USING STABLE ISOTOPES TO EXAMINE CARRY-OVER EFFECTS DURING THE FULL ANNUAL CYCLE OF A MIGRATORY BIRD, THE PRAIRIE WARBLER

Michael E. Akresh
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USING STABLE ISOTOPES TO EXAMINE CARRY-OVER EFFECTS DURING
THE FULL ANNUAL CYCLE OF A MIGRATORY BIRD, THE PRAIRIE
WARBLER

A Dissertation Presented

by

MICHAEL E. AKRESH

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2018

Wildlife and Fisheries Conservation
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To Bethany for her love and support and to Val Nolan Jr. for paving the way.
ACKNOWLEDGMENTS

I would like to thank my advisor David King for giving me the opportunity to conduct both my Master’s and Ph.D. at UMass. I am very grateful for his support, guidance, and friendship throughout the past decade and through many seasons of field work. Thanks also to my committee: Bruce Byers, Kevin McGarigal, Joe Wunderle, and additionally Pete Marra, who provided guidance throughout the project. I’m grateful to my lab mates and fellow graduate students in the Environmental Conservation department who were helpful with feedback and stats guidance with this project.

The U.S. Forest Service Northern Research Station provided the funding for the project. Additional funding came from the Smithsonian Migratory Bird Center, the Blodget Fund, the Wilson Ornithological Society, the American Ornithologists’ Union, the Cooper Ornithological Society, and the American Wildlife Conservation Foundation. The Massachusetts Division of Fisheries and Wildlife allowed us to conduct work in the Montague study site. Tim Simmons, Brian Hawthorne, and Peter Grima were helpful throughout the project. I also appreciate the Gerace Research Centre and Tom Rothfus for providing helpful support and logistics in The Bahamas. Doug Gamble kindly provided the Sal Salvador precipitation data, and I thank him for collecting and sharing the data with me. Velda Knowles, Rochelle Hanna, Erin Rothfus, Dave Trydahl, Nancy Elliot, Carol Landry, Tom Snyder, and Rusty Scates also helped greatly with logistics in The Bahamas.

I would like to thank all the field technicians for their tireless work and countless hours of help in the field. Technicians that worked in The Bahamas include Ellie Armstrong, Heather Buleje, Blaine Carnes, Emily Cook, Tim Duclos, Marie Fiola, Matt
Fuirst, Aaron Hulsey, Todd Jones, Stacy Kemphers, Alan Moss, Kathryn Peiman, Patrick Roberts, Zeke Smith, and Kittie Yang. Technicians that worked in Massachusetts include Brett Bailey, Kayla Baker, Alex Bielaski, Carly Chandler, Jen Glagowski, Tyler Maikath, Nora Papian, Kate Pelletier, Deysha Rivera, Sam Roberts, Josie Ryan-Small, Jen Smetzer, Matt Smith, Greta Turschak, Mattie VandenBoom, Jesse Wampler, Doug Weidemann, and Nathaniel Young. I am especially grateful to Brodie Kramer for working during three spring seasons and one winter season.

Thanks to my family and friends for your unwavering support. Hudson the poodle was always ready for a study break, and happy to settle back down by my feet to help write. My deepest thanks and love to Bethany, who has been with me through the adventures of field seasons and has endured extended time while I was away from home. I’m grateful for her constant support through both good times and bad. Here’s to more fun-filled days of chasing birds ahead.
ABSTRACT

USING STABLE ISOTOPES TO EXAMINE CARRY-OVER EFFECTS DURING THE FULL ANNUAL CYCLE OF A MIGRATORY BIRD, THE PRAIRIE WARBLER

MAY 2018

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To better conserve threatened species, conservationists need to understand the processes that affect species during their entire life cycle, including ‘carry-over effects’ which can occur if individuals’ previous experience influences their current or future performance. We studied prairie warblers (Setophaga discolor) to examine carry-over effects in a Nearctic-Neotropical migratory bird. Using carbon isotopes in birds’ blood as a measure of habitat moisture, we first assessed the effects of rainfall and habitat on the condition of prairie warblers wintering in The Bahamas. Annual variation in rainfall and spatial moisture interacted to influence birds’ condition: during a winter with less rainfall, most birds lost mass and muscle, but more so for birds that occupied drier habitats. During a winter with more rainfall, most birds did not lose mass or muscle regardless of habitat use.

Using stable isotopes, we assessed if winter habitat use carried over to affect birds’ phenology and reproductive success in Massachusetts, USA. We did not find evidence of carry-over effects for second-year males or females, but our sample sizes
were relatively small. In two of three years, our observations of after-second-year (ASY) males were consistent with our expectation that birds wintering in drier habitat would arrive later on the breeding grounds. We found no evidence for time-mediated constraints on reproductive performance for ASY males.

Using a winter rainfall index and carbon isotopes to indicate winter habitat moisture, we examined carry-over effects initiated during the breeding season. Juvenile birds that hatched earlier acquired wetter winter habitat during drier winters, and during all winters for male birds. Winter habitat acquired as a juvenile was used throughout the bird’s life. Hatching date can thus influence a bird’s lifetime winter habitat quality, which other studies found can influence birds’ survival and reproduction. Adult males that successfully reproduced in the previous breeding season obtained wetter, better-quality habitat in the subsequent winter season, indicating no apparent cost of caring for young on winter habitat acquisition. Overall, our novel results are important for better understanding the full annual cycle of migratory birds and how birds might be affected by climate change.
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CHAPTER 1
RAINFALL AND HABITAT AFFECT THE CONDITION OF A WINTERING MIGRATORY SONGBIRD

Introduction

Throughout the annual cycle, Nearctic-Neotropical migratory birds are vulnerable to changes in biotic factors such as habitat destruction and degradation as well as changes in abiotic factors such as drought (Faaborg et al. 2010, Wunderle and Arendt 2017). For instance, wintering migratory birds can be negatively influenced by the conversion of tropical forests to agriculture, and they can also be adversely affected by climate change (Rappole and McDonald 1994, Stuuds and Marra 2011, Achard et al. 2014). Gaining a better understanding of how ecological factors affect migratory birds throughout their life cycle, including during the less-frequently-studied wintering season, is increasingly recognized as being important for the conservation of declining populations (Calvert et al. 2009, Faaborg et al. 2010, Marra et al. 2015b).

A substantial proportion of Nearctic-Neotropical migratory bird species winter in the Caribbean (Terborgh 1989, Wunderle and Waide 1993), including species of conservation concern such as the Kirtland’s warbler (Setophaga kirtlandii) and the prairie warbler (Setophaga discolor). The Caribbean experiences a pronounced dry season beginning in December and extending to April (Wunderle et al. 2014). During dry periods, ecological systems can become stressed due to the lack of moisture (Janzen 1973, Johnson and Sherry 2001, Wunderle et al. 2014, McKinnon et al. 2015a). Moisture can vary both temporally and spatially as a function of rainfall and temperature, as well
as due to spatial variation in edaphic conditions and vegetation’s capability to retain moisture (Murphy and Lugo 1986, Wang et al. 2002). Increased moisture levels have been shown to increase avian food resources, such as insect or fruit abundance (Strong and Sherry 2000, Brown and Sherry 2006, Studds and Marra 2007, Vafidis et al. 2014). Furthermore, interactions between spatial and temporal variation in moisture are important; for instance, if rainfall amounts decline equally throughout a given area as the dry season progresses, habitats that better retain moisture tend to have more insects and fruit (Parrish and Sherry 1994, Cooper et al. 2012, Wunderle et al. 2014).

Drier habitats or conditions resulting from low rainfall can negatively affect avian body condition during the wintering period (e.g., Latta and Faaborg 2001, 2002, Smith et al. 2010, Angelier et al. 2011). Moreover, birds that are unable to maintain their body condition during the winter can have a more difficult and prolonged time in building fat and muscle reserves needed for spring migration (Studds and Marra 2007, 2011, Gerson and Guglielmo 2011, Seewagen and Guglielmo 2011, Cooper et al. 2015). Birds that winter in drier habitats or conditions may have lower survival during spring migration (Marra and Holmes 2001, Studds and Marra 2005, Johnson et al. 2006, Latta et al. 2016). If birds survive spring migration, the effects of birds’ winter habitat can still carry-over to delay individuals’ phenology (i.e., arrival to the breeding grounds) and subsequently reduce reproductive output on the breeding grounds (Marra et al. 1998, Norris et al. 2004, Reudink et al. 2009, Rockwell et al. 2012).

Many migratory bird species segregate by age or sex in wintering habitats that differ in vegetation type, structural characteristics, or moisture (Rappole and Warner 1980, Ornat and Greenberg 1990, Wunderle 1995, Murphy et al. 2001, Townsend et al.
which can then influence variation among age/sex classes in their ability to maintain body condition during the dry season (Marra and Holmes 2001). Age/sex segregation may occur because larger individuals (older birds and males) dominate and outcompete smaller individuals (younger birds and females) for better quality habitat, which is often taller or wetter vegetation (Marra et al. 1993, Marra 2000). Alternatively, sex ratios may differ among habitats because males innately select taller vegetation compared to females, regardless of size or sex-related dominance and competition (Morton et al. 1987, Morton 1990). Irrespective of the mechanism, birds of different age and sex classes can be affected differently during the winter season because of habitat segregation or dominance hierarchies within a habitat type (Marra and Holmes 2001, Mettke-Hofmann et al. 2015).

Given the importance of habitat quality and rainfall to migratory birds during the overwintering period, we undertook this study to assess effects of moisture and habitat on a wintering migratory bird, the prairie warbler, in The Bahamas. Plants in drier habitats and plants experiencing drought conditions tend to have enriched stable isotope ratios of carbon ($\delta^{13}C$; Farquhar et al. 1989, Dawson et al. 2002); these carbon isotope ratios move up the food chain from plants to herbivorous insects, and from insects to birds (Marra et al. 1998). We analyzed $\delta^{13}C$ values in the blood and claws of prairie warblers captured in representative habitats to provide an objective measure of spatial variation in moisture at the home-range scale (Marra et al. 1998, Bearhop et al. 2003, Studds and Marra 2005, Smith et al. 2010). We then tested the spatial effects of habitat vegetation and $\delta^{13}C$ values, and temporal effects of day of season, year, and daily rainfall measurements on birds’ body condition during mid- to late winter. Unlike most previous studies, we
quantitatively assessed the effects of daily rainfall with respect to individual birds’ capture dates, to better determine the influence of drought on birds’ condition. We also determined if age and sex classes were segregated by spatial variation in vegetation and moisture, and examined differences in birds’ condition over the winter among age and sex classes.

Prairie warblers are ideally suited for this study because they are Nearctic-Neotropical migrants that are declining throughout their range (Schlossberg and King 2007, Sauer et al. 2014) and are found in a variety of habitat types along a moisture gradient on their wintering grounds (Wunderle and Waide 1993, Murphy et al. 1998, 2001). Considering recent declines in precipitation in the Caribbean (Martin and Weech 2001, Heartsill-Scalley et al. 2007, Studds and Marra 2011) as well as anticipated future declines in rainfall (Neelin et al. 2006), understanding the relationship between wintering migrants and moisture could be key to their conservation.

**Methods**

**Study Site**

Between 2012-2015, we conducted our research on six study plots on San Salvador Island (24°02’N, 74°30’W), a low-elevation, relatively small (163 km²), outer island in the eastern part of The Bahamas. Plots were selected to encompass a moisture gradient and be representative of most of the main habitat types found throughout San Salvador and the southern Bahamas (Correll 1979, Smith 1986, Currie et al. 2005). Plots were located in the central to northern part of the island (see maps in Jones et al. 2013, Akresh and King 2015). Two plots (CSE, 8 ha, and CSW, 5 ha) were located in coastal
scrub habitat on primarily sandy soils and had thick, low-growing, native plant species (e.g., *Reynosia septentrionalis*, *Croton linearis*, *Erithalis fruticosa*, *Pithecellobium keyense*, *Bourreria succulenta*, *Lantana involucrata*) characteristic of Bahamian coastal scrub / coastal coppice habitat (Correll 1979, Smith 1986, Sykes and Clench 1998). There was evidence of previous, but limited, disturbance in both coastal scrub plots, and both were intersected by a paved road. Adjacent to the coastal scrub plots, a third plot (GRC, 3 ha) was located near a rain catchment basin on primarily black soils (Mooney 1905) and consisted of highly disturbed areas (previously bulldozed) and many non-native plants, including *Leucaena leucocephala*, *Casuarina equisetifolia*, *Corchorus hirsutus*, *Pluchea odorata*, and *Prunus amygdalus*. Two additional plots (JJ and LL, both 7 ha) were also on black soils and both were characterized by a mosaic of taller native, inland coppice vegetation, red mangroves (*Rhizophora mangle*), tall buttonwood (*Conocarpus erectus*), and some shorter inland coppice vegetation. The JJ plot also had areas of sabal palms (*Sabal palmetto*) and cocoplum (*Chrysobalanus icaco*) vegetation. Moisture conditions on JJ and LL ranged from dry soils to standing water. A sixth plot (FM, 7 ha) was on rocky and clay-like soils and was dominated by short buttonwood (1-4 m in height) and sawgrass (*Cladium jamaicense*), as well as patches of non-native vegetation, short inland coppice, and coastal scrub vegetation, interspersed with small ponds and some roads.

Similar to other areas throughout the Caribbean, the climate in The Bahamas follows an annual cycle of wet and dry seasons, with the dry season beginning in November or December and extending to April (Sealey 2006). There is often at least some rainfall during the winter dry season in The Bahamas, but rainfall amounts vary considerably among years (Sealey 2006, Wunderle et al. 2014). Daily rainfall data were
available from July 2012 to March 2014 from a weather station located at the Gerace Research Centre in the northeastern part of San Salvador Island (obtained from D. W. Gamble). Monthly rainfall totals were higher in fall and early winter (September-December) in the 2012-13 winter compared with the 2013-14 winter, but rainfall totals in mid- to late winter (January-25 March) were lower in 2012-13 compared to 2013-2014 (Table 1.1, Figure 1.1).

**Bird Sampling**

Birds were captured primarily during two periods, mid-winter (late December to end of January), and then again in late winter (25 February to 20 March) during three winters (2011/12, 2012/13, 2013/14), and again only in mid-winter in 2014/15. For simplicity, throughout the paper we denote the 2011/12 winter as ‘2012’, 2012/13 as ‘2013’, and 2013/14 as ‘2014’. We conducted netting only in four plots (CSE, CSW, FM, and GRC) in the initial 2012 season, and conducted only limited netting in 2015. We used target netting, passive netting, and a hybrid target/passive netting to capture birds (Wunderle et al. 2010). Target netting was conducted with one to five 12-m nets using a prairie warbler decoy and playback of either prairie warbler songs and/or chip notes, alarm ‘chatter’ calls of white-eyed vireos (*Vireo griseus*), or (less often) a mobbing call of black-capped chickadees (*Poecile atricapillus*), eastern Screech owls (*Megascops asio*), blue jays (*Cyanocitta cristata*), and American crows (*Corvus brachyrhynchos*). Passive netting was conducted with 7-17 nets (most 12-m nets and a few 6-m nets) placed 0-50 m apart and operated for one to two mornings (sunrise to 12:00 EST). Nets were moved every one to two days within the plot to cover the entire site during a winter
period (mid- or late-winter). At times, passive netting was augmented with playback, by rotating one to three speakers that broadcasted playback among individual nets for 30 minutes to an hour (Wunderle et al. 2010). On plots with tall vegetation (JJ and LL), we periodically stacked two nets on top of each other, with netting up to 5 m in height (Meyers and Pardieck 1993). For every individual capture, we noted if the bird was caught using target, passive, or the hybrid netting method.

Upon capture, we banded each prairie warbler with a United States Geological Survey aluminum band and a unique combination of three plastic color bands. We classified birds by sex and as either juveniles <1 year old (hatch-year and second-year birds), or adults >1 years old (after-hatch-year and after-second-year) using plumage and molt limits (Pyle 1997). We also measured unflattened wing chord (+/- 1 mm), tail length (+/- 1 mm), and tarsus length (+/- 0.1 mm), and mass with a digital scale (+/- 0.01 g). We scored birds’ furcular and abdominal fat levels using a standardized scale of 0-7 (DeSante et al. 2009), and, in all winters besides 2012, scored pectoral muscle using a scale between 1-4, with 1 = muscle concave, 2 = muscle in a ‘v’ shape (neither convex or concave), 3 = muscle slightly convex, 4 = muscle highly convex and sternum not visible (Latta and Faaborg 2001, Cooper et al. 2015). We also used mid-level scores (i.e., 1.5, 2.5, and 3.5) when birds’ muscle was in between the above categories. To reduce inter-observer variation, 98% of birds were measured and scored by a single observer (MA).

For a subset of the captured birds, blood samples (up to 50 uL) were collected in capillary tubes, put on ice, and later transferred to 1.5 mL micro-centrifuge tubes before placing in a freezer. In 2012 and 2013 for a subset of birds we also sampled the tip (2-3 mm) of the central claw on both feet of the individual. We sampled both blood and claws
because stable isotope ratios in whole blood (plasma and red blood cells combined) have a shorter half-life (i.e., 4-11 days; Pearson et al. 2003, Evans Ogden et al. 2004) and whole blood likely represents dietary isotopic input from a few weeks before capture to the time of capture, whereas stable isotope ratios in claw tips have a relatively long half-life (i.e., 27 days; Lourenço et al. 2015) and the isotope ratios likely represent diet a few weeks to a few months before capture (Bearhop et al. 2003, Hahn et al. 2014).

