FACTORS INFLUENCING BODY CONDITION AND ARRIVAL PHENOLOGY OF

NEOTROPICAL MIGRANTS AT A NORTHERN SPRING STOPOVER SITE

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ABSTRACT

Assessing the effect of winter habitat quality and environmental conditions on the fitness of migratory birds is important to understand factors that regulate migratory bird populations throughout the annual cycle. I evaluated the effect of winter habitat occupancy, as inferred from tissue stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values, on body condition and arrival date of seven long-distance, Nearctic-Neotropical migratory species intercepted during spring migration at Delta Marsh Bird Observatory (DMBO) southern Manitoba, Canada. Additionally, I used a long-term dataset of DMBO to assess the effect of May minimum temperature, May minimum daily temperature, and El Niño-Southern Oscillation (ENSO) index on body condition and spring arrival date. The effect of winter habitat quality on arrival day and condition index was strong for Palm Warbler (*Sethophaga palmarum*), Northern Waterthrush (*Parkesia noveboracensis*) and Alder Flycatcher (*Empidonax alnorum*). Palm Warblers using mesic winter habitats (i.e., low δ^{13}C and δ^{15}N values) were in better physical condition and arrived before individuals from more xeric habitats (with relatively higher δ^{13}C and δ^{15}N values). In Northern Waterthrush, early arrival was also related to mesic winter habitat occupancy. However, Alder Flycatcher showed an opposite trend. The effect of winter habitat on body condition and arrival phenology was more likely to be detected in species overwintering in the Caribbean. ENSO, probably through its influence on weather and food availability during winter, carried over to northern latitudes and affected both spring arrival date and condition. Condition was lower and birds arrived later during colder springs.

Furthermore, I assessed whether brighter carotenoid-based first-winter plumage colouration conferred higher annual survivorship to yearling Yellow Warblers (*Setophaga petechia*) through the occupancy of higher-quality winter habitats. Hatch-year warblers were banded and plumage brightness scored from 2008 to 2010 at DMBO and a subset was recaptured as second-year adults the following spring. I used δ^{13}C values derived from feathers and claws grown on the winter grounds to determine winter habitat occupancy of survivors. Independent of sex, I expected higher survivorship in brighter individuals and depleted δ^{13}C values in winter grown tissues as an indicator of higher quality (e.g., mesic, higher food availability) winter habitat occupancy. Survival was higher in 2009 than in 2010; however, I

did not find an effect of plumage brightness or sex on survival. Brighter colouration apparently did not confer survivorship advantages to males or female HY birds. Most individuals occupied xeric habitat during the winter independently of age, sex or plumage brightness. Further work on the winter grounds is needed in order to clarify the lack of power of winter habitat-occupancy to explain the arrival day and physical condition of most of the species on the breeding grounds, and survival in Yellow Warblers.

ACKNOWLEDGMENTS

DEDICATION

To my grandfather.

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CHAPTER 1 : GENERAL INTRODUCTION

1.1   Seasonal Interactions and Carry-Over Effects

Populations of migratory birds are influenced by interactions among different periods of the annual cycle such as wintering, breeding and migration (e.g., Newton 2004, Norris et al. 2004, Norris and Marra 2007). The concept of seasonal interactions was introduced by Fretwell (1972) who proposed that, in migratory individuals, seasonal population abundance depends on survival rates from the preceding season. Recent evidence supports this hypothesis and suggests that events that occur during one season can carry over to a subsequent season and influence individual reproductive success and population dynamics (Marra et al. 1998, Norris 2005).

Winter habitat quality is one factor that produces residual effects that carry over to subsequent seasons and influence year-round population dynamics in migratory birds (Marra et al. 1998, Norris et al. 2005). Habitat quality varies depending on the ability of the environment to provide suitable conditions to guarantee individuals survival and population persistence (Hall et al. 1997). In many environments, food availability and habitat moisture are correlated and have been identified as the most important factors determining winter habitat quality for Neotropical-Nearctic migrant songbirds (Sherry et al. 2005, Smith et al. 2010). For example, more mesic winter habitats are considered of "high quality" for insectivorous birds due to higher food availability relative to more xeric habitats (Marra et al. 1998, Studds and Marra 2005, 2011). The occupancy of mesic winter habitat has been shown to increase individual spring body condition and speed up departure dates from the wintering grounds; consequently, individuals from mesic winter habitats arrive early and in better condition to the breeding grounds than those from xeric habitats (Marra et al. 1998, Studds and Marra 2005, 2011).

Carry-over effects at the individual level can have negative effects on population size and persistence of migratory birds. Recent models predict decline of long-distance migratory bird populations over a wide geographic area on the breeding grounds as a consequence of winter habitat loss (Dolman and Sutherland 1995, Sutherland 1996). For example, Norris (2005) showed that the loss of high-quality habitat on the winter grounds for the American Oystercatcher (*Haematopus ostralegu*), a long-distance migrant, increased mortality and the number of

individuals overwintering on low quality habitats. Consequently, population size and its per capita reproductive success declined during the subsequent season.

The identification of factors that control migratory birds at the individual and population level remain poorly understood, in part, by the limited scope of conventional mark-recapture methods to track small migratory birds (Hobson 1999, Webster et al. 2002, Hobson and Norris 2008). The relatively recent use of endogenous markers such as stable-isotope assays has allowed tracking of animals without the need to follow individuals directly with exogenous markers (Hobson 2008, Hobson et al. 2010).

1.2   Stable Isotopes

Isotopes are atoms of the same element with the same number of protons but different number of neutrons (Criss 1999, Hoefs 2009). Isotopes are divided into stable and radioactive or unstable forms (Sulzman 2007). The most common stable isotopes applied to ecological research are the light elements C, N, H, O, and S. These elements comprise the bulk of animal tissues, and vary widely isotopically in nature at different environmental scales (Sulzman 2007, Wassenaar 2008). All of the light isotopes have a common or abundant ''light'' isotope (i.e., ^{12}C; 98.894%) and one or more ''heavier'' rare isotopes of interest (i.e., ^{13}C; 1.1056%; Criss 1999, Hoefs 2009).

Stable isotope ratios (e.g., ^{13}C/^{12}C and ^{15}N/^{14}N) are reported in delta (δ) notation, in per-mil units (‰) difference from an arbitrary standard material according to the following equation (Ehleringer and Rundel 1989):

$$\delta X\ (‰) = [(R_{sample}/R_{standard}) - 1] \times 1000$$

Where X (‰) represents the isotopic ratio of an element (i.e., C or N) in a sample relative to the isotopic ratio of an internationally accepted standard, R is the ratio of heavy to light isotope (i.e., ^{13}C/^{12}C or ^{15}N/^{14}N) in the sample and in the standard. For example, a sample with a δ^{13}C of -23.5‰ has a ^{13}C/^{12}C ratio that is 23.5‰ lower than of the standard. International standards for δ^{13}C and δ^{15}N are the Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen (AIR), respectively. Most laboratories have developed in-house or routine laboratory standards that have been calibrated relative to these IAEA standards allowing the assessment of the precision and accuracy of the methods (e.g., Wassenaar and Hobson 2003).

1.2.1 Carbon Stable Isotopes ($\delta^{13}C$)

Photosynthesis is the primary process that generates variation in carbon-isotope values in plant tissues (Kelly 2000). Plants with Calvin (C_3), Hatch-Slack (C_4) and Crassulacean acid metabolism (CAM) photosynthetic pathways show consistent differences in $\delta^{13}C$ values due to differences in physical and enzymatic fractionation during the fixation of atmospheric CO_2 (Marshall et al. 2007). Photosynthetic pathways begin with the diffusion of CO_2 from the atmosphere into the leaf; this diffusion has a fractionation ($\Delta\delta$) of ~4‰ due to the slower movement of molecules of $^{13}CO_2$ relative to molecules of $^{12}CO_2$. In C_3 plants, CO_2 is fixed by the enzyme ribulose bisphosphate carboxylase/oxigenase (RuBisco) which discriminates heavily against the $^{13}CO_2$ (Marshall et al. 2007). In C_4 and CAM plants, CO_2 is fixed by the enzyme phosphoenolpyruvate carboxilase (PEP) which has a higher affinity for $^{13}CO_2$ than RuBisco. Consequently, C_3 plants have depleted $\delta^{13}C$ values (-35 to -21 ‰) relative to C_4 plants (-14 to -10 ‰) (Boutton 1991, Ehleringer 1991). CAM plants show $\delta^{13}C$ values around -11‰ due to their similarity with C_4 plants during carbon assimilation (Marshall et al. 2007).

C_3 plants are associated with cooler, shaded, and humid habitats (Boutton 1991, Ehleringer 1991, Marshall et al. 2007); in contrast, C_4 and CAM plants are more abundant in dry-open habitats with higher light intensity and ambient temperatures (Teeri and Stowe 1976, Klink and Joly 1989, Sage and Coleman 2001, Marshall et al. 2007).

In addition to photosynthetic pathways, isotopic variation in C_3 plant tissues may also result from differences in water-use efficiency (Ehleringer et al. 1987, Comstock and Ehleringe 1988). In order to reduce water loss, C_3 plants in dry environments show patterns of ^{13}C enrichment due to changes in photosynthetic metabolism (Farquhar et al. 1989, Marshall et al. 2007). Transpiration, stomatal conductance and, to a lesser extent, net photosynthesis decreases under dry conditions. Even thought the diffusion of CO_2 into the leaf is reduced, the photosynthetic consumption of CO_2 inside the leaf continues at a high rate; consequently, CO_2 concentration inside the leaf falls and the $\delta^{13}C$ of CO_2 is progressively enriched (Marshall et al. 2007).

1.2.2 Nitrogen Stable Isotopes (δ^{15}N)

The range of δ^{15}N values in terrestrial plants varies between -8 and +18 ‰ (Shearer et al. 1983, Schoeninger and DeNiro 1984, Peterson and Fry 1987). Diverse processes beside photosynthesis such as climate, symbiotic associations in nitrogen fixation and nitrogen availability determine δ^{15}N values in plants (Kelly 2000). In ecosystems with mean annual temperature >-0.5ºC, foliar values of δ^{15}N are negatively correlated with mean annual precipitation (Austin and Vitousek 1998, Handley et al. 1999) and positively correlated with mean annual temperature (Amundson et al. 2003, Craine et al. 2009). Plants that are associated with mycorrhizal fungi show lower δ^{15}N values relative to non- mycorrhizal plants and varying levels of depletion depending on the kind of mycorrhizal association (Craine et al. 2009, Michelsen et al. 1996, 1998). Plants with high foliar N concentrations generally occupy sites with higher nitrogen availability (i.e., dry and warm sites) and show enrichment patterns of foliar δ^{15}N (Craine et al. 2009). Plant δ^{15}N values can also vary due to land-use practices. For example, cultivated soils typically have higher δ^{15}N values compared with uncultivated soils due to volatilization of lighter nitrogen-containing compounds (Kendall 1998, Hebert and Wassenaar 2001, Evans 2007).

1.2.3 δ^{13}C and δ^{15}N Values in Bird Tissues

The general patterns of δ^{13}C and δ^{15}N in plants and their association with mesic vs. xeric habitats allow inferences of prior habitat occupancy by migratory terrestrial birds (Hobson 2008, Hobson et al. 2010). δ^{13}C and δ^{15}N values in plants are incorporated into consumers through the food web (DeNiro and Epstein 1978); therefore, δ^{13}C and δ^{15}N values in bird tissues represent intrinsic markers of C_3- and C_4- or CAM-dominated plant communities or mesic vs. xeric sites, where the consumer fed at the time of tissue formation (Marra et al. 1998, Hobson 2008, Hobson et al. 2010).

In this study, I used stable- isotope measurements of winter-grown feathers and claws to infer winter habitat-occupancy. Feathers and claws, once formed, are metabolically inert and record the isotopic composition of the local diet at the time of growth (Hobson and Clark 1992, Chamberlain et al. 1997, Bearhop et al. 2003, Mazerolle and Hobson 2005). Hence, δ^{13}C and

δ^{15}N values of bird tissues grown at the wintering grounds are reliable markers of winter habitat-occupancy (xeric vs. mesic) during the period of tissue formation (Marra et al. 1998, Bearhop et al. 2003, Hobson 2008, Hobson et al. 2010). Most passerines typically grown their feathers over a short period or at one specific location (Pyle 1997, Bearhop et al. 2003, Wassenaar 2008); consequently, the isotopic composition of this tissue allows the determination of the habitat where the feathers were molted. Unlike feathers, claw isotopic values are integrated over a longer time scale; therefore a typical distal claw clipping (1-2 mm) represents winter habitat use of a bird 2-5 months before sampling (Bearhop et al. 2003).

1.2.4   Application of δ^{13}C and δ^{15}N Values to Track Migratory Birds

The application of δ^{13}C techniques has allowed linkage between different periods in the annual cycle of Nearctic-Neotropical long-distance migrants and identification of winter habitat quality as a limiting factor for migratory individuals. A key isotopic study assessing carry-over effects of winter habitat occupancy on migratory birds was conducted on American Redstarts (*Setophaga ruticilla*) by Marra et al. (1998). Redstarts occupying high-quality mesic areas in Jamaica showed significantly lower δ^{13}C values in blood compared with those occupying xeric habitats; and departed earlier and in better condition during spring migration. Consequently, high-quality habitat occupancy during winter resulted in higher physical condition during spring migration, early arrival to the breeding grounds in eastern North America and higher reproductive success (Marra et al. 1998, Norris et al. 2004).

More recently, using δ^{13}C values in blood and a satellite-derived measure of winter habitat moisture, Smith et al. (2010) showed that Northern Waterthrush (*Parkesia noveboracensis*) occupying wetter habitat with higher food availability, increased body mass over the winter, had higher rates of fat deposition before spring migration and departed sooner from the winter grounds than individuals from dryer habitats. Similarly, Black-throated Blue Warblers (*Dendroica caerulescens*) which occupied poor-quality Caribbean winter habitats had poorer physical condition during spring migration (Bearhop et al. 2004). In particular, the warblers with lower δ^{13}C values derived from claws were in better body condition than birds with higher δ^{13}C values.

The isotopic difference between American Redstart blood samples from mesic and xeric habitat found by Marra et al. (1998) at the Jamaican winter grounds was about 2.2‰ (wet forest -23.9‰, mangrove -22.8‰, citrus -22.2‰ and scrub -21.7‰). I categorized arrival day to the breeding grounds of American Redstarts reported by Marra et al. (1998) as early (below the 25th percentile), intermediate (between the 25th and 75th percentile) and late (above the 75th percentile). Following the same procedure, I classified Black-throated Blue Warbler spring migratory body condition reported by Bearhop et al. (2004) as low, intermediate and high. The δ^{13}C mean from muscle of AMRE arriving early differed from the late arrivals mean by -0.63‰ (Mean±SE early -3.97±0.13‰, intermediate -27.71±0.13‰, late -23.34±0.16‰). Mean δ^{13}C from claws of Black-throated Blue Warblers in high body condition differed from those in low condition by -0.64‰ (Mean±SE high -24.03±0.29‰, intermediate -23.50±0.25‰, low -23.39±0.07‰). So, previously, authors have considered relatively small tissue δ^{13}C differences among individuals to be reliable indicators of the food webs birds fed on the winter grounds and subsequently winter habitat quality.

The combination of δ^{13}C and δ^{15}N analysis has also allowed the successful tracking of habitat use by migratory birds throughout the annual cycle. For example, Chamberlain et al. (2000) inferred use of arid vs. moister winter habitats in Africa by two subspecies of Willow Warbler (*Phylloscopus trochilus trochilus* and *P. t. acredula*) based on differences in δ^{13}C and δ^{15}N values derived from flight feathers replaced at their African winter quarters prior to spring migration. The subspecies *acredula* showed higher δ^{13}C and δ^{15}N values than *trochilus*, which reflected the more xeric winter habitats of this subspecies in eastern Africa.

1.3   El Niño-Southern Oscillation (ENSO)

The Southern Oscillation (SO) is the atmospheric phenomenon related to the occurrence of El Niño (EN), and consists of fluctuations in the Pacific Ocean surface air pressure between eastern and western hemispheres in tropical and subtropical latitudes (Stenseth et al. 2003). Due to the close relationship between EN and the SO, the term ENSO is used to describe the atmosphere-ocean interaction throughout the tropical Pacific (Stenseth et al. 2003). The Southern Oscillation Index (SOI) is an accurate indicator of the two ENSO phases: La Niña and El Niño; and is based on sea-surface air pressure differences between Darwin, Australia, and the South

Pacific island of Tahiti (Philander 1990). Prolonged periods of negative SOI correspond to El Niño episodes, and consistent periods of positive SOI values to La Niña episodes (Philander 1990).

El Niño and La Niña have significant influence on temperature and precipitation patterns in North, Central and South America, and consequently on the productivity of many terrestrial and aquatic ecosystems (Philander 1990, Shabbar and Khandekar 1996, Shabbar et al. 1997). The extent and strength of ENSO effects vary regionally, and are stronger during the winter following the onset of ENSO and weaken during spring (Kiladis and Diaz 1989, Shabbar and Khandekar 1996, Shabbar et al. 1997). El Niño events induce lower temperatures and higher precipitation than average in inland Texas, northern Mexico and the Gulf Coast (Ropelewski and Halpert 1986, Kiladis and Diaz 1989); in contrast, above-normal temperature and precipitation are pronounced in southern Canada. In particular Manitoba winters are more than 3 ºC warmer during El Niño than during La Niña phase (Kiladis and Diaz 1989). During El Niño phase, northern Mexico, western and southeastern South America generally have above-average rainfall levels, whereas Central America, the Caribbean and northeastern South America have drier than average conditions (Ropelewski and Halpert 1987, Jaksic 2001). Opposite weather conditions are observed in these regions during La Niña phase.

1.3.1   Effects of El Niño-Southern Oscillation (ENSO) on Migratory Birds Populations

Large-scale climatic events such as ENSO, through its effect on seasonal weather patterns, influence long-distance migrant population dynamics (Sillett et al. 2002). In some tropical regions, El Niño events induce dry conditions which result in reduced insect abundance; in contrast, during La Niña events, precipitation and insect abundance increases dramatically (Allan et al. 1996, Holmgren et al. 2001).

