THE RELATIVE IMPORTANCE OF NATIVE FOREST AND SHADE-GROWN COFFEE PLANTATIONS FOR HABITAT USE, INDIVIDUAL FITNESS AND MIGRATION STRATEGIES OF OVERWITNERING NEOTROPICAL MIGRANT SONGBIRDS IN COLOMBIA

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Saskatoon

By

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ABSTRACT

Winter habitat quality is one of the primary ecological factors limiting self-maintenance and survival of Nearctic-Neotropical migratory birds during the non-breeding season. I assessed the relative importance of shade-grown coffee plantations vs. forest in the Colombian Andes as winter habitat for Swainson's Thrush (*Catharus ustulatus*), Gray-cheeked Thrush (*Catharus minimus*), and Canada Warbler (*Cardellina canadensis*). For Swainson's Thrush, I used daily and seasonal mass change, age ratios, density and corticosterone levels as measurements of habitat quality; and for Canada Warbler I used daily and seasonal mass change and sex ratios. Automated radio-telemetry on a continental scale was used to determine the effect of overwintering habitat occupancy on spring departure date and migration pace of Swainson's Thrush. Using light-level geolocators I assessed the link between winter habitat occupancy and migratory connectivity of Gray-cheeked Thrush, and measured population spread and its relationship with the species winter distribution. I determined migratory connectivity of Canada Warblers overwintering across the three Andean cordilleras in Colombia by analysing stable hydrogen- isotope values (δ^2H) in feathers.

Taken together, my results suggested that native forests are more suitable winter habitats than shade-grown coffee plantations for Swainson's Thrush. Native forest maintained a higher number of individuals than coffee, and in general, individuals maintained or increased their daily and seasonal body condition. On the other hand, the results for Canada Warbler are not conclusive, the quality of coffee can improve in certain circumstances such as high precipitation. My research provides the first evidence that by overwintering in native forest, birds can adjust their departure date, migration speed, and fuel up sufficiently to cover about 25% of the total length of spring migration. Migratory connectivity revealed that the effect of land-use changes on the wintering grounds is likely to be amplified on the breeding grounds through strong migratory connectivity. While market-based conservation strategies primarily promote shade-grown coffee plantations for the conservation of Neotropical migrants, my research suggest that strategies to conserve and restore native forest are also urgently needed.

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DEDICATION

To Felipe and my family. For their encouragement and unconditional love and support to pursue my dreams.

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CHAPTER 1. GENERAL INTRODUCTION

1.1. Conservation status of Nearctic-Neotropical migrants

Migratory bird species throughout the world are declining at greater rates than non-migratory species (Wilcove and Wikelski 2008). That trend is likely associated with increased mortality associated with migration itself (Sillett and Holmes 2002, Newton 2008, Altizer et al. 2011), and with overall exposure to a greater number of events occurring throughout the annual cycle such as habitat destruction and climate change (Sillett et al. 2000, Wilcove and Wikelski 2008, Faaborg et al. 2010). Nearctic-Neotropical migratory songbird populations have seriously declined in recent decades with those that overwinter in northern South America declining at greater rates than those wintering elsewhere (NABCI 2012). Persistent population declines in species over-wintering primarily in montane habitats in the northern Andes of South America are associated with habitat loss and deterioration on the wintering grounds (Jones et al. 2004a, González-Prieto et al. 2017, Kramer et al. 2018, Wilson et al. 2018). However, information about key winter habitats and limiting factors during the non-breeding season remain mostly unknown in this region of the Neotropics. Assessing winter habitat quality for Neotropical migrants and its effect on overwinter ecology and demographics is a critical line of research if we are to identify the factors driving population declines or limiting population growth, and to predict how environmental changes will impact migratory populations.

1.2. Winter habitat for Nearctic-Neotropical migratory birds

Habitat includes all of the resources, and the physical and biological conditions present in an area required by an organism (Hall et al. 1997). Habitat quality is a measure of the ability of the environment to provide suitable conditions to guarantee survival, reproductive success and population persistence (Hall et al. 1997). For Neotropical migratory songbirds, moisture and food availability are the main drivers of winter habitat quality (Sherry et al. 2005, Brown and Sherry 2006, Smith et al. 2010). In turn, these are some of the most important ecological factors limiting physical condition and survival of migrants during the winter (Sherry and Holmes 1996, Sherry et al. 2005, Studds and Marra 2005). Recent studies suggest that vegetation structure is also a significant driver of winter habitat quality for migrants. For instance, Wilson´s Warbler (*Cardellina pusilla*) overwintering in mature forest had smaller territory size, showed consistent interannual physical condition, and were more abundant than individuals overwintering in more disturbed secondary forest (Ruiz-Sánchez et al. 2017). Winter habitat quality can produce residual effects that carry over to subsequent seasons (i.e., migration and breeding), and can affect individual fitness and year-round population dynamics (Marra et al. 1998, Norris et al. 2004, Norris 2005). Most evidence supporting the critical role of winter habitat quality for migratory birds comes from studies of insectivorous songbirds overwintering in the Caribbean, where the availability of high quality habitats varies spatially and temporally in response to precipitation patterns and its influence on food abundance (Smith et al. 2010).

In American Redstarts (*Setophaga ruticilla*) overwintering in Jamaica, strong differences in food availability between moist coastal forest (hereafter mesic) and adjacent scrub habitats (hereafter xeric) led to differences in overwinter body condition, spring departure time, and arrival to the breeding grounds. Individuals overwintering in xeric habitats showed poorer physiological condition (Marra and Holberton 1998), declining body mass (Strong and Sherry 2000), lower survival (Marra and Holmes 2001), and later spring migration departure time (Marra et al. 1998) than individuals from mesic habitats. In turn, the effect of occupying poor xeric winter habitats carried out to the subsequent season and resulted in later arrival on the breeding grounds (Marra et al. 1998, Studds and Marra 2005) and lower reproductive success (Norris et al. 2004). Habitat suitability can also vary inter-annually in response to precipitation patterns. For instance, Black-throated Blue Warblers (*Setophaga caerulescens*) overwintering in high quality habitats in Jamaica had lower annual survivorship during dry El Niño years than during wet La Niña years, indicating that annual fluctuations in habitat quality and resource availability influence migratory birds even within high quality habitats (Sillett et al. 2000).

Precipitation in the Caribbean is highly seasonal, with consistent rainfall from September to November, and a marked dry season from January to March (Studds and Marra 2011). The negative effects of drought on the performance of migrants seems to be strengthened in areas where the dry season coincides with preparations for spring migration (Studds and Marra 2007). For example, in dry years, American Redstarts overwintering in xeric habitats were in poorer physical condition and delayed their spring departure relative to birds in mesic habitats. However, birds overwintering in xeric and mesic habitats had the same spring migration departure time when precipitation levels preceding spring migration were high in both habitats (Studds and Marra 2011). Precipitation patterns vary widely throughout the region occupied by migrants during the winter and how birds respond to different patterns is unknown.

1.3. Measurements of habitat quality

Measurements of apparent survival (hereafter survival), density, sex and age ratios and change in mass over the winter, have been used to assess winter habitat quality for Neotropical migrants (reviewed by Johnson 2007). However, single measurements may produce misleading conclusions about the quality of a given habitat and using more than one is recommended (Pidgeon et al. 2006, Johnson 2007). From an ornithological perspective, priority habitats for conservation should be identified by assessing habitat quality for migratory birds at the population level (Pidgeon et al. 2006).

During the non-breeding season, survival is a robust indicator of winter habitat quality for population persistence (Johnson et al. 2006). Overwinter, between-winter, and annual survival have all been used as measures of winter habitat quality for Neotropical migrants (Marra and Holmes 2001, Johnson et al. 2006, Bakermans et al. 2009). However, although mortality caused by occupying poor-quality winter habitat can be measured from overwinter survival estimates, annual and between-winter survivorship are considered more robust measures of habitat quality because they account for lethal effects of winter habitat that might not be manifested until subsequent seasons (Conway et al. 1995, Johnson et al. 2006).

Population density is expected to be higher in high quality habitats because individuals select the most suitable habitats where chances of survivorship are higher (Fretwell and Lucas 1970). However, factors such as dominance behaviour, environmental conditions, and large-scale habitat structure can lead to high densities in poor-quality habitats (Van Horne 1983). For example, socially dominant behaviour may decouple the expected relationship between habitat quality and density if density increases in poor habitats as a result of weak competitors being excluded from suitable habitats (Van Horne 1983, Johnson 2007). Short-term variation in local density may result from variability in weather conditions, which influences local food abundance and feeding opportunities (Wunderle and Waide 1993, Smith et al. 2010, Studds and Marra 2011); in this case, density might reflect short-term conditions rather than the actual quality of the habitat (Van Horne 1983). Density may not depend on winter habitat quality alone. Habitat quantity and distribution within the landscape could also influence how migrants move and distribute themselves during the non-breeding season (Van Horne 1983, Sherry and Holmes 1996). Therefore, density alone may be a misleading indicator of habitat quality. Reliable measures require estimates of other demographic parameters, such as survival, especially in species with scarce information about social relationships or responses to environmental conditions on their wintering grounds, as is the case for many Neotropical migrants.

When habitat selection is controlled by dominance, higher proportions of dominant individuals are expected in the highest quality habitats (Marra 2000). Therefore, the ratio of sex and age classes among habitats could indicate differences in habitat quality (Wunderle and Latta 2000). Sex and age segregation during the non-breeding season has been reported in several Neotropical migrants. Older male American Redstarts overwintering in Jamaica maintained high-quality territories in mangrove and moist forest, and excluded females and younger males to less suitable, second growth scrub habitat (Marra et al. 1998, Marra 2000). Male Hooded Warblers (*Wilsonia citrina*) overwintering in Mexico (Lynch et al. 1985) and male Black-throated Blue Warblers overwintering in Puerto Rico (Wunderle 1995) dominated mature forest while females were relegated to shrubby second-growth habitats. Age and sex segregation in response to differences in winter habitat suitability has also been shown in Cape May Warblers (*Setophaga tigrina*) overwintering in desert, dry forest and pine forest in Dominican Republic (Latta and Faaborg 2002). Adult males were dominant in pine forest where fruit and nectar resources were more stable throughout the winter, whereas the other two habitats were dominated by females. Consequently, males wintering in pine forest had higher overwinter persistence and higher body mass than individuals in desert or dry forest. Understanding how winter social systems influence habitat occupancy and population process is crucial to design effective conservation management for Neotropical migrants (Brown and Sherry 2006).

Measures of quality at the individual level, such as body condition can also provide reliable information about the quality of the habitat if related to differential fitness (Johnson 2007). For example, American Redstarts overwintering in poor-quality scrub habitats in Jamaica lost mass over the winter, were lighter preceding spring migration, and had lower annual survivorship than birds in high-quality mangrove forest (Marra and Holmes 2001). Using the same species as a model, Johnson et al. (2006) showed that body condition was a predictor of annual survival and suggested the combination of these two measures as the best measures of winter habitat quality for songbirds.

Measures of corticosterone levels in free-living animals are increasingly used as a biomarker of the level of exposure to stressors (Cabezas et al. 2007, Fairhurst et al. 2015), and as a physiological index of individual and population condition or health (Wikelski and Cooke 2006). Vertebrates respond to threatening or unpredictable/uncontrollable stimuli through a set of physiological and behavioural changes known as the "stress response", and in birds corticosterone is the primary glucocorticoid hormone released into the blood stream during this response (reviewed by Romero 2004). Corticosterone levels have been shown to correlate with winter habitat quality in Neotropical migrants. For instance, American Redstarts wintering in suboptimal female-biased habitats in Jamaica showed higher corticosterone baseline levels than individuals in optimal male-biased habitats. The negative relationship between baseline corticosterone levels and physical condition of birds in poor habitats suggested muscle catabolism associated with high corticosterone levels or poor condition as a result of increased foraging effort (Marra and Holberton 1998). However, the relationship between corticosterone levels in animals and fitness is intricate and at present inconclusive (Kitaysky et al. 1999, Clinchy et al. 2004, Jenni-Eiermann et al. 2008, Bonier et al. 2009), and corticosterone data in conjunction with demographic and behavioural covariables allows for better interpretation in an appropriate context.

1.4. Shade-grown Coffee Plantations

Shade-grown coffee plantations are one of the few remaining "forested" areas in mid- to high-elevation mountain ranges of Latin America (reviewed by Perfecto et al. 2005). In this agroecosystem, the native canopy is maintained or replaced and the understory is occupied exclusively by coffee (Moguel and Toledo 1999). Shade-grown coffee supports high levels of biodiversity across different taxa from insects to mammals (Perfecto et al. 1996) and provides habitat for native predators of coffee pests and pollinators that contribute to higher coffee productivity and quality (Klein et al. 2003, Ricketts et al. 2004, Karp et al. 2013). Despite the benefits provided by shade coffee, these traditional coffee plantations are rapidly disappearing. In northern Latin America, technification has transformed more than 50% of coffee production systems into agroecosystems with lower structural and floristic diversity, where intensively managed plantations are grown in full sun (Perfecto et al. 1996, Rice 1999).

The importance of shade coffee plantations for the conservation of Neotropical migratory birds is related to the observations that (1) shade-coffee plantations tend to have higher species richness and abundance than other agroecosystems (reviewed by Komar 2006), (2) species richness is comparable to natural habitats (Tejada-Cruz and Sutherland 2004), and (3) some species found in shade coffee plantations are as or more abundant in this habitat than in natural forest (Komar 2006, Bakermans et al. 2009, Gomez et al. 2013). Despite the assumed importance of shade coffee plantations for the conservation of migratory birds, species richness or abundance alone do not necessarily indicate high quality habitat or high conservation value unless they are correlated with population parameters (e.g., survivorship) or with individual physical condition, and compared with values from native habitats (Johnson et al. 2006, Komar 2006). Additionally, most of the studies reporting higher densities of Neotropical migrants in shade coffee plantations relative to native habitats have failed to account for possible differences in detectability, and their results are likely biased by higher detection probabilities in more open habitats (but see Bakermans et al. 2009, Gomez et al. 2013).

The best assessment of the quality of shade-grown coffee should include measures of quality in coffee relative to the native forest from where those plantations originated (Van Horne 1983, Vickery et al. 1992). However, this comparison is lacking across several studies evaluating the suitability of shade-grown coffee as winter habitat for Neotropical migrants (i.e., Strong and Sherry 2000, Wunderle and Latta 2000, Johnson et al. 2006, Colorado and Rodewald 2017). For instance, Wunderle and Latta (2000) evaluated the importance of shade coffee plantations as winter habitat for American Redstarts, Black-throated Blue Warbles, and Black-and-White Warblers (*Mniotilta varia*) by assessing site fidelity in shade coffee plantations in the Dominican Republic and comparing their results to fidelity reported in native forest elsewhere in the Caribbean. Values of overwinter persistence and annual return rates for each species were high and suggested that shade-grown coffee plantations provided quality winter habitat comparable to natural forest elsewhere. These authors also examined the relationship of site fidelity, sex ratios, and body condition with plantation size. These parameters did not change with plantation size, which indicated low variation in the quality of the plantation with its size. Johnson et al. (2006) found that overwinter change in body mass and annual survival of American Redstarts in shade-grown coffee were comparable to natural habitats, such as mangrove forest. However, these authors argued that to provide sound evidence to support the conservation value of shade-grown coffee plantations for migratory birds, comparative studies of the quality of shade coffee and the quality of the native forest from where these agroecosystems originated are needed.

Bakermans et al. (2009) provided the first evidence of a seasonal increase in body condition for Neotropical migrants overwintering in coffee plantations and showed that monthly and annual survival of Cerulean Warblers (*Setophaga cerulea*) holding territories in coffee plantations was "high"; although sample sizes did not allow for comparisons with forest. Using density estimates adjusted for detection probability, this study also showed that Cerulean Warblers, Blackburnian Warblers (*Setophaga fusca*), Tennessee Warblers (*Oreothlypis peregrina*) and American Redstarts overwintering in the Venezuelan Andes were up to 14 times more abundant in shade coffee plantations than in primary forest. To date, this density estimate is the only winter habitat measurement that has been compared between shade-grown coffee plantations and the native habitats from where these habitats originated.

1.5. Assessing migratory connectivity and migration strategies

Conservation of any migratory species requires knowledge of migratory connectivity or where various populations breed, stopover, and winter during their annual cycle (Webster et al. 2002, Martin et al. 2007). Recent models predict that when breeding populations from across North America converge where they overwinter (e.g., weak migratory connectivity), events like habitat loss in the winter area will influence population size over a wide area of the breeding range (Marra et al. 2006). Unfortunately, little is known about migratory connectivity for most Neotropical migrants, in part, due to the inherent limitations in conventional methods used to track small-bodied birds year-round (Bridge et al. 2011). The application of stable isotope tools to the study of animal migration, and the development of tracking techniques such as light-sensitive geolocators and continental-scale radio telemetry has improved our ability to understand migratory connectivity, and the effects of winter habitat use in subsequent stages of the annual cycle in long-distance migrants.

Stable-hydrogen isotope (δ^2H) measurements have been widely used to infer the origins of migratory organisms (Hobson and Norris 2008). In North America, the amount-weighted mean values of δ^2H in precipitation during the growing season (δ^2H_p) follow a strong latitudinal gradient and are strongly correlated with δ^2H values of bird feathers (δ^2H_f) grown across the gradient (Hobson and Wassenaar 1997). Most species of Neotropical migratory songbirds replace feathers on or close to their breeding grounds before fall migration (Pyle 1997); therefore, δ^2H_f of birds sampled during migration or at wintering sites represent intrinsic markers of the geographic location where the feathers were grown.

Light-sensitive geolocators are one of the smallest devices available to track migratory birds that are too small to carry other devices like GPS loggers or satellite tracking systems (Bridge et al. 2011). Geolocators consist of a microprocessor, a battery, a light sensor, a clock and a memory that record daily integrated measurements of light and time of noon to provide estimates of latitude and longitude (Hill 1994). Latitude is estimated by the combination of the length of the day or night and the sun elevation at sunset and sunrise, and longitude by the timing of local midday and midnight (Hill 1994). The accuracy of geolocation (±200 km, Phillips et al. 2004, Fudickar et al. 2012) is affected by factors influencing the levels of light detected by the sensor such as season, habitat and behaviour of the species, weather, artificial light sources and topography and vegetation density during migration (Fudickar et al. 2012). For example, although longitude estimation is possible and accurate throughout the year, latitude is impossible to estimate during the spring and fall equinoxes when the length of the day is about the same in all regions (Hill 1994).

The Motus Wildlife Tracking System (Motus) is an international collaborative network where researchers use coordinated automated radio-telemetry to track the movements of small individuals including insects, bats, and birds at local and continental scales (Taylor et al. 2017). Most receiving stations in the international Motus array consist of a power source, a receiver (Sensorgnome), and one or multiple antennas listening continuously on a unique frequency (currently 166.380 MHz in the Western Hemisphere). Motus uses digitally coded tags manufactured by Lotek Wireless (Newmarket, Ontario). Each tag emits pulses with a coded sequence repeated at fixed intervals (burst rate), and the combination of the code and the burst rate is used to uniquely identify each tag. All coded tags transmit under the same frequency which allows detections of tags by any receiver in the international array. Data collected by each receiver is processed through a centralized data base before it can be used by researchers. International detections throughout the Motus array have provided critical information inaccessible by other tracking techniques such as the energy contribution of critical stop-over sites and migratory strategies (Duijns et al. 2017, Gómez et al. 2017).

1.6. Study species and system

I included three Neotropical migratory species with winter ranges restricted mostly to northern South America: Swainson's Thrush (*Catharus ustulatus*), Gray-cheeked Thrush (*Catharus minimus*) and Canada Warbler (*Cardellina canadensis*) (Figure 1.1). In my study sites Swainson's Thrush and Canada Warbler were commonly found in both forest and shade-grown coffee plantations, while Gray-cheeked Thrush was restricted to remaining forest fragments.

Swainson's Thrush are morphologically and genetically separated into coastal (western subspecies, *C. u. ustulatus* and *C. u. oedicus*) and inland (eastern subspecies *C. u. alame* and *C. u. swainsoni*) groups; each group appears to maintain their ancestral migration routes (Ruegg *&* Smith 2002). The combination of banding, genetic and geolocation data have shown that coastal and inland populations follow different migratory pathways, overwinter in different locations, and show different levels of migratory connectivity (Ruegg *&* Smith 2002, Delmore *et al.* 2012, Cormier *et al.* 2013). Coastal birds migrate along the west coast of North America during spring and fall and overwinter in southern Mexico and Central America (Ruegg *&* Smith 2002, Delmore *et al.* 2012). Inland birds migrate throughout central North America to their wintering grounds in northern South America. Breeding habitats across North America include primary coniferous and deciduous riparian forest; a wider variety of habitats with dense undergrowth are used during migration and winter (Mack & Yong 2000). North American Breeding Bird Survey data indicate little overall change in the population during the last four decades (Sauer et al. 2017).

Gray-cheeked Thrush are separated into the Northern Gray-cheeked Thrush (*C. m. aliciae*) and the Newfoundland Gray-cheeked Thrush (*C. m. minimus*). The northern subspecies breeds in northern boreal forests across North America and across the Bering Sea to eastern Siberia. The Newfoundland subspecies breeds throughout the Newfoundland archipelago, Harbour Island, Nova Scotia, and likely on the north shore of the Gulf of St. Lawrence in Labrador and eastern Quebec (Whitaker et al. 2018). Breeding habitat includes dense conifer stands with thick undergrowth in the boreal forest and shrub thickets in taiga or above the tree line (Whitaker et al. 2018). This species is known to winter primarily in the northwestern Amazon basin; the limit of the winter range distribution is poorly known but is believed to extend to the base of the Colombian and Venezuelan Andes (Hilty and Brown 1986, Whitaker et al. 2018). Migration routes taken by Gray-cheeked Thrush during their over 16000 km annual journey between breeding and wintering grounds remain unknown. Recently, the Sierra Nevada de Santa Marta on the northern coast of Colombia was recognized as a critical refuelling site before presumably Amazon wintering individuals take a non-stop flight over the Caribbean Sea to North America (Bayly et al. 2013, Gómez et al. 2017). Nothing is known about the distribution, overwinter ecology, migratory routes and strategies, and breeding destinations of individuals overwintering in the Andes of South America. Information on population trends is limited due to the species remote breeding range, rugged terrain and dense habitat. Newfoundland populations (*C. m. minimus*) have experienced steep population decline since the mid-1980s (ECCC 2017). Western populations are relatively stable while northeastern populations are declining although at much lower rate than populations in Newfoundland (ECCC 2017).

Canada Warbler breeds primary across the southern boreal forest of Canada. The breeding range expands from northeast British Columbia to the northeast Atlantic coast, and south along the Appalachian Mountains (Reitsma et al. 2009). The winter distribution of Canada Warbler lies mainly within the Andean mountains of Colombia, Peru and Ecuador in northern South America. Canada Warbler is listed as “threatened” under Canada’s species at Risk Act, and over 60% of the breeding population has been lost in Canada during the last 50 years (ECCC 2017). North American Breeding Bird Survey data suggest that population declines are steepest in the east of the breeding range (Sauer et al. 2017) and are primary driven by land use practices on the wintering grounds (Wilson et al. 2018).

1.7. Thesis objectives and chapter synopses

The main objective of my thesis is to assess the relative importance of shade-grown coffee plantations vs. forest as winter habitat for Neotropical migratory songbirds in Colombia. To accomplish this, I compared measurements of habitat quality at the individual and population level between the two habitats in Swainson’s Thrush and Canada Warbler (Chapter 2). I also used state-of-the-art tracking techniques to determine the effect of winter habitat quality and occupancy on spring migration strategies of Swainson's and Gray-cheeked Thrush (Chapter 3 and 4), and to determine potential links between migratory connectivity, winter habitat, and population declines in Canada Warbler (Chapter 5).

In chapter 2, I followed the recommendations of Johnson (2007) and combined a series of indicators of habitat quality at the individual and population level. I used daily and seasonal body condition, age and sex ratios, density and stress levels to assess the quality of shade-grown coffee plantations relative to native forest. I hypothesized that a simplified vegetation composition and forest structure may be inappropriate to maintain the overwinter energy demands of Swainson's Thrush and Canada Warbler and expected shade-coffee plantations to be poorer habitat than forest.

In chapter 3, I tracked spring migration departures and migration speed from the wintering grounds to North America in Swainson's Thrush by using the Motus automated telemetry array. I hypothesized early spring migration and early arrival to the breeding grounds in individuals overwintering in more suitable native forests as has been previously shown in birds overwintering in the Caribbean islands. I predicted that by departing earlier, birds from forests would reach the breeding grounds earlier, while maintaining the same migration pace as birds leaving later from shade-coffee plantations.

In chapter 4, I used Gray-cheeked Thrush to assess the link between winter habitat occupancy, population spread, and migratory connectivity (i.e., population mixing). Population spread measures the degree to which individuals from a single breeding population spread out during the non-breeding season. According to Finch et al. (2017), the size of the winter range occupied by a given population is the underlying mechanism explaining variation in population spread. Low population spread is expected in western populations of long-distance migrants overwintering in Central America, and high population spread is expected in eastern populations overwintering in South America. Migratory connectivity is predicted by the size of the winter range and to a lesser extent by population spread; for instance, strong migratory connectivity is expected in species with large winter ranges and with low population spread. Since all populations of Gray-cheeked Thrush overwinter in South America, I expected high population spread. I hypothesized that if the size of the winter range predicts migratory connectivity, then strong migratory connectivity is expected in the Gray-cheeked Thrush based on its broad winter distribution range in South America. I also expected a link between migratory connectivity, declining breeding populations, and high levels of habitat loss in the Eastern Andes.

In chapter 5. I assessed the migratory connectivity of Canada Warbler overwintering in the three Andean Cordilleras in Colombia. If population declines in Canada Warbler are related to winter habitat events I expected strong migratory connectivity between breeding and wintering populations, and a geographic link between the breeding populations with steeper decline and regions in the Andes with high levels of habitat loss and deterioration.

1.8. Thesis format

This thesis is organized in manuscript format for publication. There is a certain degree of repetition of information throughout the text.

Chapter 2, chapter 3 and chapter 4 are in preparation for publication in peer-reviewed Journals. Chapter 5 “Topography of the Andes Mountains shapes the wintering distribution of a migratory bird” was published in full in 2017 in *Biodiversity and Distributions* in co-authorship with Nicholas J. Bayly, Gabriel J. Colorado and Keith A. Hobson. Appendix 11 “Conservation of Nearctic Neotropical migrants: The coffee connection revisited” was a guest editorial published in June 2018 in *Avian Conservation and Ecology*.

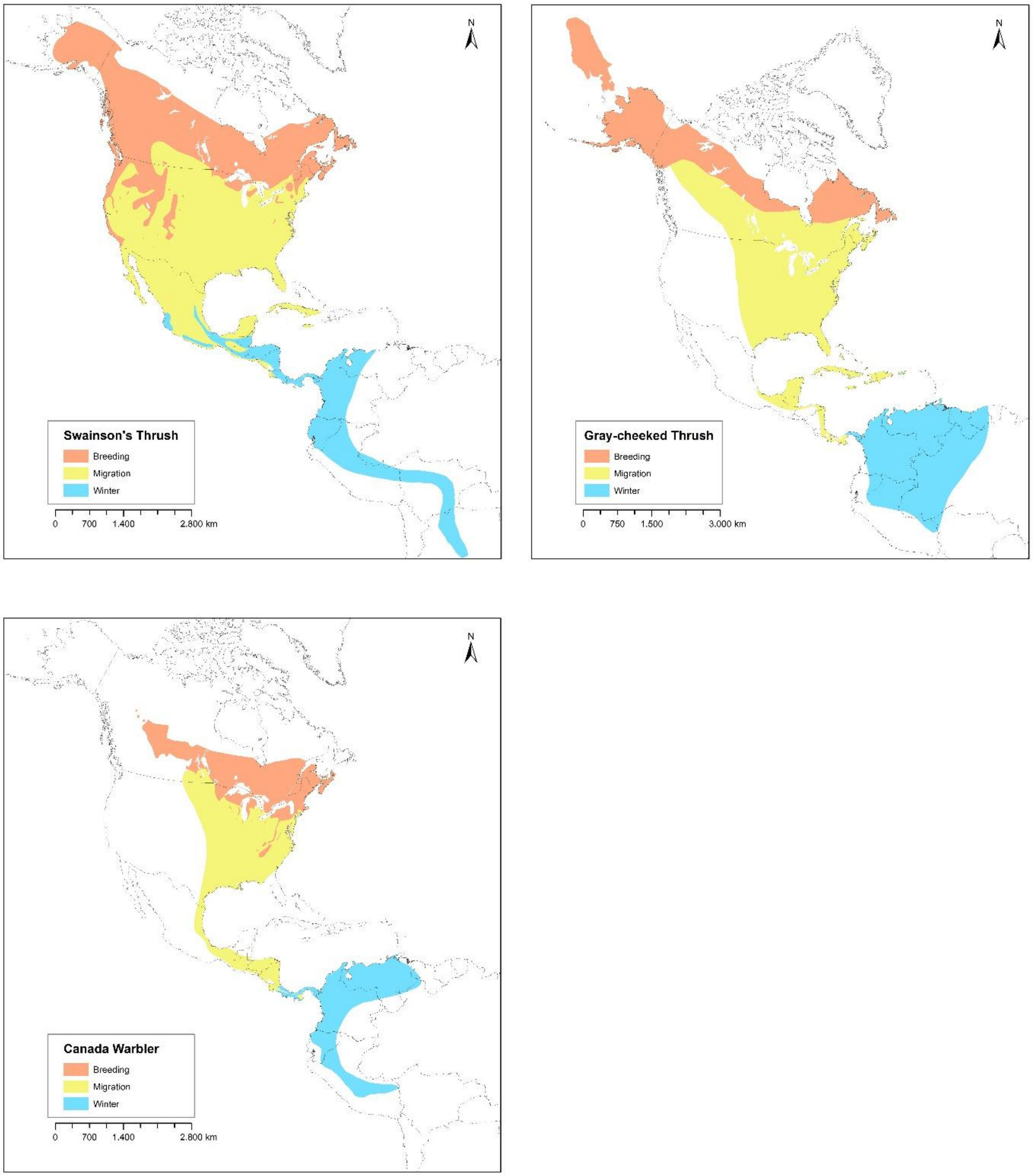

Figure 1.1 Breeding, migration, and wintering distribution of Swainson’s Thrush, Gray-cheeked Thrush, and Canada Warbler. Digital range maps were obtained from BirdLife International (2017).

CHAPTER 2. RELATIVE IMPORTANCE OF SHADE-GROWN COFFEE PLANTATIONS AS OVERWINTERING HABITAT FOR NEOTROPICAL MIGRANT SONGBIRDS IN COLOMBIA

2.1. Abstract

Winter habitat quality is one of the primary ecological factors limiting survival of migratory birds during the non-breeding season. Most studies evaluating relative habitat quality for Neotropical migrants have been conducted in Central America and the Caribbean islands; however, less is known about winter quality habitat for Neotropical migrants wintering in human-modified landscapes elsewhere in the Neotropics. We assessed the relative importance of shade-grown coffee plantations vs. forest in the Colombian Andes as winter habitat for Swainson's Thrush (*Catharus ustulatus*), and Canada Warbler (*Cardellina canadensis*) using measurements of habitat quality at the individual and population level. For Swainson's Thrush we used daily and seasonal mass change, age ratios, density and corticosterone levels; and for Canada Warbler we used daily and seasonal mass change and sex ratios.