In late January and February 2012-2014 and in January 2015, we conducted intensive area searches within the plots (Marra 2000, Latta and Faaborg 2001) where we re-sighted color banded prairie warblers banded in mid-winter or in previous years. We followed similar methods as previous studies, searching along a grid of trails in each plot and adjacent areas beginning at sunrise until bird activity declined (around 10:00 EST), and then again in the late afternoon when bird activity picked up again (approximately 15:30 to sunset). Each plot was surveyed for five days during a given winter, in which the plot was surveyed for a minimum of 10 person-hours per day, thus, totaling at least 50 person-hours per plot for a given year. At each prairie warbler sighting, observers recorded the color band combination and estimated the height at which the bird was first observed. Most birds were observed briefly (78% were tracked for a minute or less), and thus, only one observed height was recorded for each sighting.

**Vegetation Sampling**

At each net lane within plots, we estimated the average height of the canopy with a 3 m pole and recorded 3-4 of the dominant plant species within 2 m of the net lane. Vegetation at each net lane was later classified as one of the following habitat types
based on the dominant species and descriptions of vegetation communities in the literature (Correll 1979, Smith 1986, Currie et al. 2005): coastal scrub (otherwise known as coastal coppice), disturbed/non-native vegetation, short coppice (defined as inland coppice <3m in height), tall coppice (inland coppice >3m in height), short buttonwood/sawgrass-dominated vegetation, and mangrove/sabal palm/tall buttonwood/cocoplum-dominated vegetation.

**Stable Isotope Preparation and Analysis**

Claws were soaked for 2 hours in a 2:1 chloroform:methanol solution and dried in a fume hood for 48 hours. Blood was freeze-dried while in micro-centrifuge tubes and then powdered. All samples were then weighed in tin capsules and combusted in a continuous flow isotope ratio mass spectrometer (Thermo Scientific Delta V Advantage mass spectrometer coupled with a Costech ECS 4010 elemental analyzer via a Conflo IV gas interface) at the Stable Isotope Mass Spectrometry Facility at the Smithsonian Institution, Suitland, MD, USA. One in-house standard was run for every four unknowns. Stable isotope ratios ($^{13}\text{C}/^{12}\text{C}$) are reported in delta (δ) notation, in per-mil units (‰) relative to the Vienna Pee Dee Belemnite ($\delta^{13}\text{C}$) standard. Repeated analyses of blood samples from the same individual capture were replicable to within 0.2‰ (n = 25).

**Statistical Analysis**

**Moisture**

We tested if $\delta^{13}\text{C}$ values of blood from captured prairie warblers were a function of spatial variation in moisture, as reflected by vegetation type or vegetation height, and
temporal variation in moisture, as reflected by capture date, rainfall, or year. Although investigators have found that spatial variation in moisture can be captured by $\delta^{13}C$ values in bird samples (e.g., Marra et al. 1998, Bearhop et al. 2004), there are few studies that have examined how $\delta^{13}C$ values in bird samples change temporally over the winter season and in relation to rainfall. We used linear mixed models with $\delta^{13}C$ values of blood as the response variable, and in separate models, examined the capture net vegetation type or height as the main predictor variable, while also taking into account temporal effects of year and capture date. We used separate models because vegetation type was correlated with vegetation height and we were interested in testing both variables. We presented results of the effects of year and date using the model with vegetation type. In additional models, we tested the effect of rainfall on $\delta^{13}C$ values, with a main predictor variable of total rainfall at either 30, 60, 90, or 120 days prior to capture (removing the correlated capture date variable from the models), and included covariates of year and vegetation type (to account for spatial variation). In all models we included a random effect of individual; we did not include plot in the models because the vegetation at the net lanes was correlated with plot. We used the R statistical program version 3.3.1 to conduct all analyses (R Core Team 2016). We used the “lme4” and “lmerTest” packages (Bates et al. 2015, Kuznetsova et al. 2016) to conduct mixed models unless otherwise noted, and the “multcomp” package (Hothorn et al. 2008) to conduct Tukey’s tests to examine pairwise comparisons among years and vegetation types while controlling for the family-wise error rate.

To further examine temporal changes in $\delta^{13}C$ values, using paired t-tests we compared $\delta^{13}C$ values of blood between mid-winter and late winter for the same
individual birds captured during both periods. Using a linear mixed model with individual as a random effect, we also tested the relationship between δ\textsuperscript{13}C values of blood versus claws taken at the same capture from an individual bird. Since claws represent a different dietary time-span compared to blood (Lourenço et al. 2015), we would interpret a strong correlation as an indication that an individual bird was using habitat of the same amount of wetness throughout the previous few months and that there was little temporal change in δ\textsuperscript{13}C values over the previous few months.

**Age/Sex Ratios**

We tested if age/sex ratios of captured individuals varied with the vegetation type at the capture location using chi-squared tests. We also tested if vegetation height at the capture location differed among age/sex classes using mixed models with individual as a random effect. Lastly, we examined if δ\textsuperscript{13}C values of blood (as an index of habitat wetness) differed among age/sex classes using mixed models, including covariates of ordinal date and year to account for temporal variation in δ\textsuperscript{13}C values, and also including individual as a random effect. Age/sex ratios were not affected by the use of playback during capture and did not differ in plots among years (chi-squared tests within individual plots, all \( p > 0.05 \)). Thus, the differences in sex (male vs. female), age (juvenile vs. adult), and age/sex ratios (four separate groups) were compared with birds captured using all netting methods and in all years combined. We did not include within-year recaptures in these analyses, but the same individual captured in different years (6% of the population) was considered a unique sample each year because a bird’s age class was often dependent on the capture year. For the mixed models, we used likelihood ratio tests to test for significant differences among the four separate age/sex groups, by comparing a model
with and without a covariate of age/sex groups.

With the resighting data of color-banded birds, we tested if different age/sex classes were observed at different heights in the vegetation. We conducted mixed models, with height of the bird as the response variable, either sex or age as the predictor variable, and a random effect of individual.

**Body Condition and Pectoral Muscle Score**

We computed a body size index using the first principal component (PC1) from a principal component analysis of body size measurements (wing, tail, and tarsus length; PC1 explained 62% of the variance). We then computed a size-corrected body condition index, taking the residuals from the linear relationship of PC1 regressed over mass ($r = -0.50$, $p < 0.001$; Marra et al. 1998). We used linear mixed models to examine change in body condition and pectoral muscle over the winter season in the population, with body condition index or pectoral muscle score as the response variable, and day of season as the main predictor variable. We further tested the effect of day of season on condition and muscle separately for each age/sex class. In separate analyses, we also tested the effect of an interaction of day of season and either vegetation height, or vegetation type, at the capture net, or $\delta^{13}$C values of blood (indicating habitat moisture) on body condition or muscle score. Since the vegetation variables and $\delta^{13}$C values were correlated, we conducted separate models with each individual covariate to prevent multi-collinearity. For all models, we analyzed individual years separately because we often observed different results (i.e., interactions) among years. In all models with body condition as the response variable, we included an additional covariate of time after sunrise because birds
caught later in the day were in better condition ($\beta = 1.23$, SE = 0.24, $t = 5.1$, $p < 0.001$). In all models, we included a random effect of individual bird. In the few cases when mixed-effects models did not converge (likely because of low numbers of recaptured individuals), we ran simpler fixed effects models without the random effect of individual. We excluded any recaptures of the same individual captured multiple times on the same day. We also excluded captures in late March (after March 20$^{th}$), when we only had a few captures and some birds were putting on large fat loads before migration. Due to small sample sizes, we did not include captures in January 2015. Also due to small sample sizes, we were not able to examine the effects of day of season on condition or muscle within the short coppice or mangrove/sabal palm vegetation type in any year, or within the tall coppice in 2012. We could only include birds with blood samples in the analyses with $\delta^{13}$C values, and only had data to examine birds’ muscle in 2013 and 2014. Since 91% of captures had a fat score of 1 or 0, (indicating a trace or no fat), our fat scoring classification system was likely too coarse (Cooper et al. 2015) and we therefore did not further analyze fat scores.

In addition to the above analyses that focused on the populations’ body condition and muscle as a function of date, we also wanted to directly assess how variation in rainfall affected birds. Based on previous studies examining rainfall’s effect on birds, we hypothesized that total rainfall during the 30, 60, 90, or 120 days prior to an individual’s capture date (not including rainfall on the capture day) might affect birds’ condition (Angelier et al. 2011, Studds and Marra 2011, Wunderle et al. 2014). However, especially during scarce rainfall periods, total rainfall does not differentiate between many small precipitation events versus one or two large precipitation events. The size of
the precipitation event could affect evapotranspiration rates and soil moisture, which in turn could affect food resources (Wunderle et al. 2014). We therefore additionally calculated the standard deviation (SD), and the coefficient of variation (CV) of daily rainfall during the 30, 60, 90, or 120 days prior to the capture date. Importantly, SD incorporates both the mean and the variation of daily rainfall, while the CV only addresses the variation, independent of the mean, of daily rainfall during a given period.

Using an information-theoretic framework, we compared a set of a priori linear mixed models assessing the effect of the 12 rainfall variables, and rainfall interactions with habitat wetness (δ^{13}C values), vegetation type, or vegetation height at the capture net, on body condition or muscle score (Table 1.2). We did not include interactions of rainfall with δ^{13}C and capture net vegetation in the same model because these variables were correlated with each other (see Results). Instead, we used Akaike’s Information Criterion corrected for small sample sizes (AICc) and Akaike’s model weights (ω_i) to compare among the models and determine which variable interacting with rainfall best explained the variation in birds’ condition or muscle (Burnham and Anderson 2002). We additionally wanted to determine whether the rainfall variables outperformed day of season in predicting birds’ condition or muscle; therefore, we conducted additional models with day of season to compare with the rainfall models. Some rainfall variables were highly correlated with day of season, thus, we did not include any models with both date and rainfall variables (Table 1.2). In all models with body condition, we included an additional covariate of time after sunrise, and we included a random effect of individual bird in all models. We tested the two years with rainfall data (2013 and 2014) in two separate sets of models because we observed different results between years. In order to
make consistent datasets to compare models with $\Delta^{13}C$ values (those with blood samples) in our models. To assist with model convergence, we standardized all continuous variables to a mean of 0 and SD of 1. When comparing among models we used maximum likelihood in the “lme4” package. We presented models that were less than 2 $\Delta^{13}C$ from the null model and within 2 $\Delta^{13}C$ from the best model (Arnold 2010).

We likely captured a mixture of site faithful and ‘floater’ individuals in our study sites throughout the winter (Latta and Faaborg 2001, Brown and Long 2007), but in the above analyses, we did not differentiate between site-faithful and ‘floater’ birds. We documented site faithful, likely territorial, birds that were captured in December or January and resighted or recaptured in February or March, and we additionally captured individuals in mid-winter that were not detected later in the season (possible ‘floaters’). However, although birds captured in mid-winter could be classified as site-faithful or not, detectability in resighting or recapturing birds in February and March likely varied among plots and years, which confounded any simple estimates of site-faithfulness of mid-winter captures. Some birds captured in mid-winter were likely territorial (and observed in subsequent years), but were just not detected in February or March. Furthermore, we could not classify the large number of unbanded birds captured in March – these birds either could have been non-territorial and were not present within plots in mid-winter, or these birds were site-faithful, but we just failed to capture them in mid-winter (Brown and Long 2007). We therefore chose to combine all individuals when analyzing condition in the entire population.

Besides assessing change in body condition and muscle for the entire population,
we also examined changes in individual birds that were captured in mid-winter and then re-captured in late winter during the same year. We calculated the change in mass (late-winter mass minus mid-winter mass) and the change in muscle score for each individual bird. We then divided the change in mass or pectoral muscle by the number of days between the two captures, to account for capture dates and obtain daily rates of change in mass and pectoral muscle for each individual (McKinnon et al. 2015a). We first examined annual variation in the rate of change in mass and muscle. In separate models, we then examined the effect of vegetation height, δ13C value, or age/sex class on the rates of change in mass, taking into account year as a covariate. All individuals were captured and recaptured in a given winter only once during the study; therefore we conducted linear models without a random effect of individual. We did not test the effect of vegetation type due to small sample sizes. We ran similar models for effects on the change in muscle, but did not include year as a covariate because the effect of year was not significant. We conducted pairwise comparisons among age/sex classes using Tukey’s tests. For models with δ13C values, we used the δ13C values from blood samples of mid-winter captures (Smith et al. 2010); captures without mid-winter blood samples were omitted. Due to the number of parameters and low sample sizes, we could not examine effects of age/sex class within years, but we were able to examine the effects of vegetation height and δ13C within years using simple linear models.
Results

Moisture

We obtained 273 blood samples from 231 prairie warblers to examine $\delta^{13}\text{C}$ values in blood and its relationship with vegetation at the 178 net locations where prairie warblers were captured in our 6 study plots. Birds that were captured at net lanes with a taller vegetation canopy had depleted $\delta^{13}\text{C}$ values (indicating more moisture; $t = -4.6$, $p < 0.001$). Vegetation type at the capture location also explained variation in $\delta^{13}\text{C}$ values, with birds captured in coastal scrub having enriched $\delta^{13}\text{C}$ values (indicating drier home ranges) compared to birds captured in tall coppice ($z = -4.3$, $p < 0.001$), disturbed/non-native vegetation ($z = -3.3$, $p = 0.01$), and mangrove/sabal palms ($z = -2.9$, $p = 0.04$), but other pairwise comparisons among vegetation types (including short coppice and buttonwood) were not significant (all $p > 0.05$, Figure 1.2).

Examining temporal variation, $\delta^{13}\text{C}$ values differed significantly among years with 2014 and 2015 having enriched values (mean in 2014 = $-24.65 \pm 0.09$ SE, mean in 2015 = $-24.53 \pm 0.17$ SE) compared to 2012 and 2013 (mean in 2012 = $-25.29 \pm 0.17$ SE, mean in 2013 = $-25.26 \pm 0.10$ SE; the 4 pairwise comparisons, $p < 0.001$), but there was no difference between 2012 and 2013 or between 2014 and 2015 ($p > 0.05$). For years which we had rainfall data (2013 and 2014), $\delta^{13}\text{C}$ values in blood were not significantly affected by rainfall occurring 30 days prior to capture ($n = 206$, 30 days: $t = 0.1$, $p = 0.90$). However, increased rainfall during 60, 90 and 120 days prior to capture led to more depleted $\delta^{13}\text{C}$ values (indicating more moisture; 60 days: $t = -1.96$, $p = 0.05$, 90 days: $t = -3.7$, $p < 0.001$, 120 days: $t = -3.4$, $p < 0.001$, Figure 1.3). $\delta^{13}\text{C}$ values in the population also became more enriched (indicating drying) as the winter progressed ($t = \ldots$)
4.3, p < 0.001). However, for 22 individuals that we captured in mid-winter and recaptured in late winter, δ¹³C values in mid-winter (mean = -25.3‰) did not significantly differ from δ¹³C values in late-winter (mean = -25.2‰) for the same individual bird (t = -0.75, p = 0.46), and the correlation between the values was high (r = 0.67). For 67 captures of 64 birds from which we sampled both claw and blood samples, δ¹³C values in claws highly predicted δ¹³C values in blood (t = 13.2, p < 0.001, r = 0.86).

**Age/Sex Ratios**

Overall, we captured 314 individual prairie warblers on 334 occasions (excluding within-year recaptures) in 2012-15, of which 66% were juveniles and 59% were females. The four age/sex classes were captured in net lanes with different vegetation canopy height (chi-squared from likelihood ratio test = 24.0, p < 0.001; Figure 1.4); males were captured in significantly taller vegetation (t = 4.7, p < 0.001), but there was no difference between adults and juveniles (t = 0.9, p = 0.38). Captures of age/sex classes also differed among nets located in different vegetation types (chi-squared = 41.4, P < 0.001, Table 1.3); males were more likely to be captured in mangroves, sabal palms, and taller coppice (chi-squared = 28.9, p < 0.001), although adults did not significantly differ in vegetation type compared to juveniles (chi-squared = 6.2, p = 0.29). δ¹³C values in blood also significantly differed among age and sex classes (n = 238, chi-squared from likelihood ratio test = 8.0, p = 0.05, Figure 1.4), while accounting for ordinal date and year. Males had more depleted δ¹³C values compared to females (t = -1.9, p = 0.06), indicating males’ home ranges were in wetter habitat. Additionally, there was a trend for adults to have more depleted δ¹³C values compared to juveniles (t = 1.7, p = 0.09).
We resighted color banded birds and recorded their observed height in the vegetation for 113 individuals on 360 occasions. Males were observed at significantly taller heights compared to females (average height for males = 2.8m, SD = 1.9m, average height for females = 1.9m, SD = 1.3m, t = 3.8, p < 0.001), but there was no difference between adults and juveniles (t = -0.4, p = 0.66).

**Body Condition and Pectoral Muscle in the Population Sample**

Birds’ body condition and pectoral muscle changed over the winter season differently during individual years in the study (Figure 1.5). In the entire population, birds’ body condition declined from mid- to late winter in 2013 (n = 140, t = -7.2, p < 0.001), but only marginally declined in 2012 (n = 68, t = 1.8, p = 0.08), and marginally increased in 2014 (n = 145, t = 1.7, p = 0.10). Moreover, birds’ lost muscle over the winter in 2013 (t = -2.7, p = 0.007), but maintained muscle in 2014 (t = -0.7, p = 0.51). The observed differences between 2013 and 2014 appeared to correspond to variation in the amount of rainfall occurring in March (Table 1.1).