During La Niña events, Black-throated Blue Warblers overwintering in Jamaica and breeding on the east coast of North America had higher overwinter survival, higher fecundity and higher recruitment of juveniles and yearlings into the wintering and breeding population (Sillett et al. 2002). Similarly, Yellow Warblers (*Sethophaga petechia*) breeding in southern Manitoba, Canada, had higher annual production of young and adult apparent survival during La Niña events (Mazerolle et al. 2005). However, due to the spatial and temporal variation of the

influence of ENSO on precipitation in tropical and subtropical regions and the broad winter distribution of many long-distance migrants, the response of migratory populations to ENSO effects can vary. For example, Nott et al. (2002) reported higher annual reproductive success of several Neotropical migrants breeding in the Pacific Northwest of the United States during El Niño years. This pattern was attributed to higher food availability driven by increased precipitation in their xeric winter habitats of Mexico during El Niño years; and the potential carry-over effect of winter food availability on spring physical condition, arrival time on the breeding grounds and breeding success.

Recent studies suggest that changes in local weather variables, such as those observed during ENSO events, determine variation in the body condition of migratory birds. For example, abundant rainfall during the non-breeding season in the Caribbean increased food availability for American Redstarts; consequently, the birds were in better condition through the winter and were able to depart earlier from the winter grounds (Studds and Marra 2005, 2011). Similarly, drought conditions which reduce invertebrate prey biomass led to a decrease in body mass and an increased the risk of mortality in Ovenbirds (*Seiurus aurocapillus*) wintering in the Caribbean (Strong and Sherry 2000).

1.4   Condition Index

Mass changes in migrant passerines are attributed to the deposition and use of fat and to a lesser extent fat-free mass (Piersma 1990, Scott et al. 1994). In order to cope with the high energetic demands imposed by migration, long-distance migrants store subcutaneous fat which may reach 50% of total body mass (Biebach 1990, Blem 1990, Alerstam and Lindstrom 1990). Mechanisms used to achieve rapid rates of increase in body mass before migration include hyperphagia (King and Farner 1959), shift in diet selection, and increase assimilation efficiency of energy and nutrients (Bairlein 1985). Although both fat-free body mass and fat can be used for energy, the net energetic contribution of fat is considerably higher than that of fat-free body mass (Piersma 1990); therefore, energetic relationships between fat and fitness are more valuable (Schamber et al. 2009).

Body condition refers to the energetic condition of an animal and its variation is frequently attributed to changes in fat stores (Schulte-Hostedde et al. 2005). Body mass is a simple and commonly applied index of body condition and represents the sum of energy stores and structural mass (Schamber et al. 2009). As body mass does not estimate condition independently of structural size, standardizing body mass by individual size could remove potential size-related variation and increase the precision of an estimate of condition (Winker 1992, 1995). The value derived from condition index = ([mass/wing length] x 100) can be applied as an indicator of the amount of fat content in a passerine bird (Winker 1992, 1995).

Body mass usually shows a diurnal increase in birds (Thomas 2000); therefore, estimates of condition index are affected by hour of capture (Winker 1995). By regressing condition index against hour of capture, the rate of increase per hour can be estimated and corrected for.

1.4.1 Arrival date and physical condition during spring migration in migratory birds

For migratory birds, arrival date and physical condition at the breeding grounds are major determinants of individual fitness (e.g, Sandberg and Moore 1996, Smith and Moore 2003, 2005). Birds arriving earlier and in better physical condition have extra time and energy to allocate to breeding activities (Sandberg and Moore 1996). Consequently, early arriving individuals typically gain the best breeding territories, have higher mating success, better quality mates, additional time to replace lost clutches and higher reproductive success (Møller 1994, Norris 2005, Smith and Moore 2003, 2005). However, despite its benefits, arriving early to the breeding grounds increases self-maintenance costs and mortality risk due to poor or stochastic environmental conditions during early spring (i.e., bad weather, low food availability); hence, only birds in good condition would be able to better cope with the costs of early arrival (Kokko 1999, Drent et al. 2003).

1.5 Carotenoids

Carotenoids are the primary pigments responsible for the bright red, orange, and yellow colouration of bird plumage (McGraw 2006). According to the molecular structure, carotenoids

are divided in xanthophylls and carotenes. Xanthophylls are subdivided in hydroxy-carotenoids such as lutein and canary xanthophyll; and ketocarotenoids such as astaxanthin (Goodwin 1984).

The yellow plumage colouration of the Yellow Warbler is given only by lutein (McGrawn et al. 2003). In the hatch-year, the first-winter plumage of these warblers is highly variable between and within sexes; generally males are brighter than females but duller males can overlap in plumage with females (Pyle 1997, Hobson et. al 2000). Such intraspecific colour variation may signal quality, attractiveness, strategy, genetic compatibility, kinship, or individual identity (Dale 2006).

Carotenoid-based colours are an honest indicator of quality or viability (Zahavi 1975, Hamilton and Zuk 1982, Hill 1991), and confer fitness benefits to individuals (e.g., Hill 1988, 1990, 1991). Birds cannot synthesize carotenoids, and so the quality of carotenoid coloured plumage depends on carotenoid intake through the diet (Goodwin 1984); hence, only individuals in good physical condition are able to accumulate the pigments needed for maximum ornamental expression. While most of the study of the function of carotenoid-base plumage has focused on the breeding grounds, the role and advantages conferred by bright plumage during the non-breeding season have been poorly documented.

Assessing the effect of winter habitat quality and environmental conditions on the fitness of migratory birds is important to understand the factors that regulate migratory bird populations throughout the annual cycle (Webster et al. 2002, Webster and Marra 2005, Newton 2006). Despite growing evidence of the importance of winter habitat quality as a determining factor of annual survival, self maintenance, individual fitness and population dynamics (Sherry and Holmes 1996, Gill et al. 2001, Norris et al. 2004, Gunnarsson et al. 2005), to date in North America, isotopic studies assessing the carry-over effect of winter habitat on migratory birds have been focused on eastern populations of American Redstarts and Black-throated Blue Warblers overwintering on the Caribbean (Marra et al. 1998, Bearhop et al. 2004). We now need to determine the extent to which other migratory songbird species respond at the individual and population level to events experienced on the winter grounds and how these are mediated by individual quality.

1.6   Study Species

I focused on the Yellow Warbler but also examined seven additional long-distance migratory species (overwintering mostly to the south of the U.S.-Mexico border): American Redstart, *Sethophaga ruticilla*; Northern Waterthrush, *Parkesia noveboracensis*; Swainson's Thrush, *Catharus ustulatus*; Wilson's Warbler, *Cardellina pusilla*; Palm Warbler, *Sethophaga palmarum*; Alder Flycatcher, *Empidonax alnorum*; and Baltimore Oriole, *Icterus galbula*. All these species captured at the study site were migrating to their breeding areas. I selected species with different timing of spring migration through Delta Marsh Bird Observatory and from various known winter distributions (Ridgely et al. 2007, Figure 1.1, Appendix A).

After reproduction and before fall migration, most passerines undergo a pre-basic molt, which differs in extent among hatch-year and adult birds. Hatch-year birds have a partial molt (first pre-basic molt) that includes the replacement of body feathers and some wing coverts and tertials, but not flight feathers; this molt results in the first basic or first winter plumage. Adult birds have a complete molt (adult pre-basic molt) which includes the replacement of all body and flight feathers; and results in the adult basic plumage. In the winter grounds and before spring migration, adults and hatch-year birds complete the pre-alternate molt which again includes the replacement of body feathers and some wing coverts, and results in the alternative or breeding plumage (Pyle 1997). The selection of feathers sampled for δ^{13}C and δ^{15}N analysis was made based on the extension of the prealternate molt.

In Yellow Warblers, the prealternate molt includes the replacement of body feathers and some wing coverts (Pyle 1997). In Northern Waterthrushes, the prealternate molt is limited to body feathers, and in Wilson's and Palm Warblers is limited to head feathers. This molt is absent in Swainson's Thrushes and highly variable in American Redstarts and Alder Flycatchers; therefore, feathers were not sampled in these species. The Baltimore Oriole was not included in the δ^{13}C and δ^{15}N analysis because the isotope data was not available.

1.6.1   Yellow Warbler

The northern Yellow Warbler (*Sethophaga petechia*; *aestiva* group of subespecies) is the migratory form of Yellow Warbler and includes nine subspecies differentiated by plumage

colouration and morphology (Browning 1994). Two non-migratory forms are related to the northern Yellow Warbler: the Mangrove Warbler (*S. petechia*; *erithachorides* group) restricted to coastal mangroves habitat in Mexico, Central America and northern South America; and the Golden Warbler (*S. petechia*; *petechia* group) distributed throughout the Caribbean (Lowther et al. 1999).

The Northern Yellow Warbler has the broadest distribution among Wood Warblers (Parulidae) in North America (Appendix A). Within the breeding range, the species is common in riparian and scrub habitats dominated by willows and in human-disturbed areas (Briskie 1995). The population breeding at Delta Marsh, southern Manitoba, is likely to overwinter in southwest Mexico, southern Central America and northern South America (Boulet et al. 2006). During the winter, the Yellow Warbler occupies a broad diversity of habitats that range from urban areas to scrub habitats, agricultural lands and mangrove associations (Elliot 1974, Wunderle and Waide 1993, Greenberg and Ortiz 1994).

1.6.2   Other warbler species

The summer and winter ranges of all species are in presented in Appendix A. American Redstart breeds preferentially in deciduous and moist forest in North America. Breeding individuals from northwest and midwest North America are likely to winter in Mexico, and individuals from eastern North America in the Caribbean (Norris et al. 2006). During the winter, American Redstarts occupy diverse habitats including black mangrove forest, lowland forest, secondary growth, and agricultural and non-forested areas (Marra et al. 1993, Wunderle and Waide 1993, Marra et al. 1998). Sexual winter habitat segregation has been suggested as one of the mechanisms regulating winter habitat occupancy in this species; through behavioural dominance, older males maintain high quality territories in mangroves and moist forested habitats and displace females and younger males to less suitable second-growth scrub habitats (Marra et al. 1993, Marra 2000, Marra and Holmes 2001).

The Northern Waterthrush breeds in swamps, wet woodlands and mixed forest. The Caribbean distribution of Waterthrushes is restricted to mangrove associations and lowland forest (Wunderle and Waide 1993); the survival of wintering individuals might rely on the availability

of these habitats (Reitsma et al. 2002).In other areas within its winter range this species also occupies second-growth in different stages of succession and riparian forest (Eaton 1995). According to Lefebvre et al. (1994) and Reitsma et al. (2002) Northern Waterthrushes overlap winter foraging territories; however, other studies suggest that individuals defend exclusive foraging territories during the winter (Schwartz 1964, Smith et al. 2008).

Wilson's Warbler breeds generally in riparian and early successional forest. Wilson's Warbler winters in different kinds of habitats from coastal lowland forest to high-altitude cloud forest and paramos; including riparian, evergreen and deciduous forest and successional habitats (Hutto 1994, Finch 1989). It shows different winter behavioural strategies; some individuals of both sexes defend territories, others remain as winter "floaters" or join large mixed-species foraging flocks (Rappole 1988, Hutto 1994). This species shows a "leapfrog" migration pattern, individuals from northern latitudes migrate earlier and farther south than those from southern latitudes (Kelly et al. 2002).

Palm Warbler has one of the northernmost breeding distributions in North America; this species is generally associated with bogs and fens in the boreal forest of Canada and northern United States (Wilson 1996). During winter, this species resides mainly in pastures, pine forests, dry scrub, and successional and disturbed open habitats where it feeds on seeds, fruits, nectar and insects (Wunderle and Waide 1993). However, affinity for different types of winter habitats and diets varies among the Caribbean islands (Lack and Lack 1972, Wunderle 1978, Wunderle and Waide 1993).

1.6.3 Other passerines

Swainson's Thrush breeds in coniferous, hardwood and riparian forest; winters mostly in Mexico and northern South America and is less abundant in Central America (Mack and Yong 2000). During the winter, Swainson's Thrushes feed on fruit and insects (Leck 1972) mostly in primary forest at high and low elevation; this species is less abundant in second growth and open areas (Robinson et al. 1995, Mack and Yong 2000).

Alder Flycatcher breeds primarily in brush wetlands, damp open meadows with overgrown shrub thickets and areas in early successional stages; the winter range of this species

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is poorly known, but it seems to comprise the northwest of South America (Lowther 1999). During the winter, Alder Flycatchers defend territories and feed almost exclusively on insects caught in the air from exposed perches in open areas with scattered trees and early successional scrubby growth (Lowther 1999, Robinson et al. 1995).

Baltimore Oriole breeding habitat is diverse but shows preference for riparian and deciduous forest, and open woodlands (Rising and Flood 1998). This species winters from southern Mexico throughout Central America and northern South America; in the Caribbean, the species is common in Cuba and Jamaica and less abundant in Dominican Republic, Puerto Rico and the Lesser Antilles (Rising and Flood 1998). During the winter, Baltimore Orioles feed on insects, fruit and nectar (Leck 1972, Timken 1970) in a wide range of habitats that include riparian and deciduous forest, shaded plantations, and open areas with trees.

1.7   Study Area

Fieldwork was conducted during summer 2008 and from spring to fall 2009 and 2010 at Delta Marsh Bird Observatory (DMBO). DMBO is located on the forested dune-ridge which separates the southern shore of Lake Manitoba from Delta Marsh, south-central Manitoba, Canada (Figure 1.2, 98°23'W, 50°11'N, elevation 248 m). Delta Marsh is one of the largest freshwater marshes in North America and a primary stopover site for migrating songbirds (Underwood and den Haan 2000). This site represents a key staging area for Nearctic-Neotropical migrants and allows the capture of large numbers of individuals migrating to their breeding grounds during spring. The ridge forest is dominated by Peach-leaved Willow (*Salix amygdaloides*), Manitoba Maple (*Acer negundo*), Green Ash (*Fraxinus pennsylvanica*) and Cottonwood (*Populus deltoides*) (MacKenzie 1982). Every year during late spring and summer, this area experiences frequent massive emergences of aquatic insects (MacKenzie at al. 1982). A complete description of the study area can be found in MacKenzie (1982).

1.8   Thesis Outline

The general objectives of my thesis were as follows:

1. To evaluate if habitat occupancy on the winter grounds (e.g., xeric vs. mesic), inferred from $\delta^{13}C$ and $\delta^{15}N$, affect the time of arrival of seven long-distance migrants intercepted during spring migration at Delta Marsh, Manitoba, Canada.

I hypothesized higher condition index and earlier arrival to the study site for individuals that had occupied higher-quality winter habitats (i.e., mesic) as indicated by relatively lower $\delta^{13}C$ and $\delta^{15}N$ values of winter-grown feathers and claws.

2. To determine the effect of El Niño-Southern Oscillation (ENSO) operating on the winter grounds and May minimum temperature in Delta Marsh on arrival day and condition index of eight long distance migrants using a Delta Marsh Bird Observatory (DMBO) long-term data set.

I hypothesized higher condition index and earlier arrival to the study site during springs preceded by La Niña or El Niño events depending on the effects of ENSO on the winter grounds and on the potential winter grounds of the species, and during springs with higher May minimum temperature.

3. To Evaluate if, in yearling Yellow Warblers, brighter carotenoid-based first winter plumage colouration confers survivorship advantages through occupancy of higher quality winter habitats (i.e., mesic).

I hypothesized that plumage brightness, a putative indicator of individual quality, would benefit brighter individuals arriving on the wintering grounds through the acquisition of higher quality winter habitat; this would be reflected in higher survivorship of bright vs. pale birds returning to DMBO. I expected surviving individuals would more likely have occupied mesic winter habitats as indicated by relatively lower $\delta^{13}C$ values of winter-grown tissues.

I organized my thesis into four chapters. Chapters 1 and 4 are the Introduction and Synthesis, respectively. In the introduction, I provide the background for the techniques, the variables and the species included in this study; and point out the importance of studying carry-over effects and understanding the factors that limit survival, physical condition and the

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phenology of spring migration in long-distance migrants. In the synthesis, I link Chapters 1 and 2, and present the major findings and directions for future studies. Chapter 2 addresses objective 1 and 2 listed above while chapter 3 evaluates objective 3.
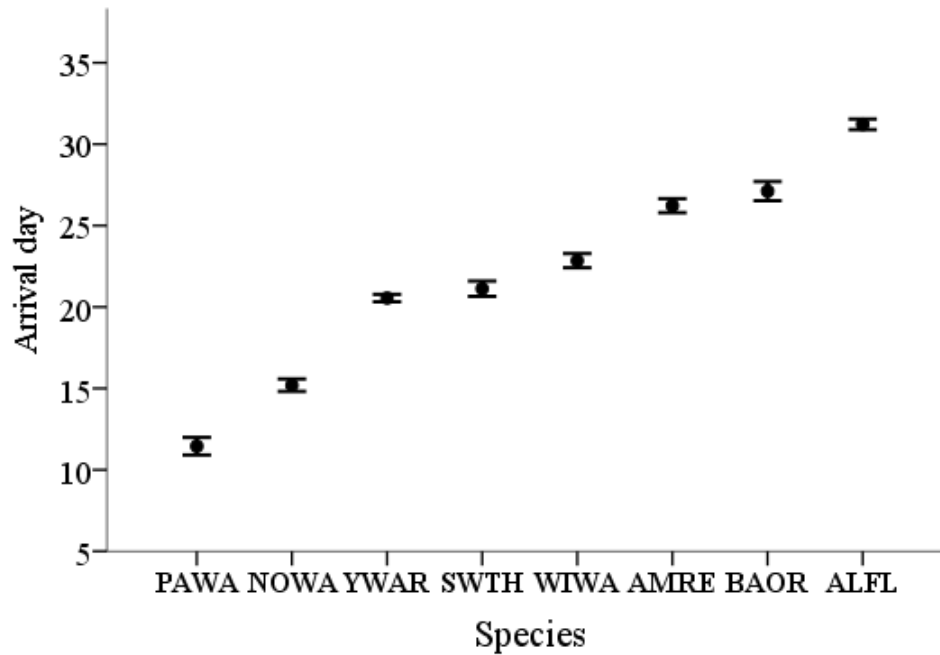
Figure 1.1. Spring migration date (mean, 95% C.I) of eight long-distance migrants passing throughout Delta Marsh Bird Observatory (DMBO), Manitoba, Canada, from 1998 to 2010. Palm Warbler (PAWA, N = 457), Northern Waterthrush (NOWA N = 851), Yellow Warbler (YWAR N = 801), Swainson's Thrush (SWTH, N = 590), Wilson's Warbler (WIWA N = 512), American Redstart (AMRE N = 570), Baltimore Oriole (BAOR N = 234) and Alder Flycatcher (ALFL N = 432). Day 1 = 1 May. (DMBO, unpublish data).
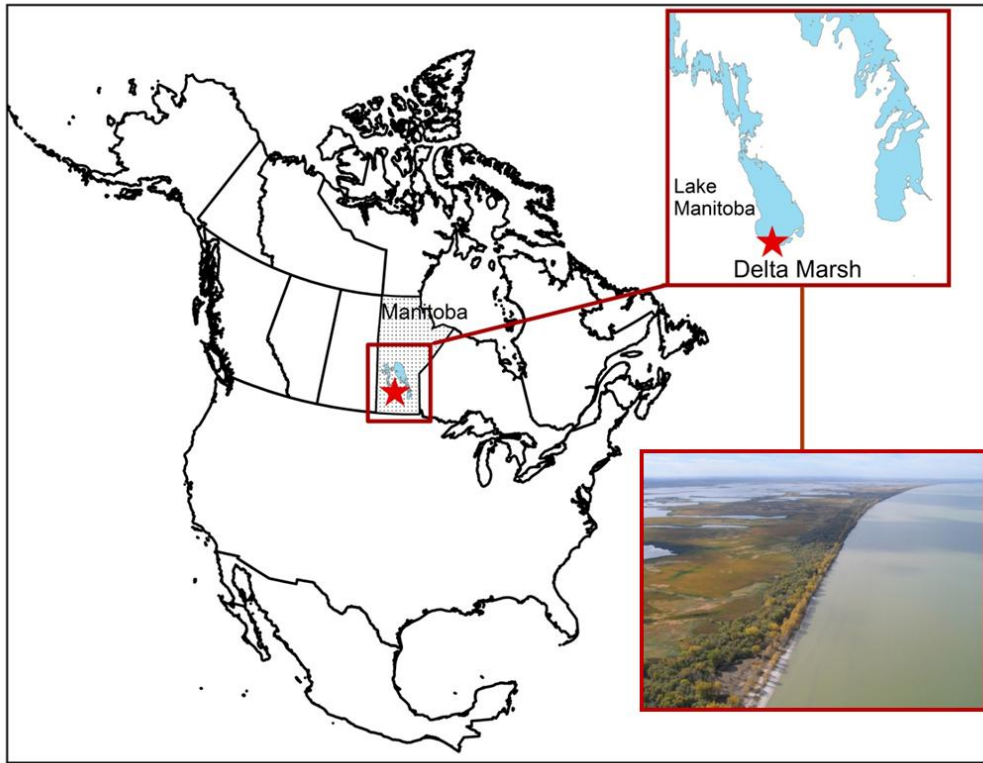
Figure 1.2. Map of the study area location. Delta Marsh, Manitoba, depicted by the red star.

