on the target species at a constant effort mist-net station (8-12 mist nets, 12 or 18 m long, 32 mm mesh, North Ronaldsay and Japanese). Mist nets were positioned strategically to maximize captures and the number of nets and their location were kept virtually constant among days and years. The station was operated during fall migration between September and November during five years 2011-2015. Nets were opened daily or every other day from dawn and remained open for 4.5 hours on average, during which time they were checked every 30-40 min. Birds were transported in individual cloth bags to a banding station where they were fitted with uniquely coded Porzana-made metal bands (band reporting website: www.aselva.co). For all captures, I recorded species, date, time of capture, age, and sex, as well as basic morphometric measurements not analyzed here (Pyle 1997).

2.2.3 Feather sampling

I collected the first primary feather from hatch-year (HY) and after hatch-year (AHY) individuals captured in the Darién, except for Red-eyed Vireo, for which only HY birds were sampled as adults molt their primary feathers on their winter grounds. The first primary feather is the first to be molted on the breeding grounds (Pyle 1997) and so is a more reliable indicator of the natal or breeding origin. After collection, feathers were placed in paper envelopes with individual information. Later, feathers were exported to Canada for isotope analyses at the Stable Isotope Laboratory of Environment Canada (Saskatoon) under permit from the Autoridad Nacional de Licencias Ambientales (ANLA) in Colombia.

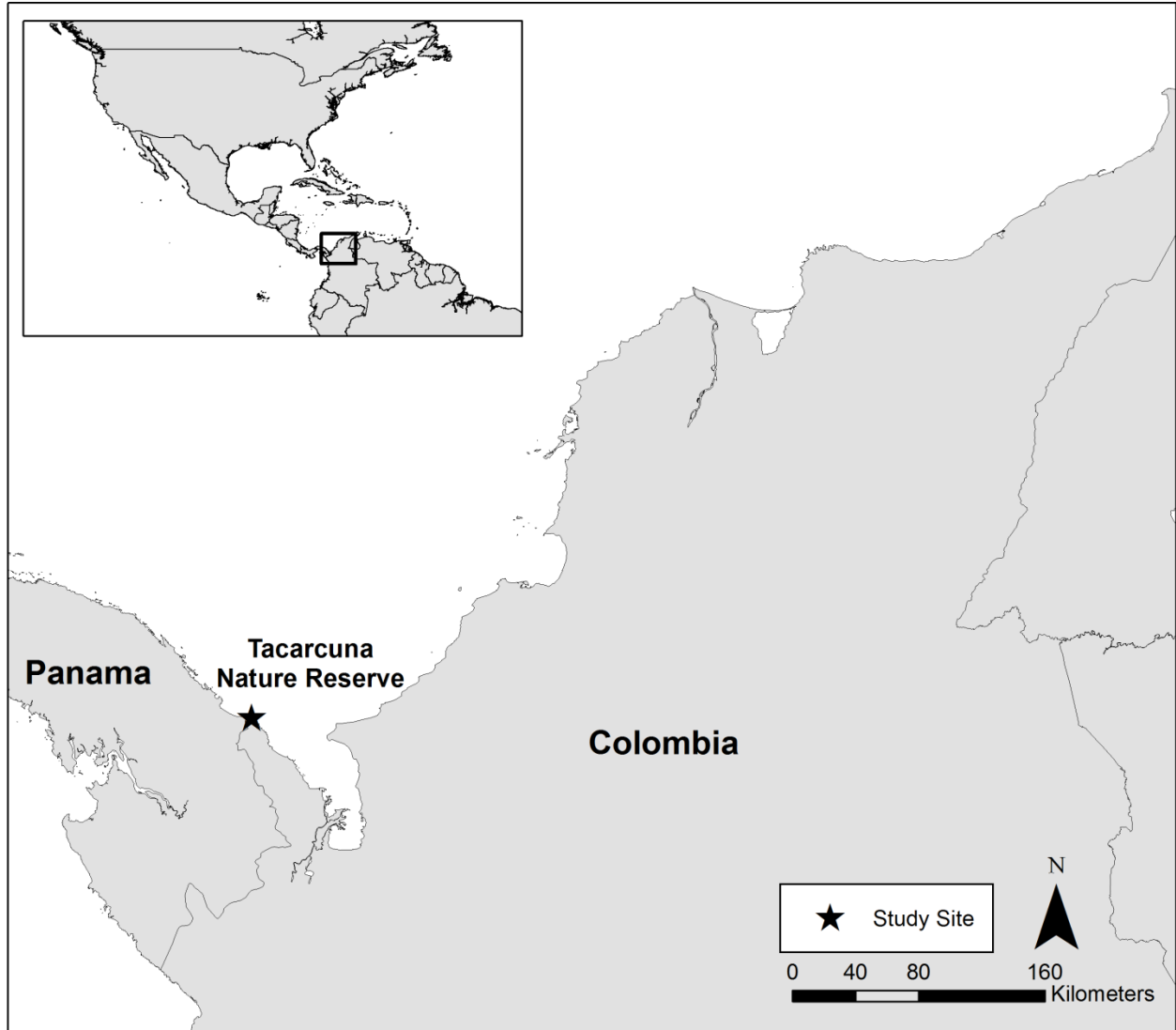


Figure 2.1 Location of study site in the Darién region of northwest Colombia: Tacarcuna Nature Reserve, Sapzurro, Darién, Colombia.

2.2.4 Feather preparation for stable isotope analyses

Feather samples were prepared in the Environment Canada stable isotope laboratory at the National Hydrology Research Centre (NHRC) in Saskatoon, Canada. Each feather sample was soaked for 5 hours in 2:1 chloroform: methanol solution, then rinsed and dried in a fume hood for 48 hr (Wassenaar 2008). The impact of exchangeable

hydrogen on isotopic measurements was corrected using the comparative equilibration method described by Wassenaar and Hobson (2003). Within analytical runs, I used Environment Canada keratin reference standards CBS (Caribou hoof: -197‰) and KHS (Kudu horn: -54.1‰) to calibrate samples. H Isotopic measurements were performed on H₂ gas derived from high-temperature (1350°C) flash pyrolysis of 350±10 ug distal vane feather subsamples in silver capsules. Resulting H gas was separated in a Eurovector 3000 (Milan, Italy) elemental analyser and introduced into an Isoprime (Crewe, UK) continuous flow isotope ratio mass spectrometer. All results are reported for non-exchangeable H expressed in the typical delta (δ) notation, in units of per mil (‰), and normalized on the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale (Wassenaar and Hobson 2006). Based on within-run replicate (n=5) measurements of laboratory keratin standards, we estimate measurement precision to be ± 2‰.

2.2.5 Timing of migration-Phenology

Phenology of fall migration was considered separately for each species. I calculated the percentage of individuals captured per day by dividing the capture total for any given day by the total number of fall captures for each of the years. For any given date, I then calculated the mean percentage across the four years but only including days on which mist-nets were opened. As mist-net effort varied among years but little among days within years, this method is expected to provide a reliable approximation to the timing of migration, without having to correct for the complex effect of mist-net effort.

2.2.6 Determination of breeding-ground origins using isotope analyses

I assigned birds to breeding areas using a likelihood-based assignment method (Royle and Rubenstein 2014). Details of my approach for assigning birds to origins in a probabilistic framework are described elsewhere (Hobson et al. 2014). Briefly, I employed algorithms relating variation in $\delta^2\text{H}_f$ to variation in amount-weighted growing season average $\delta^2\text{H}_f$ (Hobson et al. 2012). Hobson et al. (2012) provided separate isoscape calibration equations based on migratory and foraging guilds. Based on Hobson et al. (2012), I derived the $\delta^2\text{H}_f$ isoscape for non-ground-foraging species like Red-eyed Vireo, Swainson's Thrush, Yellow Warbler, Mourning Warbler, Canada Warbler, Prothonotary Warbler, Scarlet Tanager and Summer Tanager using the algorithm $\delta^2\text{H}_f = -27.09 + 0.95 \delta^2\text{H}_p$ and for ground-foraging Neotropical migrants $\delta^2\text{H}_f = -17.6 + 0.95 \delta^2\text{H}_p$ like Veery, Gray-cheeked Thrush and Northern Waterthrush. To limit assignment results to biologically plausible origins, I used digital range maps (Ridgely et al. 2011) to clip the recalibrated isoscape to the breeding range using functions in the raster package (Hijmans and Etten 2016) in the R statistical computing environment version 3.3.3. For each individual sample (bird), I assessed the likelihood that each cell in the calibrated isoscape represented a potential origin for the individual using the normal probability density function and applied a 2:1 odds ratio criterion for including each pixel as a potential source or not. Probabilities of origin surfaces were combined for all individuals in a population whereby pixel data reflected how many individuals at a given pixel were included in a final population depiction.

2.2.7 Migration patterns

To describe patterns of migration (e.g. chain vs. leapfrog), I determined the relationship between the assumed arrival date (Julian day of first capture) of each individual and its latitudinal breeding origin (isotopic $\delta^2\text{H}_f$ value) migrating through the Darién. Taking into account that other factors can affect arrival day (i.e. the response variable) besides breeding origin, I ran General Linear Models (GLMs) including the explanatory variables: $\delta^2\text{H}_f$ values (continuous), age, sex and year (categorical), as biological factors affecting arrival day. Years with small sample size were not included in the analyses depending on each species and age and sex were only included for those species for which they could be determined. If species adopted a chain migration, I expected a significant negative relation between arrival date and $\delta^2\text{H}_f$ value (González-Prieto et al. 2011) and a positive relationship for species with a leapfrog migration.

2.3 RESULTS

2.3.1 Timing of migration-Phenology

Earliest migrants at the study site were Red-eyed Vireo, Yellow Warbler, Northern Waterthrush and Prothonotary Warbler, occurring from early September, followed by Veery, Mourning Warbler and Canada Warbler, which first arrived after the 18 September (Table 2.1). Summer Tanager, Swainson's Thrush, Scarlet Tanager and Gray-cheeked Thrush typically arrived later, from late September/early October onwards. The peak of migration for the majority of species (Annex 1), apart from Yellow Warbler (19 September), was in October. Early October peaks were recorded for: Red eyed Vireo (2 October), Veery (8 October), Mourning Warbler (10 October), Prothonotary Warbler (1 and 9 October); Mid October for: Swainson's Thrush (19

October), Northern Waterthrush (14 October), Canada Warbler (11 October), Scarlet Tanager (16 and 19 October) and late October for: Gray-cheeked Thrush (20 and 21 October) and Summer Tanager (25 October).

Table 2.1 Number of 11 focal species of Neotropical long distance migrants captured by age (HY: Hatch year; AHY: After hatch-year) and sex (M: Male; F: Female), and the first and last capture dates for each species in the Tacarcuna Nature Reserve, Sapzurro, Choco, Colombia (2011- 2015).

Species	N	Age		Sex		Phenology
		HY	AHY	M	F	
Red-eyed Vireo	1373	278	664	-	-	11 Sep - 6 Nov
Veery	782	541	241	-	-	17 Sep - 5 Nov
Swainson's Thrush	1960	1434	522	-	-	26 Sep - 3 Nov
Gray-cheeked Thrush	846	545	269	-	-	30 Sep - 5 Nov
Yellow Warbler	139	86	47	56	66	12 Sep - 3 Nov
Northern Waterthrush	131	93	37	-	-	11 Sep - 3 Nov
Mourning Warbler	287	181	105	96	118	18 Sep - 3 Nov
Canada Warbler	161	146	15	52	106	20 Sep - 5 Nov
Prothonotary Warbler	282	175	106	135	140	12 Sep - 6 Nov
Scarlet Tanager	100	68	31	59	36	29 Sep - 4 Nov
Summer Tanager	120	53	64	53	58	25 Sep - 5 Nov

2.3.2 Determination of breeding-ground origins using stable isotope analyses

Species sampled in the Tacarcuna Nature Reserve in the Darién, covered a broad range of $\delta^2\text{H}_f$ values (-29‰ to -200‰) (Table 2.2). The isotope data are consistent with origins from an extremely broad geographic breeding area in North America, likely including populations from the extreme south, north, west and east of the continent (Figure. 2.2).

Table 2.2 Summary (mean, SD, 95% CI) of stable hydrogen isotope analyses of feathers ($\delta^2\text{H}_f$) captured at the Tacarcuna Nature Reserve, Sapzurro, Chocó, Colombia during fall migration between 2011 and 2015.

Species	Code	<i>N</i>	Mean (‰)	SD (‰)	95%CI (‰)	
Red-eyed vireo	REVI	169	-76	23	-150	-138
Veery	VEER	222	-93	21	-161	-34
Swainson's Thrush	SWTH	310	-134	24	-180	-50
Gray-cheeked Thrush	GCTH	159	-148	17	-174	-107
Yellow Warbler	YWAR	107	-98	15	-141	-58
Northern Waterthrush	NOWA	77	-134	24	-195	-73
Mourning Warbler	MOWA	147	-115	23	-181	-56
Canada Warbler	CAWA	69	-94	23	-200	-63
Prothonotary Warbler	PROW	153	-61	15	-138	-29
Scarlet Tanager	SCTA	63	-72	12	-96	-54
Summer Tanager	SUTA	35	-57	12	-94	-34

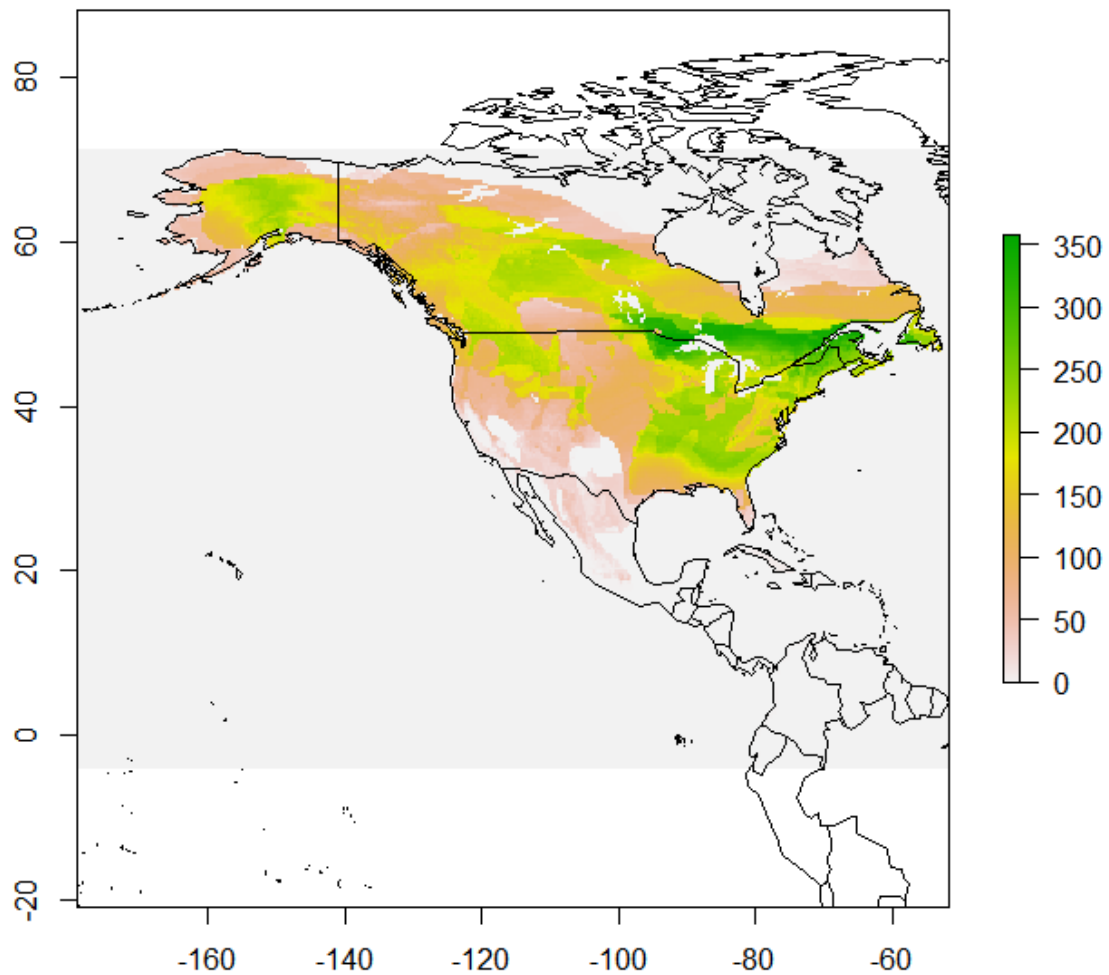


Figure 2.2 Map of the number of individuals assigned to pixels based on the 2:1 odds criteria, combining the most probable breeding origins of 11 species of Neotropical migrants (VEER, SWTH, GCTH, REVI, YWAR, NOWA, MOWA, CAWA, POWA, SCTA and SUTA), to show where the “community of migrants” is originated using isotope data from feathers of individuals captured in the Tacarcuna Nature Reserve, Darien.

Six species had origins consistent with birds arriving from across their expected breeding ranges (Veery (Figure 2.3C), Yellow Warbler (Figure 2.5A), Mourning Warbler (Figure 2.6A), Prothonotary Warbler (Figure 2.7A), Scarlet Tanager (Figure 2.7C) and Summer Tanager (Figure 2.8A)). Yellow Warbler was derived primarily from the central portion of the breeding range (Figure 2.5A). Mourning Warbler showed potential origins from across the northcentral portion of the breeding range (Figure 2.6A).

Three species showed a bias in potential origins towards the western portion of their breeding range (Swainson's Thrush (Figure 2.4A), Gray-cheeked Thrush (Figure 2.4C) and Northern Waterthrush (Figure 2.5C)). Swainson's Thrush had feather isotope values consistent with the northwest region of their breeding range (northwestern boreal of British Columbia, Alberta and Saskatchewan). My depiction also showed western Alaska as a possible origin but this may be an artifact of the isoclines of $\delta^2\text{H}_p$ in precipitation (see Hobson et al. 2014). As expected, Gray-cheeked Thrush showed the most northern origins of all *Catharus* thrushes. Northern Waterthrush showed a similar pattern of origin as the Swainson's Thrush. Finally, two species, Red-eyed Vireo (Figure 2.3A) and Canada Warbler (Figure 2.6C) likely originated primarily from eastern breeding populations.

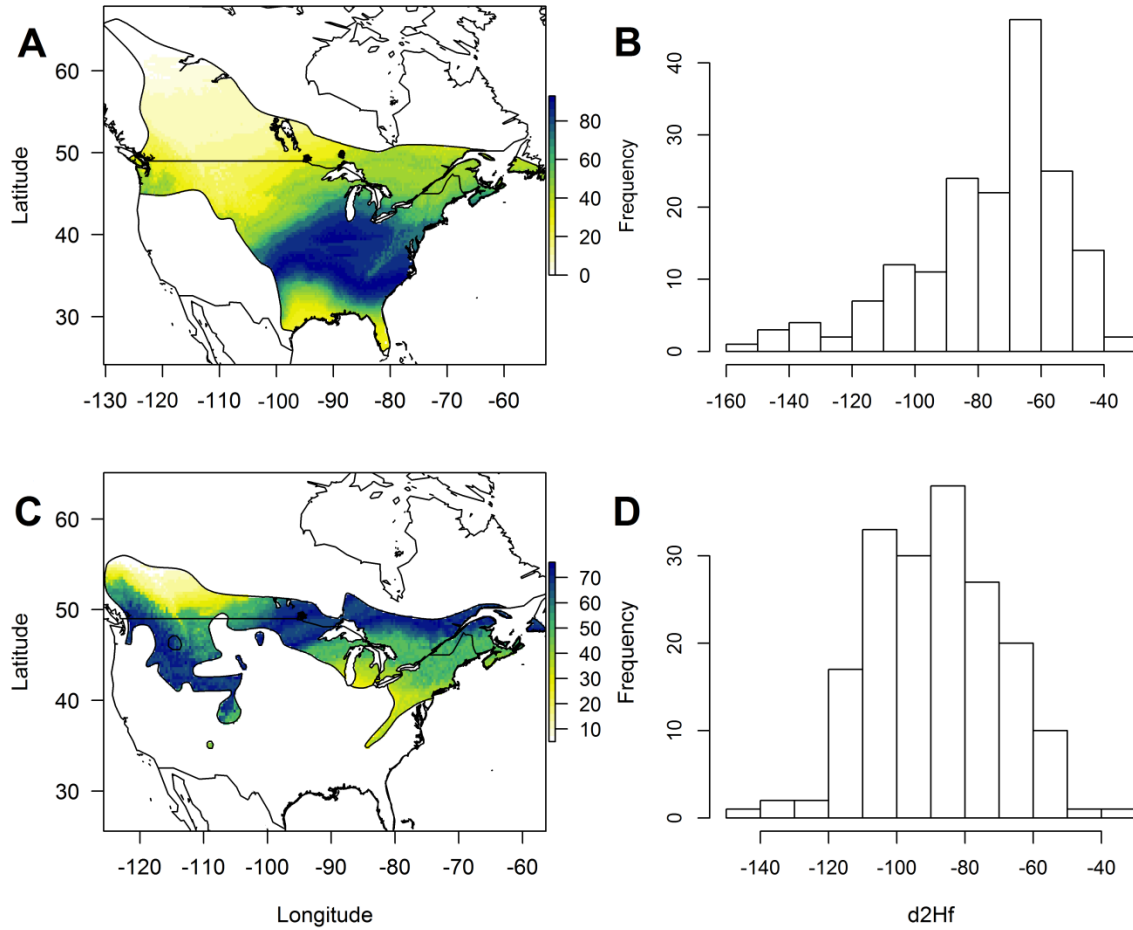


Figure 2.3 Geographic distributions of assigned origins for individuals captured in the Tacarcuna Nature Reserve, Darién, Colombia, during fall migration 2012-2015, as inferred from stable isotope (δ^2H_f) analysis. A) Red-eyed Vireo (N=169; δ^2H_f range: -150 to -138 ‰), B) Histogram of the distribution of the δ^2H_f values of Red-eyed Vireo, C) Veery (N=222; δ^2H_f range: -161‰ to -34 ‰), D) Histogram of the distribution of the δ^2H_f values of Veery.

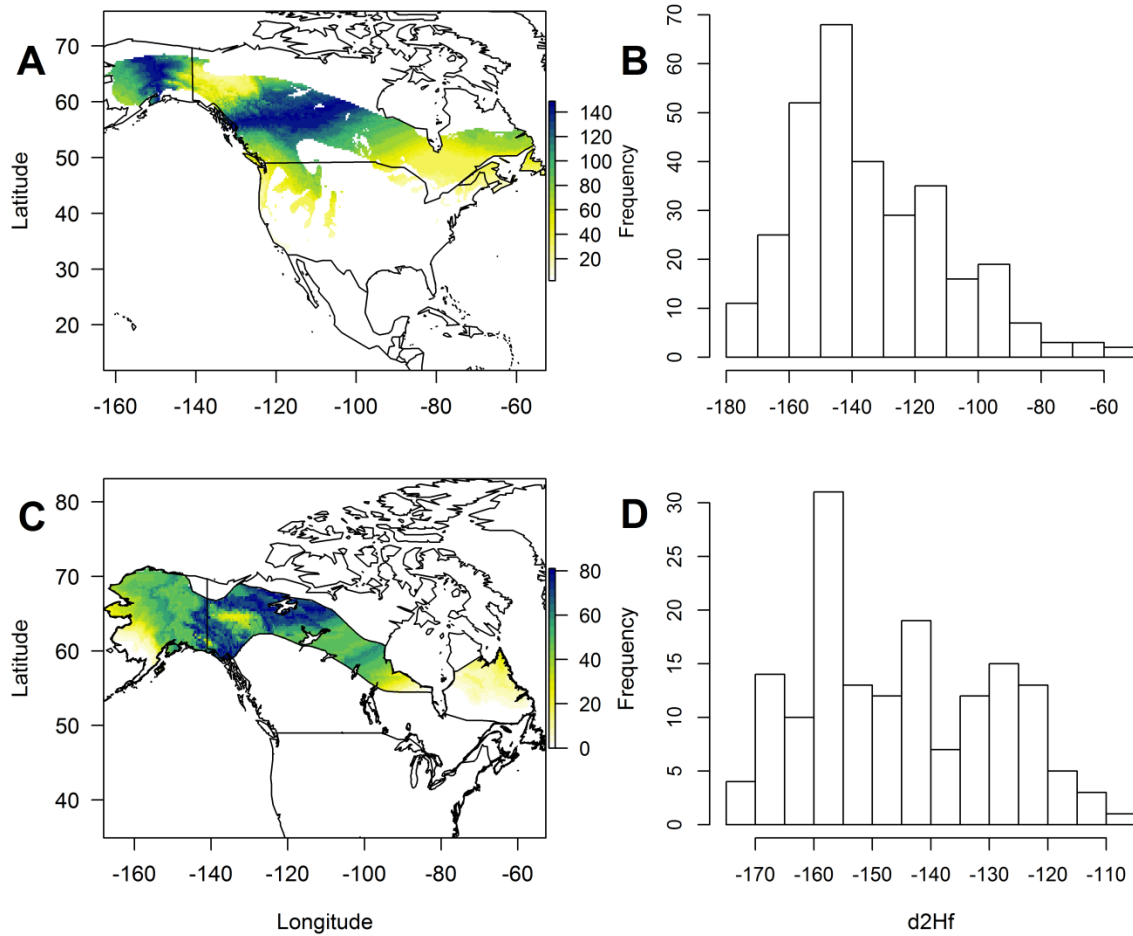


Figure 2.4 Geographic distribution of assigned origins for individuals captured in the Tacarcuna Nature Reserve, Darién, Colombia, during fall migration 2012-2015, as inferred from stable isotope (δ^2H_f) analysis A) Swainson's Thrush (N=310; δ^2H_f range: -180‰ to -50 ‰), B) Histogram of the distribution of the δ^2H_f values of Swainson's Thrush, C) Grey-cheeked Thrush (N=159; δ^2H_f range: -174 to -107 ‰) and D) Histogram of the distribution of the δ^2H_f values of Grey-cheeked Thrush.

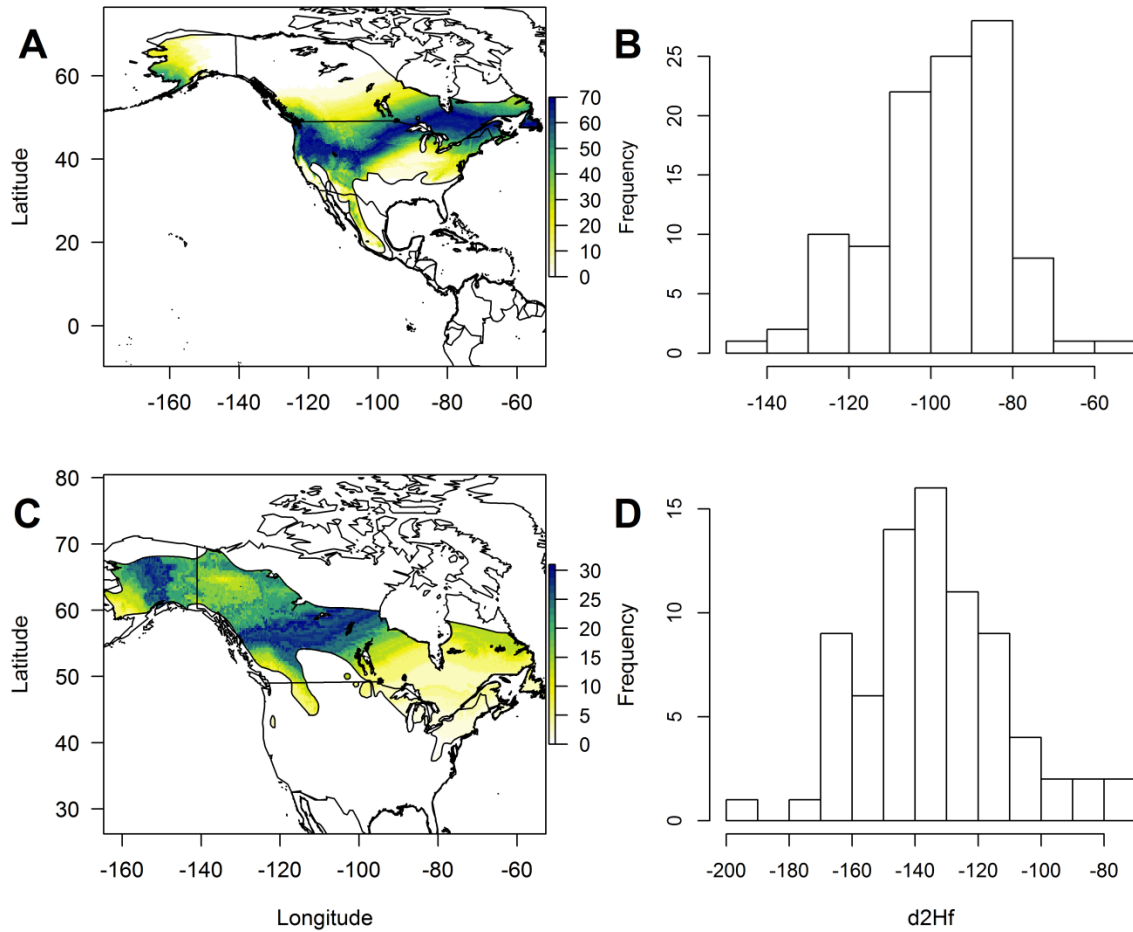


Figure 2.5 Geographic distribution of assigned origins for individuals captured in the Tacarcuna Nature Reserve, Darién, Colombia, during fall migration 2012-2015, as inferred from stable isotope (δ^2H_f) analysis. A) Yellow Warbler (N=107; δ^2H_f range: -141‰ to -58 ‰), B) Histogram of the distribution of the δ^2H_f values of Yellow Warbler, C) Northern Waterthrush (N=77; δ^2H_f range: -195 to -73 ‰) and D) Histogram of the distribution of the δ^2H_f values of Northern Waterthrush.

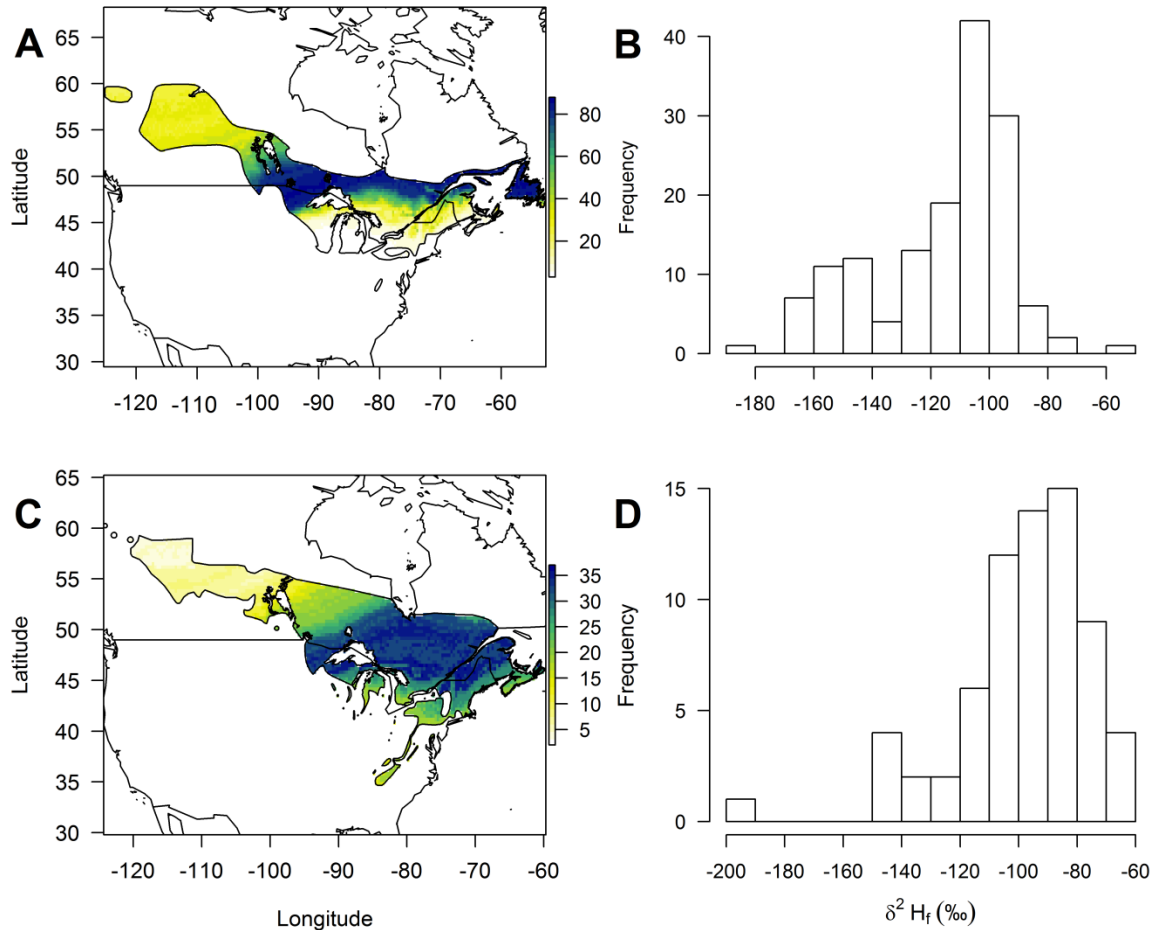


Figure 2.6 Geographic distribution of assigned origins for individuals captured in the Tacarcuna Nature Reserve, Darién, Colombia, during fall migration 2012-2015, as inferred from stable isotope (δ^2H_f) analysis. A) Mourning Warbler (N=147; δ^2H_f range: -181‰ to -56‰), B) Histogram of the distribution of the δ^2H_f values of Mourning Warbler, C) Canada Warbler (N= 69; δ^2H_f range: -200‰ to -63‰ and D) Histogram of the distribution of the δ^2H_f values of Canada Warbler.