Body condition and pectoral muscle changed at different rates within age/sex classes. In 2012, body condition declined over the winter in adult females (t = -2.6, p = 0.02) and juvenile males (t = -2.4, p = 0.06), while juvenile females (t = -0.5, p = 0.70) and adult males maintained body condition (t = -0.3, p = 0.74; Figure 1.6). In 2013, body condition declined over the winter for all age/sex classes (all p < 0.05). Additionally, muscle declined over the 2013 winter for juvenile females, juvenile males, and adult females (all p < 0.05), but muscle increased over the winter for adult males (t = 2.1, p = 0.05). Lastly, in 2014, juvenile and adult males significantly increased in condition over
the winter (p < 0.05), and juvenile and adult females maintained condition (p > 0.05). Juvenile and adult males as well as adult females maintained muscle through the 2014 winter (all p > 0.05), but juvenile females declined in muscle (t = -2.9, p = 0.009).

Examining birds captured within different vegetation types, birds captured in buttonwood, coastal scrub, and non-native vegetation maintained body condition over the 2012 and 2014 winters, and birds captured in tall coppice in 2014 also maintained condition (all p > 0.05). In 2013, birds captured in tall coppice and non-native vegetation maintained condition (p > 0.05), but birds captured in buttonwood (t = -4.5, p = 0.001) and coastal scrub vegetation (t = -6.0, p < 0.001) declined in condition over the winter. Consistent with body condition, birds maintained muscle in buttonwood, coastal scrub, non-native, and tall coppice vegetation in 2014, and maintained muscle in non-native and tall coppice vegetation in 2013 (all p > 0.05), but birds’ muscle declined in buttonwood (t = -2.9, p = 0.009) and coastal scrub (t = -4.6, p < 0.001) in 2013. There was no significant interaction of vegetation height at the capture location and day of season influencing birds’ body condition in any year (2012: t = 0.3, p = 0.77, 2013: t = 0.9, p = 0.37, 2014: t = 0.98, p = 0.33). However, in 2013, birds captured in taller vegetation increased muscle over the winter, while birds in shorter vegetation lost muscle over the winter (2013: t = 2.0, p = 0.04); there was no significant interaction in 2014 (t = 1.1, p = 0.26).

Spatial moisture, as indicated by δ^{13}C values in birds’ blood, interacted with day of season to influence birds’ body condition and muscle, but this relationship varied among years. In the winter of 2013, birds with enriched δ^{13}C (indicating drier habitats) had a greater decrease in body condition over the winter season compared to birds with depleted δ^{13}C (n = 99, body condition: t = -3.1, p = 0.02). Also, birds with enriched δ^{13}C
lost muscle over the 2013 winter season, and birds with relatively depleted $\delta^{13}C$ gained or maintained muscle ($t = -2.2$, $p = 0.03$). We found no significant interaction between day of season and $\delta^{13}C$ values affecting body condition in 2012 ($n = 56$, $t = 0.28$, $p = 0.79$) or in 2014 ($n = 100$, $t = 1.6$, $p = 0.12$), or affecting muscle in 2014 ($t = 1.3$, $p = 0.20$).

Comparing models focusing on the effects of rainfall on body condition, in 2013, the model with the lowest $AIC_c$ included an interaction between $\delta^{13}C$ values and the SD of the daily rainfall 90 days prior to birds’ captures (Table 1.4); there were no other models within 2 $AIC_c$. Birds with enriched $\delta^{13}C$ values (in drier habitats) declined in body condition as the SD of daily rainfall decreased, and birds’ body condition also declined in wetter habitats as a function of the SD of rainfall, but at a relatively lower rate of decline (interaction: $t = 4.9$, $p = 0.009$, Figure 1.7). In 2014 for body condition, there were no models less than 2 $AIC_c$ compared with the ‘null’ model, the model without variables besides time since sunrise. Examining rainfall effects on muscle in 2013, the top model included an interaction between vegetation height and the total rainfall 30 days prior to birds’ captures (Table 1.4). Birds had more muscle when there was more rainfall in the previous 30 days ($t = 3.2$, $p = 0.002$), but the interaction with vegetation height was not significant ($t = 0.19$, $p = 0.85$). In 2014 examining muscle, there were a number of top models; the best model included total rainfall 30 days prior to birds’ captures, with birds surprisingly having more muscle when there was less rainfall ($t = -2.2$, $p = 0.03$).

**Body Condition and Pectoral Muscle in Individual Recaptures**

Body condition and muscle changes were examined in 35 individuals captured in mid-winter that were recaptured in late winter, in all years combined. Daily changes in
mass and muscle varied among years: individual birds had little change in mass over the 2012 winter (n = 10, mean = 0.0003, SE = 0.0016 g/day), on average birds lost mass in 2013 (n = 13, mean = -0.0047, SE = 0.0011 g/day) and gained mass in 2014 (n = 12, mean = 0.0037, SE = 0.0019 g/day). Additionally, on average birds in 2013 lost muscle (mean = -0.0039, SE = 0.0048) and in 2014 gained muscle (mean = 0.0023, SE = 0.0046). The differences between 2013 and 2014 corresponded to variation in the amount of rainfall occurring in March (Table 1.1). Daily mass and muscle change did not significantly differ among age/sex classes in pairwise comparisons (all p > 0.05), but sample sizes were low for some age classes, especially within years.

In all years combined, there were no significant relationships with vegetation height and daily mass change (t = 0.0, p = 0.99), or daily muscle change (t = 1.4, p = 0.17), and also no significant relationships were found within years (all p > 0.05). Daily mass change was correlated with $\delta^{13}$C values in all years combined, such that birds with enriched $\delta^{13}$C values (in drier habitat) lost on average more mass over the winter, but this relationship only approached significance (t = -1.7, p = 0.1). There was also a non-significant trend in which birds with enriched $\delta^{13}$C values lost more muscle (t = -1.7, p = 0.11). Nevertheless, in the drier winter of 2013, birds with enriched $\delta^{13}$C values (in drier habitat) lost significantly more mass (n = 8, t = -2.8, p = 0.03, Figure 1.8), but there was no relationship in 2012 (n = 8, t = -0.8, p = 0.45) or 2014 (n = 9, t = -0.9, p = 0.40). $\delta^{13}$C values were not significantly correlated with daily muscle change in 2013 (t = -0.5, p = 0.61) or 2014 (t = -1.5, p = 0.17).
Discussion

Our results that prairie warblers declined in condition in a drier winter and in drier habitats is consistent with findings of other wintering Nearctic-Neotropical migratory passerines (Smith et al. 2010, Studds and Marra 2007, 2011, Wunderle et al. 2014). Other studies of prairie warblers, American redstarts, ovenbirds (*Seiurus aurocapilla*), northern waterthrush (*Parkesia noveboracensis*), and Kirtland’s warblers (*Setophaga kirtlandii*) have also shown that birds’ condition is often better maintained during wetter winters (Brown and Sherry 2006, Studds and Marra 2007, Wunderle et al. 2014, Marra et al. 2015a) or in wetter habitats during drier winters (Marra et al. 1998, Latta and Faaborg 2001, Smith et al. 2010). Collectively, these results emphasize that annual variation in rainfall can be important in influencing the degree in which spatial variation in moisture influences birds’ condition.

We found that in a drier winter, the standard deviation of daily rainfall 90 days prior to capture was a better predictor of body condition than total rainfall and ordinal date; this finding was likely due to the fact that larger precipitation events are more likely to inundate soils with moisture and have lower rates of evapotranspiration compared to smaller precipitation events (Thomey et al. 2011, Reynolds et al. 2014). We also observed that rainfall 90 days prior to capture predicted body mass in 2013 better than rainfall 30, 60 or 120 days prior to capture, suggesting that cumulative amounts of rainfall over a long period likely increases soil moisture and insects and is important during drier winters. However, we also found that birds’ pectoral muscle was more affected by rainfall 30 days prior to capture in 2013, which is consistent with a study by Angelier et al. (2011) that showed birds can be affected relatively quickly by changes in
rainfall. In our study in 2014, birds actually had lower muscle scores when rainfall totals in the previous 30 days were higher, but this relationship was likely because of a confounding effect of date, as 30-day rainfall totals were higher for birds captured in March compared to those captured in January (MA unpublished data). Although most previous studies have not examined rainfall with respect to individuals’ capture dates, Wunderle et al. (2014) found that Kirtland’s warblers’ condition in late winter was significantly affected by rainfall occurring 30, 60, and 90 days prior to capture, and the effect was most significant 30 days prior to capture.

In 2013, the drier winter in our study, birds captured in coastal scrub and buttonwood vegetation declined in both body mass and pectoral muscle. Our study suggests that relatively taller and wetter vegetation (i.e., taller coppice) provides better habitat quality compared to the shorter and drier coastal scrub vegetation. Our results are consistent with studies conducted in different vegetation communities elsewhere in the Caribbean, where short, scrubby vegetation communities are often drier and of poorer quality for migrants than taller, wetter vegetation communities (Wunderle 1995, Latta and Faaborg 2001, Marra and Holmes 2001). In our study, birds were able to maintain condition in non-native vegetation, which was wetter than coastal scrub. Our findings, along with other studies, suggest that non-native vegetation in the Caribbean can provide migratory birds with moderate to high-quality wintering habitat (Murphy et al. 2001, Johnson et al. 2006), Beltrán and Wunderle 2013).

We observed habitat segregation in age/sex classes of prairie warblers on San Salvador; males were captured and sighted in taller vegetation, and their δ¹³C values indicated home ranges in wetter habitats, while females were more likely to be captured
and sighted in drier, shorter vegetation. Our findings are consistent with other studies that have found passerine males in taller habitat during the winter (Rappole and Warner 1980, Ornat and Greenberg 1990, Wunderle 1995, Murphy et al. 2001). Interestingly, our findings are also consistent with foraging height preferences of males and female prairie warblers on their breeding grounds (Nolan 1978). Males and females may innately select habitats or intraspecific competition and dominance-related habitat selection may also be occurring (Marra 2000).

Although we are uncertain of the mechanism for age/sex segregation, the observed age and sex class segregation was correlated with birds’ condition during the winter. The older and male individuals that occupied wetter habitats often had better maintenance of body condition and muscle compared to the younger and female individuals that occupied drier habitats. For instance, adult males increased their muscle mass over the 2013 winter, while the females and juvenile males occupying relatively drier habitat lost muscle mass. The increase in condition or muscle in March for some males is likely because males were beginning to deposit reserves for migration, as males arrive on the breeding grounds earlier than females (Nolan 1978), and likely depart wintering grounds earlier than females (Studds and Marra 2011, Wunderle et al. 2014). Even though we suspect that prairie warbler females prepare for migration later in the winter season and therefore may not start depositing fat and muscle reserves in mid-March, in ideal high-quality habitats, females should at least maintain body condition and muscle, rather than decreasing condition and muscle in late winter as we observed in some years. Our results are therefore consistent with other studies that have found habitat segregation can lead to pronounced differences in effects on birds’ condition among

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We had a small sample size of recaptured individuals and this is an important caveat to consider in our study. Some of the non-significant results observed examining recaptured individuals, including within age and sex classes, might have been significant with a larger sample size and more statistical power. Additionally, in our condition analyses examining the entire population, we did not differentiate between territorial and floater birds, partly because we had relatively few recaptures of observed territorial birds in late winter. Since territorial birds may be better able to maintain body condition compared to non-territorial birds during the dry season (Smith et al. 2011), this is another important caveat to consider in our study. Nevertheless, the majority of birds captured within plots in December and January were resighted in the same plots in February (Akresh unpublished data), but we were just unable to recapture a number of these known territorial birds in March. Interestingly, results of our population sample were still mostly consistent with results from recaptured individuals (i.e., body condition relationships within years and with $\delta^{13}C$ values), indicating our findings were robust, despite likely inclusion of some floater birds in our population sample.

Our study is one of the first to closely examine effects of both spatial variables (i.e., vegetation type and height) and temporal variables (i.e., year, ordinal date, and rainfall) on $\delta^{13}C$ values in birds’ blood and claws on the wintering grounds. Consistent with other studies, $\delta^{13}C$ in birds’ samples appeared to reflect spatial variation in moisture based on vegetation communities (i.e., coastal scrub versus tall coppice and mangroves; Marra et al. 1998, Bearhop et al. 2004, Studds and Marra 2005, Smith et al. 2010).
However, we note that there was still some variation in $\delta^{13}$C values even within the same vegetation community. Using $\delta^{13}$C values as an index of spatial moisture therefore allowed us to assess important effects of spatial variation in drought-resistance at a home range scale among and within vegetation communities.

The results for the temporal effects of year, ordinal date, and rainfall on $\delta^{13}$C values were complicated. $\delta^{13}$C values became enriched (drier) over the winter in the population sample of prairie warblers, but $\delta^{13}$C values were not significantly different between mid- and late winter samples for the recaptured individuals. The size of the effect in the larger population sample was fairly small, and perhaps our sample size of recaptured individuals was too small to detect the relatively weak temporal effect of date. Interestingly, isotope values in blood versus claws were correlated in the population sample, despite claw samples likely incorporating a longer isotopic dietary time-span compared to blood (Lourenço et al. 2015), suggesting no short-term temporal effect. We also observed some variation in $\delta^{13}$C among years, but unexpectedly, 2014 had enriched $\delta^{13}$C values (indicating less moisture) compared to 2013, which matches the amounts of rainfall occurring in September-December, but not in January-March. We found a significant effect of rainfall 60 to 120 days prior to capture on $\delta^{13}$C, indicating that $\delta^{13}$C values may incorporate some temporal variation in moisture, but with an interesting time-lag. Individual C$_3$ plants that are water stressed uptake $^{13}$C at a higher rate during photosynthesis and tend to have enriched $\delta^{13}$C values (Farquhar et al. 1989, Dawson et al. 2002). A time-lag makes intuitive sense because changes in moisture must first be reflected in changes in $\delta^{13}$C values in plants during photosynthesis (Farquhar et al. 1989), and then the carbon is passed through herbivorous insects to insectivorous birds over a
period of time (Marra et al. 1998). An alternative hypothesis is that temporal changes in δ^{13}C values in birds’ blood reflect changes in the trophic levels of prairie warbler prey items consumed (i.e., more or less spiders consumed in late-winter; Diggs et al. 2011). Nonetheless, similar to our results, Studds and Marra (2005) also observed differences in δ^{13}C in American Redstarts sampled among years, and found slightly enriched δ^{13}C values for individual birds recaptured in the same habitat type in late winter compared to mid-winter. Our findings are important to consider when assessing carry-over effects using δ^{13}C values (e.g., Drake et al. 2013, Gonzalez-Prieto and Hobson 2013), as variation in δ^{13}C values among years in claw or blood samples obtained during arrival to migratory stop-over sites or breeding grounds may be indicative of temporal rainfall patterns occurring in early to mid-winter, and not during late winter. More studies would be useful to fully determine how temporal variation in moisture affects δ^{13}C values in bird samples.

**Conservation Implications**

Rainfall in the Caribbean is expected to decline and also become more variable over the next 50 years (Neelin et al. 2006, Studds and Marra 2011). Given continued development and deforestation in the tropics and limited resources to conserve habitat (Achard et al. 2014), we recommend that preservation efforts for migratory birds focus on the least drought-prone areas (Wunderle et al 2014), which in The Bahamas are sites where the freshwater table is close to the surface (Sealey 2006). Conservation areas should include high-moisture habitats (i.e., mangroves) that have been shown to be of high quality for certain species of wintering Nearctic-Neotropical migrants (Johnson et al. 2006, Smith et al. 2010). Additionally, conservation areas should include relatively
wetter sites within other vegetation communities that are often not perceived as ‘high moisture’ (i.e., inland coppice), yet our study observed that these areas also provide high-quality habitat (Wunderle et al. 2014). Conservation of a variety of vegetation communities will not only benefit threatened migratory avian species that are ‘dry forest’ specialists, such as Swainson’s warblers (*Limnothlypis swainsonii*; Strong and Sherry 2001) and Kirtland’s warblers (Wunderle et al. 2014), but also resident birds and other wildlife species that are dependent on the preservation of the entire breadth of different vegetation communities (Latta et al. 2003, Currie et al. 2005).

Climate change will likely affect birds in complex ways; for instance, some species of migratory birds are adapting to warmer springs in temperate zones by arriving earlier to the breeding grounds (Jonzén et al. 2006), yet lower rainfall in the wintering grounds will make it more difficult for migrants to acquire pre-migratory reserves and depart earlier on spring migration (Studds and Marra 2011). Females and younger individuals segregated to poorer-quality, drier habitats may be especially prone to predicted declines in rainfall (Marra and Holmes 2001), which may subsequently affect processes on the breeding grounds (Norris et al. 2004, Runge and Marra 2005, Drake et al. 2013). Our study shows that prairie warbler populations could be limited by habitat quality during the wintering season, although further studies of effects on birds’ fitness (survival and carry-over effects on reproduction) are needed. Continued research on full annual cycles of migratory passerines is important to fully understand limiting factors of populations and provide best management tools for declining and threatened species (Marra et al. 2015b).
Table 1.1. Monthly rainfall between September and March, in the 2012-2013 and 2013-2014 winters. For March, we only included rainfall up until 25 March because we did not capture birds past this date.