CHAPTER 2 : WINTERING HABITAT INFLUENCES SPRING BODY CONDITION AND
ARRIVAL PHENOLOGY OF NEOTROPICAL MIGRANTS AT A STOPOVER SITE IN
SOUTHERN MANITOBA, CANADA.

2.1   Introduction

It is now well established that migratory songbirds are influenced by interactions between
different stages of their annual cycle (e.g., Marra et al. 1998, Saino et al. 2004, Norris and Marra
2007). This involves effects of factors experienced during one season carrying over to a
subsequent season thereby producing residual effects on the fitness of individuals and
populations (Marra et al. 1998, Norris 2005, Newton 2006). Assessing the magnitude and
consequences of carry-over effects is important for understanding the factors regulating the
population dynamics of migratory birds (Webster et al. 2002, Newton 2006). However, to date,
understanding where and what factors influence populations of migratory birds has been limited
by the large spatial scales involved during the annual cycle, the number of potential ecological
constraints, and the range of potential responses of individuals to resources that vary in space and
time (Sherry and Holmes 1996).

The quality of habitat occupied by migrants during their winter and breeding seasons
affects individual fitness and population dynamics in some migratory songbirds (Sherry and
Holmes 1996, Gill et al. 2001, Gunnarsson et al. 2005). Recently, measurements of stable-carbon
isotopes ($\delta^{13}C$) in bird tissues have been used to infer prior habitat occupancy (Marra et al. 1998,
Gill et al. 2001, Bearhop et al. 2004, Norris et al. 2004, Gunnarsson et al. 2005). This approach
relies on the fact that foodweb $\delta^{13}C$ values depend on photosynthetic pathways which are in turn
influenced by ambient growing conditions (Hobson 1999, Wolf and Martinez del Rio 2000,
Hobson et al. 2010). C3 plants have lower $\delta^{13}C$ values than C4 and CAM plants (Boutton 1991,
Ehleringer 1991) and are associated with mesic habitats (Lajtha and Marshall 1994). In contrast,
C4 and CAM plants are more abundant in xeric habitats with high light intensity and ambient
temperature (Lajtha and Marsha 1994, Sage and Coleman 2001). In order to diminish water loss,
C3 plants in xeric environments have also evolved mechanisms of water-use efficiency that
favour isotopic enrichment, resulting in higher $\delta^{13}C$ values (Farquhar et al. 1989, Lajtha and
Marsha 1994, Marra et al. 1998).

Plant $\delta^{15}N$ values are influenced by climate, degree of soil exposure and anthropogenic input of nitrogen to the biosphere (Nadelhoffer and Fry 1994). $\delta^{15}N$ values are negatively correlated with rainfall (Austin and Vitousek 1998, Handley et al. 1999) and positively correlated with temperature (Amundson et al. 2003). Values of $\delta^{15}N$ also vary between agricultural and non-agricultural areas, uncultivated soils typically have lower $\delta^{15}N$ values compared with cultivated soils (Kendall 1998, Hebert and Wassenaar 2001, Evans 2007). The combination of $\delta^{13}C$ and $\delta^{15}N$ analysis of feathers and claws has allowed the successful tracking of habitat use by migratory birds throughout the annual cycle (Marra et al. 1998, Chamberlain et al. 2000, Paine et al. 2004, Bensch et al. 2006, Yohannes et al 2007).

Environmental conditions on the wintering and breeding grounds such as precipitation, temperature and primary productivity also affect the physical condition and phenology of spring migration in migrating birds. On the wintering grounds, precipitation drives primary production which, in turn, enhances foraging conditions for insectivorous birds allowing individuals to acquire adequate physical condition earlier, depart from winter grounds sooner during spring migration (Studds and Marra 2005, 2011), and arrive earlier to the breeding grounds (Saino et al. 2004). At northern latitudes, spring temperatures are one of the most important constraints shaping the phenology of migration and clutch initiation (Tøttrup et al. 2010, Mazerolle et al. 2011).

Body condition and day of arrival on the breeding grounds are important factors contributing to migratory performance and fitness of individuals (Cristol 1995, Smith and Moore 2005). Early arrival is often related to better physical condition, and both factors have been correlated with reproductive success (Møller 1994, Lozano et al. 1996, Marra et al. 1998, Kokko et al. 1999). Individuals arriving early on breeding areas usually have access to higher quality territories, start reproduction earlier, have extra time and energy to devote to reproduction, and consequently have higher reproductive success than late arrivals (e.g., Smith and Moore 2003, 2005, Norris 2005). Therefore, assessing the factors that carry over from one season to the other and constrain the condition and arrival phenology of individuals during migration is important to understand the events regulating migration and limiting populations (Newton 2006).

Here, I evaluated the effect of winter habitat occupancy as inferred from tissue $\delta^{13}C$ and $\delta^{15}N$ values on body condition and spring arrival phenology of seven long-distance Neotropical migratory species intercepted during spring migration at Delta Marsh, Manitoba, Canada. Based on the findings of Marra et al. (1998) and Bearhop et al. (2004), I hypothesized higher condition index and earlier arrival at the study site for individuals that had occupied higher quality habitats on their winter locations as indicated by relatively lower $\delta^{13}C$ and $\delta^{15}N$ values of winter-associated tissues.

2.2   Methods

2.2.1   Study Site

Field work was conducted from 1 May to 4 June, 2009 and 2010, at the forested dune-ridge which separates the southern shore of Lake Manitoba from Delta Marsh, Manitoba, Canada (98°23'W, 50°11'N). This site allowed the capture of large numbers of individuals during spring migration (Underwood and den Haan 2000).

2.2.2   Study Species and Field Methods

Seven long-distance migrants, defined as species overwintering mostly south of the U.S.-Mexico border, were selected to infer winter habitat occupancy based on $\delta^{13}C$ and $\delta^{15}N$ values of winter-grown tissues: Yellow Warbler (YWAR), *Sethophaga petechia*; American Redstart (AMRE), *Sethophaga ruticilla*; Northern Waterthrush (NOWA), *Parkesia noveboracensis*; Swainson's Thrush (SWTH), *Catharus ustulatus*; Wilson's Warbler (WIWA), *Cardellina pusilla*; Palm Warbler (PAWA), *Sethophaga palmarum*; and Alder Flycatcher (ALFL), *Empidonax alnorum*. I selected species with different timing of spring migration through DMBO and from various known winter distributions. Baltimore's Oriole (BAOR), *Icterus galbula*, was included in analyses only from the (non isotope) DMBO long-term data set.

Birds were captured at DMBO using a standardized constant-effort mist-netting protocol (Hussell and Ralph 2005). Ten mist nets were operated six hours a day from one half hour before sunrise. Captured birds were banded using US Fish and Wildlife Service aluminium bands. Age and sex determination followed the techniques outlined by Pyle (1997). Wing chord was

measured from the carpal joint to the nearest millimeter to the tip of the longest primary. Birds were weighed on an electronic balance and the mass recorded to the nearest 0.1 g.

Feathers and 1-2 mm of distal claw material were taken from each individual. The selection of feathers was made based on the extension of the prealternate molt described by Pyle (1997). Because stable isotopes in the environment are incorporated into consumers through the food web (DeNiro and Epstein 1978), isotopic information in alternate feathers were expected to be a marker of the extent to which individuals had been feeding on mesic or xeric habitat during the prealternate molt in winter. Breast feathers were collected from NOWA, head feathers from PAWA and WIWA, and inner greater coverts from YWAR. For AMRE, SWTH and ALFL, only distal portions of claws were sampled.

2.2.3 Stable Isotope Analyses

Feathers and claws were soaked for 4 h in a 2:1 chloroform:methanol solution, rinsed and dried in a fume hood for 48 h; distal vane material was removed for analysis. All samples were weighed (0.20-1.10 mg), loaded into tin capsules and combusted in a Robo-Prep elemental analyzer interfaced with a Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS). Stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) are reported in delta (δ) notation, in per-mil units (‰) relative to the Vienna Pee Dee Belmnite ($\delta^{13}C$) and atmospheric nitrogen ($\delta^{15}N$) standards, respectively. Using within-run repeated analysis of an internal laboratory standard (albumen) measurement error was estimated to be $\pm$ 0.1 ‰ and $\pm$ 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$ analyses, respectively.

2.2.4 Statistical Analysis

Condition index was estimated as [mass/wing length] x 100 (Winker 1995). Day of arrival was assumed to be equal to the day of capture for all species except YWAR. The assumption was supported by the lack of within-year recaptures at the study site. Because YWAR breeds at Delta Marsh, the day of capture does not necessarily represent day of arrival, especially for birds trapped late in the season. To avoid the incorporation of breeding YWAR in the analysis, the equation Arrival day = -1.12 * MT + 35.52 derived from Mazerolle et al. (2011) for the study population was used to predict arrival day of YWAR to DMBO in each year based on

local mean May temperature (MT). All individuals captured after the predicted day of arrival were excluded from the analysis. Arrival dates were transformed so that day one was equal to 1 May for all species.

2.2.4.1 Effect of winter habitat quality on body condition and arrival day

I modeled condition index and arrival day separately. I developed five *a priori* candidate linear models to examine factors influencing variation in condition index of NOWA, BAOR, TRFL, PAWA and SWTH; the candidate models included variables for capture time of day as a linear covariate, δ^{13}C, δ^{15}N, and the additive effect of δ^{13}C with δ^{15}N. In addition, I considered an intercept only (null) model for comparison. The inclusion of capture time allowed accounting for the potential effect of body mass increase during the day on the estimation of condition index (Winker 1992). When variation in condition was explained primarily by capture time, I corrected condition index by its rate of increase. To examine factors influencing variation in arrival day, I excluded the model containing capture time. For YWAR, WIWA and AMRE, tissues were collected during 2009 and 2010; therefore for both body condition and arrival day I considered three additional models that included the effect of year as a linear covariate, and additive effects for δ^{13}C or δ^{15}N with year.

Claw and feather δ^{13}C and δ^{15}N (hereafter δ^{13}C$_{c/f}$ δ^{15}N $_{c/f}$) values of YWAR, WIWA, PAWA and NOWA were used as markers of quality of winter habitat with models run independently for each tissue. Inferences of habitat occupancy for AMRE, SWTH and ALFL were made only from isotope measurements of claws.

I selected amongst competing models using Akaike's Information Criterion adjusted for small sample size (AIC$_c$; Burnham and Anderson 2002). This method is based on the principle of parsimony and considers the model with lowest AIC$_c$ to be the most parsimonious or the "best" of the set of candidate models. To facilitate comparison of the candidate models, I calculated Δi as the difference between each model and the model with the lowest AIC$_c$ (Δi= AIC$_{ci}$ − minimum AIC$_c$). Models with $\Delta i < 2$ are considered to be competitive with the best model, models with Δi values between 4-7 have considerable less support; and models with $\Delta i > 10$ are very unlikely (Burnham and Anderson 2002). I estimated normalized Akaike weights (Wi) to indicate the

probability that a given model was the best among the considered models (Burnham and Anderson 2002). When the best model was identified clearly (Akaike weight ≥ 0.90), inferences were made based on that model alone (Burnham and Anderson 2002).

When model selection uncertainty was evident (multiple models within $\Delta i < 4$, or the best AIC_c model not strongly weighted), I created a confidence set of models by all the top models until a cumulative $Wi \geq 0.90$ was reached and performed model averaging to obtain estimates and associated standard errors for each variable in the models. An unconditional 95% confidence interval (95% CI) was used to estimate the magnitude and direction (positive or negative) of the effect of the variable of interest on condition index and arrival day. Narrow intervals excluding zero indicate more precise estimates and a strong effect of the variable. Unconditional standard error (USE) was computed to assess the precision of the model-averaged estimated (Burnham and Anderson 2002).

When a given variable was present only in one model within the confidence set its importance was deemed as the Akaike weight of the model containing the variable; model averaging was not performed (Burnham and Anderson 2002). Slope and associated standard error (slope $\pm$ SE) are presented only for variables that were included in a model with $Wi \geq 0.5$.

When the effect of $\delta^{13}C$ or $\delta^{15}N$ values on condition index or arrival day was strong I estimated the change in body mass and the number of days difference in arrival day associated with winter habitat occupancy. I used parameter and averaged parameter estimates from the top models to predict condition index and arrival day at the most depleted and the most enriched values of $\delta^{13}C$ or $\delta^{15}N$. The difference between these values was then used as an estimate of effect size. For each species, predicted condition index was multiplied by the average wing length.

2.2.4.2 Effect of ENSO and local weather on body condition and arrival day

Effect of ENSO and local weather on body condition and arrival day was investigated using the long-term DMBO data set. A set of 13 *a priori* candidate linear models were investigated to explain variation in condition index observed in individuals of YWAR, AMRE, WIWA, SWTH, ALFL, NOWA, PAWA and BAOR arriving to Delta Marsh during spring from

1998 to 2010. The candidate models for condition index included May minimum temperature (MMT), El Niño Southern Oscillation (ENSO), year as a linear covariate, capture time, additive effects for year with ENSO, MMT, MMT and ENSO, MMT with ENSO, and intercept only (null) model. In order to assess whether seasonal (MMT) or within-season temperature had a stronger effect on condition index I considered four additional models that included mean May minimum daily-temperature during the migration period of each species (MDT), additive effects for year with MDT, MDT with ENSO and of MDT with MMT.

For arrival day, nine linear models were considered and included MMT, ENSO, condition index (CI), year as a continuous variable, additive effects for ENSO with MMT, CI with ENSO and MMT, CI with MMT, and CI with ENSO and a null model.

MMT and MDT data were obtained from an Environment Canada Meteorological Station located at DMBO. Annual mean monthly values of the standardized Southern Oscillation Index (SOI) were used to estimate ENSO conditions for each year, January to December, preceding spring migration (Philander 1990, Sillett et al. 2002, NOAA 2011). Negative values of SOI correspond with El Niño phase of ENSO and positive values with La Niña phase (Kiladis and Diaz 1989).

Consistent and strong variations in tropical precipitation patterns are related to ENSO; during El Niño phase, Mexico, northeastern and western South America generally experience above-average rainfall levels, whereas Central America and the Caribbean experience below-average rainfall levels (Ropelewski and Halpert 1987, Jaksic 2001). Opposite weather conditions are observed in these regions during La Niña phase. Due to interspecific variation in the winter distribution of the species studied and the regional variation of the effects of ENSO, I expected either a positive or negative effect of ENSO on arrival day and condition index. Model selection and the assessment of the magnitude and direction of the effect of the parameters of interest were conducted using the same AIC_c based approach described above.

2.3 Results

2.3.1 δ^{13}C and δ^{15}N Values in claws and feathers

Low $\delta^{13}C_c$ values in SWTH, NOWA and WIWA suggested that those species occupied mesic habitats during the winter; however, high $\delta^{15}N_c$ values in NOWAs showed that this species is likely to overwinter in more disturbed or agriculturally influenced environments (Figure 2.1). Most SWTHs migrating throughout DMBO seemed to occupy moist habitats, this species showed the narrowest range of $\delta^{13}C_c$ and $\delta^{15}N_c$ values and the lowest means (Figure 2.1). In contrast, $\delta^{13}C$ and $\delta^{15}N$ values of PAWA, YWAR, TRFL and AMRE indicated that those species potentially occupied more open, xeric winter habitats (Figure 2.1). For NOWA, WIWA, PAWA and YWAR these results were supported by $\delta^{13}C$ and $\delta^{15}N$ values derived from feathers. Additionally, both $\delta^{15}N_c$ and $\delta^{15}N_f$ values, and $\delta^{13}C_f$ values suggested that YWARs occupied drier and/or more disturbed areas than the other species (Figure 2.1).