For Swainson's Thrush, the rate of daily and seasonal mass gain changed as a function of the interaction between habitat and age, and for Canada Warbler as a function of the interaction between habitat and sex. Daily mass gain in Swainson's Thrush varied between habitats and years; in general, the rate of increase was higher in forest for both ages in 2013 and in forest for adults in 2014. For Canada Warbler, the rate of daily mass gain was higher in males than in females; males gained more mass during the day in forest than in coffee and the opposite was observed in females. The rate of daily mass increase in Swainson's Thrush was lowest in 2015, and for both species, seasonal mass during mid-winter was lowest also in the same year. We attribute the low daily and seasonal condition during 2015 to the effects of the extreme El Niño-Southern Oscillation (ENSO) event observed during winter 2015 which induced severe drought in our study sites. Seasonal changes in mass in Canada Warbler showed that while males and females in forest maintained their mass, females in coffee lost up to 0.5 g from early to mid-winter which corresponds to 6% of total body mass. The probability of occurrence of Swainson's Thrush was higher in forest than in coffee each year; however, the probability of being in forest decreased by 44% in 2015 relative to 2013 and by 22% relative to 2014. In contrast, the probability of occurrence of Canada Warbler was higher in coffee than in forest in most years, and the probability of being in forest increased substantially during 2015 relative to 2013 and 2014. Density of Swainson’s Thrush was twice as high in forest than in coffee, suggesting that the carrying capacity of Andean Montane forest is higher than in shade-grown coffee. Corticosterone values were higher during winter 2013 than during winter 2014, and in both years, values were higher in forest. These findings suggest that elevated values of corticosterone in higher density situations might be adaptive by increasing foraging activity. Taken together, our results suggested that for Swainson´s Thrush native forests are more suitable winter habitats than shade-grown coffee plantations. However, the suitability of coffee increases substantially under certain conditions such as rainy years.

2.2. Introduction

Winter habitat quality is one of the most important ecological factors limiting self-maintenance and survival of Neotropical migratory songbirds during the winter (Sherry and Holmes 1996, Sherry et al. 2005, Studds and Marra 2005). The quality of habitat occupied by migrants during their winter season can also produce residual effects that carry over to subsequent seasons (i.e., migration and breeding), and affect individual fitness and year-round population dynamics (Marra et al. 1998, Norris et al. 2004, Norris 2005). To date, most studies that have assessed the effect of winter habitat quality on overwinter performance have been conducted on insectivorous birds overwintering on Caribbean islands. There, strong differences in food availability between moist coastal forest and adjacent scrub habitats, and between the wet and dry season, allowed the identification of gradients in moisture and food abundance as the most important factors determining winter habitat quality (Sherry et al. 2005, Smith et al. 2010).

Most studies that have assessed effects of winter habitat quality on overwinter performance and spring migration of Neotropical migrants have been conducted in the Caribbean islands in habitats with relatively food-rich or food-poor conditions. However, less is known about the suitability of winter habitats in human-modified landscapes elsewhere in the Neotropics, despite high rates of forest loss and increasing agricultural development. Within human modified landscapes, agroecosystems are the predominant land cover in much of the region occupied by Neotropical migrants during the winter. Therefore, it is critical that we assess the ability of these agroecosystems to maintain populations of migratory species. Assessing winter habitat quality for

Neotropical migrants and its effect on overwinter ecology and demographics therefore remains critical if we are to identify factors driving population declines or limiting population growth, and to predict how environmental changes will impact migratory populations.

Most Neotropical migratory songbirds overwintering in northern South America depend on mid-elevation forests across the Andean mountains. However, over 90% of Andean forests have been cleared (Henderson et al. 1991) and agroecosystems are the predominant land cover in much of region occupied by Neotropical migrants during the winter (Díaz-Bohórquez et al. 2014). Within this agroecological matrix, traditional shade-grown coffee plantations are one of the few remaining forest-like habitats left for Neotropical migrants in mid- to high-elevation mountain ranges in northern South America (Reviewed by Perfecto et al. 2005). Higher migratory species richness and abundance in shade-grown coffee plantations than in other agroecosystems and natural forest have enhanced the perceived importance of this habitat for conservation of Neotropical migrants (reviewed by Komar 2006). However, species richness or abundance alone do not necessarily indicate high quality habitat or high conservation value unless correlated with population parameters (e.g., density or survival), or with individual physical condition and compared to native habitat (Johnson et al. 2006, Komar 2006). It follows that despite the assumed importance of shade coffee plantations for the conservation of migratory birds, the quality of shade coffee relative to the native forests from where they were carved is still to be addressed (but see Bakermans et al. 2009, Bayly et al. 2016).

Different measures, including apparent survival, density, sex and age ratios and change in mass over the winter, have been used to assess winter habitat quality for Neotropical migrants (reviewed by Johnson 2007). However, individual measurements may produce misleading conclusions about the quality of a given habitat and using more than one measure is recommended (Pidgeon et al. 2006, Johnson 2007). To date, the relative suitability of shade-grown coffee plantations for overwinter survival, body condition and population density of migratory birds has been evaluated for a few, primarily insectivorous species (Strong and Sherry 2000, Wunderle and Latta 2000, Bakermans et al. 2009). The only study assessing the quality of shade-coffee plantations relative to forests found that Cerulean Warblers (*Setophaga cerulea*), Blackburnian Warblers (*Setophaga fusca*), Tennessee Warblers (*Oreothlypis peregrina*) and American Redstarts overwintering in the Venezuelan Andes were more than 10x more abundant in shade coffee plantations than in primary forest (Bakermans et al. 2009). However, it is unclear whether higher overwintering density in shade grown coffee plantations was correlated with other proxies of habitat quality (i.e., survival, body condition); and if higher density was driven by habitat quality, dominant behaviour, lack of natural habitats in the landscape or other factors.

We used daily and seasonal changes in physical condition, age and sex ratios, density, and measures of Corticosterone as a biomarker of the level of exposure to stressors to determine the relative quality of shade coffee plantations vs. native forest as winter habitat for Swainson's Thrush and Canada Warbler wintering in northern South America. We hypothesized that a simplified vegetation composition and forest structure may be inappropriate to maintain the overwinter energy demands of Swainson's Thrush and Canada Warbler and expected shade-coffee plantations to be poorer habitat than forest. Consequently, we expected birds overwintering in coffee to have lower daily and seasonal condition than birds in forest. Specifically, we expected lower total daily and seasonal mass gain in coffee than in forest. Precipitation in our study sites peaks in October and decreases until the onset of the dry season in December (Figure 2.1). Precipitation decreases steeply from December until the onset of the second rainy season at the beginning of March. Based on findings in the Caribbean, we expected decreasing body mass as the dry season progressed from December to the end of February in coffee, and stable or increasing mass in forest. For Canada Warbler we additionally expected an increase in condition in March with the onset of the rainy season.

Population density is expected to be higher in high quality habitats because individuals select the most suitable habitats where chances of survivorship are higher (Fretwell and Lucas 1970). However, factors such as dominance behaviour (competitive exclusion), environmental conditions, and large-scale habitat structure can also lead to high densities in poor-quality habitats (Van Horne 1983). For example, socially dominant behaviour may decouple the expected relationship between habitat quality and density if density increases in poor habitats as a result of weak competitors being excluded from suitable habitats (Van Horne 1983, Johnson 2007). In turn, when habitat selection is controlled by dominant behaviour, higher proportions of dominant individuals are expected to occur in the highest quality habitats, as illustrated by adult male American Redstarts in Jamaica (Marra 2000). Therefore, the ratio of sex and age classes among habitats could indicate differences in habitat quality (Wunderle and Latta 2000). Following on from the above, lower density of overwintering migrants in forest might be expected if older males displace young and females to poor quality shade-grown coffee plantations.

In birds, patterns of corticosterone secretion can be modulated daily and seasonally in response to normal and predictable changes in the environment or life-history stages such as reproduction, moult or migration (Romero 2002). Corticosterone is also the primary glucocorticoid hormone released into the blood stream by the vertebrate hypothalamic–pituitary–adrenal (HPA) axis during the stress response (reviewed by Romero 2004). Feather corticosterone reflects plasma hormone levels during the period of feather growth and can be used as a long-term and integrated measure of HPA activity (Bortolotti et al. 2008). We expected higher exposure to stressors (e.g., low food availability, competition, habitat loss, predation risk) in shade-grown coffee plantations which would be reflected in higher corticosterone values than in forest.

Comparative studies of the quality of shade coffee and the quality of native forest from where these agroecosystems originated are needed to provide sound evidence to support the conservation value of shade-grown coffee plantations for Neotropical migrants (Johnson et al. 2006). Only by combining multiple proxies for habitat quality is it possible to understand the complexities of overwinter habitat quality and provide unbiassed assesments as has been demonstrated by previous studies in the Neotropics (Johnson 2007, Bayly et al. 2016).

2.3. Methods

2.3.1. Study sites

Field work was carried out during the winters of 2013, 2014, and 2015 (December to March) in three study sites located on the western slope of the East Andean Cordillera in Colombia. Study sites were separated by 5 km and were dominated by shade-grown coffee plantations with pastures and small patches of secondary forest. We selected sites where shade-coffee plantation and secondary forest were located at approximately the same elevation and not more than 1 km apart. The location of the sites are listed as follows: “Hacienda La Fragua” 04°18’54.18”N, 74°32’19.29”W (Coffee 1400m forest 1500m), “Los Vientos” ” 04°21’56.23”N, 74°31’19.31”W (coffee and forest 1350); and “La Vuelta” ” 04°19’31.13”N, 74°28’54.69”W (coffee 1400 and forest 1700 m).

In the three sites, shade in coffee plantations was provided by residual native trees remaining from the original native forest. Native shade species included *Inga* ssp., *Simarouba amara*, *Cordia* *alliodora*, *Trichanthera gigantean*, *Sebastiania commersoniana*, *Alfaroa colombiana*, *Anacardium excelsum*, *Senna spectabilis*, and *Hevea pauciflora*. In all sites, coffee had at least 40% shade during the dry season and plantations in La Fragua and Los Vientos were Rainforest Alliance certified (SAN 2017).

Median precipitation across the Andean coffee region in Colombia ranges between 1100 and 7359 mm/year; most of the region receives above 2000 mm/year. Within the coffee region, our study sites are characterized by drier than average conditions with median precipitation of 1103 mm/year, which in part enforces the maintenance of the shade in the coffee plantations to meet optimal production conditions. Precipitation in our study sites followed a bimodal pattern with two rainy seasons from March to June and from September to November, and two dry seasons from December to February and from July to August (Cenicafé 2011).

2.3.2. Captures

Captures were conducted during eight days a month in each habitat by alternating four days in coffee and four days in forest to reduce disturbance and mist net avoidance. Birds were captured from 06:00 to 11:00 h and from 15:00 to 17:30 h using mist nets (30 mm mesh). The placement and number of mist nets was determined by topography and designed to maximize capture rates. Canada Warblers were captured from 1 December to 25 March, and Swainson's Thrush from 1 December to 28 February in order to exclude birds during migration.

All captured birds were fitted with a US Fish and Wildlife Service numbered aluminium band and processed and released at the capture site. We determined age and sex following plumage characteristics outlined by Pyle (1997); and recorded wing chord (±1 mm) and body mass (±0.1 g, using an electronic balance) for each bird at first capture and in all birds recaptured at least one day after their initial capture. Individuals were aged as hatch year and after hatch-year during December, and as second year and after second-year after 31 December (Pyle (1997). We refer to hatch-year and second-year birds as immatures, and to after hatch-year and after second-year as adults.

2.3.3. Variable width line transects

Across sites, we conducted 211 transects in coffee and 153 in forest from December to the end of February. In 2013 transects were conducted only during January and February. In La Fragua we established one transect of 600 m (n=37) in coffee and one of 500 m in forest (n=39), in Los Vientos we surveyed two transects of 300m in coffee (n=76, 38 in each) and one of 500m in forest (n=40); and in La Vuelta we established three transects of 200 m in coffee (n=98) and two of 200m in forest (n=74). Transects were walked at steady pace starting at 16:00 h in all sites, the duration of the transects varied according to their length; however, all were finished by 17:00 h. The perpendicular distance from the centre of the transect to each Swainson's Thrush heard or seen was recorded at the nearest m (Buckland et al. 2001).

2.3.4. Corticosterone

We compared stress levels for birds occupying shade-grown coffee plantations and forest by measuring corticosterone values of feathers induced to grow on the wintering grounds during 2013 (coffee n=8, forest n=11) and 2014 (coffee n=21, forest n=27). Three external greater wing coverts were sampled from each Swainson's Thrush at first capture (feathers grown on the breeding grounds); re-grown winter feathers were collected during subsequent recaptures.

Corticosterone levels in feathers were obtained by using a methanol-based extraction technique (Bortolotti et al. 2008). Samples were randomized and processed in two batches. We assessed the recovery efficiency of each extraction by including three feather samples spiked with approximately 5000 d.p.m. of ^{3}Hcorticosterone (Amersham Biosciences Corp., Piscataway, NJ, USA). Recovery efficiency in the reconstituted samples in each extraction was 93.3%. Corticosterone concentration was determined using radioimmunoassay (RIA). Within and between assay variability was determined as the coefficient of variation resulting from repeated measurement of six samples spiked with a known amount of corticosterone. Samples were measured in four RIA with an intra-assay coefficient of variation of 4% and an inter-assay coefficient of variation of 10%, and mean (±SD) limit of detection (ED80) of 23.89±4.35 pg corticosterone-feather/assay tube. Corticosterone values are expressed as pg corticosterone per mm of feather (pg/mm), which provides a reliable estimate of corticosterone levels in feathers per unit time of feather growth (Bortolotti et al. 2008). Corticosterone extractions were performed at the University of Saskatchewan, Canada.

2.3.5. Statistical analysis

2.3.5.1. Index of body condition and repeatability

We used mass as an index of body condition. Mass alone is a reliable indicator of energy reserves and it has been argued that mass alone is a better index than other more commonly used indices such as mass corrected by wing length (Labocha and Hayes 2012). We investigated the use of mass as an index of body condition by estimating its repeatability. Within-year repeatability was calculated using within- and between-variance components in a Linear Mixed Effects Model (LMM) with the restricted maximum-likelihood method (REML, nlme package in R; Pinheiro and Bates 2000) with bird identity as a grouping random factor in the model. We could not estimate repeatability between years because most individuals were not recaptured across years. We estimated repeatability as $R = \delta^{2}\alpha/(\delta^{2}\alpha + \delta^{2}_{\text{€}})$ where $\delta^{2}\alpha$ is the between-individual variance and $\delta^{2}_{\text{€}}$ is the within-individual variance (Nakagawa and Schielzeth 2010). Mass was highly repeatable, in 2013 R= 66%, and 2014 and 2015 R=72%. Measurement errors are included in the residual variance ($\delta^{2}_{\text{€},}$ within-individual). In the case of mass, measurement errors are expected to be small since we used an electronic scale (±0.1 g); therefore, we assumed that much of the within-individual variance of mass is caused by actual changes in a bird's body mass. We estimated the phenotypic plasticity (Nakagawa and Schielzeth 2010), or how changeable mass was during the overwintering period as 100-*R*. The phenotypic plasticity of mass was 34% in 2013, and 28% in 2014 and 2015, these values represent how changeable this trait was. In 2014 and 2015 the repeatability of mass corrected by wing length was lower than the repeatability of mass (2013 R= 66%, 2014 R= 61%, and 2015 R= 64%).

For Canada Warbler, we estimated the overall repeatability of mass because we did not have enough data for each year. As in Swainson's Thrush, the repeatability of mass (R= 63%) was higher than mass corrected by wing length (R=58%).

2.3.5.2. Daily and seasonal change in mass – by site

The objective of modelling changes in body mass was to predict the pattern of daily and seasonal mass change. First, we assessed whether there were differences in daily and seasonal patterns of mass change between sites (Appendix 1). We ran two separate linear models for Swainson's Thrush to assess how daily and seasonal mass changed with the interaction between site, year and habitat (Appendix 1A). Smaller sample sizes in Canada Warbler precluded us from looking at daily and seasonal changes in mass across years so the models only included the interaction between site and habitat (Appendix 1B). All Swainson's Thrush gained mass daily across years and sites. In general, mass change was higher in forest than in coffee in 2013 and 2014, only in 2014 in Los Vientos birds gained 0.05g more during the day in coffee than in forest. In 2015, birds gained less mass in forest in La Fragua and Los Vientos and gained 0.01g more in forest than in coffee in La Vuelta. The patterns of seasonal mass change varied slightly across years and sites, in 2013 and 2014, mass increased over the season and the rate of increase was slightly higher in forest than in coffee. Only in Los Vientos mass decreased slightly in both habitats (steeper in forest) in 2013 and in forest in 2014. During 2015 mass declined in all sites and habitats, the decline was the same in forest and coffee in La Vuelta and steeper in forest in La Fragua and Los Vientos.

Canada Warblers gained mass during the day in all sites, but we did not find large differences between rates of daily mass gain between forest and coffee in each site. Canada Warblers in La Fragua slightly gained mass over the season, and the increase was higher in forest than coffee. In Los Vientos and La Vuelta body mass slightly declined over the season (decline < 0.01g) and the decline was steeper in forest in Los Vientos. We consider that the differences between the coefficients across sites were not large enough to conclude and the trends in daily and seasonal mass change across years and habitats were inconsistent. We present our results using data across the three sites pooled; this also enabled us to show that effects we found were consistent across three different sites and therefore likely reflect what was happening in the wider landscape.

2.3.5.3. Daily and seasonal change in mass – pooling sites

After pooling sites, we conducted three different analyses for each species (i) population daily changes in body mass; and (ii) seasonal mass changes at the population and (iii) at the individual level. We analyzed data separately for each year and for all three years combined. Daily and seasonal mass change analysis at the population level included all birds at first capture. We confirmed whether the population-level pattern of seasonal mass change was maintained at the individual level by analysing only data of recaptured individuals. For Canada Warbler, we considered the winter period from 1 December to 30 March, and for Swainson´s Thrush from 1 December to 28 February. Day 1 was equal to 1 December for both species.

We conducted the (i) population daily changes in body mass; and (ii) the seasonal mass changes at the population and (iii) at the individual level in a two-stage process. First, we assessed whether trends in daily (i.e., changes with capture time) and seasonal mass change (i.e., changes with capture day) were linear or non-linear (Swainson's Thrush Appendix 2, Canada Warbler Appendix 3) by running a linear model (I), a quadratic model (I + I2) and a polynomial model (I + I2 + I3). "I" was capture time for analyses of population daily changes in body mass, and capture day for analyses of population seasonal change in body mass analysis. To assess the seasonal pattern of mass change at the individual level based on recapture data, we used a modified version of the method presented by Bayly et al. (2012), where the dependent variable Change in Body Mass was calculated as the change in mass between first capture and subsequent recaptures; for birds recaptured more than once only the last recapture of the season was used. We then modelled change in body mass as a function of the number of days since the bird was captured (Appendix 2 and 3).

In all analyses, we compared models by calculating the relative support that each model received from Akaike's information criterion corrected for small sample sizes (AIC_c). To facilitate comparison of the candidate models, we calculated Δi as the difference between each model and the model with the lowest AIC_c ($\Delta i = AIC_{ci} -$ minimum AIC_c). Models with Δ $AIC_c < 2$ were considered equally plausible (Burnham and Anderson 2002).The trend in daily and seasonal mass change showed by the top ranked model (Appendix 2 and 3) was selected to be included in stage 2.

2.3.5.4. Daily change in mass at the population level

Results of the first stage of the analysis for Swainson's Thrush indicated a consistent linear pattern in daily mass change for each year, and a quadratic pattern for pooled data (Appendix 4A, Table 2.1 A). For Canada Warbler, model selection suggested a consistent linear pattern of daily change in body mass across years and when all years were pooled (Appendix 5A, Table 2.2 A). In the second stage, all models were run for each species as follows. We examined whether body mass changed with capture time and incorporated the covariates habitat (coffee and forest), age (immature and adult), sex (male and female, only for Canada Warbler), and year (three-level factor:

2013, 2014 and 2015). Variables were entered as an interaction with capture time to ensure that we modelled the effect of these variables on the rate of daily mass change and not as an additive effect (Swainson's Thrush Table 2.1 A, Canada Warbler Table 2.2 A).

In all analyses, we selected among competing models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002) as described earlier. The top ranked model was used to predict daily and seasonal trajectories of body mass. Seasonal coefficients were multiplied by 30 and expressed as a monthly rate of mass change.

2.3.5.5. Seasonal change in mass at the population level

In the first stage, model selection suggested that for Swainson's Thrush the pattern of seasonal change in mass was linear during each year, and quadratic when years were combined (Appendix 4B, Table 2.1 B). For Canada Warbler the pattern was linear during each year and when years were pooled (Appendix 5B, Table 2.2 B). In the second stage we modelled body mass as a function of capture day, habitat, age, sex (only for Canada Warbler), and year. Variables were entered as an interaction with capture day to ensure that we modelled the effect of these variables on the rate of daily mass change and not as an additive effect. We entered capture time as an additive effect in each model to account for daily increases in body mass (Swainson's Thrush Table 2.1 B, Canada Warbler Table 2.2 B).

2.3.5.6. Seasonal change in mass at the individual level

Data were pooled across 2013, 2014, and 2015 because few birds were recaptured within each year. Model selection suggested that the pattern of seasonal change in mass gain was linear for both species (Appendix 2C and 3C). We modelled change in body mass (mass change between first capture and last recapture, Bayly et al. 2012) as a linear function of habitat, age, sex (only for Canada Warbler), and year. Variables were entered as an interaction with day (number of days since the bird was first captured) to ensure that we modelled the effect of these variables on the rate of seasonal mass change and not as an additive effect (Swainson's Thrush Table 2.1 C, Canada Warbler Table 2.2 C).). The difference between capture and recapture time was entered as an additive effect in each model to account for diurnal changes in body mass (Bayly et al. 2012).

2.3.5.7. Age and sex habitat segregation

We used Generalized Linear Models (GLM) with habitat (coffee=0, forest=1) as a response variable to assess the likelihood that individual Swainson's Thrush and Canada Warbler occupied forest or coffee during the non-breeding season. For Swainson's Thrush we compared a set of four candidate models, including a null model, to test whether there were differences in habitat selection between years, ages, or if habitat selection varied with the interaction of year and age (Appendix 8A). Due to smaller sample sizes for Canada Warbler, we included sex instead of age in the candidate model set (Appendix 8B). Model selection was carried out using AIC_c. Models with Δ $AIC_c < 2$ were considered equally plausible (Burnham and Anderson 2002).

We used the coefficients from the top model to obtain the odds, odd ratios, and converted odds ratios to percent changes of the odds of being in forest (Table 2.3). We used the DHARMa package in R to check model assumptions (Hartig 2018) . DHARMa standardizes the model residuals to values between 0 and 1 and can be interpreted as intuitively as residuals from a linear regression. We visually examined a qq-plot to detect overall deviations from uniformity, and a plot of the residuals against the predicted values. Visual inspection of the residuals was supported by conducting One-sample Kolmogorov-Smirnov test in order to test for the overall uniformity of the residuals.

2.3.5.8. Density

Overwinter density (D = number per unit area) of Swainson's Thrush in forest and shade coffee habitats was estimated by the distance-based line transects approach (Buckland et al. 2001). The probability of detecting birds was expected to differ between structurally complex primary forest and more simplistic shade-grown coffee plantations. The distance-based sampling approach estimates density within a sampling area adjusting for the detectability of the individuals, providing unbiased density estimates (Buckland et al. 2001). We analyzed data using the Conventional Distance Sampling (CDS) engine in Distance 7.1. Histograms of the detection data showed the presence of heaping every 5 m and outliers. Heaping arises when observers round the estimated distances to convenient values. Heaps were mitigated by grouping the data in five intervals, outliers were removed by right-truncating the largest 5% of distances of the data in both habitats (i.e., detections at far distances >38m).

We considered six *a priori* models for the detection function that included the uniform, half-normal, and hazard-rate key functions. Key functions were adjusted by adding a cosine, simple polynomial or a hermite polynomial series expansion to improve the fit of the model to the distance data (Table 2.4 A, B). Data across sites were combined and stratified by habitat (the factor affecting detectability), and an estimate of density was made for each stratum. We selected amongst models using AIC_c, and densities were estimated using the model receiving the greatest support from AIC_c. The fit of all competing models was assessed using chi-square test (Buckland et al. 2001). Density estimates are reported as individuals/ha.

2.3.5.9. Corticosterone

We assessed the effect of habitat, year, age and the interaction of habitat and age, habitat and year, and year and age on corticosterone values of feathers grown on the winter grounds (Table 2.5). We selected amongst competing models using AIC_c. Models with Δ $AIC_c < 2$ were considered equally plausible (Burnham and Anderson 1998). Model coefficients and 95% confidence intervals (95% CI) were used to estimate the magnitude and direction (positive or negative) of the effect of each variable in the top model on winter corticosterone values. Narrow intervals excluding zero indicate more precise estimates and a strong effect of the variable (Burnham & Anderson, 2002).

2.4. Results

2.4.1. Daily and seasonal patterns of body mass in Swainson's Thrush

We modelled daily and seasonal mass change in 1119 individuals captured over the three field seasons (2013 n= 221, 2014 n= 396, 2015 n=502). We found a consistent pattern of change in daily and seasonal body mass during each year and when years were pooled (Appendix 4, Table 2.1). In each year, the model receiving the greatest support showed that daily and seasonal mass changed as a function of the interaction between habitat and age (Appendix 4). When years were pooled, within-annual patterns were maintained; with adults and immatures in both forest and coffee showing the lowest rate of daily and seasonal mass gain during the winter of 2015. We present and discuss our model predictions based on the results of years combined Table 2.1).

2.4.2. Daily change in mass – Swainson’s Thrush

When data were pooled across years, a quadratic model containing the interaction between capture time, year, habitat and age received the greatest support (Table 2.1 A). This model suggested that, in general, mass increased during the morning, reached a plateau early in the afternoon and slightly decreased at the end of the afternoon (Table 2.1 A, Figure 2.2 A, B). In general, adults were heavier than immatures, and during each year the rate of mass increase was higher for adults than for immatures in all habitats. Results within age and habitats varied among years; for immatures the rate of daily mass increase was higher in forest than in coffee in 2013, and higher in coffee than in forest during 2014 and 2015 (Figure 2.2 A). For adults, the rate of daily mass increase was higher in forest than in coffee in 2013 and 2014, and higher in coffee at the end of the day during 2015 (Figure 2.2 B). The increase in mass during the morning was strong for adults in all years and habitats, and for immatures in forest and coffee in 2014, decrease in mass at the end of the afternoon was not supported (i.e., 95%CI included zero, Appendix 6A).

2.4.3. Seasonal change in mass at the population level – Swainson’s Thrush

When data were pooled across years, a quadratic model containing the interaction between day, year, habitat and age received the greatest support (Table 2.1 B). During winter 2015, immatures in forest and coffee showed strong mass loss from early to mid-winter. The rate of monthly mass loss was similar in both habitats (Appendix 6B forest= -1.85±0.03, coffee=-1.96±0.03), birds recovered mass during late winter but the recovery was steeper in coffee than in forest (Figure 2.2 C). Adults in forest increased their mass from mid- to late-winter in 2013 and maintained their mass during 2014; in 2015, mass declined slightly at the end of the season. Mass of adults in coffee at the end of the season in 2015 was lower than during previous years in the same habitat; however, this mass was higher than the mass of birds in forest during the same period (Figure 2.2 C). During each year, immatures reached their highest condition at the end of the season in coffee, the same was observed in adults during 2013 and 2015. Across the three years the highest condition at the end of the season was reached by adults and immatures in coffee in 2013, followed by adults in forest in the same year. In contrast, the condition of immatures in forest in 2013 declined and reached the lowest values at the end of the season.

2.4.4. Seasonal mass change at the individual level – Swainson's Thrush

We modelled seasonal mass change in 109 individuals recaptured over the three seasons (2013 *n*= 18, 2014 *n*= 26, 2015 n=30). The highest ranked model was the null model, followed by the model that suggested an increase in mass as the season progressed while controlling for capture time (Table 2.1 C, Figure 2.3 A). However, confidence intervals overlapped zero and so any increase in mass over the season was not strong.

2.4.5. Daily and seasonal body condition in Canada Warbler

We modelled daily and seasonal changes in body-mass in 222 individuals captured over the three winters (2013 *n*= 62, 2014 *n*= 71, 2015 n=89). Results of daily and seasonal mass change were consistent within years and when years were combined, the highest ranked models contained the interaction between time, habitat and sex (Appendix 5, Table 2.2 A, B). We present and discuss our model predictions based on the results of years combined (Table 2.2 A, B).

2.4.6. Daily change in mass – Canada Warbler

The highest ranked model suggested that mass during the day changed linearly as a function habitat and sex and their interaction (Table 2.2 A). Model coefficients suggested that the rate of daily mass gain was higher in males than in females; males gained more mass during the day in forest than in coffee, and the opposite was observed in females (Figure 2.4 A, Appendix 7A). We could not assess the effect of the interaction of time, habitat and sex in 2014 due to small sample sized for females in forest (n=4).

2.4.7. Seasonal change in mass at the population level – Canada Warbler

When years were combined, two quadratic models received the greatest support from AIC_c and indicated a difference in overwinter mass between habitats and sexes (top ranked model Table 2.2 B), and between habitats and years (second ranked model Table 2.2 B). In general, mass was higher in males than in females. Model estimates suggested that males in forest and coffee, and females in forest maintained their mass during the winter. Females in coffee showed the lowest overwinter mass. The top model predicted that females in coffee lose up to 0.5g from early to late-winter (18 February); however, these individuals reached the condition of females in forest at the end of the season (Appendix 7B, Figure 2.4 B). The second ranked model showed that condition was lower over most of the winter in both habitats in 2015, and birds reached the highest condition in coffee during late winter in 2013 (Appendix 7B, Figure 2.4 D).

2.4.8. Seasonal mass change at the individual level – Canada Warbler

We modelled seasonal mass change in 74 individuals recaptured over the three seasons (2013 *n*= 22, 2014 n= 44, 2015 n=43). The top ranked model included the interaction between capture day and year and suggested that overwinter condition decreased from 2013 to 2015 (Table 2.2 C, Figure 2.3 B).

2.4.9. Age and sex ratios – Swainson’s Thrush

We modelled winter habitat occupancy in 1154 Swainson’s Thrush captured over the three years. Results from model selection suggested that for Swainson’s Thrush the likelihood of being in forest or coffee changed according to year (Appendix 8A). During each year the odds of being in forest were higher than coffee (Table 5); however, these odds were reduced in 2015 by 44% relative to 2013 and by 22% relative to 2014 (Table 2.3 A). The model including the interaction between year and Thrush age suggested that, within adults, the odds of being in forests decreased in 2014 and 2015 relative to 2013 by 11%. While in 2013 and 2014 the probability of occurrence of adults in forest was lower than in immatures, in 2015 the probability of adults being in forest increased by 31% relative to immatures. Visual inspection of residual plots and the results of the One-sample Kolmogorov-Smirnov test (D = 0.02, p>0.05) indicated that the model assumptions were met.

2.4.10. Age and sex ratios – Canada Warbler

We modelled winter habitat occupancy in 234 Canada Warblers captured over the three years. Model selection suggested that for Canada Warbler the likelihood of being in forest changed according to year (Appendix 8B). Odd ratios obtained from the highest ranked model suggested that the odds of being in forest were lower than the odds of being in coffee during each year (Table 2.3 B). However, these results were conclusive only in 2014. During 2013 and 2015 the higher probability of occurrence in coffee was not substantial (i.e., 95% CI included zero). In 2015 the probability of occurrence in forest increased by 14% relative to 2013 and by 167% relative to 2014 (Table 2.3 B). Odd ratios obtained from the second ranked model (Appendix 8B suggested that the difference in the probability of occurrence between males and females in forest in 2013 was not substantial; however, during 2014 and 2015 the proportion of males in forest increased to 96% and 87%, respectively (Table 2.3 B).

Within sexes, females were more likely to occupy forest than coffee in 2015 relative to 2014, and males were more likely to occupy forest in 2015 and 2014 relative to 2013 (Table 2.3 B). Visual inspection of residual plots and the results of the One-sample Kolmogorov-Smirnov test (D = 0.038, p>0.05) indicated that the model assumptions were met.

2.4.11. Density – Swainson's Thrush

We conducted 212 transects in coffee and detected 761 Swainson's Thrush, and 153 transects in forest with 1119 detections. Detection-adjusted density estimates derived by the top ranked model (Table 2.4 A) showed that across sites and years the density of Swainson's Thrush was twice as high in forest (D=4.3 individuals/ha, 95% CI 3.8 to 4.9) than in coffee (D= 2.3 individuals/ha, 95% CI 2.0 to 2.6). Lack of difference in detection probability between forest and coffee was likely related to the fact that 69% of individuals were recorded by auditory rather than visual detections (P_{coffee}=0.7, 95% CI 0.6 to 0.7; P_{forest}=0.6, 95% CI 0.6 to 0.6).