<table>
<thead>
<tr>
<th>Month</th>
<th>Rainfall in 2012-13 (mm)</th>
<th>Rainfall in 2013-14 (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>September</td>
<td>146.3</td>
<td>41.5</td>
</tr>
<tr>
<td>October</td>
<td>358.0</td>
<td>252.6</td>
</tr>
<tr>
<td>November</td>
<td>127.3</td>
<td>102.4</td>
</tr>
<tr>
<td>December</td>
<td>57.8</td>
<td>15.7</td>
</tr>
<tr>
<td>January</td>
<td>9.9</td>
<td>34.2</td>
</tr>
<tr>
<td>February</td>
<td>51.3</td>
<td>54.9</td>
</tr>
<tr>
<td>March</td>
<td>16.7</td>
<td>30.3</td>
</tr>
</tbody>
</table>
Table 1.2. Candidate model set examining rainfall variables and date on prairie warbler body condition and muscle score. Time was not included in muscle score models and thus those models had one less parameter. The rainfall variable in a given model was either total, SD, or CV of daily rainfall 30, 60, 90, or 120 days prior to capture. VegHtatNet = vegetation canopy height at the capture net, VegTypeatNet = vegetation type at the capture net, K = number of parameters.

<table>
<thead>
<tr>
<th>Model No.</th>
<th>Fixed-effect Variables</th>
<th>K</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Time</td>
<td>4</td>
</tr>
<tr>
<td>2 to 14</td>
<td>Time+(Rainfall Variable or Date)</td>
<td>5</td>
</tr>
<tr>
<td>15 to 27</td>
<td>Time+(Rainfall Variable or Date)* $\delta^{13}$C</td>
<td>7</td>
</tr>
<tr>
<td>28 to 40</td>
<td>Time+(Rainfall Variable or Date)*VegHtatNet</td>
<td>7</td>
</tr>
<tr>
<td>41 to 53</td>
<td>Time+(Rainfall Variable or Date)*VegTypeatNet</td>
<td>15</td>
</tr>
</tbody>
</table>
Table 1.3. Age and sex of prairie warbler captures among vegetation types in San Salvador Island, between 2012-2015. Presented are within-vegetation type percentages, with total numbers (n) in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>Buttonwood</th>
<th>Coastal Scrub</th>
<th>Mangrove and Palm</th>
<th>Non-native</th>
<th>Short Coppice</th>
<th>Tall Coppice</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Juvenile Female</strong></td>
<td>47 (23)</td>
<td>42 (58)</td>
<td>13 (2)</td>
<td>41 (26)</td>
<td>60 (6)</td>
<td>24 (12)</td>
</tr>
<tr>
<td><strong>Adult Female</strong></td>
<td>16 (8)</td>
<td>24 (33)</td>
<td>0 (0)</td>
<td>24 (15)</td>
<td>20 (2)</td>
<td>12 (6)</td>
</tr>
<tr>
<td><strong>Juvenile Male</strong></td>
<td>24 (12)</td>
<td>18 (25)</td>
<td>73 (11)</td>
<td>21 (13)</td>
<td>0 (0)</td>
<td>45 (22)</td>
</tr>
<tr>
<td><strong>Adult Male</strong></td>
<td>12 (6)</td>
<td>16 (22)</td>
<td>13 (2)</td>
<td>14 (9)</td>
<td>20 (2)</td>
<td>18 (9)</td>
</tr>
<tr>
<td><strong>Total Male</strong></td>
<td>36 (18)</td>
<td>34 (47)</td>
<td>86 (13)</td>
<td>35 (22)</td>
<td>20 (2)</td>
<td>63 (31)</td>
</tr>
<tr>
<td><strong>Total Adult</strong></td>
<td>28 (14)</td>
<td>40 (55)</td>
<td>13 (2)</td>
<td>38 (24)</td>
<td>40 (4)</td>
<td>30 (15)</td>
</tr>
</tbody>
</table>
Table 1.4. The top models (<2 ΔAIC<sub>c</sub>) assessing rainfall variables and date on prairie warbler body condition and muscle score, separately for 2013 and 2014. No models were presented for body condition in 2014 because no models were less than 2 ΔAIC<sub>c</sub> from the null model. Presented are the models, number of parameters (K), Akaike’s Information Criterion value corrected for small sample sizes (AIC<sub>c</sub>), difference in AIC<sub>c</sub> from the top model (ΔAIC<sub>c</sub>), and model weight (ω<sub>i</sub>).

<table>
<thead>
<tr>
<th></th>
<th>K</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ω&lt;sub&gt;i&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Body Condition 2013</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>90DaySD*Isotope</td>
<td>7</td>
<td>36.18</td>
<td>0</td>
<td>0.7</td>
</tr>
<tr>
<td><strong>Muscle 2013</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30DayTotal*Veg.Height</td>
<td>6</td>
<td>195.91</td>
<td>0</td>
<td>0.26</td>
</tr>
<tr>
<td>30DayTotal</td>
<td>4</td>
<td>196.12</td>
<td>0.22</td>
<td>0.24</td>
</tr>
<tr>
<td><strong>Muscle 2014</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30DayTotal</td>
<td>4</td>
<td>200.57</td>
<td>0</td>
<td>0.13</td>
</tr>
<tr>
<td>30DaySD</td>
<td>4</td>
<td>200.83</td>
<td>0.27</td>
<td>0.12</td>
</tr>
<tr>
<td>90DayCV</td>
<td>4</td>
<td>200.92</td>
<td>0.36</td>
<td>0.11</td>
</tr>
<tr>
<td>90DayCV*Isotope</td>
<td>6</td>
<td>201.26</td>
<td>0.69</td>
<td>0.09</td>
</tr>
<tr>
<td>90DayTotal</td>
<td>4</td>
<td>201.79</td>
<td>1.22</td>
<td>0.07</td>
</tr>
<tr>
<td>90DaySD</td>
<td>4</td>
<td>202.41</td>
<td>1.84</td>
<td>0.05</td>
</tr>
</tbody>
</table>
Figure 1.1. Daily rainfall (mm) between January and March, in the 2012-2013 and 2013-2014 winters.
Figure 1.2. Relationship between $\delta^{13}$C values of prairie warbler blood with the vegetation type at the capture net in 2012-2015. Points represent means and error bars are ± 1 standard error.
Figure 1.3. Total rainfall 90 days prior to capture and effect on $\delta^{13}\text{C}$ values in 2013 and 2014. Solid line represents simple regression line (without covariates or random effects), while grey shading represents the 95% CI.
Figure 1.4. Vegetation canopy height (m) at capture locations of different age and sex classes, and $\delta^{13}\text{C}$ values of blood, (more negative indicating more habitat moisture), in different age and sex classes.
Figure 1.5. Prairie warbler body condition as a function of day of season in 2012, 2013, and 2014. Solid lines represent simple regression lines, while grey shading represents the 95% CI.
Figure 1.6. Prairie warbler body condition as a function of day of season and age/sex classes in 2012, 2013, and 2014. Solid lines represent simple regression lines (without covariates or random effects) for the relationships within each plot-year, while grey shading represents the 95% CI.
Figure 1.7. The partial residuals of the relationship between prairie warbler body condition index as a function of the interaction between $\delta^{13}C$ and the SD of daily rainfall 90 day prior to the capture date during the drier winter of 2013 on San Salvador. Both predictor variables were standardized with a mean of 0 and a standard deviation of 1. The left and right facets show the relationship between rainfall and body condition when the $\delta^{13}C$ value is -1.3 or 1.3 standard deviations from its mean, respectively. The middle facet shows the relationship when $\delta^{13}C$ is at its mean. More negative $\delta^{13}C$ values (the left graph) indicate birds that used wetter habitat. The best-fit lines were created using the “visreg” package in R, based on the mixed model analysis.
Figure 1.8. Rate of daily change in mass (g/day) as a function of $\delta^{13}C$ values of blood, for individuals captured in mid-winter and recaptured in late-winter. Solid lines represent regression lines, while grey shading represents the 95% CI. There was a significant relationship only in 2013.
CHAPTER 2
CARRY-OVER EFFECTS OF WINTER HABITAT ON BREEDING SEASON
PHENOMENA IN A MIGRATORY BIRD POPULATION

Introduction

Migratory bird populations are dependent on habitat quality at multiple sites throughout their annual cycle, and recent studies have found that birds at a given site may be greatly affected by habitat quality or events that occurred in a previous period during their lifecycle (Marra et al. 1998, Sillett et al. 2000, Harrison et al. 2011). In the last few decades, new knowledge of these carry-over effects is becoming instrumental in better understanding the ecology and evolution of migratory birds, determining limiting factors of population growth, and improving conservation efforts for declining bird populations (Webster et al. 2002, Norris and Marra 2007). Understanding carry-over effects is especially important for conservation, as conservation or management efforts at one site along the migratory route could be ineffective if birds are negatively influenced by marginal habitat elsewhere (Norris 2005).

Marra et al. (1998) conducted a breakthrough study, in which stable isotope ratios of carbon ($\delta^{13}C$) in bird tissue were used to link birds studied on the wintering grounds with birds observed on the breeding grounds. Studies have shown that a strong correlation exists between $\delta^{13}C$ in birds’ tissue, blood, and claws and winter habitat moisture (Marra et al. 1998, Bearhop et al. 2003, Norris et al. 2005). The correlation between moisture and $\delta^{13}C$ in birds is due to differences in the ratio of $^{13}C$ to $^{12}C$ (known as $\delta^{13}C$) in $C_4$ and CAM plants, which are found in dry habitats, versus $C_3$ plants, which
are found in wet habitats. As well, δ¹³C values differ within C₃ plants found in dry versus wet areas (Marshall et al. 2007). Carbon isotope ratios, inherently different in the vegetation along the moisture gradient, then moves up the food chain from plants to herbivorous insects, and from insects to birds (Marra et al. 1998).

Besides having a strong relationship with δ¹³C, winter habitat moisture also correlates highly with winter habitat quality for certain migratory birds (Marra et al. 1998, Studds and Marra 2005, Smith et al. 2010). As the winter dry season progresses in the Caribbean, wetter habitats tend to have more insects and fruit than drier habitats, and thus provide more food resources for wintering migrants (Latta and Faaborg 2002, Wunderle et al. 2014, Cooper et al. 2015). In the Dominican Republic, Latta and Faaborg (2001) observed that prairie warblers (Setophaga discolor) declined in body condition in dry scrub habitat but body condition remained constant in less xeric, upland habitat. American redstarts (Setophaga ruticilla) that winter in drier, poor-quality habitat have reduced physical condition and delayed spring departure dates, which leads to later arrival dates and lower reproductive success on the breeding grounds (Marra et al. 1998, Norris et al. 2004, Reudink et al. 2009). For a number of other migratory passerines, studies have found birds in wetter winter habitats arrive earlier and/or in better condition to a migratory stop-over site (Bearhop et al. 2004, Gonzalez-Prieto and Hobson 2013, Paxton and Moore 2015), which presumably would then lead to birds’ arriving earlier and having more time and energy to reproduce on the breeding grounds (Tonra et al. 2011).

Although winter habitat moisture is important for a number of avian species on the wintering grounds and effects of moisture can carry over to influence birds in a subsequent location, some studies of Nearctic-Neotropical passerines have found weak or
no carry-over effects of winter habitat moisture, including studies on magnolia warblers
(*Setophaga magnolia*), yellow warblers (*Setophaga petechia*), and Kirtland’s warblers
(*Setophaga kirtlandii*; Boone et al. 2010, Rockwell 2013, Drake et al. 2014a). Carry-over
effects can even vary within species, for instance, multiple studies have observed
significant and important carry-over effects for American redstarts wintering in the
Caribbean (Marra et al. 1998, Norris et al. 2004, Reudink et al. 2009, Tonra et al. 2011,
Rushing et al. 2016), yet no relationship was found for redstarts arriving during migration
at a study site in Ontario, where birds were arriving from habitat relatively more
homogenous in moisture in Central America (Gonzalez-Prieto and Hobson 2013).
Moreover, for yellow warblers, a significant carry-over effect of winter moisture on
reproductive output occurred for second-year females in British Columbia, but no
relationships were found for other age-sex classes in the same population, as well as none
observed for a yellow warbler population breeding in the arctic (Drake et al. 2013, Drake
et al. 2014a). Carry-over effects are therefore not ubiquitous among Nearctic-Neotropical
migratory passerines, and more research is needed to better understand variation among
species, populations, and age and sex classes. For some species, winter habitat moisture
may not be an important driver of winter habitat quality (Boone et al. 2010), while for
other species, arrival date and reproductive success may be more influenced by other
environmental conditions and processes during the bird’s life cycle (Rockwell et al. 2012,
Drake et al. 2014b).

Prairie warblers are Nearctic-Neotropical migratory passerines that winter
primarily in the Caribbean and breed in early-successional habitats in the eastern United
States (Nolan et al. 2014). Prairie warblers have experienced dramatic range-wide
declines in the past few decades and are currently a species of conservation concern (Schlossberg and King 2007, Sauer et al. 2014). Although ongoing forest management is necessary to create and maintain suitable early-successional breeding habitat (Schlossberg and King 2009, King et al. 2011, King and Schlossberg 2014), we currently do not know if conserving high-quality winter habitat is also important for maintaining populations due to carry-over effects limiting prairie warbler fitness on the breeding grounds. To address this knowledge gap, we studied carry-over effects for prairie warblers on the breeding grounds in a managed early-successional site in Massachusetts. Specifically we examined if prairie warbler winter habitat use, assessed indirectly by examining δ¹³C in claws and red blood cells of birds captured on arrival in Massachusetts, can carry-over to explain patterns in arrival dates, body condition upon arrival, pairing success, first-egg date, and apparent reproductive success on the breeding grounds. Since winter habitat quality for prairie warblers does appear to vary among wet and dry habitats (Latta and Faaborg 2001, Chapter 1), we hypothesize that birds in wetter winter habitats will arrive on the breeding grounds earlier and in better condition, experience greater pairing success and earlier first-egg dates, and have higher apparent reproductive success compared to birds over-wintering in drier habitats.

**Methods**

**Study Site**

We conducted the study from 2009-2013 at the Montague Plains Wildlife Management Area (MPWMA), in Western Massachusetts, U.S.A. (N 42° 34’, W 72° 31’) as part of an ongoing study on prairie warblers starting in 2008 (Akresh et al. 2015).
The MPWMA is a pitch pine-scrub oak barren that is actively managed for habitat restoration and fuels reduction to reduce wildfire risk and promote biodiversity. Prairie warblers are one of the most abundant songbirds breeding within the MWPWA, and nest in scrub-oak barrens, thinned pitch pine stands and power line corridors (see King et al. 2011, Akresh et al. 2015 for more details). We sampled birds within 9 study plots within the study site ranging in area from 4 to 29 ha (Akresh and King 2016).

**Bird Sampling**

During 2009-2013 we established individual male arrival dates by monitoring study plots intensively every 2-3 days starting in mid- to late April before the first prairie warbler arrived until June when almost all the males had arrived. During each visit we surveyed the entire plot for singing males and sighted previously color-banded and unbanded birds to estimate individual male arrival dates. The earliest date during each season that we first observed an individual was considered the arrival date. Since males are conspicuous, sing upon arrival to the study site, and plots were covered extensively early in the season, we believe we detected most arriving males during the first visit that they were present. Although the first day a male was detected could have been 1-2 days after the individual’s actual arrival date, all plots were sampled on the same 2-3 day schedule; therefore, this measurement error was equally distributed among males and should not bias analyses of individual-based effects on arrival date (Rockwell et al. 2012). We delineated territories by recording 1-10 locations of singing males during each visit using handheld global positioning system (GPS) units, and we also plotted the singing locations relative to landmarks on treatment maps and aerial photographs. The
presence of many returning color-banded males (Akresh et al. 2015) and the above mapping procedure allowed us to delimit territories for males that we did not catch and color band during their first day of arrival.

During 2011-2013, we captured both previously banded and unbanded males soon after their estimated arrival date using targeted mist-netting with prairie warbler song playback and a decoy. While we primarily targeted males, we also incidentally captured some females early in the breeding season. Previously unbanded birds were banded with a United States Geological Survey aluminum band and a unique color combination of 2-3 plastic color bands. Birds were classified upon capture by age class (After-second Year = ASY or Second Year = SY) and sex using plumage, breeding condition, feather wear, and molt limits (Pyle 1997). We then measured birds’ wing chord (+/- 1 mm), tail length (+/- 1 mm), and tarsus length (+/- 0.1 mm), weighed birds using an electronic scale (+/- 0.1 g), and sampled the tip (2-3 mm) of the central claw on both feet of the bird. In 2011 and 2012, for a subset of birds we also collected blood samples (up to 50 uL). Blood samples were put on ice and then later spun in a centrifuge for 8 min at 13000 rpm on the same day as sampled. The plasma and red blood cells (RBC) were separated using a Hamilton syringe and then frozen.

Of the males captured upon arrival, we captured and obtained claws of 78% of the males within 3 days of their estimated arrival, 94% within 1 week, and 100% within 12 days. Since claw tips represent dietary isotopic input a few weeks to a few months before capture and δ13C isotopes in claws can have a relatively long half-life (i.e., 27 days; Lourenço et al. 2015); the sampled claws of these captured males should reflect the birds’ wintering habitat (Bearhop et al. 2003, Hahn et al. 2014). Indeed, we recaptured 10
individual males 10-21 days (mean = 16 days) after their initial capture and re-sampled these birds (sampling different claws, the tips of the outer claws and/or the hallux): 70% of the claws from re-sampled birds had $\delta^{13}$C values within 0.3‰ of the initial capture, and 90% had values within 0.7‰. Therefore, claws from birds captured even weeks after arrival should represent isotopic input from birds’ wintering habitat. We could not determine female arrival dates because females were more difficult to detect on arrival, often moved among multiple territories early in the season, and were less likely to return to the study site as banded birds. Nevertheless, given claws’ $\delta^{13}$C half-life (Lourenço et al. 2015) and our above findings on re-sampled males, we believe that any birds captured and sampled in May (including females) were likely sampled early enough in the breeding season for claws to represent the birds’ wintering habitat (Dale and Leonard 2011), and we therefore included these birds in our analyses.