The correlation between $\delta^{13}C$ values from feathers and from claws within individuals was weak and significant only for YWAR and NOWA (YWAR $r^2 = 0.09$, $P < 0.05$; NOWA $r^2 = 0.12$, $P < 0.05$; WIWA $r^2 = 0.03$, $P = 0.18$; PAWA $r^2 = 0$, $P = 0.98$). The correlation between $\delta^{15}N$ values derived from feathers and claws was also weak and significant in YWAR, NOWA and WIWA (YWAR $r^2 = 0.28$, $P < 0.05$; NOWA $r^2 = 0.1$, $P < 0.05$; WIWA $r^2 = 0.19$, $P < 0.05$; PAWA $r^2 = 0$, $P = 0.96$).

2.3.2 Effect of Winter Habitat Quality on Physical Condition

The highest-ranked models for condition index and arrival day included the winter-quality occupancy variables, $\delta^{13}C$ and $\delta^{15}N$, derived from claws and feathers (Table 2.1, 2.2). For condition index, model selection uncertainty was evident; with none of the top models receiving $\geq 90\%$ of the support (Table 2.1). Therefore, I report model-averaged slope and unconditional standard error (USE) for each parameter included in the confidence set (Table 2.1, 2.2).

Model averaging revealed that only $\delta^{13}C$ values derived from claws in ALFL and from feathers in PAWA had a strong effect on condition index (95% UCI excluded zero, Appendix B). The results from feathers in PAWA were supported by negative estimates derived from claws (Appendix B). For ALFL, condition index was positively related with $\delta^{13}C$ (Appendix B, Figure

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2.2); ALFL condition index was highest in birds occupying the most xeric winter habitats and lowest in most mesic habitats. I estimated an increase in body mass of approximately 3 g from the most mesic (i.e., $\delta^{13}C_c$ of -23.0‰) to the most xeric habitats (i.e., $\delta^{13}C_c$ of -20.4‰). Conversely, PAWA from mesic habitat had higher condition index than birds that had wintered in xeric habitats (negative 95% UCI, Appendix B, Figure 2.2). I estimated an increase in body mass associated to winter habitat quality of 2 g from the most xeric (i.e., $\delta^{13}C_f$ of -21.0‰) to the most mesic (i.e., $\delta^{13}C_f$ of -24.7‰) habitats, which represented 14.4% of the average body mass. The results from model averaging also suggested inter-annual variation in condition index; AMRE, WIWA and YWAR had higher condition index in 2010 than in 2009 (Appendix B).

Two models were within the confidence set of models for condition index of YWAR based on analysis of claws and feathers respectively (Table 2.1). The top model included the effect of $\delta^{15}N$ and year and the second the effect of $\delta^{13}C$ and year (Table 2.1); hence I estimated the weighted average effect of year but not the effect of $\delta^{15}N$ or $\delta^{13}C$. The effect of $\delta^{15}N$ or $\delta^{13}C$ on condition index was assessed based on the weight of the model containing that variable. Models containing $\delta^{15}N$ received $\geq 74\%$ of the support in contrast with models containing $\delta^{13}C$ which received $\leq 21\%$ based on analysis of feathers and claws respectively (Table 2.1). This suggests that $\delta^{15}N$ was a better predictor of variation in condition index than $\delta^{13}C$ values, though the effect was not strong (Appendix B).

2.3.3 Effect of Winter Habitat Quality on Arrival Day

For PAWA and NOWA, the best models for variation in arrival day contained both $\delta^{13}C$ and $\delta^{15}N$ values derived from PAWA feathers and NOWA claws which received 90 and 94% support respectively (Table 2.2).

PAWA $\delta^{13}C_f$ estimates derived from the highest ranked model (Table2) suggested that birds from xeric habitats (i.e., higher $\delta^{13}C$) passed through the study site before birds from mesic habitats (Appendix B). In contrast, the results from $\delta^{13}C_c$ model averaging showed that PAWA from mesic habitats (i.e., lower $\delta^{13}C$) passed through the study site before birds from xeric habitats (Appendix B, Figure 2.3). On average, birds from the moistest habitats (-24.3‰) arrived 9 days ahead of birds from the most xeric habitats (-15.7‰). Analysis of $\delta^{15}N_f$ values supports

the $\delta^{13}C_c$ model, with birds the most depleted samples (3.7‰) arriving 5 days ahead of birds with the most enriched (10.1‰) feathers (Appendix B).

In NOWA, claw and feather $\delta^{13}C$ suggested earlier arrival of birds from more mesic habitats (Figure 2.3). The top model containing the variable $\delta^{13}C_c$ received 94% support (Table 2.2); birds from the moistest habitats (-29.2‰) arrived seven days sooner than birds from the driest habitats (-19.4‰) (Appendix B). Similarly, model averaged parameter estimates for the effect of $\delta^{13}C_f$ also suggested a strong wintering ground influence on arrival date (Appendix B); birds from the moistest habitats ($\delta^{13}C_f$ -29.2‰) arrived nine days sooner than birds from the driest habitats (-19.4‰). In contrast, ALFL showed a negative relationship between wintering-ground habitat and arrival date, with birds from the most xeric habitats (-20.4‰) arriving approximately 3 days earlier than birds from the most mesic (-23.0‰) habitats (Appendix B, Figure 2.4).

In NOWA the top model containing the variable $\delta^{13}C_c$ received 94% support (Table 2.2), and suggested earlier arrival of birds from more mesic habitats (Appendix B, Figure 2.3). Birds from the moistest habitats (-29.2‰) arrived seven days sooner than birds from the driest habitat (-19.4‰). Similarly, model averaged parameter estimates for the effect of $\delta^{13}C_f$ also suggested a strong wintering ground influence on arrival date (Appendix B, Figure 2.4); birds from the moistest habitats ($\delta^{13}C_f$ -29.2‰) arrived nine days sooner than birds from the driest habitats (-19.4‰).

Model selection suggested that for WIWA and AMRE, the model including $\delta^{15}N$ values ($\delta^{15}N_f$ for WIWA) and year was the best model explaining the variation in arrival day, receiving 98% support in each case (Table 2.2). WIWA with the lowest $\delta^{15}N_f$ values (3.7‰) arrived 2 days before individuals with highest values (9.7‰, Appendix B). The same pattern was found in $\delta^{13}C$ and $\delta^{15}N$ values derived from claws, with those models receiving 64 and 34% support respectively (Table 2.2; Appendix B). Conversely, AMRE with the lowest $\delta^{15}N$ values (2.4‰) arrived 4 days later than individuals with highest values (11.1‰; Appendix B).

YWAR, AMRE and WIWA arrived earlier in 2010 than in 2009. Parameter estimates suggest that YWAR arrived approximately 2.5 days earlier in 2010 than 2009 (claw data set 95% U CI = -3.35, -1.58; feather data set -3.19, -1.46; Appendix B). Inter-annual variation in arrival date was even larger for AMRE and WIWA. AMRE arrived approximately 5.2 (± 0.8) days

earlier in 2010, than 2009 while WIWA arrived approximately 4.9 days (± 1.03) earlier in 2010 than 2009. Earlier arrival of WIWA in 2010 compared to 2009 was also supported by the results of model averaging conducted for the claws data set (Appendix B).

2.3.4 Effect of MMT, MDT, ENSO and Year on Body Condition

MMT was within the confidence set of models for condition index in all species. However, the presence of MDT, ENSO and year within the confidence set varied (Appendix C). Results from model averaging suggested that for YWAR, AMRE, WIWA, NOWA and BAOR condition index increased strongly with MMT (Appendix D). For SWTH and PAWA the models containing MMT received 91% and 14% of support respectively (Appendix C); and parameter estimates also indicated an increment in condition with MMT (Appendix D). For ALFL model averaging suggested that the effect of MMT was not strong.

Only AMRE and PAWA showed evidence that condition index was influenced by ENSO; birds were in better condition in springs following "La Niña" events than during springs after "El Niño" events (Appendix D). Only YWAR displayed a strong linear trend in body condition index over time, with body condition decreasing from 1998 to 2010 (Appendix D). WIWA and BAOR also displayed declining body condition over time; however, the effect of year was comparatively weak for these species (Appendix D).

2.3.5 Effect of MMT, Condition Index, ENSO and Year on Arrival Day

The model including condition index, ENSO and MMT had 97% support of being the best model for YWAR and 100% support for WIWA (Appendix E). Both YWAR and WIWA arrived earlier during warmer springs preceded by La Niña events (Appendix F). YWAR in better condition arrived earlier than birds in poorer condition; in contrast, WIWA in better condition arrived later (Appendix F). In ALFL, the only model within the confidence set containing condition index received 83% support (Appendix E), providing considerable support for an effect of condition on arrival day. Early arrival in ALFL was associated to high condition index (Appendix F).

None of the models for the other species showed W$i \geq 0.9$, hence model averaging was conducted for the parameters in the models within the confidence set (Appendix E). The results

suggested a strong effect of MMT and condition index on the day of arrival for most species. Notably, AMRE, PAWA, ALFL and BAOR arrived later during cold springs. Even though the effect of MMT was not strong for NOWA and SWTH (Appendix F) the negative estimates of that variable also revealed a trend toward late arrival with lower temperatures.

AMRE, NOWA and SWTH in poor condition arrived earlier than birds in better condition. Similarly to YWAR and WIWA, ALFL arrived earlier during springs preceded by La Niña events (Appendix F). None of the species showed changes in arrival day to Delta Marsh over time.

2.4   Discussion

2.4.1 δ^{13}C and δ^{15}N Values in claws and feathers

Strong and high significant relationships between δ^{13}C and δ^{15}N values from feathers and claws within individuals were expected since it was assumed that claws and feathers were synthesized in the same habitat and around the same time of year. However, weak correlation between isotope values from those tissues suggested that feathers and claws might not reveal the same information about winter habitat occupancy. Prealternate feathers (winter-grown feathers) represent a short-term integration of winter diet (Bearhop et al. 2002); in contrast, 1-2 mm of distal claws is expected to represent an integration of diet assimilated during a period of two to five months prior to the date of collection (Bearhop et al. 2003). However, precise winter habitat occupancy inferences from feathers depend on the knowledge of the moulting cycle of the species, the extension and timing of the prealternate moult, and on the accuracy of sampling feathers that have been replaced on the winter grounds. For WIWA, PAWA and NOWA the prealternate moult is limed to the head or body feathers, and contrast between basic and alternate feathers is often difficult to assess (Pyle 1997). I suggest that for these species winter habitat inferences from claws are potentially more reliable than inferences from feathers. Currently, the only tissues that have been used to infer winter habitat occupancy in long-distance migrants captured during spring migration or at their breeding sites are muscle (Marra et al. 1998), claws (Bearhop et al. 2004) and blood (Norris 2004). Further studies are needed in order to assess the

accuracy of winter habitat inference from feathers in species with moult limited to body or head feathers.

2.4.2 Wintering Grounds

My isotopic investigation of tissues grown on Neotropical wintering grounds and sampled at a spring migration stopover site in North America revealed strong effects of assumed winter habitat quality on body condition and arrival date for some (PAWA, ALFL, NOWA) but not all of the migrant passerines I investigated. As expected, PAWA that had occupied mesic habitats during the winter were in better physical condition and arrived before individuals from more xeric habitats. In contrast, ALFL from xeric areas arrived first and in better condition than birds from more mesic habitats. In winter, ALFL prefer open areas, forest and scrubby growth in early succession stages (Lowther 1999, Robinson et al. 1995); therefore, these habitats might be more advantageous for this particular species during the non-breeding season. Feathers and claw δ^{13}C values derived from NOWA clearly suggested that mesic winter habitat occupancy resulted in early arrival to the study site; however I did not observe any isotope pattern related to body condition.

Carry-over effects of winter habitat quality, inferred from δ^{13}C values, on spring departure condition and day of arrival has been shown previously in AMRE (Marra et al. 1998) and Black-throated Blue Warblers (*Dendroica caerulescens*) (Bearhop et al. 2004) originating from Caribbean overwinter habitats. More mesic habitats presumably have higher food availability, allowing birds from these areas to acquire condition for migration faster than individuals from more xeric habitats and depart first from the wintering grounds (Marra et al. 1998, Studds and Marra 2005, 2011).

For AMRE, I expected a strong effect of tissue δ^{13}C on arrival time as seen in several previous studies (Marra et al 1998, Marra and Holmes 2001, Studds and Marra 2005, 2011). However, I found only a strong negative effect of δ^{15}N values. Plant δ^{15}N values can vary in response to climate, soil type, and land-use practices (Nadelhoff er and Fry 1994, Handley et al. 1999, Amundson et al. 2003, Kendall 1998, Hebert and Wassenaar 2001, Evans 2007). Therefore, it is difficult to fully interpret possible mechanisms responsible for birds with higher δ^{15}N values arriving first.

The hypothesized positive effect of mesic winter habitat occupancy, inferred from δ^{13}C on arrival day and condition index was observed most strongly in PAWA and NOWA. PAWA and NOWA are strongly linked to Caribbean within winter range (Eaton 1995, Wilson 1996, Sherry and Holmes 1997); in contrast, AMRE populations migrating through southern Manitoba likely overwinter in Mexico vs. the Caribbean (Stewart 1989, Norris et al. 2006). These findings suggest that intra-specific variation in the effect of mesic winter habitat is influenced by the geographical winter distribution of the species, and that such an effect is more likely to be detected in species overwintering on the Caribbean. However, I acknowledge that lack of effect of winter habitat occupancy variables on arrival day and condition index might be due the lack of winter habitat segregation in the sampled individuals, as seems to be the case of SWTHs.

Variability in body condition and arrival day was further explained by the effect of ENSO. AMRE and PAWA were in better condition during springs preceded by La Niña events than during springs following El Niño events. A positive effect of La Niña years was also observed on the arrival day of YWAR, WIWA and ALFL. In wet areas of tropical regions El Niño events induce dry conditions which results in reduced insect abundance; in contrast, during La Niña events precipitation and insect abundance increases dramatically (Allan 1996, Holmgren et al. 2001).

Mazerolle et al. (2011) did not find an effect of ENSO on spring arrival dates of YWAR from 1974 to 2003 to the study site, and suggested that the effect of ENSO did not carry over to the breeding areas. However, recent studies suggest that ecological conditions experienced on the wintering grounds influence long-distance migrants at the population level during the following season. For example, higher plant productivity on the Caribbean winter grounds of AMRE resulted in higher abundance of eastern breeding populations during the subsequent season (Wilson et al. 2011). My findings suggest that in some long-distance migrants moving through southern Manitoba, the effect of ENSO on ecological conditions on the winter grounds can carry over to northern latitudes and influence body condition and day of arrival during spring migration.

2.4.3 Spring Stopover

ENSO also affects precipitation and temperature patterns in North America (Shabbar and Khandekar 1996, Shabbar et al. 1997). In the Canadian prairies where the study site was located, El Niño events induce warmer and dryer conditions than average. Such effects are stronger during the winter following the onset of ENSO and weaken during spring (Shabbar and Khandekar 1996, Shabbar et al. 1997). In northern latitudes, warmer temperatures during spring have been shown to advance plants budburst (Beaubien and Freeland 2000, Marra et al. 2005) and insects' emergence (Gilbert and Raworth 1996, Thomas et al. 2001). Although those conditions could be beneficial for migratory birds during spring by, for example, enhancing food availability during migration, my findings generally supported the effect on spring arrival of ENSO on winter grounds.

The results from the analysis of the DMBO long-term data set clearly suggest a strong effect of May minimum temperature (MMT) on physical condition and arrival day for most of the long-distance migrants I examined. Low temperature represents the greatest physical restriction for insects' emerging in northern latitudes (Corbet 1964, Gilbert and Raworth 1996). Additionally, lower food availability during colder springs enhance the thermoregulatory cost of migration by increasing the rates of energy consumption (Dawson et al. 1983) and can limit the ability of birds to rebuild energy stores (Marra et al. 2005).

NOWA, PAWA and SWTH were among the earliest migrants throughout the study site, and the only species where low condition index was related to both the colder springs and the lowest daily temperatures during their period of migration. Early migrants are threatened by increased energy demands imposed by low temperatures and bad weather during early spring as well as low food availability (Møller 1994). I suggest that individuals arriving earlier to the study site trade off having lower body condition and potentially higher mortality risk with the pay-offs of early arrival.

ALFL was the latest spring migrant to arrive to Delta Marsh; and the only species where the effects of MMT and MDT on condition index were not strong. ALFL was one of the two species (along with YWAR) where individuals that arrived earlier were in better condition than late arrivals. MDT during ALFL's period of migration was higher than the mean daily minimum

temperature for the period of migration of the other species and so this delayed timing of migration may be an adaptation for aerial insectivores.

Plasticity in spring arrival of long-distance migrants is thought to be constrained by endogenous circannual rhythms triggered by photoperiod at the wintering grounds (Kok et al. 1991, Berthold 1996, Gwinner 1996). However, recent studies have shown that long-distance migrants can modify their arrival in response to environmental conditions on the wintering grounds (Cotton 2003, Saino et al. 2004, Studd and Marra 2011), en route (Ahola et al. 2004, Marra et al. 2005) and at the breeding areas (Both et al. 2005, Mazerolle et al. 2011). For example, flexibility in the phenology of migration of long-distance migrants in response to spring temperature at stopover and breeding sites has been recently shown in Europe and North America (Ahola et al. 2004, Both et al. 2005, Marra et al. 2005, Buskirk et al. 2009, Tøttrup et al. 2010, Mazerolle et al. 2011), where in general birds migrated earlier during warmer years.

Modification of rates of migration in response to spring temperature has been identified as one of the mechanisms controlling variation in spring arrival in long-distance migrants (Ahola et al. 2004, Marra et al. 2005). In Britain, Huin and Sparks (1998) showed that Barn Swallows (*Hirundo rustica*), a long-distance insectivorous bird, had higher rates of migration and arrived earlier during warmer years. Similarly, Marra et al. (2005) found that in eastern North America, several species of long-distance migrants including SWTH, NOWA, YWAR, WIWA, AMRE and PAWA slowed their migratory progression in response to cold temperatures along the migratory route and consequently delayed their arrival time to stopover sites. In both studies, delayed spring arrival was attributed to the constraint imposed by temperature to insect emergence and availability. Mazerolle et al. (2011) also suggested that plasticity in spring arrival date of YWAR captured at the study site between 1974 and 2004 was likely to be caused by adjustments to the rate of migration in response to spring temperature. My findings reinforce the hypothesis of year-to-year flexibility in the phenology of spring migration of long-distance migrants in response to variation in environmental conditions (Marra et al. 2005, Mazerolle et al. 2011).