2.4.12. Corticosterone – Swainson's Thrush

The best model explaining corticosterone values during the winter included the interaction between habitat and year and received 93% support (Table 2.5). Estimates derived from this model suggested that corticosterone values were higher during winter 2013 than during winter 2014, and in both years, values were higher in forest (2013 coffee 21.20±1.48 pg/mm 95% CI 18.3, 24.2; 2013 forest 25.34±1.26 pg/mm 95% CI 22.8, 27.9; 2014 coffee 17.63±0.91 pg/mm 95% CI 15.8, 19.5; and 2014 forest 20.62±0.80 pg/mm 95% CI 19.0, 22.2). Within forest, corticosterone values were negatively correlated with mass at initial capture (Appendix 9). Differences in feather corticosterone within forest were not related to age (adult n=14 corticosterone 20.91 pg/mm, immature n=24 corticosterone =22.61 pg/mm, Welch Two Sample t-test P>0.05).

2.5. Discussion

2.5.1. Swainson’s Thrush

Estimates of daily and seasonal change in body mass showed a strong effect of age, habitat and year. In general, the rate of daily mass gain was lower in 2015 for all ages and habitats, and the decline in mass from early to mid-winter was steepest for immatures in both habitats. Adults in forest showed their lowest mass at the end of the season in 2015. We attribute the low daily and seasonal condition of Swainson´s Thrush during 2015 to the effects of El Niño-Southern Oscillation (ENSO). The Southern Oscillation Index (SOI) is an indicator of the two ENSO phases: La Niña and El Niño; prolonged periods of negative SOI correspond to El Niño episodes, and consistent periods of positive SOI values to La Niña episodes (Philander 1990). Measures of the SOI during winter 2015 (December 2015 to February 2016) indicate one of the strongest El Niño events on record (NOAA 2017).

El Niño events have significant influence on temperature and precipitation and consequently on the productivity of many terrestrial ecosystems (Philander 1990, Shabbar and Khandekar 1996, Shabbar et al. 1997). For instance, in the Caribbean, and Central and Northern South America, El Niño induces drier than average conditions (Ropelewski and Halpert 1987, Jaksic 2001). Studies in the Caribbean and Central America suggest that, by limiting food availability, drought conditions like those observed during El Niňo years can affect habitat quality and have negative effects on overwinter physical condition (Strong and Sherry 2000, Latta and Faaborg 2002) and survival of insectivorous Neotropical migrants (Sillett et al. 2000, Marra and Holmes 2001). Less is known about the direct effect of ENSO conditions on frugivorous species overwintering in South America. ENSO induced drier than average conditions in our sites; for instance, total local precipitation from December to February was 297 mm in 2013, 273 mm in 2014, and 68 mm in 2015 (Cenicafé 2016a, b, c, 2017). This dramatic decrease in precipitation during the 2015 El Niño likely affected fruit availability for Swainson’s Thrush since water availability controls the phenology of many Neotropical forest plants (Reich and Borchert 1984) and fruit peaks coincide with the onset of the rainy season (van Schaik et al. 1993). Consistent with our findings, a similar pattern was observed at a spring stopover site in Costa Rica, where Swainson’s Thrush and other Neotropical frugivorous species showed lower physical condition during an El Niño year likely in response to reduced fruit availability (Wolfe and Ralph 2009).

Higher condition of thrushes in coffee at the end of the season for most birds across years might be related to birds in coffee leaving earlier and perhaps starting to refuel earlier. The high daily and seasonal condition reached by birds in 2013 was likely related to high precipitation during that year. Precipitation was particularly high in November (236 mm, compared with 141 mm in 2014 and 116 mm in 2015) before or during Thrush arrival which might have driven high food availability during the beginning of the season and acted as a buffer during the onset and progression of the dry season.

Studies in the Andes of Venezuela and Colombia suggest that shade-grown coffee plantations provide quality habitat for Neotropical migrants (Bakermans et al. 2009, Colorado and Rodewald 2017). For example, some species overwintering in shade-grown coffee increased their daily and overwinter body condition and had high overwinter survival and high between-seasons return rates (Bakermans et al. 2012, Colorado and Rodewald 2017). However, the best assessment of the habitat quality of shade-grown coffee should include measures of habitat quality in coffee relative to the local native forest from where those plantations were carved (Van Horne 1983, Vickery et al. 1992) and this comparison is lacking across several studies evaluating the suitability of shade-grown coffee as winter habitat for Neotropical migrants (i.e., Strong and Sherry 2000, Wunderle and Latta 2000, Johnson et al. 2006, Colorado and Rodewald 2017). During the winter period, avian density has been the only measure of the quality of shade-grown coffee plantations relative to the native Andean forest from where the plantations originated. In the Andes of Venezuela, the detectability-corrected density of American Redstart, Blackburnian Warbler, Cerulean Warbler, and Tennessee Warbler was over ten times higher in shade-grown coffee than in forest (Bakermans et al. 2009). However, density alone is not a reliable measure of habitat quality (Van Horne 1983, Sherry and Holmes 1996) and it is unclear whether higher density in shade grown coffee plantations was driven by habitat quality, dominance behaviour or other factors. In contrast with the results of Bakermans et al. (2009), our results suggest that the carrying capacity of Andean Montane forest is higher than in shade-grown coffee, as density estimates indicated that forest can maintain twice as many Swainson's Thrush than shade-grown coffee plantations. We suggest that a complex vegetation composition and likely higher density of native fruiting trees in forest, make this habitat more suitable than shade-coffee for Swainson's Thrush during the winter.

Probability of occurrence of adults and immatures during 2013 and 2014 suggest that immatures were not displaced from forest by adults. Indeed, the odds of adults occupying forest during those years were lower than the odds of immatures occupying the same habitat. However, in contrast with adults, the condition of immatures decreased significantly from early to mid-winter in forest in 2013, and slightly decreased over the season in 2014. This suggests that although immature birds can access the forest, they might be outcompeted by despotic behaviour of adults. Age ratios in 2015 suggested that habitat selection was mediated by dominance behaviour since the number of adults in forest increased by 31%, and the odds of immatures occupying forest were the lowest during that year. The body condition of adults in forest declined slightly over the season in 2015, while immatures showed the lowest rate of daily mass gain and reached their lowest seasonal mass over the three years of study. The higher proportion of adults in forest in 2015 likely resulted from higher competition with immatures in response to limited resources resulting from the severe drought induced by the strong El Nino year (Marra 2000). Our hypothesis that population was structured by dominance behaviour in 2015 is supported by the differential patterns of body condition changes of adults and immatures in forest from early to mid-winter (Brown and Sherry 2006). We suggest that by varying behavioural strategies, adult Swainson’s Thrush can dominate higher quality habitats such as forest during years when food availability is limited and maintain their seasonal body condition by excluding immatures from the forest when needed.

Our results from feather corticosterone analyses showed that during winter 2013 and 2014, corticosterone values were higher in forest than in coffee. Since the corticosterone values we report here reflect plasma hormone levels during the period of feather replacement, these values represent a long-term and integrated measure of baseline level, stressors, and the magnitude of stress responses by thrushes in each habitat (Bortolotti et al. 2008). Individuals with elevated baseline corticosterone levels are expected to have lower physical condition than individuals with lower corticosterone levels (Bonier et al. 2009). For instance, American Redstarts wintering in suboptimal female-biased habitats in Jamaica, lost body mass, had higher corticosterone baseline levels, and had a weaker adrenocortical response relative to individuals in optimal male-biased habitats (Marra and Holberton 1998). In individuals overwintering in suboptimal areas, elevated corticosterone values might reflect higher foraging effort needed to cope with lower food availability (Holberton and Dufty Jr 2005).

Our results across the two years showed that with the exception of immatures in 2013, birds in forest either maintained or increased their mass over the winter. Although corticosterone baseline values and the magnitude of the stress response of Swainson’s Thrush in each habitat is unknown, this suggests that feather corticosterone values recorded between habitats did not vary in response to factors such as food availability or poor energy reserves as seen in American Redstarts and other species (Marra and Holberton 1998, Jenni-Eiermann et al. 2008). Additionally, long-term chronic effects of elevated corticosterone values associated with poor resource availability include catabolism of skeletal muscles to provide an energy source, which in turn would be reflected in poor or declining condition of birds in forest relative to coffee (Wingfield and Silverin 1986, Berdanier 1989, Gray et al. 1990, Astheimer et al. 1992)**.** Within forest, corticosterone values were negatively correlated with mass at initial capture suggesting that mass of individuals with the higher corticosterone values in forest is compromised, but not to a point to reach values similar or lower than the mass of birds in coffee (Appendix 9).

Since Thrush density in the forest was twice that in coffee, birds in forest likely contended with higher competition driven by higher density. That density difference might explain elevated levels of feather corticosterone found in thrushes occupying forest. Competition among thrushes in forest might be exacerbated by the presence of resident or other Neotropical migrants with food or habitat needs similar to Swainson's Thrush such as Gray-cheeked Thrush (*Catharus minimus*) which winters exclusively in forests in our study sites. Our findings suggest that elevated values of corticosterone in higher density situations might be adaptive by increasing foraging activity, or by regulating aggressive behaviours involved in food acquisition or defence (Van Duyse et al. 2004, Landys et al. 2007, 2010).

Birds in forest might avoid potentially damaging effects of elevated corticosterone levels by minimizing the adrenocortical response and the secretion of additional corticosterone above its already elevated level. Indeed, the modulation of corticosterone secretion is a mechanism used during migration to meet energetic demands. During migration, baseline corticosterone levels are elevated in order to trigger and maintain migratory fattening (e.g., by increasing food intake Landys et al. 2004, Holberton et al. 2008), while the acute corticosterone stress response is suppressed in order to protect skeletal muscle needed for flight (Holberton et al. 1996, Long and Holberton 2004). We suggest that the cost associated with high density and elevated corticosterone levels in forest may be offset by the benefits of occupying a high-quality habitat. Our results suggest that when density is not considered, measures of habitat quality such as physical condition, age and sex ratios, and corticosterone values can lead to misleading conclusions.

Taken together, our findings suggest that native forest is a higher-quality winter habitat for Swainson's Thrush than coffee. Our analysis of density showed that forest can hold twice as many Swainson's Thrush than coffee, and in general the odds of all birds occupying forest were higher than the odds of occupying coffee. However, immatures tended to maintain higher daily and seasonal physical condition in coffee likely due to lower density and competition with adults. However, the relative quality of forest and coffee were not stable over time as daily and seasonal condition varied among years. Daily body condition was lowest during 2015 for all ages and habitats, and the odds of adults being in forest increased by over 30% suggesting that intraspecific competition increased and dominant adults preferred the best habitat. Our results provide the first evidence that the direct effects of global climatic events such as El Niño events have detrimental effects on the quality of habitat for Neotropical migrants in South America.

2.5.2. Canada Warbler

Taken together, winter habitat quality measurements suggest that for Canada Warbler, the suitability of forest and coffee changes temporally likely in response to precipitation patterns. Males maintained higher daily and seasonal mass in forest than in coffee. Our top ranked model for seasonal change in mass predicted that while males and females in forest maintained their overwinter body condition, females in coffee lost up to 0.5 g which corresponds to 6% of total body mass from early- to late-winter. Decline in body mass over the winter is a strong predictor of annual survival probability in American Redstarts (Marra and Holmes 2001, Johnson et al. 2006). For instance, Individuals overwintering in several natural and agricultural habitat suffered a 6.8% reduction in annual survival probability due to just a loss of 0.1 g over the winter(Johnson et al. 2006). Small sample size limited the ability to determine if the patterns of seasonal mass change in males and females resulted from the direct effect of habitat or from annual variation in precipitation. However, the second highest ranked model for mass change over the season included a strong effect of year, as seen in Swainson's Thrush, such that condition over most of the winter in both habitats was lower in 2015. We suggest that drought conditions induced by El Niño amplified the negative effects of seasonal drought on winter habitat quality, physical condition and potentially annual survival.

Annual patterns of winter habitat occupancy in Canada Warblers were inconclusive and varied between years. Our analysis of sex ratios showed that the difference in the probability of occurrence between males and females in forest in 2013 was not substantial, during 2014 and 2015 the proportion of males in forest increased to 96% and 87%, respectively. This suggests that forest was preferred by dominant individuals during the driest years and females were forced into lower quality shade-grown coffee plantations. In turn, lower survival or the negative effects of poor winter habitat occupancy by females can carry over to the breeding grounds and limit the number of breeding females and their reproductive success (Marra and Holmes 2001, Studds and Marra 2005, 2007).

Our results suggest that both shade-grown coffee plantations and forest are suitable winter habitats for Canada Warblers, however their suitability varies in response to precipitation patterns. Higher mass in males in forest could be related to the preference of this habitat during the driest years. In turn, this preference during driest years is likely related to microhabitat structure and food availability. Canada Warblers forage at mid-levels between 5 m and 15 m above the ground (Céspedes and Bayly in press) and are often seen along creeks where vegetation in mid-levels is denser (pers. Obs). In our study sites, there are more creeks in coffee than forest. However, during El Niño year, creeks running along the coffee plantations where completely dry, while creeks in the forest maintained some water and likely higher insects' availability which might explain higher condition of males in forest. Further studies involving microhabitat structure and food availability are needed to clarify the relationship found between habitat preference and seasonal changes in mass. Assessing winter habitat quality is a fundamental step to direct attention to regions where conservation efforts will have a greater impact on population viability, and our results suggest that conserving remaining mountain forest on the wintering grounds is critical for Neotropical migrants.

Our findings suggest that extreme climatic events such as El Niño of 2015 have negative effects on habitat quality for frugivorous and insectivorous Neotropical migrants overwintering in the Andes of northern South America. Frequency of extreme El Niño events is expected to increase linearly with global mean temperature and have long lasting effects on precipitation patterns and, in turn, on winter habitat quality for Neotropical migrants (Wang et al. 2017). Phenotypic plasticity allows individuals to cope rapidly and effectively with the effects of environmental variation such as drought or other harsh weather conditions (Martin and Wiebe 2004, Charmantier et al. 2008, Moreno and Møller 2011). However, these mechanisms may be ineffective above a threshold of unpredictable climatic extremes (Martin and Wiebe 2004, Moreno and Møller 2011). The responses of birds to extreme and unpredictable climatic events might be further challenged with the predicted increased frequency of extreme El Niño events which might disrupt the time needed for populations to recover (Moreno and Møller 2011).

Predicted increase in temperature across montane elevations is also expected to affect the distribution of key habitats for Neotropical migrants. For example, warmer climate would reduce climatic suitability for Arabica coffee at low elevations and increase suitability of higher areas; consequently, the altitudinal range suitable for Arabica coffee in the Andes is predicted to move from currently 500–1500 masl to 1000–2800 masl. The potential upward expansion of the coffee-growing areas would result in the loss of shade-grown coffee plantations at lower elevation and would increase land-use pressure on high-altitude forest (Ovalle-Rivera et al. 2015). Under this scenario, maintenance of wintering populations of Neotropical migrants at low elevations would depend on the ability of the species to follow shifting winter habitats and colonise suitable areas outside of their current ranges, or on conservation measures to mitigate the effects of global warming at lower elevations (i. e., increasing shade in coffee plantations).

Table 2.1 Candidate model set for predicting A) daily and B) seasonal body mass change in Swainson’s Thrush overwintering in Colombia from 1 December to 28 February during the winters of 2013, 2014, and 2015. C) Models looking at seasonal mass change in individuals.

Analyses	Model	K[a]	AICc	Δ*i* [b]	W*i*[c]	Cum. W*i*
A. Daily mass change	T:Year:H:Age + T2:Year:H:Age	26	4362.62	0	1	1
	T:H:Age + T2:H:Age	10	4379.81	17.19	0	1
	T:Year:H+ T2:Year:H	14	4396.30	33.69	0	1
	T	4	4419.32	56.70	0	1
	T:H	6	4422.15	59.53	0	1
	Null	2	4469.30	106.69	0	1
B. Seasonal mass change	D:Year:H:Age + D2:Year:H:Age+T	27	4374.40	0	1	1
	D:H:Age + D2:H:Age+T	11	4388.83	14.44	0	1
	D:Year:H+ D2:Year:H+T	15	4402.62	28.23	0	1
	D:H + D2:H+T	7	4419.00	44.60	0	1
	D+T	5	4419.91	45.51	0	1
	Null	2	4469.30	94.91	0	1
C. Individual seasonal mass change (Recaptures)	Null	2	374.53	0	0.39	0.39
	I+Time	4	375.26	0.73	0.27	0.66
	I:Age+Time	5	376.82	2.23	0.12	0.78
	I:Year+Time	6	377.19	2.65	0.10	0.88
	I:Habitat+Time	5	377.37	2.84	0.09	0.97
	I:Habitat:Age+Time	7	381.19	6.70	0.01	0.98

[a] Number of parameters

[b] Δ*i* (Δ*i*= AIC_{ci} – minimum AICc)

[c] Akaike weight represents support for each model

T= Capture time, H=Habitat, D=Capture day (Day 1= 1 December), I= number of days between first capture and recapture.

Table 2.2 Candidate model set for predicting A) daily and B) seasonal body mass change in Canada Warbler overwintering in Colombia from 1 December 1 to 30 March during the winters of 2013, 2014, and 2015. C) Models looking at seasonal mass change in individuals.

Analyses	Model	K[a]	AICc	Δ*i*[β]	W*i*[c]	Cum. W*i*
A. Daily mass change	Time:H:Sex	6	309.7	0	0.99	0.99
	Time	3	320.97	11.27	0	0.99
	Time:Year:H	8	321.27	11.57	0	1
	Time:H	4	322.95	13.25	0	1
	Time:H:Age	6	324.32	14.62	0	1
	Null	2	339.23	29.53	0	1
B. Seasonal mass change	D:H:Sex+ D^2:H:Sex+Time	11	310.53	0	0.53	0.53
	D:H:Year+ D^2:H:Year+Time	15	311.6	1.07	0.31	0.83
	D+ D^2+ Time	5	313.2	2.67	0.14	0.97
	D:H+ D^2:H+Time	7	316.59	6.06	0.03	1
	D:H:Age+D^2:H:Age+Time	11	321.82	11.29	0	1
	Null	2	339.23	28.7	0	1
C. Individual seasonal mass change (Recaptures)	I:Year+Time	6	55.5	0	0.69	0.69
	I+Time	4	59.02	3.5	0.12	0.81
	I:Age+Time	5	60.64	5.1	0.05	0.86
	I:Sex+Time	5	60.76	5.3	0.05	0.91
	I:Habitat+Time	5	61.31	5.8	0.04	0.95
	I:Habitat:Sex+Time	7	61.74	6.2	0.03	0.98
	I:Habitat:Age+Time	7	62.53	7	0.02	1
	Null	2	87.22	31.7	0	1

[a] Number of parameters

[b] Δ*i* (Δ*i*= AIC$_{ci}$ – minimum AICc)

[c] Akaike weight represents support for each model

H=Habitat, D= Capture day (Day 1= 1 December), I= number of days between first capture and recapture.

Table 2.3 Odds of being in forest and 95% confidence intervals (CI) obtained from coefficients of models that received the greatest support explaining winter habitat occupancy in A) Swainson's Thrush and B) Canada Warbler.

Species	Model	Variable	Odds	95%CI	Odd ratios	odd ratios	% change*
A. Swainson's Thrush	Year	2013	2.5	1.9 to 3.3	2015/2013	0.56	-44
		2014	1.8	1.5 to 2.2	2015/2014	0.78	-22
		2015	1.4	1.2 to 1.7			
	Year:Age	2013:Ad	1.9	1.2 to 3.2			
		2014:Ad	1.7	1.2 to 2.3	Ad 2015/2013	0.89	-11
		2015:Ad	1.7	1.2 to 2.3	Ad 2015/2014	1	0
		2013:Imm	2.8	2.0 to 3.9	2013 Ad/Imm	0.68	-32
		2014:Imm	1.9	1.5 to 2.5	2014 Ad/Imm	0.89	-11
		2015:Imm	1.3	1.1 to 1.7	2015 Ad/Imm	1.31	31
B. Canada Warbler	Year	2013	0.7	0.4 to 1.2	2015/2013	1.14	14
		2014	0.3	0.2 to 0.5	2015/2014	2.67	167
		2015	0.8	0.6 to 1.3			
	Year:Sex	2013: ♀	0.7	0.4 to 1.5	2013 ♂/♀	0.93	-7
		2014: ♀	0.2	0.1 to 0.4	2014 ♂/♀	1.96	96
		2015: ♀	0.6	0.3 to 1.1	2015 ♂/♀	1.87	87
		2013: ♂	0.7	0.3 to 1.4	♀2015/2013	0.82	-18
		2014:Im	0.4	0.2 to 0.7	♀2015/2014	3.14	214
		2015:Im	1.1	0.6 to 2.0	♂ 2015/2013	1.66	66
					♂ 2015/2014	3	200

*% change= increase or decrease of birds in forest.

Table 2.4 A) Models considered for the detection function of Swainson's Thrush in shade-grown coffee plantations and forest in the Colombian Andes. B) Goodness of the fit statistics for models fitted to the detection data of Swainson's Thrush.

A. Model	K[a]	AICc	Δi^{β}	W*i* [c]
Uniform+cosine	2	5396.03	0	0.93
Hazard-rate+simple polynomial	4	5398.1	2.07	0.05
Hazard-rate+cosine	4	5398.1	2.07	0.01
Half-normal+cosine	4	5399.74	3.71	0.01
Uniform+simple polynomial	5	5400	3.97	0
Half-normal+hermit polinomial	2	5401.15	5.11	0
B. Model	Habitat	X^2	df	p
Uniform+cosine	Coffee	0.82	3	0.84
	Forest	2.2	3	0.53
Hazard-rate+simple polynomial	Coffee	0.6	2	0.74
	Forest	0.52	2	0.77
Hazard-rate+cosine	Coffee	0.6	2	0.74
	Forest	0.52	2	0.77
Half-normal+cosine	Coffee	0.53	2	0.77
	Forest	2.17	2	0.34
Uniform+simple polynomial	Coffee	0.96	2	0.62
	Forest	0.05	1	0.82
Half-normal+hermit polinomial	Coffee	3.28	3	0.35
	Forest	4.86	3	0.18

[a] Number of parameters

[b] Δi (Δi= AIC_{ci} – minimum AICc)

[c] Akaike weight represents support for each model

Table 2.5 Results of model selection examining the effect of winter habitat (shade-grown coffee plantations and forest), age (immature and adult) and year (2013, 2014, 2015) on corticosterone values of Swainson's Thrush overwintering in the Eastern Andes of Colombia.

Model	K[a]	AICc	Δi^{β}	W*i* [c]	Cum. W*i*
Habitat:Year	5	388.72	0	0.93	0.93
Year	3	394.5	5.78	0.05	0.98
Habitat	3	397.73	9.01	0.01	0.99
Year:Age	5	398.36	9.64	0.01	1
Habitat:Age	5	400.99	12.27	0	1
Null	2	404.21	15.49	0	1
Age	3	405.08	16.36	0	1

[a] Number of parameters

[b] Δi (Δi= AIC_{ci} – minimum AICc)

[c] Akaike weight represents support for each model

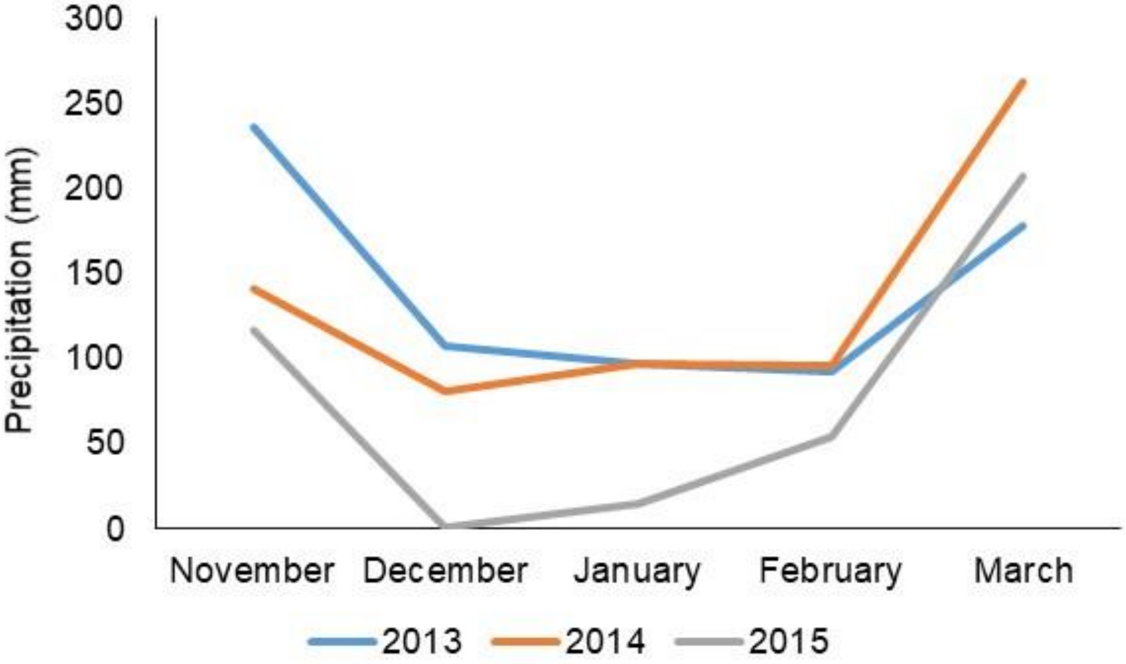

Figure 2.1 Precipitation (mm) patterns in the study sites from November to March in 2013, 2014 and 2015. Data were obtained from a meteorological station located in the municipality of Tibacuy at 1538 m asl (04°22’N 74°26’W) and operated by “Federación Nacional de Cafeteros de Colombia” (Cenicafé 2016a, b, c, 2017)

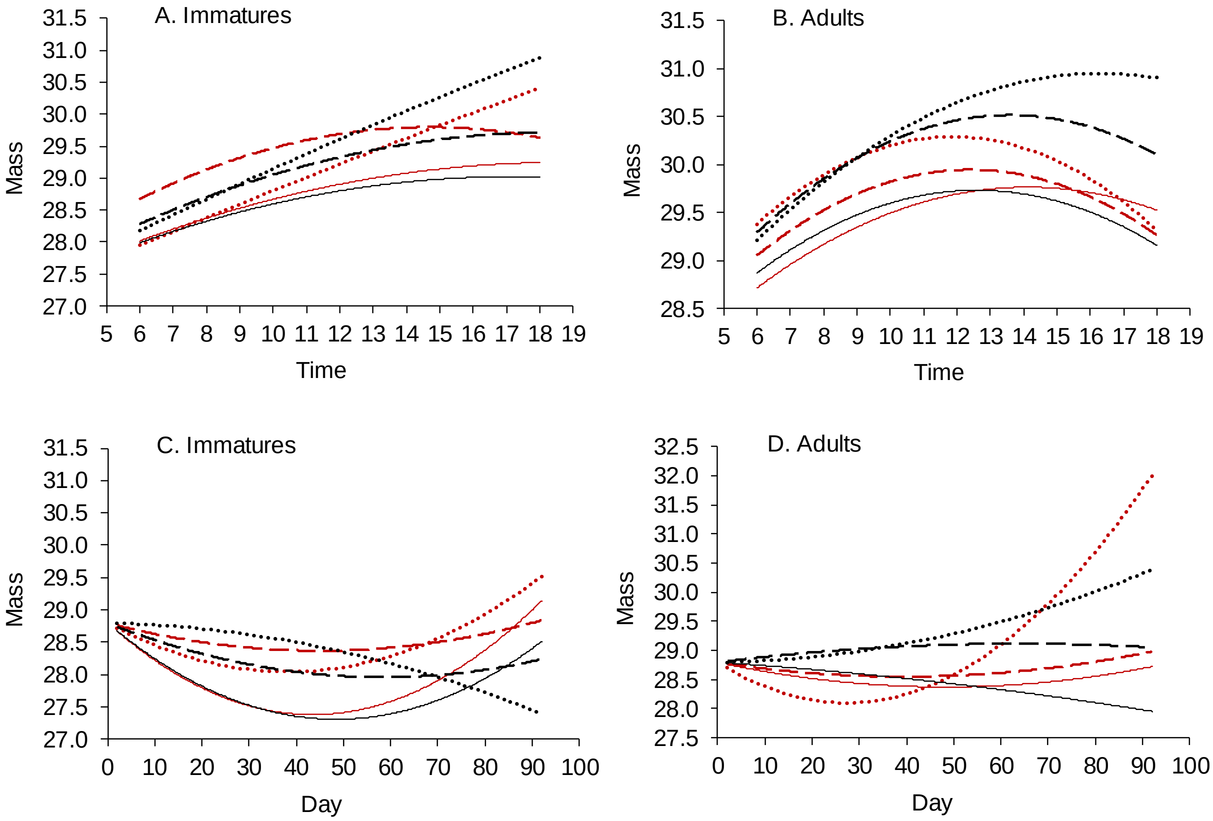

Figure 2.2 Daily and seasonal body mass (g) change in immature and adult Swainson's Thrush captured in shade-grown coffee plantations (red) and forest (black) in the Colombian Andes during 2013 (dotted line), 2014 (dashed line) and 2015 (solid line). Lines are the predicted trajectory of the top ranked model Time:Year:Habitat:Age + Time^2:Year:Habitat:Age for daily changes in mass (Table 2.1 A), and the model Day:Year:Habitat:Age + Day^2:Year:Habitat:Age+Time for seasonal mass change (Table 2.1 B). Model coefficients are presented in Appendix 6.

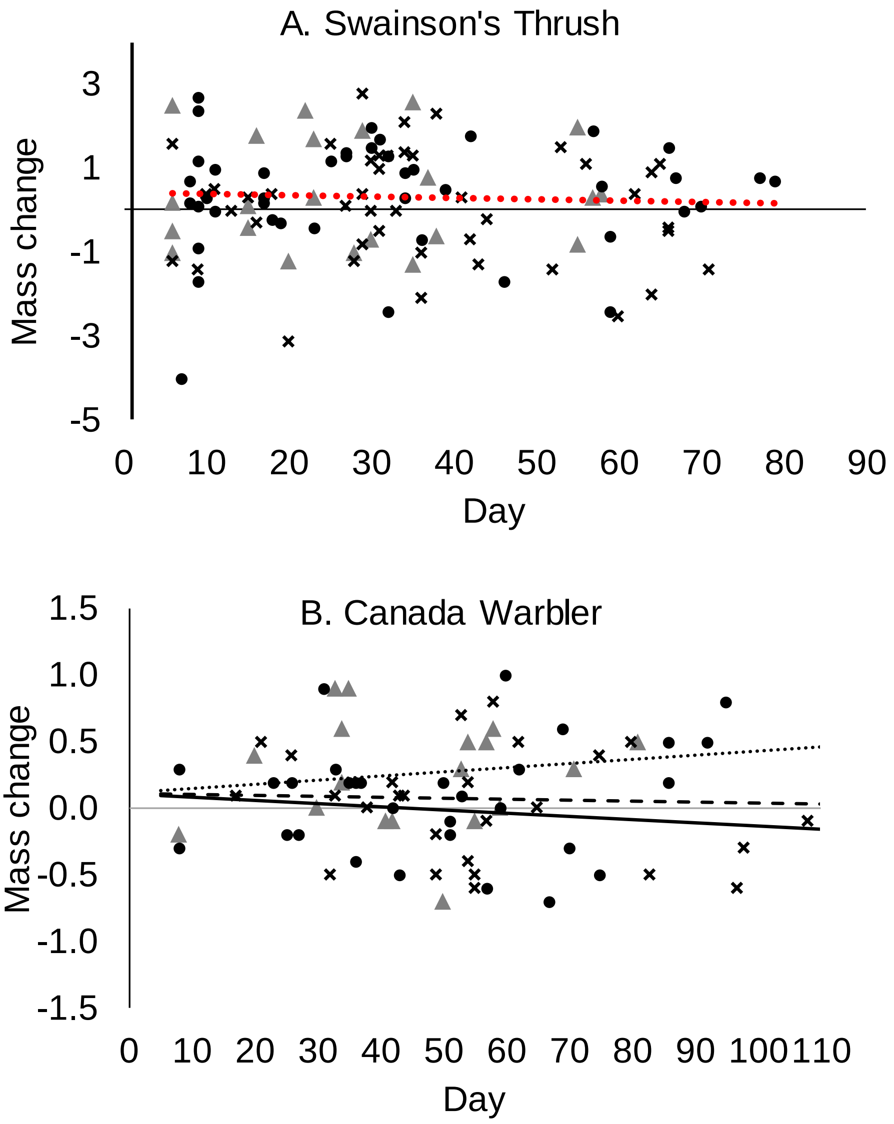

Figure 2.3 Body-mass changes in overwintering A) Swainson's Thrush and B) Canada Warbler captured on more than one occasion in relation to the number of days since first capture in the Eastern Andes of Colombia in 2013 (triangles), 2014 (crosses) and 2015 (dots). Swainson's Thrush: The line is the predicted trajectory of mass gain from the model: body-mass change = (0.37) + (-0.003*I) + 0.05 where "I" is the number of days since first capture. Coefficient estimates were derived from the model body-mass change ~I+Time (Table 2.1 C). Canada Warbler: Lines are the predicted trajectory of mass gain from the following model: 2013 body-mass change = (0.1) + (0.003*I) + 0.1 (dotted line), 2014 body-mass change = (0.1) + (-0.003*I)+0.1 (dashed line), and 2015 body-mass change = (0.1) + (-0.001*I)+0.1 (solid line). Coefficient estimates were derived from the model body-mass change~I:Year+Time (Table 2.2 C).