We also examined all of the RBC samples that we obtained from males captured upon arrival. For males with an estimated arrival date and a RBC sample, 71% were captured within 3 days of estimated arrival, 94% within 1 week, and 100% within 9 days. Studies have found that isotope values from RBC samples can represent winter habitat moisture for birds captured very soon after arrival (Norris et al. 2004, Norris et al. 2005, Rockwell 2013). However, stable isotope ratios in RBC samples have a shorter half-life than claws (7-30 days; Hobson and Clark 1993, Klaassen et al. 2010, Lourenço et al. 2015) and are metabolically active, and thus may also represent some dietary input from migration (Norris et al. 2005, McKinnon et al. 2012).

We monitored prairie warbler territoriality, pairing success, first-egg laid on the territory (first-egg date), and apparent reproductive success by visiting each territory for
30-60 minutes between 5:30 and 14:00 every 2-4 days throughout the breeding season. Males were considered territorial if they bred within the site or if they were observed at least twice in a given territory over a period longer than 10 days (Bibby et al. 1992). We located nests within territories by observing parent behavior and conducting systematic searches. Nests were marked with flagging placed 10-20 m from the nest and monitored every 2-4 days until the nestlings fledged or the contents of the nest had disappeared. Most nests were found during the building stage, although some were found after laying and for those we estimated the first-egg date based on the nest’s hatch date (Nolan 1978). For first-egg dates, we excluded nests where the first egg of the nest was laid after 7 June, since we could not be certain that these were first nests in the territory rather than re-nests after a nest failure. We additionally excluded nests found on territories on which we later found evidence of an earlier nesting attempt or we were otherwise led to believe we had missed the male’s first nest (i.e., due to the presence of a female early in the season; Byers et al. 2015).

We classified males as paired if 1) the male exhibited mating behavior with a female (e.g. mate-guarding or copulation) or 2) the male sang exclusively near a nest within his territory and/or was observed feeding young. We determined if adults fledged young by monitoring nests until we observed fledging, searching for fledglings in territories where nests could have fledged based on the stage of the nestlings’ development in the previous nest check, and by searching territories for adults feeding fledglings in territories where we did not locate a successful nest. In these latter territories where we just found adults feeding fledglings, we did not know the exact number of fledglings. Therefore, when analyzing data on the number of fledglings, we only included
territories with found nests (~90% of the territories). We never observed polygamous males or double-broods, yet given many visits to the territories we are confident we were aware of the majority of reproductive efforts within the extensively surveyed plots. In certain years, due to the large number of territories in the study site, some plots were not surveyed extensively for reproductive success.

Stable Isotope Preparation and Analysis

We analyzed stable isotopes from claw and RBC samples at the Stable Isotope Mass Spectrometry Facility at the Smithsonian Institution, Suitland, MD, USA. Claws were soaked for 2 hours in a 2:1 chloroform:methanol solution and dried in a fume hood for 48 hours. RBC samples were freeze-dried and powdered. All samples were then weighed into tin capsules and then combusted in a continuous flow isotope ratio mass spectrometer (Thermo Scientific Delta V Advantage mass spectrometer coupled with a Costech ECS 4010 elemental analyzer via a Conflo IV gas interface). One in-house standard was run for every four unknowns. Stable isotope ratios ($^{13}$C/$^{12}$C) are reported in delta (δ) notation, in per-mil units (‰) relative to the Vienna Pee Dee Belemnite ($\delta^{13}$C) standard. Repeated analyses of RBC samples from the same individual capture were replicable to within 0.2‰ (n = 4).

Statistical Analysis

Direct and Indirect Pathways

Carry-over effects of winter habitat can manifest themselves in the form of direct relationships between winter habitat moisture (assessed using $\delta^{13}$C values) and breeding
phenology, body condition upon arrival, or breeding performance measures (Marra et al. 1998, Rushing et al. 2016), or in an indirect pathway on breeding performance through influences on breeding phenology (Norris et al. 2004, Drake et al. 2013). As a result, we explored the direct effects of $\delta^{13}C$ on arrival dates, body condition upon arrival, pairing success and apparent reproductive success, and also explored indirect pathways testing if any influences of winter habitat on birds’ arrival dates then subsequently affected birds’ pairing success or reproductive output. We also explored a 4-step indirect pathway examining if any influence of $\delta^{13}C$ values on arrival dates would then affect first-egg dates, which lastly could affect reproductive output (Drake et al. 2013). Unless noted, we analyzed SY and ASY males separately because individuals of different age classes exhibit different constraints throughout their annual cycle, which can lead to differences in the importance of seasonal interactions (Drake et al. 2013). Moreover, age class affects male arrival dates and other breeding phenomena in our study site (Akresh et al. 2015); thus, analyzing the population as a whole may obscure within age-class patterns. For similar reasons we analyzed females separately from males (Drake et al. 2013, Rushing et al. 2016), although we could not examine female age classes separately due to small sample sizes. Since non-territorial males could have been northward-bound migrants or otherwise could have continued on to disperse to territories outside of the study site, we excluded these birds from our analyses unless noted. We used the R statistical program version 3.2.1 to conduct all analyses (R Core Team 2016), and the nlme package (Pinheiro et al. 2015) to run linear mixed-effects models unless otherwise noted.

To test for carry-over effects on male arrival dates, we created linear models with arrival date as the response variable and $\delta^{13}C$ values of claws or RBCs as the predictor
variable. Processes that affect birds in both the wintering grounds (i.e., rainfall) and the breeding grounds (i.e., nest predator abundance) often vary among years (Schmidt and Ostfeld 2003, Studds and Marra 2007); therefore, when possible we examined yearly variation in our analyses. We tested for interactions between the effect of year and δ¹³C of claws on arrival date, using a linear mixed model with a random effect of individual bird for ASY males, and a linear fixed-effects model for SY males. Since we found a significant δ¹³C of claws and year interaction for ASY males, we analyzed data and presented results separately for each year using linear fixed-effect models. We did not find a significant interaction with year and δ¹³C of claws for SY males, so we first examined SY males with all years combined, but with year as a covariate. In our exploratory examination of the data for SY males, we did note a slightly different trend during 2011 and 2012 compared to 2013, so we ran additional analyses separating 2013 from the other two years, but still including year as a covariate when examining 2011 and 2012 combined. When possible, we also conducted the above tests using the δ¹³C values of RBCs, instead of claws, as the predictor variable. We omitted males that we were unable to capture and obtain their isotope signature in May. Arrival dates after June 1 were also omitted, as these late arrivals could have been birds immigrating into the study site from the surrounding area (Nolan 1978).

To test if δ¹³C values in claws or RBCs affected male body condition upon arrival, we computed a size-corrected body condition index using a principal component analysis on body size measurements (wing, tail, and tarsus length), and taking the residuals from the linear relationship of the first principal component (PC1; 60% of the variance explained) regressed over mass (r = 0.39, p < 0.001; Marra et al. 1998). Using
this body condition index as the response variable, we analyzed $\delta^{13}$C values in claws as the predictor variable for SY males using a linear fixed-effect model and for ASY males using a mixed-effects model with individual as a random effect. In addition, we included covariates of year, time of capture, and the number of days birds were captured after their estimated arrival date on the breeding grounds, to control for daily and annual variation in body condition. We did not find significant interactions for the effect of year and $\delta^{13}$C values in claws for either SY or ASY males, and therefore we pooled years in our analyses. We additionally ran a similar, fixed-effects model to test the effects of $\delta^{13}$C values in RBCs (instead of claws) on body condition for ASY males, but the sample size of RBCs was too small to run a model for SY males. We did not examine $\delta^{13}$C effects on body condition or arrival date for females because we were uncertain of the timing of their arrival to the breeding grounds.

We then tested if there was a direct effect of $\delta^{13}$C values in claws on male pairing success. There were very few unpaired males, therefore to assist with model convergence we examined pairing success by pooling ASY and SY males, and left out year and individual covariates. We then analyzed the data using a Generalized Linear Model (GLM) fit to a binomial distribution. We also tested for indirect effects of $\delta^{13}$C on pairing success through the influence of a male’s arrival date. As we already examined the effect of $\delta^{13}$C on arrival dates, we continued the pathway by testing if arrival date predicted pairing success, again pooling ASY and SY males due to the small sample size of unpaired males and using a GLM fit to a binomial distribution. We also examined a similar model, but included a covariate of age class to account for differences in pairing
success just due to age. In these analyses we excluded any plots or territories in which we did not adequately survey for reproductive success in a given year.

We also assessed if first-egg dates were a function of male arrival dates. We used first-egg date as the response variable and for ASY males our predictor variables were arrival date and year, with a random effect of individual. We did not find any significant interactions with the effects of arrival date and year for ASY males, and therefore pooled years in this analysis. For SY males we just examined arrival date as a predictor as sample sizes were small within years. We only included territories that we obtained the arrival date and first-egg date.

We examined reproductive performance in two ways: first, we examined whether or not an adult successfully fledged prairie warbler young, and second, we examined the number of young fledged if successful (Jones et al. 2014, Byers et al. 2016). We did this approach partly because the number of fledglings per male, including counts of zero young fledged, did not fit a simple Poisson distribution (Akresh et al. 2015). We therefore conducted Zero-altered Poisson (ZAP) regressions, otherwise known as hurdle models, which effectively fit fledging success to a binomial distribution, and fit fledgling count if successful to a zero-truncated Poisson distribution (Zuur et al. 2009). Using the glmmADMB package (Skaug et al. 2015), for ASY males we conducted mixed-effects ZAP models with individual as a random effect, and for SY males we conducted fixed-effects ZAP models. We separately tested the direct effect of $\delta^{13}$C on the two reproductive performance measures, and also tested the indirect effects of male arrival date and laying date on reproduction. We did not find interactions with predictor variables and year, therefore we pooled years for the analyses but included a covariate of
year in the models to account for yearly variation in reproductive performance (Akresh et al. 2015). However, due to small sample sizes in the analyses of SY males with δⁱ³C values in claws, first-egg date, and the number of fledglings, to assist with model convergence we did not include year as a covariate. For the above analyses with arrival and first-egg date, we only included males in plots where we extensively examined reproductive success for every male, and for all analyses we only included territories with known fledging success and arrival dates, first-egg dates, or δ¹³C values (depending on the model). Since we analyzed pairing success separately, we excluded the few territories with unpaired males. We also examined the direct effects of δ¹³C on reproduction for females, but only tested fledging success and did not examine yearly variation because of small sample sizes. To test this, we pooled SY and ASY females and used a simple GLM fit to a binomial distribution. We could not examine indirect pathways of δ¹³C on reproductive performance of females, because we did not know female arrival dates and the sample size of females that we collected claws from and had known first-egg dates was not adequate for analysis. Because of the small sample size of RBCs, for almost all reproductive success analyses we just examined effects of δ¹³C in claws, with the exception of also assessing the effects of δ¹³C in RBCs on fledging success for ASY males.

For all analyses with δ¹³C values or body condition upon arrival we only used data from 2011-13, because we did not collect claw samples or capture birds upon arrival in 2009-2010. However, for analyses without these variables (i.e., the effects of arrival on first-egg date or reproductive success), we chose to examine a broader dataset from 2009-2013 in order to increase sample sizes and power, especially for SY males. Since we
account for year and examine any possible yearly interactions in the data, we believe adding data from 2009-2010 for these analyses should not bias our results.

**Examining Between Age/Sex Classes and Territoriality**

For many warbler species, older males dominate high-quality, often wetter, winter habitat forcing younger males and females into marginal habitat (Marra 2000, Mettke-Hofmann et al. 2015, Chapter 1). As a result, we also explored if different age-sex classes had different δ¹³C isotope signatures, perhaps reflecting age- or sex-specific habitat segregation on the wintering grounds. For males, we then also tested if any differences in δ¹³C between age classes would carry-over to affect differences in breeding phenology, body condition upon arrival, and breeding success between male age classes. We first tested if δ¹³C values of females differed from those of territorial males using a linear mixed model, including an interaction with year and a random effect of individual. Since we observed a significant interaction with year, we examined and presented analyses for each year separately in fixed effects models. For territorial males, we then conducted separate linear mixed models with a response variable of either δ¹³C, body condition upon arrival, or first-egg date, male age class as the predictor variable, a covariate of year, and a random effect of individual bird. There were no significant interactions between male age class and year for any of the models, therefore we did not examine models within individual years. We only examined δ¹³C values in claws, due to small sample sizes of RBCs. When examining body condition, we again included additional covariates of time of capture and the number of days males were captured after they arrived on the breeding grounds. We examined differences in reproductive performance
in SY versus ASY males using ZAP models, including a covariate of year and random effect of individual.

Although non-territorial males may have dispersed outside our study site to breed, some of these birds could have been ‘floater’ males that may be inferior compared to territorial males (Zack and Stutchbury 1992, Cooper et al. 2009). To test if non-territorial males wintered in different habitats as territorial males, we used a linear mixed model, with a response variable of δ13C values in claws, and predictors of territoriality (yes or no) and year, including individual bird as a random effect. We tested for and found no significant interaction of territoriality and year.

**Examining Repeatability**

Individuals of many warbler species exhibit high fidelity to the same wintering territory over multiple years (Holmes and Sherry 1992, Latta and Faaborg 2001). If birds winter in the same habitat over multiple years and there are strong carry-over effects of winter habitat on birds’ arrival, one might expect a high within-individual consistency in arrival dates, especially relative to others in the population. Conversely, if birds have high winter habitat fidelity, but low consistency in arrival timing, other factors besides winter habitat may be driving birds’ arrival dates. To test annual consistency, we examined within-individual variability in δ13C values in claws and arrival dates, as well as body condition upon arrival and first-egg dates, by computing analyses on repeatability (intraclass correlation coefficient) using the rptR package (Nakagawa and Schielzeth 2010) for birds that we observed over multiple years. Since arrival and first-egg dates differ between male age classes, we only examined ASY males for these analyses. Due to
small sample sizes, we pooled SY and ASY males when examining repeatability of $\delta^{13}$C and body condition.

**Results**

**Direct Carry-over Effects**

The relationship between $\delta^{13}$C values in claws or RBCs and male arrival dates varied among years and age classes. For ASY males, in 2011 there was a trend for birds using wetter winter habitats (more depleted $\delta^{13}$C values) to arrive earlier based on claw samples ($n = 49, t = 1.95, p = 0.06, r^2 = 0.07$; Figure 2.1), and this relationship was more significant based on RBC samples ($n = 15, t = 2.2, p = 0.05, r^2 = 0.27$; Figure 2.1). In 2012, the relationship between $\delta^{13}$C values and ASY male arrival date was significant using claws ($n = 39, t = 2.63, p = 0.01, r^2 = 0.16$) and again the variables were more correlated using RBCs ($n = 12, t = 2.1, p = 0.06, r^2 = 0.32$). In 2013, we found no effect of $\delta^{13}$C in claws on ASY males’ arrival date ($n = 30, t = -1.64, p = 0.11$). For SY males, we did not find a relationship between $\delta^{13}$C values in claws and arrival dates in all years combined ($n = 36, t = 0.42, p = 0.67$), in just 2011 and 2012 combined ($n = 19, t = 1.22, p = 0.24$, Figure 2.2), or in just 2013 ($n = 17, t = -0.58, p = 0.57$). There was also no significance between $\delta^{13}$C values in RBCs and SY arrival dates in 2011 and 2012 combined, taking into account year, although the sample size was small ($n = 7, t = 2.0, p = 0.11$).

For ASY males, body condition upon arrival was not significantly affected by $\delta^{13}$C values in claws ($n = 112, t = 1.20, p = 0.25$), or by $\delta^{13}$C values in RBCs ($n = 27, t = -1.10, p = 0.28$), while taking into account other covariates (time of day, number of days...
since arrival, and year) in the models. As well, body condition had no relationship with 
$\delta^{13}C$ values in claws for SY males ($n = 33, t = 0.57, p = 0.57$).

For ASY and SY males pooled, $\delta^{13}C$ in claws did not directly affect pairing
success ($n = 133, z = -0.84, p = 0.40$). For ASY males, we did not find any direct effects
of $\delta^{13}C$ in claws or RBCs on fledging success (claws: $n = 77, z = -0.42, p = 0.68$, RBCs:
$n = 18, z = 1.21, p = 0.23$) or effects of $\delta^{13}C$ in claws on the number of fledglings if
successful ($n = 31, z = -0.36, p = 0.72$). Additionally, no direct effects of $\delta^{13}C$ in claws
were observed for SY males on fledging success ($n = 23, z = 1.43, p = 0.15$) or number of
fledglings ($n = 8, z = 0.63, p = 0.53$). Lastly, no direct effect of $\delta^{13}C$ in claws on fledging
success was observed for females ($n = 20, z = -0.25, p = 0.81$).

**Continuing Indirect Pathways of Carry-over Effects on Reproductive Performance**

In 2009-2013, males that arrived to the breeding grounds earlier had a higher
probability of pairing successfully ($n = 287, z = -3.41, p < 0.001$, Figure 2.3), and this
relationship was still significant after accounting for the influence of age class on pairing
success ($z = -2.26, p = 0.02$). For ASY males, we did not find a significant effect of
arrival date on first-egg date ($n = 122, t = 0.82, p = 0.42$). In contrast to ASY males,
earlier arriving SY males did significantly have earlier first-egg dates ($n = 28, t = 2.12, p
= 0.04; Figure 2.4$).