I have shown that for long-distance migrants overwintering in the Caribbean, the effect of mesic winter habitat occupancy inferred from $\delta^{13}C$ analysis carry over to northern latitudes and

affects spring condition index and arrival day. Studies are needed in order to assess whether the $\delta^{13}C$ gradient between xeric and mesic habitats in the Caribbean is consistent in other regions where my studied populations might be wintering. Individuals captured at Delta Marsh derived from a broad range of potential wintering grounds and it is not clear whether these individuals are occupying a moisture gradient throughout their winter range. Similarly, due to the variation of the effect of ENSO on local weather throughout tropical regions, different responses are expected from individuals from different wintering regions (Nott et al. 2002; Sillet et al. 2002; Mazerolle et al. 2005).

Table 2.1. Results of model selection examining the effect of winter habitat occupancy on condition index of seven long-distance migratory birds captured at Delta Marsh Bird Observatory (DMBO), Manitoba, during spring migration in 2008 and 2009. Nine candidate models were considered for each species, the models listed represent the $\geq$ 90% confidence set determined by selecting up to the first model with a cumulative Wi $\geq$ 0.9. Four-letter codes for the species are described in the methods.

Species	Model	K^a	AICc	Δi^b	Wi^c	Cum. Wi
YWAR claw	$\delta^{15}N$ + year	4	268.62	0	0.78	0.78
	$\delta^{13}C$ + year	4	271.33	2.71	0.20	0.98
YWAR feather	$\delta^{15}N$ + year	4	276.36	0	0.74	0.74
	$\delta^{13}C$ + year	4	278.83	2.48	0.21	0.95
AMRE claw	$\delta^{15}N$ + year	4	271.13	0	0.65	0.65
	year	3	274.88	3.75	0.10	0.75
	$\delta^{13}C$ + year	4	275.12	3.98	0.09	0.84
	$\delta^{13}C$ + $\delta^{15}N$	4	275.14	4	0.09	0.93
WIWA claw	$\delta^{13}C$ +year	4	128.95	0.00	0.34	0.34
	year	3	129.60	0.63	0.25	0.59
	$\delta^{15}N$ +year	4	130.00	10.53	0.20	0.79
	Intercept	2	132.32	33.68	0.06	0.85
	$\delta^{13}C$	3	132.60	36.46	0.06	0.91
WIWA feather	$\delta^{15}N$	3	109.63	0	0.53	0.53
	$\delta^{15}N$ + year	4	110.82	1.20	0.29	0.82
	$\delta^{13}C$ + $\delta^{15}N$	4	111.83	2.20	0.18	1
NOWA claw	$\delta^{15}N$	3	209.80	0.00	0.69	0.69
	$\delta^{13}C$ + $\delta^{15}N$	4	211.47	1.67	0.30	0.99
NOWA feather	$\delta^{13}C$	3	214.37	0	0.45	0.45
	$\delta^{15}N$	3	214.62	0.25	0.4	0.85
	$\delta^{13}C$ + $\delta^{15}N$	4	216.57	2.20	0.15	1
PAWA claw	$\delta^{13}C$	3	53.62	0	0.71	0.71
	$\delta^{13}C$ + $\delta^{15}N$	4	56.50	2.88	0.17	0.88
	$\delta^{15}N$	3	58.57	4.95	0.06	0.94
PAWA feather	$\delta^{13}C$	3	40.35	0	0.65	0.65
	$\delta^{13}C$ + $\delta^{15}N$	4	41.63	1.28	0.34	0.99
SWTH claw	$\delta^{15}N$	3	143.65	0	0.49	0.49
	$\delta^{13}C$	3	144.12	0.46	0.39	0.88
	$\delta^{13}C$ + $\delta^{15}N$	4	146.41	2.76	0.12	1
ALFL claw	$\delta^{13}C$	3	97.92	0	0.74	0.74
	$\delta^{13}C$ + $\delta^{15}N$	4	100.16	2.23	0.24	0.98

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

Table 2.2. Results of model selection examining the effect of winter habitat occupancy on arrival day of seven long-distance migratory birds captured at Delta Marsh Bird Observatory (DMBO), Manitoba, during spring migration in 2009 and 2010. Nine candidate models were considered for each species, the models listed represent the $\geq 90\%$ confidence set determined by selecting up to the first model with a cumulative W$i \geq 0.9$. Four-letter codes for the species are described in the methods.

Species	Model	K[a]	AICc	Δi^{β}	Wi^{c}	Cum. Wi
YWAR claw	δ^{15}N+year	4	534.89	0	0.85	0.85
	δ^{13}C+year	4	538.30	3.40	0.15	1.00
YWAR feather	δ^{15}N+year	4	556.68	0	0.60	0.60
	δ^{13}C+year	4	557.46	0.79	0.40	1.00
AMRE claw	δ^{15}N+year	4	610.34	0	0.98	0.98
WIWA claw	δ^{13}C+year	4	323.70	0	0.64	0.64
	δ^{15}N+year	4	324.97	1.27	0.34	0.98
WIWA feather	δ^{15}N+year	4	314.76	0	0.98	0.98
NOWA claw	δ^{13}C + δ^{15}N	4	320.77	0	0.94	0.94
NOWA feather	δ^{13}C	3	324.19	0	0.53	0.53
	δ^{13}C + δ^{15}N	4	324.88	0.69	0.37	0.90
	δ^{15}N	3	327.46	3.27	0.10	1.00
SWTH claw	δ^{15}N	3	187.09	0	0.62	0.62
	δ^{13}C	3	189.13	2.04	0.22	0.84
	δ^{13}C+δ^{15}N	4	189.75	2.66	0.16	1.00
ALFL claw	δ^{13}C	3	135.26	0	0.41	0.41
	δ^{15}N	3	136.42	1.15	0.23	0.64
	Intercept	2	136.57	1.31	0.21	0.85
	δ^{13}C+δ^{15}N	4	137.20	1.93	0.15	1.00
PAWA claw	δ^{13}C	3	144.66	0	0.73	0.73
	δ^{13}C + δ^{15}N	4	147.11	2.45	0.22	0.95
PAWA feather	δ^{13}C + δ^{15}N	4	116.67	0	0.90	0.90

[a] Number of parameters
[b] Δi (Δi= AIC$_{ci}$ – minimum AICc)
[c] Akaike weight represents support for each model
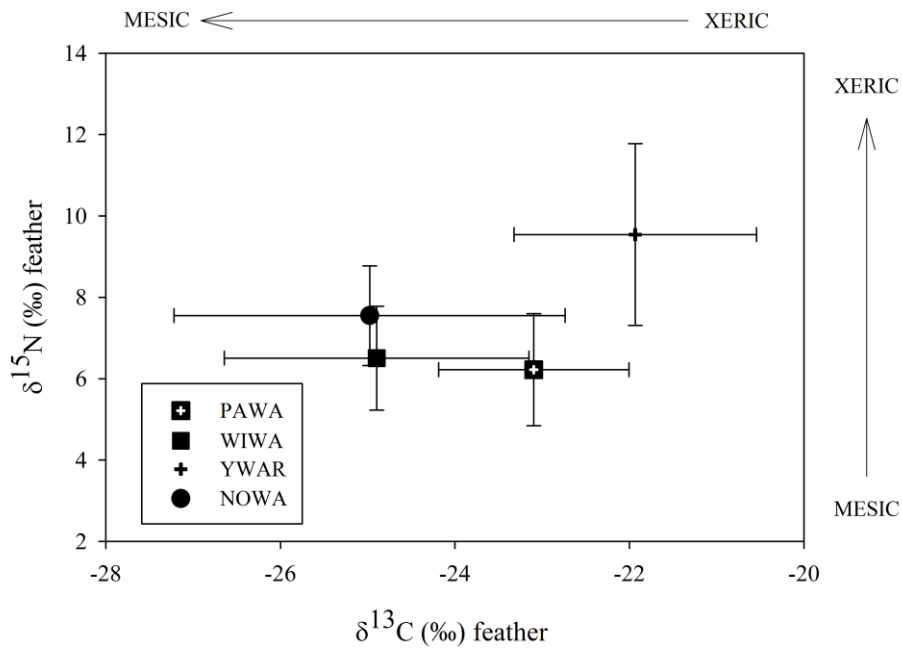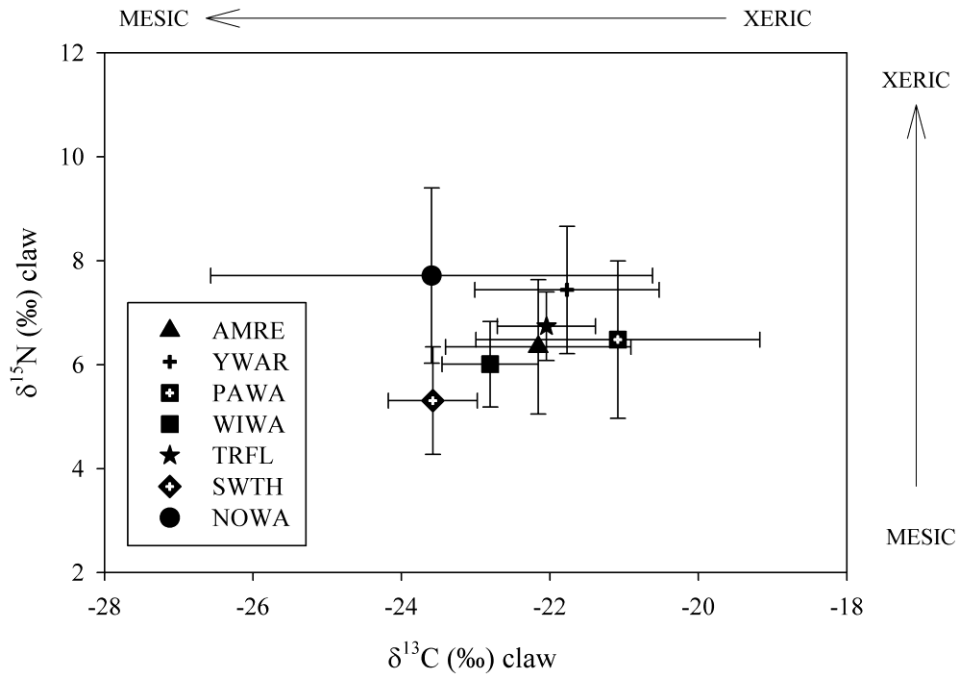
Figure 2.1. Mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values of claws and feathers of seven long-distance migratory birds sampled at Delta Marsh Bird Obsevatory (DMBO), Manitoba, during spring migration in 2009, and 2009 and 2010 (YWAR, AMRE and WIWA). Four-letter codes for the species are described in the methods.

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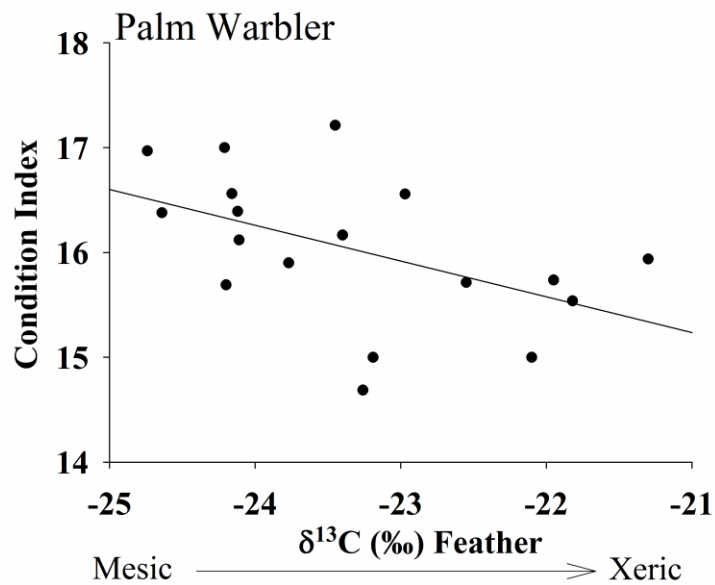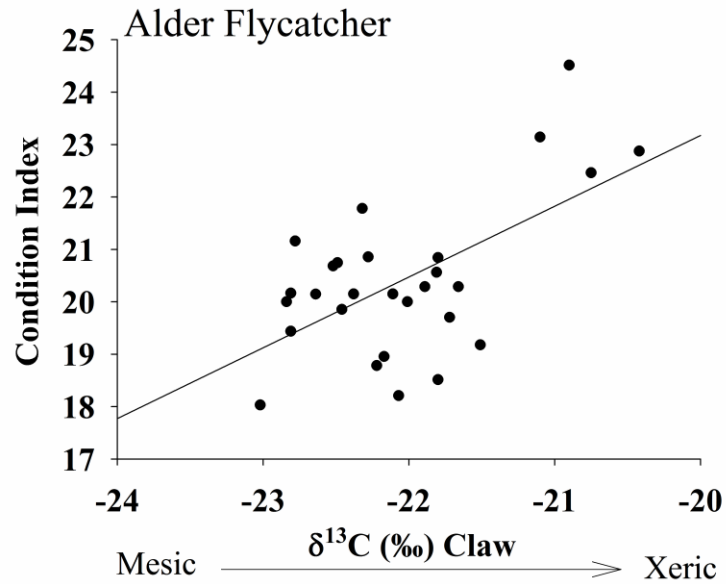
Figure 2.2. Effect of winter habitat occupancy on condition index of Alder Flycatcher (*Empidonax alnorum)* and Palm Warbler (*Sethophaga palmarum*) captured at Delta Marsh Bird Observatory, southern Manitoba, during spring migration 2010. Winter habitat occupancy was inferred from δ13C (‰) values derived from claws and feathers grown on the wintering grounds.

Figure 2.3. Effect of winter habitat occupancy on arrival day of Palm Warbler (*Sethophaga palmarum*) and Northern Waterthrush (*Parkesia noveboracensis*) captured at Delta Marsh Bird Observatory, southern Manitoba, during spring migration 2010. Day 1= 1 May. Winter habitat occupancy was inferred from $\delta^{13}C$ (‰) values derived from claws and feathers grown on the wintering grounds.
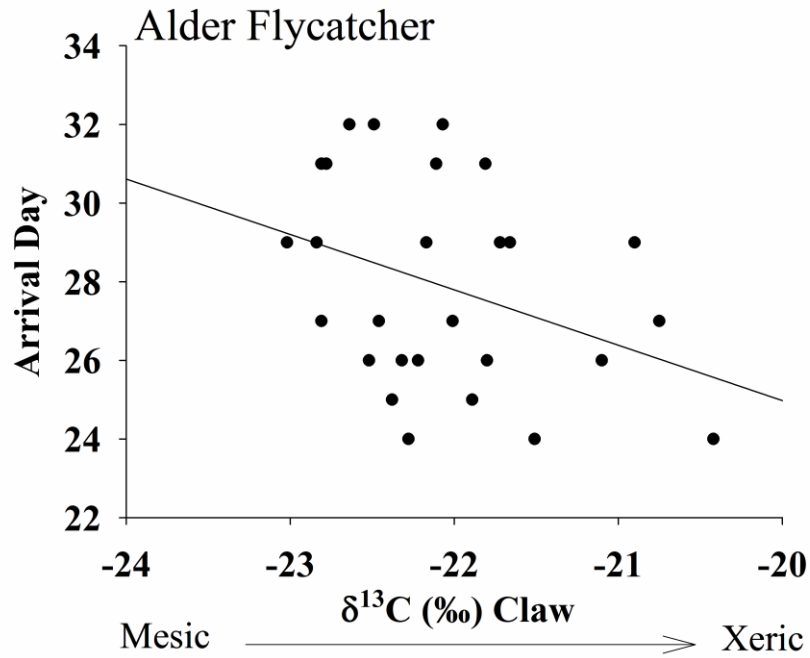
Figure 2.4. Effect of winter habitat occupancy on arrival day of Alder Flycatcher (*Empidonax alnorum*) captured at Delta Marsh Bird Observatory, southern Manitoba, during spring migration 2010. Day 1= 1 May. Winter habitat occupancy was inferred from δ^{13}C (‰) values derived from claws growth at the wintering grounds.

CHAPTER 3 : PLUMAGE COLORATION AND WINTER HABITAT OCCUPANCY OF YEARLING YELLOW WARBLERS: CONSEQUENCES FOR ANNUAL SURVIVAL

3.1   Introduction

Carotenoids are one of the three main mechanisms for the production of colour in birds and carotenoid levels have been widely accepted as a reliable condition-dependent signal of quality (Zahavi 1975, Hamilton and Zuk 1982, Hill 1991, Griffith and Pryke 2006, Hill 2006). Birds cannot synthesize carotenoids; therefore the display of coloured plumage depends on the acquisition of these pigments through the diet (Goodwin 1984). Besides carotenoid intake, carotenoid-based colouration can be affected by nutritional state during molt, (Hill and Montgomerie 1994, Hill et al. 2002), health and imunocompetence (Thompson et al. 1997, Møller et al. 2000, Brawner et al. 2000, Saks et al. 2003). Therefore, only individuals with access to adequate carotenoid intake and in good physiological status should be able to accumulate the pigments needed for maximal colouration expression.

In several Nearctic-Neotropical migrants, occupation of winter territories is highly influenced by behavioural dominance (Lynch et al. 1985, Morton 1990, Wunderle 1992, Lopez and Greenberg 1990, Marra 2000). Rohwer (1975, 1982) suggested that brighter plumage colouration favored competition over resources during the non-breeding season by signaling individual quality (i.e., individual ability and social status) and assumed that such signaling should work both between and within age classes. The quality of habitat occupied by migrant individuals during the winter is a contributing factor to self-maintenance, annual survival and consequently fitness (Sherry and Holmes 1996, Gill et al. 2001, Gunnarsson et al. 2005, Marra et al. 2006). Winter habitat occupancy can produce residual effects on the individuals that carry over to the subsequent season (Marra et al. 1998, Norris et al. 2004, Norris 2005). For example, Icelandic Black-tailed Godwit (*Limosa limosa*) overwintering in high quality sites in the UK (i.e., with higher prey density) arrived earlier to the breeding grounds, acquired higher quality breeding sites, bred more successfully, and had higher annual survival that individuals from poorer-quality wintering habitats (Gill et al. 2001, Gunnarsson et al. 2005). American Redstarts (*Setophaga ruticilla*) residing in low-quality xeric winter habitats (i.e., low food availability) decreased their energetic condition over the winter (Marra and Holberton 1998), departed later

and in lower physical condition in spring migration (Marra et al. 1998, Studds and Marra 2005), and had lower overwinter survival than individuals from high-quality mesic habitats (Marra and Holmes 2001).