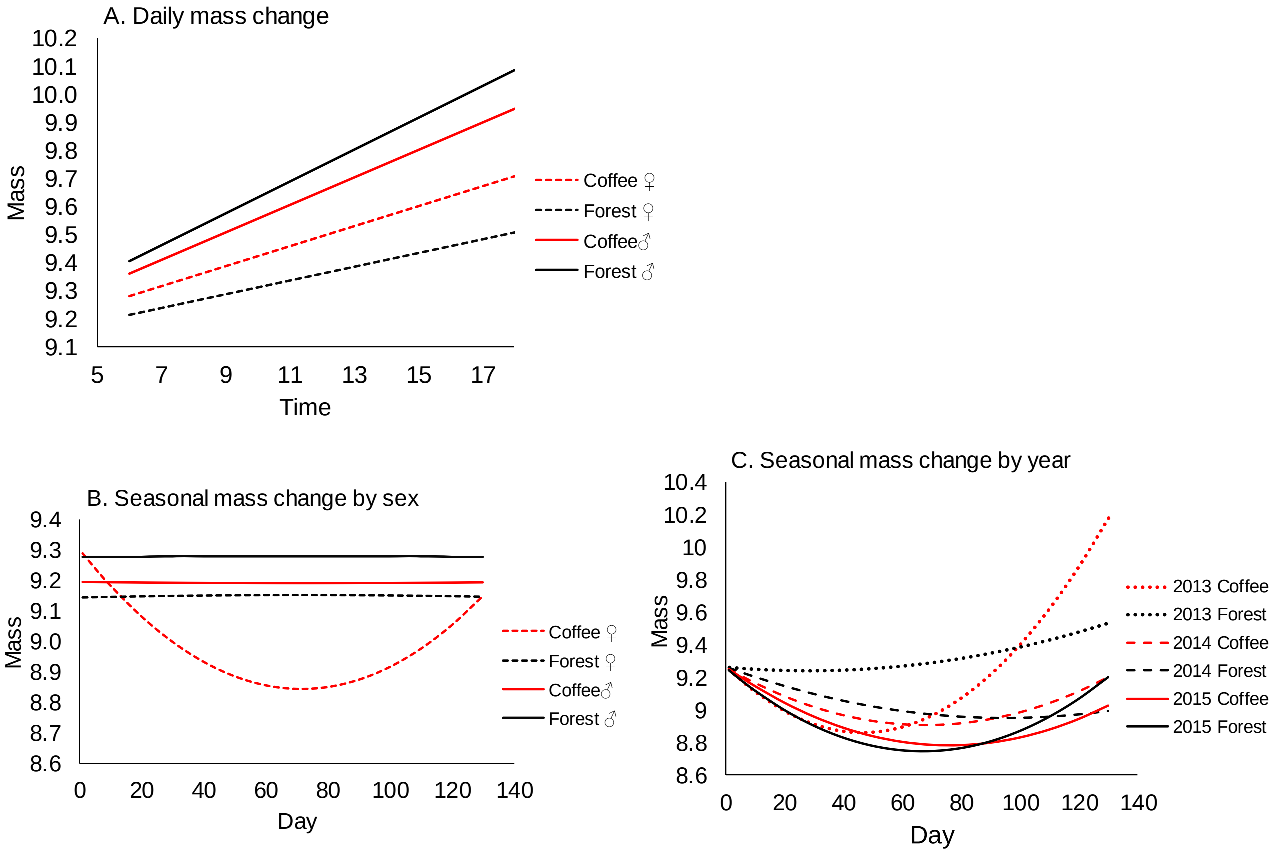

Figure 2.4 Daily and seasonal body mass change in Canada Warbler captured in shade-grown coffee plantations (red) and forest (black) in the Colombian Andes during 2013 (dotted line), 2014 (dashed line) and 2015 (solid line). A) Lines are the predicted trajectory of the top ranked model Time:Habitat:Sex for daily changes in mass (Table 2.2 A), B) and C) are the predicted trajectories of the two highest ranked models explaining seasonal mass change Day:Habitat:Sex+ Day^2:Habitat:Sex+Time, and Day:Habitat:Year+ Day^2:Habitat:Year+Time (Table 2.2 B). Model coefficients are presented in Appendix 7.

CHAPTER 3. EFFECT OF WINTER HABITAT ON SPRING DEPARTURE AND MIGRATION SPEED IN SWAINSON'S THRUSH: WHY LEAVE EARLY WHEN YOU CAN STAY LONGER AND CATCH UP?

3.1. Abstract

Selection for early arrival to the breeding grounds has implications for departure time from wintering sites and speed of migration in long-distance Neotropical migrants. Assessing these factors has been limited by an inability to track migratory birds directly from their wintering grounds to stopovers or breeding destinations. We used an automated radio tracking system (MOTUS) on a continental scale to determine the effect of winter habitat (shade coffee vs. forest) use by Swainson's Thrush (*Catharus ustulatus*) on spring departure date from the Andean mountains of South America and total speed of spring migration. We found a strong effect of habitat and Thrush age on departure date (n= 121). Adult birds in forest departed six days later than adults in coffee and immatures in forest departed three days later than immatures in coffee. When controlling for departure date, birds wintering in forest migrated in spring faster than birds wintering in coffee and the pattern was maintained along the migration path (n=40). Since migration speed is correlated with fuel load, birds wintering in forest likely reached higher fuel loads than birds wintering in shade-grown coffee before migration. Birds overwintering in forest departed later and migrated faster and so can compensate for a late departure while decreasing the risks associated with migration. Such facultative adjustment to winter conditions reveals previously unappreciated complexity in migratory decisions by long-distance migrants.

3.2. Introduction

Selection for fast and timely spring migration derives from fitness benefits conferred by early arrival to the breeding grounds (Alerstam 2011, Nilsson et al. 2013). Rapid migration also minimizes the costs and risks associated with migration itself, and can lead to arriving ahead of other individuals, which in turn allows more time to be allocated to other activities like breeding or moult (Newton 2008). The total duration of migration depends on the migratory route and on the total speed of migration. In turn, total speed of migration depends on stopover behaviour, time allocated to migratory flights and to a lesser degree, on travel speed. Birds can increase their total speed of migration by decreasing the length or number of stopovers, or by flying for more hours during each migratory flight (Nilsson et al. 2013). Migration timing is under endogenous control (Gwinner 1996); however, phenotypic responses in timing can arise from environmental conditions experienced on the wintering grounds (Cotton 2003, Saino et al. 2004, Studds and Marra 2011), en route (Ahola et al. 2004, Marra et al. 2005, Tottrup et al. 2010, González-Prieto and Hobson 2013), or at the breeding sites (Both et al. 2005, Mazerolle et al. 2005). For instance, winter habitat occupancy can affect spring departure dates and carry over to subsequent seasons thereby producing residual effects on fitness of individuals and populations (Marra et al. 1998, Norris 2005, Newton 2006). Declining overwinter body mass (Strong and Sherry 2000), later departure during spring migration (Marra et al. 1998), later arrival on the breeding grounds (Marra et al. 1998, Studds and Marra 2005), and lower reproductive success (Norris et al. 2004) have all been related to occupancy of poor winter habitats. Understanding the direct effects of winter habitat on departure decisions and its cascading effects on spring migration pace and arrival to the breeding grounds is important to understand the factors regulating migration and limiting populations throughout the annual cycle.

Most indirect evidence supporting the critical role of winter habitat on spring migration departure dates and subsequent effect on fitness comes from insectivorous songbirds overwintering on Caribbean islands, where the availability of high quality habitats varies spatially and temporally (Sillett et al. 2000, Studds and Marra 2007, Smith et al. 2010, Studds and Marra 2011). Less is known about the effect of winter habitat for birds overwintering on continents or in human modified landscapes such as shade-grown coffee agroecosystems, which are the predominant land cover in much of the region occupied by Neotropical migrants during the winter (Díaz-Bohórquez et al. 2014). Neotropical migrants overwintering in shade-grown coffee plantations in South America increase their body condition during early, mid (Bakermans et al. 2009), and late winter (Colorado and Rodewald 2017), in contrast to patterns recorded in the Caribbean. However, whether increasing condition in coffee is optimal relative to forest, or whether it has any subsequent effect on the onset of migration or later in the annual cycle is unknown.

Information about winter habitat occupancy of birds captured during migration (González-Prieto and Hobson 2013, Paxton and Moore 2015) or on the breeding grounds (Norris et al. 2004, 2005) has been inferred from stable carbon ($\delta^{13}C$) isotope measurements of winter grown tissues. Assessing the direct relationship between the occupancy of suitable winter habitats, early departure from the wintering grounds, and early arrival to the breeding grounds has been limited by the difficulty of tracking migratory birds directly from their wintering grounds to spring stopovers or breeding destinations. Tracking studies using light-level geolocators deployed in North America have shown that earlier departure from the wintering grounds in South America is correlated with earlier arrival to the breeding grounds (Jahn et al. 2013), and that this "early" schedule is maintained throughout the full annual cycle (Callo et al. 2013). However small sample sizes and the lack of spatial resolution of geolocators have precluded an assessment of whether earlier departures from wintering sites are linked to winter habitat occupancy or other factors.

We used an automated radio tracking system on a continental scale to determine the effect of winter habitat on spring migration departure date, migration pace and arrival date within the breeding range of a Nearctic-Neotropical migratory landbird, Swainson's Thrush (*Catharus ustulatus*). Swainson's Thrush are morphologically and genetically separated into coastal (western subspecies, *C. ustulatus* and *C. oedicus*) and inland (eastern subspecies *C. u. alame* and *C. u. swainsoni*) groups. Each group appears to maintain their ancestral migration routes (Ruegg and Smith 2002), following different migratory pathways and overwintering in different locations (Ruegg and Smith 2002, Delmore et al. 2012, Cormier et al. 2013). Birds overwintering in South America migrate throughout central North America and belong to the inland group. In our study sites, this species occupies both shade-grown coffee and forest during the winter.

We hypothesized that earlier spring migration and earlier arrival dates to the breeding range would occur in birds overwintering in the most suitable habitats, as was previously shown for birds overwintering in the Caribbean. The effect of winter habitat occupancy on spring migration pace has not previously been addressed. We predicted that by departing earlier, birds from more suitable native forests would reach the breeding range earlier, while maintaining the same migration pace as birds leaving later from shade-coffee plantations.

3.3. Methods

3.3.1. Study sites

We captured Swainson's Thrush between 10 January and 15 March in 2015, 2016 and 2017 in two study sites located on the western slope of the Colombian Eastern Andes: Hacienda La Fragua

(04°18’54.18”N, 74°32’19.29”W) at 1,500 m, and Los Vientos (04°21’56.23”N, 74°31’2.31”W) at 1,350 m. Sites were operated simultaneously, in each site we had one banding station in a shade-coffee plantation and one in secondary forest. Birds were fitted with radio tags only in La Fragua during 2015 and 2016, and in both sites in 2017. Birds were captured during eight days a month in each habitat from 06:00 to 11:00 h and from 15:00 to 17:30 h using mist nets (36 mm mesh) and by alternating four days in shade-grown coffee and four days in forest. Birds were fitted with a numbered US Fish and Wildlife Service aluminium band, processed, and released at the capture site. Individuals were aged as after second year (hereafter adult) and second year (hereafter immature) according to Pyle (1997), and we recorded wing chord (±1 mm) and body mass (±0.1 g, using an electronic balance) prior to release.

3.3.2. Tag deployment

To track spring departure dates and continental movements we fitted 185 Swainson’s Thrush (29 in 2015, 64 in 2016, and 92 in 2017) with digitally-coded radio transmitters using leg-loop harnesses made of elastic thread (Rappole and Tipton 1991, Naef-Daenzer 2007). We used three transmitter types from Lotek (Lotek Wireless, Newmarket, ON, Canada); NTWB-2 (0.35 g), NTQB-3-2 (0.67 g) and NTWB-4-2 (1 g). The total weight of transmitter and harness was always less than 5% of the body weight of wintering birds (mean weight 30 g ±2.1 g, range 24.8 to 39.2 g).

3.3.3. Departure from wintering site.

We determined spring departure dates (hereafter departure date) from our study sites by using telemetry data from an automated telemetry station consisting of one tower with three nine-element Yagi antennas (~15 km detection range) connected to a SensorGnome receiver. The location of the station allowed birds in forest and shade-coffee plantations to be detected simultaneously. We visually inspected the changes in signal strength over time for each tag and considered departure dates reliable when the maximum signal strength of the last set of detections followed a characteristic curve for a migratory departure (Mills et al. 2011). During distinctive departure flights the receivers detected a rapid increase in signal strength from a lower baseline or no signal to a high level, followed by a decline. We assessed the effect of habitat on departure date by running an analysis that included a full dataset of all birds tagged that had reliable departure dates (2015 n=28, 2016 n=44, 2017 n=49).

3.3.4. International radio telemetry

Radio-tagged individuals were tracked at the continental scale using the Motus Wildlife Tracking System (hereafter "Motus", Taylor et al. 2017), an international collaborative network consisting of over 300 coordinated automated radio-telemetry arrays tuned to a specific frequency (166.380 MHz) throughout the Americas. All international detections of radio-tagged Swainson's Thrush linked to the Motus frequency were filtered to exclude false signals distinguishable by less than three consecutive signal bursts (Sjöberg et al. 2015). For each Motus array where birds were detected we obtained geographic coordinates and used the time of the first signal as arrival date.

3.3.5. Statistical analyses

3.3.5.1. Departure dates and migration pace

We modelled departure dates using General Linear Models (GLM). Model selection was carried out using Akaike's information criterion adjusted for small sample size AICc (Burnham and Anderson 2002). Models with ΔAICc < 2 were considered equally plausible. The candidate model set for the analysis included Habitat, Age, Year, and the interaction of Habitat:Age, Habitat:Year, and Year:Age (Table 3.1). Models were selected using package "AICcmodavg" in R (Mazerolle 2017).

We used the number of days elapsed between international detections and departure from our study sites as our measure of migration pace (Gómez et al. 2017). International detections were clustered within four areas and therefore were grouped into the following four main regions according to latitude: South (8.4° to 9.4°), Gulf Coast (27.2° to 30.4°), Great Lakes (41.5° to 45.0°), and North (48.5° to 50.4°).

3.3.5.2. Effect of spring departure date and winter habitat on spring migration pace.

We assessed the effect of departure date and winter habitat on migration pace in two stages. First, we ran linear mixed-effects models to evaluate the effect of departure date and region on the pace of spring migration (Table 3.2). We included individual (ID) as a random effect to account for birds with more than one international detection. In a separate analysis we assessed the effect of habitat, habitat and the interaction with departure date, age, and the additive effect of habitat and age on migration pace. We accounted for birds with more than one detection and the significant variation in migration pace between regions by including individual (ID) and region as random effects (Table 3.3). Model assumptions were assessed using residual diagnostic plots (Pinheiro and Bates 2000); all analyses were performed using the used R package “nlme” (Pinheiro et al. 2018).

3.3.5.3. Effect of spring departure date and migration pace on arrival date within known breeding range.

We included only individuals detected within the known breeding range of Swainson’s Thrush (n=12). We ran two simple linear models to assess whether departure date or migration pace had an effect on arrival to the breeding range. All analyses were performed in the statistical software program R, v. 3.3.3 (R Development Core Team 2017).

3.4. Results

3.4.1. Departure from winter grounds during spring migration

Swainson’s Thrush departed the wintering grounds between 1 April and 6 May in spring 2015 (n=28), between 31 March and 4 May in spring 2016 (n=44), and between 23 March and 6 May in 2017 (n=49). The peak of migration was 13 April ±8 days in spring 2016, and 18 April ±11 days in spring 2017. Of the 185 birds radio-tagged during the three years, 22% (40 birds) were detected during their northward spring migration (2015 n=3, 2016 n=12, 2017 n=25, Figure 3.1). Seven additional birds were detected during 2017 but were not included in the analysis because their departure date from the wintering grounds could not be reliably determined.

3.4.2. Effect of winter habitat on spring departure dates.

The best model explaining spring departure date included the interaction between habitat and age and received 86% support (Table 3.1). Estimates derived from this model suggested that adult birds in forest departed six days later than adults in coffee (adults forest 50±1.6 d, 95% CI 47.0, 53.2 d, adult coffee 44±1.4 d 95% CI 41.5, 47.0 d, Figure 3.2), and immatures in forest departed three days later than immatures in coffee (immature forest 49±1.5 d 95% CI 46.3, 52.2 d, immature coffee 46±1.7 d 95% CI 42.4, 49.2 d).

3.4.3. Effect of spring departure date and habitat on migration pace.

We found strong support for an effect of spring departure date and its interaction with region on spring migration speed (Table 3.2). The speed of migration was different between regions which is attributable to the distance of each region from the winter sites (i.e., birds arrived faster to Panama than to the Great Lakes Region) and likely the location of stopover regions. The negative relationship between spring departure date and migration speed was maintained within each region, suggesting that birds that departed later from their wintering grounds migrated faster (Figure 3.3).

Models included in the second stage of the analysis (Table 3.3) were selected based on the result that birds from forest departed later and that birds that departed later migrated faster. The highest ranked model included habitat and the interaction with departure date (Table 3.3). However, when birds from forest and coffee departed on the same day differences in migration pace between the two habitats were not substantial (Forest:Departure -0.45 d ±0.1 95% CI -0.6,-0.3 d; Coffee:Departure -0.49 d ±0.1 95% CI -0.7,-0.3 d).

3.4.4. Effect of winter departure date and migration pace on arrival date within the breeding range.

Birds departing earlier from their wintering grounds and migrating faster tended to arrive earlier to the breeding range; however, this effect was not significant (β Departure = 0.11, $P > 0.05$; β Pace = 0.13, $P > 0.05$; Figure 3.4).

3.5. Discussion

Our finding that birds overwintering in forest departed later, and that later birds migrated faster challenges the conventional wisdom about the benefits of earlier winter departure. Migrating late and at higher pace could have potential advantages in the annual cycle of long-distance migrants. For instance, birds overwintering in forest might reduce the thermoregulation cost of arriving too early to North America and reduce total energy expenditure of migration by making longer flights and fewer or shorter stopovers (Wikelski et al. 2003). Departing later and spending less time migrating and at stopovers may also reduce mortality risk by reducing exposure to stochastic events, predation (Dierschke 2003), parasites and pathogens (Gill et al. 2009). We showed that birds wintering in forest compensate for late departure by migrating faster, potentially enabling them to catch up to those earlier departing birds from coffee.

The negative relationship we found between departure date and spring migration speed has been described in other long-distance migrants leaving from stopover sites during spring (Duijns et al. 2017, Gómez et al. 2017) and fall migration (Deppe et al. 2015). Late departure from stopover sites and fast migration are associated with high fuel loads at departure (Deppe et al. 2015, Duijns et al. 2017, Gomez et al. 2017). We suggest that the same might apply to birds departing later from their wintering grounds. Birds overwintering in forest might have stayed longer than birds in coffee and deposited larger fuel reserves allowing them to increase the total speed of migration by having fewer or shorter stopovers (Duijns et al. 2017), or by making longer and more direct flights to their breeding destination (Gomez et al. 2017). Birds departing later from the wintering grounds could also have increased their total migration speed by selecting favourable winds at departure and en route thereby increasing fly speed (Erni et al. 2002, Dossman et al. 2016) or by flying for longer, extending normally nocturnal flights into the day. Indeed, recent studies show that late birds can increase their spring migration pace by selecting more optimal wind patterns relative to earlier migrants (Deppe et al. 2015, Duijns et al. 2017).

Although we did not evaluate differences in food availability or pre-migratory rates of fuel deposition in forest vs. shade-grown coffee, migration speed is typically correlated with fuel deposition rate (Houston 2000, Gómez et al. 2017). This suggests that birds in forest likely reached higher fuel loads than birds in shade-grown coffee before migration. Birds in forest could have achieved higher fuel loads by staying longer. Alternatively, forest may have offered exceptionally high fuelling rates in combination with low predation risk, which in turn may have allowed for more efficient and intensive foraging (Bayly et al. 2016). We suspect it may be an important strategy for birds in high-quality winter habitat such as forest to spend more time in such sites they know well and reduce the risk of uncertainty while investing less time in fuelling, reaching migratory condition faster, and maximizing migration speed. The effect of winter habitat quality on migratory strategy and its energy contribution to spring migration has been largely unappreciated. We suggest that Andean forests are high quality habitats allowing birds to achieve higher departure fuels while decreasing the risks incurred during migration. The effect of age on departure date, with adult birds departing six days later than immature birds in forest, supports this hypothesis since the success of this strategy might depend on the experience of birds finding the resources, and knowledge and experience navigating the migratory route, locating critical stopover sites, and selecting optimal wind conditions (Newton 2008).

Departing earlier or migrating faster did not result in a significantly earlier arrival to the breeding range. The ultimate breeding destination, arrival date, and breeding success of the 12 birds detected in the breeding range is unknown, which prevents us from making inferences about whether leaving later and migrating faster has more fitness benefits than leaving earlier and migrating slower. Besides the total speed of migration, the duration of migration and consequent arrival to the breeding grounds also depends on the migration route and the breeding destination (Nilsson et al. 2013). It follows, that besides leaving earlier or migrating faster, taking a migration route through Central America or over the Caribbean to North America can determine the total duration of migration and arrival patterns at the ultimate breeding grounds. The same may apply to birds taking the central versus eastern flyway in North America. For instance, in birds detected in Saskatchewan during the last two weeks of May, which migrated the same distance from the wintering grounds and likely followed the same migratory route, early arrival was related to later departure from the wintering sites and faster migration pace. However, birds detected in Saskatchewan departed earlier from the winter grounds and on average migrated 1197 km longer than birds detected in eastern North America suggesting that early departure is likely to be related to the total length of migration.

The Motus international telemetry array also revealed information about the spring migration routes of Swainson's Thrush overwintering in the Colombian Andes. Detections along the border between Colombia and Panama and subsequent detections on the Gulf Coast suggest a migratory route through Central America, followed by a trans-Gulf crossing, perhaps leaving from the Yucatan Peninsula. Birds spent on average 3±3 days to reach Panama (n=12) and 23±7 days to reach the northern coast of the Gulf of Mexico (n=18), which suggests that birds undertook additional stopovers after entering Central America and before crossing the Gulf of Mexico. These results are supported by detections of the same individuals in Panama and in the Gulf coast (n=5) who spent 20±5 days in Central America before making landfall on the Gulf Coast. The broad longitudinal spread of the detections on the breeding range suggests that individuals are also taking different migration routes in North America and have widely separated final destinations (>2500 km). Birds in the northern region (latitude >48°) were detected in Quebec (n=2) and Saskatchewan (n=4), Canada. Both birds detected in Quebec were also detected on the Gulf Coast and likely took the east flyway to Quebec, while birds in Saskatchewan migrated 1000 km farther and were not detected earlier in the spring.

The importance of winter habitat quality on migratory strategies and its energy contribution to migration has been largely unappreciated. Our results provide compelling evidence that by occupying native forest remnants in the Andes of South America Swainson's Thrush can adjust migratory decisions. It follows that besides providing winter habitat, occupying native forest can significantly influence spring migratory strategies by reducing the cost and risks associated with a longer migration.

3.6. Acknowledgments

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Table 3.1 Results of linear models in order to assess the effect of winter habitat occupancy on spring migration departure dates of Swainson’s Thrush overwintering in shade-grown coffee plantations and forest in the Eastern Andes of Colombia.

Model	K[a]	AICc	Δi^{β}	W*i* [c]	Cum. W*i*
Habitat:Age	5	872.9	0	0.86	0.86
Habitat	3	877.71	4.8	0.08	0.94
Age	3	878.72	5.82	0.05	0.99
Habitat:Year	7	882.43	9.53	0	1
Year:Age	7	883.1	10.2	0	1
Null	2	886.24	13.33	0	1
Year	4	888.62	13.34	0	1

[a] Number of parameters
[b] Δi (Δi= AIC_{ci} – minimum AICc)
[c] Akaike weight represents support for each model

Table 3.2 Results from Linear Mixed-effects Models used to assess the effect of winter departure date on the pace of spring migration of Swainson's Thrush overwintering in the Eastern Andes of Colombia. ID= Individual.

Model	K[a]	AICc	Δ*ι*[β]	W*i*[c]	Cum. W*i*
Pace~Departure*Region +(1|ID)	10	370.03	0	1	1
Pace~Departure+Region+(1|ID)	7	382.28	12.26	0	1
Pace~Region+(1|ID)	6	392.6	22.57	0	1
Pace~Departure*Age +(1|ID)	6	501.6	131.58	0	1
Pace~Departure +(1|ID)	4	512.31	142.29	0	1

[a] Number of parameters

[b] Δ*i* (Δ*i*= AIC_{ci} – minimum AICc)

[c] Akaike weight represents support for each model

Table 3.3 Results of Linear Mixed-effects models used to assess the effect of winter habitat on the pace of spring migration of Swainson’s Thrush overwintering in shade-grown coffee plantations and forest in the Eastern Andes of Colombia. ID= Individual.

Model	K[a]	AICc	Δi^{β}	Wi^{c}	Cum. Wi
Pace~ Habitat:Departure+(ID | Region)	7	418.73	0	0.98	0.98
Pace~ Age+(ID | Region)	6	427.55	8.81	0.01	1
Pace~Habitat+Age+(1|ID)	7	430.08	11.35	0	1
Pace~Habitat +(1|ID)	6	441.66	22.92	0	1

[a] Number of parameters
[b] Δi (Δi= AIC$_{ci}$ – minimum AICc)
[c] Akaike weight represents support for each model

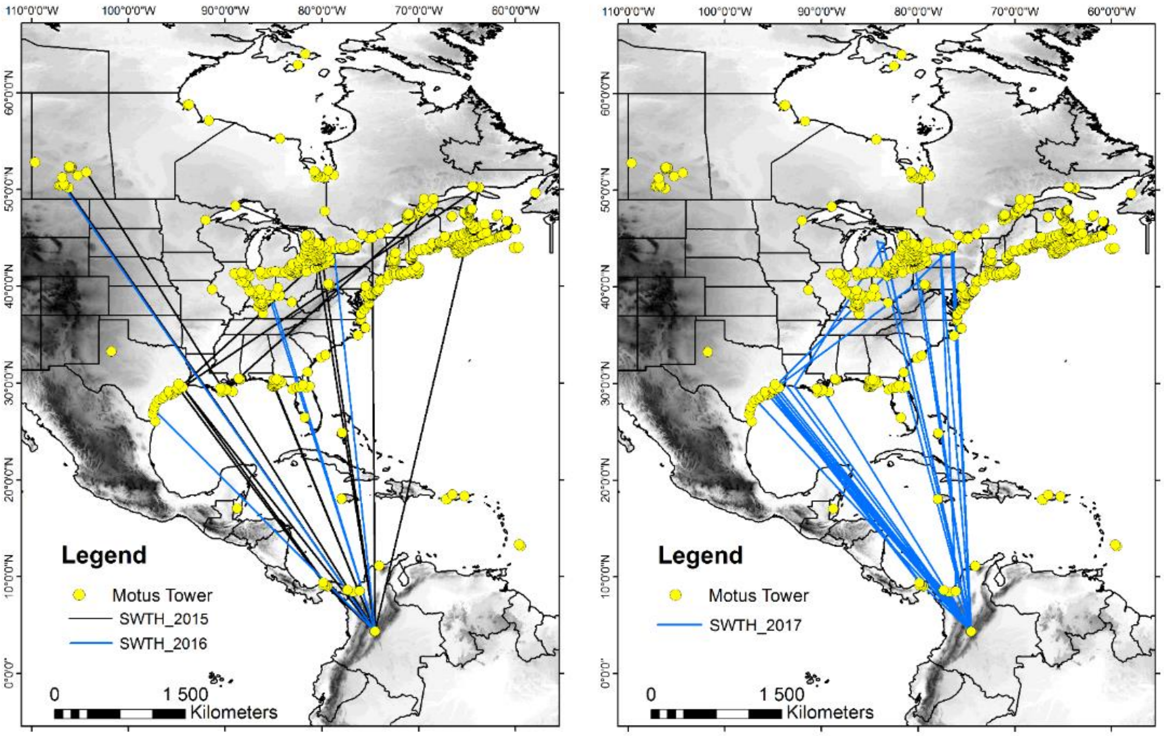

Figure 3.1 Trajectories of forty radio tagged Swainson's Thrush from the wintering grounds in the western slope of the Eastern Andes of Colombia and detected at continental scales using the Motus Wildlife Tracking System (yellow dots, https://motus.org). Lines indicate shortest distance between detections and are not migration routes.

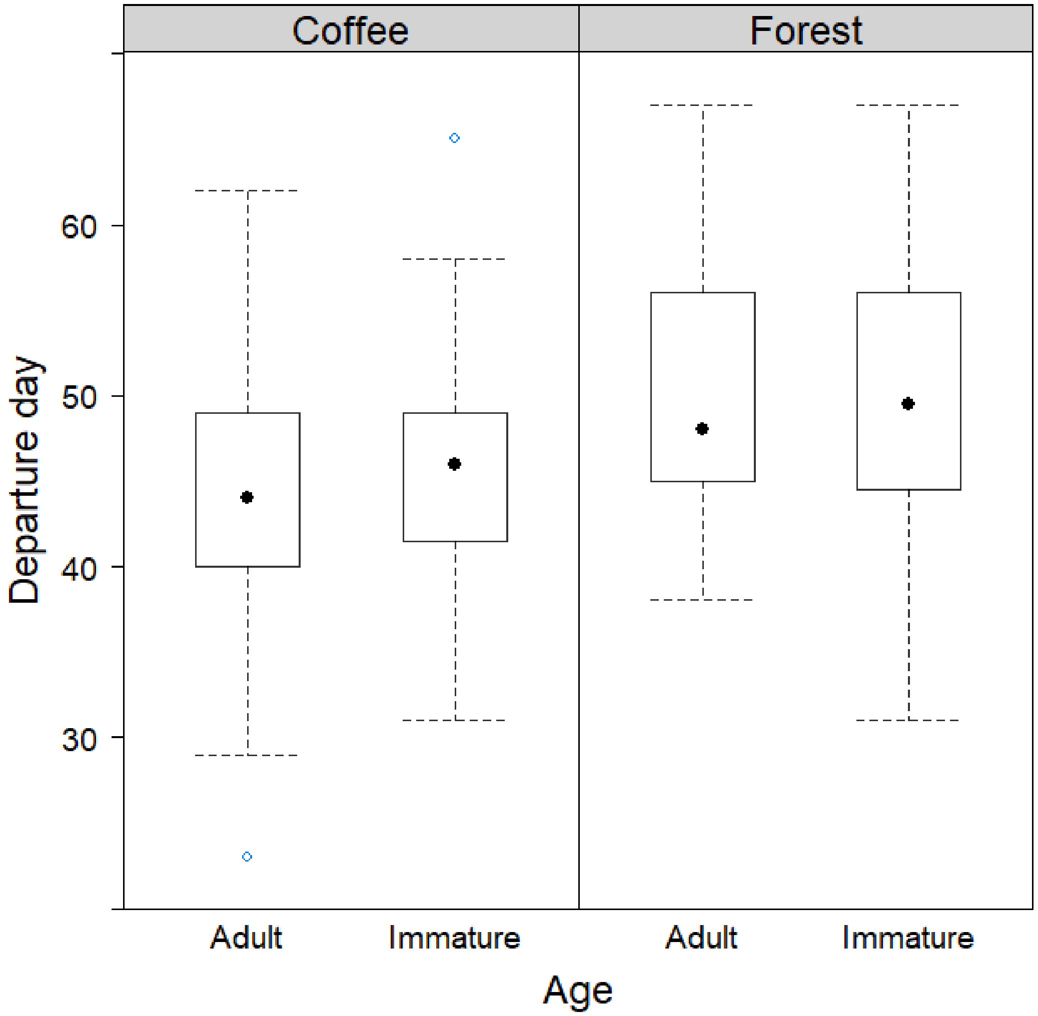

Figure 3.2 Median spring departure date of adult and immature Swainson's Thrush overwintering in shade-grown coffee plantations and forest in the Colombian Andean mountains. Day 1= 1 March. Data from spring departures in 2015 (n= 28), 2016 (n=44) and 2017 (n=49). Upper and lower boundaries of boxes show the 25th and 75th percentiles, respectively.