For ASY males, we did not find a significant effect of arrival date on fledging
success (if successful mean arrival date = 5 May, not successful = 6 May, $n = 137, z = -
1.21, p = 0.23$), or number of fledglings if successful ($n = 64, z = 0.35, p = 0.73$) while
accounting for yearly variation. We also found no significant relationships for SY males
while accounting for yearly variation (fledging success: n = 34, z = 1.44, p = 0.15, 
number of fledglings: n = 16, z = 1.44, p = 0.15), although there was a slight trend for 
later arriving SY males to be more successful (if successful, mean arrival date = 9 May, 
not successful = 12 May).

For ASY males, we did not find a significant effect of first-egg date on fledging 
success (successful and non-successful mean first-egg date = 26 May, n = 91, z = -1.46, p 
= 0.14), or number of fledglings if successful (n = 46, z = 0.54, p = 0.59) while 
accounting for yearly variation. For SY males, there was a non-significant trend for males 
to successfully fledge young if they had earlier first-egg dates (if successful, mean first-egg date = 28 May, not successfully = 30 May, n = 21, z = -1.48, p = 0.14), and there was 
no effect of first-egg date on the number of fledglings (n = 11, z = 1.28, p = 0.2).

**Examining Variation between Age Classes, Sex, and Territoriality**

Territorial males had significantly more depleted δ¹³C values in claws (indicating 
wetter winter habitat) compared to females in 2011 (males: mean = -21.95‰ +/- 0.10 SE, 
females: mean = -21.42‰ +/- 0.21 SE, n = 74, t = -2.10, p = 0.04) and in 2012 (males: 
mean = -21.72‰ +/- 0.10 SE, females: mean = -21.11‰ +/- 0.33 SE, n = 61, t = -1.95, p 
= 0.06), but not in 2013 (n = 72, t = 1.0, p = 0.30). There were no significant differences 
in δ¹³C values in claws between non-territorial versus territorial males (n = 204, t = -1.26, 
p = 0.22), or territorial SY males versus territorial ASY males (n = 171, t = 0.37, p = 
0.71). SY males did have slightly worse body condition upon arrival compared to ASY 
males, with taking into account other covariates (n = 145, t = -2.18, p = 0.04). Moreover, 
ASY males arrived significantly earlier than SY males, and ASY males had higher
pairing success (99%) compared to SY males (91%) between 2009-2013 (Akresh et al. 2015). While taking into account yearly variation, SY males had slightly later first-egg dates (mean = May 28, SE = 0.7 days) compared to ASY males (mean = May 26, SE = 0.3 days, t = 2.44, p = 0.02). ASY males did not significantly differ in fledging success ($z = -1.31, p = 0.19$), or number of fledglings ($z = -0.83, p = 0.41$) compared with SY males.

**Repeatability**

We collected claws from the same individual male in 2 different years for 29 returning birds, and in 3 consecutive years for 5 birds. $\delta^{13}$C values in claws were highly repeatable among years for the same individual bird (R = 0.72, 95% CI = 0.52 to 0.84, p < 0.001). Body condition on arrival was also repeatable among years for the same individual males (same sample size as claws minus 1 individual, R = 0.55, 95% CI = 0.27 to 0.84, p < 0.001). Between 2009 and 2013, we estimated arrival dates in 2 different years for 53 individual ASY males, in 3 different years for 20 males, in 4 years for 8 males, and in 5 years for 1 male. Arrival dates were significantly repeatable for the same individual ASY male (R = 0.23, 95% CI = 0.06 to 0.39, p = 0.003), but less so than $\delta^{13}$C values and body condition upon arrival. We estimated first-egg dates in 2 different years for 24 individual ASY males, in 3 different years for 6 males, and in 4 years for 2 males. First-egg dates were not significantly repeatable for the same ASY male over multiple years (R = 0.15, 95% CI = -0.15 to 0.45, p = 0.15).
Discussion

We found that ASY males arrived earlier to the breeding grounds from wetter winter habitats in 2011 and 2012; this is consistent with observed carry-over effects of winter habitat moisture in the Caribbean on arrival to the breeding grounds for American redstarts (Marra et al. 1998, Norris et al. 2004, Tonra et al. 2011), as well as on arrival to migratory stop-over sites for other passerines (Bearhop et al. 2004, Gonzalez-Prieto and Hobson 2013, Paxton and Moore 2015). Our results support the hypothesis that birds in wetter winter habitats may have had increased body condition during the dry season and subsequently earlier departure times, leading to earlier arrival on the breeding grounds (Marra et al. 1998, Latta and Faaborg 2001, Studds and Marra 2005, Chapter 1).

In 2013, we observed that ASY males did not arrive earlier from wetter winter habitats, and we believe this relationship may have been influenced by patterns of rainfall on the wintering grounds. In wetter winters with increased rainfall and presumably increased insect abundance in all habitat types, among-habitat moisture levels may not be as important and food resource abundance may not limit birds’ condition even in drier habitats (Brown and Sherry 2006, Studds and Marra 2007, Studds and Marra 2011, Chapter 1). We do not know the precise location that our breeding population overwinters; as a result, matching up specific winter rainfall patterns to our findings is difficult (Rockwell et al. 2012). However, we can examine North Atlantic Oscillation (NAO) index values, which some studies have found negatively correlates with higher precipitation in the Caribbean (Malmgren et al. 1998, Jury et al. 2007). Interestingly, the average of the monthly means of the NAO index between January and March (noaa.gov; 2011 = 0.14, 2012 = 0.95, 2013 = -0.57), as well as the mean NAO index in March (2011...
(2013), follows a pattern in which there could have been potentially higher precipitation in the populations’ wintering grounds in 2013. Therefore, rainfall and habitat could be interacting to influence birds’ condition on the wintering grounds (Chapter 1), which then subsequently carries over to affect arrival dates for ASY males in our population.

Our results are similar to a study done on Kirtland’s warblers, in which the effects of winter habitat moisture on male arrival dates to the breeding grounds only occurred in some years (Rockwell 2013). However, unlike our study, Rockwell (2013) observed that the carry-over effect of winter habitat moisture was not influenced by differences in winter rainfall amounts among years. Additionally, Rockwell et al. (2012) observed that winter rainfall predicted differences in arrival dates among years for SY males. In contrast, mean arrival dates in our population did not appear to vary yearly due to winter rainfall, as measured by NAO index values (Akresh unpublished data). Moreover, unlike Kirtland’s warblers (Rockwell 2013, Wunderle et al. 2014), we believe that our results of carry-over effects on ASY males were probably not due to late-winter shifts in habitat use on the wintering grounds. In a separate study, we observed relatively high within-winter site fidelity on the wintering grounds in The Bahamas and Jamaica (Akresh unpublished data), and this has also been observed in the Dominican Republic (Latta and Faaborg 2001), although some studies suggest prairie warblers are less territorial in Puerto Rico (Staicer 1992, Baltz 2000). Very high repeatability of δ^{13}C for the same birds sampled in multiple years in our breeding site further suggests that birds reside in similar winter habitats among years, and we presume are likely to be site faithful during the winter as well (Holmes and Sherry 1992).
Besides winter rainfall and habitat, we cannot rule out that additional factors that we did not examine could be important in influencing arrival dates in certain years, such as wind speed and weather during migration (Drake et al. 2014b, Finch et al. 2014), or leafing phenology and climate conditions on the breeding grounds (Møller 1994, Brown and Brown 2000). Although δ\(^{13}\)C values were highly repeatable in multiple years, arrival date repeatability was much lower, and no repeatability carried over to first-egg date. As a result, other factors may be overriding the consistency of winter habitat moisture to diminish an individual’s consistency of arrival date relative to others in the population (Conklin et al. 2013).

We found a stronger relationship with ASY male arrival date and δ\(^{13}\)C values in RBC samples compared to δ\(^{13}\)C values in claw samples. Avian claws grow conically, and the base of the claw may differ in isotope signature compared to the tip of the claw when sampled upon arrival (Mazerolee and Hobson 2005, Hahn et al. 2014). Minute differences in the size of the sampled claw tips among individuals therefore could have added variation in the claw samples. Furthermore, because of the small size of the sampled prairie warbler claws, a proportion of the sampled conical tips may have also contained some blood, depending on the wear of the claw and the location of the quick for each individual claw (MA personal observation). The addition of some whole blood in some of the claw samples likely imparted ‘noise’ in the samples (the samples being less likely to indicate winter habitat), because the stable isotope ratios in whole blood have a short half-life (i.e., 4-11 days; Pearson et al. 2003, Evans Ogden et al. 2004) and likely represents some dietary isotopic input during migration. Moreover, regardless of the time period that the claws and blood represent, claws and blood differ in isotopic
values because of differences in isotopic discrimination factors (in other words, how the isotope ratios integrate into the sample types; Lourenço et al. 2015), thus adding additional noise to any claws that contain some blood. In contrast to claws, RBCs likely have little sampling variability among individuals, and this could have lead to our observation of a stronger relationship of $\delta^{13}C$ values in RBCs with ASY male arrival date. Interestingly, RBCs likely incorporate more dietary isotopic input during migration because they are metabolically active (Norris et al. 2005). Thus, the results from RBCs may indicate that males using both wetter wintering ground habitat, and wetter migratory stopover sites, arrive earlier on the breeding grounds compared to birds using drier migratory and wintering habitats. If RBCs did incorporate more isotopic input during migration compared to claws, an alternative explanation of the stronger relationship with arrival date using RBCs is that moisture in stopover sites could be relatively more influential in affecting males’ phenology compared to moisture in the wintering grounds. Although there are a number of recent studies showing winter habitat moisture can influence birds’ condition and phenology (Marra et al. 1998, Smith et al. 2010, Chapter 1), unfortunately few studies have examined migratory stopover quality in relation to habitat moisture for Nearctic-Neotropical migratory passerines. In support of our results, Wolfe and Ralph (2009) observed that the body condition of some passerine species passing through Costa Rica during spring migration was correlated with the El Niño–Southern Oscillation (ENSO) cycle, likely because of variation in rainfall and moisture among years and subsequent influence on food resources available during migration.

Many Nearctic-Neotropical migrants exhibit age- or sex-specific habitat selection on the wintering grounds, with younger and female birds typically segregated to marginal
habitats (Marra 2000, Mettke-Hofmann et al. 2015, Chapter 1). Consistent with other studies, we observed that males obtained wetter winter habitat compared to females in two of the three years. We did not detect differences in winter habitat use between male age classes, and we failed to find a relationship between \( \delta^{13}C \) values and breeding phenology or reproductive success for females and SY males. Drake et al. (2013) also observed variation in carry-over effects on different age and sex classes, but they also were unable to attribute this variation to age- or sex-related dominance of wetter winter habitats (Marra and Holmes 2001), because \( \delta^{13}C \) values in their study did not vary among age/sex classes. Norris et al. (2004) found indirect carry-over effects on reproductive performance were stronger for female American redstarts compared to males, while Rushing et al. (2016) observed direct carry-over effects on reproductive success for just male American redstarts, but not for females. Overall, these studies did not present a clear theory for why the observed differences in carry-over effects between age and sex classes occurred, although Rushing et al. (2016) suggested that their results may have been skewed since females were sampled for claws late in the breeding season. In our study, the small sample sizes within years for females (n = 8 in 2011 and 2012) and SY males could have influenced our ability to detect significant relationships with reproductive success and/or arrival dates. Indeed, during 2011 and 2012 the relationship between SY male arrival date and \( \delta^{13}C \) values in claws did have a similar amount of variance explained \( (r^2 = 0.11) \) compared to the significant relationships found for ASY males in 2011 \( (r^2 = 0.07) \) and in 2012 \( (r^2 = 0.16) \), but unfortunately we do not know if additional samples of SY males would have led to a significant relationship. We cannot completely rule out that there was some error in estimating arrival dates which could
have affected our results, especially for unbanded SY birds before capture. Given that the majority of territorial SY males (77%) were unbanded before capture (compared to 37% for ASY males), and banded SY males sometimes moved within the study site early in the season before settling on a territory (Akresh unpublished data), our estimates of SY arrival dates may have had lower precision compared to ASY birds.

Despite very high overall pairing success, we found that males in the entire population were more likely to pair if they arrived early to the breeding grounds. However, this relationship was mainly driven by late arriving, unpaired SY males, as almost all (99%) of the ASY males paired in our study site. If there was a true carry-over effect of winter habitat on SY male arrival dates, but we did not detect it because of low precision or power, this could then have been a pathway for winter habitat moisture to have a significant effect on bird’s fitness. For American redstarts, studies have shown that winter habitat wetness influences arrival date (Marra et al. 1998, Ruedink et al. 2009), and in a separate study, Lozano et al. (1996) observed that within both age classes, male redstarts that arrive relatively earlier are more likely to pair with females. Rushing et al. (2016) documented a direct effect of winter habitat quality on pairing success for SY males, but not for ASY males, attributing this to differences in individual quality between age classes. Differences in individual quality between SY and ASY males could have been driving differences in pairing success in our study as well.

Our observation that arrival date did not affect first-egg dates for ASY males contrasts with other studies reporting a positive relationship between early arrival and early laying dates for males (Nolan 1978, Cooper et al. 2011, Tonra et al. 2011, Rockwell et al. 2012, Drake et al. 2013). However, with the exception of Drake et al. (2013), most
other studies examined the entire male population, and did not test relationships within age classes. Indeed, we observed a significant difference between ASY and SY male first-egg dates, which was likely driven by the difference in arrival times, and we observed a significant relationship with arrival and first-egg date when pooling male age classes (MA unpublished data). Since ASY males arrive weeks before females begin laying eggs, and a number arrive even before the first female is observed on the study site, variation within ASY male arrival times may not be important for time-mediated pairing with females. In contrast to ASYs, earlier-arriving SY males did have earlier first-egg dates compared to later-arriving SY males. Early-arriving SY males arrive at similar times as early-arriving females, and therefore can begin pairing and nesting earlier than later-arriving SY males.

Lastly, the date of arrival or laying did not affect prairie warbler reproductive performance; thus, at least for the measures of reproductive output examined, birds do not appear to be limited by time constraints. Our results contrast with a number of studies that have observed relationships with time constraints and reproductive success (Norris et al. 2004, Tonra et al. 2011, Rockwell et al. 2012), but are consistent with a few studies that have found no relationships (Drake et al. 2014a, Senner et al. 2014). The comparatively weak relationship between arrival and reproductive success could be related to specific features of our study system. Most of the males in our study were ASY, and we observed that even if ASY males arrived relatively late, these males often fought and re-gained their previously owned territory from an earlier-arriving intruder. Other studies have also noted high ASY territory fidelity for prairie warblers and other passerines (Nolan 1978, Lanyon and Thompson 1986, Joos et al. 2014). Therefore, in our
study site there may be a window of arrival time (i.e., the first 15-20 days) in which varying arrival date does not influence reproductive output (and during this window almost all of the ASY males arrive), but after this period, (for mostly SY males) there are time-mediated negative consequences such as reduced pairing success and later first-egg dates. Nevertheless, the lack of finding an effect of $\delta^{13}C$ on SY male arrival dates, or a difference in $\delta^{13}C$ between SY and ASY males, fails to provide a pathway for winter habitat wetness to carry over to affect pairing or first-egg date in our study system.

We conducted our research in a northeastern pitch pine-scrub oak barren, which is subject to extreme and variable temperature regimes, including unseasonable late frosts that delay leafing phenology (Motzkin et al. 2002). Delayed leaf-out subsequently affects prairie warblers’ nest site selection and in some years may increase nest depredation early in the season (Akresh 2012), which could obscure relationships between early arrival/laying and increased reproductive success. Furthermore, our site in Massachusetts is at the northern edge of the prairie warbler range and time-mediated effects on reproduction could be more important farther south where a longer breeding season permits enough time for double brooding for early-arriving individuals (Nolan 1978, Drake et al. 2014a). In our study, even the earliest fledged nests (in mid-June) apparently did not allow enough time for adults to re-nest and complete a double brood. Finally, we observed low daily nest survival (0.958; Akresh 2012) similar to other studies on prairie warblers (Nolan 1978, Slay 2010 for review), so many of the first nests of the breeding season were depredated. Since individual first-nests failed at different numbers of days after laying and both early- and late-laying females re-nested multiple times after first-nest failures, the effect of first-egg date on reproductive success was diminished. We
previously showed that reproduction output significantly varied among years in our site (Akresh et al. 2015); therefore, other aspects that affect annual variation in reproductive output may be more important than time constraints in our study, such as food resources or predator abundance (Rodenhouse and Holmes 1992, Clotfelter et al. 2007).

Perhaps ASY males wintering in wetter habitats, and subsequently arriving early in some years, are benefitting in other ways that we did not examine (McKellar et al. 2013). For instance, early-successional breeding habitat used by prairie warblers is often destroyed naturally or by forest management, and returning males disperse from previous territories that were completely mowed or burned to locate new suitable breeding territories (Akresh et al. 2015). As a result, there may often be an advantage to arriving to the breeding grounds early before females arrive, especially if the male chooses to survey and disperse to a new, more suitable or higher-quality territory (Betts et al. 2008). Moreover, males that have arrived before females can be ready to pair with the earliest-arriving females, who may be of higher quality (Nol and Smith 1987, McKellar et al. 2013). We also did not examine effects of winter habitat wetness and arrival on extra-pair paternity, which could be an important pathway affecting birds’ fitness (Ruedink et al. 2009).