Benefits conferred by brighter carotenoid-based plumage colouration during the non-breeding season and its potential effects on annual survival remains poorly studied. Understanding the factors that influence survival during different stages of the annual cycle of migratory birds is important for the determination of processes that regulate migratory populations (Sillett and Holmes 2002, Sillett et al. 2002, Mazerolle et al. 2005). The aim of this study was to assess whether brighter carotenoid-based first-winter plumage colouration conferred higher annual survivorship to yearling Yellow Warblers' (YWAR) through the occupancy of higher quality winter habitats. Juvenile YWAR require about a year to achieve their full adult basic plumage. The first-winter plumage colouration is acquired largely before fledging, therefore the colour display depends in part on carotenoids provided by the parents during nestling growth (Tschirren et al. 2003, Fitze et al. 2003a, b).YWAR first-winter plumage is highly variable between and within sexes, generally males are brighter than females but duller males can overlap in plumage with females; this plumage is replaced before spring migration (Pyle 1997, Hobson et. al 2000). Delays in acquiring adult plumage benefit inexperienced immature individuals by signalling competitive abilities between age classes and reducing aggressiveness from adults on the non-breeding grounds (Rohwer 1975, Rohwer et al. 1980, Rohwer and Butcher 1988, Rohwer 1986). Although this hypothesis explains the function of differences in plumage colouration between age classes, high inter-individual variability still remains within age classes and the importance of such variation remains unknown for young birds.

I selected YWAR as a study species due to the high plumage colouration variability (Pyle 1997, Hobson et al. 2000), its occupancy of a wide range of habitat on the winter grounds (Elliot 1974, Wunderle and Waide 1993, Greenberg and Ortiz 1994) and high return rate of yearling individuals to the study site which allows survival estimations of the local population. Based on the benefits conferred by bright carotenoid-based colouration I hypothesized that within sexes, brighter yearling birds will have higher annual survival than pale yearlings. I used stable-isotope (δ^{13}C) analysis of winter-grown tissues to infer winter habitat occupancy in returning individuals. I hypothesized that if brighter carotenoid-based colouration confers survivorship advantages by

mediating the occupancy of more suitable winter habitats, then $\delta^{13}C$ values of returning individuals should reflect higher-quality winter habitat occupancy.

3.2   Methods

3.2.1   Study Site and Field Methods

Field work was carried out at Delta Marsh Bird Observatory (DMBO), Manitoba (50º11′N, 98 º23′W) from 2008 to 2010. Hatch-year (HY) Yellow Warblers (*Sethophaga petechia*) were captured from 12 July to 20 August using a standardized constant-effort mist-netting protocol (Hussell and Ralph 2005). The last day of sampling was established prior to fall migration in order to restrict the analysis to HY birds produced at the study site.

Ten mist nets were operated six hours a day from 30 minutes before sunrise at the forested dune-ridge which separates the southern shore of Lake Manitoba from Delta Marsh. Captured birds were banded using US Fish and Wildlife Service aluminum bands aged and sexed according to Pyle (1997) and plumage brightness measurements were performed (see below). During 2009 and 2010, recaptures were conducted from 1 May to 30 September following the same mist-netting protocol.

3.2.2   Coloration Assessment

Hatch year (HY) males and females were visually separated into pale and bright categories based on the overall brightness of the yellow breast plumage (Hobson et al. 2000). I validated the visual classification system by quantifying HY colour relative to a continuous scale using the RGB colour model; in this model, red, green, and blue combine additively to produce a resultant color (Wiebe and Bortolotti 2002, Montgomerie 2006).

The validation of the visual classification involved 240 randomly chosen individuals, 120 from 2008 and 120 from 2009; YWARs were stratified into four groups: bright males, bright females, pale males and pale females. Each individual was photographed under a tripod mounted digital camera (Canon PowerShot SX100 IS) and under uniform light conditions. The digital images of Yellow Warbler breast regions were uploaded to the computer program ImageJ (Rasband 1997). For each image, a uniform yellow breast section of 100 pixels was randomly

selected; then choosing the Color Histogram plug-in an average score for each red, green and blue variable in the RGB color model was calculated (Montgomerie 2006).

3.2.3   Stable Isotopes Analysis

Mesic and xeric habitats typically differ in carbon-stable isotope values (δ^{13}C) of foodwebs, due to differences in photosynthetic pathways and water-use efficiency mechanisms (Farquhar et al. 1989, Lajtha and Marsha 1994). In general, δ^{13}C values of plants are lower in mesic than in xeric habitats (Boutton 1991, Ehleringer 1991, Lajtha and Marsha 1994, Sage and Coleman 2001, Marra et al. 1998). These values are incorporated into birds' tissues through the supporting food web and so the nature of previous winter habitats occupied by birds subsequently captured at breeding areas the following spring can be inferred from δ^{13}C values of feathers and portions of claws growth on the winter grounds (Marra et al. 1998, Bearhop et al. 2004).

From each individual recaptured, I sampled alternate feathers grown during the winter. Feathers were soaked for 4 h in a 2:1 chloroform:methanol solution and dried in a fume hood for 48 h; distal vane material was removed for analysis. Distal claw tissue (1-2 mm) was additionally taken from each individual. All samples were weighed (0.2-1.1 mg), loaded into tin cups and combusted in a Robo-Prep elemental analyzer interfaced with a Europa 20:20 continuous-flow isotope-ratio mass spectrometer (CFIRMS). Stable isotope ratios (^{13}C/^{12}C) are reported in delta (δ) notation, in per-mil units (‰) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

Where X is ^{13}C, and R is the corresponding ^{13}C/^{12}C ratio. The $R_{standard}$ value for δ^{13}C is the Vienna Pee Dee Belemnite (VPDB) standard. Using within-run repeated analysis of an internal laboratory standard (albumen) measurement precision was estimated to be ± 0.1 ‰.

3.2.4   Statistical Analysis

3.2.4.1 Coloration assessment

Both visually determined and RGB brightness values were included into a Discriminant Function Analysis (DFA) to determine whether a pale or bright bird was correctly classified. Predictor variables were the red, blue and green values from the RGB colour model. I performed

six DFA, four to test the separation of bright and pale birds within each sex in each year (i.e., separation of bright and pale females in 2008); and two where I combined values from 2008 and 2009 and tested the separation into pale and bright within each sex.

3.2.4.2 Survival analysis

In order to assess if apparent annual survival (ϕ) of HY Yellow Warblers varied as a function of sex, plumage colouration, and year, I fitted nine Cormack-Jolly-Seber (CJS) models to the mark-recapture data following procedures outlined by Lebreton et al. (1992) and by Burnham and Anderson (2002).

All models were developed and assessed using program MARK (White and Burnham 1999). I began the survival analysis by developing a fully parameterized model where apparent survival probabilities varied as function of the interaction of year (y), sex (s) and plumage brightness (c); I allowed recapture probabilities (p) to change as function of sex or year ($\phi s*y+c*y+s*c\ ps/y$) but not by the additive effect or the interaction of both because it diminished the fit of the full model. In order to check for model fit, I calculated median c-hat (ĉ) for the full model using the method implemented in MARK, (White and Burnham 1999). In total, I fit 20 candidate models where I allowed survival to vary as function of different combination of the variables and their main effects (Table 3.2).

Model selection was based on Akaike's Information Criterion, corrected for small sample sizes (AICc; Burnham and Anderson 2002). Under this approach, the model with the lowest AICc is selected as the "best" or most parsimonious model; the model that explains most of the variance with the lowest number of parameters. In order to assist model comparison I estimated Δi as the difference between each model and the model with the lowest AIC_c ($\Delta i = AIC_{ci} -$ minimum AICc); models with $\Delta i < 2$ are considered to be as good as the most parsimonious model (Burnham and Anderson 2002). Normalized Akaike weights (Wi) were calculated in order to indicate the relative likelihood of each model within the candidate set of models. A model with Wi >0.90 is 90% likely of being the best model and inferences can be made from that model along (Burnham and Anderson 2002).

When there was uncertainty in model selection (i.e., where different models had $\Delta i < 2$ or $Wi < 0.90$), I incorporated such uncertainty by reporting model-averaged parameter estimates (Burnham and Anderson 2002). From each model I took the estimates of a parameter θ, weighted them by the Wi value of the model and averaged the weighted estimates over all models in the candidate set containing parameter θ. I calculated 95% confidence intervals and associated standard error for year, sex and plumage brightness in order to assess the magnitude and direction of their effect on apparent survival; positive intervals excluding zero indicated a strong positive effect of the parameter (Burnham and Anderson 2002).

3.2.4.3 Isotope information from winter grounds

I fitted a General Linear Model (GLM) in order to assess the effect of year, sex and plumage colouration on $\delta^{13}C$ values of recaptured second-year (SY) individuals (banded the previous year as hatch year). I combined sex and plumage brightness information in a single variable (sex/colour) with three categories: bright female, bright male and pale male; pale females were not included in the analysis because isotope data was not available.

In order to assess winter habitat occupancy differences related to sex and age, I combined the $\delta^{13}C$ information of SY with $\delta^{13}C$ information of adult individuals (more than a year old). I fitted a general linear model (GLM) with $\delta^{13}C$ values as the response variable and the interaction of sex and age as explanatory variable. I ran separate models for feathers and claws. All statistical analyses were conducted using R (R development Core team 2008). Significance for statistical tests was accepted at $P < 0.05$.

3.3   RESULTS

3.3.1   Coloration Assessment

The variables red and green were highly correlated; therefore only red and blue were used as predictors of visually classified plumage brightness. For females and males in 2008 the Discriminant Function Analysis (DFA) revealed a significant association between groups and all predictors, accounting for 82.6% and 80.7% of between group variability respectively. The cross validated classification showed that overall 95% females and 96.7% males were correctly

classified into pale and bright categories (Table 3.1). In 2009, the association between groups and predictors was also significant and accounted for 56% of the variation for females and 76% in males. The cross validated classification showed that overall 83.3% females and 96.7% males were correctly classified into pale and bright (Table 3.1).

When I performed the DFA for 2008 and 2009 together the results showed that the association between groups and predictors was also significant and accounted for 65% of the variation for females and 68% in males. The cross validated classification showed that in general 87.5% females and 90.8% males were correctly classified into pale and bright categories (Table 3.1).

3.3.2 Survival Analyses

Model selection based on AICc suggested that the three top models were the most parsimonious ($\Delta I < 2$), the accumulative Akaike weight was 0.46 indicating that 46% of the support in the data was for those models (Table 3.2). Since none of the models clearly showed better support in relation to other candidate models (i.e., none of the models had W$i \geq 0.90$), I used model averaging to incorporate uncertainty in the estimation of the survival estimates. The results showed that survival was higher in 2009 than in 2010; however, the survival estimates within sex did not show major differences (Table 3.3).

In order to assess the magnitude of the effect of year, colouration and sex on apparent survival, I derived 95% confidence intervals and associated standard error from the model containing only the main effect of those variables. My results suggested an effect of year on apparent survival only when the recapture probability remained constant; 95% CI was negative and did not included zero. The models did not show support for the effect of plumage brightness and sex on survival (Table 3.4).

3.3.3 Isotope Information from Winter Grounds

Recaptured SY birds showed high δ^{13}C values in claws and feathers during both years (Table 3.5). Results from the GLM suggested no significant differences between the δ^{13}C values

derived from claws and feathers of bright females, bright males and pale males (claws: year*sex/colour $F_{2,53} = 2.96$, $P = 0.06$; feathers: year*sex/colour $F_{2,59} = 0.95$, $P = 0.4$).

Differences in $\delta^{13}C$ values, derived from both claws and feathers, between age and sex classes were not statistically significant (claws $F_{3,155} = 2.5$, $P = 0.07$; feathers $F_{3,168} = 1.8$, $P = 0.16$). $\delta^{13}C$ values for each sex and age class are shown in Table 3.6.

3.4   Discussion

The annual apparent survival analysis based on capture-recapture data of yearling Yellow Warblers at their natal sites at Delta Marsh showed that survival was higher in 2009 than in 2010. Lower survival in 2010 might be related to the effect of long-scale climatic events, such as ENSO, on precipitation patterns and food availability on the winter grounds (Sillett et al. 2000, Nort et al. 2002). The YWAR population at Delta Marsh is likely to overwinter in southwest Mexico, southern Central America and northern South America (Boulet et al. 2006) where precipitation declines during El Niño and increases during La Niña years (Ropelewski and Halpert 1987, Jaksic 2001). La Niña conditions persisted during winter 2008 and spring 2009; in contrast, El Niño conditions occurred during winter 2009 and spring 2010 (NOOA 2011). Low food availability on the winter grounds induced by El Niño conditions could have increased overwinter mortality or lowered pre-migratory physical condition and enhanced mortality during spring migration.

Neither sex nor carotenoid-based colouration had any clear effect on annual apparent survival. Bright carotenoid-based colouration is related to high individual's quality (Zahavi 1975, Hamilton and Zuk 1982); therefore I expected that YWAR with brighter yellow breast colouration had higher annual survival than dull individuals. Studies assessing the relationship between carotenoid-based colouration and survival are few and have shown contrasting results. For example Hill (1993) reported that in House Finches (*Carpodacus mexicanus*), yearling female survival was not related to plumage brightness. Horak et al. (2001) found that males and female yearling Great Tits (*Parus major*) with brighter carotenoid-based ventral plumage colouration had higher annual survivorship than dull individuals. My results suggested that, at

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least in the studied population, brighter colouration did not confer survivorship advantages to males or female HY birds.

Winter habitat occupancy inferred from $\delta^{13}C$ values of winter-grown tissues showed that independent of sex or plumage brightness, all survivors had resided in generally xeric habitats during the non-breeding season (Table 3.5). The results contrast with my expectations and with previous studies suggesting that mesic habitat occupancy is related to higher survival. For example, American Redstarts overwintering in xeric habitat, with low food availability, decreased their energetic and physical condition over the winter and had lower annual survival (Marra and Holberton 1998, Marra and Holmes 2001). However, my findings agreed with few previous studies of long-distance Nearctic-Neotropical migrants that showed carotenoid-based colouration did not have any direct relationship with the quality of winter habitats (Reudink et al. 2009, Germain et al. 2010).

Winter habitat segregation by sex has been suggested as one of the mechanisms regulating winter habitat occupancy in several migratory species. The mechanism is presumably through behavioural dominance, older males displace females and younger males to less suitable habitats (Lynch et al. 1985, Morton 1990, Wunderle 1992, Lopez and Greenberg 1990, Marra 2000). I evaluated the possibility of yearling individuals being displaced to poorer habitats by adults by examining differences in $\delta^{13}C$ values between age, sex and the interaction of both. Feather and claw $\delta^{13}C$ values suggested that both adults and yearlings resided in winter habitats with similar $\delta^{13}C$ values.

To date, strong isotopic effects of winter habitat occupancy in Nearctic-Neotropical migratory passerines (inferred from δ13C) has been shown only in species overwintering in the Caribbean where some of the population inhabits moist mangroves and others dry shrub (Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004). The population of YWAR breeding at Delta Marsh likely overwinters in southwest Mexico, southern Central America and northern South America (Boulet et al. 2006). The Mangrove Warbler (S. petechia; erithachorides group) is a YWAR subspecies native to tropical mangroves and whose distribution overlaps with my migrant subspecies (Browning 1994). If migrant YWARs are generally excluded from higher-quality mesic habitat by the resident Mangrove Warbler then this would clearly interfere with my ability

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to detect habitat segregation isotopically in my study population of migrants. Further studies of isotope patterns and habitat occupancy on the breeding grounds are needed in order to confirm my hypothesis.

Table 3.1. Cross-validated classification of bright males, bright females, pale males and pale females hatch year Yellow Warblers visually classified at Delta Marsh Bird Observatory during summer 2008 and 2009. The Red and Blue values from a RGB colour model were derived from photographs and included as predictive variables into a Discriminant Function Analysis to determine whether a pale or bright bird was correctly classified.

Sex/year	Visual classification		DFA classification (%)		
	Colour	N	Pale	Bright	Total
Females 2008	Pale	30	90	10	100
	Bright	30	0	100	100
Males 2008	Pale	30	93.3	6.7	100
	Bright	30	0	100	100
Females 2009	Pale	30	90	10	100
	Bright	30	23.3	76.7	100
Males 2009	Pale	30	93.3	6.7	100
	Bright	30	0	100	100
Females 2008-2009	Pale	60	88.3	11.7	100
	Bright	60	13.3	86.7	100
Males 2008-2009	Pale	60	93.3	6.7	100
	Bright	60	11.7	88.3	100

Table 3.2. Summary output from competing capture-recapture models developed for hatch year Yellow Warblers captured and released at Delta Marsh, Manitoba, from 2008 to 2010. Rates of survival (ɸ) and recapture (P) were modeled as function of year (y), sex (s), plumage brightness (c), and combinations (+) and interactions (*) of these explanatory variables.

Model	K	Deviance	AICc	Δi	Wi
Φs+t, Ps	5	5.21	773.27	0.00	0.2126
Φt , Ps	4	7.79	773.84	0.57	0.1600
Φs*t, Ps	6	4.97	775.05	1.77	0.0877
Φs+c+t, Ps	6	5.20	775.28	2.00	0.0781
Φc+t, Ps	5	7.74	775.81	2.53	0.0600
Φs+t, Pt	4	10.32	776.37	3.10	0.0452
Φs, Pt	4	10.33	776.38	3.11	0.0449
ɸs+t, P	4	10.37	776.42	3.14	0.0442
Φs, Ps	4	10.61	776.66	3.39	0.0391
Φt, P	3	13.21	777.25	3.98	0.0291
Φc*t, Ps	6	7.53	777.61	4.34	0.0243
Φs*c, Ps	6	8.02	778.09	4.82	0.0191
Φs+c+t, Pt	5	10.29	778.35	5.08	0.0168
Φs+c, Pt	5	10.31	778.37	5.09	0.0167
Φs*t, P	5	10.32	778.38	5.11	0.0165
ɸs+c+t, P	5	10.35	778.41	5.14	0.0163
Φs+c, Ps	5	10.51	778.57	5.30	0.0150
Φc+t, Pt	4	12.97	779.02	5.75	0.0120
ɸc+t, P	4	13.17	779.22	5.94	0.0109
Φc, Pt	4	13.18	779.23	5.96	0.0108

Table 3.3. Model-averaged survival parameter estimates (ɸ) and associated unconditional standard error (U. SE) computed for hatch year Yellow Warblers captured and released at Delta Marsh. Manitoba. from 2008 to 2010.