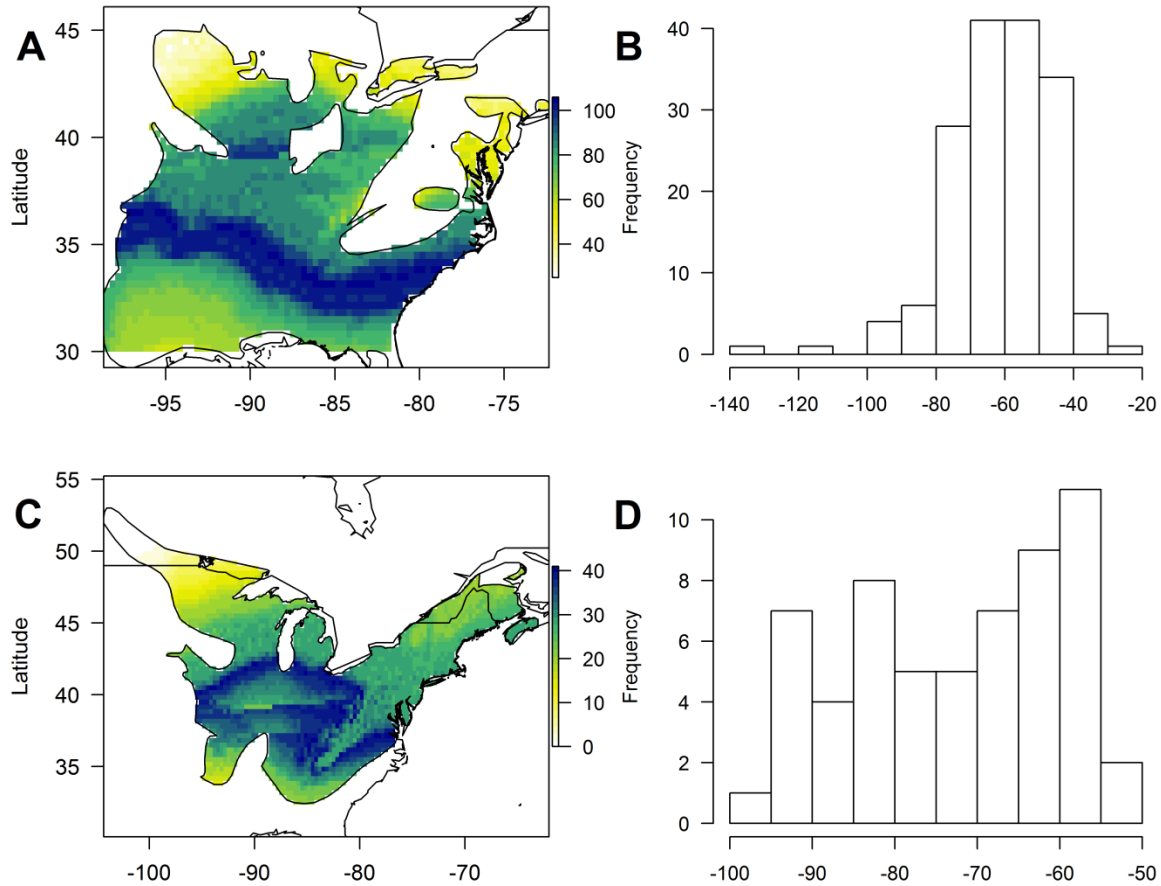


Figure 2.7 Geographic distribution of assigned origins for individuals captured in the Tacarcuna Nature Reserve, Darién, Colombia, during fall migration 2012-2015, as inferred from stable isotope ($\delta^2\text{H}_f$) analysis. A) Prothonotary Warbler (N= 153; $\delta^2\text{H}_f$ range: -138‰ to -29‰), B) Histogram of the distribution of the $\delta^2\text{H}_f$ values of Prothonotary Warbler, C) Scarlet Tanager (N=63; $\delta^2\text{H}_f$ range: -96‰ to -54 ‰) and D) Histogram of the distribution of the $\delta^2\text{H}_f$ values of Scarlet Tanager.

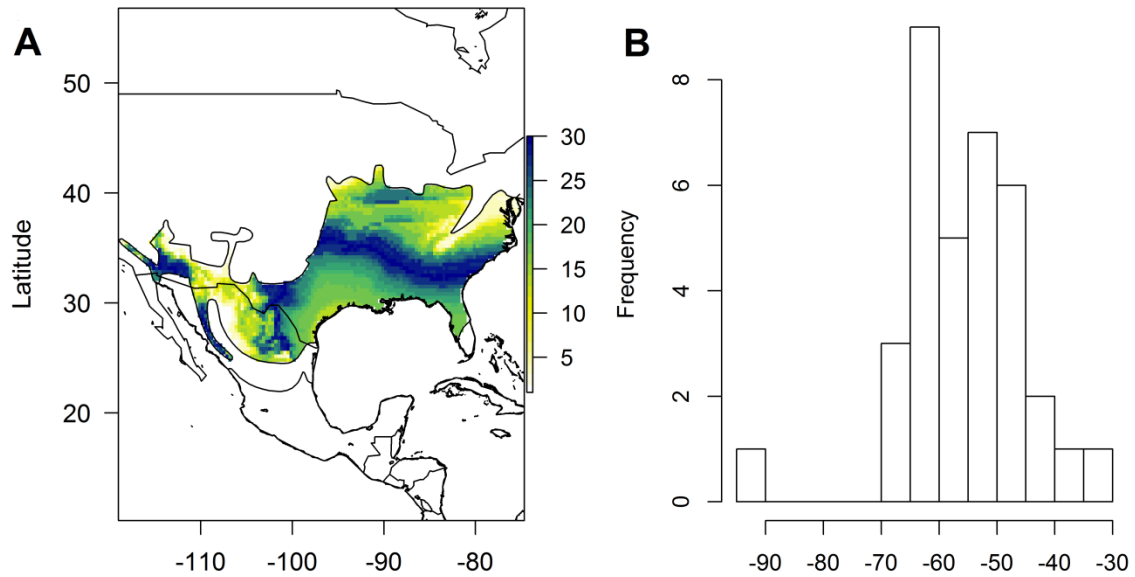


Figure 2.8 Geographic distribution of assigned origins for Summer Tanager captured in the Darién, Colombia, during fall migration, 2011 to 2015, as inferred from stable isotope ($\delta^2\text{H}_f$) analysis (N=35; $\delta^2\text{H}_f$ range: -94‰ to -34‰) and B) Histogram of the distribution of the $\delta^2\text{H}_f$ values of Summer Tanager.

2.3.3 Migration patterns

I found a significant negative relationship between arrival day and the values of δ^2H_f for Red-eyed vireo ($F_{1,169}=38$, $P<0.001$), Yellow Warbler ($F_{1,95}=17$, $P<0.001$), Mourning Warbler ($F_{1,108}=7.801$, $P=0.0061$) and Northern Waterthrush ($F_{1,67}=26$, $P<0.001$), indicating that they used chain migration. A positive relationship was found for Swainson's Thrush ($F_{1,351}=24.5$, $P<0.001$) and Gray-cheeked Thrush ($F_{1,172}=4.2$, $P=0.0419$), suggesting a leapfrog migration pattern. I did not find a significant relationship between arrival time and δ^2H_f for Veery ($F_{1,243}=1.98$, $P=0.1603$), Canada Warbler ($F_{1,57}=0.53$, $P=0.4679$), Prothonothary Warbler ($F_{1,173}=0.1$, $P=0.7884$), Scarlet Tanager ($F_{1,60}=0.9$, $P=0.3559$), and Summer Tanager ($F_{1,34}=0.38$, $P=0.8466$).

In addition to breeding origin, arrival day was also affected by age and year in Gray-cheeked Thrush ($F_{3,170}=8.295$, $P<0.001$) (Figure 2.9E), Northern Waterthrush ($F_{4,64}=9.6$, $P<0.001$) (Figure 2.11A) and Morning Warbler ($F_{6,103}=6.647$, $P<0.001$), age in Swainson's Thrush ($F_{2,350}=21.66$, $P<0.001$), and year in Red-eyed vireo ($F_{2,168}=49$, $P<0.001$) (Figure 2.10A). In contrast, arrival date was only affected by age in Canada Warbler ($F_{2,56}=5.53$, $P=0.0064$; Figure 2.12A), year in Scarlet Tanager ($F_{2,59}=4.08$, $P=0.0217$; Figure 2.13A), age and year in Prothonothary Warbler ($F_{1,173}=0.1$, $P=0.7884$; Figure 2.12A). Arrival date in Summer Tanager was not affected by any factor ($F_{5,30}=0.7957$, $P=0.5614$; Figure 2.13C).

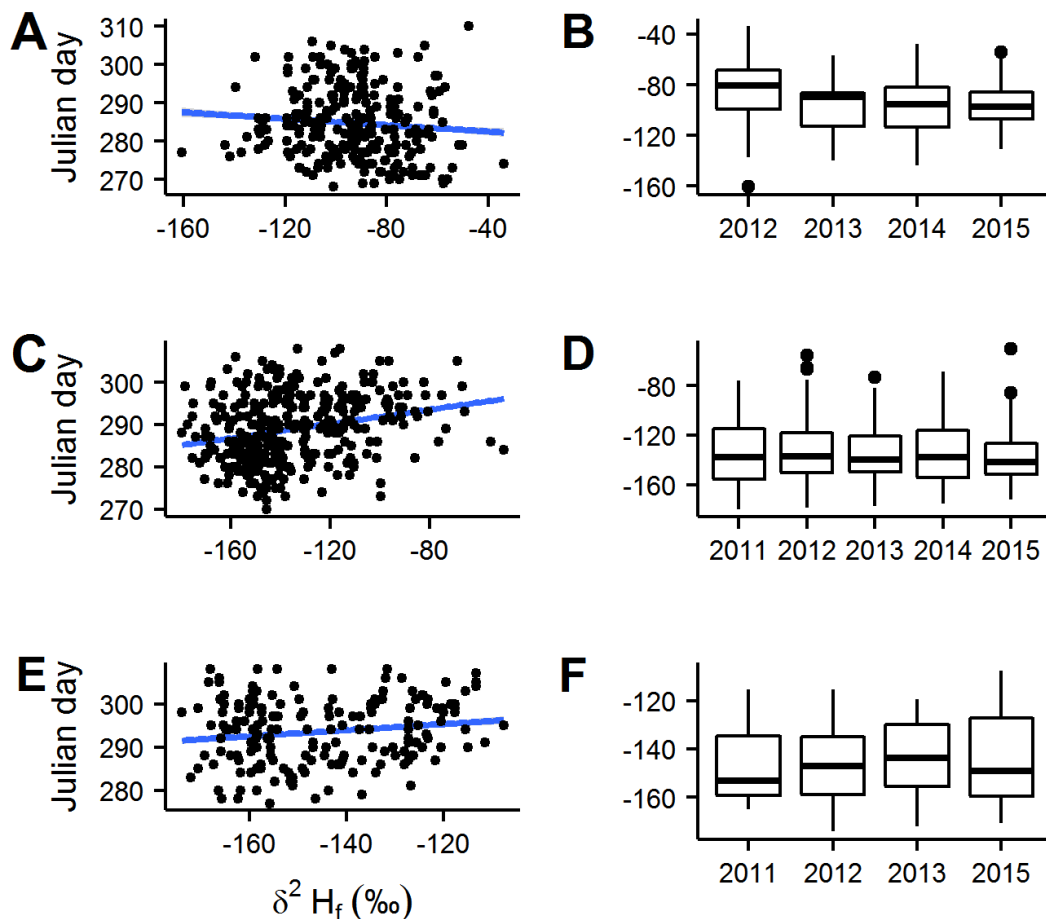


Figure 2.9 A-C-E. Relationship between the ($\delta^2\text{H}_f$) values and Julian day (270 = 27 Sep, 280 = 7 Oct, 290 = 17 Oct, 300 = 27 Oct and 310 = 6 Nov) of arrival to the Tacarcuna Nature Reserve, Darién. A) Veery (*Catharus fuscescens*) B) Median isotope value of ($\delta^2\text{H}_f$) of Veery per year, C) Swainson's Thrush (*Catharus ustulatus*), D) Median isotope value of ($\delta^2\text{H}_f$) of Swainson's Thrush per year, E) Gray-cheeked Thrush (*Catharus minimus*) and F) Median $\delta^2\text{H}_f$ of Gray-cheeked Thrush per year. Upper and lower boundaries of boxplot boxes show the 25th and 75th percentiles, respectively in each boxplot figure B-D-F.

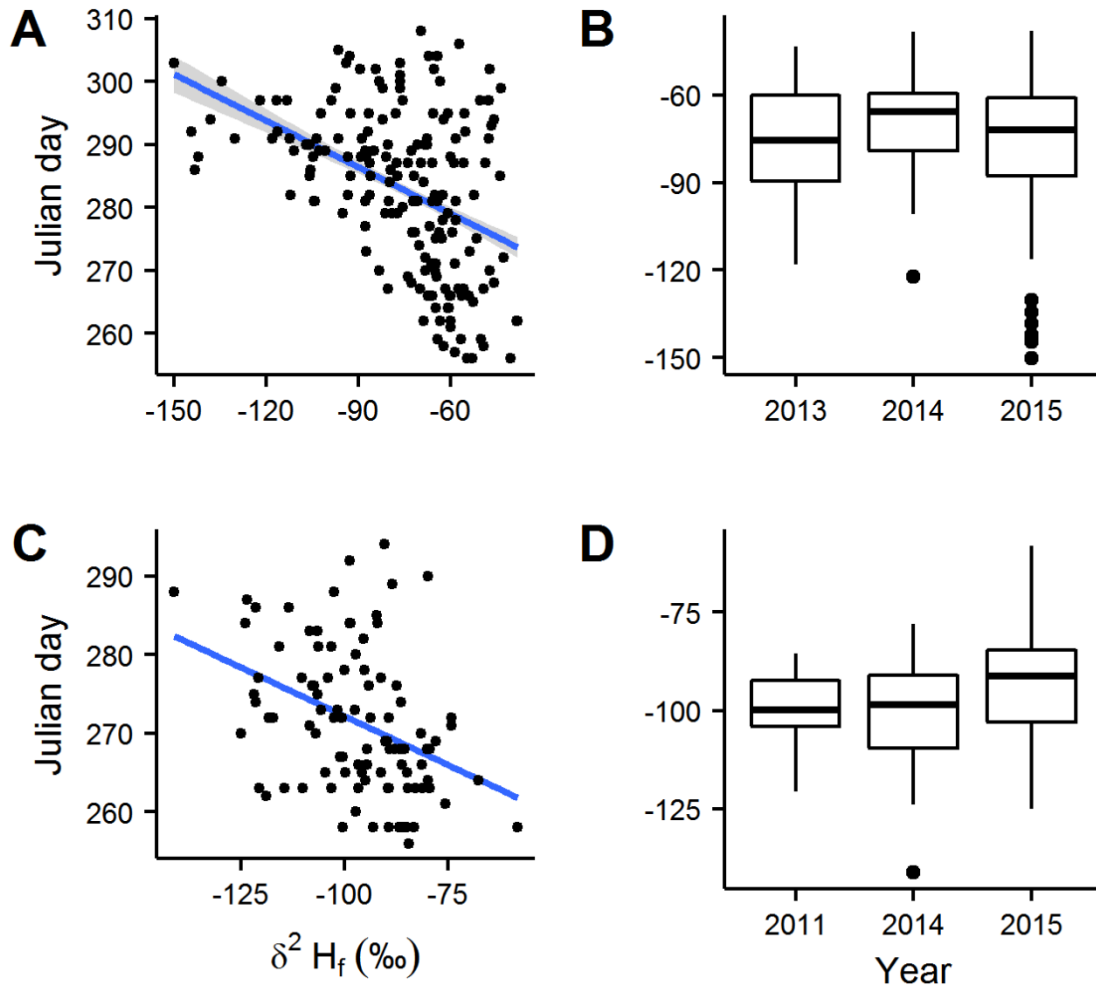


Figure 2.10 A-C. Relationship between the ($\delta^2 H_f$) values and Julian day (260 = Sep 17, 270 = 27 Sep, 280 = 7 Oct, 290 = 17 Oct, 300 = 27 Oct and 310 = 6 Nov) of arrival to the Tacarcuna Nature Reserve, Darién. A) Red-eyed Vireo (*Vireo Olivaceus*), B) Median isotope value of ($\delta^2 H_f$) of Red-eyed Vireo per year and C) Yellow Warbler (*Setophaga petechia*) and D) Median $\delta^2 H_f$ of Yellow Warbler per year. Upper and lower boundaries of boxplot boxes show the 25th and 75th percentiles, respectively in each boxplot figure B-D.

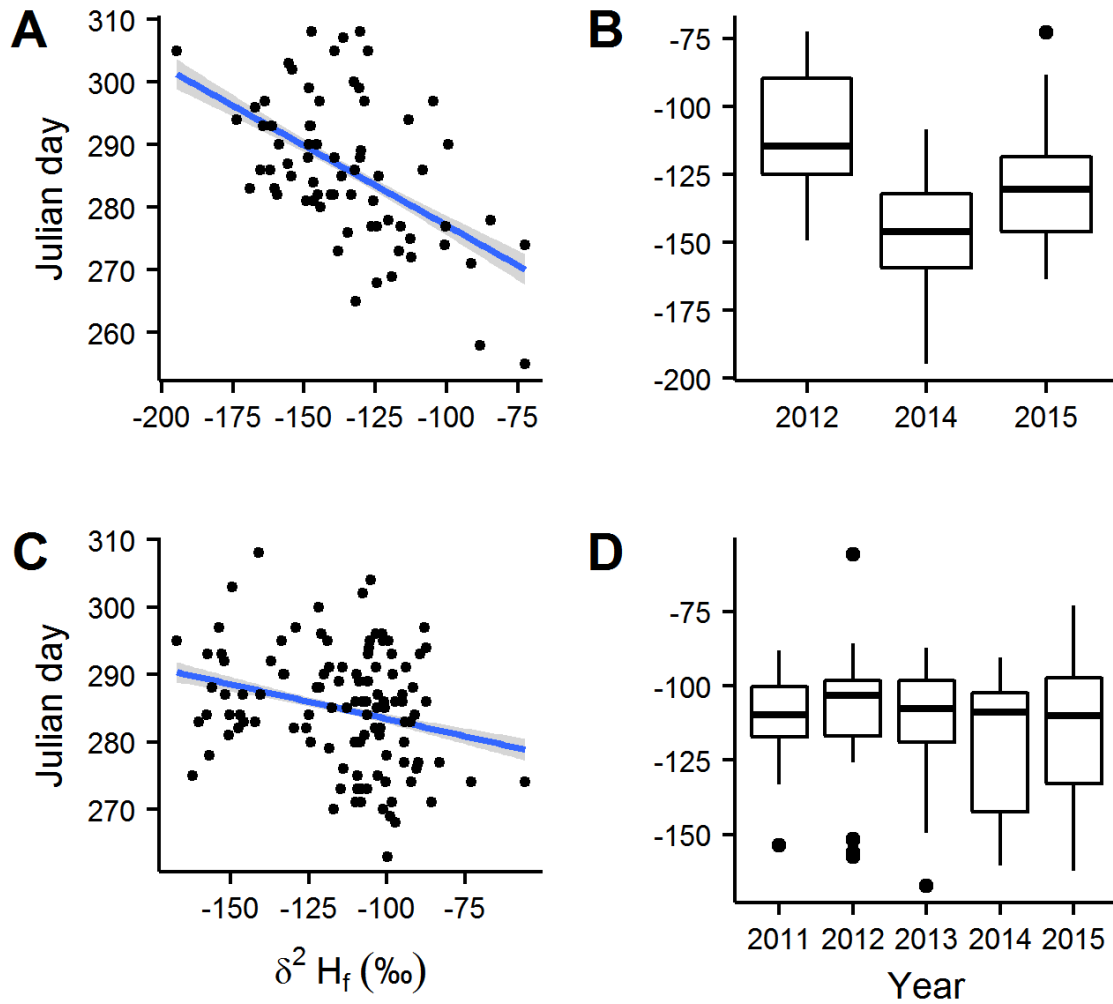


Figure 2.11 Relationship between the ($\delta^2 H_f$) values in feathers and the Julian day (260 = Sep 17, 270 = 27 Sep, 280 = 7 Oct, 290 = 17 Oct, 300 = 27 Oct and 310 = 6 Nov) which represents the arrival date of individuals arriving to the Tacarcuna Nature Reserve, Darién. A) Northern Waterthrush (*Parkesia noveboracensis*), B) Median $\delta^2 H_f$ value of Northern Waterthrush per year, C) Mourning Warbler (*Geothlypis philadelphia*), D) Median $\delta^2 H_f$ value of Mourning Warbler per year. Upper and lower boundaries of boxplot boxes show the 25th and 75th percentiles, respectively in each boxplot figure B-D.

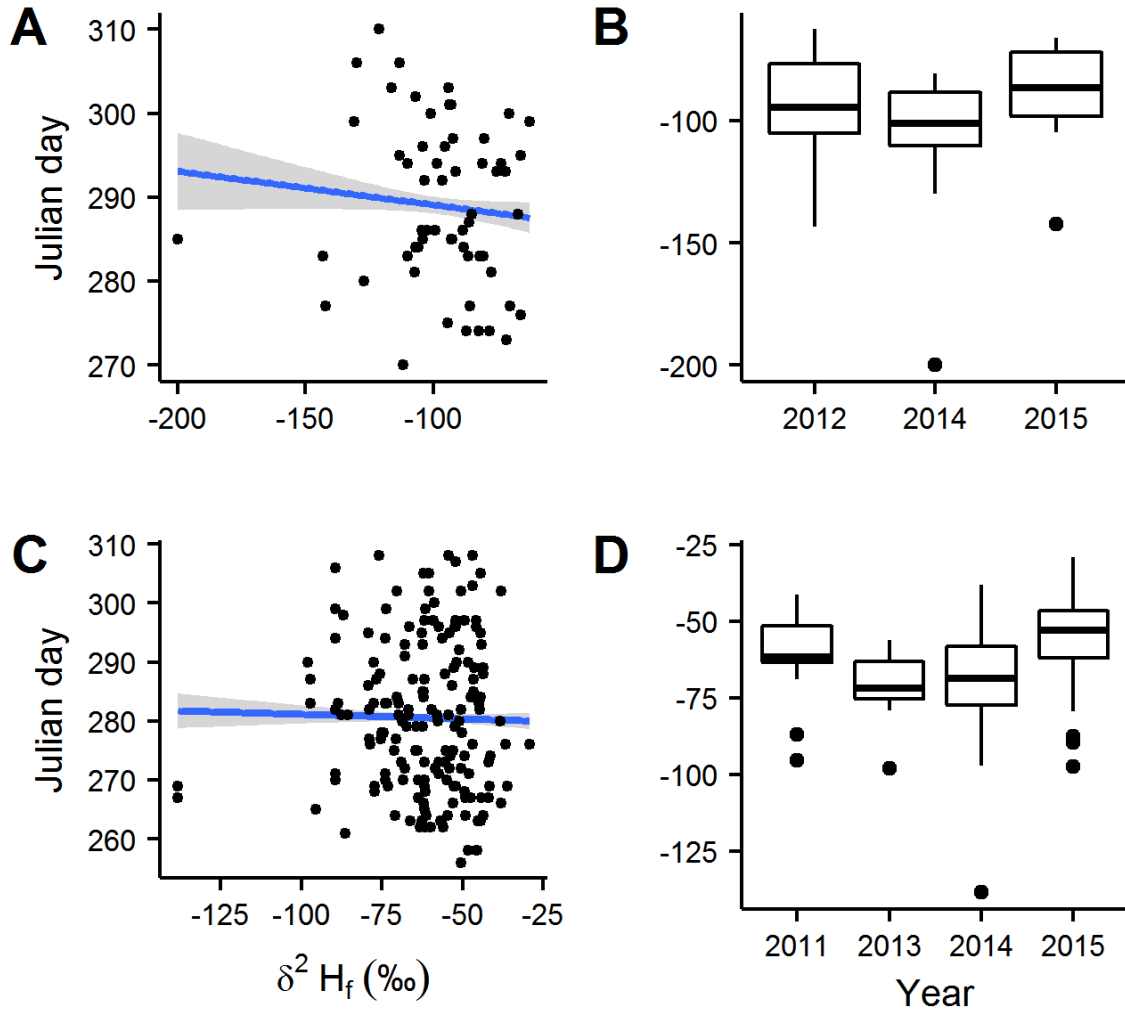


Figure 2.12 A-C. Relationship between $\delta^2\text{H}_f$ and the Julian day (260 = Sep 17, 270 = 27 Sep, 280 = 7 Oct, 290 = 17 Oct, 300 = 27 Oct and 310 = 6 Nov) which represents the arrival date of individuals arriving to the Tacarcuna Nature Reserve, Darién. A) Canada Warbler (*Cardellina canadensis*), B) Median $\delta^2\text{H}_f$ of Canada Warbler per year, C) Prothonotary Warbler (*Protonotaria citrea*) and D) Median isotope value of $\delta^2\text{H}_f$ of Prothonotary Warbler per year. Upper and lower boundaries of boxplot boxes show the 25th and 75th percentiles, respectively in each boxplot figure B-D.

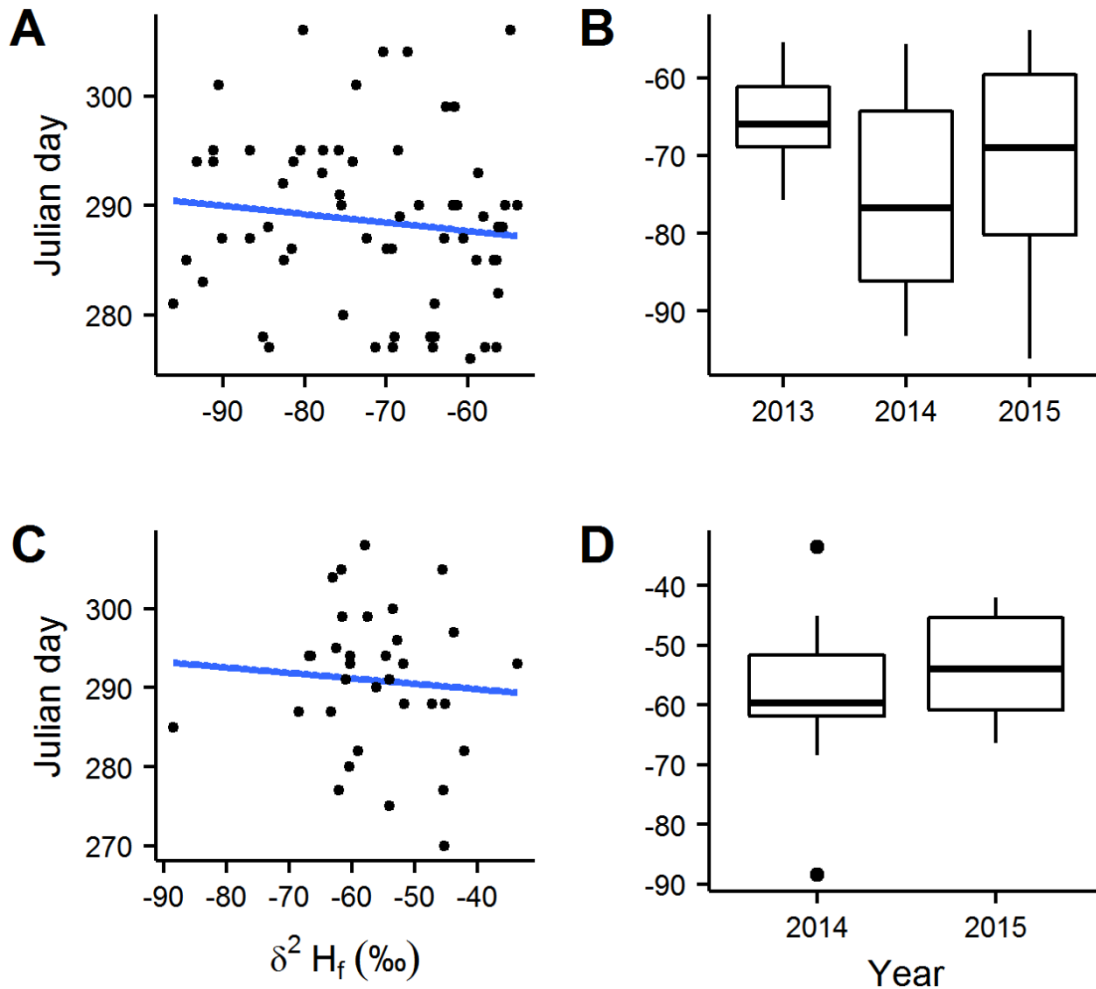


Figure 2.13 A-C. A-C. Relationship between $\delta^2 H_f$ and Julian day (270 = 27 Sep, 280 = 7 Oct, 290 = 17 Oct and 300 = 27 Oct) which represents the arrival date of individuals arriving to the Tacarcuna Nature Reserve, Darién. A) Scarlet Tanager (*Piranga olivacea*), B) Median $\delta^2 H_f$ of Scarlet Tanager per year, C) Summer Tanager (*Piranga rubra*) and D) Median $\delta^2 H_f$ of Summer Tanager per year. Upper and lower boundaries of boxplot boxes show the 25th and 75th percentiles, respectively in each boxplot figure B-D.

2.4 DISCUSSION

Birds from across North America, encompassing varying proportions of their breeding range, converged on the study site located in the Darién during fall migration. Within species, more than half (Veery, Yellow Warbler, Mourning Warbler, Prothonotary Warbler, Scarlet Tanager and Summer Tanager or 55%) showed isotopic values consistent with the presence of individuals from throughout their breeding range. This is consistent with the idea that the Darién region acts like an important area concentrating widely distributed populations into a tiny area of land (Bayly et al. 2014; Gómez et al., 2014, Cardenas et al. 2017). This has important implications for conservation, as loss of stopover habitat here could impact an entire species, not just one or a few of its populations. This highlights the vulnerability of migratory birds at natural geographic areas during migration and the need to increase conservation efforts in these regions (Bayly et al. 2013, 2014).

I also describe for the first time the phenology of migration and the patterns of migration for eleven migrants (Red-eyed Vireo, Veery, Swainson's thrush, Gray-cheeked Thrush, Yellow Warbler, Mourning Warbler, Northern Waterthrush, Canada Warbler, Prothonotary Warbler, Scarlet Tanager and Summer Tanager, showing the effect of breeding origin and therefore, distance traveled on arrival time during *en route* migration. The majority of the species followed a chain migration, while only two showing a leap frog migration pattern, possibly as a strategy to reach on time not only wintering grounds.

2.4.1 Breeding origins and connectivity

Stopover sites located in front of ecological barriers may be as important as other locations as breeding and wintering grounds (Morris et al. 1994). Especially, when they are located at important areas that receives large concentrations of birds migrating from different locations, as it was shown by my results in the Darién. In this study, half of the species showed a marked concentration of birds from across their breeding range. I believe that this result is explained largely by the strategic location of this study site, located in the southeast portion of Central America corridor at the gateway to South America. In comparison with North America, it is way smaller in area, where the Isthmus of Panama narrows to less than 70 km in parts. For this reason, its geography allows it to gather individuals from a variety of breeding areas. Few other places are known to concentrate such high numbers of passerines besides the northern coast of the Gulf of Mexico, where they converge during migration towards South America (Moore et al. 1990; Gauthreaux and Belser 1999; Bayly et al. 2014).