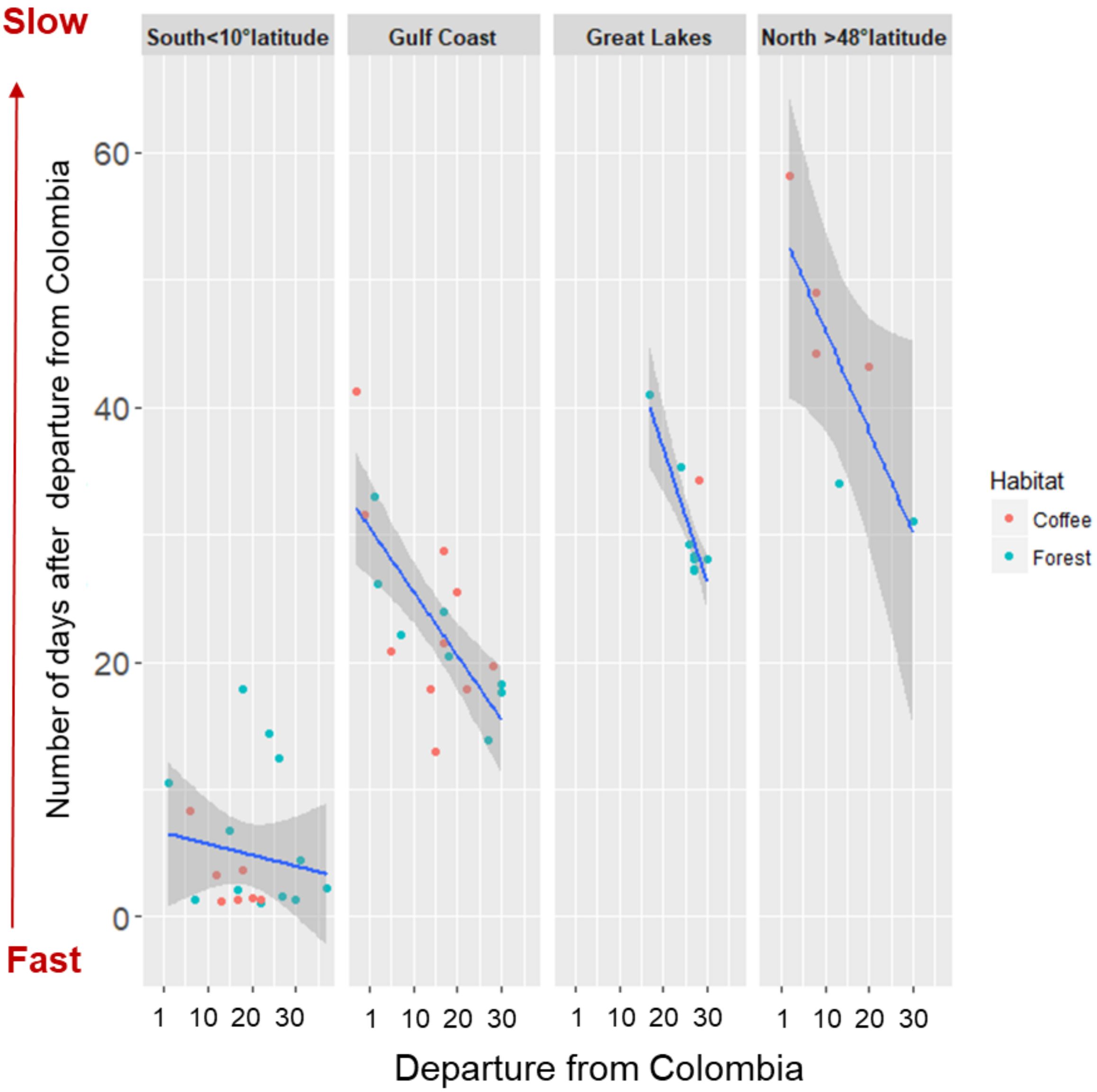

Figure 3.3 Estimates of the relationship between spring departure day of Swainson's Thrush overwintering in forest and shade-grown coffee plantations in South America and migration pace (number of days after departure from Colombia). Birds departing later from the wintering grounds migrated faster and this pattern was maintained within each region. Day 1= 1 March, the grey area represents 95% confidence interval for the predicted relationship. Regions were divided based on latitude as follows: South (8.4° to 9.4°), Gulf Coast (27.2° to 30.4°), Great Lakes (41.5° to 45.0°), and North (48.5° to 50.4°).

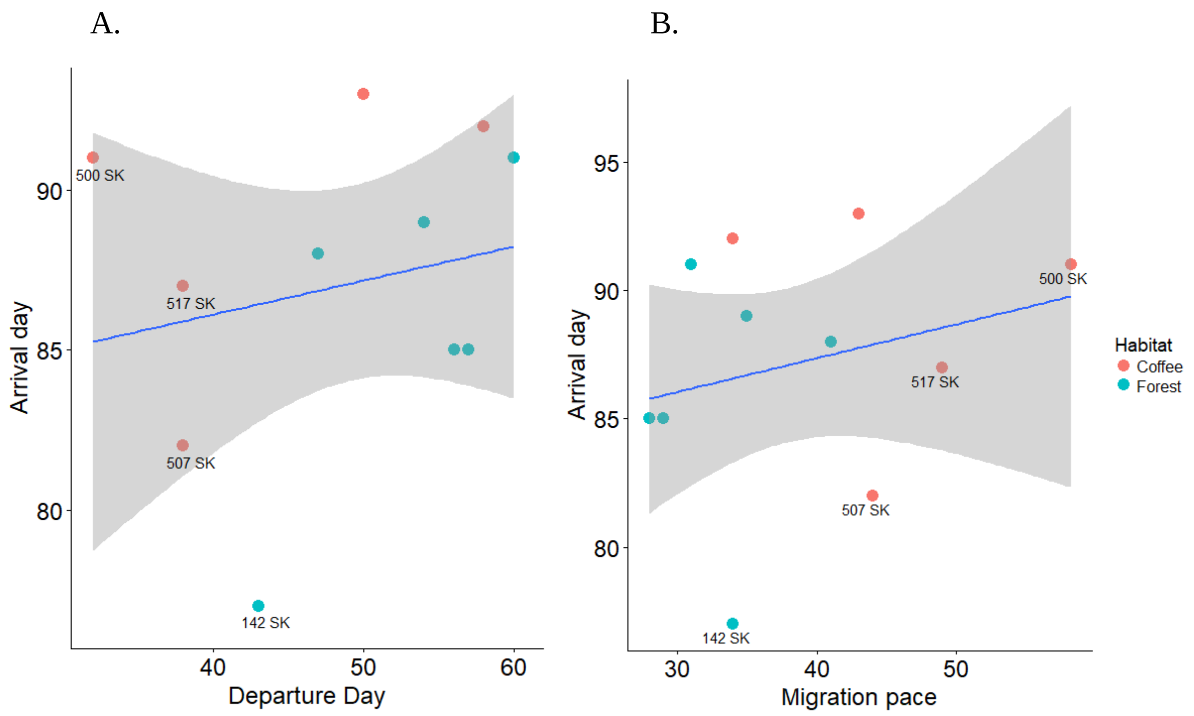

Figure 3.4 Estimates of the relationship between A) departure date from the wintering grounds, B) migration pace (number of days after departure from Colombia), and arrival date to the breeding range of Swainson's Thrush radio tagged in shade-grown coffee plantations and forest is the East Cordillera in the Colombian Andean mountains. Day 1= 1 March. SK= Birds detected in Saskatchewan, Canada and tag number. The grey area represents 95% confidence interval for the predicted relationship.

CHAPTER 4. STRONG MIGRATORY CONNECTIVITY IN A LONG-DISTANCE NEOTROPICAL MIGRANT SONGBIRD: THE GRAY-CHEEKED THRUSH

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4.1. Abstract

Establishing patterns of migratory connectivity can provide insight into how populations are geographically and temporally linked during their annual cycle and how those links may be influenced by a variety of factors. We determined the coarse-scale migratory connectivity and migration routes of Gray-cheeked Thrush (*Catharus minimus*) overwintering in the northern Andes of South America during the winter of 2014 and 2015. We used light-level geolocators and an intercontinental radio-telemetry array (Motus) to show strong migratory connectivity between these sites and breeding grounds, low population spread, and considerable flexibility in migration routes. Despite a boreal breeding range spanning over 4000 km, birds migrated to the northeast portion of their breeding range corresponding to northern Labrador, northeastern Quebec and eastern Nunavut, Canada. Population spread on the breeding grounds was less than 10% of the maximum width of the North American breeding range. Spring and fall migration routes included both a Central American and a trans-Gulf of Mexico route whereas trans-Caribbean Sea migration routes during both seasons were less common. Our findings represent an exception to the expected pattern of high population spread described for Neotropical migrants overwintering in South America. We suggest that the low population spread found in Gray-cheeked Thrush may be the result of habitat distribution and availability since populations in the Andes are restricted to highly isolated forest patches. Strong migratory connectivity enhances vulnerability to habitat loss but allows for targeted conservation actions. While forest-dependent species in the Neotropics are predicted to lose more than half of their current winter range as a consequence of climate change, preserving Andean winter populations of Gray-cheeked Thrush depends on winter habitat conservation strategies that

will also include a renewed focus on high quality stopover sites found along the Central American and Caribbean routes that we describe.

4.2. Introduction

Migratory bird species throughout the world are declining at greater rates than non-migratory species (Wilcove and Wikelski 2008). That trend is likely associated with increased mortality associated with migration itself (i.e., migratory culling, Sillett and Holmes 2002, Newton 2008, Altizer et al. 2011) and with overall exposure to a greater number of events or factors occurring throughout the annual cycle (Sillett et al. 2000, Faaborg et al. 2010) and with their potential to interact in time and space through carry over effects (Webster et al. 2002, Martin et al. 2007). For instance, the occupancy of poor winter habitats can produce detrimental effects on individuals that can carry over to the breeding season and influence population dynamics by affecting recruitment and fecundity (Marra et al. 1998, Norris 2005, Webster and Marra 2005, López-Calderón et al. 2017). During migration, fuel loads acquired at critical stopover sites determine subsequent flight range and pace of migration, which, in turn, can affect survival by compromising the capacity for crossing geographic barriers (Bayly et al. 2013, Gómez et al. 2017). Effective conservation of populations of migratory birds is thus more challenging than for non-migratory populations and there is obviously an urgent need to find ways to mitigate threats that can be encountered internationally and at continental scales.

Migratory connectivity, or the degree to which migratory birds from a given breeding area winter together and vice versa, has become a useful concept in the field of avian conservation (Taylor and Norris 2010). In general, species showing weak connectivity, whereby individuals from populations across the breeding grounds overlap and mix on the wintering grounds, are considered to be more resilient to habitat loss or climate change occurring on the wintering grounds because the effect of any given perturbation or threat at a given site is spread across many breeding sites (but see Finch et al. 2017). As such, the last decade has seen considerable effort and expense directed to tracking migrant birds and to documenting linkages between various stages of their annual cycle. This work has been facilitated to a large degree by various new tools ranging from intrinsic genetic and stable isotope markers to extrinsic miniaturized devices such as light-sensitive geolocators and VHF transmitters (Hobson and Norris 2008, Bridge et al. 2011, Taylor et al. 2017).

In their recent review of 712 individuals from 98 populations of 45 species, from tagging studies in the Neotropics and Afro-Palearctic flyways, Finch et al. (2017) concluded that there is little evidence for strong migratory connectivity among long-distance migratory birds with the mean inter individual distance of birds from the same breeding population on the wintering grounds being 743 km. However, they also argued that the concept of migratory connectivity should be interpreted in terms of population spread on the wintering grounds relative to the extent of geographical spread (relative size) of the wintering grounds. We used Gray-cheeked Thrush, a species only found in forest in our study sites, to assess the link between winter habitat occupancy, population spread, and migratory connectivity (i.e., population mixing). Population spread measures the degree to which individuals from a single breeding population spread out on their winter grounds. According to Finch et al. (2017), the size of the winter range occupied by a given population and, to a lesser extent, breeding longitude are the underlying mechanisms explaining variation in between population spread. In the context of North America, low population spread is expected in western breeding populations overwintering in Central America where land availability limits population spread. In contrast, high population spread is expected in eastern breeding populations overwintering in South America where land availability is higher. Migratory connectivity is predicted by the size of the species' winter range and to a lesser extent by population spread; for instance, strong migratory connectivity is expected in species with large winter ranges and with low population spread (Finch et al. 2017).

In the New World, populations of Nearctic-Neotropical migratory birds have seriously declined in recent decades with those that overwinter in South America declining at greater rates than those wintering elsewhere (NABCI 2016). Despite the importance of understanding migratory connectivity to identify population limiting processes, the migration strategies and population-specific winter locations used by Neotropical migrants in South America are poorly known (Faaborg et al. 2010, González-Prieto et al. 2017). The Gray-cheeked Thrush is a Nearctic-Neotropical migratory songbird that has a broad breeding distribution in the boreal forest across North America from Alaska to Newfoundland, and in northeastern Siberia (Whitaker et al. 2018). This species is known to winter primarily in the northwestern Amazon basin; the limit of the winter range distribution is poorly known but is believed to extend to the base of the Colombian and Venezuelan Andes (Hilty and Brown 1986, Whitaker et al. 2018). Thus, based on the analysis by Finch et al. (2017) Gray-cheeked Thrush is typical of a species with generally high population spread, given that all breeding populations from across North America winter in South America where land availability would favour high population spread. We hypothesized that if the size of the winter range predicts migratory connectivity, then strong migratory connectivity is expected in the Gray-cheeked Thrush based on its broad winter distribution range in South America.

Migration routes taken by Gray-cheeked Thrush during their over 16000 km annual journey between breeding and wintering grounds remain unknown. Recent studies have provided some information about likely breeding destinations (Ungvari-Martin et al. 2016), spring migration strategies (Gómez et al. 2017), and stopover ecology (Bayly et al. 2013) of presumably Amazon wintering populations. Stable-hydrogen isotope analyses (δ^2H) of feathers (δ^2H_f) grown on the breeding ground suggest that at least some Gray-cheeked Thrush overwintering in the western Amazon basin originate from the northwest part of their breeding range (Ungvari-Martin et al. 2016). Recently, the Sierra Nevada de Santa Marta on the northern coast of Colombia was recognized as a critical refuelling site before individuals take a trans-oceanic flight to North America (Bayly et al. 2013, Gómez et al. 2017). Higher numbers of historical and recent records in Panama and the Darién region, Colombia, than along the northern coast of South America during the fall suggest that this species might migrate primarily through Central America during its southward migration or across the western Caribbean Sea (Gómez et al. 2014). However, nothing is known about the distribution, overwinter ecology, migratory routes and strategies, and breeding destinations of Gray-cheeked Thrush overwintering in the Andes of South America.

Here, we combine tracking technologies to provide the first information about migratory connectivity, spring and fall migration routes, year-round phenology of migration, and important stopover sites for a population of Gray-cheeked Thrush overwintering in the Andes of northern South America. Our approach also allowed us to test the expectation of weak connectivity in this long-distance migrant and to consider conservation objectives for this and other Neotropical migrant species.

4.3. Methods

4.3.1. Study site

We captured Gray-cheeked Thrush in two study sites located on the western slope of the Eastern Andes of Colombian: Los Vientos (04°21’56.23”N, 74°31’2.31”W) at 1,350 m, and Hacienda La Fragua, Vereda Batavia (04°18’54.18”N, 74°32’19.29”W) at 1600 m. These sites are dominated by shade-grown coffee plantations, with pastures and small patches of secondary forest. Gray-cheeked Thrush were found only in forest patches.

4.3.2. Captures

Birds were captured daily from 1 December to 30 March during winters of 2013, 2014, 2015 and 2016. Birds were captured during eight days a month in each site from 06:00 to 11:00 h and from 15:00 to 17:30 h using mist nets (36 mm mesh). Most birds were caught using passive mist-netting; however, some were lured to the nets using playback of calls. All Gray-cheeked Thrush were fitted with a numbered US Fish and Wildlife Service aluminium band and a single colour band indicating the year and were processed and released at the capture site. We recorded age (Pyle 1997), wing chord length (±1 mm) and body mass (±0.1 g, using an electronic balance) prior to release. Birds were sexed genetically following Griffiths et al. (1998) using blood samples collected from the brachial vein using a sterilized needle (27-gauge) and a heparinized capillary tube.

4.3.3. Light-level geolocators

We attached light-level geolocators (Intigeo-P65 with 14-mm-long stalk; Migrate Technology v3.12.4; Coton, Cambridge, UK) using leg-loop backpack harnesses (Rappole and Tipton 1991), and 1 mm silicone string sized according to the Naef-Daenzer (2007) formula. Geolocators and harnesses weighed 1.0 (±0.1 g), and all geolocator batteries lasted the duration of the logging period. During winter 2014 nine out of 19 geolocators (47%) were deployed on birds previously banded during winter 2013 and returning to our study sites. During winter 2015 six out of 19 geolocators were placed on recaptured birds initially banded during winter 2013. In 2014, five geolocators were deployed in La Fragua and 14 in Los Vientos; in winter 2015 all geolocators were deployed in Los Vientos.

4.3.4. Radio transmitters

To track spring departure dates and continental movements we fitted nine Gray-cheeked Thrush (only during spring 2016) with digitally-coded radio transmitters using leg-loop harnesses made of elastic thread (Rappole and Tipton 1991, Naef-Daenzer 2007). Eight transmitters were deployed in Los Vientos and one in La Fragua. We used two transmitter types from Lotek (Lotek Wireless, Newmarket, ON, Canada): NTQB-3-2 (0.67 g, burst rate 10 s, battery life 124 d) and NTWB-2 (0.35 g, burst rate 17 s, battery life 68 d). Total weight of transmitter and harness was always less than 5% of body weight. We determined spring departure dates by using telemetry data from an automated telemetry station consisting of one tower with three nine-element Yagi antennae (~15 km detection range) connected to a SensorGnome receiver. Radio-tagged individuals were tracked at a continental scale using the Motus Wildlife Tracking System (hereafter "Motus",Taylor et al. 2017), an international collaborative network consisting of over 300 coordinated automated radio-telemetry arrays tuned to a specific frequency (166.380 MHz) throughout the Americas.

All international detections of radio-tagged Gray-cheeked Thrush linked to the Motus frequency were filtered to exclude false signals distinguishable by less than three consecutive signal bursts per minute. Time of the first signal at each Motus array was used as arrival and the time of the last signal as departure (Sjöberg et al. 2015). The geographic great-circle-distance between international detections were calculated with the R package geosphere v1.3-8 (Hijmans et al. 2014).

4.3.5. Statistical analysis

4.3.5.1. Light-level analysis

We defined twilight events using the function twilightCalc in the GeoLight R package (Lisovski and Hahn 2012). We chose a light threshold of 1.5 to demarcate all twilight events, and visually assessed each twilight period. Annotated twilights were exported to TAGS format and put into FlightR (Rakhimberdiev et al. 2017). Workflow in FlightR followed the steps described in Rakhimberdiev et al. (2017).

To calibrate the relationship between measured and expected light levels, we used two calibration periods (when tags stayed at known positions), one after deployment before the bird left the wintering grounds and when the bird was back on the wintering grounds. FlightR uses a template fit for calibration where for each tag, the linear relationship between the light levels measured during the calibration period (observed) and the theoretical light levels is found. We determined the start and end of the calibration periods visually by plotting the calibration slopes for sunsets and sunrises for every day of the tracking period using the function plot_slopes_by_location as described in Rakhimberdiev et al. (2017).

We limited the spatial extent that FlightR uses to estimate the position of birds by allowing birds to stay or occur anywhere inland, and 480 km from the shoreline over sea (i.e., birds were "allowed" to fly over the Gulf of Mexico). To avoid states of residence over water, we used a spatial mask where birds were allowed to stay only within 50 km of shore. We constrained positions to areas between -130º W, 4 º S to 59 º E, 61º N based on the species year-round distribution. Finally, we used the function run.particle.filter to optimize the FlightR model with 1 million particles and without an automated outlier exclusion. We also estimated stopover sites during the full annual cycle using the function stationary.migration.summary where stationary periods longer than three twilights (i.e., 1.5 days) were considered stopovers (Rakhimberdiev et al. 2017).

4.3.5.2. Migratory connectivity

We used population spread as a measure of migratory connectivity by calculating the mean pairwise distance between individuals tagged with geolocators (Finch et al. 2017). All distances are reported as great-circle-distance and were calculated with the R package geosphere v1.3-8 (Hijmans et al. 2014). Only data obtained from geolocators were used for our migratory connectivity analysis.

4.4. Results

4.4.1. Light-level geolocators

We deployed 19 geolocators during each non-breeding season. During the non-breeding season spanning 2015/2016, we recovered four (21%) geolocators deployed during 2014/2015; three of these birds had overwintered at our sites during the non-breeding season of 2013/2014. During the 2016/2017 season we recovered three (16%) of the geolocators deployed in the 2015/2016 season; one of the birds was a recapture from 2013. All recovered birds had geolocators and each unit recorded data from deployment until recovery (mean= 320±60 days). During the two years in both study sites, tagged birds had higher return rates than untagged birds. In the 2015/2016 season in La Fragua we recaptured 14% of tagged birds (n=14) and 9% of untagged birds (n=11); in Los Vientos we recaptured 40% of tagged birds (n=5) and 30% of untagged birds (n=10). In the 2016/2017 season in Los Vientos we recaptured 16% of tagged birds (n=19) and 8% of untagged birds (n=12).

4.4.2. Migratory connectivity

All birds tagged with geolocators migrated to the northeast portion of their breeding range corresponding to northern Labrador, northeastern Quebec and eastern Nunavut, Canada. The distance between individuals during the breeding season ranged from 87 km to 906 km. Mean distance between individuals (i.e. population spread) was 377 ± 207km, spanning about 10% of the maximum width of the species' breeding range.

4.4.3. Arrival and departure from breeding grounds

Mean departure date from the wintering grounds was 10 May (±9 days), mean arrival to the breeding grounds was 7 June (±8 days). On average, birds spent 107±6 days on the breeding grounds (Table 4.1). Mean departure date from the breeding grounds was 21 September (±6 days) and mean arrival date on the wintering grounds was 13 November (±11 days).

4.4.4. Spring migration routes

Our results suggest that birds followed both Central American (with a trans-Gulf crossing) and trans-Caribbean Sea migration routes with two stopovers before reaching the breeding grounds. After leaving the wintering grounds, birds had their first stopover either in North America (birds 303 and 314), Central America (birds 097,302, and 316), northern Colombia (bird 114), or likely in Cuba (bird 300, Figure 4.1, Appendix 10). Bird 303 arrived to its first stopover in northwest Alabama in approximately 3 days, and bird 314 arrived to northwest Kentucky in approximately seven days of which four were spent on the north coast of the Gulf of Mexico after crossing the Gulf (Figure 4.1). Birds 097, 302 and 316 had a stopover of 8 ±1 days in Central America. After the stopover, bird 302 followed a circum-Gulf route while 097 and 306 followed a trans-Gulf route (Figure 4.1). Stopover data suggest that birds 114 and 300 followed a trans-Caribbean Sea migration route. Bird 114 stopped in northern Colombia for 13 days before flying to a second stopover site in south-west Mississippi. Bird 300 was the only individual with evidence for a stopover in the Caribbean islands before reaching North America.

The mean length of spring migration was 28±7 days (Table 4.1). Bird 114 (adult, sex unknown), had the earliest departure from the wintering grounds (28 April 2016), the slowest spring migration (48 days), and was the only bird with four spring stopovers. Bird 316 (adult female), had the latest departure date (28 May 2015), the latest arrival to the breeding grounds (21 June 2015), and spent the shortest time on the breeding grounds (98 days, Table 4.1). Bird 303 (adult male), had the fastest spring migration (20 days) and arrived first to the breeding grounds (26 May 2015).

4.4.5. Fall migration routes

The mean length of fall migration was 53±10 days. Fall migration was longer than spring migration with birds spending 66±8 % of the total annual migration time during the fall (Table 4.1). Our results suggest that Gray-cheeked Thrush used two fall migration routes (Figure 4.1). Most birds arrived in Central America after a trans-Gulf flight and then migrated through Central America to the wintering grounds. Birds flew directly from Central America to the winter grounds. Only bird 097 used a trans-Caribbean Sea fall migration route flying from southern Florida or Cuba to the northern coast of Colombia. After entering South America (passing 12 degrees latitude on the northern coast of Colombia) this bird took a further 29 days to reach its wintering grounds (over half of the full length of fall migration); but did not appear to stop over for longer than 1.5 days at any site during that period.

Birds had between 2 and 5 stopovers during fall migration (Table 4.1, Figure 4.1, Appendix 10). Bird 302 was the only one with 5 fall stopovers and had the slowest fall migration (67 days, Table 1). Five out of the seven birds stopped during 10±2 days south of their breeding grounds in Quebec.

4.4.6. Radio-tagged birds

We obtained international detections from six of the nine birds radio-tagged during spring 2016. Three birds were detected by the Motus station “Palmeras” on the northern coastal plain of Colombia, approximately 496 km from the wintering sites and 60 km from the coast (Figure 4.2). The first detection for all other birds was over 3000 km from the winter grounds and suggested that birds were migrating along the eastern flyway to the breeding grounds potentially in the eastern part of the breeding range as indicated by our geolocator results.

4.5. Discussion

4.5.1. Breeding grounds and migratory connectivity

A striking result of our study was that despite a pan-boreal breeding range, all of our tracked (geolocator) individuals returned to a fairly narrow breeding region in the northeastern portion of the range corresponding to northern Labrador, northeastern Quebec and Nunavut, Canada. Moreover, those birds also detected by Motus were consistent with a general movement to that region. Notwithstanding the spread in ultimate breeding locations, this suggests strong connectivity between breeding and wintering sites and stands as an exception to the pattern found by Finch et al. (2017) in their meta-analysis of long-distance migrants in the New and Old World. If strong migratory connectivity is expected in species with relatively large winter ranges despite the degree of population spread (Finch et al. 2017), then strong migratory connectivity is expected to be common in species such as the Gray-cheeked Thrush whose winter range extends over 30º longitude and 2700 km wide in South America. We suggest that for species overwintering primarily in South America such as the Gray-cheeked Thrush, habitat distribution and availability might outweigh the effect of the size of the breeding range and breeding longitude on the patterns of population spread described by Finch et al. (2017). Indeed, although species overwintering in South America may have broad winter ranges, the amount of available land for species with Andean distribution is limited. The effect of limited land availability across the Andes on population spread of forest-dependent species is likely to be enhanced by limited habitat availability. For instance, Gray-cheeked Thrush populations overwintering in the Colombian Andes are restricted to highly isolated forest patches compared to the more extensive Amazon basin where the majority of this species is assumed to winter, and low population spread should be expected. Our results suggest that the strong migratory connectivity found in Gray-cheeked Thrush is mainly driven by low population spread and likely by parallel migration.

4.5.2. Wintering grounds

Our results from geolocators and radio telemetry data suggest that Gray Cheeked-Thrush spent the full winter at our study sites. We did not observe mid-winter intra-tropical migration as described for closely related species like Swainson’s Thrush (*Catharus ustulatus*) overwintering in Central America (Delmore et al. 2012, Cormier et al. 2013), and eastern (Heckscher et al. 2011) and western (Hobson and Kardynal 2015, Kardynal and Hobson 2017) populations of Veery (*Catharus fuscescens*) overwintering in the Amazon basin. Our results suggest that Gray-cheeked Thrush wintering at our study sites depend on Andean forest for overwinter survival and for preparation for spring migration This species was not recorded using adjacent agroecosystems such as shade coffee plantations. Our results also suggest that most birds flew over 2000 km to their first stopover, which indicates than Andean habitats played a crucial role in fuelling the first leg of spring migration.

4.5.3. Migration

Gray-cheeked Thrush showed a variety of migratory routes during both spring and fall migration. Flexibility in migratory routes has been described within and between individuals and has been attributed to availability of suitable stopover habitats, variation in physical condition, and unpredictable environmental conditions found en route (Heckscher et al. 2011, Vardanis et al. 2011, López-López et al. 2014, Stanley et al. 2015). Recent evidence suggests that variation in migratory route is also associated with long migratory distance, and the presence of large ecological barriers in the migration route such as the Caribbean Sea, and might decrease the risk associated with ocean crossing by optimizing migration timing and route (La Sorte and Fink 2017).

During spring, most individuals took a Central America-trans-Gulf migration route; only two birds showed a trans-Caribbean Sea route to North America. Although a trans-Caribbean Sea migration from the northern coast of South America is within the Gray-cheeked Thrush potential flight range capacity (Bayly et al. 2013, Gómez et al. 2017), most birds used a detour through Central America during spring migration and avoided the shorter but overwater migration. Absence of coastal refuelling options for birds leaving South America throughout the 400-km gap between the Sierra Nevada de Santa Marta and the Darien might have added to the significant barrier effect of crossing the Caribbean Sea and shaped the evolution of a Central America migratory route.

Since the success of long over-sea migratory flights depends, in part, on energy acquired before crossing (Newton 2008), taking a trans-Caribbean Sea route might depend on the capacity of winter habitats to provide enough energy to fuel the migratory journey to a suitable stopover site in the Caribbean. That seemed the case for bird 300 which stopped in Cuba for 10 days, two days after departing from the winter grounds. Other individuals crossing the Caribbean Sea seemed to refuel in non-coastal sites like bird 114 which crossed the Caribbean after a stopover of 13 days in northern Colombia approximately 400 km south of the coast. This stopover duration is the same as observed and predicted in Gray-cheeked Thrush stopping in the Sierra Nevada de Santa Marta, northeast Colombia, before crossing the Caribbean Sea (Gómez et al. 2017).

Three of the radio tagged birds were detected on the northern coast of Colombia about 500 km from their wintering site, one of the birds stopped during seven days and likely crossed the Caribbean Sea after the stopover. These results were consistent with our findings from geolocators and suggest that Andean wintering populations are following a more westerly spring migration route than Amazon wintering populations stopping in the Sierra Nevada de Santa Marta 360 km northeast from where radio-tagged birds were detected.

4.5.4. Conservation Implications

The strong connectivity and flexibility of migration route and strategy we observed in Gray-cheeked Thrush have implications for conservation. Tracked individuals originated from the north-east part of the breeding range where populations of the Northern Gray-cheeked Thrush (*C. m. aliciae*) are showing steeper decline (ECCC 2017). This suggests that the loss of native winter habitat and lack of adaptation to shade-grown coffee plantations might be a key driver of declines for eastern populations of Gray-cheeked Thrush overwintering in the Andes. Strong migratory connectivity is expected to reduce dispersal rates limiting the ability of the population to adapt to land-use changes and diminishing the probability of individuals from less affected areas to counteract declines (Webster et al. 2002, Jones et al. 2008, but see Finch et al. 2017). In the Gray-cheeked Thrush and other Neotropical migrants that depend on forests during winter, negative effects of strong connectivity might be increased by limited habitat availability and ongoing deforestation (Pereira et al. 2012) across the Andes which can potentially eliminate focal winter populations.

Inter-individual flexibility in the migration route and strategy may increase the response of long-distance migrants to environmental variation during migration (La Sorte and Fink 2017). However, since the success of migration is expected to be determined by the capacity of the individuals to meet energy requirements en route (Alerstam and Lindstrom 1990, Newton 2004, Bayly et al. 2013); the success of migration of Andean winter populations might ultimately depend on the quality of the stopovers found along the Central America and Caribbean routes described during spring and fall migration.