Year	Bright female		Pale female		Bright male		Pale male	
	ɸ	U. SE	ɸ	U. SE	ɸ	U. SE	ɸ	U. SE
2009	0.2258	0.13	0.2250	0.13	0.1478	0.06	0.1480	0.06
2010	0.3314	0.20	0.3270	0.20	0.2236	0.13	0.2201	0.13

Table 3.4. β Estimates, standard error (SE) and 95% Confidence Interval derived from the models including the main effect of year (y), plumage brightness (c) and sex (s).

Model	β±SE	95% CI
φt. P	-0.124±0.06	-0.247, -0.002
φt. Ps	-0.110±0.06	-0.227, 0.008
φs. P	0.074±0.04	-0.008, 0.156
φs. Ps	-0.237±0.17	-0.570, 0.096
φs. Pt	0.052±0.03	-0.015, 0.118
φc. P	-0.002±0.04	-0.090, 0.085
φc. Ps	0.018±0.04	-0.066, 0.103
φc. Pt	-0.006±0.04	-0.075, 0.063

Table 3.5. Mean (SD‰) stable-carbon isotope ratios of second year Yellow Warbles' alternate feathers and claws sampled at Delta Marsh Bird Observatory during 2009 and 2010. $\delta^{13}C$ values represent winter habitat occupancy during the year when the individuals were initially banded as hatch year.

Season	N	Feathers δ13C	N	Claws δ13C
Winter 2008	25	-21.8±1.2	15	-21.7±0.7
Winter 2009	43	-21.6±1.4	45	-22.2±0.9
Winter*	68	-21.6±1.3	60	-22.1±0.9

Winter*$\delta^{13}C$ values from winter 2008 and 2009 combined.

Table 3.6. Mean (±SE) stable-carbon isotope ratios of Yellow Warbler claws and feathers grown at the wintering grounds and sampled at Delta Marsh Bird Observatory, southern Manitoba, Canada; during spring migration in 2009 and 2010.

Year	Age/Sex	δ^{13}C Claw		δ^{13}C Feather	
		N	Mean ± SE	N	Mean ± SE
2009	ASY/Male	23	-21.8 ± 0.2	23	-22.2 ± 0.3
	ASY/Female	13	-21.4 ± 0.2	15	-22.0 ± 0.3
	SY/Male	25	-21.6 ± 0.1	28	-21.4 ± 0.2
	SY/Female	11	-21.9± 0.3	18	-22.4 ± 0.3
2010	ASY/Male	15	-21.9 ± 0.2	15	-21.7 ± 0.3
	ASY/Female	9	-22.0 ± 0.3	9	-21.9 ± 0.3
	SY/Male	48	-22.1 ± 0.1	48	-21.6 ± 0.3
	SY/Female	15	-22.5 ± 0.3	16	-21.7 ± 0.3

CHAPTER 4 : SUMMARY AND SYNTHESIS

Long-distance Nearctic-Neotropical migrants are influenced by interactions between different seasons of their annual cycle (Fretwell 1972, Marra et al. 1998, Saino et al. 2004, Norris and Marra 2007). For example, events during the non-breeding season such as the quality of habitats occupied (Marra et al. 1998) or other environmental conditions (Studds and Marra 2011) produce residual effects that carry over to the subsequent breeding season and presumably affects fitness of migratory birds at the individual and population level (Sillett et al. 2002, Norris et al. 2004). Linking events during different stages of the annual cycle in small, long-distance migrants have been constrained by the limitations of conventional mark-recapture techniques to track migratory birds year-round (Hobson 1999, Webster et al. 2002, Hobson and Norris 2008). However, the recent application of endogenous markers, such as naturally occurring ratios of stable isotopes in animals, have received considerable attention because of their usefulness for tracking migratory birds without the need for individuals to be marked and recaptured (Hobson 1999, Hobson 2008, Hobson and Norris 2008, Hobson et al. 2010).

For my thesis research, I relied on carbon- and nitrogen-stable isotope (δ^{13}C, δ^{15}N) values from winter-grown tissues to infer the occupancy of high (i.e., mesic) vs. poor (i.e., xeric) quality winter habitats. In Chapter 2, I used isotopic information of birds returning to their breeding grounds in North America, to assess the carry-over effect of winter-habitat occupancy on arrival day and condition index during spring migration of seven long-distance migratory songbirds. Based on the findings of Marra et al. (1998) and Bearhop et al. (2004), I expected higher condition index and earlier arrival to the study site for individuals that had occupied higher-quality habitats. Inter-specific differences in the effect of winter habitat quality on arrival day and condition index might be influenced by the geographical winter distribution of the species, and such an effect is more likely to be detected in species overwintering on the Caribbean.

Recent studies have shown that besides winter habitat-occupancy, environmental conditions on the wintering and breeding grounds, such as precipitation amount, temperature and primary productivity also influence spring physical condition and phenology of spring migration (Saino et al. 2004, Marra et al. 2005, Studds and Marra 2011, Tøttrup et al. 2010). I used a DMBO, long-term, data set to determine the effect of El Niño events (ENSO), May minimum

temperature (MMT) and May minimum daily temperature (MDT) on body condition and spring arrival date.

The effect of ENSO, probably through its influence on precipitation and food availability on the winter quarters (Allan 1996, Holmgren et al. 2001, Sillett et al. 2002), carried over to northern latitudes and affected both spring arrival date and physical condition in some, but not all, of the species studied. Differences observed in the effect of ENSO on condition and arrival day among species is potentially related to the strength to which the individuals captured at Delta Marsh are geographically connected throughout the annual cycle (Webster et al. 2002, Marra et al. 2006). For example, due to the variation of the effect of ENSO on local weather throughout tropical regions (Ropelewski and Halpert 1987, Stenseth et al. 2003), individuals disperse over a broad geographic area in their wintering grounds might thus respond differently to El Nino and La Nina events, and the effect might not be detected. Further studies on Neotropical migrants using regions with consistent influence of ENSO are needed to determine whether interspecific variation in condition and arrival day in response to ENSO are the consequence of weak connectivity among the individuals captured or to a weak effect of ENSO on precipitation and primary productivity on the winter grounds.

The effect of MMT on arrival day and condition index was strong; during colder springs, most species arrived later and in lower physical condition. The variation in arrival day in response to MMT reinforced the hypothesis of phenology of spring migration flexibility of long-distance migrants (Marra et al. 2005, Mazerolle et al. 2011). Only in late migrants such as Alder Flycatcher was condition index not affected by MMT; whereas only early migrants such as Palm Warbler, Northern Waterthrush and Swainson's Thrush were affected by lower MDT. Low ambient temperatures found *en route* by long-distance migrants limit body condition and such an effect is likely to be stronger in species that migrate earlier. For most species, early arrival was related to a low condition index; I suggest that individuals arriving earlier risk having a lower body condition (and potentially higher mortality) as a trade off to potential benefits from arriving earlier to the breeding grounds.

Survival is affected by multiple events during different stages of the annual cycle of migratory birds (Sherry and Holmes 1995). When Fretwell (1972) suggested the seasonal

interaction hypothesis, he argued that events during the breeding season carried over to influence winter survival and that, in turn, winter survival influenced the densities of breeding populations. In chapter 3, I evaluated whether brighter, first-winter plumage carotenoid-based colouration acquired on the natal areas conferred survivorship advantages to yearling Yellow Warblers seeking to occupy quality winter habitats.

The expression of bright, carotenoid-based colouration is energetically demanding (Hill 2000) and is highly influenced by environmental factors including parasites and food access at the time of the moult (Hill 2006). Hence, carotenoid-based colouration has been suggested as an honest indicator of birds quality (Zahavi 1975, Hamilton and Zuk 1982). Independently of sex, I expected brighter individuals to have higher annual survival and predicted high-quality winter occupancy of survivors. However, neither sex nor carotenoid-based colouration had any effect on the annual apparent survival of yearling Yellow Warblers. Winter habitat occupancy inferred from δ^{13}C values of winter-grown tissues showed that independently of sex, age or plumage brightness all YWAR had overwintered in habitats with similar moist characteristics. At least in my study population, brighter carotenoid-based colouration did not confer survival benefits to yearling YWAR, and apparently survivorship in this species was not limited by the occupancy of mesic winter habitats.

Information about the mechanisms mediating winter habitat-occupancy in YWAR and its interaction with other resident forms of the species on the wintering quarters remains poorly understood. Although δ^{13}C and δ^{15}N values revealed that, apparently, this species was not limited by winter habitat quality; direct observation on the wintering grounds would help us to better understand the lack of isotopic patterns observed in winter-grown tissues sampled at the breeding areas.

Isotopic studies assessing the carry-over effects of winter habitat-occupancy on Neartcic-Neotropical migrants has been conducted only on eastern populations of American Redstarts and Black-throated Blue Warblers overwintering on the Caribbean (Marra et al. 1998, Bearhop et al. 2004). Both studies detected δ^{13}C differences between tissues of birds overwintering in presumed wet forest (i.e., mangrove and lowland tropical forest) and scrub habitats. However, there is no evidence yet of whether isotopic gradients are likely to be detected away from

mangrove associations or in other areas of the Neotropics where the populations under this study might also be wintering.

Habitat segregation on the wintering grounds between the sexes has been suggested as one of the mechanisms regulating winter habitat-occupancy in both American Redstarts and Black-throated Blue Warblers (Wunderle 1995, Marra et al. 1993). Through behavioural dominance, older males maintain high-quality territories in mangroves and moist forested habitats and displace females and younger males to less suitable, second-growth, scrub habitats (Ornat and Greenberg 1990, Marra et al. 1993, Marra 2000, Marra and Holmes 2001, Wunderle 1995). This behavioural mechanism of winter habitat occupancy might enhance the detection of C- and N-isotope differences between ages and sex classes. Further work on the winter grounds should be conducted in order to assess if the lack of power of winter habitat-occupancy to explain the arrival day and physical condition of most of the species on the breeding grounds, and survival in YWAR was consequence of poor isotopic patterns on their wintering areas, winter habitat occupancy strategies or other mechanisms.

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APPENDIX A. Breeding, migration and wintering distribution of Yellow Warbler (Sethophaga petechia), American Redstart (Sethophaga ruticilla), Northern Waterthrush (Parkesia noveboracensis), Swainson's Thrush (Catharus ustulatus), Wilson's Warbler (Cardellina pusilla), Palm Warbler (Sethophaga palmarum), Alder Flycatcher (Empidonax alnorum) and Baltimore Oriole (Icterus galbula) captured during spring migration (1998-2010) at Delta Marsh Bird Observatory, southern Manitoba, Canada. Digital range maps were obtained from Ridgely et al. (2007).