My study site was previously shown to be important during fall migration for Swainson's and Gray-cheeked thrushes (Gómez et al. 2014), as well as for other species of diurnal Neotropical migrants (Bayly et al. 2014). However, species migrating through the Darién region may have alternative migration routes to reach South America. For example, Veery are regular trans-Caribbean migrants, especially among eastern-breeding individuals (Heckscher et al. 2011). Gómez et al. (2014) suggested that the lower abundance of Veery captured in the Darién relative to other species of thrushes, could be the result of a smaller population originating from the western side of its breeding range. Later, Hobson and Kardynal (2015), showed how individuals of

Veery originating from the west side of the breeding distribution, crossed towards the eastern part of North America prior to crossing the Caribbean Sea, on a similar route to birds from the east (Heckscher et al. 2011). Isotope results presented here support the assumption suggested by Gómez et al. (2014), and part of the population of Veery originating in the west portion of its breeding range may cross Central America or take a trans Gulf route to reach the Darién. This route of migration would extend that presented by Heckscher et al. (2011).

2.4.2 Timing of migration

Understanding migration timing through stopover sites assists with the identification of which species co-occur in time and have the potential to interact, and also to define the most active times of migration when potential food competition is likely to be the greatest (Deppe and Rotenberry 2005) and when risk of collision with human-made structures is greatest (Longcore et al. 2012). At our study site, the peak of migration for the majority of species (10), apart from Yellow Warbler, was in October which follows patterns found further north in Belize (Bayly & Gomez, 2011) and the Yucatan (Deppe and Rotenberry 2005).

2.4.3 Migration Patterns

Red-eyed vireo, Yellow Warbler, Northern Waterthrush and Mourning Warbler, showed evidence of a chain migration pattern, in which individuals from southern latitudes arrived before those from northern latitudes. This pattern has been found in short-distance migrants such as Orange-crowned Warblers, Common Yellowthroat (Kelly, 2006) and in Sharp-shinned hawks (Smith et al. 2003) but not in migrants travelling to South America.

In contrast, Swainson's Thrush and Gray-cheeked Thrush, showed evidence for a leapfrog migration pattern, in which individuals from the northern latitudes arrived before those from the south. Individuals originating from farther north could be arriving earlier either by migrating faster or leaving earlier from the breeding grounds (McKinnon et al. 2015). Leap frog migrants can also reduce intraspecific competition by avoiding stopover sites used by more southern breeders (Berthold 1993). Therefore, leap frog migration can be seen as a form of differential migration behavior (as with chain migration) (Gauthreaux 1982).

For species like Swainson's Thrush (Willson et al. 2008) or Gray Catbird (Hobson et al. 2007) no relationship was found between the timing of fall passage and latitudinal origin along the Gulf coast. In my study, Veery showed no clear pattern of migration. However, Veery demonstrated a chain migration pattern at a stopover site located in the Sierra Nevada of Santa Marta in north-east Colombia (González-Prieto et al. 2011), suggesting that patterns of migration may also vary depending on location and time.

2.4.4 Implications for the conservation of Neotropical migratory birds

The high concentration of Neotropical migratory birds during fall migration confirms the ecological function of the Darién during *en route* migration. Therefore, it is not only important for concentrating birds but also as a site where potentially a large proportion of the breeding population of several species refuel or rest before reaching their wintering sites in South America. This was known for raptors (Bayly et al. 2014) but had not been demonstrated in landbirds that are capable of oversea crossings. This region appears similar to other areas in the Neotropics like Veracruz and the Yucatan Peninsula in Mexico. Basic knowledge of regional patterns of migration through the

region will assist in designing conservation strategies that should include the urgent need to reduce rates of deforestation in the Darién (Bayly et al., 2014; Renjifo et al., 2017) to protect declining species of Neotropical migrants, like the Canada Warbler (Cardenas-Ortiz et al. 2017), and other Neotropical migrants.

CHAPTER 3. FACTORS INFLUENCING THE ARRIVAL BODY CONDITION OF A GROUP OF NEOTROPICAL MIGRATORY BIRDS IN THE DARIÉN REGION OF COLOMBIA

3.1 INTRODUCTION

Every year, millions of Neotropical migratory birds undertake long-distance migrations towards wintering sites located in South America. Some of these migrants fly distances of >6,500 km (Heckscher et al. 2011). Such long journeys require birds to make stopovers in strategic areas in Central or northern South America to refuel (Stutchbury et al. 2007; Heckscher et al. 2011; Renfrew et al. 2013; Cohen et al. 2014).

Migration is a time of exceptional energetic demands (Cohen et al. 2014), Berthold 2001) and when most mortality occurs (Sillett and Holmes 2002; Newton 2006) (Newton 2006). Thus, the choice of migratory routes and the availability of stopover sites that allow adequate refueling are important components of migration strategies (Arizaga et al. 2011; Labocha and Hayes 2011). Fuel load is a measure of energy available for migration and has been used in several studies as an index of body condition (Alerstam and Lindström 1990; Lindström and Alerstam 1992; Cardenas-Ortiz et al. 2017) directly related to energy reserves (Labocha and Hayes 2011). Changes in body condition reflect changes in the energy reserves available to birds for migration (Lindström and Alerstam 1992; Arizaga and Bairlein 2011; Bayly et al. 2013). Body condition on arrival at a stopover site can therefore be used to assess which factors have the greatest impact on the energy reserves of birds *en route* during fall migration.

The elevated energetic requirements during migration imply that body condition may influence migration strategies, potentially acting on the duration (Gómez et al.

2017) and route and stopover use. Body condition has also been found to influence survival on migration (Baker et al. 2004). However, for many Neotropical migrants it is still unclear what factors influence body condition during migration, as measured at stopover sites. Diverse factors including breeding origin (i.e. distance travelled), age, sex, interannual variation, body size, migration route or climatic events may all affect body condition.

One of the most significant climatic events experienced by Neotropical migrants is the El Niño–Southern Oscillation (*ENSO*), an irregular periodic variation in winds and sea surface temperatures over the tropical eastern Pacific Ocean, affecting much of the tropics and subtropics (Nott et al. 2002). The warming phase is known as El Niño leading to reduced rainfall across much of Central and northern South America. The cooling phase is known as La Niña and gives rise to increased rainfall and linking to increased productivity.

Climatic variation induced by ENSO commonly influences biological systems. However, climatic variability and its effect on bird migration remains poorly understood, especially in the Neotropics (Wolfe and Ralf, 2009). Variation in climatic conditions as a result of the combination of La Niña and El Niño phases in the (ENSO) cycle may affect the body condition of Neotropical birds arriving to stopover sites by increasing or decreasing the availability of food resources necessary for the successful completion of migration (Wolfe & Ralph, 2009). Migrants that depend on insects for refueling during stopover may not be strongly affected by El Niño, because in the tropics, insects are generally considered to be abundant year-round (Levey and Stiles 1992), although in strongly seasonal tropical habitats this may not be true. In contrast, migrants that

depend on fruit resources for refueling may be affected by El Niño when fruit becomes scarce, due to dry conditions which inhibit fruiting in tropical forests (Wolfe et al. 2009).

To determine which factors most strongly influence body condition on migration through the Neotropics, I evaluated the impact of several factors on arrival body condition in a group of 11 Neotropical migrants moving through the Darién region of Colombia. I aimed to determine: 1) whether individuals from northern origins arrive to the Darién in poorer body condition than those from southern origins, 2) if migrants are affected by the ENSO cycle, whereby El Niño years resulted in poorer body condition on arrival relative to la Niña years, 3) whether larger individuals arrived in better body condition than smaller individuals and 4) if species known to migrate mostly over water arrived in lower body condition relative to those that migrate mostly overland.

3.2 METHODS

3.2.1 Study site and data collection

I studied a group of 11 long distance migrants: Red-eyed Vireo (*Vireo olivaceus*), Veery (*Catharus fuscescens*), Swainson's Thrush (*Catharus ustulatus*), Gray-cheeked Thrush (*Catharus minimus*), Yellow Warbler (*Setophaga petechia*), Northern Waterthrush (*Parkesia noveboracensis*), Mourning Warbler (*Geothlypis philadelphia*), Canada Warbler (*Cardellina canadensis*), Prothonotary Warbler (*Protonotaria citrea*), Scarlet Tanager (*Piranga olivacea*) and Summer Tanager (*Piranga rubra*), at a constant-effort mist-net station in the Tacarcuna Nature Reserve, Chocó, Colombia (08 ° 39'41.53"N, 77 ° 22'06.74"W; ~100 m asl). The station was located near the village of Sapzurro close to the border of Colombia and Panama. Habitat consisted of seasonal tropical humid forest interspersed with small clearings for agriculture and houses.

Fall migrations were monitored between 2011 to 2015 using 8 to 15 mist-nets (12 or 18 m long, 32-mm mesh) between mid-September and early November. Nets were positioned strategically to maximize captures and the number of nets and their location were kept virtually constant among days and years. Nets were opened daily beginning at dawn and remained open for 4.5 h on average, and were checked every 30-40 min. Captured birds were banded with uniquely coded Porzana-made metal bands (band reporting website: www.aselva.co). For all species, I recorded date and time of capture, age and sex (Pyle 1997), visible subcutaneous fat score (Kaiser 1993), pectoral muscle score (Redfern and Clark 2001), wing chord (± 1 mm), and body mass (± 0.1 g) using an electronic balance (Fast Weigh digital pocket scale, model M-500). In addition, I collected the first primary feather of individuals of each species to determine breeding origins based on stable hydrogen isotope ($\delta^2\text{H}_f$) analyses.

I prepared feather samples in the Environment Canada stable isotope laboratory at the National Hydrology Research Centre (NHRC) in Saskatoon, Canada. Each feather sample was soaked for 5 h in 2:1 chloroform: methanol solution then rinsed and dried in a fume hood for 48 h (Hobson and Wassenaar 2008). The impact of exchangeable hydrogen on isotopic measurements was corrected using the comparative equilibration method (Wassenaar and Hobson 2003). Within analytical runs, Environment Canada keratin reference standards CBS (caribou [*Rangifer tarandus*] hoof = -197‰) and KHS (kudu [*Tragelaphus* spp.] horn = -54.1‰) were used to account for exchangeable H and to calibrate samples. H isotopic measurements were performed on H_2 gas derived from high temperature (1350°C) flash pyrolysis of 350 ± 10 μg of distal-vane feather subsamples in silver capsules. Resulting H gas was separated

in a Eurovector 3000 (Milan, Italy) elemental analyzer and introduced into an Isoprime (Crewe, UK) continuous-flow isotope ratio mass spectrometer. All results are reported for non-exchangeable H expressed in the typical delta (δ) notation, in units per mil (‰), and normalized on the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale (Wassenaar and Hobson 2006). Based on within-run replicate (N = 5) measurements of laboratory keratin standards, measurement precision was estimated to be $\pm 2\text{‰}$.

3.2.2 Body condition, lean body mass and fuel reserves

To describe body condition, lean body mass (LBM) for each species was estimated using a group of individuals with no visible fat deposits (fat score = 0). LBM represented the average body mass of a bird with no energy reserves and was calibrated to body size by regressing body mass against wing length for the sample of birds described above (Lindström and Alerstam 1992).

Taking the LBM estimates, I calculated fuel load for each individual using the following equation that expresses fuel reserves as a percentage of LBM (Lindström and Alerstam 1992) : $\text{Fuel load reserves} = ((\text{body mass} - \text{LBM}) / \text{LBM}) * 100$. Fuel load is a measure of the amount of energy stored by a bird during migration (Bayly et al. 2013; Gómez et al. 2014; Cardenas-Ortiz et al. 2017) and therefore is an appropriate proxy for body condition in migrating birds (Arizaga and Bairlein 2011). The advantage of using fuel load to describe body condition is that it provides an estimate of the percentage of energy carried by an individual on arrival at a stopover. The percentage is corrected for the size of each species and can therefore be used to compare fuel reserves between species of different sizes.

3.2.3 Climate conditions-ENSO

For the years 2011–2015, average Southern Oscillation index (SOI) values were derived from monthly index data available through the National Oceanic and Atmospheric Administration's Climate Prediction Center (NOAA 2017). The SOI was used to measure the strength of ENSO in Central America, as has been done in previous climate studies (Ropelewski and Halpert 1996; Sillett et al. 2000). A strong positive value indicates La Niña conditions (high precipitation), and a strong negative value indicates El Niño conditions (low precipitation).

3.2.4 Modelling fuel load on arrival

To evaluate those factors influencing arrival body condition, I created a model set in which fuel load on arrival was the response variable. Modelling was carried out in the program R version 3.3.3 and model selection was carried out using Akaike's information criterion (AIC), comparing Δi values, where Δi was the difference between each model and the model with the lowest AIC (i.e. $\Delta i = \text{AIC} - \text{minimum AIC}$), and Akaike model weights (W_i). Model average verification was performed for models with $\Delta i < 2$.

To understand the effect of breeding origin on fuel load, I designed two model sets. The first set (Table 3.1), was designed for sexually monomorphic species and the second for the sexually dimorphic species. Models included various combinations of the explanatory variables: Breeding origin (BO) – the continuous variable isotope value $\delta^2\text{H}_f$ as a proxy for breeding latitude; age (A) – a two level factor, HY: Hatch year <1 Year old and AHY: After hatch year > 1 Year old, Sex (S) – a two level factor, Female and Male and finally the ENSO index (E) - a two level factor, El Niño and La Niña.

To understand the effect of body size and routes of migration on body condition, a third model set was designed (Table 3.1) including the following explanatory variables: Breeding origin (BO) - a continuous variable, Wing length (unflattened wing) (W) – a continuous variable, as an estimate of body size per species and migration route (R) – a two level factor, over land (Migrating mostly by land) and over water (Migrating mostly over water). I did not use the variable species in this analysis because most of the variation would be driven by this factor. Instead, I used wing length as an estimate of body size. This metric, has been taken as a standard measure of body size in small passerines (Spencer 1984). Migration routes were based on a literature review about the most probable route of migration for the majority of individuals per species during fall migration (Cardenas-Ortiz et al. 2017, Cohen et al. 2014, Gómez et al. 2014, Heckscher et al. 2011, Mowbray 1999, Robinson 2012, al. 1999). I assigned migration routes as follows: Over land species - Canada Warbler, Mourning Warbler, Scarlet Tanager, Summer Tanager, Yellow Warbler, and Over water - Red-eyed vireo a trans-Gulf migrant, Veery, Swainson's Thrush, Gray-cheeked Thrush, Prothonotary Warbler a trans-Gulf migrant, and Northern Waterthrush a trans-Gulf, circum-Gulf, and trans-Caribbean migrant.

Table 3.1 Model set used to determine how fuel load varies per species as a function of the variables: Fuel load (F), age (A), sex (S), breeding origin (BO), ENSO index (E), route of migration (R) and wing cord (W), at the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011- 2015).

Set of models 1	Explanation
$F=A+BO+E$	Fuel load varies as linear function of age, breeding origin and ENSO
$F=A+BO$	Fuel load varies as linear function of age and breeding origin
$F= A+E$	Fuel load varies as linear function of age and ENSO
$F=BO+E$	Fuel load varies as linear function of breeding origin and ENSO
$F=A$	Fuel load varies as linear function of age
$F=BO$	Fuel load varies as linear function of breeding origin
$F=E$	Fuel load varies as linear function of ENSO
$F=Null$	Fuel load vs null model
Set of models 2	Explanation
$F= A+S+BO+E$	Fuel load varies as linear function of age, sex, breeding origin and ENSO
$F=A+S+BO$	Fuel load varies as linear function of age, sex, breeding origin
$F=A+S+E$	Fuel load varies as linear function of age, sex and ENSO
$F=E+BO+S$	Fuel load varies as linear function of ENSO, breeding origin and sex
$F=E+BO+A$	Fuel load varies as linear function of ENSO, breeding origin and age
$F=A+S$	Fuel load varies as linear function of age and sex
$F=A+BO$	Fuel load varies as linear function of age and breeding origin
$F= A+E$	Fuel load varies as linear function of age and ENSO
$F=S+BO$	Fuel load varies as linear function of sex and breeding origin
$F=S+E$	Fuel load varies as linear function of sex and ENSO
$F=BO+E$	Fuel load varies as linear function of breeding origin and ENSO
$F=A$	Fuel load varies as linear function of age
$F=S$	Fuel load varies as linear function of sex
$F=BO$	Fuel load varies as linear function of breeding origin
$F=E$	Fuel load varies as linear function of ENSO
$F=Null$	Fuel load vs null model
Set of models 3	Explanation
$F=BO+R+W$	Fuel load varies as linear function of breeding origin, route and wing length
$F=BO+R$	Fuel load varies as linear function of breeding origin and route
$F=BO+W$	Fuel load varies as linear function of breeding origin and wing length
$F=W+R$	Fuel load varies as linear function of wing and route
$F=W$	Fuel load varies as linear function of wing length
$F=R$	Fuel load varies as linear function of route

F=BO
F=N

Fuel load varies as linear function of breeding origin
Fuel load vs null model

3.3 RESULTS

For all species, fuel loads on first capture showed considerable variation from -25 to 30% LBM.

3.3.1 Factors affecting body condition - breeding origins and ENSO

More than a single top model (i.e. $\Delta AIC \leq 2$) was found for the majority of species, where model weights warranted a model averaging approach to approximating model coefficients. I considered only the conditions prior to migration (Average value during one year before migration). Also, after comparing AIC values and weights between two variables (ENSO conditions prior to migration (Annual) versus ENSO conditions during migration), ENSO conditions prior to migration showed the stronger support to be included in each model.



Veery: The top two models encompassed 70% of the model weights (Table 3.2). Following model averaging, I found no support for an effect of breeding origin, given that 95% confidence intervals for the coefficient included zero (Table 3.13) (Figure 3.1). In contrast, body condition varied according to the ENSO index. Individuals migrating during El Niño years arrived with lower body condition than individuals migrating during La Niña years (Table 3.13) (Figure 3.2). Also, HY birds arrived in lower body condition than AHY birds (Table 3.13).



Swainson's Thrush: Four top models encompassed 79% of the model weights (Table 3.3). Following model averaging, I found support for an effect of breeding origin on body condition, given that 95% confidence intervals for the coefficient did not include zero (Table 3.13) (Figure 3.1). Therefore, birds from more southerly regions arrived in better condition than northerly birds (Figure 3.3). In contrast, the ENSO index or age on did not show a support, given that 95% confidence intervals for all coefficients included zero (Table 3.13) (Figure 3.1).



Gray-cheeked Thrush: Two top models encompassed 55% of the model weight (Table 3.4). I did not perform model averaging since the null model was among the best models. I found no support for an effect of the ENSO index on body condition, given that 95% confidence intervals for the coefficient included zero (Table 3.13).



Northern Waterthrush: Two top models encompassed 52% of the model weights (Table 3.5). I did not perform model averaging since the null model was among the best models. I found no support for an effect of breeding origin or age on body condition, given that 95% confidence intervals for the coefficient included zero (Table 3.13) (Figure 3.1).



Yellow Warbler: Three top models encompassed 54% of the model weights (Table 3.6). Following model averaging, I found no support for an effect of breeding origin and age, given that 95% confidence intervals for the coefficient included zero (Table 3.13) (Figure 3.1). In contrast, I found support for an effect of the factor sex, given that 95% confidence intervals for the coefficient did not include zero (Figure 3.1). Males arrived with lower body condition than females (Table 3.13).



Mourning Warbler: Three top models encompassed the 49% of the model weights, including the null model (Table 3.7). Following model averaging, I found no support for an effect of age or sex, given that 95% confidence intervals for the coefficient included zero (Table 3.13) (Figure 3.1).



Canada Warbler: Four top models encompassed 57 % of the model weights (Table 3.8). Following model averaging, I found no support for an effect of the breeding origin, age and sex on body condition, given that 95% confidence intervals for the coefficient included zero (Table 3.13) (Figure 3.1).



Prothonotary Warbler: Two top models encompassed 54% of the model weights (Table 3.9). Following model averaging, I found no support for an effect of breeding origin on body condition, given that the 95% confidence intervals for the coefficient included zero (Table 3.13) (Figure 3.1). In contrast, I found support for an effect of the

factor ENSO index and age, given that 95% confidence intervals for the coefficient did not include zero. Individuals migrating during El Niño years arrived with lower body condition than individuals migrating during La Niña years (Table 3.13) (Figure 3.2). Also, HY individuals arrived with better body condition than AHY (Table 3.13).



Red-eyed vireo: Three top models encompassed 76% of model weights (Table 3.10). Following model averaging, I found no support for an effect of the breeding origin and ENSO index on body condition; given that 95% confidence intervals for the coefficient included zero (Table 3.13) (Figure 3.1). In contrast, I found support for an effect of the factor age, given that 95% confidence intervals for the coefficient did not include zero. HY individuals arrived with lower body condition than AHY individuals (Table 3.13).



Scarlet Tanager: Two top models encompassed 54% of model weights (Table 3.11). Following model averaging, I found support for an effect of the factor sex on body condition, given that 95% confidence intervals for the coefficient did not include zero (Figure 3.1). Males arrived with lower body condition than females (Table 3.13).



Summer Tanager: Four top models encompassed 59% of model weights (Table 3.12). Following model averaging, I found no support for an effect of breeding origin, age and sex on body condition, given that 95% confidence intervals for the coefficient included zero (Table

3.13) (Figure 3.1).

Table 3.2 Table Associated AICc, Δi , and W_i values for models of fuel load (F) as a function of breeding origins (BO), age (A), and ENSO (E) of Veery arriving to the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011 – 2015). N = 220.

Model	Intercept	Age	Enso	B. Origin	DF	logLik	AICc	Δi	W_i
F = A + E	15.8	+	-2.70		4	-840.01	1688.2	0.00	0.41
F = A + BO + E	19.6	+	-2.52	0.05	5	-839.31	1688.9	0.69	0.29
F = BO + E	20		-2.38	0.07	4	-841.03	1690.2	2.03	0.15
F = E	13.2		-2.66		3	-842.99	1692.1	3.87	0.06
F = A + BO	20.3	+		0.06	4	-842.49	1693.2	4.96	0.03
F = A	15.2	+			3	-843.73	1693.6	5.35	0.03
F = BO	20.6			0.09	3	-843.86	1693.8	5.61	0.03
F = Null	12.7				2	-846.49	1697.0	8.83	0.01

Table 3.3 Associated AICc, Δi , and W_i values for models of fuel load (F) as a linear function of breeding origin (BO), age (A) and ENSO (E) of Swanson's Thrush arriving to the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011 – 2015). N = 306.

Model	Intercept	Age	Enso	Breeding Origin	Df	logLik	AICc	Δi	W_i
F = A + BO	20.7	+		0.06	4	-1180.41	2369.0	0.00	0.24
F = A + BO + E	20.46	+	-0.94	0.06	5	-1179.47	2369.1	0.19	0.22
F = BO + E	21.1		-1.02	0.05	4	-1180.75	2369.6	0.68	0.17
F = BO	21.41			0.06	3	-1181.85	2369.8	0.82	0.16
F = E	13.81		-1.06		3	-1182.82	2371.7	2.76	0.06
F = Null	13.95				2	-1184.00	2372.0	3.07	0.05
F = A + E	12.65	+	-1		4	-1181.98	2372.1	3.13	0.05
F = A	12.7	+			3	-1183.03	2372.1	3.19	0.05

Table 3.4 Associated AICc, Δi , and W_i values for models of fuel load (F) as a linear function of breeding origin (BO), age (A) and ENSO (E) of Grey-cheeked Thrush arriving to the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011 – 2015). N = 153.

Model	Intercept	Age	Enso	Breeding Origin	Df	logLik	AICc	Δi	W_i
F = E	10.41		1.60		3	-567.77	1141.7	0.0	0.36
F = Null	11.1				2	-569.51	1143.1	1.39	0.18
F = BO + E	8.83		1.60	-0.01	4	-567.74	1143.8	2.05	0.13
F = A + E	10.39	+	1.60		4	-567.77	1143.8	2.11	0.13
F = BO	9.64			-0.01	3	-569.48	1145.1	3.42	0.07
F = A	11.03	+			3	-569.50	1145.2	3.46	0.06
F = A + BO + E	8.83	+	1.60	-0.01	5	-567.74	1145.9	4.19	0.05
F = A +BO	9.63	+		-0.01	4	-569.48	1147.2	5.52	0.02

Table 3.5 Associated AICc, Δi , and W_i values for models of fuel load (F) as a linear function of breeding origin (BO), age (A) and ENSO (E) of Northern Waterthrush arriving to the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011- 2015). N = 77.

Model	Intercept	Age	ENSO	Breeding Origin	Df	logLik	AICc	Δi	W_i
F = Null	2.10				2	-272.07	548.3	0.00	0.31
F = BO	-4.39			-0.05	3	-271.34	549.0	0.71	0.22
F = A	2.63	+			3	-271.99	550.3	2.00	0.11
F = A +BO	-5.22	+		-0.06	4	-270.88	550.3	2.02	0.11
F = E	2.06		0.27		3	-272.05	550.4	2.12	0.11
F = BO + E	-4.44		0.27	-0.05	4	-271.32	551.2	2.89	0.07
F = A + E	2.57	+	0.22		4	-271.97	552.5	4.19	0.04
F = A + BO + E	-5.23	+	0.15	-0.06	5	-270.88	552.6	4.30	0.04

Table 3.6 Associated AICc, Δi , and W_i values for models of fuel load (F) as a linear function of breeding origin (BO), age (A), sex (S) and ENSO (E) of Yellow Warbler arriving to the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011- 2015). N = 102.

	Model	Intercept	Age	ENSO	Sex	Breeding Origin	Df	logLik	AICc	Δi	W_i
63	F = S + BO	-2.9			+	-0.08	4	-336.47	681.3	0.00	0.27
	F = S	4.79			+		3	-338.05	682.3	1.00	0.17
	F = A + S + BO	-2.4	+		+	-0.079	5	-336.36	683.3	1.99	0.10
	F = E + BO + S	-2.6		-0.231	+	-0.077	5	-336.40	683.4	2.08	0.10
	F = A + S	5.24	+		+		4	-337.90	684.2	2.86	0.07
	F = Null	3.44					2	-340.18	684.5	3.13	0.06
	F = BO	-2.9				-0.065	3	-339.15	684.5	3.20	0.06
	F = A + S + BO + E	-2.2	+	-0.204	+	-0.077	6	-336.31	685.5	4.15	0.03
	F = A + S + E	5.26	+	-0.37	+		5	-337.73	686.1	4.74	0.03
	F = A	4.03	+				3	-339.95	686.2	4.80	0.03
	F = A + BO	-2.3	+			-0.064	4	-338.96	686.3	4.98	0.02
	F = E	3.46		-0.254			3	-340.10	686.4	5.10	0.02
	F = S + E	-2.8		-0.099		-0.064	4	-339.14	686.7	5.34	0.02
	F = BO + E	-2.8		-0.099		-0.064	4	-339.14	686.7	5.34	0.02
	F = A + E	4.02	+	-0.214			4	-339.90	688.2	6.86	0.01
	F = E + BO + A	-2.2	+	-0.063		-0.063	5	-338.95	688.5	7.18	0.01

Table 3.7 Associated AICc, Δi , and W_i values for models of fuel load (F) as a linear function of breeding origin (BO), age (A), sex (S) and ENSO (E) of Mourning Warbler arriving to the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011- 2015). N = 110.

	Model	Intercept	Age	ENSO	Sex	Breeding Origin	Df	logLik	AICc	Δi	W_i
g	F = Null	4.182					2	-367.59	739.3	0.00	0.22
	F = S	3.556			+		3	-366.97	740.2	0.87	0.15
	F = A	4.789	+				3	-367.12	740.5	1.18	0.13
	F = BO	3.509				-0.01	3	-367.57	741.4	2.07	0.08
	F = E	4.193		0.02			3	-367.59	741.4	2.11	0.08
	F = A + S	4.135	+		+		4	-366.65	741.7	2.40	0.07
	F = S + BO	2.515			+	-0.01	4	-366.92	742.2	2.93	0.05
	F = A + BO	3.969	+			-0.01	4	-367.09	742.6	3.27	0.04
	F = A + E	4.735	+	-0.17			4	-367.10	742.6	3.29	0.04
	F = S + E	3.517		0.01		-0.01	4	-367.57	743.5	4.23	0.03
	F = BO + E	3.517		0.01		-0.01	4	-367.57	743.5	4.23	0.03
	F = A + S + BO	3.015	+		+	-0.01	5	-366.60	743.8	4.48	0.02
	F = A + S + E	4.081	+	-0.17	+		5	-366.63	743.8	4.55	0.02
	F = E + BO + S	2.484		-0.03	+	-0.01	5	-366.92	744.4	5.13	0.02
	F = E + BO + A	3.836	+	-0.19		-0.01	5	-367.06	744.7	5.41	0.02
	F = A + S + BO + E	2.876	+	-0.19	+	-0.01	6	-366.57	746	6.66	0.01

Table 3.8 Associated AICc, Δi , and W_i values for models of fuel load (F) as a linear function of breeding origin (BO), age (A), sex (S) and ENSO (E) of Canada Warbler arriving to the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011 – 2015). N = 59.

	Model	Intercept	Age	ENSO	Sex	Breeding Origin	Df	logLik	AICc	Δi	W_i
2	F = Null	1.83					2	-182.73	369.7	0.00	0.25
	F = S	1.33			+		3	-182.23	370.9	1.22	0.13
	F = A	0.89	+				3	-182.56	371.6	1.89	0.10
	F = BO	0.40				-0.01	3	-182.61	371.7	1.99	0.09
	F = E	1.87		-0.31			3	-182.64	371.7	2.03	0.09
	F = A + S	-0.77	+		+		4	-181.66	372.1	2.40	0.07
	F = S + BO	-0.78			+	-0.02	4	-181.99	372.7	3.05	0.05
	F = A + BO	-0.15	+			-0.01	4	-182.49	373.7	4.05	0.03
	F = A + E	1.04	+	-0.23			4	-182.52	373.8	4.10	0.03
	F = S + E	0.61		-0.26		-0.01	4	-182.55	373.8	4.16	0.03
	F = BO + E	0.61		-0.26		-0.01	4	-182.55	373.8	4.16	0.03
	F = A + S + BO	-0.62	+	-0.43	+		5	-181.49	374.1	4.44	0.03
	F = A + S + E	-2.38	+		+	-0.02	5	-181.50	374.1	4.46	0.03
	F = E + BO + S	-0.58		-0.49	+	-0.02	5	-181.77	374.7	5.00	0.02
	F = E + BO + A	0.07	+	-0.20		-0.01	5	-182.45	376	6.37	0.01
	F = A + S + BO + E	-2.10	+	-0.40	+	-0.02	6	-181.36	376.3	6.66	0.01

Table 3.9 Associated AICc, Δi , and W_i values for models of fuel load (F) as a linear function of breeding origin (BO), age (A), sex (S) and ENSO (E) of Prothonotary Warbler arriving to the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011 – 2015). N = 145.

	Model	Intercept	Age	Enso	Sex	Breeding Origin	Df	logLik	AICc	Δi	W_i
g	F = A + E	-0.96	+	2.00			4	-508.81	1026	0.00	0.39
	F = E + BO + A	-2.22	+	2.08		-0.02	5	-508.71	1028	1.96	0.15
	F = A + S + BO	-1.27	+	2.02	+		5	-508.74	1028	2.02	0.14
	F = E	0.96		1.98			3	-511.17	1029	2.62	0.11
	F = A + S + BO + E	-2.42	+	2.10	+	-0.02	6	-508.66	1030	4.03	0.05
	F = S + E	-0.03		2.05		-0.02	4	-511.11	1031	4.62	0.04
	F = BO + E	-0.03		2.05		-0.02	4	-511.11	1031	4.62	0.04
	F = A	0.06	+				3	-512.43	1031	5.14	0.03
	F = E + BO + S	-0.01		2.04	+	-0.02	5	-511.11	1033	6.76	0.01
	F = A + BO	0.91	+			0.01	4	-512.39	1033	7.16	0.01
	F = A + S	-0.07	+		+		4	-512.42	1033	7.23	0.01
	F = Null	1.94					2	-514.62	1033	7.42	0.01
	F = A + S + E	0.81	+		+	0.01	5	-512.37	1035	9.28	0.00
	F = BO	2.98				0.02	3	-514.55	1035	9.37	0.00
	F = S	2.08			+		3	-514.60	1035	9.47	0.00
	F = S + BO	3.05			+	0.02	4	-514.53	1037	11.5	0.00

Table 3.10 Associated AICc, Δi , and W_i values for models of fuel load (F) as a linear function of breeding origin (BO), age (A), and ENSO (E) of Red-eyed Vireo arriving to the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011 – 2015). N = 171.