**Conclusion**

Overall, we observed varied results among years and among age and sex classes when testing the hypothesis that winter habitat wetness carries over to effect phenomena on the breeding grounds for prairie warblers. Winter rainfall and winter habitat may interact to influence birds’ phenology (e.g., breeding ground arrival dates), especially for
ASY males. We tentatively suggest that winter habitat wetness may not have strong carry-over effects on prairie warbler reproductive performance, at least in our study system. In our study area, rather than focusing on winter or migratory habitat, the creation and maintenance of suitable early-successional breeding habitat could be more productive in sustaining prairie warbler populations (King and Schlossberg 2014). More research on prairie warblers examining carry-over effects at other locations throughout the species range, testing other carry-over pathways (i.e., influences of weather during migration), and assessing habitat’s and climate’s direct effect on birds’ survival is needed to help determine when and where this species is limited in their full annual cycle.

Our study adds to a growing literature base on winter to breeding season carry-over effects, including studies that found compelling and important effects (Marra et al. 1998, Norris et al. 2004, Tonra et al. 2011), varied effects among age- and sex- classes or among years (Rockwell 2013, Drake et al. 2013, Rushing et al. 2016), and completely no effects (Lourenço et al. 2011, Drake et al. 2014a, McKinnon et al. 2015b). Even though these combined studies have focused on only a few species of passerine birds, they suggest that the importance of carry-over effects on birds’ ecology and fitness can vary drastically among avian species, and among and within populations in different geographic locations. The apparent inter- and intraspecific variance is important to consider when including carry-over effects in population limitation models (Sherry and Holmes 1995, Norris 2005, Runge and Marra 2005).
Figure 2.1. After-second Year (ASY) male arrival dates and relationships with $\delta^{13}$C in bird’s claws or red blood cells (RBC) sampled on arrival to the breeding grounds in Montague, MA during 2011-2013. Points represent individual birds, black lines represent the best-fit regression lines, and shading represents the 95% confidence intervals.
Figure 2.2. Second Year (SY) male arrival dates and relationships with $\delta^{13}$C in bird’s claws sampled on arrival to the breeding grounds in Montague, MA during 2011-2013. Points represent individual birds, black lines represent the best-fit regression lines, and shading represents the 95% confidence intervals.
Figure 2.3. Predicted probability of pairing success as a function of male arrival date (ages pooled) in the breeding grounds in Montague, MA during 2009-2013. Main black line and shading represents the regression curve and 95% confidence interval. Additional short black lines on the top and bottom of the figure represent data points for individual birds, spaced out slightly to enhance visibility.
Figure 2.4. Second Year (SY) male first-egg dates and significant relationship with arrival dates to the breeding grounds in Montague, MA during 2009-2013. Points represent individual birds, the black line represents the best-fit regression line, and shading represents the 95% confidence interval.
CHAPTER 3
EXAMINING CARRY-OVER EFFECTS DURING THE FULL ANNUAL CYCLE
FOR JUVENILES AND ADULTS IN A MIGRATORY BIRD

Introduction

Migratory animals are affected by processes occurring at multiple sites throughout their annual cycle and recent studies have shown that processes occurring at a given location or time can even ‘carry-over’ to affect an individual at a subsequent location or time (Myers 1981, Marra et al. 1998, O’Connor et al. 2014). Carry-over effects (COEs) have been shown to exist for a wide variety of animals, including insects, amphibians, fish, birds, and mammals (Harrison et al. 2011, Marshall and Morgan 2011, O’Connor et al. 2014) and are important to better understand animals’ ecology and improve conservation efforts for threatened species (Norris and Marra 2007).

Carry-over effects can occur between any two periods in an individual’s life, but processes affecting an individual during development can be expressed differently than those occurring when the individual is an adult (Senner et al. 2015). Processes occurring early in life that later affect the individual are often called ‘silver spoon’ or developmental effects, and can permanently affect the intrinsic quality of an individual and subsequently the animal’s fitness throughout its lifetime (Van de pol et al. 2006, Tilgar et al. 2010, Saino et al. 2012, Gill et al. 2014). In contrast, processes that affect individuals as adults can carry-over to influence individuals later in their life, but the effects often do not inherently change the quality of the individual and may dissipate in later periods of life (i.e., no ‘domino’ effects; Lourenco et al. 2011, Senner et al. 2014).
Nevertheless, differences between COEs initiated during early versus adult life may be more complicated due to environmental factors (e.g., poorly-developed individuals may still have high fitness in ideal environmental conditions) and individuals’ behavior (e.g., site fidelity; Lindström 1999).

Using novel tools such as stable isotopes, corticosterone levels, and light-level geolocators, recent studies have shown COEs can occur for small, Neartic-Neotropical migratory birds (Norris et al. 2004, Latta et al. 2016, Cooper et al. 2017). Researchers have been able to examine COEs using stable isotopes because a gradient exists in stable carbon isotope signatures among wet and dry wintering habitats of migratory birds; this gradient correlates highly with habitat quality for certain passerines wintering in the Caribbean (Marra et al. 1998, Latta and Faaborg 2001, Smith et al. 2010). For instance, during a drier winter, prairie warblers’ (*Setophaga discolor*) body condition and muscle declined at a higher rate in drier habitats, where birds had enriched carbon isotope values, compared to wetter habitats (Chapter 1). American redstarts (*Setophaga ruticilla*) that winter in drier, poor-quality habitat have delayed spring departure dates, which leads to later arrival dates and lower reproductive success on the breeding grounds (Studds and Marra 2005, Reudink et al. 2009, Rushing et al. 2016). We observed a similar carry-over effect of wintering habitat on breeding arrival dates in prairie warblers, although we found relatively weak cascading effects on reproductive success likely due to the local breeding environment (Chapter 2).

Despite continued increases in our understanding of COEs in a variety of taxa, only very recently have studies on migratory birds begun to examine COEs initiated during the breeding season, effects cascading through the entire annual cycle, and inter-
generational interactions between parents and young during the entire year (Catry et al. 2013, van Gils et al. 2016, Saino et al. 2017). Studies have shown that juvenile birds that hatch earlier in the breeding season have more time before fall migration to develop and increase fat reserves, and early-hatched juveniles may also leave earlier for migration (Morton 1992, Mitchell et al. 2011, 2012, Meller et al. 2013). Continuing through a bird’s lifecycle, birds that leave for migration earlier and in better condition could arrive on the wintering grounds earlier and in better condition, and may be more likely to acquire higher quality habitat in their first wintering season (Smallwood 1988, Stutchbury 1994, Wunderle et al. 1995). A non-mutually exclusive hypothesis is that nestlings that hatch earlier, or are in better condition, develop physiologically as ‘better quality’ individuals (Merilä and Svensson 1997, Lindström 1999, Cam and Aubry 2011), and as a result, are able to outcompete conspecifics for better-quality winter habitat (Verhulst et al. 1997, Marra 2000, Mettke-Hofmann et al. 2015). Brood size could also affect the parental care received by each juvenile (Maigret and Murphy 1997, Saino et al. 1997), which could influence juvenile condition and carry-over to affect winter habitat acquisition. Despite the importance of understanding the mechanisms influencing winter habitat acquisition (Stutchbury 1994), few studies have examined winter habitat acquisition as a result of developmental effects, likely because of the difficulty in tracking juvenile migratory birds. Full annual cycle COEs for juveniles may occur as well, if COEs initiated on the breeding grounds continue a complete pathway from wintering grounds to the breeding grounds the following year.

For adult birds, there is a long history of researchers examining the cost of reproduction during the breeding season and COEs on subsequent breeding seasons
(Williams 1966, Stearns 1976, O’Connor et al. 2014), but relatively few studies have examined reproductive costs that carry-over to the subsequent wintering period after breeding (Inger et al. 2010, Hoye et al. 2012). For adults that successfully reproduce, caring for young can increase adults’ stress, and affect the timing of their molt and preparation for migration (Mulvihill et al. 2009, Stutchbury et al. 2011, Done et al. 2011). Birds that fledge young later in the breeding season may molt later and depart for migration later (Evans Ogden and Stutchbury 1996, Bogdanova et al. 2011, Mitchell et al. 2012, Fayet et al. 2016), and late-departing migrants may subsequently arrive on the wintering grounds later (McKinnon et al. 2016, Cooper et al. 2017, but see Stutchbury et al. 2011). Adults that arrive on the wintering grounds later may acquire poorer wintering habitat (Wunderle et al. 1995). However, early-arriving adult birds may not choose to acquire better quality winter habitat due to preferences to stay and be behaviorally dominant in their previous winter home range (Holmes and Sherry 1992, Marra 2000, Latta and Faaborg 2001). Furthermore, instead of departing for migration earlier, early-breeding males may continue to stay on the breeding grounds in autumn to defend their breeding territories and possibly even obtain mates for the following breeding season (Nolan 1978, Weggler 2000, Mills 2005). Thus, an alternative hypothesis is that better quality males who are likely to fledge young on the breeding grounds are able to outcompete poorer-quality males and obtain high-quality habitat on the wintering grounds, regardless of the cost of raising young during the previous breeding season (Gunnersson et al. 2005, Rushing et al. 2016).

To further our understanding of the full annual cycle of migratory birds, we conducted a study on COEs initiated during the breeding season in different age and sex
classes of prairie warblers, a Nearctic-Neotropical migratory passerine that winters primarily in the Caribbean and breeds in the eastern United States (Nolan 1978). Prairie warblers have experienced dramatic range-wide declines in the past few decades (Schlossberg and King 2007, Sauer et al. 2014) likely because of declines in shrubland breeding habitat (King and Schlossberg 2014), or perhaps due to effects of decreasing winter rainfall as a result of climate change (Martin and Weech 2001, Neelin et al. 2006, Studds and Marra 2011). Given influential processes occurring over prairie warblers’ entire range, understanding the full annual cycle of this species is important for conservation and management (Marra et al. 2015b), and can serve as a case study for other migratory birds. In our study, we used stable isotopes of carbon to represent winter habitat quality (Marra et al. 1998, Chapter 1), and we examined COEs initiated early in life as well as later during adulthood. Specifically, we first tested for juveniles if nestling condition, hatching date, or brood size affected the habitat quality acquired during the following winter. We also examined full cycle relationships between nestlings and arrival dates the following breeding season. For adult male birds, we examined winter habitat acquisition as a function of reproductive success during the previous breeding season, or hatching date if the male successfully reproduced. We also tested the repeatability of winter habitat use over multiple years to examine site fidelity. Lastly, we determined if winter habitat or breeding ground arrival dates influenced the hatch date of a male’s successful nest, which could in turn create an intergenerational pathway of effects. We often examined relationships within wet versus dry winters, because rainfall can interact with habitat quality to affect birds on their wintering grounds (Studds and Marra 2007, 2011, Chapter 1). We hope that our research on the full annual cycle of a migratory bird
allows researchers to begin to understand the limiting factors of populations and provide the best management tools for declining and threatened species (Marra et al. 2015b).

**Methods**

**Study Site**

We conducted the study from 2009-2015 at the Montague Plains Wildlife Management Area (MPWMA), in Western Massachusetts, U.S.A. (N 42° 34’, W 72° 31’) as part of an ongoing study (Akresh et al. 2015). The MPWMA is a pitch pine-scrub oak barren that is actively managed by the Massachusetts Division of Fisheries and Wildlife. Prairie warblers reside and nest in scrub-oak barrens, thinned pitch pine stands and power line corridors in the study site (see King et al. 2011, Akresh et al. 2015 for more details). We studied birds primarily within 9 study plots within the study site ranging in area from 4 to 29 ha; a few birds dispersed outside of the study site and were observed on adjacent power line corridors (Akresh and King 2016, Akresh et al. 2017).

**Bird Surveying and Sampling**

During 2009-2013, we monitored study plots intensively every 2-3 days starting in mid- to late April before the first prairie warbler arrived until June when almost all the males had arrived to establish individual male arrival dates (Akresh et al. 2015). In 2014-15, we surveyed study plots approximately once a week, thus we did not get as precise arrival dates during these years. During each visit we surveyed the entire plot for singing males and sighted previously color-banded and unbanded birds to estimate individual male arrival dates. In 2009-2013, the earliest date during each season that we first
observed an individual was considered the arrival date. We delineated territories by recording 1-10 locations of singing males during each visit using handheld global positioning system (GPS) units, and we also plotted the singing locations relative to landmarks on treatment maps and aerial photographs. The presence of many returning color-banded males, and the above mapping procedure, allowed us to delimit territories for males that we did not catch and color band during their first day of arrival.

During 2008-2015, we captured and banded prairie warbler males using targeted mist-netting with prairie warbler songs and a decoy. We also captured some females throughout the breeding season. Some of the returning color-banded birds were originally color-banded as nestlings, and we attempted to capture every natal return that we observed on our study site. Previously unbanded birds were banded with a United States Geological Survey aluminum band and a unique color combination of 2-3 plastic color bands. Birds were classified upon capture by age class (After-second Year = ASY or Second Year = SY) and sex using plumage, breeding condition, feather wear, and molt limits (Pyle 1997). Between 2011-2015, we attempted to capture birds in late April and May within a week or two of their arrival date, and sampled the tip (2-3 mm) of the central claw on both feet of the bird. For a subset of birds in 2011 and 2012, we also collected blood samples (up to 50 uL). Blood samples were put on ice, spun within 12 hours in a centrifuge for 8 min at 13000 rpm, the plasma and red blood cells (RBC) separated using a Hamilton syringe, and the RBC samples were then frozen.

Since claw tips represent dietary isotopic input a few months before capture and $\delta^{13}C$ isotopes in claws can have a relatively long half-life (i.e., 27 days; Lourenco et al. 2015), the sampled claws of birds captured soon after arrival should reflect the birds’
wintering habitat (Bearhop et al. 2003, Hahn et al. 2014). Between 2011-2015 we recaptured 13 individual males 10-29 days (mean = 16 days) after their initial capture and re-sampled these birds (sampling different claws, the tips of the outer claws and/or the hallux): on average, claws from re-sampled birds had δ^{13}C values only 0.34‰ (SD = 0.26‰) different from the δ^{13}C values of the initial captures. Therefore, claw samples from birds captured even weeks after arrival should represent isotopic input from birds’ winter habitat use. Given recent research on claw δ^{13}C half-life (Lourenco et al. 2015) and our above findings on re-sampled males, we believe that any birds captured and sampled in May and the first week of June were likely captured early enough in the breeding season for claws to represent the birds’ wintering habitat (Dale and Leonard 2011).

We note that using claw tips has some disadvantages and δ^{13}C values from RBCs can provide an alternative measure of winter habitat use. Avian claws grow conically, and the base of the claw may differ in isotope signature compared to the tip of the claw when sampled upon arrival (Mazeroolee and Hobson 2005, Hahn et al. 2014). Claw tips from small birds may have variation among individuals because of variation in claw wear, minute differences in the size of the clipped sample, and the possibility that some claw samples contain a small amount of blood which may impart noise into the sample (MA personal observation). In contrast, blood samples likely do not have as much sampling variability, but stable isotope ratios in RBC samples have a shorter half-life (7-30 days; Hobson and Clark 1993, Klaassen et al. 2010, Lourenco et al. 2015), and are metabolically active. Previous studies have observed that RBCs can represent winter habitat moisture for birds captured very soon after arrival (Norris et al. 2004, Norris et al.
2005, Rockwell 2013) because spring migration for some Nearctic-Neotropical migrants only takes a few weeks (Ewert et al. 2012). In our study, all of the males with RBC samples were captured within 9 days of arrival. Nevertheless, because RBC are metabolically active and have a shorter isotopic half-life, they may also represent some dietary input from migration (Norris et al. 2005, McKinnon et al. 2012).

In 2009-2013, we monitored prairie warbler territoriality and apparent reproductive success by visiting each territory for 30-60 minutes between 5:30 and 14:00 every 2-4 days throughout the breeding season. In 2014-2015, we monitored territories approximately every week. We located nests within territories by observing parent behavior and conducting systematic searches. Nests were marked with flagging placed 15-20 m from the nest and monitored every 2-4 days until the nestlings fledged or the contents of the nest had disappeared.

We determined if adults fledged young by monitoring nests until we observed fledging, searching for fledglings in territories where nests could have fledged based on the stage of the nestlings’ development in the previous nest check, and by searching territories for adults feeding fledglings in territories where we did not locate a successful nest. In these latter territories where we just found adults feeding fledglings, we could not determine the hatch date. Therefore, when analyzing hatch dates in territories of adult males, we only included territories with found nests (~90% of the successful territories). We never observed polygamous males or double-broods, yet given many visits to the territories we are confident we were aware of the majority of reproductive efforts within the extensively surveyed plots. In certain years, due to the large number of territories in the study site, some plots were not surveyed extensively for reproductive success.
In successful nests, when nestlings were approximately 8 days old, we color-banded nestlings, measured their tarsus length (± 0.1 mm) and weighed them with a digital scale (± 0.1 g). We were able to obtain a precise hatch date for each nest by aging young nestlings (0-2 days old) based on their size, amount of down, presence of feather sheaths, and behavior (Nolan, 1978). For nests that were found empty on day 8 (nestlings typically fledge when 9-10 days old, but can fledge on day 8; Nolan, 1978), we determined nest failure by systematically searching for fledglings in the territory during visits every 2-3 days (Akresh et al. 2015).