AMERICAN REDSTART

- Breeding
- Migration
- Wintering

NORTHERN WATERTHRUSH

- Breeding
- Migration
- Wintering

SWAINSON'S THRUSH

Breeding
Migration
Wintering

WILSON'S WARBLER

Breeding
Migration
Wintering

ALDER FLYCATCHER

Breeding

Migration

Wintering

BALTIMORE ORIOLE

Breeding

Migration

Wintering
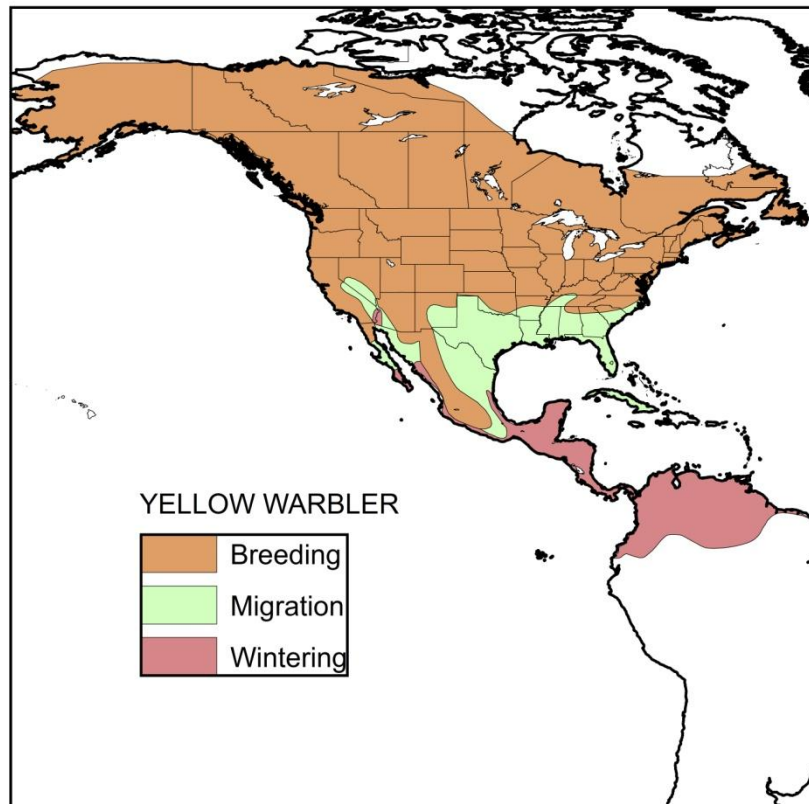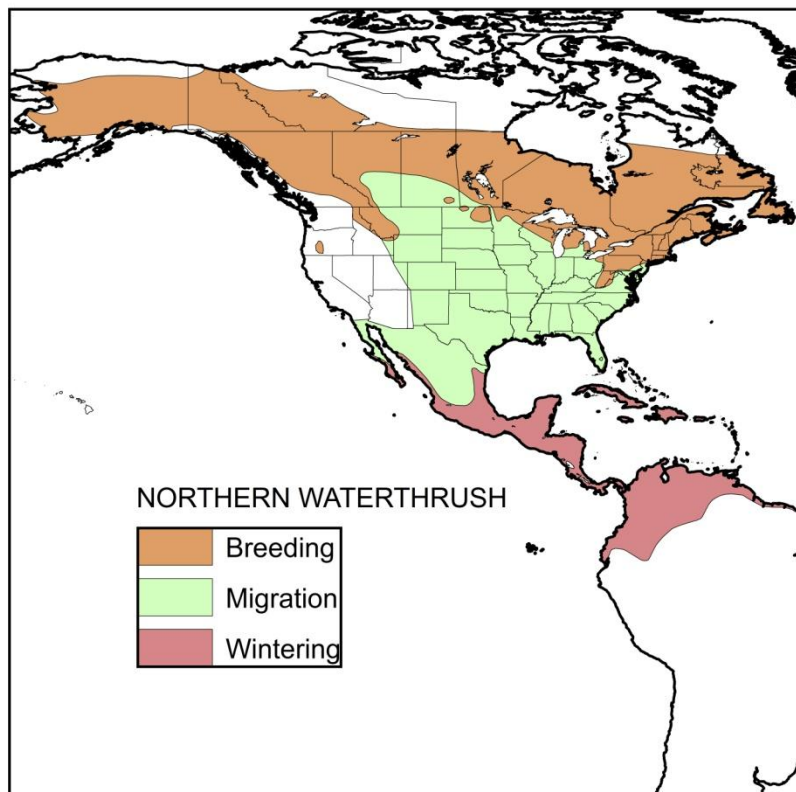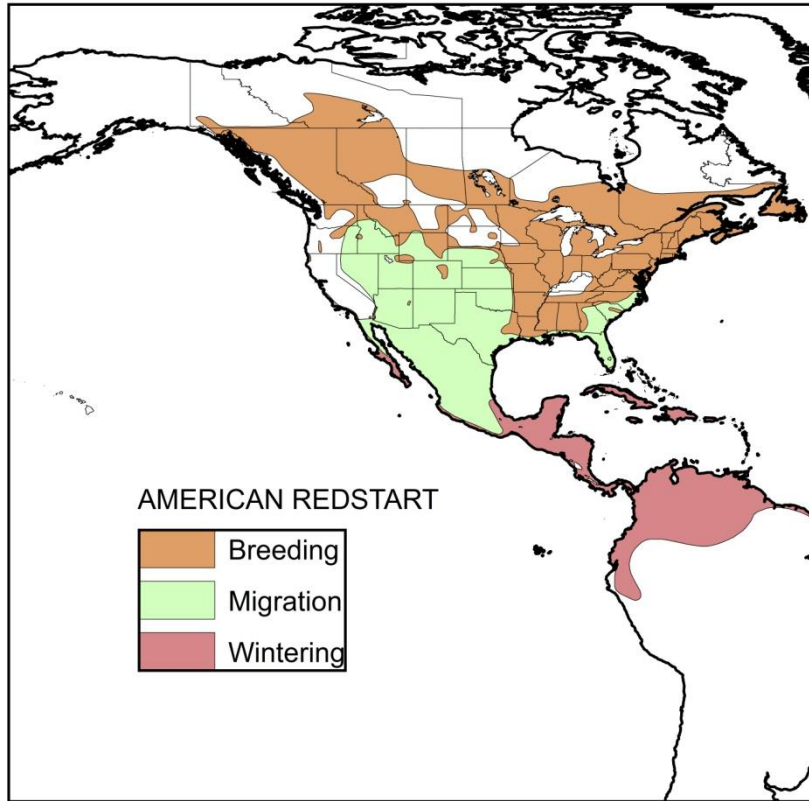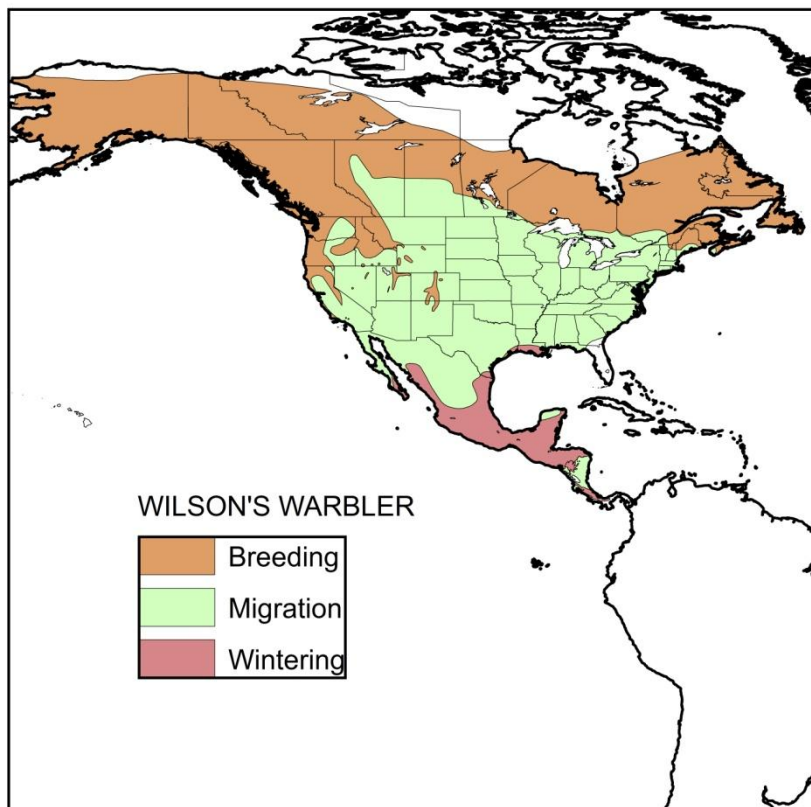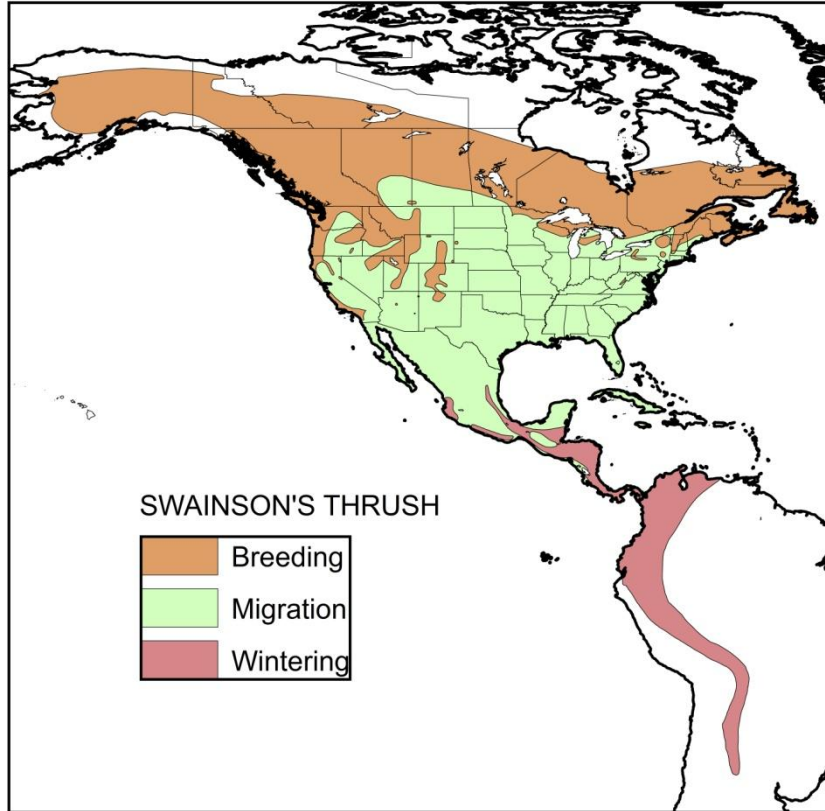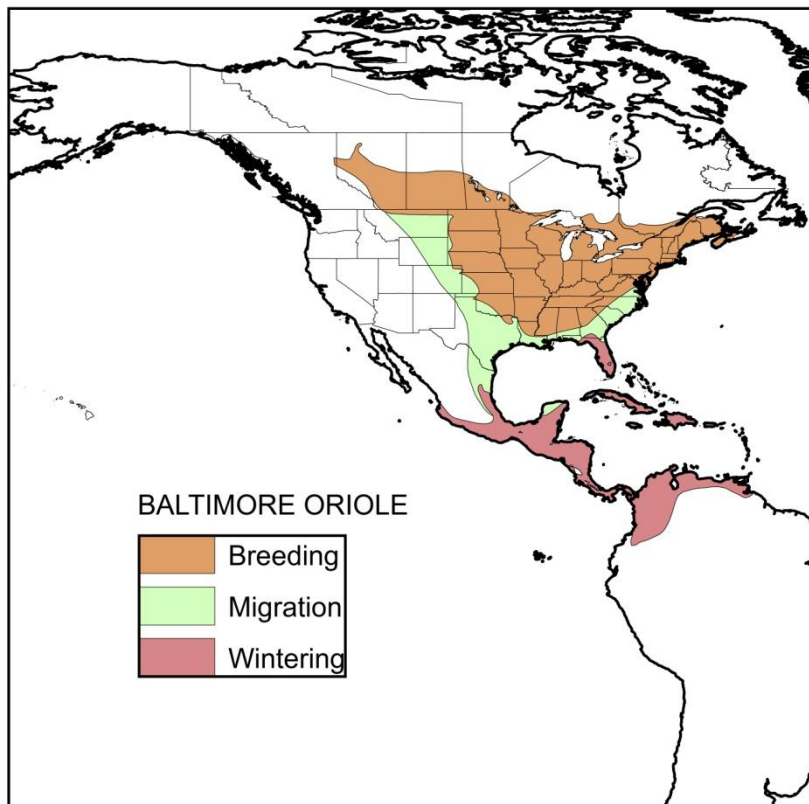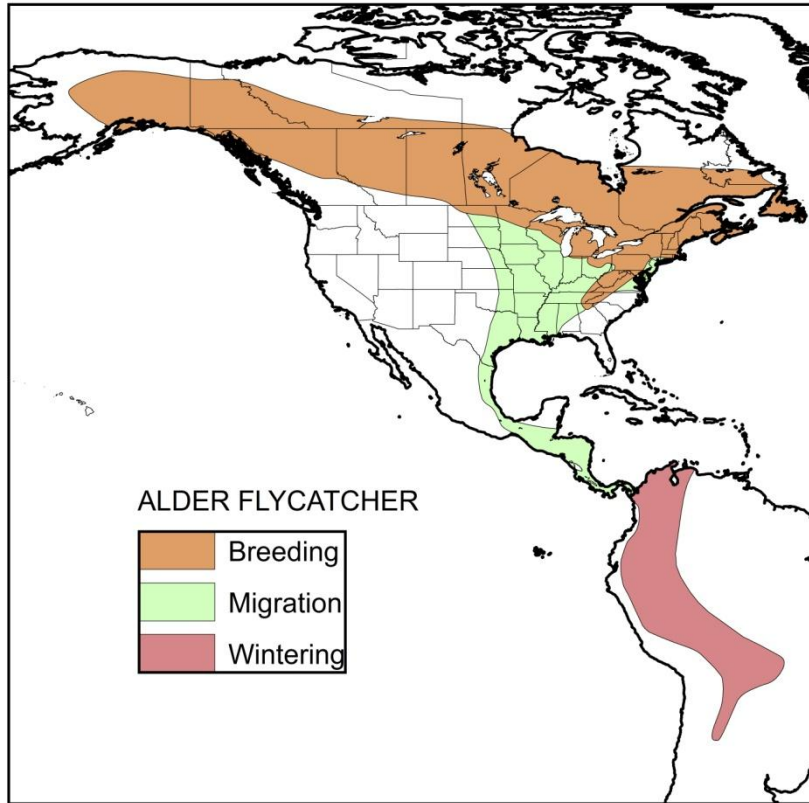
APPENDIX B. Model-averaged estimates (Est.) for parameters of the condition index and arrival day models within the 90% confidence set for seven long-distance migratory birds captured at Delta Marsh Bird Observatory (DMBO), Manitoba, during spring migration in 2009 and 2010.

Species		$\delta^{13}C$		$\delta^{15}N$		Year	
		Est. (±USE)	95% CI	Est.(±USE)	95% CI	Est.(±USE)	95% CI
Condition index	YWAR[C]	-0.1 ± 0.14*		0.07 ± 0.01*		0.77 ± 0.23	**0.32, 1.22**
	YWAR[F]	0.05 ± 0.08*		-0.03 ± 0.05*		0.8 ± 0.22	**0.38, 1.23**
	AMRE[C]	-0.05 ± 0.11	-0.26, 0.17	-0.15 ± 0.1	-0.35, 0.06	0.76 ± 0.28	**0.2, 1.31**
	WIWA[C]	-0.24 ± 0.32	-0.38, 0.86			0.8 ± 0.36	**0.09, 1.5**
	WIWA[F]			-0.34 ± 0.12	0.56, -0.11		
	NOWA[C]			0.28 ± 0.15	-0.02, 0.58		
	NOWA[F]	-0.09 ± 0.11	-0.31, 0.14	-0,08 ± 0.22	-0.52, 0.36		
	PAWA[C]	-0.14 ± 0.1	-0.35, 0.06	0.03 ± 0.13	-0.22 , 0.28		
	PAWA[F]	-0.38 ± 0.17	**-0.71, -0.05**				
	ALFL[C]	1.42 ± 0.39	**0.66, 2.18**	-0.29 ± 0.42	-1.11, 0.54		
	SWTH[C]	-0.1 ±1.03	-2.11, 1.91	0.38 ± 0.57	-0.75, 1.51		
Arrival day	YWAR[C]	0.13 ± 0.23*		0.08 ± 0.18*		-2.47 ± 0.45	**-3.35, -1.58**
	YWAR[F]	0.06 ± 0.16*		0.11 ± 0.01*		-2.33 ± 0.44	**-3.19, -1.46**
	AMRE[C]			-0.47 ± 0.3*		-5.18 ± 0.8*	
	WIWA[C]	1.26 ± 1.0*				-4.35 ± 1.29	**-6.87, -1.83**
	WIWA[F]			0.41 ± 0.4*		4.9 ± 1.03*	
	NOWA[C]	0.52 ± 0.2*		-0.45 ± 0.46	-0.35, 0.44		
	NOWA[F]	0.74 ± 0.3	**0.15, 1.32**	3.78 ± 0.57	-0.34, 1.91		
	PAWA[C]	0.92 ± 0.38	**0.17, 1.67**				
	PAWA[F]	-0.4 ± 0.81*		0.72 ± 0.5*			
	ALFL[C]	-1.32 ± 0.76	-2.81, 0.17	-1 ± 0.81	-2.58, 0.59		
	SWTH[C]	0.24 ± 1.61	-2.92, 3.39	1.28 ± 0.91	-0.5, 3.06		

[C]= Claws
[F]=Feathers
95% CI= 95% confidence interval
U SE= Unconditional standard error
* Estimate derived from a single model
Bold= 95% CI suggesting a strong effect of the variable

APPENDIX C. Results of model selection examining factors affecting condition index of eight long-distance migratory birds captured at Delta Marsh Bird Observatory (DMBO), Manitoba, during spring migration from 1998 to 2010. Nine candidate models were considered for each species, the models listed represent the ≥ 90% confidence set, determined by selecting up to the first model with a cumulative Wi ≥ 0.90. Four-letter codes for the species are described in the methods.

Species	MODEL	K[a]	AICc	Di[b]	Wi[c]	Cum. Wi
AMRE	MMT+ENSO	4	172.10	0.00	0.52	0.52
	Year+MMT+ENSO	5	172.29	2.00	0.20	0.72
	MMT	3	172.35	3.00	0.15	0.86
	MDT+MMT	4	172.47	4.00	0.08	0.94
YWAR	Year+MMT	4	243.89	0.00	0.65	0.65
	Year+MMT+ENSO	5	244.00	2.00	0.29	0.94
WIWA	Year+MMT+ENSO	5	147.24	0.00	0.46	0.46
	Year+MMT	4	147.29	0.54	0.35	0.81
	MMT+ENSO	4	147.51	2.68	0.12	0.93
NOWA	MDT+MMT	4	328.46	0.00	0.61	0.61
	MMT	3	328.74	2.88	0.15	0.76
	MMT+ENSO	4	328.84	3.83	0.09	0.85
	Year+MMT	4	328.85	3.90	0.09	0.93
ALFL	Year+MMT	4	188.09	0.00	0.30	0.30
	MMT	3	188.20	1.11	0.17	0.47
	Year	3	188.23	1.47	0.14	0.61
	Year+MMT+ENSO	5	188.28	1.93	0.11	0.73
	MMT+ENSO	4	188.40	3.13	0.06	0.79
	Year+MDT	4	188.42	3.33	0.06	0.85
	Year+ENSO	4	188.43	3.46	0.05	0.90
SWTH	MDT+MMT	4	282.00	0.00	0.91	0.91
BAOR	MMT	3	108.39	0.00	0.32	0.32
	Year+MMT	4	108.42	0.28	0.28	0.60
	MMT+ENSO	4	108.59	1.96	0.12	0.71
	MDT+MMT	4	108.59	1.97	0.12	0.83
	Year+MMT+ENSO	5	108.61	2.23	0.10	0.94
PAWA	MDT+ENSO	4	1368.15	0.00	0.80	0.80
	MMT+ENSO	4	1371.69	3.55	0.14	0.94

MMT: Mean May minimum temperature
MDT: Mean minimum daily temperature
ENSO: El Niño Southern Oscillation
[a]Number of parameters
[b]Δi (Δi= AIC$_{ci}$ – minimum AICc)
[c]Akaike weight represents support for each model

APPENDIX D. Model-averaged estimates (Est.) for parameters of the condition index models within the 90% confidence set for of eight long-distance migratory birds captured at Delta Marsh Bird Observatory (DMBO), Manitoba, during spring migration from 1998 to 2010.

Species	MMT		MDT	ENSO		Year	
	Est.±U SE	95% CI	Est.±U SE	Est.±U SE	95% CI	Est.±U SE	95% CI
YWAR	0.13±0.02	**0.1, 0.16**				-0.06±0.01	**-0.08 , -0.04**
AMRE	0.13±0.02	**0.09, 0.17**		0.23±0.11	**0.02, 0.44**		
WIWA	0.16±0.02	**0.11, 0.21**		0.17±0.1	-0.03, 0.37	-0.03±0.01	-0.05, 0
NOWA	0.13±0.03	**0.06, 0.2**	0.03±0.02*				
BAOR	0.34±0.07	**0.2, 0.48**		0.13±0.37	-0.59, 0.85	-0.06±0.04	-0.15, 0.03
SWTH	0.41±0.06*		0.13±0.04*				
PAWA	0.10±0.03*		0.06±0.01*	0.41±0.11	**0.19, 0.63**		
ALFL	0.10±0.05	0, 0.2		0.06±0.26	-0.44, 0.57	0.05±0.03	0, 0.1

MMT: Mean May minimum temperature
MDT: Mean minimum daily temperature
ENSO: El Niño Southern Oscillation
95% CI= 95% confidence interval
U SE= Unconditional standard error
* Estimate derived from a single model
Bold= 95% CI suggesting a strong effect of the variable

APPENDIX E. Results of model selection examining factors affecting arrival day of eight long-distance migratory birds captured at Delta Marsh Bird Observatory (DMBO), Manitoba, during spring migration from 1998 to 2010. Nine candidate models were considered for each species, the models listed represent the ≥90% confidence set, determined by Cum. Wi ≥0.9. Four-letter codes for the species are described in the methods.

Species	Model	K[a]	AICc	Δi[b]	Wi[c]	Cum. Wi
YWAR	CI+ENSO+MMT	5	398.23	0	0.97	0.97
WIWA	CI+ENSO+MMT	5	301.61	0	1	1
AMRE	CI+MMT	4	346.22	0	0.53	0.53
	CI+ENSO+MMT	5	346.28	0.59	0.40	0.93
NOWA	CI	3	537.41	0	0.48	0.48
	CI+MMT	4	537.56	1.52	0.22	0.70
	CI+ENSO	4	537.59	1.8	0.20	0.90
	CI+ENSO+MMT	5	537.76	3.49	0.08	0.98
PAWA	CI+MMT	4	287.17	0,00	0.34	0.34
	CI+ENSO+MMT	5	287.21	0.46	0.27	0.60
	MMT	3	287.23	0.58	0.25	0.85
	ENSO+MMT	4	287.33	1.67	0.15	1
ALFL	CI+ENSO+MMT	5	221.77	0,00	0.83	0.83
	ENSO+MMT	4	222.10	3.23	0.17	1
SWTH	CI	3	374.66	0,00	0.33	0.33
	CI+ENSO	4	374.73	0.69	0.23	0.56
	CI+MMT	4	374.76	0.92	0.21	0.77
	CI+ENSO+MMT	5	374.81	1.47	0.16	0.93
BAOR	CI+MMT	4	136.30	0,00	0.30	0.30
	CI+ENSO+MMT	5	136.31	0.09	0.28	0.58
	ENSO+MMT	4	136.38	0.74	0.21	0.79
	MMT	3	136.38	0.75	0.20	0.99

CI: Condition index
ENSO: El Niño Southern Oscillation
MMT: Mean May minimum temperature
[a]Number of parameters
[b]Δi (Δi= AIC_{ci} – minimum AICc)
[c]Akaike weight represents support for each model

APPENDIX F. Model-averaged estimates for parameters of the arrival day models within the 90% confidence set for of six long-distance migratory birds captured at Delta Marsh Bird Observatory (DMBO), Manitoba, during spring migration from 1998 to 2010. MMT: May minimum temperature.

Species	MMT		Condition Index		ENSO	
	Est.±U SE	95% CI	Est.±U SE	95% CI	Est.±U SE	95% CI
YWAR	-0.57 ± 0.04*		-0.27 ± 0.09*		-0.1 ± 0.22*	
WIWA	-0.91±0.11*		1.23 ± 0.2*		-2 ± 0.45*	
AMRE	-0.65±0.1	**-0.85, -0.46**	0.52±0.19	**0.14, 0.89**		
PAWA	-1.02±0.14	**-1.29, -0.75**	0.41 ±0.24	-0.07, 0.88	-0.68±0.59	-1.84, 0.48
ALFL	-0.61±0.07	**-0.76, -0.47**	-0.24 ± 0.11*		-1.83±0.38	-2.57, -1.09
BAOR	-0.48±0.14	**-0.75, -0.21**	-0.2±0.12	-0.43, 0.04		
SWTH	-0.13±0.12	-0.36, 0.1	0.31±0.09	**0.14, 0.49**	-0.64±0.55	-1.71, 0.43
NOWA	-0.06±0.09	-0.24, 0.12	0.38±0.12	**0.15, 0.6**	0.2±0.5	-0.79, 1.18

MMT: Mean May minimum temperature
ENSO: El Niño Southern Oscillation
95% CI= 95% confidence interval.
U SE= Unconditional standard error.
Bold= 95% CI suggesting a strong effect of the variable
* Estimate derived from a single model