Model	Intercept	Age	Enso	Breeding Origin	Df	logLik	AICc	Δi	W_i
F = A	13.16	+			3	-608.06	1222.3	0.00	0.42
F = A +BO	14.38	+		0.01533	4	-607.91	1224.1	1.80	0.17
F = A + E	13.55	+	-0.4558		4	-607.95	1224.1	1.86	0.17
F = Null	10.62				2	-610.61	1225.3	3.02	0.09
F = A + BO + E	14.69	+	-0.4316	0.0147	5	-607.81	1226.0	3.71	0.07
F = BO	11.4			0.01025	3	-610.55	1227.2	4.97	0.04
F = E	10.7		-0.1266		3	-610.60	1227.3	5.08	0.03
F = BO + E	11.46		-0.1065	0.01006	4	-610.54	1229.3	7.05	0.01

Table 3.11 Associated AICc, Δi , and W_i values for models of fuel load (F) as a linear function of breeding origin (BO), age (A), sex (S) and ENSO (E) of Scarlet Tanager arriving to the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011- 2015). N = 60.

	Model	Intercept					Df	logLik	AICc	Δi	W_i
		Age	Enso	Sex	Breeding	Origin					
g	F = A + E	-0.96	+	2.00			4	-508.81	1025.9	0.00	0.39
	F = E + BO + A	-2.22	+	2.08		-0.02	5	-508.71	1027.9	1.96	0.15
	F = A + S + BO	-1.27	+	2.02	+		5	-508.74	1027.9	2.02	0.14
	F = E	0.96		1.98			3	-511.17	1028.5	2.62	0.11
	F = A + S + BO + E	-2.42	+	2.10	+	-0.02	6	-508.66	1029.9	4.03	0.05
	F = S + E	-0.03		2.05		-0.02	4	-511.11	1030.5	4.62	0.04
	F = BO + E	-0.03		2.05		-0.02	4	-511.11	1030.5	4.62	0.04
	F = A	0.06	+				3	-512.43	1031.0	5.14	0.03
	F = E + BO + S	-0.01		2.04	+	-0.02	5	-511.11	1032.7	6.76	0.01
	F = A + BO	0.91	+			0.01	4	-512.39	1033.1	7.16	0.01
	F = A + S	-0.07	+		+		4	-512.42	1033.1	7.23	0.01
	F = Null	1.94					2	-514.62	1033.3	7.42	0.01
	F = A + S + E	0.81	+		+	0.01	5	-512.37	1035.2	9.28	0.00
	F = BO	2.98				0.02	3	-514.55	1035.3	9.37	0.00
	F = S	2.08			+		3	-514.60	1035.4	9.47	0.00
	F = S + BO	3.05			+	0.02	4	-514.53	1037.4	11.5	0.00

Table 3.12 Associated AICc, Δi , and W_i values for models of fuel load (F) as a linear function of breeding origin (BO), age (A), Sex (S) and ENSO (E) of Summer Tanager during fall migration arriving to the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011 – 2015). N = 32.

Model	Intercept	Age	Enso	Sex	Breeding Origin	Df	logLik	AICc	Δi	W_i
F = Null	9.406					2	-119.58	243.6	0.00	0.24
F = A	11.62	+				3	-118.797	244.5	0.88	0.16
F = S	7.615			+		3	-119.236	245.3	1.76	0.10
F = BO	16.27				0.12	3	-119.348	245.6	1.98	0.09
F = E	10.28		-1.84			3	-119.368	245.6	2.02	0.09
F = A + S	9.759	+		+		4	-118.36	246.2	2.63	0.07
F = A + BO	16.1	+			0.08	4	-118.691	246.9	3.29	0.05
F = A + E	11.84	+	-0.80			4	-118.759	247.0	3.43	0.04
F = S + E	18.6		-2.21		0.15	4	-119.046	247.6	4.00	0.03
F = BO + E	18.6		-2.21		0.15	4	-119.046	247.6	4.00	0.03
F = S + BO	13.07			+	0.09	4	-119.108	247.7	4.12	0.03
F = A + S + BO	9.705	+	-2.40	+		5	-118.073	248.5	4.88	0.02
F = A + S + E	12.23	+		+	0.04	5	-118.332	249.0	5.4	0.02
F = E + BO + S	14.5		-3.58	+	0.11	5	-118.422	249.2	5.58	0.02
F = E + BO + A	17.39	+	-1.20		0.10	5	-118.611	249.5	5.96	0.01
F = A + S + BO + E	13.45	+	-2.58	+	0.07	6	-118.009	251.4	7.80	0.01

Table 3.13 Model averaged coefficients of top models for only the species that had more than one model with $\Delta i < 2$ and 95% confidence intervals, to explain factors affecting body condition at arrival time in the Tacarcuna Nature Reserve, Darién Colombia 2011-2015. VEER: Veery, SWTH: Swainson's Thrush, GCTH: Gray-cheeked Thrush, NOWA, NOWA: Northern Waterthrush, YWAR: Yellow Warbler, MOWA: Mourning Warbler, CAWA: Canada Warbler, PWAR: Prothonotary Warbler, REVI, Red-eyed Vireo, SCTA: Scarlet Tanager and SUTA: Summer Tanager.

Species	Variable	β	SE	L 95% CI	U 95% CI
VEER	(Intercept)	17.400	3.094	11.335	23.464
	Age: HY	-3.570	1.686	-6.874	-0.266
	ENSO: Niño	-2.623	1.003	-4.588	-0.658
	B. Origin	0.046	0.040	-0.031	0.124
SWTH	(Intercept)	20.863	3.70	13.619	28.107
	Age: HY	2.292	1.40	-0.453	5.038
	B. Origin	0.059	0.03	0.005	0.112
	ENSO: Niño	-0.972	0.69	-2.328	0.384
GCTH	(Intercept)	10.642	0.9291	8.821	12.463
	ENSO: Niña	1.601	0.8675	-0.099	3.301
NOWA	(Intercept)	-0.003	4.634	-9.085	9.080
	B. Origin	-0.048	0.041	-0.129	0.032
	Age: HY	-0.810	2.036	-4.799	3.180
YWAR	(Intercept)	-0.422	5.149	-10.512	9.669
	Sex: M	-2.966	1.357	-5.625	-0.308
	B. Origin	-0.080	0.046	-0.169	0.010
	Age: HY	-0.631	1.389	-3.354	2.092
MOWA	(Intercept)	4.151	0.919	2.349	5.953
	Sex: M	1.466	1.338	-1.157	4.088
	Age: HY	-1.261	1.327	-3.861	1.339

CAWA	(Intercept)	1.325	1.688	-1.984	4.634
	Sex: M	1.467	1.518	-1.509	4.442
	Age: HY	1.111	2.010	-2.829	5.051
	B. Origin	-0.015	0.032	-0.076	0.047
PWAR	(Intercept)	-1.304	2.045	-5.311	2.704
	Age: HY	3.052	1.417	0.275	5.830
	ENSO: Niña	2.020	0.755	0.539	3.500
	B. Origin	-0.020	0.047	-0.112	0.072
REVI	(Intercept)	13.521	1.805	9.984	17.059
	Age: HY	-3.435	1.520	-6.415	-0.456
	B. Origin	0.015	0.029	-0.041	0.071
	ENSO: Niña	-0.456	0.960	-2.337	1.425
SCTA	(Intercept)	21.125	3.545	14.029	28.221
	Sex: M	-20.264	4.576	-29.425	-11.102
SUTA	(Intercept)	10.737	5.536	-0.114	21.588
	Age: HY	-4.438	3.770	-11.827	2.952
	Sex: M	3.016	3.891	-4.611	10.643
	B. Origin	0.123	0.193	-0.256	0.501

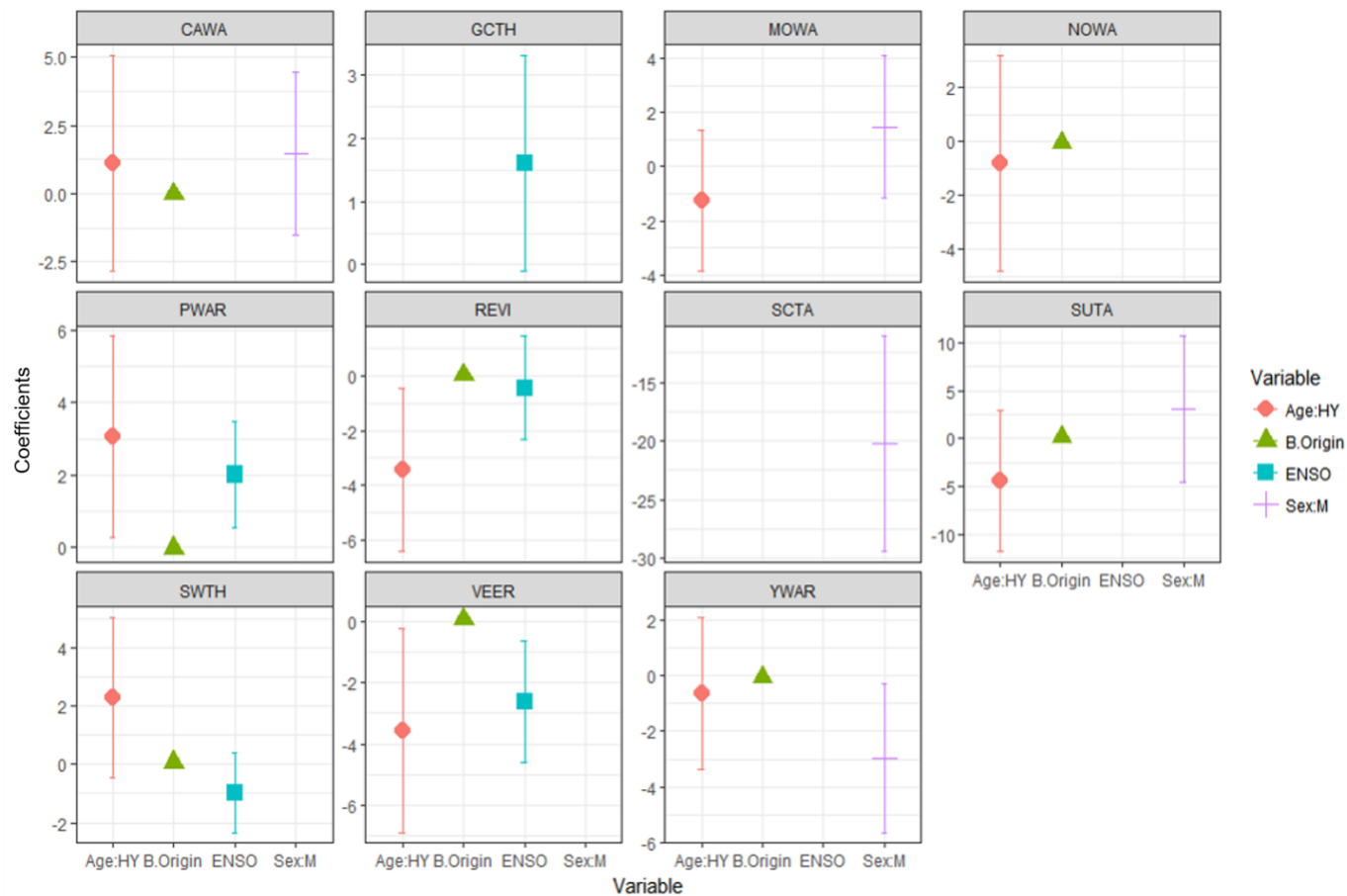


Figure 3.1 Coefficients of each variable included in the models and 95% confidence intervals for the species: CAWA: Canada Warbler, GCTH: Gray-cheeked Thrush, MOWA: Mourning Warbler, NOWA: Northern Waterthrush, PWAR: Prothonotary Warbler, REVI: Red-eyed vireo, SUTA: Scarlet Tanager, SUTA: Summer Tanager, SWTH, Swainson's Thrush, VEER: Veery and YWAR: Yellow Warbler.

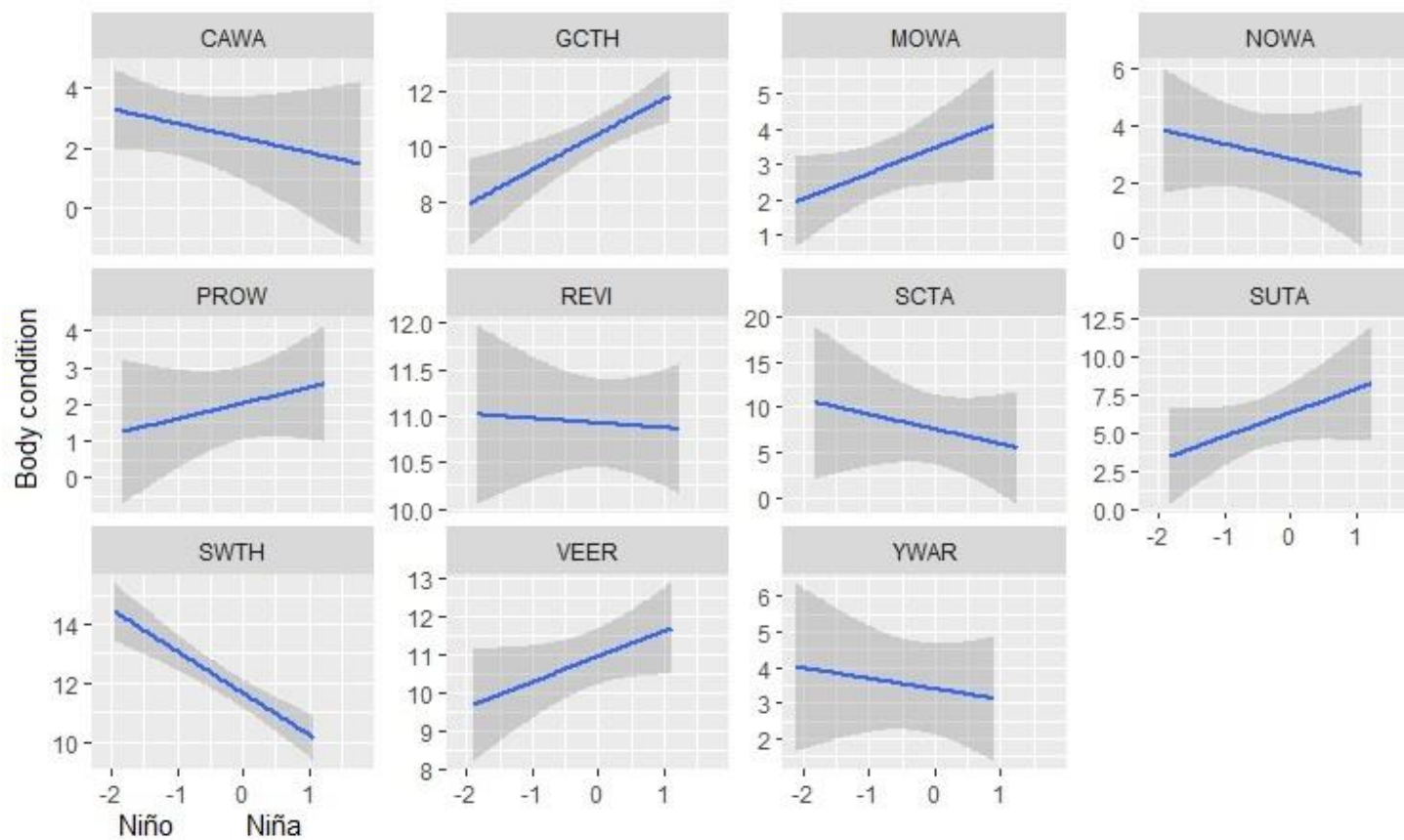


Figure 3.2 Relationship between body condition and the ENSO index (Negative values indicate El Niño years and positive values indicate La Niña Years) for the species: CAWA: Canada Warbler, GCTH: Gray-cheeked Thrush, MOWA: Mourning Warbler, NOWA: Northern Waterthrush, PWAR: Prothonotary Warbler, REVI: Red-eyed Vireo, SUTA: Summer Tanager, SWTH: Swainson's Thrush, VEER: Veery and YWAR: Yellow Warbler.

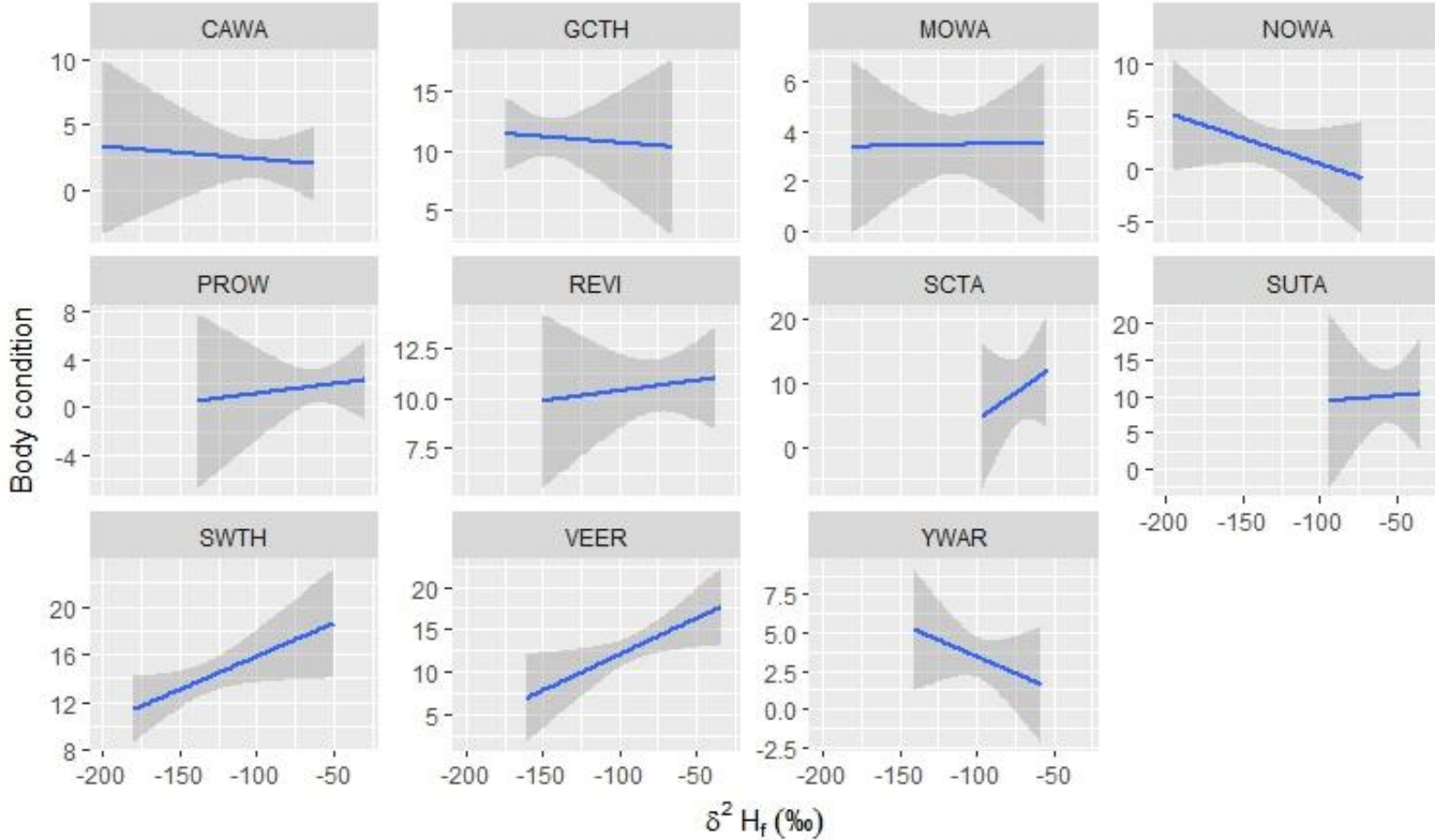


Figure 3.3 Relationship between body condition and the ($\delta^2 H_f$) values (Breeding origin) in feathers of the species: CAWA: Canada Warbler, GCTH: Gray-cheeked Thrush, MOWA: Mourning Warbler, NOWA: Northern Waterthrush, PROW: Prothonotary Warbler, REVI: Red-eyed vireo, SUTA: Summer Tanager, SWTH: Swainson's Thrush, VEER: Veery and YWAR: Yellow Warbler.

3.3.2 Body size and routes of migration affecting body condition

I found three top models describing factors influencing fuel load at arrival that encompassed 89% of the model weights (Table 3.14). Following model averaging we found limited support of breeding origin and the route of migration, given that 95% confidence intervals for the coefficient included zero (Table 3.15). In contrast, the factor body size (Wing length) indicated that birds of larger body size arrived to the Darién with better body condition than smaller birds.

Table 3.14 Associated AICc, Δ_i , and W_i values for models of fuel load (F) as a function of breeding origins (BO), route of migration (R) and Wing length (W) of arriving to the Tacarcuna Nature Reserve, Darién, Colombia. Fall migration (2011-2015).

Model	Intercept	Route of migration	Breeding Origin	Wing length	Df	logLik	AICc	Δ_i	W_i
F = W	-12.46			0.25	3	-5559.9	11125.8	0.00	0.43
F = BO + W	-12.09		0.01	0.26	4	-5559.44	11126.9	1.09	0.25
F = W + R	-12.11	+		0.25	4	-5559.62	11127.3	1.46	0.21
F = BO + R + W	-11.77	+	0.01	0.25	5	-5559.2	11128.4	2.63	0.12
F = BO + R	2.953	+	-0.02		4	-5619.36	11246.7	120.93	0.00
F = R	4.715	+			3	-5621.8	11249.6	123.81	0.00
F = BO	5.899		-0.03		3	-5651.36	11308.7	182.93	0.00
F = NULL	8.738				2	-5656.65	11317.3	191.5	0.00

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Table 3.15 Model averaged coefficients of top models to explain factors affecting body condition at arrival time of a group of 11 Neotropical migrants in the Tacarcuna Nature Reserve, Darién Colombia 2011-2015.

Variable	β	SE	L 95% CI	U 95% CI
(Intercept)	-12.27	1.54	-15.30	-9.25
Wing length	0.2538	0.02	0.22	0.29
B. Origin	0.0079	0.01	-0.01	0.02
Route: Overwater	0.5612	0.76	-0.93	2.05

3.4 DISCUSSION

My findings suggest that body condition of long-distance Neotropical migrants during fall migration, is affected by several factors such as breeding origin, climate events like El Niño–Southern Oscillation (*ENSO*), age and sex, body size and route of migration. However, the effect of factors such as the breeding origin and the El Niño–Southern Oscillation (*ENSO*) on body condition were not as strong as predicted and did not show enough support to explain the body condition at arrival time in most of the species selected in this study. This could be a result of small sample sizes for some species and years, limiting the power of our models to explain better the data. In contrast, the most powerful factor affecting more species was body size. Birds with longer wing length arrived in better body condition than smaller birds, no matter the route of migration.

3.4.1 Effect of breeding origin on body condition

My findings showed breeding origin as one of the factors affecting body condition at arrival for only Swainson's Thrush. However, while origin appeared in the top model for 7 species, its effect is not clear as 95% confidence intervals for 6 of the 7 species included zero. In most species, coefficients were positive suggesting that there may be an effect by which birds from more southerly regions arrive in better condition. However, it did not have a strong effect for the rest of the species. Therefore, if northern populations migrate furthest then they may have larger reserves and a different fueling/stopover strategy. The reason why, it is still unknown. However, body condition at arrival time may be more related to distance to wintering grounds instead of stopover sites and it may be a factor shaping migratory strategies (Gomez et al 2014). However, more studied is needed in order to confirm this assumption.

Another possible explanation of this result is that body condition may be related to where birds last stopped over, rather than how far they have travelled. A single stopover can have a substantial effect on fuel load and increase it substantially, (Gómez et al. 2017). Thus if more northerly populations stop over closer to the Darién than southern populations, northern birds could arrive in better condition.

3.4.2 Effect of the ENSO index on body condition

Few studies have evaluated the direct effects of El Niño events in tropical forest animals (Bermingham et al. 1998). Variable community-level fruit production has induced fluctuations in the abundance of species of frugivorous mammals in Panama (Wright et al. 1999). However, we still do not have much information about how ENSO affects migratory birds. The species for which an effect of ENSO was detected on my site were Veery and Prothonotary Warbler. Individuals arrived in lower body condition during El Niño years (2011 and 2013) compared to La Niña years (2012, 2014 and 2015).

Veery is highly frugivorous during migration (Gómez et al. 2014) and it followed our prediction of being impacted by dry conditions during an El Niño year that can lead to low fruit availability. In Costa Rica, Swainson's Thrushes showed the same pattern during spring migration (Wolfe and Ralph 2009). In contrast, the rest of my frugivorous species as, Swainson's Thrush, Gray-cheeked Thrush, Scarlet Tanager and Summer Tanager did not show the same response. Nonetheless, top models contained ENSO for Swainson's Thrush and Gray-cheeked Thrush, and it is possible that high inter-individual variation masked the effect of ENSO in our data. Alternatively, this group of species may stopover in other localities in Central America before reaching my site and

so again, stopover history before reaching the Darién could have complicated my ability to detect an effect of ENSO in these species.

However, Prothonotary Warbler which is mostly insectivorous showed also lower body condition during El Niño years. This result is important because it shows that the body condition of some insectivorous species can also be affected during El Niño years.

Prothonotary Warbler is associated with aquatic areas that can be reduced if conditions are dryer. This could cause less production of insects or additional movement of birds looking for optimal foraging areas, resulting in lower body condition. However more study is needed in order to confirm this result in other areas.

In itself, this multi-species comparison is useful and suggests that Veery and Prothonotary warbler have a migration strategy which puts them more at risk in El Niño years.

In keeping with my prediction, arrival body condition of insectivores such as Red-eyed vireo, Yellow Warbler, Mourning Warbler, Northern Waterthrush, Canada Warbler was apparently not affected by ENSO. Wolfe & Ralph (2009) found similar results in Eastern Wood-Pewee, Northern Waterthrush, Prothonotary Warbler and Canada Warbler. They suggested that the lack of correlation between body condition and ENSO may be explained by the foraging behavior and dietary plasticity of these species during migration. Dietary plasticity, involving the use of fruit and insects, may buffer them from climatic variability and subsequent trophic cascades (Levey and Stiles 1992).

3.4.3 Effect of age and sex on body condition

Age affected the arrival body condition in Veery, Red-eyed Vireo and Prothonotary Warbler. HY individuals of Veery and Red-eyed Vireo arrived to the Darién with lower

fuel load than AHY birds. This finding was expected due to the fact that young birds often require a longer time to gain migratory fuel than adults, migrate with lower fuel loads, stay longer at stopover sites, and take longer to complete their journeys (Newton 2008). These differences have been attributed in part due to their lower experience and social status. HY birds gain experience during autumn migration (Arizaga and Bairlein 2011, Newton 2008), consequently, in most cases AHY birds are more efficient when foraging due to their greater experience besides being socially dominant over HY birds throughout the non-breeding season (Lundberg 1985; Moore et al. 2003). In contrast, HY individuals of Prothonotary Warbler arrived in better body condition than AHY, suggesting that AHY individuals can also suffer during migration and not necessarily arrive always in better condition than HY individuals. More study is needed to understand why.

The factor sex affected the body condition at arrival in Yellow Warbler and Scarlet Tanager. Males of both species arrived to the Darién in lower body condition than females. Most of the time females migrate further on average, and winter at lower latitudes than males (Cristol 1992; Newton 2008). I believe that it is possible that males carry less energy stores as a result of the distance that they need to travel, however more study is needed to understand why males of some species can experience this pattern.

3.4.4 Body size and routes of migration affecting body condition

Birds migrating across geographical barriers such as the Caribbean Sea or flying over Central America need to adjust their physiology accordingly. Wing morphology clearly affects flight efficiency (Pennycuik 2008) and therefore body condition. However, wing

length is also shaped by often opposing selection pressures (Milá et al. 2008). Longer wings are favoured in long-distance migrants (Bowlin and Wikelski 2008; Newton 2008; Pennycuick 2008; Nowakowski et al. 2014). Shorter-distance migrants or those that stop more frequently have rounded and shorter wings (Senar et al. 1994; Milá et al. 2008) that favour manoeuvrability (Alatalo et al. 1984; Swaddle and Lockwood 2003).

Our results showed that larger birds (Veery, Swainson's Thrush, Gray-cheeked Thrush, Scarlet Tanager and Summer Tanager arrived in better body condition than smaller birds (Yellow Warbler, Northern Waterthrush, Mourning warbler, Canada Warbler, Prothonotary Warbler, and Red-eyed Vireo) as we predicted. Contrary to our predictions, birds did not show differences based on their presumed migration route by land or by water. In terms of flight efficiency, bigger birds have higher aspect ratios, in comparison with smaller birds. Small birds in general have lower lift to drag ratios than large ones, and have higher basal metabolism (Pennycuick 2015). I expected to see lower body condition in birds migrating across the Caribbean Sea compared to overland migrants that can presumably refuel more frequently (Newton 2008). However, thrushes migrating across the Gulf of Mexico and across the Caribbean Sea arrived in similar body condition as tanagers that migrate across Central America. Among the smaller birds, the warblers and vireo showed the same pattern and arrived in lower body condition. Their route of migration did not affect this result.

3.4.5 Further considerations

My study is the first attempt to understand factors affecting body condition and the potential migration strategies of long-distance migrants after crossing the Caribbean compared to those migrating through Central America. However, it is difficult to detect

the broad level effects we were hoping to detect due to several reasons. For example, the high variation in strategy between individuals could hide more general patterns. Also by including birds from across the migration, it is possible that each set of birds experienced very different conditions when migrating as wind direction, temperature and precipitation that I was not able to analyze and these may have hidden other general patterns.

In the future, it would be worth to analyze the data for shorter time periods to see if other patterns become clearer. Also, interannual variation is another factor that could be affecting the results and it would be important to include it in future analyses.

Recent studies indicate that long-distance migrants can differ genetically from shorter distance migrants of the same species as was shown in Wilson's Warbler (Bazzi et al. 2016). Therefore, this is definitely another factor that needs to be included in future studies including more Neotropical migrants linking intrinsic and extrinsic selection factors on stopover ecology.

CHAPTER 4. FALL MIGRATION AND BREEDING ORIGINS OF CANADA WARBLERS MOVING THROUGH NORTHERN COLOMBIA¹

4.1 INTRODUCTION

Despite considerable interest and effort on the part of ecologists over the years, the migration ecology of Nearctic-Neotropical migrant birds remains poorly understood, especially outside of North America (Faaborg et al. 2010). This knowledge gap is especially alarming when considering the number of landbirds migrating to the Neotropics every year and the dramatic population declines experienced by many over the last three decades (Faaborg et al. 2010). For example, populations of Canada Warblers (*Cardellina canadensis*), long-distance migratory passerines, have declined at an annual rate of 2.1% since 1966 (Sauer et al. 2011). The causes of this decline are unknown (Becker et al. 2012), but likely causes include the loss of forest habitat (Reitsma et al. 2010) and an increase in urban development in forest landscapes (Miller 1999).

Among the knowledge gaps that inhibit our ability to design effective conservation strategies for Canada Warblers is a lack of knowledge about where individuals spend the winter or where they stop during migration. Migratory connectivity is a term that helps quantify the degree to which individuals from the same breeding areas migrate to the same wintering areas (Trierweiler et al. 2014), and migratory

¹ CARDENAS-ORTIZ, L., N.J. BAYLY, G.J. COLORADO and K.A. HOBSON. 2017. Fall migration and breeding origins of Canada Warblers moving through northern Colombia. *Journal field of ornithology* 88: 53–64.

stopover sites are integral components of this connectivity (González-Prieto et al. 2011). Therefore, establishing patterns of migratory connectivity at the population level is important, linking breeding and wintering grounds as well as migratory stopover sites (Hobson et al. 2014). The use of endogenous markers, like measurements of naturally occurring ratios of stable isotopes in avian tissues, has been shown to be useful in assigning origins and determining connectivity patterns (Hobson and Wassenaar 2008). The most useful stable isotope measurements to date for tracking long-distance migrant birds are those of hydrogen ($\delta^2\text{H}$), which are strongly influenced by continent-wide isotope patterns in amount-weighted precipitation (Hobson and Wassenaar 2008). In North America, most Neotropical migrants grow flight feathers in their breeding areas prior to fall migration. Isotopic signals of origin are then fixed into these feathers and can be sampled at other locations to infer origins (Hobson 2011). However, little is known about the breeding origins of long-distance migrants arriving at most stopover sites like the Darién region of Colombia and few investigators have collected feather samples at stopover sites in Colombia to address this knowledge gap (González-Prieto et al. 2011).