Migration is one of the greatest sources of mortality and a critical period during the annual cycle of migratory birds (Sillett et al. 2000, Newton 2008, Klaassen et al. 2014). Yet, for Neotropical migrants overwintering in South America, research efforts toward the study of migration and the identification of critical stopover sites are limited. Recent research shows that stopover habitats in northern Colombia can provide up to 40% of the energy required for a successful spring migration of presumably Amazon Gray-cheeked Thrush (Bayly et al. 2013, Bayly et al. 2016). However, for Andean Gray-cheeked Thrush and for most populations of Neotropical migrants the energy contribution of a stopover site to spring or fall migration is unknown. Having determined annual-cycle movements of Gray-cheeked Thrush overwintering in the Colombian Andes, defining conservation priorities requires fine-scale research to determine habitat use and quality, and distribution at stopover sites found along the Central American and Caribbean routes we have described.

In contrast to Swainson’s Thrush and Canada Warbler, which are commonly found in forest and adjacent shade coffee plantations in our study sites, Gray-cheeked Thrush were found exclusively in forest. Coastal montane forests are also preferred over shade-coffee plantations at a critical spring stopover site in northern South America for populations of Gray-cheeked Thrush overwintering in the Amazon basin (Bayly et al. 2016). Recent studies suggest that the combined effects of agriculture expansion and climate drying represent a major threat to wet forest bird communities in the Neotropics as species associated with warm or dry environments are more likely to thrive in agricultural landscapes (Frishkoff et al. 2016, Karp et al. 2017). It follows that Neotropical migrants relying on forests during the non-breeding season such as the Gray-cheeked Thrush are particularly vulnerable to global change. While ongoing deforestation in northern South America has already reduced Andean forests to 10% of their original cover (Henderson et al. 1991), forest-dependent resident Neotropical species that avoid agriculture are predicted to lose more than half of their current range as a consequence of climate change (Frishkoff et al. 2016). While deforestation continues to be the biggest threat to tropical communities (Pereira et al. 2012) maintaining Andean populations of Gray-cheeked Thrush depends clearly on the conservation of Andean montane forests and on the maintenance of healthy breeding habitats in the boreal region (NABCI 2012).

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Table 4.1 Migration summary of Gray-cheeked Thrush tagged at two wintering sites in the Eastern Andes of Colombia. The number of stopover sites used during the full annual cycle were obtained using the function stationary.migration.summary in the R package FlightR. Stationary periods longer than three twilights (i.e., 1.5 days) were considered stopovers (Rakhimberdiev et al. 2017). Total length of stopovers and duration of migration during each season are presented as number of days.

Migration	Geolocator number							Mean± SD
	97	114	300	302	303	314	316	
Number of spring stopovers	2	4	2	2	2	2	2	
Total spring stopover length	14	29	17	15	15	18	13	17±6
Spring migration length	23	43	28	29	20	27	24	28±7
Number of fall stopovers	2	3	3	5	4	4	2	
Total fall stopover length	17	34	46	62	42	53	25	40±16
Fall migration length	54	41	53	67	50	64	41	53±10
Time on breeding grounds	105	104	116	112	112	102	98	107±6

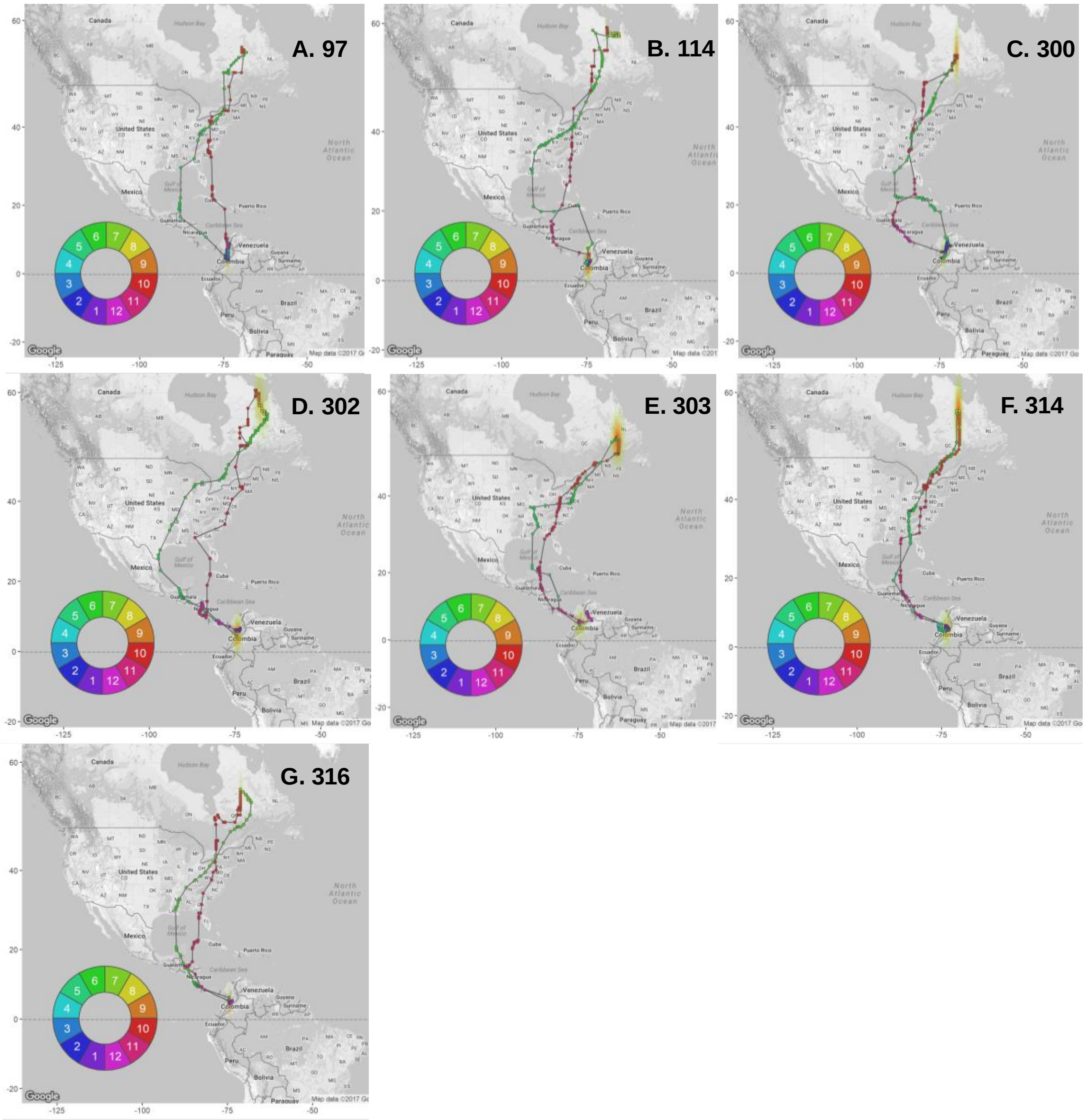

Figure 4.1 Movements of Gray-cheeked Thrush tagged in the Andes of South America and tracked to their breeding grounds in eastern North America. Medians of estimated positions (by latitude and longitude) for each twilight are represented as coloured dots connected with lines. Colour of each dot corresponds to the colour of the months (on the colour-wheel), during which the twilight occurred. Shades of orange represent where birds spent most of the time (utilization distribution). A) bird 097 immature female, B) bird 114 adult unknown sex, C) bird 300 adult female, D) bird 302 adult male, E) bird 303 adult male, F) bird 314 adult female, G) bird 316 adult females. Only birds 300 and 316 were tagged in the study site La Fragua, other birds were tagged in Los Vientos. Study site are 5 km from each other.

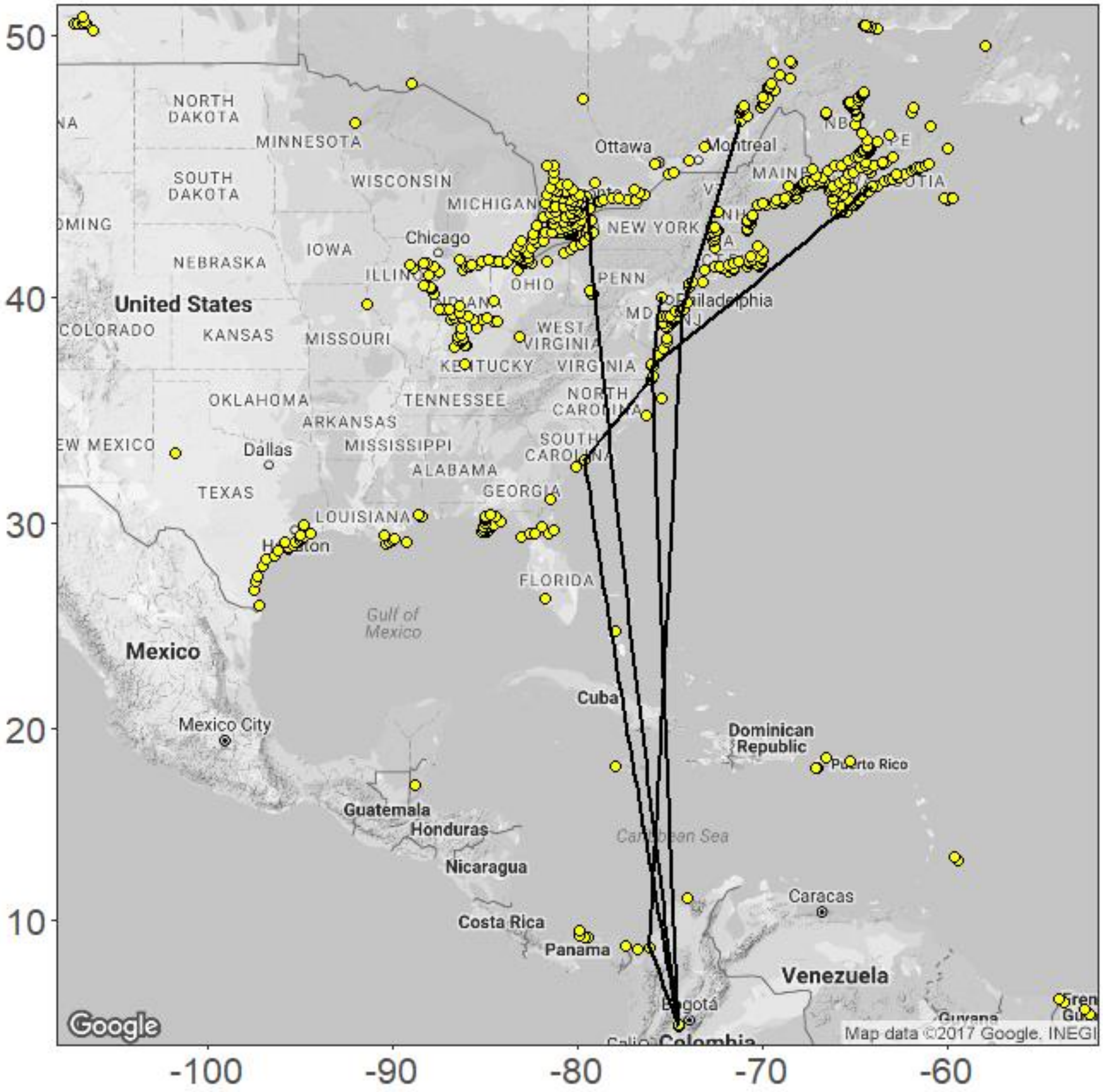

Figure 4.2 Six radio-tagged individuals were detected at continental scales using the Motus Wildlife Tracking System (yellow dots, https://motus.org). Three individuals were detected on the northern coast of Colombia before heading to North America. Detections further north suggest that the birds were likely migrating to the northeastern part of their breeding range. Solid lines indicate shortest distance between detections and are not migration routes.

CHAPTER 5. TOPOGRAPHY OF THE ANDES MOUNTAINS SHAPES THE WINTERING DISTRIBUTION OF A MIGRATORY BIRD

5.1. Abstract

In birds, patterns of migratory connectivity are influenced by landscape structure experienced throughout the annual cycle. Assessing how landscape patterns drive the movements and distributions of migratory species is important for understanding the evolution of migration and determining conservation priorities. We determined migratory connectivity in the Canada Warbler (*Cardellina canadensis*), a declining Neotropical migratory bird, and evaluated the degree to which the Andean mountains influence winter population distribution in this montane forest specialist. We inferred breeding and natal origins of Canada Warblers overwintering in seven study regions across the Western, Central, and Eastern Andes of Colombia by analysing stable hydrogen isotope values (δ^2H) in feathers and assigning wintering populations to breeding origins using an established feather δ^2H isoscape for North America. We found strong evidence for parallel migration between breeding and wintering sites, giving rise to moderately strong migratory connectivity between breeding and wintering regions. The model best explaining population distribution in the Colombian Andes implied that populations were most similar within basins or valleys. Such segregation is notable, given that basins are separated by less than 300 km on the wintering grounds, while breeding populations may be separated by more than 3000 km from east to west. Our results suggest that the high spine of each Andean cordillera acts to shape the winter distribution of individuals from different breeding populations. To our knowledge, this is the first demonstration that the topography of the Andean mountains can shape the winter distribution of populations of a migratory bird. The strength of migratory connectivity found in Canada Warblers may inhibit evolutionary responses to environmental change, and the more rapid population declines recorded in some eastern breeding populations may be related to habitat loss and local environmental conditions in the Eastern Andes, where individuals from these populations were more likely to overwinter.

5.2. Introduction

Mountains have long been recognized both as barriers and as insular environments that shape the distribution and population structure of countless organisms (Vuilleumier 1969, Ruggiero and Hawkins 2008). Indeed, montane habitats have been equated to islands, giving rise to speciation or divergence between populations inhabiting isolated mountain tops or cordilleras (Vuilleumier 1970). While the role of mountains in shaping population structure is well recognized in resident species (Gutiérrez-Pinto et al. 2012), the same is not true for migratory species, and yet, many migratory birds are montane specialists during at least one phase of their annual cycle (Rappole et al. 2000).

The tropical Andes (hereafter the Andes) of Colombia are divided into three cordilleras and are widely recognized for their high diversity and levels of endemism across a range of resident taxa – driven in part by the geographic isolation of montane habitats among cordilleras (Kattan et al. 2004). The three cordilleras are separated by dry and deep basins; the Cauca basin separates the West and Central cordilleras, and the Magdalena basin separates the Central and East cordilleras. Montane forests are also interrupted at high elevations (> 3000 m), where the slopes of each cordillera are separated by ridgelines often above 4000 m. If the complex topography of the Colombian Andes defines metapopulations in resident species of birds and other organisms (Gutiérrez-Pinto et al. 2012, Muñoz-Ortiz et al. 2015), the same may apply to migratory species. Indeed, a number of studies have shown the differential use of Caribbean islands and Central America by populations of migratory birds (Rubenstein et al. 2002, Norris et al. 2006), and so, it follows that the Andes could act as 'islands in the sky' for migratory montane specialists. Such a relationship has never been examined before but by determining the breeding ground origin of individuals wintering in the different Andean cordilleras, we can determine the degree to which the topography of the Andes structures migratory populations.

Determining the origins of migratory species from across their non-breeding grounds is also a question of critical importance to understand their full life-cycle ecology, to model population dynamics, and to determine conservation priorities (Webster et al. 2002, Marra et al. 2015). Indeed, our lack of knowledge of the migratory connectivity between declining breeding ground populations and their non-breeding grounds is a major barrier to designing effective conservation actions for a wide range of migratory organisms (Faaborg et al. 2010, Reichlin et al. 2010). Having determined the degree of connectivity, we can ask, for example, how seasonal interactions may affect demography (Marra et al. 2015), and through modelling population dynamics, we can identify population-limiting factors (Holmes 2007). Further, the degree of connectivity between populations is expected to affect their vulnerability to land-use change, with strong connectivity increasing the probability of extinction in individual populations (Webster et al. 2002, Jones et al. 2008). Indeed, where migratory populations segregate on either their breeding or wintering grounds, they can form metapopulations, just like resident species, rendering individual populations vulnerable as a result of restricted gene flow (Esler 2000).

Several species of Nearctic–Neotropical migratory birds occupy montane habitats in the Andes during the non-breeding period, including species of conservation concern such as the Olive-sided Flycatcher (*Contopus cooperi*), Cerulean Warbler (*Setophaga cerulea*), Golden-winged Warbler (*Vermivora chrysoptera*) and Canada Warbler (*Cardellina canadensis*) (Davidson et al. 2011, IUCN 2016, NABCI 2016). These species have experienced persistent population declines over the last 50 years (Sauer et al. 2017), and it is suspected that land-use changes in the Andes are partly responsible (Jones et al. 2004, Colorado et al. 2012). For instance, the Canada Warbler global population is estimated to have declined by 66% since 1966 (Sauer et al. 2017). Canada Warbler breeds primarily in the boreal forest stretching 4000 km inland from the north-east Atlantic coast and south into the southern Appalachian Mountains (Reitsma et al. 2009), while its winter distribution lies mainly within the highly deforested and fragmented Andes of northern South America (Henderson et al. 1991, Armenteras et al. 2003). It is therefore essential to determine the connectivity among populations in the non-breeding and breeding grounds, in order to identify population-limiting processes and to design effective strategies to reverse declines.

In this study, we determined natal and breeding origins of Canada Warblers overwintering in Colombia by analysing stable hydrogen isotope ratios (δ^2H) in feathers grown on their North American breeding grounds and sampled at multiple sites spread across the three Andean cordilleras. In North America, the amount-weighted average values of deuterium in precipitation during the growing season (δ^2H_p) follow a strong latitudinal gradient. As metabolically inactive animal tissues (e.g. claws, feathers) incorporate and retain isotopic values of the geographic location at the time the tissue was grown, these tissues can be used as intrinsic markers to determine potential areas of origin (Chamberlain et al. 1997, Hobson and Wassenaar 1997). Both juvenile and adult Canada Warblers grow their feathers on their breeding grounds, and as a result, their feathers reflect the isotopic values of the region where they were grown (Hobson 2005).

We used these inferred origins to answer the following questions: (1) Do either the high spines of each Andean cordillera or the low valleys of each inter-Andean basin act to shape the distribution of Canada Warbler populations wintering in Colombia as they do in resident species? (2) What is the degree of migratory connectivity between breeding and Andean wintering populations? (3) Do populations of Canada Warbler show either latitudinal or longitudinal structure in the Andes?

5.3. Methods

5.3.1. Study sites

We collected feathers in seven study regions spanning all three of the Andean cordilleras in Colombia (the Eastern, Central and Western Andes), including a north–south gradient. Within each region, one or more sites were sampled (Table 5.1; Fig. 5.1). Sites were grouped within regions according to their proximity and geographic considerations.

5.3.2. Tissue sampling

We sampled feathers from Canada Warblers during the winters (1 December to 31 March) of 2013/2014 (Cundinamarca only) and 2014/2015 (all regions). Birds from Cundinamarca and Jericó were caught by passive mist-netting. Individuals from the other regions were detected using playback of both male song and calls, and subsequently lured with playback to a 9- or 12-m mist net. Each individual was banded, aged and sexed following Pyle (1997), and the first primary feather was collected. As this feather is grown first following breeding (Pyle 1997), it best represents the geographic location where moult was initiated. Feathers were exported from Colombia to Canada under Permit No. 00511 issued by the Autoridad Nacional de Licencias Ambientales (ANLA). Feathers were stored and labelled in sealed paper envelopes until analysed at the National Hydrology Research Centre of Environment Canada in Saskatoon, Canada.

5.3.3. Stable isotope analysis

All feathers were cleaned of surface oils in a 2:1 chloroform: methanol solution, rinsed and then dried in a fume hood. A feather subsample (0.33–0.37 mg) from the distal end of the feather vane was removed, weighed into silver capsules and loaded into an Elemental analyser (Eurovector, Milan, Italy). The H_2 resulting from high-temperature flash pyrolysis (1350 °C) was analysed by Continuous Flow Isotope Ratio Mass Spectrometry (CF-IRMS) using an Isoprime (Manchester, UK) mass spectrometer. Three calibrated keratin standards (CBS: -197‰, SPK: -121.6‰ and KHS: -54.1‰) were used to correct for the effect of uncontrolled isotopic exchange between non-carbon-bound hydrogen in feathers and ambient water vapour using the comparative equilibrium approach described by Wassenaar and Hobson (2003, 2006) . Stable isotope ratios $^2H/^1H$ are reported in delta (δ) notation, in per mil units (‰) relative to Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation (VSMOW-SLAP). Within-run measurement error (n=5) of the keratin laboratory reference materials corrected for linear instrumental drift were < 2‰ (SD).

5.3.4. Statistical analysis

5.3.4.1. Variation in the breeding ground origin of individuals across the Andes

We tested the hypotheses that either the high spine of each Andean cordillera or the low inter-Andean valleys act as mechanisms shaping the distribution of Canada Warbler populations wintering in Colombia. We modelled δ^2H_f values as a function of Andean slope (east slope of West cordillera, west slope of Central cordillera, east slope of Central cordillera, west slope of East cordillera and east slope of East cordillera), basin (Cauca River, Magdalena River and Orinoco/Amazon slope of the East cordillera here after Piedmont) and region. By splitting the three cordilleras into five slopes, we expected isotopic differentiation for each slope if the low valleys in each basin are shaping the distribution of populations; we expected the high ridges of each cordillera to shape the distribution if there is isotopic differentiation amongst basins. Each factor was entered into our linear models as a unique variable. We also included a null model (Table 5.2). An examination of the data revealed that one region, Santander, had extreme negative δ^2H_f. Therefore, we developed two model sets, a set including all regions (Table 5.2 A) and a set excluding Santander (Table 5.2 B). We selected among competing models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c, Burnham and Anderson 2002). This method considers the model with lowest AIC_c to be the most parsimonious of the set of candidate models. We estimated delta AIC_c (ΔAIC_c) to determine the strength of evidence for each model (Burnham & Anderson, 2002). Model selection was carried out using the package 'AICcmodavg' (Mazerolle 2017) in program R Version 3.2 (R Development Core Team, 2015).

5.3.4.2. Establishing origins

We assigned origins of Canada Warblers captured on their wintering grounds following a spatially explicit approach similar to that of Hobson et al. (2014). We used digital range maps (BirdLife International 2017) to extract the breeding range of the Canada Warbler from a GIS-based model of expected amount-weighted growing-season average precipitation (δ^2Hp) from Terzer et al. (2013) in ARCGIS Spatial Analyst (v10.2.1, Esri Redlands, CA, USA).

We used the transfer function, linking feather δ^2H (δ^2H_f) of non-ground-foraging Nearctic–Neotropical migrants with δ^2H_p, $\delta^2H_f = -17.57 + 0.95\ \delta^2H_p$, reported by Hobson et al. (2012) to transform the δ^2H_p isoscape rastermap for the species' range into a δ^2H_f isoscape at the same spatial scale. Each raster cell (20 km^2) represented a local δ^2H_f value. We assessed the likelihood that each cell within the δ^2H_f isoscape represented a potential origin for each bird sampled using equation 1:

Equation 1

$$f(y^* \mid \mu_c, \sigma_c) = \left(\frac{1}{\sqrt{2\pi}\sigma_c}\right)\exp\left[-\frac{1}{2\sigma_c{}^2}(y^* - \mu_c)^2\right]$$

where $f(y^* \mid \mu_c, \sigma_c)$ is the probability that any given cell (pixel) on the map represents a potential origin for an individual (origin y*), given an expected mean (μ_c) δ^2H_f based on the predicted value within the calibrated isoscape and the expected standard deviation (σ) of δ^2H_f between individuals growing their feathers at the same locality. We used a value of $\sigma = 14.4‰$ as the standard deviation of the residuals based on the regression equation reported by Hobson et al. (2012).

In order to estimate 'probability of origin', we used the normalized likelihoods calculated from equation 1 to obtain a set of spatially explicit probability densities for each individual. To assign all individuals to the base map, we reclassified the spatially explicit probability densities into likely versus unlikely origins by specifying 2:1 odds ratios. We identified the set of cells that defined the upper 67% of estimated 'probabilities of origin' and coded those as '1' (likely) and the rest as '0' (unlikely). Each bird was assigned to multiple potential origins within the isoscape at the same time. The results of the assignment for each individual were summed and mapped on the δ^2H_f isoscape, to obtain the likely origin of the population.

All geographic assignments were performed by employing the packages ‘raster’ (Hijmans and van Etten 2012), ‘maps’(Becker and Wilks 2018), and ‘maptools’ (Bivand and Lewin-Koh 2016) (Bivand & Lewin-Koh, 2016) with Program R Version 3.2 (R Development Core Team, 2015) and ArcGIS (v10.2.1, Esri Redlands).

5.3.4.3. Latitudinal and longitudinal structure in the Andes

To determine how origin varied with latitude and longitude, we modelled δ^2H_f values as a function of the latitude and longitude of each capture site; we used site instead of region to obtain more geographic resolution. We developed two sets of models, a set including all sites and a set excluding sites in Santander. Each set included a priori linear and quadratic models with variables for latitude, longitude, the additive and the interaction effect of latitude with longitude, and a null model (Table 5.3). We selected among competing models using AIC_c adjusted for small sample sizes as described above (Burnham & Anderson, 2002). Model coefficients and 95% confidence intervals (95% CI) were used to estimate the magnitude and direction (positive or negative) of the effect of each variable in the top model on δ^2H_f values. Narrow intervals excluding zero indicate more precise estimates and a strong effect of the variable (Burnham and Anderson 2002).

5.4. Results

5.4.1. Variation in the breeding ground origin of individuals across the Andes

For the initial set of models including Santander, the AICc values suggested that the main factor driving differences in δ^2H_f values was region (Table 5.2 A, Fig. 5.2a). An examination of the data revealed that the extreme negative δ^2H_f values of Santander were primarily responsible for this result. When Santander was excluded from the analysis, region received little support, and the model including basin received the greatest support (Table 5.2 B), such that δ^2H_f values were predicted to increase from the westernmost to the easternmost basin (Fig. 2b).

5.4.2. Geographic assignments

The Canada Warbler's breeding range cuts across two broad isotopic regions, which allowed us to use the δ^2H_f isoscape to assign overwintering birds to north-west and south-east breeding origins. Based on our findings of consistently different δ^2H_f values between basins and of unexpectedly low δ^2H values for birds overwintering in Santander, we present separate depictions of the likely breeding origins of Canada Warblers from each of the basins, and for birds overwintering in Santander (Fig. 5.1).

Canada Warblers overwintering in each basin had different probabilities of origin, such that those from the Cauca basin were more likely to originate from the northern and western reaches of the breeding range, those from the Magdalena Basin from the northern and central regions of the breeding range and those from the piedmont from the south-eastern part of the range (Fig. 5.1). Birds from Santander were predicted to have origins at the extreme western limit of the breeding range.

5.4.3. Relationship between breeding origin and latitude and longitude on the wintering grounds

We found effects of both latitude and longitude on the predicted breeding/natal origins (δ^2H_f values) of Canada Warblers overwintering in the Colombian Andes, when analysing all sites (Table 5.3 A) and when using a reduced data set without sites in Santander (Table 5.3 B). When including all sites, a quadratic relationship between latitude and δ^2H_f values received the greatest support (Table 5.3 A, Fig. 5.3a), and model coefficients and their 95% CI imply that overwinter latitude is a moderately strong predictor of breeding/natal origins (Coefficients: Latitude = 131.8, 95% CI -50.5, 182.3; Latitude^2 = -13.74, 95% CI -18.6, -8.8). This pattern was driven by highly negative δ^2H_f values in the sites located in the southernmost (Valle) and northernmost (Santander) regions. When excluding sites in Santander (extreme negative values), longitude was the strongest predictor of natal/breeding origin (Table 5.3 B), supporting a linear relationship (Fig. 5.3b), in which δ^2H_f values become increasingly positive (more easterly origins) as one moves west to east (coefficients: Longitude= 9.7, 95% CI 6.2, 13.2).

5.5. Discussion

Our results provide evidence of a large-scale longitudinal geographic gradient in the origins of Canada Warblers overwintering in the Colombian Andes, giving rise to moderately strong migratory connectivity between breeding and wintering regions. This geographic gradient of origin resulted in differential use of the three basins we sampled in Colombia, suggesting that the high spine of each cordillera may act to shape the winter distribution of individuals from different populations. Given that the maximum distances between basins in Colombia is just 300 km and the minimum distance is only 50 km, the level of isotopic differentiation between basins is remarkable for a migratory bird that flies over 8000 km annually and whose breeding range spans over 3000 km in North America. To our knowledge, this is the first demonstration that the topography of the Andean mountains can act to shape connectivity patterns among populations of a migratory bird.

5.5.1.1. Migratory connectivity and its origins

Assigning wintering or migrating birds to east or west origins in North America using the δ^2H isoscape alone is often imperfect because the isoscape follows a latitudinal rather than a longitudinal pattern (Hobson et al. 2012). However, the cline of the δ^2H isoscape across the breeding distribution of the Canada Warbler provided sufficient longitudinal resolution to infer both west versus east origins, as well as the north versus south origins of birds.

Our geographic assignments showed that western breeders were more likely to winter in the Western Andes (Cauca basin), and eastern breeders in the Eastern Andes (Piedmont), giving rise to a parallel migration system. A similar longitudinal geographic gradient of origin has been inferred in several species of Nearctic–Neotropical migrants (Boulet and Norris 2006, Norris et al. 2006, García-Pérez and Hobson 2014, Rushing et al. 2014, Hobson et al. 2015) and it is often attributed to the legacy of Pleistocene glaciations when many species were confined to forested refuges in the southwest and the south-east of North America (Ruegg et al. 2006, Newton 2008). However, while Pleistocene events might have shaped the breeding distribution, migration routes and genetic differentiation of some Nearctic–Neotropical migrants, less is known about past wintering distributions of these species or the processes that affected population distributions and migratory pathways further south.

Intense uplift in the northern Andes during the Neogene (mid-Miocene to Pliocene) drove dramatic large-scale landscape changes in northern South America, which are hypothesized to have fragmented the previously continuous distributions of resident populations (Gutiérrez-Pinto et al. 2012), leading to the structuring of populations, speciation and the high levels of biodiversity observed in the Neotropics today (Smith et al. 2014). We hypothesize that if during the evolution of migration, North American breeding ranges evolved from ancestral areas in current overwintering ranges (e.g., Cox 1985, but see Barker et al. 2014), then the uplift of the Andes might have played a role in shaping the population distribution in Andean wintering long-distance migrants. Montane forest isolation and fragmentation in the Andes, driven by glacial–interglacial cycles during the Pleistocene glaciations, may also have contributed to population distribution structuring (Hooghiemstra and der Hammen 2004). In the case of the Canada Warbler, it is unclear whether the east–west breeding distribution drove the differential use of the Andes by wintering populations or vice versa. Molecular approaches could help us understand whether the winter distribution of Canada Warblers across the Colombian Andes is maintained by population genetic structure, as has been shown for closely related species overwintering elsewhere in the Neotropics (Ruegg et al. 2014).

The model best explaining the origin of Canada Warbler populations in the Colombian Andes implied that isotopic values were most similar within basins or watersheds. This implies that the high ridgelines of the Andes (often > 4000 m) may act to structure the distribution of populations to some degree, as seen in some resident species complexes; for example, some species are present in more than one Andean cordillera within the Magdalena valley but are replaced by a sister species in the Cauca valley (Cadena et al. 2007). Given that Canada Warblers largely occupy elevations between 1000 m and 2250 m (Bayly pers. obs.), the high ridges (> 4000 m) are likely to be more of a barrier than valley bottoms (300–1000 m) as observed in some resident species occupying similar elevational ranges in the Andes (Valderrama et al. 2014). Unexpectedly, we found marked isotopic differentiation between populations occupying the northern extent (Santander) versus the southern extent of the western slope of the Eastern Andes, although this result must be treated cautiously due to the small sample size from Santander ($n = 6$). Nevertheless, close examination of the biogeography of the region reveals that a number of endemic bird species are found only within the area sampled in Santander (Renjifo et al. 2014), whose distributions are limited by barriers that include both high ridges and low dry valleys (Graham et al. 2010). The extreme western origin of birds in Santander remains one of the most surprising findings of this study and more sampling in that region is warranted to determine whether the pattern will hold with increased sample sizes.