Canada Warblers are generally assumed to circumvent the Gulf of Mexico on fall migration and continue to South America via Central America (CMS 2014), but some individuals are known to migrate over the Gulf of Mexico (CMS 2014), as suggested by a small number of annual records from Florida and the Yucatan Peninsula (eBird 2016). Further south, our knowledge becomes increasingly scant and it is unknown whether birds cross the Caribbean or the Pacific from Central America to Colombia or whether most birds migrate overland. If the latter is true, the Darién region connecting the two

landmasses may act as an important area for Canada Warblers, as previously shown for other species (Bayly et al. 2014, Gómez et al. 2014).

Southward migration of Canada Warblers is believed to begin between July and August and the first individuals arrive at wintering areas between late September in Colombia and early October in Peru (CMS 2014). However, the species' phenology during fall migration in the tropics has not been studied, and we also know little about the habitats used by Canada Warblers during migration and if there is habitat segregation by sex and age.

Most long-distance migrants cannot store sufficient energy reserves for one continuous migration flight (Kaiser 1999), so they rely on a series of stopover sites to replenish their energy reserves. Body mass and visible fat scores can be used as indicators of energy reserves (Labocha and Hayes 2011) and to determine if birds need to make a stopover or continue migrating. However, no information is available concerning the arrival body condition of Canada Warblers during migration through Central America or Colombia.

I analyzed banding data from Canada Warblers captured at two migration monitoring stations located on Colombia's Caribbean coast during fall migration: the Darién (four years) and the Sierra Nevada de Santa Marta (three years, hereafter SNSM). Birds arriving in the Darién would largely be expected to have arrived via Central America, although some birds may have done so following flights over the Caribbean. In contrast, individuals captured in the SNSM would likely have used a trans-Caribbean route. This assumption is consistent with differing capture rates for Veeries (*Catharus fuscescens*) and Swainson's Thrushes (*Catharus ustulatus*) in the

Darién and the SNSM (Gómez et al. 2013, 2014), and geolocator tracks showing that Veeries are primarily trans-Caribbean migrants (Heckscher et al. 2011), whereas Swainson's Thrushes migrate via Central America (Delmore et al. 2012). Considering the potentially differing role of each site, our objectives were to determine: 1) the breeding origins of Canada Warblers migrating through northern Colombia, 2) the relative importance of the two migration pathways (trans-Caribbean and Central American, 3) the phenology of migration at each site, 4) if there are differences in the age and sex composition of Canada Warblers at the two sites, 5) the body condition of Canada Warblers at the time of arrival in Colombia, and 6) if Canada Warblers used our study sites for refueling during multi-day stopovers.

4.2 METHODS

Canada Warbler was studied in two regions on Colombia's Caribbean coast. The Darién, located in northwest Colombia where Central America connects to South America, may act as an important geographic for migratory birds traveling overland through Central America to South America (Gomez et al. 2014, Bayly et al. 2014). The SNSM, an isolated mountain range in northeastern Colombia at a latitude equivalent to southern Nicaragua and ~450 from the Darién, is most likely to receive birds whose migration route crosses part of the Caribbean Sea, given its more northerly and easterly position relative to the Darién .

In the Darién, I worked in the Tacarcuna Nature Reserve (08°39'41.53"N, 77°22'06.74"W; ~100 m asl) located near the village of Sapzurro and the border of Colombia and Panama (Figure 4.1). The habitat consisted of seasonal tropical humid

forest interspersed with small clearings for agriculture and houses. In the SNSM, we collected data at two sites that differed in elevation, including Quebrada Valencia Nature Reserve ($11^{\circ}14'22.35''\text{N}$, $73^{\circ}47'55.34''\text{W}$), consisting of tropical humid lowland forest between 100 and 200 m asl, and Hacienda La Victoria ($11^{\circ}7'19.84''\text{N}$, $74^{\circ}5'34.14''\text{W}$), consisting of tropical pre-montane forest and shade-coffee plantations at elevations between 1100 and 1300 m asl.

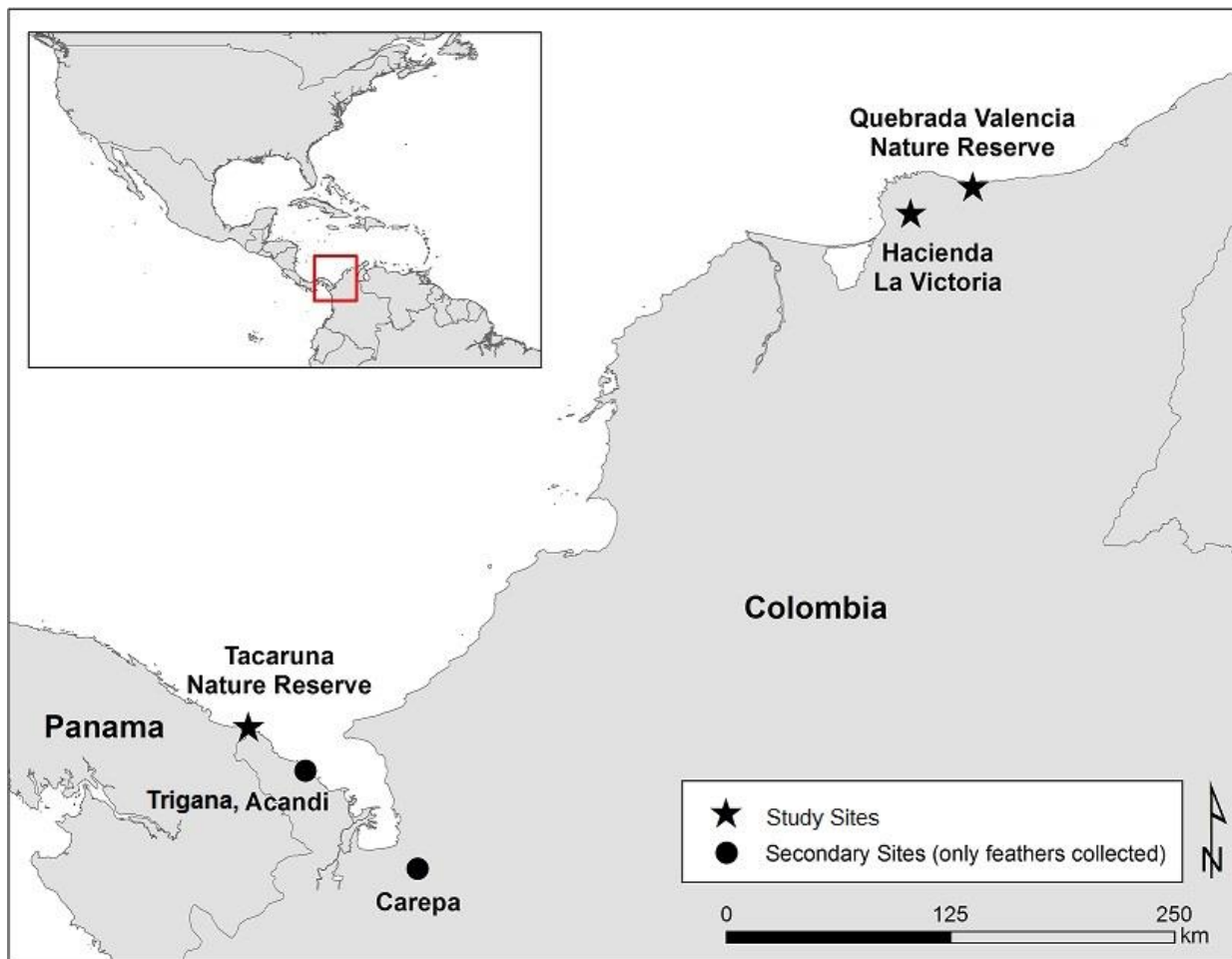


Figure 4.1 Location of my three main study sites in northern Colombia. Tacarcuna Nature Reserve (Darién), Hacienda La Victoria and Quebrada Valencia Nature Reserve (Sierra Nevada de Santa Marta). At the secondary sites, Trigana, Acandí and Carepa, we only collected feather samples for our study.

4.2.1 Data collection

Constant-effort mist-net stations consisting of 8 to 15 mist-nets (12 or 18 m long, 32-mm mesh) were established to monitor fall migration at each of study site. Mist-nets were positioned strategically to maximize captures and the number of nets and their location were kept virtually constant among days and years. Each mist-net station was operated during at least three fall migrations (September through November) between 2009 and 2015 (Table 4.1). Nets were opened either daily or every other day beginning at dawn, remained open for 4.5 h on average, and were checked every 30-40 min. Captured birds were banded with uniquely coded Porzana-made metal bands (band reporting website: www.aselva.co). For all Canada Warblers, I recorded date and time of capture, age and sex (based on plumage, Pyle 1997), visible subcutaneous fat score (Kaiser 1993), pectoral muscle score (Redfern and Clark 2001), wing chord (± 1 mm), and body mass (± 0.1 g) using an electronic balance (Fast Weigh digital pocket scale, model M-500).

I collected the first primary feather from HY and AHY individuals captured in the Darién. The first primary feather is one of the first to be molted on the breeding grounds (Pyle 1997) and so is a more reliable indicator of natal or breeding origin. After collection, feathers were placed in paper envelopes with individual information. I also analyzed 153 tail feather samples collected between 2011 and 2014 by GC at two stations south of our Darién banding station: Carepa, Antioquia ($7^{\circ}46'26''\text{N}$, $76^{\circ}39'55''\text{W}$) and Trigana, Acandí ($8^{\circ}22'37''\text{N}$, $77^{\circ}07'57''\text{W}$).

Feather samples were prepared in the Environment Canada stable isotope laboratory at the National Hydrology Research Centre (NHRC) in Saskatoon, Canada.

Each feather sample was soaked for 5 h in 2:1 chloroform: methanol solution then rinsed and dried in a fume hood for 48 h (Hobson and Wassenaar 2008). The impact of exchangeable hydrogen on isotopic measurements was corrected using the comparative equilibration method (Wassenaar and Hobson 2003). Within analytical runs, we used Environment Canada keratin reference standards CBS (caribou hoof = -197‰) and KHS (kudu horn = -54.1‰) to account for exchangeable H and to calibrate samples. H isotopic measurements were performed on H₂ gas derived from high-temperature (1350°C) flash pyrolysis of 350 ± 10 ug of distal-vane feather subsamples in silver capsules. Resulting H gas was separated in a Eurovector 3000 (Milan, Italy) elemental analyzer and introduced into an Isoprime (Crewe, UK) continuous-flow isotope-ratio mass spectrometer. All results are reported for non-exchangeable H expressed in the typical delta (δ) notation, in units per mil (‰), and normalized on the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale (Wassenaar and Hobson 2006). Based on within-run replicate (*N* = 5) measurements of laboratory keratin standards, I estimated measurement precision to be ± 2‰.

Table 4.1 . Number of Canada Warblers captured by year and survey effort at each of our three study sites, including date range, total mist-net effort expressed in mist-net hours (1 mist-net hour = one 12-m net x 1 hour), and total number of effective survey days. CR = capture rate.

Site	Year	Date range	Mist-net hours (days)	Captures	CR (Ind/day)
Darién - Tacarcuna Nature Reserve	2011	13 Sep - 31 Oct	1755.4 (49 days)	79	3.8
	2012	25 Sep - 5 Nov	1596.3 (42 days)	35	1.5
	2014	17 Sep - 6 Nov	2459.6 (51 days)	31	1.6
	2015	11 Sep - 3 Nov	2375.1 (57 days)	15	0.8
SNSM - Quebrada Valencia	2009	20 Sep - 3 Nov	2096.0 (37 days)	0	0
	2010	29 Sep- 1 Nov	2137.3 (33 days)	0	0
	2011	29 Sep- 1 Nov	1912.7 (33 days)	0	0
SNSM - Hacienda La Victoria	2009	27 Sep - 13 Nov	1291.3 (41 days)	0	0
	2010	30 Sep - 4 Nov	1342.3 (33 days)	1	0.03
	2011	21 Sep - 30 Oct	1688.7 (39 days)	0	0

4.2.2 Data analysis

Canada Warblers breed across a broad longitudinal and latitudinal gradient in North America and can be usefully split into eastern and western breeders using the Manitoba-Ontario border. This corresponds conveniently to expected $\delta^2\text{H}_f$ values as being $< -110\text{‰}$ for western birds and $> -110\text{‰}$ for eastern birds due to the nature of the $\delta^2\text{H}_f$ isoclines (Hobson et al. 2014). Although arbitrary, we considered this delineation useful because eastern and western breeding populations of Canada Warblers differ in abundance (higher breeding density in the east), population trends (more significant declines in the east), and response to spruce budworm defoliation (Sleep et al. 2009). In addition, because breeding populations potentially represent a bimodal distribution of origin, depicting each mode separately using our probabilistic methods was more appropriate (Wunder 2010). I assigned birds to breeding areas using a likelihood-based assignment method (Royle and Rubenstein 2014). Details of our approach for assigning birds to origins in a probabilistic framework are described elsewhere (Hobson et al. 2014). Briefly, I employed algorithms relating variation in $\delta^2\text{H}_f$ to variation in $\delta^2\text{H}_p$ (Hobson et al. 2012). Hobson et al. (2012) provided separate isoscape calibration equations based on migratory and foraging guilds. For Canada Warblers, I calibrated an isoscape for non-ground-foraging Neotropical migrants ($\delta^2\text{H}_f = -27.09 + 0.95 \delta^2\text{H}_p$). To limit assignment results to biologically plausible origins, I used digital range maps (Ridgely et al. 2011) to clip the recalibrated isoscape to the breeding range using functions in the raster package (Hijmans and Etten 2016) in the R statistical computing environment. For each sample (bird), I assessed the likelihood that each cell in the calibrated isoscape represented a potential origin for the individual using the

normal probability density function and applied a 2:1 odds ratio criterion for including each pixel as a potential source or not. Probabilities of origin surfaces were combined for all individuals in a population whereby pixel data reflected how many individuals at a given pixel were included in a final population depiction. This analysis was done with R version 3.0.1 (R Development Core Team 2013).

4.2.3 Darién vs. Sierra Nevada de Santa Marta

Sampling effort at both sites was uneven. To determine the degree to which each region was used by Canada Warblers on fall migration, I first calculated mist-net effort by year, where one mist-net hour = one 12-m net open for one hour. I then calculated capture rate (CR) for each site and year, where $CR = \text{number of captures per 1000 mist-net hours}$.

4.2.4 Timing of migration

Phenology of fall migration was considered only for the Darién because only one Canada Warbler was captured in the SNSM. I calculated the percentage of individuals captured per day by dividing the capture total for any given day by the total number of fall captures for each of the three years. For any given date, I then calculated the mean percentage across the three years, but only including days when mist-nets were opened. Because mist-net effort varied among years, but little between days within years, we expected this method to provide a reliable approximation of the timing of migration without having to correct for the complex effect of mist-net effort. I also examined possible differences between the sexes and age groups in the mean and median dates of capture using *t*-tests.

4.2.5 Age and sex ratios and body condition

I estimated the ratio of immature (hatch-year) and adult (after hatch-year) birds and the ratio of males to females in Canada Warblers captured during each of four years in the Darién. Using chi-square analysis, I examined whether either ratio showed inter-annual variation.

To determine body condition and estimate the fuel reserves of Canada Warblers migrating through the Darién, I first estimated lean body mass (LBM) of 71 individuals (fat score = 0). LBM is expected to represent the average body mass of a bird with no energy reserves and was estimated by regressing body mass against wing length for a sample of birds with no visible fat reserves (Lindström and Alerstam 1992). To quantify fuel reserves, I used the following equation that expresses fuel reserves as a percentage of LBM (Lindström and Alerstam 1992): Fuel reserve = $((\text{body mass} - \text{LBM}) / \text{LBM}) * 100$.

4.2.6 Stopover behavior and potential flight range

Stopover duration and fuel deposition rate are normally estimated from birds captured more than once. However, no Canada Warblers were recaptured so we considered the propensity for a stopover based on their fuel reserves at the time of initial capture (see above). To estimate potential flight ranges, I used the program Flight (Pennycuick 2008) using values for departure fuel load based on the fuel reserves of captured birds.

Wingspan (18.2 ± 0.50 cm) and wing area (61.22 ± 2.97 cm²) were estimated for Canada Warblers based on a subsample ($N = 5$) of birds captured in the Darién. Flight simulations were conducted for all captured individuals. Starting altitude was set at 100 m, cruising altitude at 1000 m, and muscle fraction at 0.17 (Default value, Pennycuick

2008). Body drag coefficient was set at 0.1, which is the default value recommended for small passerines (Pennycuik 2008). Values are presented as means \pm 1 SD.

4.3 RESULTS

4.3.1 Breeding origins and connectivity patterns

The Darién region concentrated individuals from across their breeding range. However, δ^2H_f values revealed that most (56/70, or 80%) likely originated from the eastern rather than the western portion (14/70, or 20%) of their breeding range (Figure 4.1 A, B). This delineation was based on observation of the expected δ^2H_f values separating the range (northeast: δ^2H_f values > 110 ‰, northwest: < 110 ‰; see Hobson et al. 2014) and corresponds approximately to the longitude of eastern Manitoba and western Ontario, Canada. Most birds captured in the Darién from the northeastern portion of their breeding range had δ^2H_f values consistent with those expected from Quebec and Ontario (mean = -90.16 ± 12.14 , $N = 42$, range = -109 ‰ to -63 ‰). In the northwest, birds had δ^2H_f values consistent with those expected from west-central Saskatchewan and Alberta (mean = -125 ± 14 ‰, $N = 13$, range = -148 ‰ to -110 ‰). Additionally, the δ^2H_f values obtained from the two nearby sites showed similar breeding origin ranges. Most of the latter samples likely originated from the eastern (127/153, 83%) ($X = -84.08 \pm 16$ ‰, $N = 127$, range = -110 ‰ to -27 ‰) rather than the western portion (26/153, 17%) ($X = -139 \pm 21$ ‰, $N = 26$, range = -200 ‰ to -111 ‰) of their breeding range (Fig. 4.1 C, D). The -27 ‰ sample originated in the northeastern range corresponds either to a feather grown or replaced on wintering grounds (likely) or one showing an extreme coastal effect (unlikely).

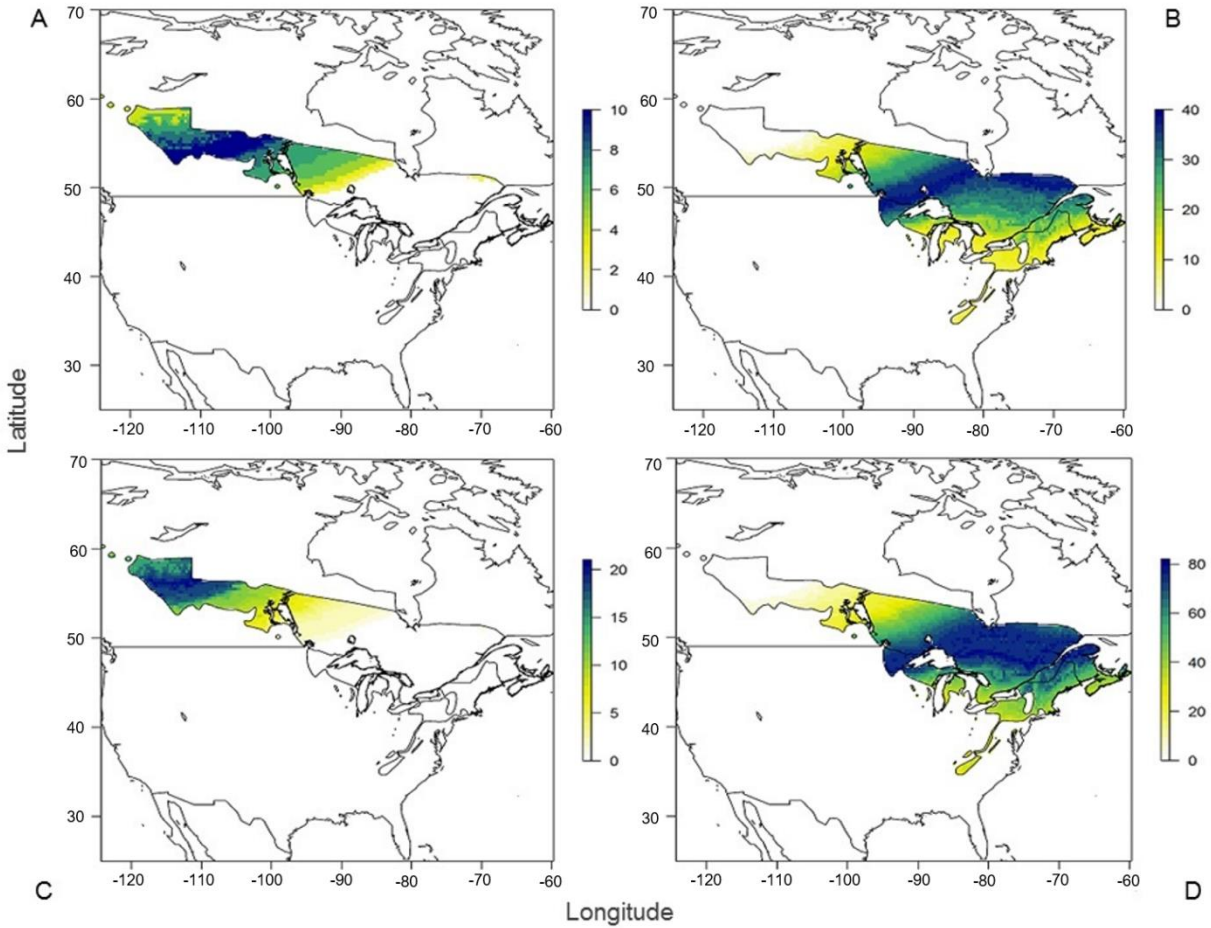


Figure 4.2 Geographic distribution of assigned origins for Canada Warblers captured in the Darién, Colombia, during fall migration, as inferred from stable isotope ($\delta^2\text{H}_f$) analysis (A and B: samples collected in Tacarcuna Reserve; C and D: samples collected in Carepa-Antioquia and Triganá-Chocó). (A) Individuals assigned to the western extent of the breeding distribution (14 samples; $\delta^2\text{H}_f < -110$ ‰) and (B) Individuals assigned to the eastern extent of the breeding distribution (56 samples; $\delta^2\text{H}_f > -110$ ‰), (C) Individuals assigned to the western extent of the breeding distribution (26 samples; $\delta^2\text{H}_f < -110$ ‰), and (D) Individuals assigned to the eastern extent of the breeding distribution (127 samples; $\delta^2\text{H}_f > -110$ ‰).

4.3.2 Darién vs. Sierra Nevada de Santa Marta

I captured 162 individuals in the Darién over a four-year period. In the SNSM, mist-netting during three fall migration seasons at two stations resulted in just a single capture in the Hacienda la Victoria despite similar total mist-net effort for the Darién and the SNSM (Table 4.1). In 2011, when the three mist-net stations were run simultaneously, 72 birds were captured in the Darién and none were captured in the SNSM.

4.3.3 Timing of migration-phenology

The earliest a Canada Warbler was captured at the Darién site was 20 September 2011, and the single capture in the SNSM was on 30 October 2010. The phenology of migration through the Darién occurred between 20 September and 5 November, with a peak in mid-October (71% of total captures between 9 and 22 October). Mean arrival date of Canada Warblers did not vary among years (ANOVA, $F_{3,159} = 1.4$, $P = 0.25$), however, phenology differed with age ($t_{1,7} = 9.3$, $P < 0.001$; Figure. 4.3) and sex ($t_{1,7} = 9.4$, $P < 0.001$; Figure. 4.4). AHY birds arrived earlier (mean = 10 October \pm 2.9 days) than HY birds (16 October \pm 2.6 days), and males arrived earlier (mean = 12 October \pm 3.5 days) than females (15 October \pm 4.0 days).

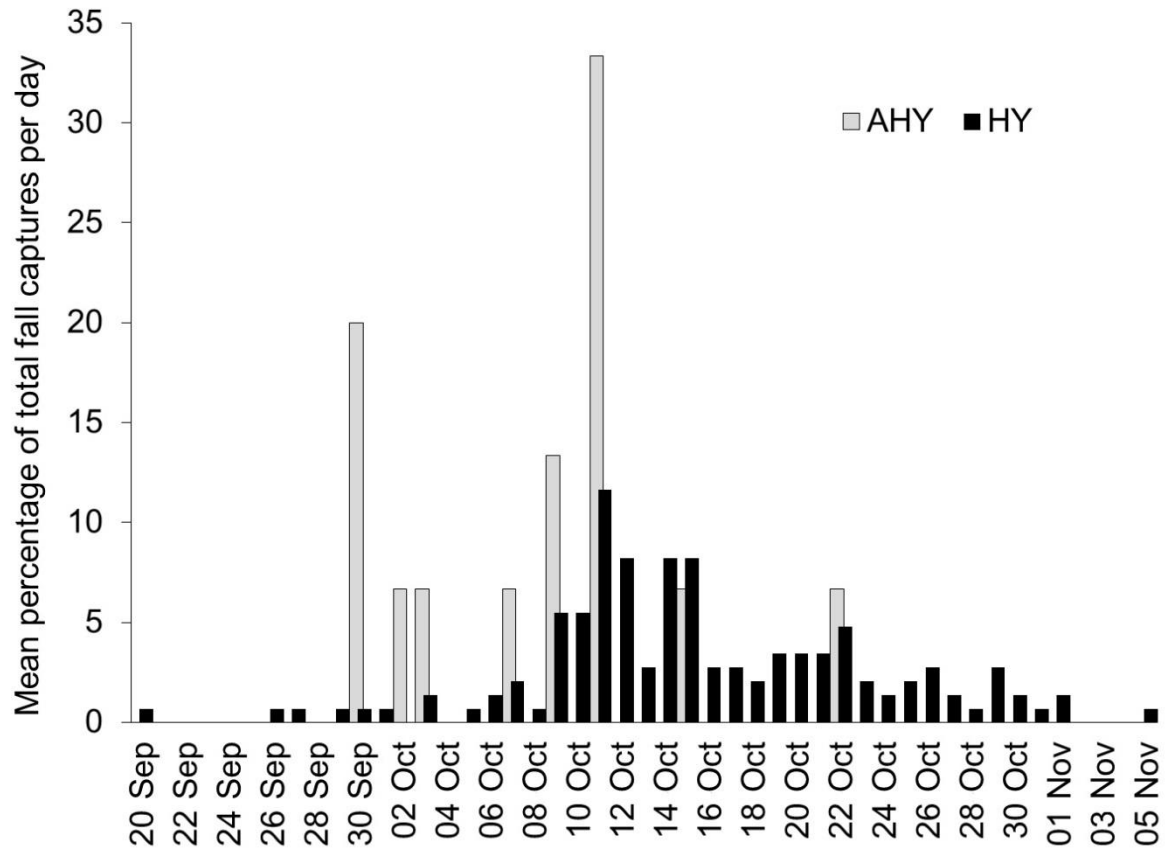


Figure 4.3 Average phenology of fall migration of after hatch-year (AHY) and hatch-year (HY) Canada Warblers migrating through the Darién in northwest Colombia during 2011, 2012, 2014, and 2015.

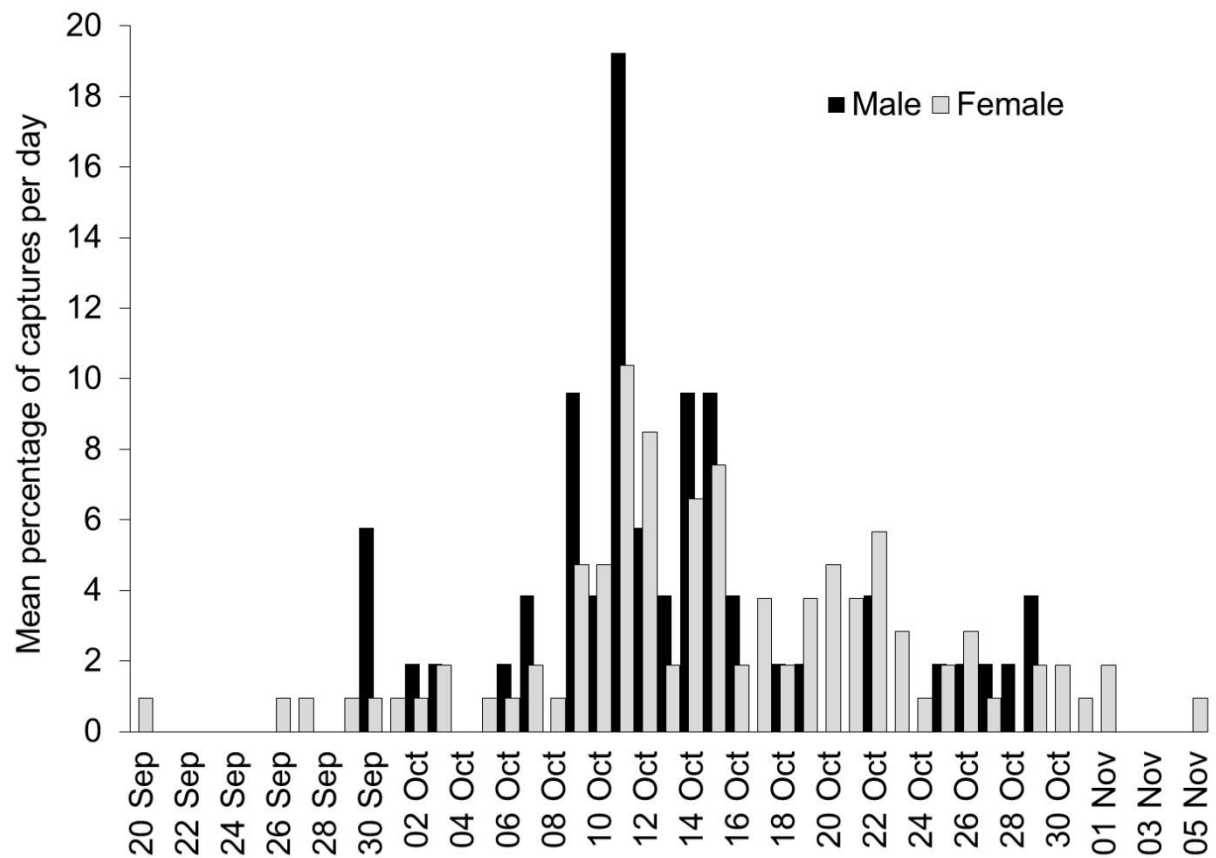


Figure 4.4 Average phenology of fall migration for male and female Canada Warblers migrating through the Darién in northwest Colombia during four years (2011, 2012, 2014 and 2015).

4.3.4 Age and sex ratios

I captured 146 HY and 15 AHY individuals in the Darién between 2011 and 2015 and a single HY in the SNSM between 2009 and 2011. The number of captures declined across years in the Darién despite increasing sampling effort. This decline is largely due to a decrease in HY birds captured compared to AHY birds, which were more stable over time (Figure. 4.5A). Age ratios differed among years ($\chi^2_{3,158} = 43.3$, $P < 0.001$), with 2011 and 2012 having higher ratios of HY to AHY birds than 2014 and 2015. Sex ratios also differed among years ($\chi^2_{3,154} = 10.5$, $P = 0.015$), with a higher proportion of females than males in 2011 and 2012 than in 2014 and 2015 (Table 4.2, Figure. 4.5B).

Table 4.2 Summary of arrival times and age and sex ratios in the Tacarcuna Nature Reserve, Darién.

Year	Mean arrival day \pm SD (days)				Age and sex ratios	
	HY	AHY	Female	Male	HY/AHY ^a	Female/Male
2012	17 Oct \pm 7.5	7 Oct	17 Oct \pm 7.3	10 Oct \pm 9.1	35:1	8:1
2014	19 Oct \pm 9.2	10 Oct \pm 1.1	19 Oct \pm 9.2	16 Oct \pm 9.5	7:1	1:1
2015	13 Oct \pm 9.1	10 Oct \pm 1.1	9 Oct \pm 9.4	8 Oct \pm 10.0	2:1	1:1

^aHY = Hatch-year bird; AHY = After-hatch-year bird

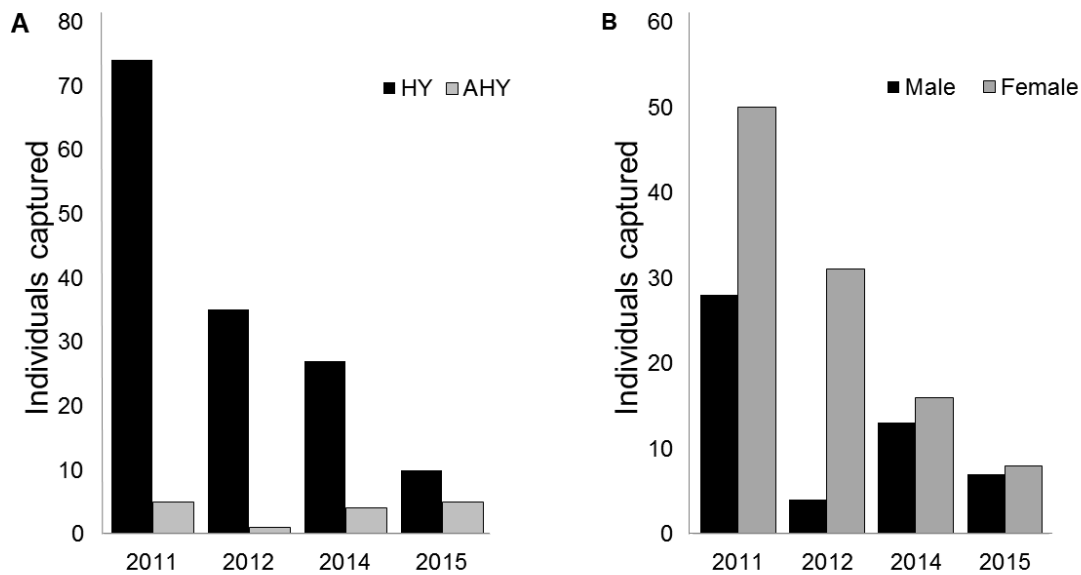


Figure 4.5 Number of A) immature (HY) and adult (AHY) and (B) male and female Canada Warblers captured in the Tacarcuna Reserve, Darién, Colombia, by year.

4.3.5 Body condition, stopover behavior and potential flight range

Lean body mass (LBM) of Canada Warblers was estimated by regressing body mass against wing length for a group of birds with fat score zero. Body mass was positively correlated with wing length ($r = 0.46$, $P < 0.001$, $N = 19$), giving rise to the regression equation: $LBM = 1.5423 + (0.1161 \times \text{wing length})$ and an estimated LBM of 8.85 g for a bird of mean wing length (63 mm). Fuel reserves were categorized as small (<10% of LBM), medium (10 - 30%), and large (>30%). Most birds arrived with low (88%) or medium (12%) fuel reserves (Figure. 4.6), with fuel loads ranging from – 13 to 18% LBM. Flight ranges calculated for Canada Warblers captured in the Darién ranged from 0 to 1061 km, with 46% of birds having predicted flight ranges of 0 km, 31% between 50

and 200 km, 13% between 250 and 400 km, 8% between 450-600 km, and 4% of 1061 km (Figure. 4.7).

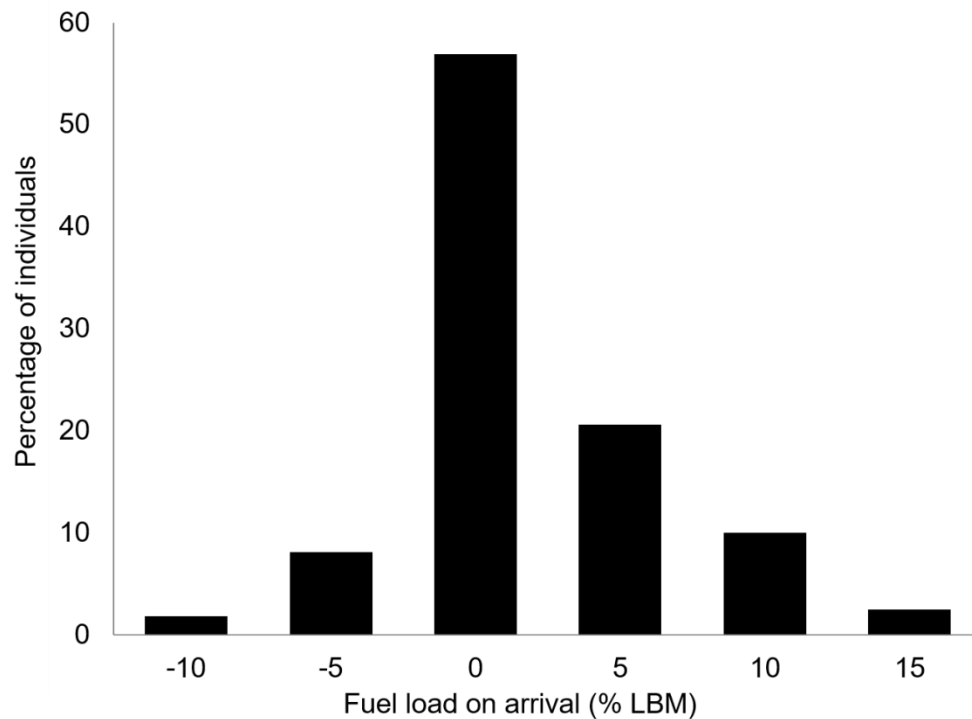


Figure 4.6 Histogram of fuel load at first capture of Canada Warblers in the Tacarcuna reserve, Darién. A value of zero or below means that birds were first captured with lean body mass (LBM), which is equivalent to having no visible fat reserves.

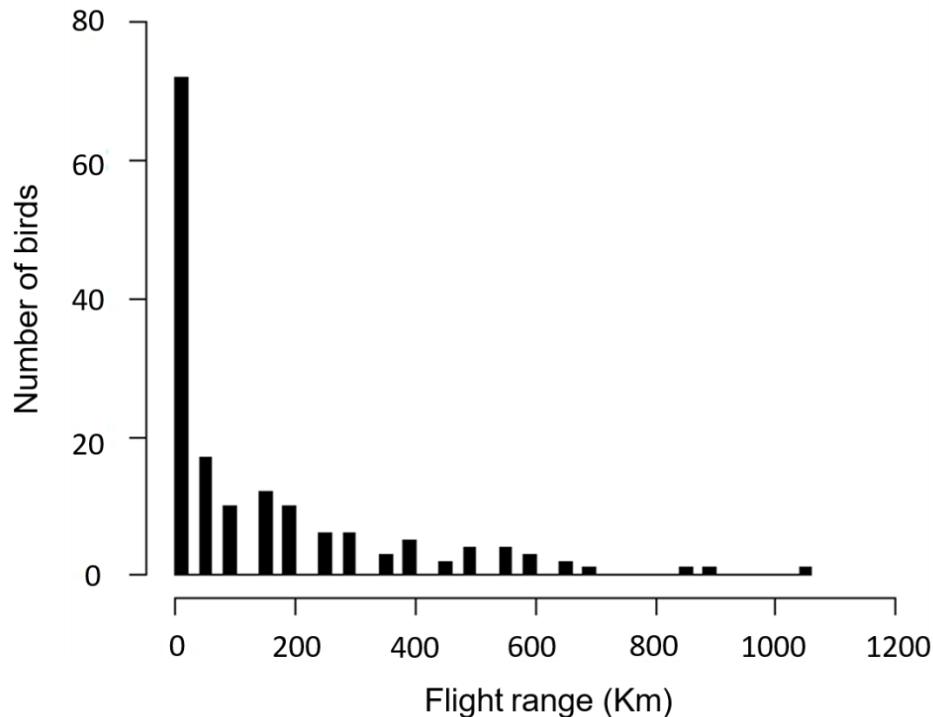


Figure 4.7 Histogram of expected flight ranges for each Canada Warbler (N = 161) captured in the Darién, Colombia. Flight range was calculated using the program Flight (Pennycuick 2008) and was based on the fuel load at first capture of each individual captured in the Tacarcuna reserve across four years.

4.4 DISCUSSION

My results provide support for the hypothesis that Canada Warblers likely take an overland migratory route through or parallel to Central America rather than crossing the Caribbean. At the Darién stopover site, we also found evidence for the potential importance of this area for refueling by Canada Warblers, with many captured birds having low fuel reserves. However, the lack of recaptures suggests potential local movements to more profitable areas, possibly at higher elevations. The preponderance of females and HY birds suggests that adults and males take another route and/or have

different patterns of habitat use (e.g., Marra 2000). It is notable that captures of HY birds have declined in the Darién over the last five years and, importantly, my stable isotope approach suggests that eastern breeding areas in North America may be contributing a greater proportion of HY recruits into the wintering population than western breeding areas. However, we cannot exclude the possibility that HY birds from western populations take different routes and are therefore underrepresented in our sample. Taken together, these results suggest that this important geographical area (The Darién) provides valuable information for monitoring this and other species of Neotropical migrants *en route* to South America (Bayly et al. 2014, Gómez et al. 2014).

4.4.1 Migration route: Darién vs. Sierra Nevada de Santa Marta

The few records of Canada Warblers from the eastern Gulf Coast, Florida, West Indies, Bahamas, Bermuda, Puerto Rico, Jamaica, and Cuba (Pashley 1988, Dunn and Garrett 1997) suggest a low probability of individuals crossing the Caribbean Sea directly (Cramp and Perrins 1994). Our results support this hypothesis, with only a single capture over several years in northeast Colombia, where the geography of the South American continent dictates that migratory birds most likely arrive by an oversea route (Bayly et al. 2012). In contrast, Canada Warblers were relatively abundant in the Darién, supporting the hypothesis that most individuals migrate via the Central American landmass to South America or at least follow the coastline rather than crossing the open sea.

4.4.2 Timing of migration-phenology

The first individuals arrived in the Darién between 20 and 30 September. This is consistent with reported arrivals in other countries located to the north of Colombia,

including Guatemala (8 September –7 October), Honduras (21 September – 7 October; Monroe 1968) and Costa Rica (and early September – 20 October; Bent 1953). No recent information exists concerning migration and stopover areas for Canada Warblers in Central America. Ridgely and Tudor (1989) reported movements in late September and early October in Panama, the country nearest to my study site. In contrast, following a late September arrival at our study site, birds continued arriving into early November, with most individuals (71%) captured between 9 and 22 October.

4.4.3 Population structure

The fall migration of Canada Warblers in the Darién was dominated by HY birds, but the proportion of HY birds differed among years. HY birds showed a declining trend in number of captures over the years. Other studies conducted during the fall in coastal areas of North America have also revealed greater numbers of HY birds than AHY birds in Maine (Morris et al. 1994), Texas (Rappole et al. 1979), and Pennsylvania (Leberman and Clench 1971). The Darién study site was located close to the Caribbean Sea and HY birds may use this route more than adults, as would be expected from the “coastal effect”, i.e., immature birds are more likely to migrate along and make landfall on coasts (Ralph 1975). Alternatively, more HY birds are expected to be present in the fall due to production on the breeding grounds, but ratios of HYs in my study were generally higher than would be expected from the breeding season alone.

I also captured more females than males, which may occur if routes differ between sexes or, more likely, if males and females use different habitats. However, another possible explanation is that my study site was in a lowland area (humid tropical forest on the Caribbean coast at 70 m elevation) and may not represent optimal habitat.

Wintering Canada Warblers are associated with Andean forest between 1000 and 1800 m in elevation (Hilty 1980, Paynter 1995, Reitsma et al. 2010), suggesting that montane habitats in the Darién should be explored for this species. The capture of more HY and female birds also suggests that the habitat at my study site was not optimal because dominant AHYs and males have been found to predominate in high-quality winter habitats in other species of migratory warblers (Johnson 2007).

4.4.4 Body condition and stopover

Canada Warblers arrived at my field site in the Darién with relatively low fuel loads and ~50% of individuals likely had insufficient energy reserves to continue migrating. I would therefore expect many individuals to undertake a stopover at my study site. However, no individuals were recaptured so stopover duration and relative mass gain are unknown. The lack of recaptures contrasts with that of *Catharus* thrushes in the Darién (Gómez et al. 2014), where 6-10% of individuals were recaptured, despite *Catharus* thrushes arriving with larger fuel loads on average, and also with studies of Canada Warblers on the Atlantic coast of Maine (recapture rate = 1.7% during spring and 4.3% during fall; Morris et al. 1994). Other possible explanations for the lack of recaptures include: 1) Canada Warblers generally use forests at mid-level elevations and are therefore less likely to be recaptured, 2) birds adopt a strategy of one-day stopovers and short flights (Arizaga et al. 2011), and 3) the Darién study site represented low-quality habitat and birds made short-distance movements away from the study site in search of suitable habitat.

The reason for the lack of recaptures and evidence for stopovers may be a combination of the above three factors. Indeed, Canada Warblers may have a lower

recapture probability compared to *Catharus* thrushes in part because they may migrate in shorter steps and therefore have shorter stopover durations, as the proposed overland migration route via Central America would imply. The high proportion of females and immature birds captured also supports the idea that my site was low-quality habitat (Johnson 2007). Because the nearest wintering areas are ~200 km from our Darién study site and the core of the winter distribution is ~700 km away, many birds may have only needed a one-day stop before flying to their final destination.

4.4.5 Conservation

The Darién region appears to be an important passage region for Canada Warbler from across their breeding range during fall migration. In particular, females and immature birds appear to rely on the coastal region as part of their migration strategy, but it remains unclear whether they either attempt to or can replenish their energy reserves there. My data suggest a general decline in population over the years that is consistent with the decline in numbers reported in breeding areas. My limited dataset suggests that a decrease in the number of hatch-year birds may reflect either a decrease in productivity or an increase in hatch-year mortality. Alternatively, HY birds may simply be using other routes through time. Determining the factors driving this decline in capture rates of hatch-year birds is important and, particularly, whether it is related to reduced productivity or increased mortality during fall migration or changes in movements. Further studies of the fall migration of Canada Warblers along the length of their migration route are needed to better understand if changes in productivity or mortality rates during migration may be driving population declines.

CHAPTER 5. GENERAL CONCLUSIONS

Understanding *en route* ecology migration is difficult because it is challenging to track birds and quantify the effect of individual factors on overall population trends. Research is needed on many species simply to identify geographic distributions, patterns of migration, phenology, pathways of migration, sexual segregation during migration and basic ecology in general (Faaborg et al. 2010, Hobson. et al 2014, Bayly et al. 2014).

Although migrants experience high rates of mortality during migration, little is known about which populations in which species are most threatened and how this is affected by geographical origin and migratory connectivity. Indeed, once species migrate, we lack information about the places where those individuals stopover in Central and South America and the strategies and routes undertaken by them in order to complete successful migrations.

Thanks to the development of stable isotope methods to identify links between breeding and wintering sites (Hobson et al. 2014), I was able to investigate migratory connectivity and the effect of breeding origins as factors affecting stopover ecology. This and other tools are now shedding new light on previously intractable questions.

In chapter 2, I described the breeding origins of several Neotropical migrants using a strategic stopover area that has been considered very important for diurnal migrants (Bayly et al. 2014), but never before for nocturnally migrating passerines. Few places in the world have a narrow geography in area dimensions to congregate vast numbers of birds. The term “funnel shaped migration” occurs when many species with large breeding distributions, especially at higher latitudes, which often congregate through vast funnels to relative small resting areas (Berthold 1993). This term applies

perfectly to the community of migrants analyzed in this study which originated in northern Canada and United States. Despite the fact that I did not have the opportunity to analyse the breeding origins of more species for my thesis, about 35 species of long-distance migrants were registered either by observations or captures during the time that the samples of this study were collected. Therefore, the same type of study I conducted for 11 species is recommended for several others.

In Chapter 2, I also described patterns of migration that are very important in order to understand the degree of effect of factors as the breeding origin in the phenology of migration. Also, my approach to determining breeding origins represents an important precedent, especially when dealing with species of concern or declining. This is because the isotope approach allows for a rapid and comparatively inexpensive means of establishing the degree of connectivity of the whole populations, especially when they pass through reduced geographic areas. This type of analysis needs to be repeated in the future in other species throughout their flyways, to allow matching their breeding origins with their important stopover areas. This is one of the most important steps to design conservation actions aimed towards migratory birds, taking into account that migration is one of the times when most of their mortality occurs. Therefore, conserving the habitats that represent important stopover sites are key factors to reduce bird migration mortality. Although not all the species showed a specific pattern of migration, I found that the majority of the species followed a chain migration and only two species followed a leap frog migration. The rest of the species did not show a clear pattern, which it could be related with the quality of the data analyzed and the amount of data collected. Also, other questions need to be explored in the future in order to

expand our understanding of the structure of migration through the Darién and other regions. For example, it is important to determine how migratory birds can have different patterns of migration according not only to their breeding origin but also, according to their age or sex. Protandry, or differential migration according to sex, has been documented for several species in the breeding grounds (Morbey and Ydenberg 2001; Maggini and Bairlein 2012). Understanding patterns of arrival and use of stopover sites according to age and sex is tractable using conventional banding approaches but, as I have demonstrated, the stable isotope approach greatly expands the potential of this area of research.

In chapter 3, I focused on the arrival body condition of these same group of species. Breeding origins had a strong effect on the body condition of Swainson's Thrush. Individuals from the northerly latitudes arrived in lower body condition than those from the southerly latitudes. It is possible that the other six species can also follow the same pattern based on the model coefficients. However, more data is needed in order to confirm this possibility.

El Niño–Southern Oscillation (*ENSO*) also had an effect on the arrival body condition of Veery and Prothonotary Warbler, demonstrating for the first time, that El Niño years can affect the arrival body condition of not only frugivorous but also insectivorous species. The factor age affected the arrival body condition of Veery and Prothonotary Warbler. However, we found that Veery HY individuals did not necessarily arrive with lower body condition compared to AHY individuals. HY individuals also arrived in better body condition than AHY, as Prothonotary Warbler showed in my study

site. Males of Yellow Warbler and Scarlet Tanager arrived with lower body condition than females.

Regarding to the effect of the factor of migration route (Over land or water) in arrival body condition, I found not difference of individuals migrating either over land or over water. Both arrived in poor body condition. This was the first attempt of analyzing this kind of data that involves lots of assumptions. Therefore, it is necessary to know a lot more about each individual species to be able to detect effects of this factor in body condition in future attempts analyzing this kind of data.

At the community level, the most explanatory factor affecting body condition was body size. Larger individuals arrived in better body condition than smaller individuals.

In Chapter 4, I described more detailed results that have improved our knowledge of the migratory ecology of Canada Warbler, a species of concern in Canada. Although long distance migrants can use different migratory routes during migration (Hecksher et al. 2011, Hobson and Kardynal 2015), the high numbers of individuals captured in our site allowed us to conclude that its most probable migration route is across Central America. There is a long way to go in order to prioritize resources in order to protect this species; however, this finding helps us narrow down where to focus ongoing research efforts in order to identify key stopover regions. This result is very important because it gave us the route that we need to prioritize in terms of efforts in conservation investing economic support in places that are truly indispensable for the whole population. Even though our site was important for females and immatures, we need further explorations as suggested by Cardenas et al (2017) to find the important stopovers for males and adults in higher altitudes of the Darién region in Colombia. Also the inclusion of other

study areas in Central America where the specie is known to be abundant such as the highlands of Honduras and Nicaragua and the Serrania de Talamanca in Costa Rica and Panama will help us to have a better picture of the ecology of Canada Warbler. Otherwise the efforts of conservation during en route migration will not be enough to protect this species.

5.1 Conservation and research actions in the future

My research provided new knowledge regarding migratory patterns of Neotropical migrant songbirds through the Darién. This incredible region is geographically important and unique, because it fulfills the function of connecting North with South America. It is located in front of the Caribbean coast at 70 m above the Sea level at the boundary with Panama (Bayly et al. 2014), and it makes part of the ecoregion of the Chocó-Darién. This wet rain forest extends from eastern Panama to North western Colombia. The ecoregion of Darién-Chocó has also a high diversity and endemism with regard to fauna. It is a spot of avian endemism of the Neotropics and its falls within two endemic bird areas one in Central America and one in South America (Stattersfield et al. 1995).

However, the high biodiversity of the Darién is at risk due to the constant human growth of loss of habitat in the region. Protected areas here are limited in size considering the size of the ecoregion and the great diversity of different ecosystems, and thus the protection system is clearly deficient (Dinerstein et al. 1995). The rate of deforestation almost two decades ago was estimated in 600 km² per year (Budowski 1989). Nowadays, it is likely higher. The northern areas of Darién and Urabá, in

Colombia are used primarily to the production of bananas and cattle ranching. Southern areas are mostly plantations dedicated to the business of oil palm and extraction of timber for paper pulp (Barnes 1993; Davis et al. 1997). Due to this situation, these regions require with great urgency a great effort in order to conserve them.

Extensive areas of lowland forests and medium elevations in the region of the Darién represents one of the last opportunities to conserve not only large areas of intact forest, but also an incredibly biodiversity including migratory birds (WWF 2017). This group of birds tend to be more abundant at medium elevation gradients as it has been seen in other regions of Colombia in the northwestern section of South America (Gómez et al. 2015). The gradient of elevation of the region from 60m to 1,845 m at the tallest peak -Cerro Tacarcuna, in the Serranía del Darién, is a key characteristic that allows the study of natural altitudinal migration for migratory birds, a phenomenon that is increasingly rare in the tropics as its forests are being destroyed (WWF 2017). Therefore in my view, this region has lots of potential for effective conservation. The study of altitudinal migration of migratory birds at higher elevations is the project that I would like to perform during my next four years, with the aim to confirm whether the process of sexual segregation and different use of habitat is performed by migratory birds before reaching their wintering sites in South America. Also the exploration of other areas in the Pacific coast of the Choco region in Colombia would be interesting because the Pacific side has been not explored in terms of bird migration. With this information we could quantify the real importance of the whole region of the Darién. Also it would help us to calculate the percentage of the population of certain species of interest using the area. In addition, it would also allow us to confirm, whether the coasts

are definitively more important for females and immature birds, confirming the process of coastal effect experienced by migratory birds during migration (Ralph 1975) and the real importance of coastal forest vs inland or mountain forest.

Finally, the last objective of studying more the region of the Chocó-Darién would be focused with the aim to establish more areas for bird conservation “AICA” (Área Importante para la Conservación de las Aves/Important Area for the Conservation of Birds). During autumn, 338 species, or about 52% of all North American migrant bird species, fly to wintering areas in the Neotropics (Rappole and Morton 1985). For instance, in my study site, more than 10% of the population of Neotropical birds use the area during migration. The establishment of a new AICA that will allow us to guarantee a protected stopover for at least 35 species of migratory land birds detected in the area is feasible. Although the establishment of AICAS is a good tool in a local scale, we also need to propose the conservation of more extensive areas in order to contribute to the protection of the ecoregion of the Choco-Darién. In Colombia, where most of the ecoregion is found, the largest protected areas cover an area equal to only about 1% of the total original habitat, and these areas are quite distant from each other. On the Colombian side, a total of approximately 2,013 km² of the ecoregion is protected in national parks or 2.5% of the total ecoregion (Davis et al. 1997). Bordering on the east with the Darién National Park, in Panama, is the Los Katios National Park, covering an area of 720 km². Additional areas must be delineated and their protection promoted (INDERENA 1993). Much additional work is needed. There is information but it is insufficient or limited to small areas. More detailed ecological studies are needed on the ecoregion. Therefore in my view, the establishment of more areas devoted for

conservation under the name of a new National Park that connects Colombia and Panama would be the best option in order to protect long term the emblematic “Tapon del Darién”, guaranteeing the survival of not only migratory birds, but also the ecological system that allows to live numerous species of vertebrates and plants.

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APPENDIX A

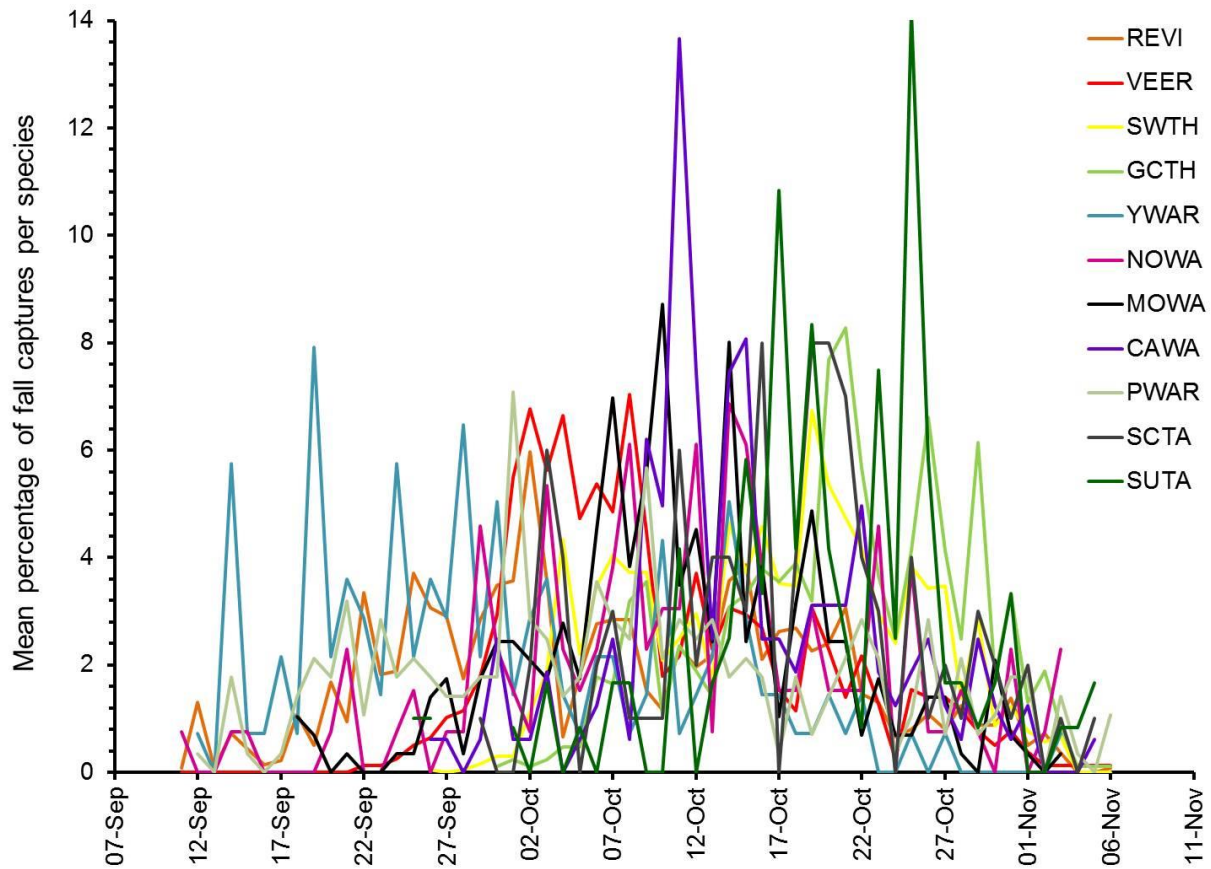


Figure A.1.1. Average phenology of fall migration of Red eyed Vireo (REVI), Veery (VEER), Swainson's Thrush (SWTH), Gray-cheeked Thrush (GCTH), Yellow Warbler (YWAR), Northern Waterthrush (NOWA), Mourning Warbler (MOWA), Canada Warbler (CAWA), Prothonotary Warbler (PWAR), Scarlet Tanager (SCTA) and Summer Tanager(SUTA), migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

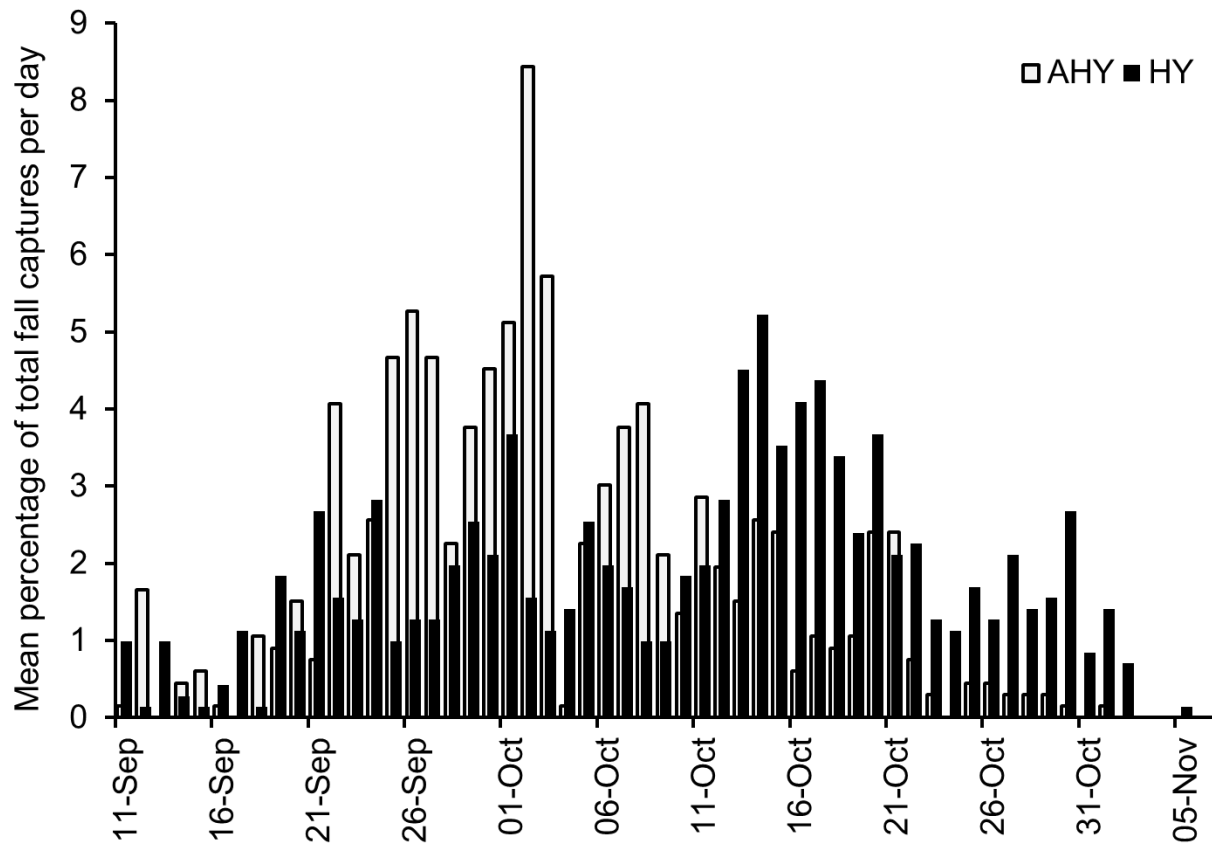


Figure A.1.2. Average phenology of fall migration of after hatch-year (AHY) and hatch year (HY) Red-eyed Vireos migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

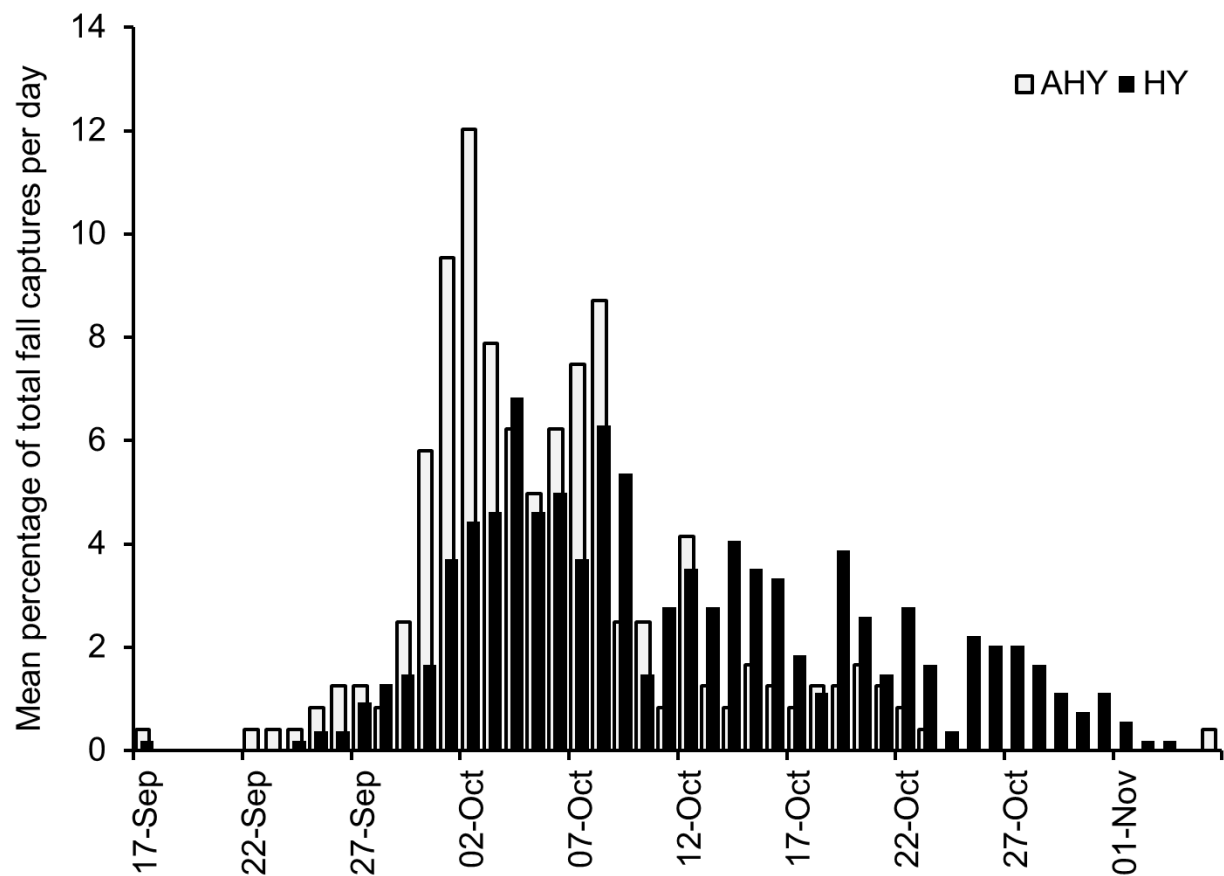


Figure A.1.3. Average phenology of fall migration of after hatch-year (AHY) and hatch year (HY) Veeries migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