5.5.1.2. Considerations for the conservation of migratory birds wintering in the Andes

Population declines in the Canada Warbler and other Nearctic–Neotropical migrants that spend the non-breeding season in the Andes are often associated with habitat loss and deterioration on the wintering grounds (Jones et al. 2004b, Colorado et al. 2012). The Canada Warbler shows a predominantly Andean distribution in northern South America, a region where over 90% of the Andean forest has been cleared (Henderson et al. 1991). For instance, in Colombia, 69% of the Andean forest was converted to grazing and agricultural land by 1998 (Etter et al. 2006), and the montane forest, where Canada Warblers are abundant, is one of the most fragmented ecosystems across the Colombian Andes (Armenteras et al. 2003). In addition, agroforestry systems such as shade coffee plantations, a habitat widely used by Canada Warblers (authors' pers. obs.), have been rapidly disappearing since the 1970s, with more than 60% of shade coffee being converted to sun coffee by 1990 in Colombia alone (Perfecto et al. 1996). These rapid and wide-reaching transformations in the Andes have no doubt played a role in the dramatic population declines of a number of Nearctic–Neotropical migratory birds, but such declines may be amplified by moderately strong connectivity between breeding and wintering populations in species like the Canada Warbler.

Increasing connectivity is expected to reduce gene flow and dispersal rates, rendering populations less able to adapt to a changing landscape and reducing the probability of individuals from less affected areas counteracting declines through dispersal (Webster et al. 2002, Jones et al. 2008). Given the moderately strong migratory connectivity between the wintering and breeding populations of Canada Warblers reported here, steeper population declines in specific regions of eastern North America (Sauer et al. 2017) could be related to differential rates of habitat loss or variation in habitat quality across the Colombian Andes. Indeed, the Magdalena Valley and the northern extent of the Eastern Andes, where most of the population was comprised of individuals from eastern North America, have been the regions most affected by deforestation and fragmentation associated with agricultural and grazing lands expansion (Rodríguez et al. 2004, Rodríguez-Eraso et al. 2013).

Further, environmental conditions are more diverse in the Eastern Andes, and its northern extent where we conducted our study (i.e. above 3° N) is characterized by lower precipitation during the driest period (January–March, Jaramillo-Robledo and Chaves-Córdoba 2000), which overlaps with the latter half of the overwinter period and preparations for spring migration. Seasonal fluctuations in rainfall are a key driver of seasonal changes in primary productivity and insect abundance in the tropics (Wolda 1980, Schloss et al. 1999) and dry conditions likely reduce habitat quality for migratory and resident birds through effects on food availability (Poulin et al. 1992, Marra and Holmes 2001, Williams and Middleton 2008, Studds and Marra 2011). Indeed, it has been shown that the residual effect of occupying drier habitats during the winter (e.g. reduced survival, lower body condition, delayed migration) can carry over to subsequent seasons and affect individual fitness and year-round population dynamics (Marra et al. 1998, Norris et al. 2004, Norris 2005). The potentially detrimental effects of drier conditions during the pre-migratory period in the northern Eastern Andes of Colombia are likely to be heightened by continued habitat loss, and the intensification and increased frequency of broad-scale climatic events with climate change (Timmermann et al. 1999, Cai et al. 2014), like the El Niño Southern Oscillation (ENSO), which induces drier than average conditions in Central and northern South America (Trenberth and Caron 2000).

Nonetheless, knowing where the populations in steepest decline are spending the non-breeding season is a major advance in our knowledge and is the first step to designing conservation actions for those populations most at risk. Indeed, from a conservationist's point of view, strong connectivity brings considerable advantages as it greatly increases the probability that targeted actions will actually assist those populations of greatest concern. Having demonstrated moderately strong connectivity for Canada Warbler populations overwintering in the Colombian Andes, a critical next step is to determine connectivity from across the non-breeding range, by sampling additional individuals from Costa Rica, Panama, Venezuela, Ecuador and Peru.

5.6. Acknowledgements

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Table 5.1 Locality data for study regions and study sites where Canada Warblers were captured in Colombia.

Study region	Study Sites	Department	Basin	Samples	Coordinates
East Slope of Western Andes					
Valle	Chicoral	Valle	Cauca	8	3°34′N 76°34′W
Jerico	Jericó	Antioquia	Cauca	15	5°48′N 75°48′W
	Támesis	Antioquia	Cauca	8	5°45′N 75°42′W
West Slope of Central Andes					
Fredonia	Fredonia	Antioquia	Cauca	6	5°56′N 75°39′W
East Slope of Central Andes					
Tolima	Ambalá	Tolima	Magdalena	7	4°28′N 75°12′W
West Slope of Eastern Andes					
Cundinamarca	La Fragua	Cundinamarca	Magdalena	50	4°18′N 74°31′W
	Los Vientos	Cundinamarca	Magdalena	24	4°21′N 74°31′W
	La Vuelta	Cundinamarca	Magdalena	21	4°19′N 74°28′W
Santander	Mesa de los Santos	Santander	Magdalena	2	6°55′N 73°03′W
	Reserva Bomarea	Santander	Magdalena	1	7°08′N 73°02′W
	San José de Suaita	Santander	Magdalena	3	6°09′N 73°25′W
East Slope of the Eastern Andes					
Boyacá	Santa María	Boyacá	Piedmont	15	4°50′N 73°15′W

Table 5.2 Results of model selection process examining the effect of region, Andean slope, and basin on breeding/natal origins (inferred from δ^2H values in flight feathers, δ^2H_f) of Canada Warblers overwintering in the Colombian Andes. A) All study regions were included; B) Santander was removed due to the anomalously negative δ^2H values in this region.

A. All regions	K^a	AIC_c	$\Delta AIC_c{}^b$	$w_i{}^c$	Cum. w_i
δ^2H_f ~Region	9	1396.09	0	1	1
δ^2H_f ~Basin	4	1434.77	38.67	0	1
δ^2H_f ~Slope	6	1438.69	45.59	0	1
δ^2H_f ~1	2	1566.47	170.38	0	1
B. Without Santander	K^a	AIC_c	$\Delta AIC_c{}^b$	$w_i{}^c$	Cum. w_i
δ^2H_f ~Basin	4	1340.14	0	0.82	0.82
δ^2H_f ~Slope	8	1343.99	3.85	0.12	0.94
δ^2H_f ~Region	6	1345.45	5.31	0.06	1
δ^2H_f ~1	2	1566.47	226.34	0	1

[a] Number of parameters

[b] $\Delta AIC_c = AIC_c$ - minimum AIC_c

[c] w_i = Akaike weight represents support for each model

Table 5.3 Results of a model selection process examining the relationship between natal/breeding origins (inferred from δ^2H values in flight feathers, δ^2H_f) of Canada Warblers and longitude and latitude of wintering sites sampled in the Colombian Andes. A) All study sites were included; B) Sites in Santander were removed due to the anomalously negative δ^2H values in this region.

A. All study sites	K[a]	AIC_c	ΔAIC_c[b]	w_i[c]	Cum. w_i
δ^2H_f ~ Lat+I(Lat^2)	4	1409.34	0	0.50	0.50
δ^2H_f ~ Lat+I(Lat^2) + Lon	5	1410.43	1.10	0.29	0.79
δ^2H_f ~ Lat+I(Lat ^2)+ Lon+I(Lon ^2)	6	1411.12	1.78	0.21	1
δ^2H_f ~ Lat+Lon	4	1433.04	23.70	0	1
δ^2H_f ~ Lat+ Lon+I(Lon ^2)	5	1433.17	23.84	0	1
δ^2H_f ~ Lat:Lon	3	1434.77	25.43	0	1
δ^2H_f ~ Lat	3	1435.33	25.99	0	1
δ^2H_f ~ Lon+I(Lon ^2)	4	1443.36	34.02	0	1
δ^2H_f ~ Lon	3	1447.13	37.79	0	1
δ^2H_f ~ Lon~1	2	1449.49	40.15	0	1
B. Without sites in Santander	K[a]	AIC_c	ΔAIC_c[b]	w_i[c]	Cum. w_i
δ^2H_f ~ Lon	3	1338.43	0	0.48	0.48
δ^2H_f ~ Lon+I(Lon ^2)	4	1340.42	1.99	0.18	0.66
δ^2H_f ~ Lat+Lon	4	1340.53	2.10	0.17	0.83
δ^2H_f ~ Lat+ Lon+I(Lon ^2)	5	1342.55	4.12	0.06	0.89
δ^2H_f ~ Lat+I(Lat ^2)+Lon	5	1342.59	4.16	0.06	0.95
δ^2H_f ~ Lat+I(Lat ^2) : Lon	4	1343.10	4.67	0.05	1
δ^2H_f ~ Lat:Lon	3	1361.61	23.18	0	1
δ^2H_f ~Lat	3	1362.64	24.21	0	1
δ^2H_f ~1	2	1449.49	111.06	0	1

[a] Number of parameters

[b] $\Delta AIC_c = AIC_c$ - minimum AIC_c

[c] w_i = Akaike weight represents support for each model

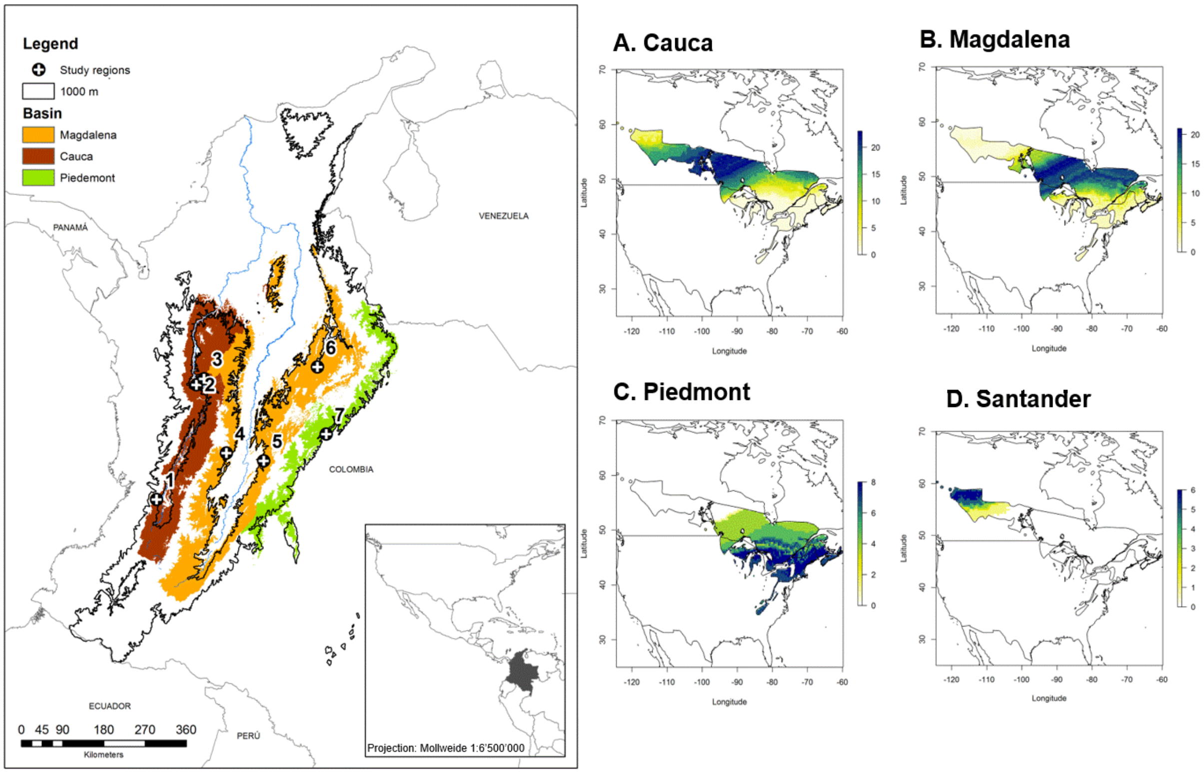


Figure 5.1 Left: Distribution map for the Canada Warbler across three basins in Colombia (Biomodelos 2015). Study regions are numbered as follows: 1 - Valle; 2 - Jerico; 3 - Fredonia; 4 - Tolima; 5 - Cundinamarca; 6 - Santander; 7 – Boyacá. Right hand map: Predicted breeding-natal origins based on an analysis of δ^2H_f values from feathers of birds wintering in: A) Cauca basin (*n* = 35); B) Magdalena basin (*n* = 102); C) Piedmont (*n* = 15); D) Santander (*n* = 6).An increasing probability of origin from a given region of the breeding distribution is represented by increasingly darker colours e.g. birds from the Cauca are most likely to come from the west of the breeding distribution (blue region), birds from the Piedmont from the southeast etc.

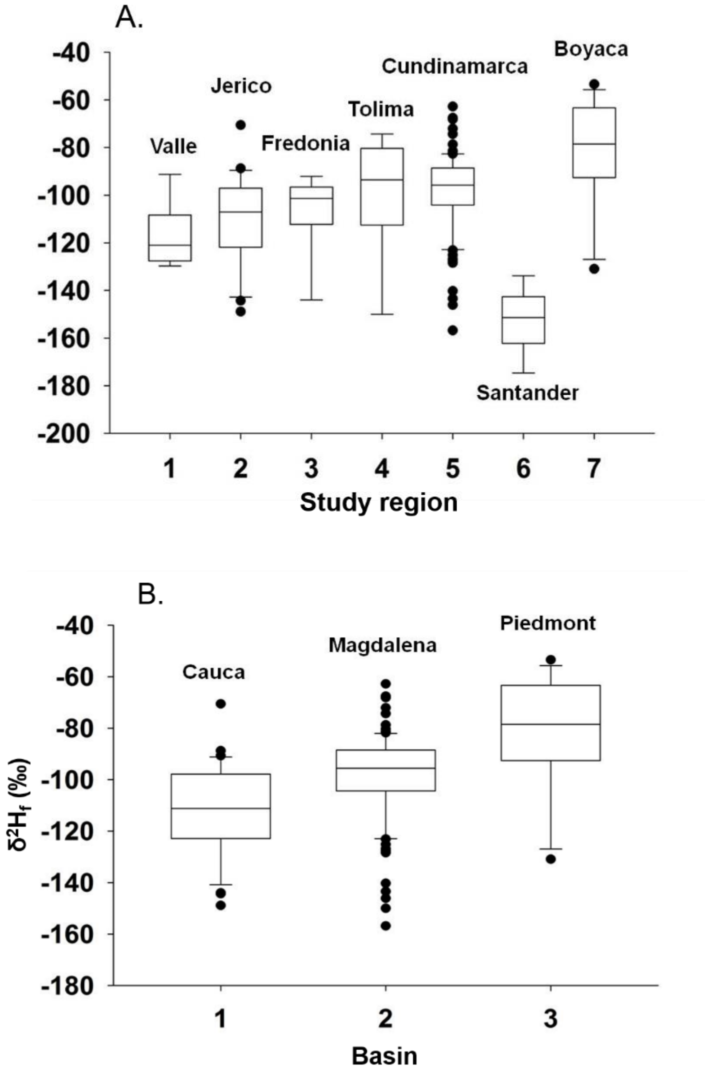


Figure 5.2 Feather δ^2H values (δ^2H_f) of Canada Warblers sampled in the Colombian Andes during the winter of 2014. A) δ^2H_f values in each study region and B) δ^2H_f values in each basin. Study regions and basins are organized longitudinally from west to east. Median, 10th, 25th, 75th, and 90th percentiles as vertical boxes with error bars are shown.

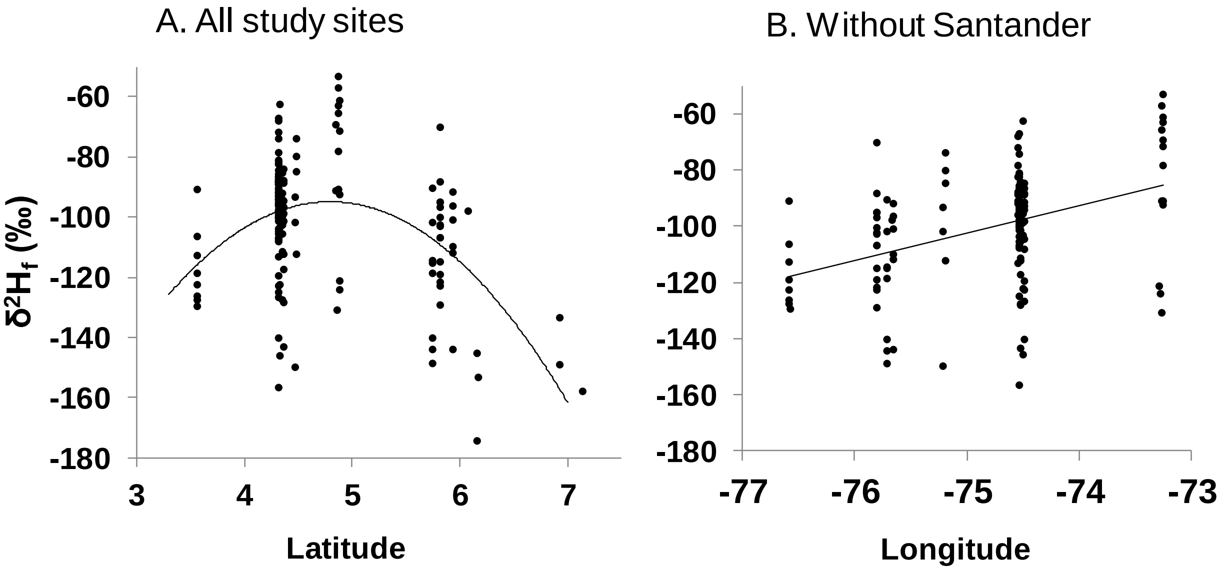


Figure 5.3 Changes in δ^2H values in feathers (δ^2H_f) of Canada Warblers sampled in the Colombian Andes during winter of 2014. A) When all sites were considered, latitude was the strongest predictor of natal/breeding origins of Canada Warblers. B) When sites in Santander were excluded (extreme negative values), longitude was the strongest predictor of natal/breeding origins, suggesting that the east-west geographic gradient of origin in North America is maintained from east to west in the Colombian Andes. The solid line is the predicted trajectory of δ^2H_f values from the following models: A) $\delta^2H_f = -410.9 + 131.8*Lat + –13.7*Lat^2$, where Lat is the latitude of the sampling sites in the Colombian Andes; and B) $\delta^2H_f = 621.7 + 9.7*Lon$, where Lon is the longitude of the sampling sites in the Colombian Andes. Coefficient estimates were derived from the top models in Table 5.3 A and 5.3 B respectively.

CHAPTER 6. SYNTHESIS

For several decades shade-grown coffee plantations have been recognized for their importance for conservation of Neotropical migratory birds. However, few studies have assessed the quality of shade-grown coffee plantations as winter habitat by comparing the quality of plantations to the mid-elevation forest from which they originated (i.e., Johnson et al. 2006, Bakermans et al. 2009). In addition few measurements of habitat quality have been used, with author's typically relying on density (Bakermans et al. 2009), which can be misleading when considered in isolation. The goal of this research was to assess the relative quality of shade-grown coffee plantations versus remaining forest as winter habitat for Swainson's Thrush (*Catharus ustulatus*) and Canada Warbler (*Cardellina canadensis*) wintering in Colombia (chapter 2), as well as assess the implications for species that do not use coffee plantations, like the Gray-cheeked Thrush (chapter 4). In order to assess the conservation value of these habitats at continental scales I also determined migratory strategies and migratory connectivity and assessed their relationship with habitat occupancy using an international automated telemetry array (Motus, chapter 3), geolocators (chapter 4), and stable isotopes (chapter 5). This research is unique because for the first time, measures of winter habitat quality at the population and individual level, along with state-of-the-art tracking technologies were combined to assess the suitability of two of the main habitats used by Neotropical migratory songbirds in northern South America. These varied perspectives allowed me to provide a composite picture of the effect of winter habitat on overwinter ecology, demographics, and migration strategies of Neotropical migrants.

In chapter 2, I compared four measures of winter habitat quality (daily and seasonal changes in body mass, age and sex ratios, density and stress levels) in Swainson's Thrush and two (daily and seasonal changes in body mass, and age and sex ratios) in Canada Warblers. My findings suggest that forest is a more suitable habitat than shade-grown coffee plantations as winter habitat for Swainson's Thrushes. However, the suitability of shade-grown coffee plantations increased during rainy years. Although Canada Warblers were more likely to occupy shade-grown coffee, the probability of males occupying forest increased during drier years. For both species mass declined from early to mid-winter, which coincides with the driest period in the study sites, although this decline was less pronounced in adult Swainson's Thrush overwintering in forest. These results build on previous research conducted in the Caribbean which suggest that habitat quality varies spatially and temporally in response to precipitation patterns and its influence on food abundance (Smith *et al.* 2010, Sillett *et al.* 2002).

My research provides the first direct evidence suggesting that severe drought from large-scale climatic events such as El Niño has detrimental effects on the quality of forest and shade-grown coffee plantations alike as winter habitats for Neotropical migrants (chapter 2). Daily and seasonal condition in Swainson's Thrush and Canada Warbler was lowest during the 2015/2016 non-breeding period, which coincided with one of the strongest El Niño events on record. By combining density and seasonal change in body mass as measures of winter habitat quality for Swainson's Thrush, I also provide evidence that El Niño events amplify the detrimental consequences of the dry season and can compromise the carrying capacity and quality of natural habitats. For instance, even though forest supported twice as many birds as coffee, seasonal body condition of adults in this habitat slightly increased in 2013 and 2014 and only decreased during the El Niño year. Although in general immatures lose mass over the winter, the decrease was steeper during the El Niño year in both habitats. My research suggests that the detrimental consequences of drought on winter habitat quality for insectivorous and frugivorous Neotropical migrants in northern South America are likely to be enhanced by the expected intensification and increased frequency of El Niño events with climate change (Timmermann et al. 1999, Cai et al. 2014).

Although winter habitat segregation by age and sex is widespread in some Neotropical migrants, my results show for the first time that the patterns of habitat occupancy arising from social mechanisms can change temporarily in response to habitat quality (chapter 2). For example, the number of dominant adult Swainson´s Thrush and dominant male Canada Warbler in forest increased during the El Niño year suggesting that competition for limited resources also increased. This is consistent with previous research showing that, when individuals of varying abilities compete to access limiting resources, dominance hierarchies emerge (Marra 2000). This finding contributes to the understanding of the factors regulating winter habitat occupancy and consequences of carry over effects.

The wintering period cannot be considered in isolation from other stages of the annual cycle such as migration or the breeding season. Indeed, the effects of winter habitat occupancy can affect migration schedules and carry over to subsequent seasons thereby producing residual effects on fitness of individuals and populations (Marra et al. 1998, Norris 2005, Newton 2006). However, assessing the direct effects of winter habitat occupancy on subsequent stages of the annual cycle of Neotropical migrants has been limited by an inability to track migrants directly from their wintering grounds to stopovers or breeding sites. By using automated VHF telemetry on a continental scale, I linked two different stages of the annual cycle and demonstrated that winter habitat occupancy affects migratory decisions and spring migration pace of Swainson's Thrush (chapter 3). Birds overwintering in forest departed later and migrated faster, and this pattern was maintained along the migratory trajectory. This suggests that during the pre-migratory period, birds in forest reached higher fuel loads than birds in coffee, and that food supply is likely the ultimate factor influencing optimal departure decisions. My research challenges the conventional wisdom about the benefits of earlier departure and shows for the first time that occupancy of Andean forests allows birds to depart later and fly faster, potentially decreasing costs associated with a longer migration.

Corticosterone is crucial in regulating daily and seasonal responses to energetic demands; and elevated levels in thrushes in forest (Chapter 2) are likely to be beneficial during the pre-migratory fattening process. For example, corticosterone promotes fat and protein catabolism to produce glucose, and in circumstances when food availability is high, elevated levels of corticosterone promote fattening (Beck et al. 2016). My study system precludes the estimation of fuelling rates (i.e., wintering and migrating birds mix during spring migration), however it is likely that the effect of elevated corticosterone levels in birds in forest during the winter carried over to the pre-migratory period and enhanced fuelling. This mechanism would allow bird in forest to reach high fuel loads and consequently migrate faster.

Despite the wide use of shade-coffee plantations by Neotropical migrants, Gray-cheeked Thrush avoided this agroecosystem and was found exclusively in forest during my research. Unlike Swainson's Thrush, Gray-cheeked Thrush spent the entire winter in montane forest, which makes this habitat critical for overwinter survival and preparation for spring migration. I showed that Andean forests are fuelling the first leg of spring migration since most birds travelled over 2000 km from the wintering grounds to their first spring stopover (chapter 4). Taken together, chapter 3 and 4 show the effect of winter habitats on migratory strategy and its energy contribution to spring migration which has been largely unappreciated.

Once critical winter habitats for Neotropical migrants have been identified, a second major challenge in conserving any migratory species is to determine migratory connectivity or where various populations breed, stop-over, and winter during their annual cycle (Webster et al. 2002). Knowledge of winter habitat needs, migratory connectivity, and a life-cycle conservation approach is critical to allocate funding effectively for protecting migratory bird populations (Martin et al. 2007). In chapters 4 and 5, I used geolocators and stable isotopes to provide a comprehensive picture of how information about migratory connectivity patterns, winter habitat loss and deterioration, and winter habitat quality can be combined to identify potential population-limiting processes, and to understand possible mechanisms driving population declines in Neotropical migrants.

A striking result of our geolocator analysis (chapter 4) was the strong migratory connectivity shown by the Gray-cheeked Thrush (Finch et al. 2017). Population spread was low which contrasts with the expectations of Finch et al. (2017) for eastern breeding populations of Neotropical migrants overwintering in South America. I suggested that although species overwintering in South America may have broad winter ranges, the amount of available land for Andean wintering species is limited. The effect of limited land availability across the Andes is likely to be enhanced by limited habitat availability for forest-dependent species which in turn might outweigh the effect of a broad winter range on expected patterns of population spread. By combining winter habitat use with migratory connectivity I established a link between declining eastern breeding populations and severe winter habitat loss, and suggest that strong migratory connectivity might amplify the negative effects of habitat loss for forest dependent species wintering in the Andes (Webster et al. 2002, Jones et al. 2008).

In chapter 5, by using stable hydrogen isotope analysis (δ^2H), I identified moderately strong migratory connectivity in Canada Warblers, and provided the first demonstration that the topography of the Andean mountains can act to shape the winter distribution of populations of a migratory bird. My findings for migratory connectivity alongside those related to winter habitat quality (chapter 2) provide critical information about the wintering ground conditions that are likely driving dramatic declines in Canada Warbler populations (Wilson et al. 2018). First, I showed that populations in steep decline in eastern North American are likely to overwinter in the northern extent of the Eastern Andes and across the Magdalena valley, regions severely affected by habitat loss and deterioration (chapter 5, Rodriguez et al 2004, Rodriguez-Erazo et al 2013). Second, in the Magdalena valley, where my study sites were located, female Canada Warblers were forced into shade-grown-coffee plantations where their overwinter physical condition is compromised (chapter

2). Body mass decline in females overwintering in shade-grown coffee plantations is likely to affect overwinter survival or produce negative residual effects that carry over to subsequent seasons and affect individual fitness and population dynamics (Johnson et al. 2006, Marra et al. 1998, Norris et al. 2004, Norris 2005). Indeed, recent research (Wilson et al. 2018) based on the connectivity results presented in González-Prieto et al. (2017, chapter 5) showed that declining recruitment across the breeding range, and steeper decline in abundance and apparent survival in eastern breeding populations is primarily related to land uses changes in the Andean winter grounds. Taken together, chapters 2, 4, and 5 suggest that the negative effects of winter habitat loss and poor winter habitat quality are likely to be amplified by moderately strong migratory connectivity in Canada Warbler and Gray-cheeked Thrush.

While my results suggest that conservation actions to protect, restore, or connect remnants of montane forest are clearly needed, the conservation value of shade-grown coffee plantations cannot be neglected. With only about 10% of the native forest in the northern Andes of South America remaining, shade coffee plantations are the only forest-like habitats left at montane elevations across several important wintering regions in the Neotropics. Furthermore, when winter habitat occupancy is affected by dominance behaviour, shade-grown coffee plantations might be the only habitat accessible to excluded individuals despite the potentially negative effects on survival. In Appendix 11, I summarized the main historical land-use changes that have transformed the Andean landscape; and that, in part, have driven conservation efforts of Neotropical migrants towards shade-grown coffee plantations. The findings of my research, along with the current requirements for shade-grown coffee certifications suggest that a re-evaluation of the criteria for these market-based conservation strategies and landscape conservation approaches are urgently needed.

Appendix 1. Analysis of daily and seasonal body mass changes by site in Swainson's Thrush and Canada Warbler.

Coefficients the model assessing the effect of the interaction site:habitat:year in daily and seasonal changes in mass in Swainson's Thrush and of the interaction habitat:site for Canada Warbler for pooled years.

A. Swainson's Thrush

	2013		2014		2015	
Habitat	Coffee	Forest	Coffee	Forest	Coffee	Forest
Daily mass change						
Fragua	0.12±0.02	0.15±0.02	0.09±0.02	0.09±0.02	0.08±0.02	0.07±0.02
Vuelta	0.12±0.03	0.18±0.03	0.12±0.03	0.15±0.02	0.08±0.02	0.09±0.02
Vientos	0.08±0.04	0.12±0.02	0.14±0.03	0.09±0.02	0.06±0.03	0.04±0.02
Seasonal mass change						
Fragua	0.30±0.30	0.30±0.18	0.03±0.18	0.06±0.12	0.00±0.12	-0.27±0.09
Vuelta	0.21±0.24	0.24±0.18	0.15±0.18	0.60±0.18	-0.15±0.12	-0.15±0.12
Vientos	-0.06±0.30	-0.12±0.12	0.06±0.15	-0.15±0.18	-0.06±0.15	-0.30±0.12

B. Canada Warbler

	Coffee	Forest
Daily mass change		
Intercept 9.12		
Fragua	0.04±0.01	0.04±0.01
Vientos	0.03±0.01	0.03±0.01
Vuelta	0.03±0.01	0.04±0.01
Seasonal mass change		
Intercept 9.62		
Fragua	0.03±0.03	0.06±0.06
Vientos	-0.09±0.06	-0.12±0.06
Vuelta	-0.03±0.06	-0.01±0.06

Appendix 2. Modelling to assess patterns of daily and seasonal mass change in wintering Swainson´s Thrush.

Models assessing the pattern of (A) daily and (B) seasonal body mass change at the population level (i.e., all individuals at first capture) in Swainson’s Thrush overwintering in the Colombian Andes during winters 2013, 2014, and 2015; and when years were pooled (All). (C). Change in body mass was calculated as the change in mass between first capture and the subsequent recapture; T= time, D= day, I= number of days since the bird was captured.

Year	Model	K[a]	AICc	Δ*i*[b]	W*i*[c]	Cum. W*i*
A. Population daily mass change						
2013	T	3	907.04	0	0.56	0.56
	T + T2	4	908.48	1.44	0.27	0.83
	T+ T2+ T3	5	909.44	2.4	0.17	1
2014	T	3	1538.5	0	0.56	0.56
	T + T2	4	1539.7	1.21	0.3	0.86
	T+ T2+ T3	5	1541.3	2.73	0.14	1
2015	T	3	1944.9	0	0.45	0.45
	T + T2	4	1945.7	0.81	0.3	0.75
	T+ T2+ T3	5	1946.1	1.21	0.25	1
All	T + T2	4	4419.3	0	0.59	0.59
	T + T2+ T3	5	4421.3	2	0.22	0.81
	T	3	4421.6	2.24	0.19	1
B. Population seasonal mass change						
2013	D+D2	4	930.08	0	0.53	0.53
	D	3	931.5	1.43	0.26	0.8
	D+D2+D3	5	932	1.92	0.2	1
2014	D	3	1551	0	0.44	0.44
	D+D2	4	1551.2	0.2	0.4	0.83
	D+D2+D3	5	1552.9	1.93	0.17	1
2015	D	3	1956.2	0	0.56	0.56
	D+D2	4	1957.1	0.92	0.35	0.91
	D+D2+D3	5	1959.9	3.75	0.09	1
All	D+D2	4	4466.3	0	0.49	0.49
	D+D2+D3	5	4466.8	0.47	0.39	0.88
	D	3	4469.1	2.76	0.12	1
C. Individual seasonal mass change						
All	I	3	376.5	0	0.49	0.49
	I + I2	4	377.61	1.11	0.28	0.77
	I + I2+ I3	5	377.98	1.48	0.23	1

[a] Number of parameters

[b] Δ*i* (Δ*i*= $\mathrm{AIC}_{\mathrm{ci}}$ – minimum AICc)

[c] Akaike weight represents support for each model

Appendix 3. Modelling to assess patterns of daily and seasonal mass change in wintering Canada Warbler.