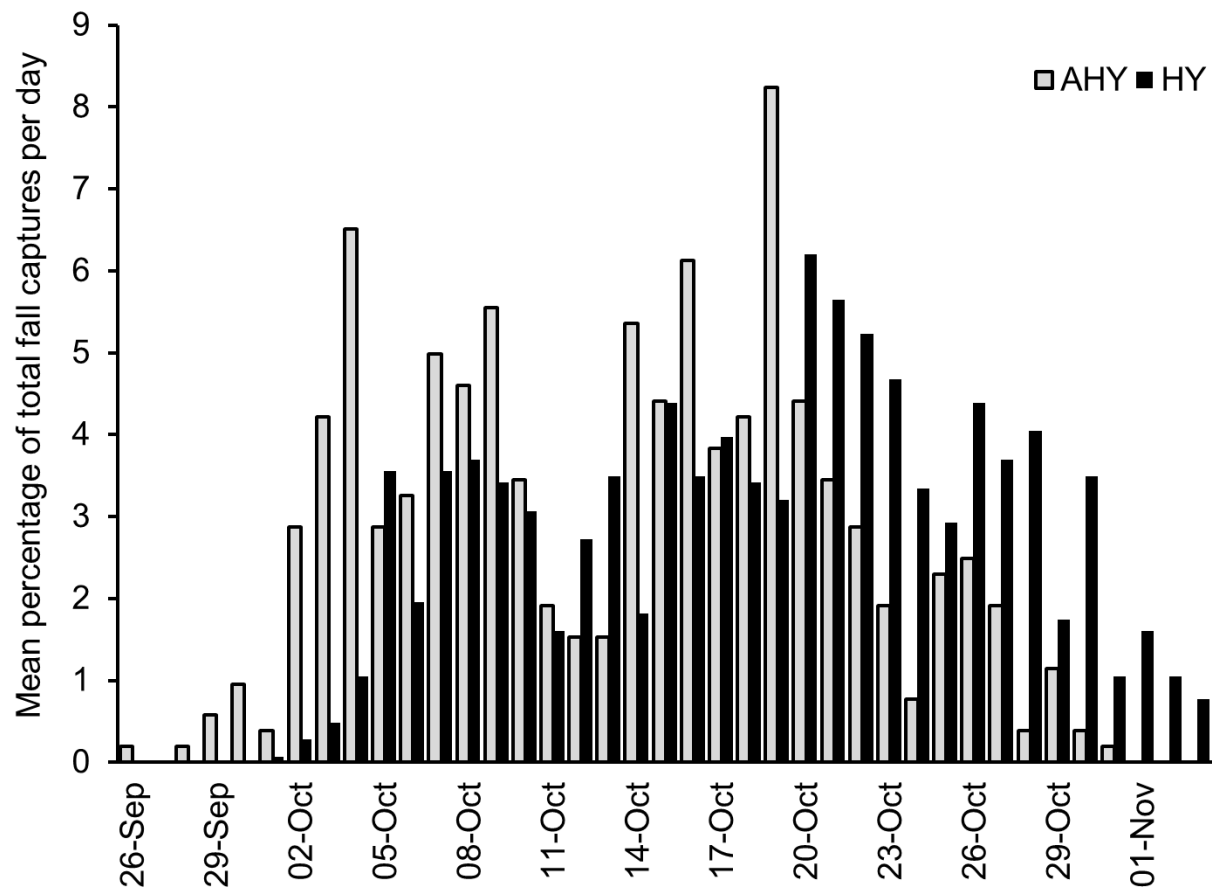


Figure A.1.4. Average phenology of fall migration of after hatch-year (AHY) and hatch year (HY) Swainson's Thrush migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

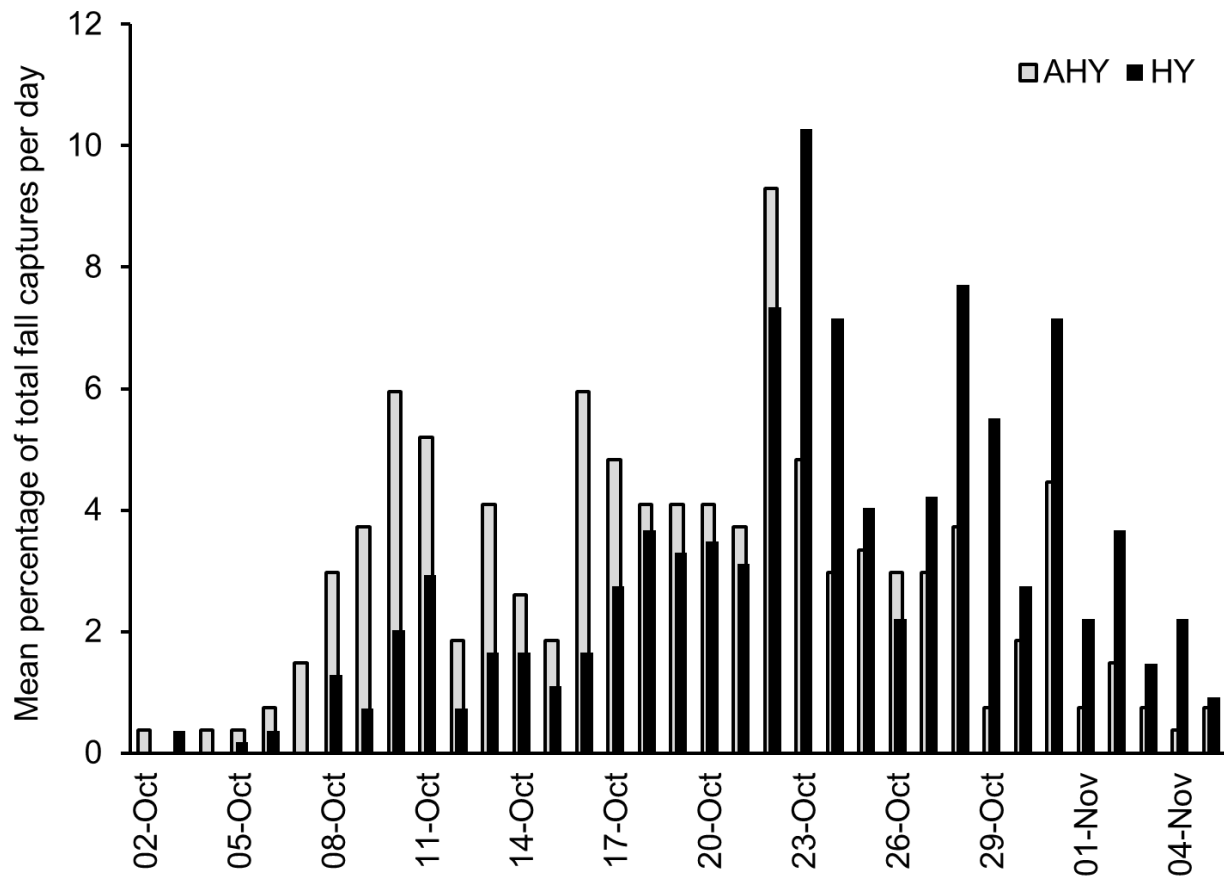


Figure A.1.5. Average phenology of fall migration of after hatch-year (AHY) and hatch year (HY) Gray-cheeked Thrush migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

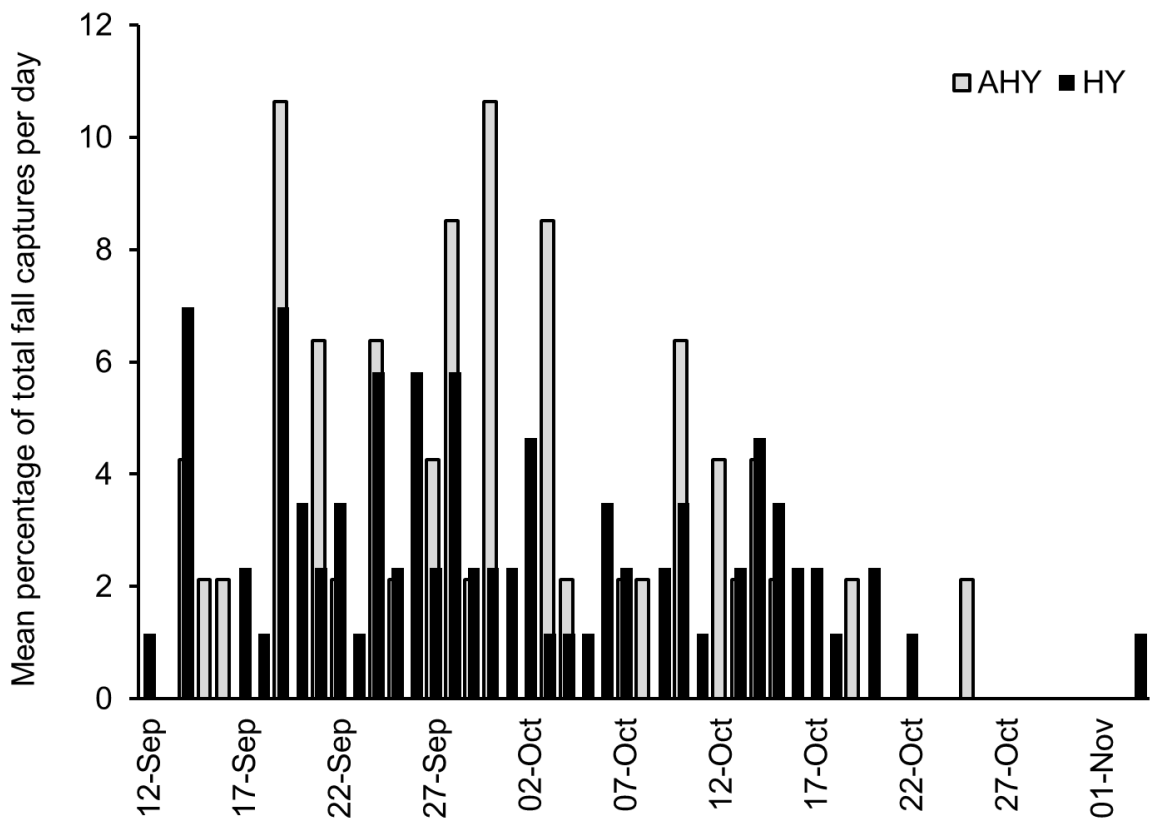


Figure A.1.6. Average phenology of fall migration of after hatch-year (AHY) and hatch year (HY) Yellow Warblers migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

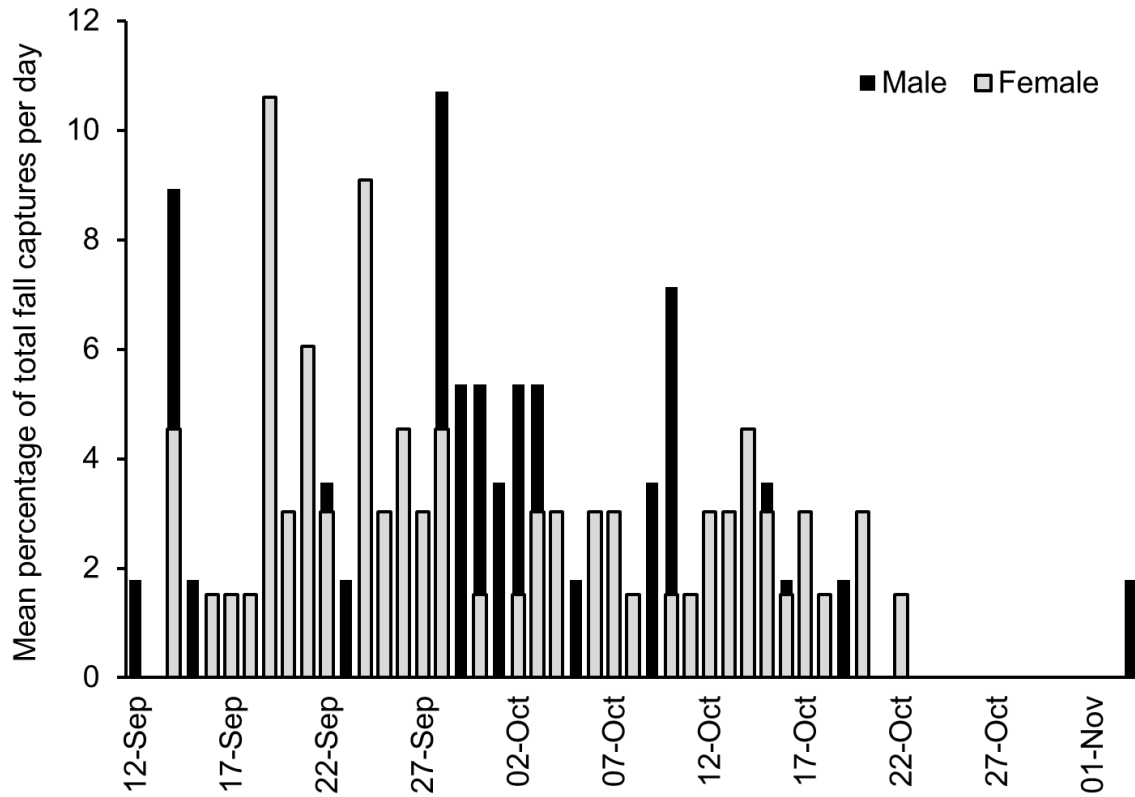


Figure A.1.7. Average phenology of fall migration of male and female of Yellow Warblers migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

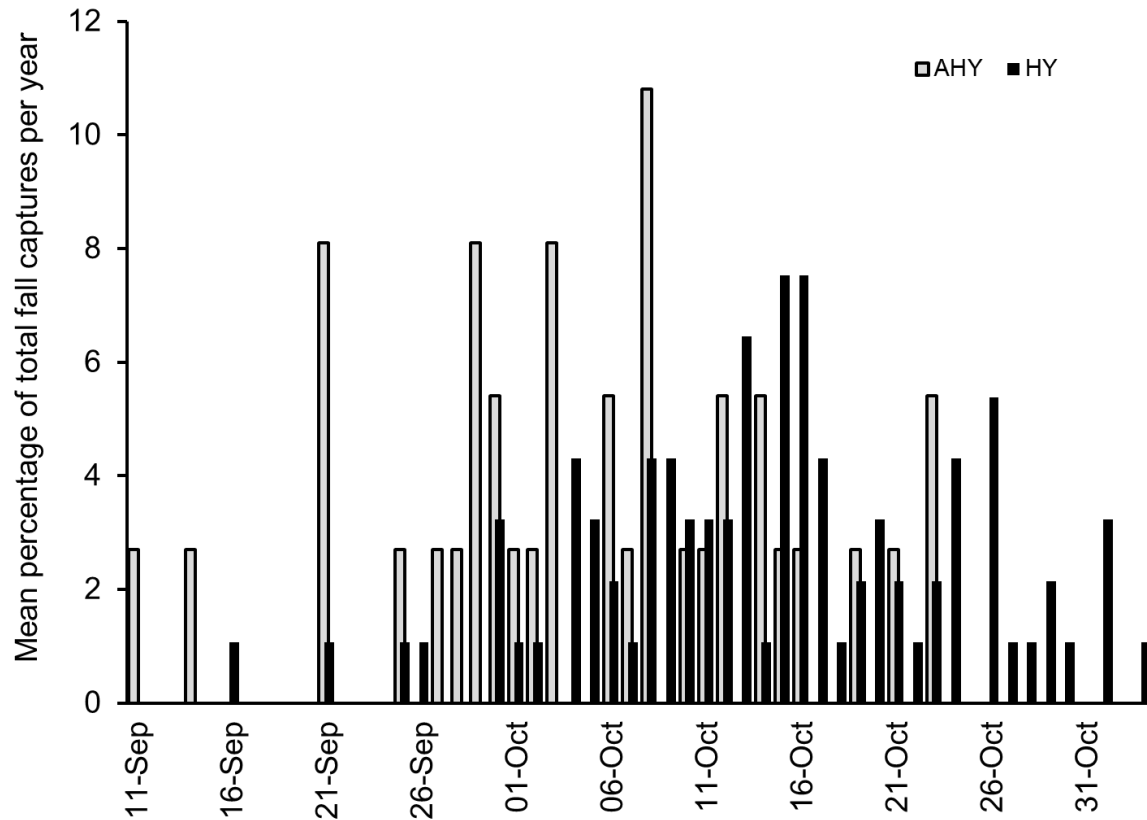


Figure A.1.8. Average phenology of fall migration of after hatch-year (AHY) and hatch year (HY) Northern Waterthrushes migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

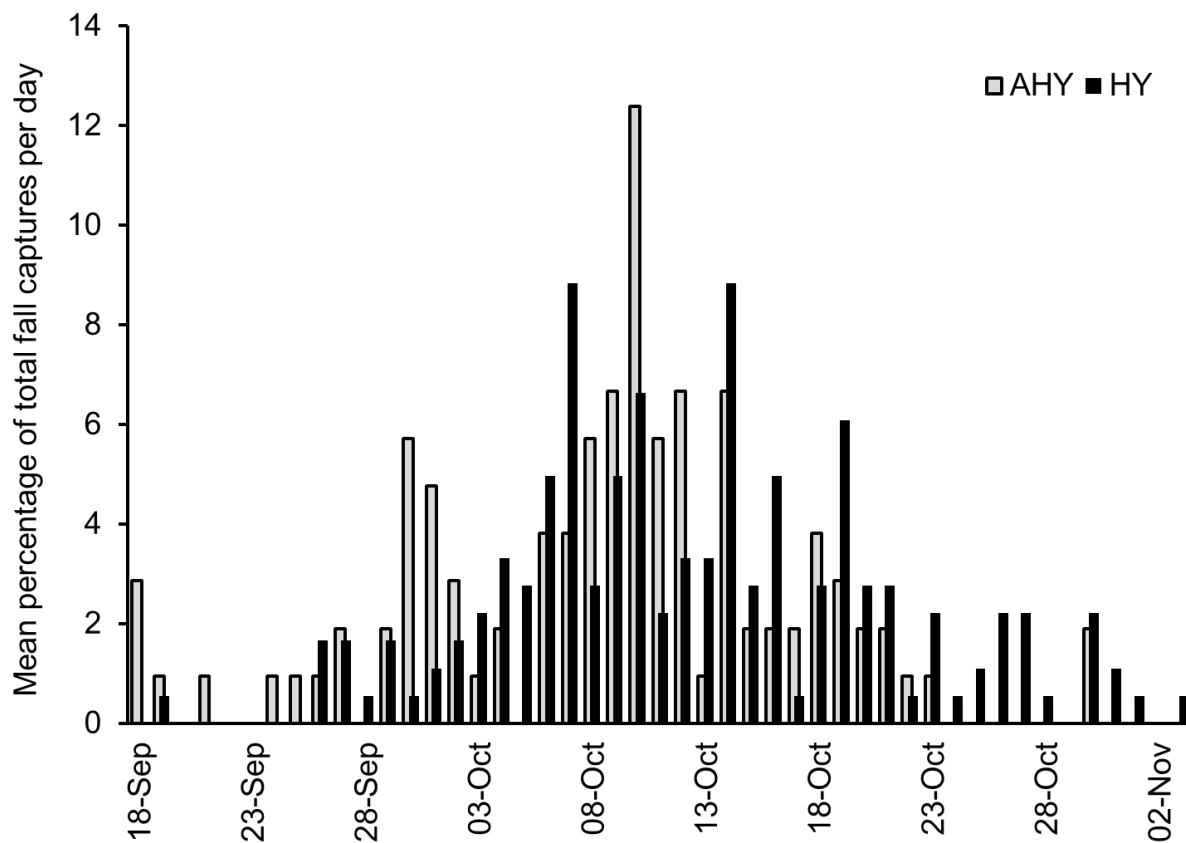


Figure A.1. 9. Average phenology of fall migration of after hatch-year (AHY) and hatch year (HY) of Mourning Warblers migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

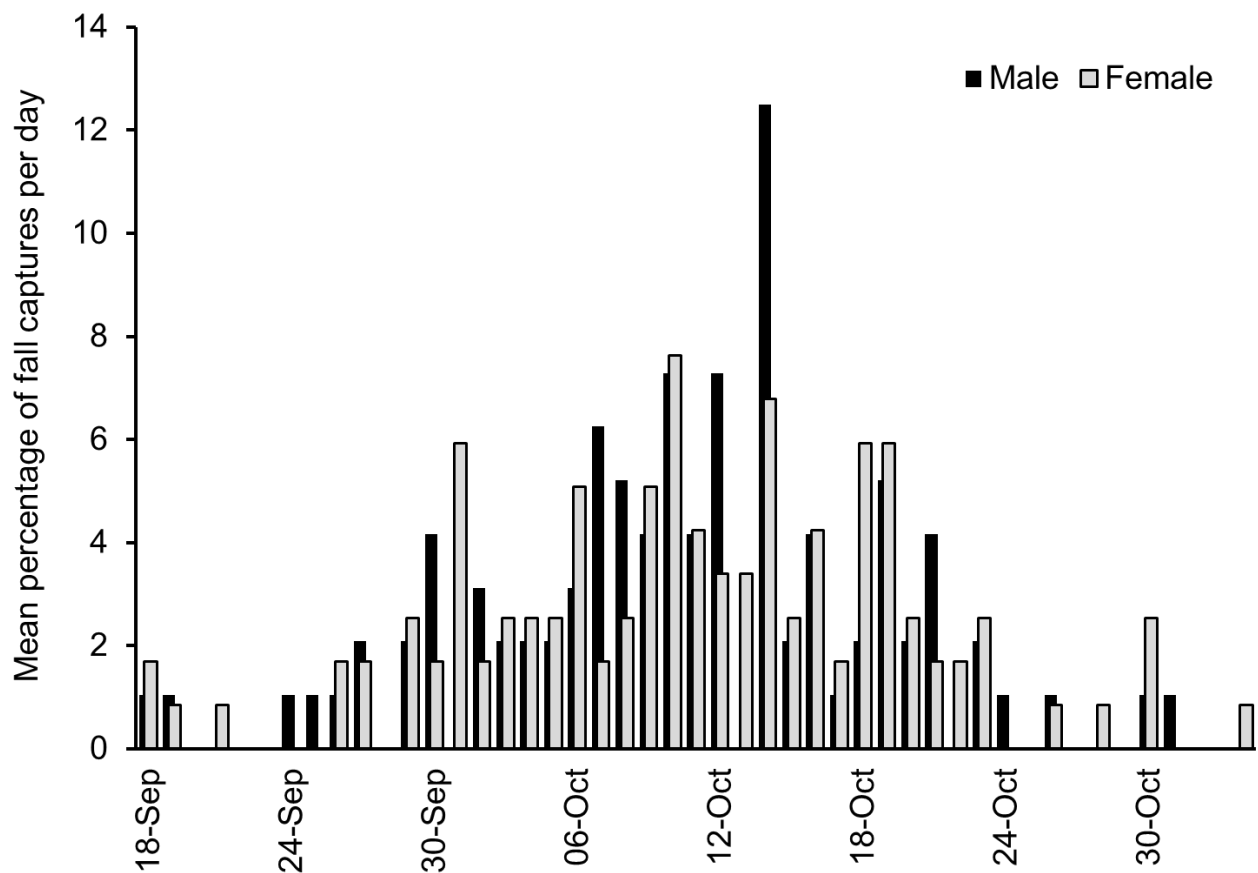


Figure A.1.10. Average phenology of fall migration of male and female of Mourning Warblers migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

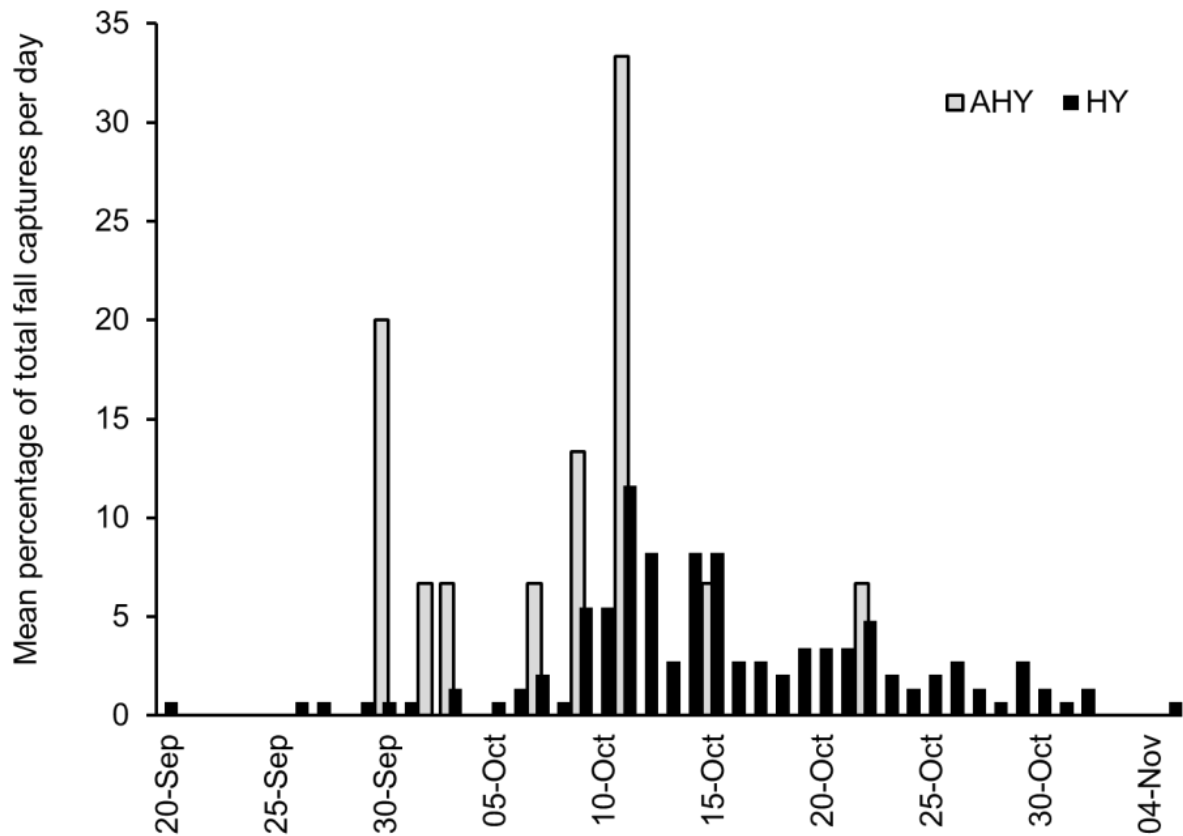


Figure A.1.11. Average phenology of fall migration of after hatch-year (AHY) and hatch year (HY) of Canada Warblers migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

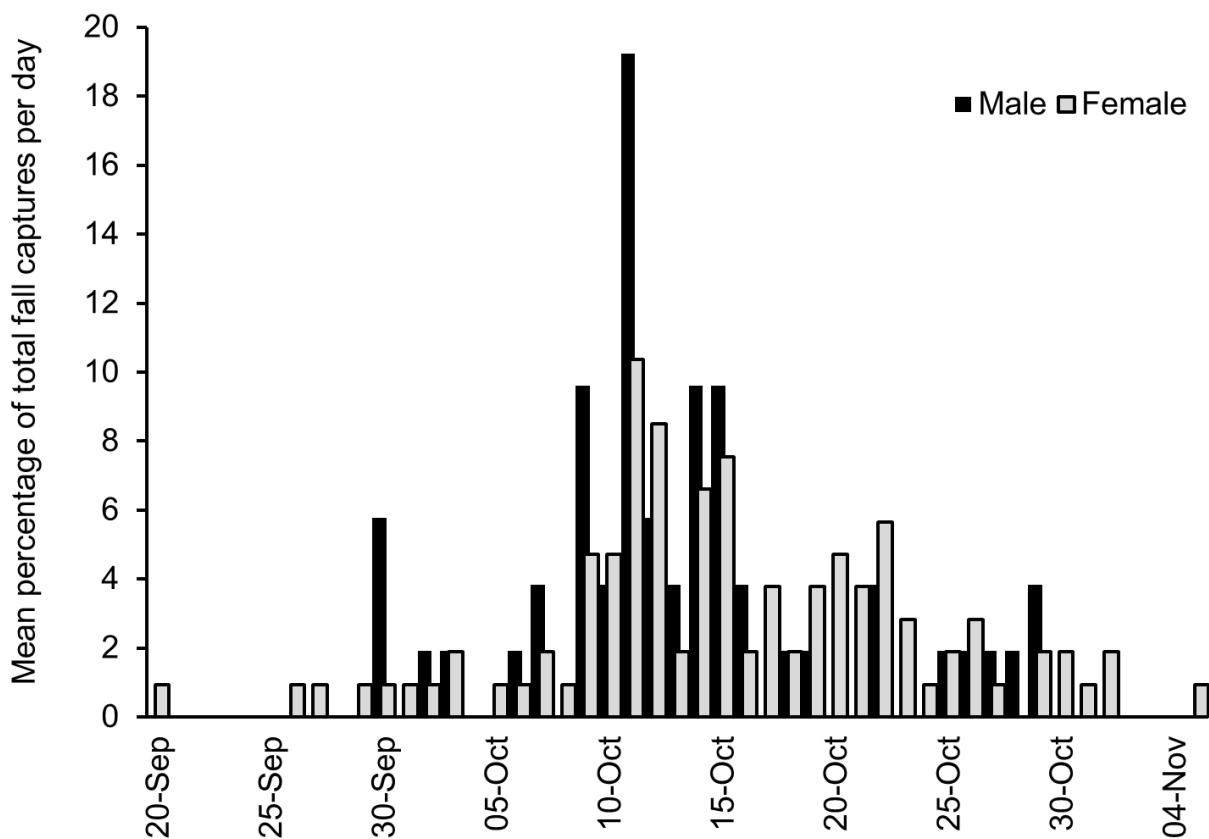


Figure A.1.12. Average phenology of fall migration of male and female of Canada Warblers migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

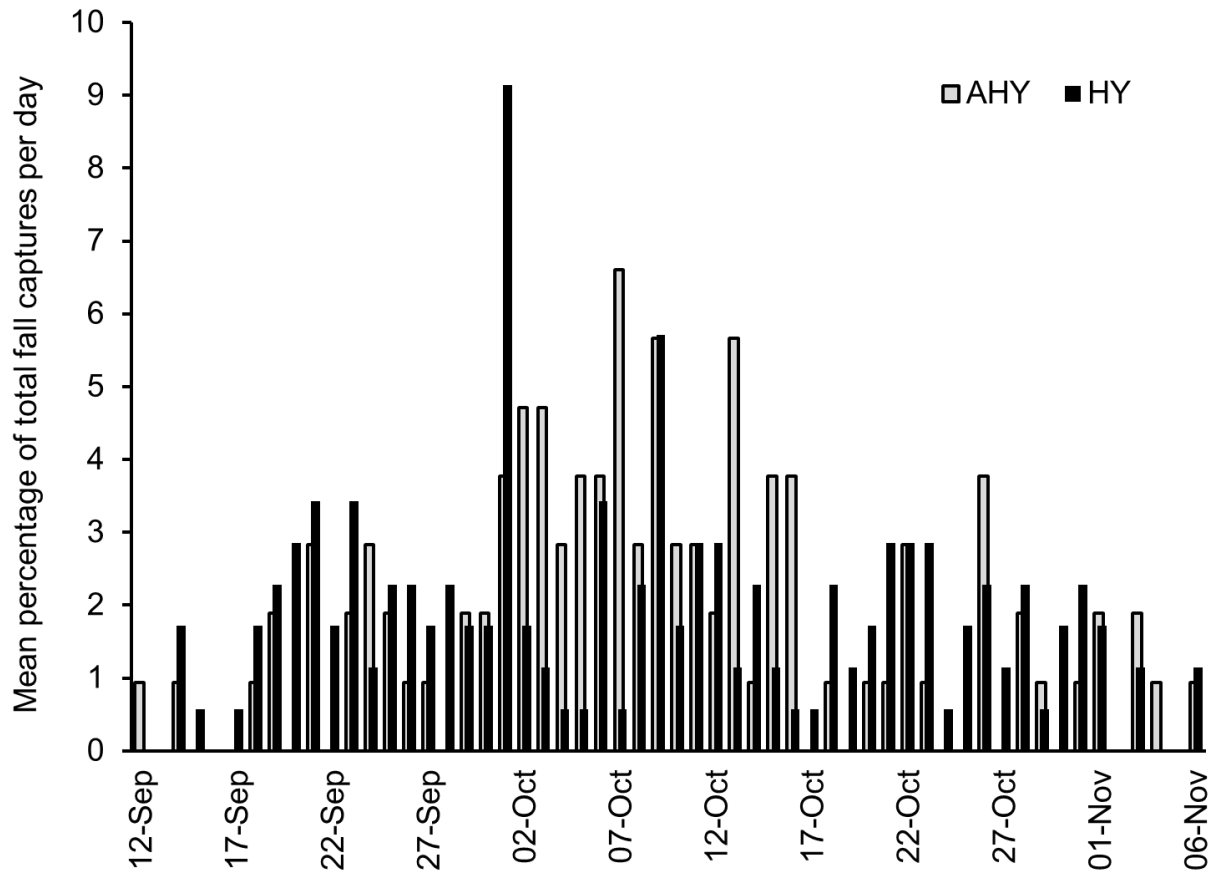


Figure A.1.13. Average phenology of fall migration of after hatch-year (AHY) and hatch year (HY) of Prothonotary warblers migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

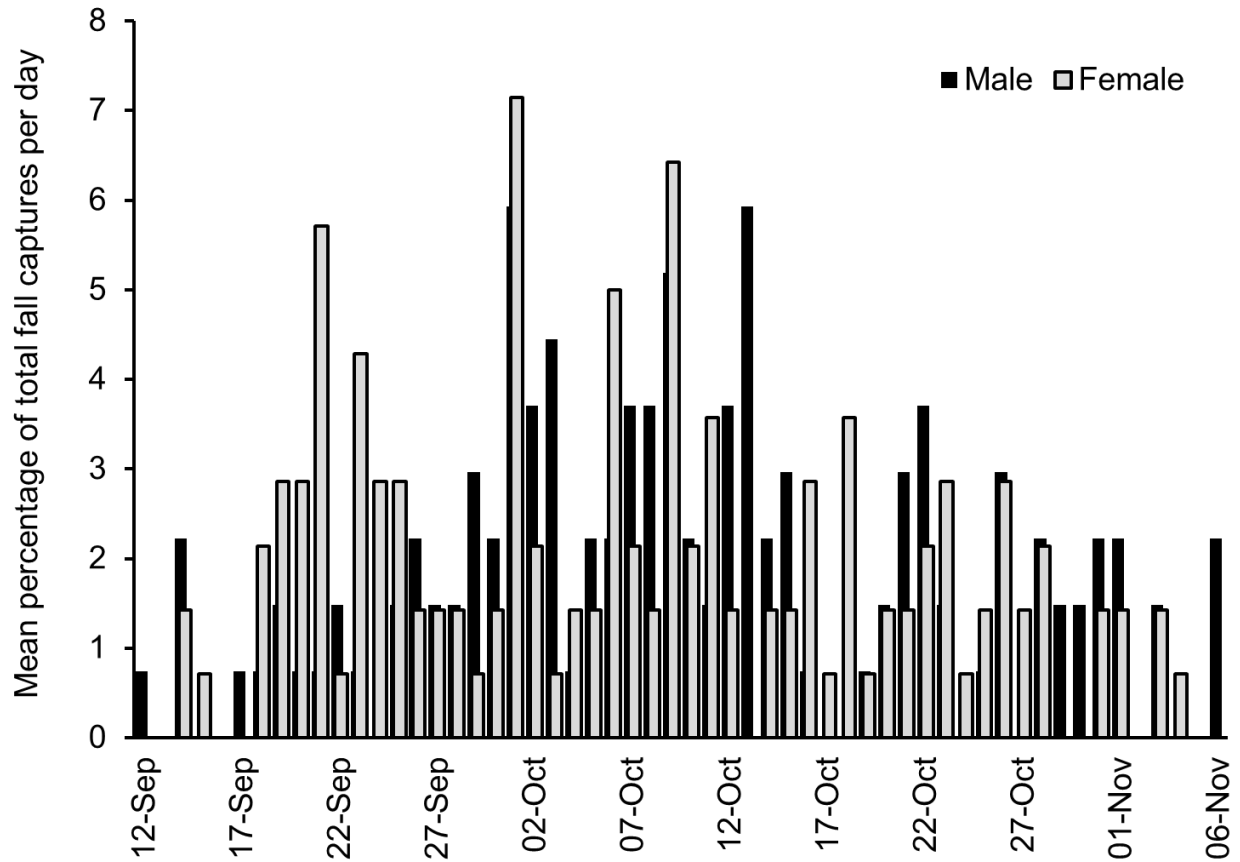


Figure A.1.14. Average phenology of fall migration of male and female of Prothonotary warblers migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

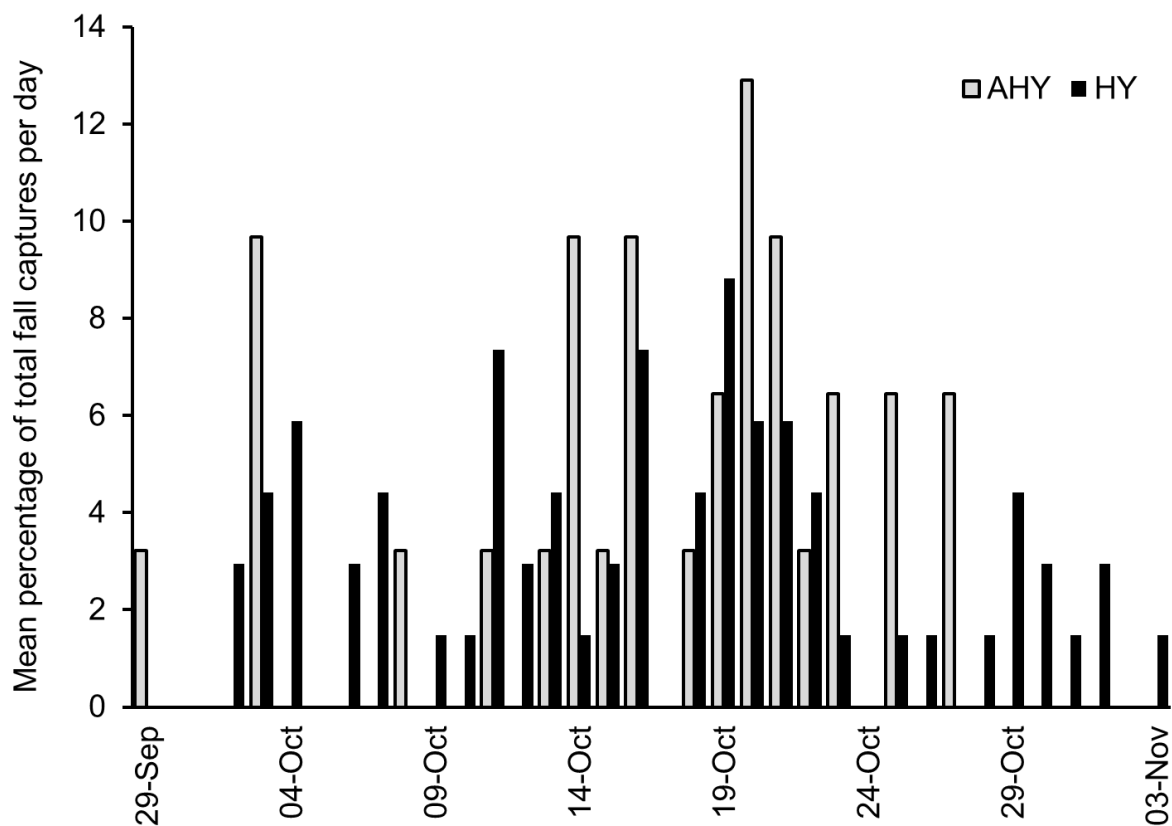


Figure A.1.15. Average phenology of fall migration of after hatch-year (AHY) and hatch year (HY) of Scarlet Tanagers migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

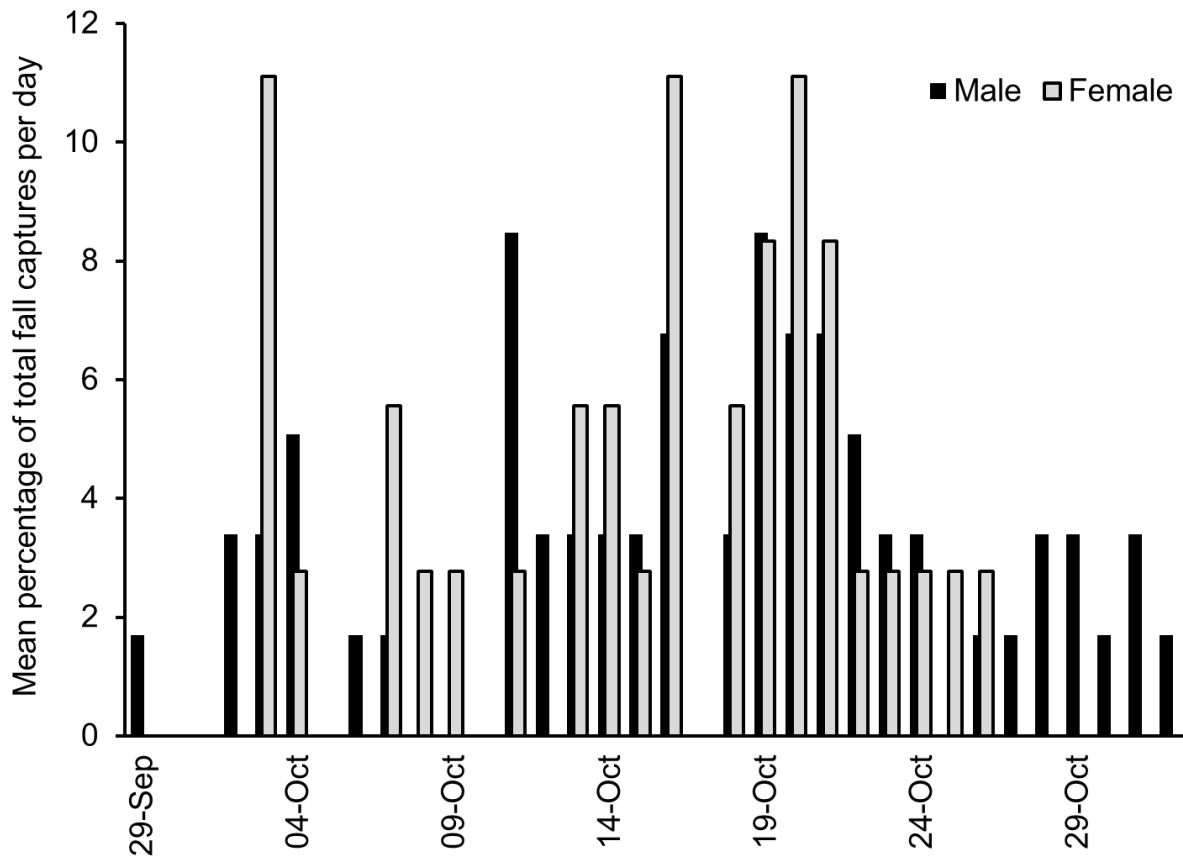


Figure A .1.16. Average phenology of fall migration of male and female Scarlet Tanagers migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

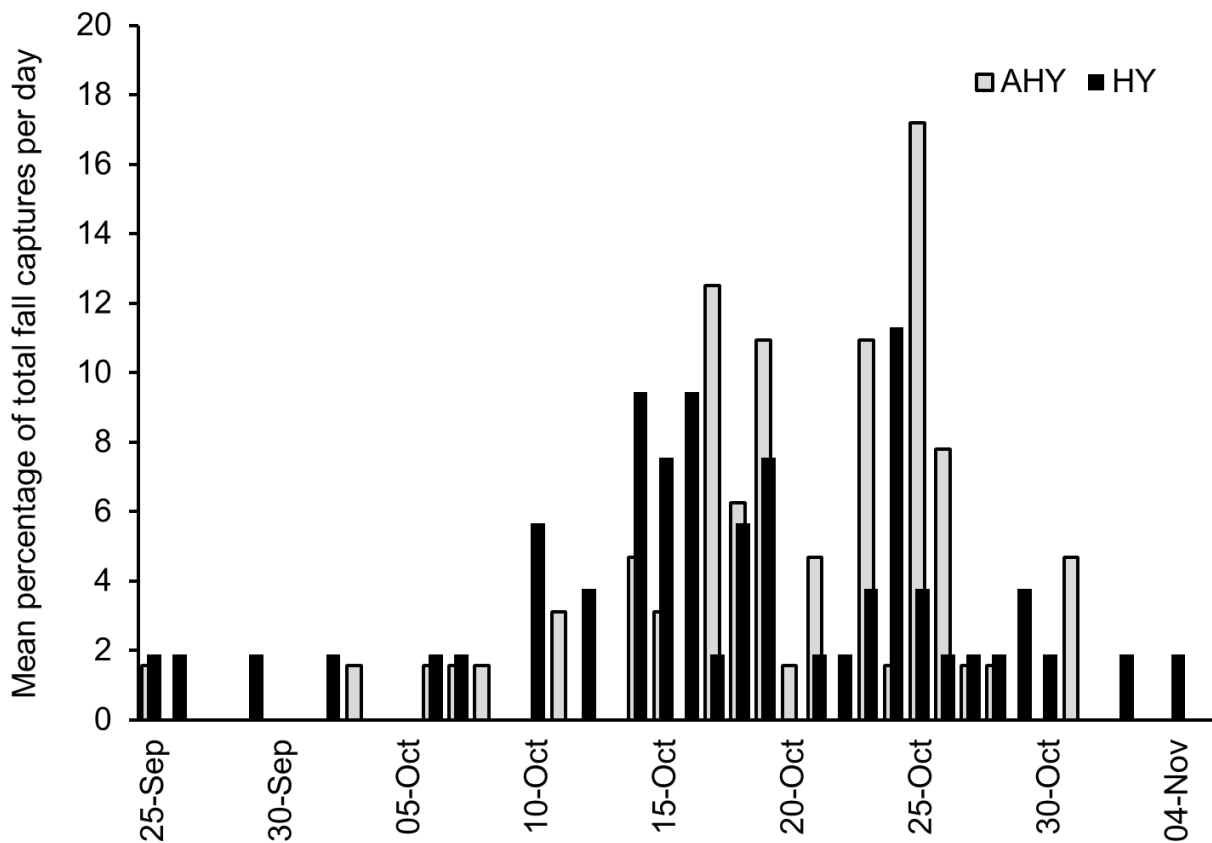


Figure A.1.17. Average phenology of fall migration of after hatch-year (AHY) and hatch year (HY) of Summer Tanagers migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

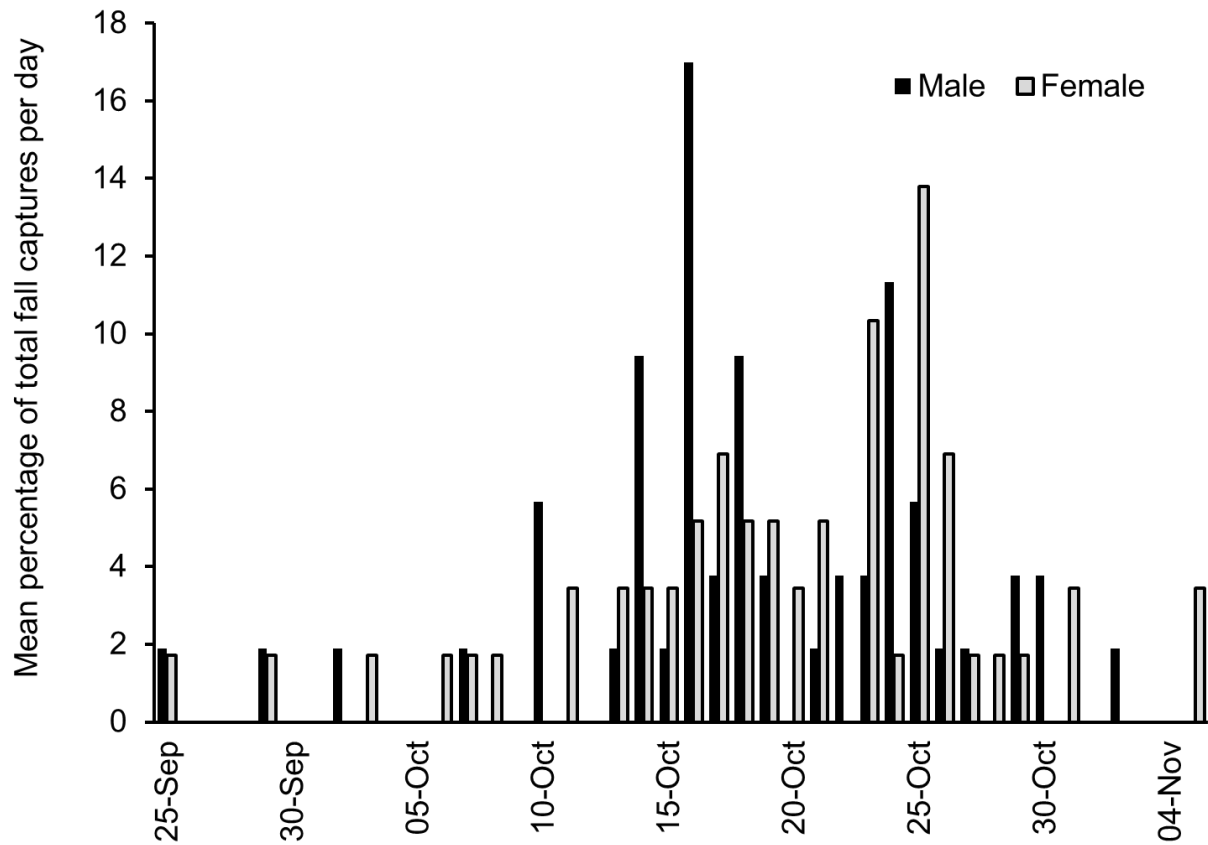


Figure A.1.18 Average phenology of fall migration of male and female Summer Tanagers migrating through the Tacarcuna Reserve, Darién, Colombia (2011, 2012, 2014 and 2015).

APPENDIX B

Figure B.3.1 Distributions of fuel load at first capture per species arriving in the Tacarcuna Nature Reserve. VEER: Veery, SWTH: Swainson's Thrush, GCTH: Gray-cheeked Thrush Gray-cheeked Thrush, REVI: Red-eyed Vireo, YWAR: Yellow Warbler, NOWA: Northern Waterthrush, MOWA: Mourning Warbler, CAWA: Canada Warbler, POWA: Prothonotary Warbler, SCTA: Summer Tanager, SUTA: Summer Tanager.

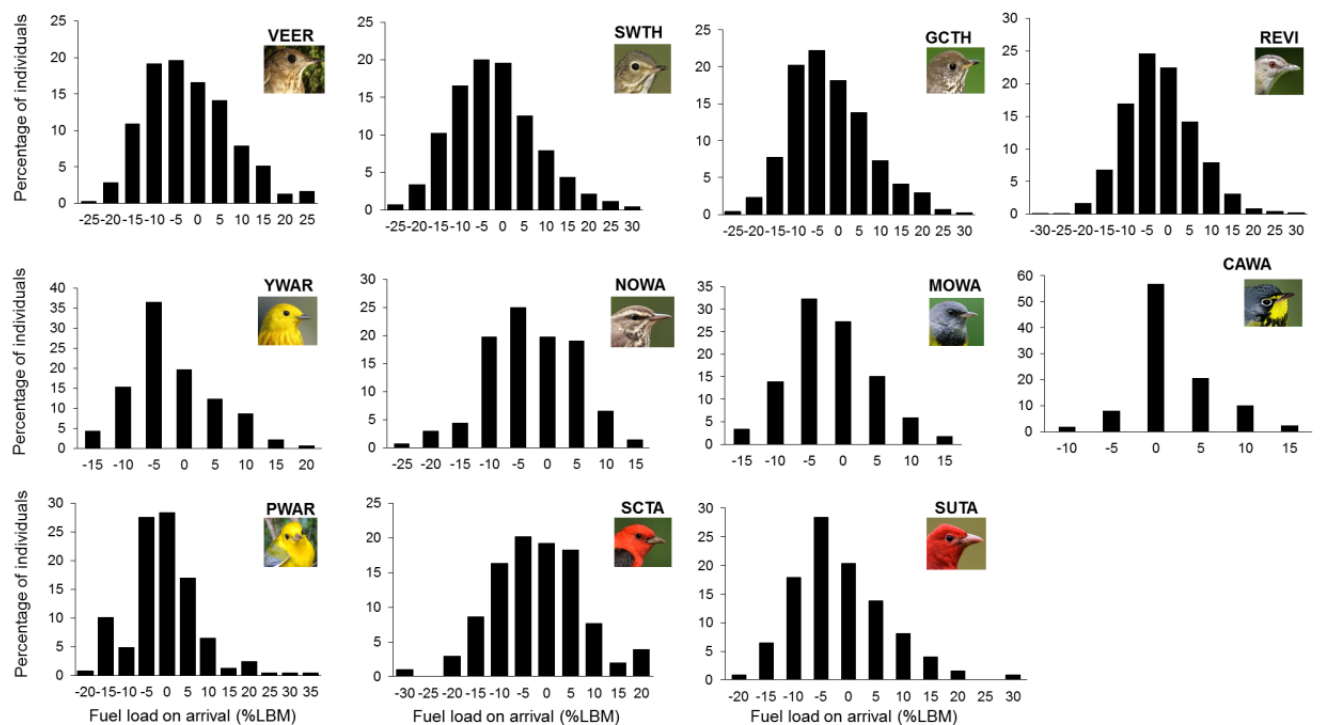


Figure B.3.2 Box and whisker plots showing variation in annual fuel load according to El Niño and La Niña of 11 species of Neotropical migrants (CAWA: Canada Warbler, GCTH: Gray-cheeked Thrush, MOWA: Mourning Warbler, NOWA: Northern Waterthrush, PROW: Prothonotary Warbler, REVI: Red-eyed vireo, SCTA: Scarlet Tanager, SUTA: Summer Tanager, SWTH: Swainson's Thrush, VEER: Veery, YWAR: Yellow Warbler) arriving to the Darién, Colombia in the fall during El Niño and La Niña years, 2011 - 2015.

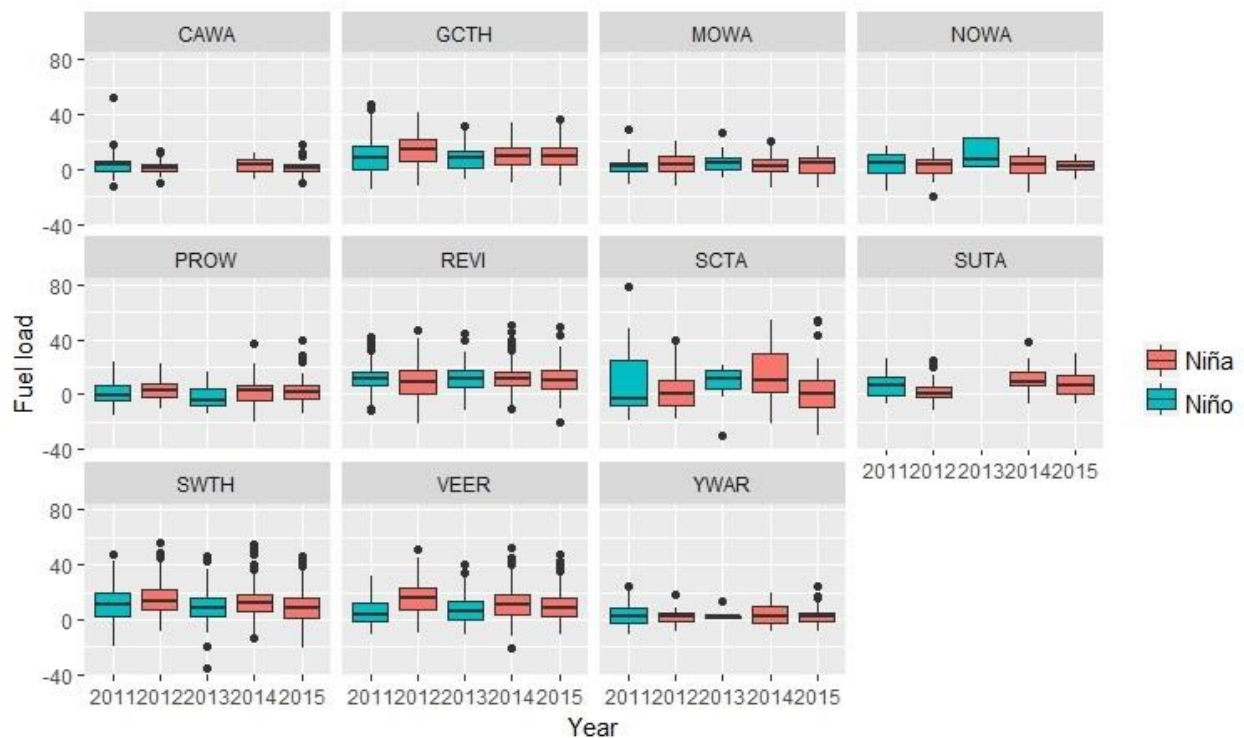


Table B.3.1 Summary of mean fuel load (% of LBM \pm SD) according to the age (A), sex (S) and year per species (VEER: Veery, SWTH: Swainson's Thrush GCTH: Gray-cheeked Thrush, NOWA: Northern Waterthrush, YWAR: Yellow Warbler, MOWA: Mourning Warbler, CAWA: Canada Warbler, PWAR: Prothonotary Warbler, REVI: Red-eyed vireo, SCTA: Scarlet Tanager and SUTA: Summer Tanager) captured in the Tacarcuna Nature Reserve 2011-2015. Table continue next page.

	Species	A/S	Year									
			2011		2012		2013		2014		2015	
			N		N		N		N		N	
147	VEER	HY	96	5.3 \pm 9.4	104	16.4 \pm 11.6	90	8.2 \pm 10.8	158	11.2 \pm 11.2	177	9.9 \pm 10.2
		AHY	34	6.2 \pm 9.6	73	15.9 \pm 10.7	11	4.7 \pm 4.2	71	12.1 \pm 8.6	58	11.6 \pm 9.9
	SWTH	HY	228	11.9 \pm 12.5	358	15.0 \pm 11.0	358	15.0 \pm 11.0	362	13.0 \pm 10.3	466	9.5 \pm 11.0
		AHY	63	12.2 \pm 12.2	162	14.5 \pm 10.0	77	10.1 \pm 11.5	135	13.1 \pm 9.9	157	8.3 \pm 12.3
	GCTH	HY	88	8.5 \pm 12.4	119	-	67	7.8 \pm 8.4	201	10.6 \pm 9.9	137	9.4 \pm 8.8
		AHY	31	9.1 \pm 11.9	77	13.4 \pm 10.3	36	7.1 \pm 8.0	100	8.3 \pm 9.1	59	12.0 \pm 9.0
	NOWA	HY	31	4.5 \pm 7.3	18	4.5 \pm 7.7	-	-	29	1.0 \pm 8.9	15	2.1 \pm 3.8
		AHY	13	2.8 \pm 9.9	5	(-4) \pm 10.7	5	11.4 \pm 10.8	7	4.2 \pm 8.4	12	3.0 \pm 6.2
	YWAR	HY	53	1.3 \pm 5.5	42	4.0 \pm 6.8	11	2.0 \pm 6.5	10	4.1 \pm 4.3	3	10.0 \pm 4.3
		AHY	34	1.6 \pm 6.7	20	3.4 \pm 5.8	6	12.0 \pm 7.9	40	3.7 \pm 7.2	12	2.4 \pm 8.4
		F	13	5.0 \pm 10.1	5	2.2 \pm 2.7	2	8.5 \pm 7.7	18	6.3 \pm 8.0	29	3.7 \pm 7.6
		M	17	2.0 \pm 6.1	5	0.0 \pm 6.3	3	1.3 \pm 1.5	13	0.92 \pm 7.2	26	2.3 \pm 4.2
	MOWA	HY	53	1.3 \pm 5.5	42	4.0 \pm 6.8	11	2.0 \pm 6.5	10	4.1 \pm 4.3	3	10.0 \pm 4.3
		AHY	34	1.6 \pm 6.7	20	3.4 \pm 5.8	6	12.0 \pm 7.9	40	3.7 \pm 7.2	12	2.4 \pm 8.4
		F	48	0.7 \pm 5.2	38	3.2 \pm 6.0	12	5.8 \pm 9.0	24	5.1 \pm 6.9	8	2.7 \pm 9.8
		M	39	2.3 \pm 6.9	24	4.7 \pm 7.3	5	5.0 \pm 7.5	26	2.5 \pm 6.5	7	5.2 \pm 6.6
	CAWA	HY	74	3.4 \pm 8.0	33	1.5 \pm 5.1	-	-	27	2.8 \pm 5.0	10	2.2 \pm 7.7
		AHY	5	3.6 \pm 2.5	1	2.4 \pm	-	-	4	3.0 \pm 5.6	32	0.3 \pm 7.3

	PWAR	F	49	3.5 ± 9.3	29	1.5 ± 5.1	-	-	16	1.8 ± 5.3	8	3.9 ± 7.6
		M	28	3.7 ± 3.7	4	4.3 ± 4.1	-	-	13	3.5 ± 4.4	7	$(-0.7) \pm 6.6$
		HY	30	$(-0.5) \pm 7.4$	28	3.7 ± 6.1	9	$(-4.2) \pm 9.7$	61	1.0 ± 7.9	54	4.3 ± 9.6
		AHY	19	3.9 ± 10.0	14	2.4 ± 9.9	4	4.0 ± 3.0	38	2.7 ± 9.0	32	0.3 ± 7.3
	REVI	F	26	2.3 ± 8.8	15	0.1 ± 6.1	3	$(-1.3) \pm 5.9$	47	1.8 ± 7.6	47	1.6 ± 9.0
		M	23	$(-0.1) \pm 8.7$	24	5.1 ± 8.1	7	$(-0.1) \pm 9.6$	50	2.1 ± 8.9	38	3.7 ± 8.4
		HY	132	11.1 ± 9.8	117	8.7 ± 8.7	105	10.6 ± 9.9	178	10.7 ± 10.2	278	10.0 ± 10.1
		AHY	116	11.3 ± 8.0	47	11.7 ± 8.4	30	13.5 ± 8.4	189	11.6 ± 7.8	309	11.5 ± 8.11
	SCTA	F	-	-	-	-	-	-	-	-	46	7.0 ± 9.7
		M	-	-	-	-	-	-	3	11.6 ± 4.7	12	15.5 ± 10.8
		HY	6	9.5 ± 25.2	16	4.6 ± 16.7	5	2.0 ± 19.7	13	12.0 ± 20.8	28	3.0 ± 18.2
		AHY	3	$(-10.0) \pm -8.1$	9	1.7 ± 14.3	2	17.5 ± 2.1	14	17.7 ± 18.1	5	6.8 ± 28.1
	SUTA	F	4	18.8 ± 26.3	10	7.6 ± 16.5	4	16.5 ± 4.7	4	16.5 ± 4.7	9	18.6 ± 26.0
		M	5	$(-9.6) \pm 6.8$	15	1.0 ± 14.9	3	$(-7.0) \pm -12.0$	14	6.5 ± 17.9	24	$(-2) \pm 13.1$
		HY	13	6.1 ± 9.6	20	1.2 ± 1.0	-	-	9	6.8 ± 8.8	10	9.9 ± 11.7
		AHY	6	8.0 ± 7.8	40	2.3 ± 7.2	-	-	13	13.8 ± 9.9	-	-
		F	8	10.9 ± 9.7	33	1.0 ± 5.7	-	-	13	10.2 ± 11.6	2	$(-2) \pm 7.0$
		M	9	4.1 ± 7.5	23	2.8 ± 7.3	-	-	9	12.2 ± 7.1	11	9.8 ± 10.2