Models assessing the pattern of (A) daily and (B) seasonal body mass change at the population level (i.e., all individuals at first capture) in Canada Warbler overwintering in the Colombian Andes during winters 2013, 2014, and 2015; and when years were pooled (All). (C). The dependent variable change in body mass was calculated as the change in mass between first capture and the subsequent recapture; T= time, D= day, I= number of days since the bird was captured.

Year	Models	K[a]	AICc	Δi[b]	Wi[c]	Cum. Wi
A. Population daily mass change						
2013	T	3	84.58	0	0.5	0.5
	$T + T^2$	4	85.9	1.32	0.26	0.77
	$T + T^2 + T^3$	5	86.12	1.54	0.23	1
2014	T	3	108.08	0	0.69	0.69
	$T + T^2$	4	110.26	2.18	0.23	0.92
	$T + T^2 + T^3$	5	112.42	4.34	0.08	1
2015	T	3	128.67	0	0.66	0.66
	$T + T^2$	4	130.76	2.09	0.23	0.89
	$T + T^2 + T^3$	5	132.25	3.58	0.11	1
All	T	3	320.97	0	0.66	0.66
	$T + T^2$	4	322.94	1.97	0.25	0.91
	$T + T^2 + T^3$	5	324.89	3.91	0.09	1
B. Population seasonal mass change						
2013	$D+D^2$	4	80.57	0	0.57	0.57
	D	3	82.28	1.71	0.24	0.81
	$D+D^2+D^3$	5	82.83	2.26	0.19	1
2014	D	3	115.29	0	0.59	0.59
	$D+D^2$	4	116.94	1.65	0.26	0.85
	$D+D^2+D^3$	5	117.93	2.64	0.16	1.01
2015	$D+D^2$	4	141.61	0	0.47	0.47
	D	3	142.19	0.58	0.35	0.82
	$D+D^2+D^3$	5	143.57	1.96	0.18	1
All	$D+D^2$	4	335.65	0	0.66	0.66
	$D+D^2+D^3$	5	337.24	1.59	0.3	0.96
	D	3	341.23	5.58	0.04	1
C. Individual seasonal mass change						
All	I	3	107.63	0	0.45	0.45
	$I+I^2$	4	107.94	0.31	0.39	0.84
	$I+I^2+I^3$	5	109.76	2.13	0.16	1

[a] Number of parameters

[b] Δi (Δi= AIC_{ci} – minimum AICc)

[c] Akaike weight represents support for each model

Appendix 4. Swainson's Thrush: Modelling of daily and seasonal wintering mass change by year.

Candidate model set for predicting (A) daily and (B) seasonal body mass change in Swainson's Thrush overwintering in Colombia from 1 December to 28 February during the winters of 2013, 2014, 2015. T=First capture time, H=Habitat, D=Capture day (Day 1= 1 December).

Year	Model	K[a]	AICc	Δ*i*[b]	W*i*[c]	Cum. W*i*
A. Population daily mass change						
2013	T:H:Age	6	905.32	0	0.51	0.51
	T:H	4	906.6	1.28	0.27	0.78
	T	3	907.04	1.72	0.22	1
	Null	2	930.12	24.79	0	1
2014	T:H:Age	6	1532.24	0	0.94	0.94
	T	3	1538.52	6.28	0.04	0.98
	T:H	4	1540.25	8.01	0.02	1
	Null	2	1549.14	16.9	0	1
2015	T:H:Age	6	1936.77	0	0.98	0.98
	T	3	1944.93	8.16	0.02	0.99
	T:H	4	1946.71	9.94	0.01	1
	Null	2	1957.92	21.15	1	1
B. Population seasonal mass change						
2013	D:H:Age+D^2:H:Age+T	11	896.65	0	0.97	0.97
	D:H+D^2:H+T	7	904.11	7.46	0.02	1
	D+D^2+T	5	908.75	12.1	0	1
	Null	2	930.12	33.47	0	1
2014	D:H:Age+T	7	1532.4	0	0.97	0.97
	D+T	4	1540.28	7.88	0.02	0.99
	D:H+T	5	1542.33	9.93	0.01	1
	Null	2	1549.14	16.74	0	1
2015	D:H:Age+D^2:H:Age+T	11	1929.88	0	1	1
	D+D^2+T	5	1943.71	13.83	0	1
	D:H+D^2:H+T	7	1944.36	14.48	0	1
	Null	2	1957.92	28.03	0	1

[a] Number of parameters

[b] Δ*i* (Δ*i*= AIC_{ci} – minimum AICc)

[c] Akaike weight represents support for each model

Appendix 5. Canada Warbler: Modelling of daily and seasonal wintering mass changes by year.

Candidate model set for predicting (A) daily and (B) seasonal body mass change in Canada Warbler overwintering in Colombia from 1 December 1 to 30 March during the winters of 2013, 2014, 2015. H=Habitat, D= First capture day (Day 1= 1 December).

Year	Model	K[a]	AICc	Δi[b]	W*i*[c]	Cum. W*i*
A. Population daily mass change						
2013	Time:H:Sex	6	83.15	0	0.46	0.46
	Time	3	84.58	1.43	0.22	0.68
	Null	2	84.68	1.53	0.21	0.89
	Time:H	4	86.03	2.88	0.11	1
2014	Time:Sex	4	104.59	0	0.78	0.78
	Time	3	108.08	3.49	0.14	0.91
	Time:H	4	109.21	4.63	0.08	0.99
	Null	2	113.36	8.77	0.01	1
2015	Time:H:Sex	4	122.34	0	0.94	0.94
	Time	2	128.67	6.34	0.04	0.98
	Time:H	3	130.48	8.15	0.02	1
	Null	1	142.72	20.38	0	1
B. Population seasonal mass change						
2013	D:H + D^2:H+ Time	7	78.37	0	0.6	0.6
	D+ D^2+ Time	5	79.02	1.11	0.35	0.95
	Null	2	84.68	6.31	0.03	0.97
	D:H:Sex+ D^2:H:Sex+Time	11	84.69	6.31	0.03	1
2014	D:Sex+ Time	5	109.71	0	0.43	0.43
	D+ Time	4	109.94	0.23	0.38	0.81
	D:H+Time	5	112.25	2.53	0.12	0.93
	Null	2	113.36	3.65	0.07	1
2015	D+ D^2+ Time	5	124.39	0	0.83	0.83
	D:H+ D^2:H+Time	7	128.83	4.43	0.09	0.92
	D:H:Sex+ D^2:H:Sex+Time	11	129.11	4.71	0.08	1
	Null	2	142.72	18.32	0	1

[a] Number of parameters
[b] Δi (Δi= AIC_{ci} – minimum AICc)
[c] Akaike weight represents support for each model

Appendix 6. Swainson's Thrush: Coefficients estimated from top models of daily and seasonal winter mass changes.

Coefficient estimates and ± standard error obtained from the top model predicting daily (A) and seasonal (B) mass change in Swainson's Thrush from data across years.

Model	I	I2
A. Daily mass change		
2013:Forest:Adult	0.54±0.16	-0.02±0.01
2014:Forest:Adult	0.58±0.15	-0.02±0.01
2015:Forest:Adult	0.50±0.15	-0.02±0.01
2013:Coffee:Adult	0.62±0.19	-0.03±0.01
2014:Coffee:Adult	0.54±0.16	-0.02±0.01
2015:Coffee:Adult	0.45±0.16	-0.02±0.01
2013:Forest:Immature	0.28±0.15	0.00±0.01
2014:Forest:Immature	0.34±0.14	-0.01±0.01
2015:Forest:Immature	0.28±0.15	-0.01±0.01
2013:Coffee:Immature	0.23±0.17	0.00±0.01
2014:Coffee:Immature	0.44±0.16	-0.01±0.01
2015:Coffee:Immature	0.28±0.15	-0.01±0.01
B. Seasonal mass change		
2013:Forest:Adult	0.03±0.6	0.01±0.00
2014:Forest:Adult	0.30±0.6	0.00±0.00
2015:Forest:Adult	-0.16±0.3	0.00±0.00
2013:Coffee:Adult	-1.53±0.9	0.03±0.00
2014:Coffee:Adult	-0.38±0.06	0.01±0.00
2015:Coffee:Adult	-0.53±0.06	0.01±0.00
2013:Forest:Immature	-0.05±0.03	0.00±0.00
2014:Forest:Immature	-0.86±0.03	0.01±0.00
2015:Forest:Immature	-1.85±0.03	0.02±0.00
2013:Coffee:Immature	-1.18±0.06	0.02±0.00
2014:Coffee:Immature	-0.57±0.06	0.01±0.00
2015:Coffee:Immature	-1.96±0.03	0.02±0.00

Appendix 7. Canada Warbler: Coefficients estimated from top models of daily and seasonal wintering mass changes

Coefficient estimates and ± standard error obtained from the top model predicting (A) daily and (B) seasonal mass change in Canada Warbler across years.

Model	I	I2
A. Daily mass change		
Coffee:Female	0.04±0.01	
Forest:Female	0.02±0.01	
Coffee:Male	0.05±0.01	
Forest:Male	0.06±0.01	
B. Seasonal mass change		
Coffee:Female	-0.30±0.15	0.00±0.00
Forest:Female	-0.60±0.30	0.00±0.00
Coffee:Male	-0.30±0.15	0.00±0.00
Forest:Male	-0.06±0.30	0.00±0.00
Coffee:2013	-0.60±0.30	0.01±0.01
Forest:2013	-0.06±0.30	0.00±0.00
Coffee:2014	-0.01±0.12	0.00±0.00
Forest:2014	-0.30±0.30	0.00±0.00
Coffee:2015	-0.30±0.30	0.00±0.00
Forest:2015	-0.06±0.30	0.00±0.00

Appendix 8. Generalized Lineal Models evaluating habitat occupancy in Swainson's Thrush and Canada Warbler

Generalized Lineal Models evaluating the likelihood of individuals of (A) Swainson's Thrush and (B) Canada Warbler occupying forest or coffee in the Colombian Andes during the winters of 2013, 2014 and 2015 in relation to year, age, and the interaction between year and age.

Models	K[a]	AICc	Δi[b]	W*i*[c]	Cum. W*i*
A. Swainson's Thrush					
Year	3	1510.98	0	0.77	0.77
Year:Age	6	1513.80	2.82	0.19	0.96
Null	1	1517.48	6.50	0.03	0.99
Age	2	1519.46	8.49	0.01	1
B. Canada Warbler					
Year	3	302.48	0	0.75	0.75
Year:Sex	6	305.07	2.59	0.21	0.96
Sex	2	309.78	7.29	0.02	0.98
Null	1	309.78	7.30	0.02	1

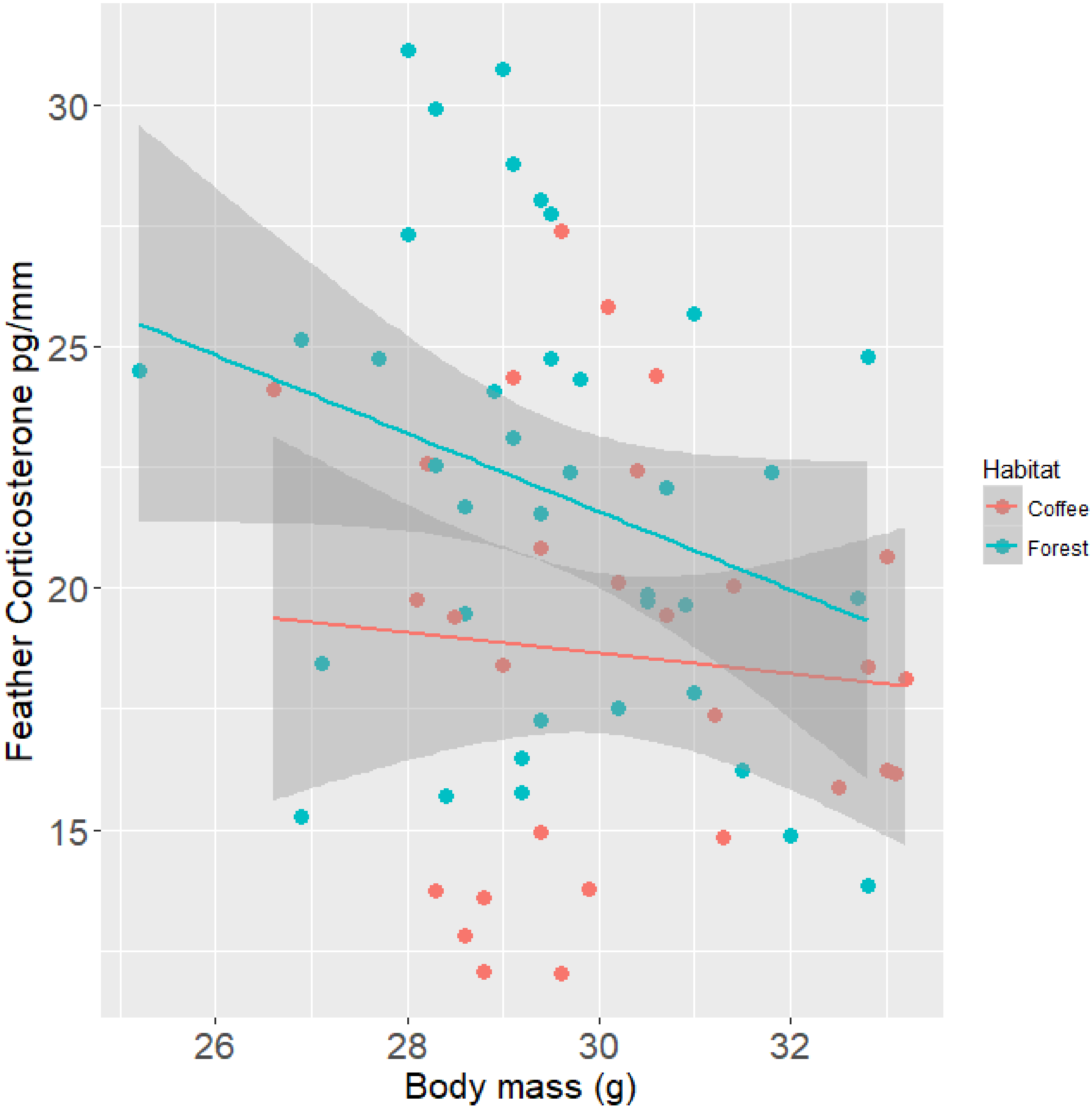
[a] Number of parameters

[b] Δi (Δi= AIC_{ci} – minimum AICc)

[c] Akaike weight represents support for each model

Appendix 9. Relationship between mass and corticosterone levels in Swainson's Thrush occupying forest and shade-grown coffee plantations in winter.

Relationship between mass at first capture and corticosterone values during the winter in Swainson's Thrush overwintering in shade-grown coffee plantations and forests in the Colombian Andes.



Appendix 10. Spring and fall stopovers results for Gray-cheeked Thrush

Spring and fall stopovers estimated with the function stationary.migration.summary in “FlightR”. Stationary periods longer than three twilights (i.e., 1.5 days) were considered stopovers. Stopover length= Number of days. ± standard error.

Geolocator	Season	Site	Latitude	Longitude	Stopover length
114	Spring	Cuba	21.6±3	-79.89±3	10
	Spring	Ontario	43.65±3	-77.89±2	7
	Breeding	Quebec	54.45±0	-69.68±1	116
	Fall	Ontario	49.5±6	-79.62±1	14
	Fall	Honduras	14.85±3	-88.49±1	32*
	Fall	Costa Rica	9.45±2	-83.85±2	
302	Spring	Guatemala	15.75±3	-90.7±2	8
	Spring	Ontario	45.45±2	-78.26±3	7
	Breeding	Quebec	56.7±0	-66.36±2	112
	Fall	Quebec	51.3±4	-71.29±4	13
	Fall	New York	43.2±5	-72.83±2	4
	Fall	Florida/Cuba	26.1±5	-82.26±1	4
	Fall	Nicaragua	13.5±3	-84.68±1	31
	Fall	Panama	8.55±1	-79.65±1	9
314	Spring	Kentucky	37.35±3	-83.65±2	12
	Spring	Quebec	49.05±2	-72.27±3	6
	Breeding	Quebec	56.7±0	-69.7±1	102
	Fall	Quebec	47.25±6	-74.92±2	10
	Fall	Pennsylvania	42.75±6	-80.21±1	14
	Fall	Honduras	15.3±5	-86.27±2	29*
	Fall	Panama	9±2	-81.26±3	
303	Spring	Alabama	33.75±6	-87.62±2	6
	Spring	Minnesota	39.15±3	-76.68±2	9
	Breeding	Quebec	51.75±0	-63.18±1	112
	Fall	Quebec	47.25±5	-69.92±2	8
	Fall	New York	43.65±5	-75.08±2	6
	Fall	Virginia	38.25±5	-80.59±1	13
	Fall	Yucatan	19.8±6	-86.61±2	15

Continuation Appendix 10

Geolocator	Season	Site	Latitude	Longitude	Stopover length
114	Spring	Northern Colombia	9.45±5	-74.62±1	13
	Spring	Mississippi	31.05±1	-91.04±0	4
	Spring	Pennsylvania	41.4±3	-78.52±3	6
	Spring	Quebec	54±2	-70.45±3	6
	Breeding	Quebec/Nunavut	58.95±1	-68.86±3	104
	Fall	Quebec	53.1±6	-73.46±2	8
	Fall	Virginia	36.9±4	-79.33±0	18
	Fall	Nicaragua	13.95±4	-85.03±1	8
316	Spring	Costa Rica	9.9±2	-84.25±2	7
	Spring	Quebec	49.05±2	-72±3	6
	Breeding	Quebec	55.35±1	-71.2±1	98
	Fall	Quebec	50.4±7	-78.55±1	13
	Fall	Panama	9.45±2	-82.69±2	12
97	Spring	Yucatan	20.25±2	-88.07±1	8
	Spring	West Virginia	39.15±3	-81.6±3	6
	Breeding	Quebec	54.9±0	-68.87±1	105
	Fall	New York	43.65±4	-74.42±1	4
	Fall	Caribbean	24.3±5	-78.39±1	13

Appendix 11. Conservation of Nearctic Neotropical migrants: The coffee connection revisited.

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Populations of Nearctic-Neotropical migratory songbirds that overwinter in South America are declining at greater rates than those wintering elsewhere (NABCI 2012). Persistent population declines over the last 50 years in species over-wintering primarily in montane habitats in the northern Andes of South America are associated with habitat loss and deterioration on the wintering grounds (Jones et al. 2004a, González-Prieto et al. 2017, Kramer et al. 2018, Wilson et al. 2018). For instance, species of conservation concern such as the Cerulean Warbler (*Setophaga cerulea*), Canada Warbler (*Cardellina canadensis*), and Olive-sided Flycatcher (*Contopus cooperi*) have a predominantly Andean wintering distribution and have experienced steep declines in their populations in recent decades (Sauer et al. 2017).

The tropical Andes represent an exclusive wintering region for several Neotropical migrants and are recognized for their elevated biological richness and high levels of endemism across a range of resident taxa. Yet, this region has lost over 90% of its original vegetation cover (Henderson et al. 1991). The current extent and spatial pattern of habitat transformation observed in the Andes are the result of historic and ongoing anthropogenic processes (Etter et al. 2008). For example, in Colombia, land use changed from crop cultivation in the sixteenth century to a system dominated by grazing in modern times. The continuous expansion of cattle pastures since the mid-1800s has been one of the major drivers of long-lasting transformations of the Andean landscape (Etter et al. 2008). As result, the landscape at montane altitudes (1000-3500 m.a.s.l) is composed of a mosaic where exotic grasses and crops are the predominant vegetation cover, and the remaining montane forests are highly fragmented (Armenteras et al. 2003, Rodríguez-Eraso et al. 2013).

Unprecedented rates of loss of natural habitats used by Neotropical migrants have directed conservation efforts towards shade-grown coffee plantations, which are one of the few remaining “forested” areas in mid- to high-elevation mountain ranges in Latin America (Perfecto et al. 2005).

The Colombian Andes, and the coffee growing region of northern South America, have experienced two key landscape-scale transformations associated with coffee production (Guhl-Corpas 2006). First, during the initial establishment of coffee plantations (1850-1970), natural forest was replaced by shade-grown coffee plantations where the native canopy was maintained or replaced, and the understory was replaced by coffee bushes (Moguel and Toledo 1999). From the 1970s to the present time, technological modifications transformed shade-grown coffee plantations into agroecosystems with lower structural and floristic diversity, where intensively managed plantations are grown in full sun (Perfecto et al. 1996, Rice 1999).This change to “sun coffee” arose to increase coffee production and in response to the spread of the devastating coffee rust (*Hemileia vastatrix*) disease in Latin America. By reducing shade through the removal of shade trees, conditions for the growth and dispersal of the fungus decreased. These dramatic transformations in the Andean landscape have no doubt played a role in the steep population declines of a number of Nearctic–Neotropical migratory birds overwintering in the Andes of northern South America.

The conservation value of shade-grown coffee for Neotropical migrants in northern South America is related, in part, to its distribution. Ideal conditions for coffee production in Colombia are found in the Andean mountains between 1200 and 1800 m, which overlaps with the elevation belt holding the highest concentration of migratory landbird species in the country (Díaz-Bohórquez et al. 2014). The importance of shade coffee plantations for conservation of Neotropical migratory birds is also related to the observations that shaded-coffee plantations tend to have higher species richness and abundance than other agroecosystems (Reviewed by Komar 2006) or species richness is comparable to natural ecosystems (Tejada-Cruz and Sutherland 2004). Some species found in shade coffee plantations are as or more abundant in shade coffee plantations than in natural forest habitats (e.g., Canada Warbler; Cerulean Warbler; Blackburnian Warbler*, Setophaga fusca;* Tennessee Warblers, *Oreothlypis peregrina;* Ovenbird, *Seiurus aurocapilla,* Swainson’s Thrush, *Catharus ustulatus*) (Komar 2006, Bakermans et al. 2009, Gomez et al. 2013). Some species overwintering in shade-grown coffee increase their daily and overwinter body condition and have high overwinter survival, and high between-season return rates (Bakermans et al. 2009, Colorado and Rodewald 2017).

Shade coffee production systems and terminology vary widely across Latin America from rustic or traditional systems where coffee is grown under the natural forest, to technified shade systems where the forest is removed and replaced (Gobbi 2000). In Colombia, coffee is technically considered shade-grown when the density of any shade species is higher than 50 trees per hectare, and semi-shaded when the shade density is between 20 and 50 trees per hectare (Moreno 2007). The shade can be composed by a single species forming a single vertical stratum, or by various species of, for example, leguminous nitrogen-fixing trees of the genera *Inga*, *Albizzia*, *Leucaena*, or *Erythrina* which form a multi-stratum. As a strategy to diversify farmer's income, native (i.e., *Cordia alliodora*) or introduced (i.e., *Pinus oocarpa* or *Eucalyptus grandis*) species of commercial interest are also often used as shade (Farfán-Valencia 2007).

Shade-grown coffee supports high levels of biodiversity across different taxa from insects to mammals (Perfecto *et al.* 1996), and bird species richness often declines with agricultural intensification (Perfecto et al. 2003). Shade trees in coffee plantations provide important ecological services including soil protection against erosion, replenishment of organic matter throughout leaf litter production, carbon sequestration and, perhaps most importantly for farmers, nitrogen fixation (Rice 1999, Soto-Pinto et al. 2009). This agroecosystem also provides habitat for native predators of coffee pests including migratory birds and for pollinators that contribute to higher coffee productivity and quality (Klein et al. 2003, Ricketts et al. 2004, Karp et al. 2013). Despite the value of the services provided by shade trees in coffee plantations, these traditional management practices are rapidly disappearing. In Colombia alone, sun coffee plantations increased from 36% in 1997 to 56% in 2013, while shade-grown coffee decreased from 23% in 1997 to 10% in 2013 with the steepest decline occurring between 2007 to 2013 (Escobar 2013).

Coffee drinkers can contribute to the conservation of surrogate habitats for wintering Neotropical migrants by becoming informed, choosing certified coffees that promote sustainable agricultural practices, and by contributing to the growth of the shade coffee market by increasing demand. Coffee certification programs have three main categories that assign environmental, social and or economic value to coffee: shade-grown, organic and fair trade. Shade-grown certifications that contribute to the protection of winter habitat for migratory birds include Bird Friendly and Rainforest Alliance. The Bird Friendly certification was developed by the Smithsonian Migratory Bird Center and is based on decades of research aimed at understanding the habitat needs of birds and other wildlife in shade-grown coffee plantations. All Bird Friendly coffee is certified Organic, and additional certification standards include a canopy height of 12m, a minimum 40% canopy cover measured during dry season after pruning, and a complex floristic diversity and structure. The Rainforest Alliance certification promotes sustainable agriculture by protecting soils and water sources, decreasing waste, and improving living conditions in coffee farms. To obtain certification, farms must maintain at least 15% of the native vegetation or a minimum canopy cover of 40% measured before pruning and during the rainy season when foliage is denser, and a minimum of 12 native species as shade in the coffee plantations, as well as complying with several infrastructural and management requirements (SAN 2017). One of the current challenges of shade-grown certification programs to provide robust benefits for the conservation of winter habitat of Neotropical migrants is the mismatch between the certification at the farm scale and the scale at which desired conservation results are needed (Tscharntke et al. 2015). The limitations of dispersed certified farms for habitat conservation need to be considered by the certification programs and landscape approaches are clearly needed (Tscharntke et al. 2015).

Coffee is the second-most traded commodity in the world and its popularity has led to several innovations to meet rising demand. Changes in coffee systems to increase production have included the reduction or elimination of shade trees, the intense use of pesticides and synthetic fertilizers, and the development of new coffee varieties that allow for higher yields and resistance to sun and diseases (Arcila-Pulgarín 2007). For instance, broad-spectrum organophosphate pesticides are widely sprayed on coffee bushes to control the coffee borer beetle (*Hypothenemus hampei*). In several regions of the Neotropics, fumigation overlaps with the overwintering period of migrant songbirds and/or with preparations for migration in spring (December to March). Such practices will affect the suitability of shade coffee plantations as overwinter habitat for Neotropical migrants by decreasing insect availability if not by causing direct physiological effects on birds. Organic certified coffee assures consumers that several synthetic herbicides, pesticides and fertilizers were not used during coffee production. In North America, the United States Department of Agriculture (USDA) Organic certified coffee is produced under the standards established by the USDA National Organic Program, and the Canada Organic certification standards are regulated by the Canadian Food Inspection Agency (CFIA). While complying with shade standards is not a requirement for this certification, by consuming Organic coffee we can support clean production systems that provided healthy ecosystems and healthy coffee. Fairtrade certification guarantees that coffee producers organized in cooperatives or associations receive a Fairtrade Premium and at least a minimum price per pound set by Fairtrade International to cover production costs and act as a safety net when market prices fall below sustainable levels. While Organic and Fairtrade certified producers may obtain some economic benefit from their certification status, their farms may not necessarily protect as much biodiversity or provide quality winter habitat for migrants, in contrast to shade-certified farms (Philpott et al. 2007).

Rigorous and consistent assessment of the effect of certifications on the environment and on farmers livelihood assets are scarce; however, certifications are more likely to generate more positive than negative impacts on ecological and economic sustainability (Bray and Neilson 2017, DeFries et al. 2017). Economic benefits for farmers might be more closely associated with enhanced yields, increased resilience, reduced dependence on agrochemicals and increased access to credit than with price premiums or overall household income. Less quantifiable benefits may include improved farm and risk management, arguably better health and safety practices, improved local soil and water quality, and an increase in physical capital by investing certification premiums on farm equipment. Despite the incentives, certification costs such as modifying or implementing production, management and administration systems to fulfill standards, and the cost of actually obtaining and maintaining certifications represent a barrier for some farmers since the financial gains may not be enough to outweigh costs (Philpott et al. 2007). Smallholder farmers and laborers in rural areas in the tropics are one of the lowest income groups in the world (Cruz et al. 2015) and likely do not have access to the information or cannot afford the cost of certification (DeFries et al. 2017). There is a clear need to develop mechanisms to ensure that low income farmers have the opportunity to benefit from participation in market-based conservation strategies (Gobbi 2000).

In optimal areas for coffee production where coffee is grown with and without shade, shade improves the physical aspects of the bean (e.g., colour, size, density) and cup quality, which ultimately improves farmer’s profits (Vaast et al. 2006). Incorporating robust technical support during shade-grown certification processes to improve coffee quality may provide economic incentives to produce shade-grown coffee while compensating the decrease in productivity associated with shade in several regions of Latin America. The price premiums of high coffee quality can surpass more than 100% of the market price of standard coffee quality (Vaast et al. 2006), and can reduce exposure and vulnerability to the devastating effects of low coffee prices on the landscape (i.e., replacement of shade coffee to cattle pastures) and rural economies in Latin America (Bacon 2005).

Two species of coffee are commercially cultivated worldwide *Coffee arabica* (Arabica) and *Coffee canephora* (Robusta). Arabica is the most widely consumed in the world and the principal variety grown throughout Latin America. Coffee production requires specific conditions of soil, temperature, and precipitation (Arcila-Pulgarín 2007). These conditions, along with socioeconomic factors vary between and within countries and determine farming practices, and the selection of coffee varieties that adjust to the production system. For instance, shade is required in regions of Colombia above 9°N where coffee is produced at lower altitudes and higher temperatures, and in Andean regions with bimodal precipitation patterns, extended soil moisture deficits, and high solar radiation intensity (Arcila-Pulgarín 2007). It follows, that shade-grown coffee certification standards are challenging or unrealistic to meet in many regions with heavy annual cloud cover, high rain fall, and high humidity without compromising yields. Indeed, in the Andean mountains of Colombia sun coffee production has increased in those regions. In the central region of the Central Andes of Colombia the production of sun coffee increased to 80% between 1997 to 2013, while in drier and warmer regions at the northern extent of the Eastern Andes and along the Caribbean coast the increase was only 15% in the same period (Escobar 2013). While increasing participation by setting lower standards is not optimal, more comprehensive market-based conservation strategies that facilitate their adoption and success in regions where sun coffee prevails are needed. For example, forest restoration and connecting corridors in regions less suitable for shade coffee might offer an alternative to farmers to engage in conservation of winter habitat for Neotropical migrants, while gaining benefits such as increased rates of pollination and resilience to pests (Ricketts et al. 2004, Imbach et al. 2017).

Despite the importance of shade-grown coffee plantations for overwintering or staging Neotropical migrant songbirds, this habitat clearly cannot replace native forest. Indeed, the conservation value of shaded coffee may be higher in areas of high deforestation and those lacking protected areas, where plantations may be the only forest-like habitat suitable for migrants (Perfecto et al. 1996, Bakermans et al. 2009). Neotropical migrants have been forced into this agroecosystem in response to the loss of natural habitat, and the quality of shade coffee relative to the native forests from where they were carved is still to be fully addressed (but see Bakermans et al. 2009, Bayly et al. 2016). While conservation efforts to maintain shade-coffee plantations are critical, efforts to restore or protect remaining forest are also needed.

Wide-reaching transformations in the Andean landscape and the rapid loss of shade-grown coffee plantations have surely contributed to the dramatic population declines in several Neotropical migrants. For instance, over 60% of the Canada Warbler population has been lost over the last four decades (Sauer et al. 2017). Over 50% of its winter range is located within the Andes of Colombia, and land use changes in Andean winter grounds are likely the primary source of population decline (Wilson et al. 2018). In the face of this worrying situation, we can choose to be part of the solution for winter habitat loss for Neotropical migrants by informing other citizens and making ethical coffee choices. While novel evaluation criteria and procedures are urgently needed for the future success of certification programs (DeFries et al. 2017), certified shade-grown coffee gives us the option to reduce the social and environmental effects of our coffee consumption, and to directly contribute to the conservation of winter habitat for Neotropical migrants. Besides environmental benefits, the premium we pay can improve the living conditions of millions of farmers and labourers dependent on the coffee culture. A good start would be that passionate birders, researchers, and conservation biologists are consistent with the message we preach and make sure that our morning coffee was grown under shade.

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