**Stable Isotope Preparation and Analysis**

Claws were soaked for 2 hours in a 2:1 chloroform:methanol solution and dried in a fume hood for 48 hours. RBC samples were freeze-dried and powdered. All samples were then weighed in tin capsules and combusted in a continuous flow isotope ratio mass spectrometer (Thermo Scientific Delta V Advantage mass spectrometer coupled with a Costech ECS 4010 elemental analyzer via a Conflo IV gas interface) at the Stable Isotope Mass Spectrometry Facility at the Smithsonian Institution, Suitland, MD, USA. One in-house standard was run for every four unknowns. Stable isotope ratios ($^{13}$C/$^{12}$C) are reported in delta ($\delta$) notation, in per-mil units (‰) relative to the Vienna Pee Dee Belemnite ($\delta^{13}$C) standard. Repeated analyses of RBC samples from the same individual capture were replicable to within 0.2‰ (n = 4).
Statistical Analysis

We first tested if COEs initiated during the breeding season affected winter habitat acquisition for both returning banded nestlings and adults. By catching birds upon arrival and sampling claws and blood from returning, previously banded birds, we were able to determine returning birds’ winter habitat moisture (Marra et al. 1998). We assumed that the returning birds maintained a home range throughout the wintering season, such that an individual’s winter home range acquired in the fall was the same home range used throughout the winter season. In the wintering grounds, most prairie warblers are territorial and have been shown to maintain home ranges throughout the wintering season in the Dominican Republic, The Bahamas, and Jamaica (Latta and Faaborg 2001, Akresh Chapter 1, Akresh unpublished data).

In a previous study (Chapter 2), we examined effects of winter habitat moisture on arrival dates to the breeding grounds, body condition upon arrival, nest initiation dates, pairing success, and reproductive success. In our present study, we also assess full annual cycle pathways by examining the effects of breeding ground phenomena during year (t-1) on winter habitat acquisition, and any subsequent carry-over effects on breeding ground phenomena during year (t) that we found in our previous study. Additionally, for natal returns, we examined full cycle effects of breeding ground phenomena at year (t-1) on breeding ground phenomena at year (t). We hypothesize that better quality nestlings (i.e., those that hatched earlier or those in better condition) may arrive earlier to the breeding grounds, regardless of the winter habitat acquired. Lastly, we tested intergenerational effects by examining if a male’s winter habitat influences their nestlings’ hatch dates. We used the R statistical program version 3.3.1 to conduct all
analyses (R Core Team 2016), and the “lme4” and “lmerTest” packages (Bates et al. 2015, Kuznetsova et al. 2016) to conduct mixed models when necessary. We defined significant results as $p < 0.05$. However, given small sample sizes in many of our analyses, we also highlight non-significant trends because $p$-values can be unreliable in testing against the null hypothesis when sample sizes are small (Halsey et al. 2015).

For natal returns, we used linear models to test effects on winter habitat acquisition. We calculated a size-corrected nestling body condition index by taking the residuals from a linear relationship of tarsus length regressed over mass ($r = 0.60$, $t = 4.4$, $p < 0.001$). The tarsi of individual nestlings when banded were highly correlated with the tarsi measurements of the same individuals captured as adults ($r = 0.85$, $t = 9.4$, $p < 0.001$); therefore, tarsus was a good measure of nestling body size (Nolan 1978). We used $\delta^{13}C$ values of claws (from samples of birds captured in the following year) to indicate winter habitat moisture as the response variable, and in separate univariate models, examined the nestlings’ hatch date, body condition, or brood size as the predictor variable. Nestlings’ body condition and hatch date were correlated ($r = -0.44$), with later-hatched nestlings having worse body condition ($n = 35$, $t = -2.8$, $p = 0.008$), and we thus did not put these two predictor variables in the same model to reduce co-linearity. We first examined tests combining sexes, but we also tested effects on males and females separately. Males often use taller and wetter vegetation on the wintering grounds compared to females (Latta and Faaborg 2001, Murphy et al. 2001, Chapter 1 and 2); thus, effects on winter habitat acquisition may differ between sexes. We defined brood size as the number of nestlings in the nest when banded, including cowbird nestlings. A fixed effect of year did not significantly affect $\delta^{13}C$ values (likelihood ratio tests of
models with and without year: all $p > 0.05$); we therefore did not include year in the above models. The sample size of natal returns with RBC samples was too small for analysis ($n = 5$).

Despite the non-significant effect of individual years, we hypothesized that in wetter winters with more rainfall there would be less pressure for birds to acquire wetter habitats (chapter 1, Studds and Marra 2007, 2011). Therefore, birds might be affected by breeding phenomena differently during wet versus dry winters. Unfortunately, we do not know precisely where our breeding population overwinters in the Caribbean; as a result, matching up specific winter rainfall patterns is difficult. However, we can examine North Atlantic Oscillation (NAO) index values, which some studies have found negatively correlates with higher precipitation in the Caribbean (Malmgren et al. 1998, Jury et al. 2007). The average of the monthly means of the NAO index varied among years between January and March (noaa.gov; 2011 = 0.14, 2012 = 0.95, 2013 = -0.57, 2014 = 0.81, 2015 = 1.52), as well as for just March (2011 = 0.61, 2012 = 1.27, 2013 = -1.61, 2014 = 0.80, 2015 = 1.45). Based on the NAO index, we deemed 2013 as a wetter winter, and the other four years as drier winters, and examined models testing effects separately during wet or dry winters.

For adult males, we tested if fledging success affected winter habitat acquisition in 2011-2015, using a linear mixed model with $\delta^{13}C$ values of claws as the response variable and fledging success (defined as fledging at least one prairie warbler) as the predictor variable. For males that fledged young, we also examined the effect of the hatch date of the males’ nest on winter habitat acquisition ($\delta^{13}C$ values of claws). We included in the above models random effects of individual bird and year. We additionally tested
effects specifically during wet or dry winters, based on the NAO index, without the random effect of year. Lastly, we had a large enough sample size to test males’ $\delta^{13}C$ values of RBCs and the relationship with fledging success the previous year, and we included a fixed effect of year (2011 or 2012) in this model. Sample sizes of RBCs were too small to test the effect of hatch date. We did not examine the number of young fledged because this was highly correlated with fledging success as most males fledged either 3 or 4 young (Akresh et al. 2015). We unfortunately did not capture enough returning banded females with reproductive data the previous season to assess winter habitat acquisition for adult females.

Given that we hypothesized birds might acquire different winter habitats due to reproductive success the previous breeding season, we wanted to assess repeatability of winter habitat use in 2011-15, using $\delta^{13}C$ values of claws (Hjernquist et al. 2009). To test this, we examined within-individual variability in $\delta^{13}C$ signatures by computing analyses on repeatability (intraclass correlation coefficient) using the “rptR” package (Nakagawa and Schielzeth 2010) for birds that we observed over multiple years. We first conducted a test for all individuals captured multiple times, regardless of age. We then conducted a separate test for individuals that were captured first as a SY, and then later captured as an ASY in a following year (examining just the first year that we caught the individual as an ASY, if the bird was captured multiple times as an ASY).

To examine full annual cycle effects, we used linear models to test if male nestlings that hatched earlier or were in better condition arrived to the breeding grounds earlier in the following year, using nestlings banded in 2009-2012 and arrival date data from 2010-2013. We tested relationships with arrival date additionally in dry versus wet
winters, classifying 2010 as a wet winter based on the NAO index (2010: Jan.-March = -1.32, March = -0.88).

To examine intergenerational effects, we tested if a male’s winter habitat or breeding arrival date affected the hatch date of the males’ nestlings. Since we tested earlier the effect of hatch date on nestlings’ acquired winter habitat, this analysis would complete a pathway to assess an intergenerational circular effect of winter habitat. Using linear mixed models, we set the hatch date of the males’ nestlings as the response variable, and in separate models, tested the effect of δ13C values of claws or males’ arrival date as the predictor variable, with year and individual as random effects. The model with arrival dates used data from 2009-2013, while the model with δ13C values of claws used data from 2011-2013. We only examined hatch dates of nests that successfully fledged at least one prairie warbler young. The sample size was too small to examine a model with δ13C values of RBC.

**Results**

**Natal Returns**

Between 2011 and 2015, we captured and obtained isotope samples from 24 male and 13 female SY birds that were originally banded as nestlings the previous breeding season. In all years and sexes combined, there was a trend in which birds that hatched earlier in the breeding season had more depleted δ13C values of claws (indicating they acquired wetter winter habitat; t = 1.8, p = 0.08). Within sexes, males that hatched earlier had significantly more depleted δ13C values (t = 2.5, p = 0.02, Figure 3.1a), but there was no significant relationship in females (t = -0.4, p = 0.71). During four winters in which the mean NAO index was relatively high (likely indicating drier winters), birds (males
and females combined) that hatched earlier had significantly more depleted δ^{13}C values 
(n = 25, t = 2.9, p = 0.008, Figure 3.1b), but there was no significant relationship during 
the wetter winter when the mean NAO index was low (n = 12, t = -0.7, p = 0.52).

In all years and sexes combined, there was a non-significant trend for nestlings in 
better condition to have more depleted δ^{13}C values upon capture the following year 
(indicating they acquired wetter winter habitat; n = 35, t = -1.9, p = 0.07). We found a 
similar trend for just males (n = 22, t = -1.7, p = 0.11, Figure 3.1c), but there was no 
relationship for females (n = 13, t = -0.8, p = 0.45). When the mean NAO index was 
relatively high (drier winters), nestlings in better condition had slightly more depleted 
δ^{13}C values (n = 23, t = -1.7, p = 0.11, Figure 3.1d), but there was no relationship when 
the mean NAO index was low (n = 12, t = 0.1, p = 0.89). We found no significant effects 
of brood size on δ^{13}C values for all birds combined, within sexes, or during wet or dry 
winters (all p > 0.05); 81% of the nestlings were from brood sizes of 3 or 4.

Returning Adult Males

In 2011-2015, we captured and obtained claw samples from 72 males and RBC 
samples from 14 males that we had reproductive success data during the previous 
breeding season. In all years combined, adult males that fledged young in the previous 
year had lower δ^{13}C values in claws (indicating birds acquired wetter winter habitat; t = - 
2.1, p = 0.05, Figure 3.2), as well as lower δ^{13}C values in blood (t = -3.3, p = 0.008).

With claw samples, there was a trend for an effect of reproductive success on δ^{13}C values 
during drier winters (n = 55, t = -1.7, p = 0.10), but not during the wetter winter (n = 17, t 
= -1.1, p = 0.29). In all years combined, there was no significant relationship between the 
hatch date of the successful nest in the previous year and the δ^{13}C values of claws (n =
37, t = 1.0, p = 0.35). In the wetter winter when the mean NAO index was low, there was a trend in which males that hatched young earlier in the season obtained wetter winter habitat (had more depleted δ¹³C values; n = 7, t = 2.3, p = 0.07), but the sample size was low with a few individual birds highly influential in the model. In dry winters when the mean NAO index was high, there was no relationship with adult male’s hatch date on winter habitat acquisition (n = 30, t = -0.3, p = 0.80).

The δ¹³C values of claws were highly repeatable among years for the same individual bird (n = 44 birds caught 98 times, R = 0.77, 95% CI = 0.64 to 0.86, p < 0.001), indicating fidelity in winter habitat moisture over multiple years. For birds that were first captured as a SY, and then recaptured in a following year as an ASY, the δ¹³C values of claws were still highly repeatable (n = 14 birds, R = 0.88, 95% CI = 0.64 to 0.96, p < 0.001, Figure 3.3).

**Full Cycle Effects of Nestlings**

We found no relationships between SY males’ arrival date, and the same individuals’ hatch date, condition or brood size as a nestling the previous year (p > 0.05). We also found no significance testing the above relationships during specifically wet or dry winters (all p > 0.05).

**Intergenerational Effects**

Winter habitat (δ¹³C values of claws) did not directly affect the hatch date of males’ successful nests (n = 43, t = 0.5, p = 0.62). We previously found that ASY males in wetter winter habitat (more depleted δ¹³C values) did arrive earlier to the breeding grounds in some years (Chapter 2). However, we only found a non-significant trend for
earlier arriving males having earlier hatch dates of successful nests (n = 113, t = 1.6, p = 0.12).

**Discussion**

Our study provides the first evidence that developmental processes such as hatching date and nestling condition can carry-over to influence winter habitat acquisition in a migratory bird. Winter habitat acquisition is important because Nearctic-Neotropical migratory passerines residing in wetter habitats are more likely to maintain body condition and muscle during the winter dry season (Chapter 1, Latta and Faaborg 2001, Smith et al. 2010), which can then influence birds’ survival and reproduction (Marra and Holmes 2001, Norris et al. 2004, Studds and Marra 2007, 2011, Johnson et al. 2006, Latta et al. 2016).

We found developmental COEs on winter habitat acquisition were significant for males and not for females, and occurred during drier winters and not wetter winters based on the NAO index. Previous studies have found that prairie warbler males use wetter winter habitat compared to females (Latta and Faaborg 2001, Chapter 1 and 2), although we did not observe a difference between sexes in our sample of natal returns (Figure 3.1). Moreover, we had a small sample size of female natal returns, some of which (n = 6) were captured during the wetter winter of 2013. Perhaps developmental effects are more important in predicting winter habitat quality for males, but the small female sample size prevents us from making any definitive conclusions on differences among sexes. Indeed, combining sexes, we observed a significant effect of hatch date during what likely were winters with less rainfall (high NAO index). Studies have shown birds often maintain
body condition in most habitat types (wet or dry) during winters with more rainfall (Brown and Sherry 2006, Studds and Marra 2007, Wunderle et al. 2014, Chapter 1). Therefore, during wetter winters juvenile birds may have less selection pressure to compete for and maintain territories in wetter habitats throughout the season.

Our results are consistent with previous research that birds of varying quality compete for better-quality territories on the wintering grounds (Stutchbury 1994, Marra 2000, Latta et al. 2016), although unfortunately we cannot fully differentiate if migratory timing, pre- or post-migratory body condition, or individuals’ innate quality led to early-hatching juveniles obtaining better-quality winter habitat. Interestingly, nestling body condition had a much weaker relationship with winter habitat acquisition compared with hatching date. Perhaps migratory timing is more important for winter habitat acquisition compared to body condition, but since we did not track or catch birds in the post-fledging period or on arrival to the wintering grounds, we cannot fully examine the relative importance of timing versus condition.

Based on isotope values, we observed that birds used winter habitats of similar moisture levels in multiple years, and juvenile birds even maintained similar winter habitat moisture levels when they were adults. Our results indicate prairie warblers may not ‘upgrade’ into better-quality, wetter winter habitat when they become older, but rather birds appear to stay in the same habitat type throughout their life. Our findings contrast with at least one study that found American redstarts can upgrade into better-quality winter habitat if it experimentally becomes available (Studds and Marra 2005). Prairie warblers exhibit high annual survival in our breeding population (at least 72%; Akresh et al. 2015). Thus, perhaps there is relatively little natural turnover of established
territories on the wintering grounds, and newly-available, unoccupied winter territories are instead acquired by juvenile birds, as is often the case on the breeding grounds (Akresh et al. 2015). Our results are consistent with studies showing high annual site fidelity for certain populations of wintering migratory passerines (Holmes and Sherry 1992, Latta and Faaborg 2001).

Combining developmental COEs and high winter site fidelity, we observed that a nestling’s hatch date can be a true ‘silver spoon’, in that the date a bird hatches can affect the individual’s winter habitat quality for the rest of its life. Although few other studies have examined winter habitat acquisition, other studies have observed that nestlings’ development can affect birds’ natal dispersal and breeding habitat selection, which can then influence their lifetime reproductive success (Verhuist et al. 1997, Van de Pol et al. 2006, Tilgar et al. 2010). Our study also ties into research on other passerines that have observed nestlings that fledge earlier, or those in better condition, have higher survival in their first year of life (Mitchell et al. 2011, McKim-Louder et al. 2013). Higher survival of early-hatched nestlings could be due to a number of factors, such as higher survival during the post-fledging period or during fall migration. Alternatively, as our results show, early-hatched nestlings can acquire better quality winter habitat, which could then influence survival during spring migration (Johnson et al. 2006, Latta et al. 2016).

For returning adult birds, we observed that males that fledged young successfully in the previous breeding season obtained wetter winter habitat. Our study is therefore consistent with the notion that better-quality males (i.e., those that fledge young; Byers et al. 2016) outcompete poorer-quality males and obtain high-quality habitat on the wintering grounds (Gunnarsson et al. 2005). Our findings contrast with studies that have
observed fledging young can be stressful and costly for adult birds and reproduction can carry-over to affect birds’ winter habitat acquisition (Inger et al. 2010, Bogdanova et al. 2011, Hoye et al. 2012, Latta et al. 2016). Our study focused on reproductive COEs on male birds, and possibly reproductive costs are greater and subsequent carry-over effects are more important for females (Mills 2005, Morris et al. 2015, Bleu et al. 2016). One inconsistency with our results is that males that fledged young in the previous year obtained wetter winter habitat, but surprisingly in our study site, birds that had wetter winter habitat did not fledge more young in the subsequent breeding season (Chapter 2). The above findings were the result of using datasets spanning different years with some different individuals, thus, possibly variation among years in breeding success (Akresh et al. 2015) led to inconsistencies between these two results. Interestingly, we observed a more significant relationship of fledging success on winter habitat acquisition for adult males using RBCs compared to claw samples, which is consistent with our previous results that found a stronger relationship between isotope values of RBCs and male arrival date, compared to using isotope values of claws (Chapter 2). Thus, RBCs may be a more accurate measure of moisture and a better indicator of winter habitat quality, as long as birds are captured soon after arrival. Alternatively, since RBCs likely incorporate some dietary input from migration (Norris et al. 2005, McKinnon et al. 2012), stronger relationships with RBCs could indicate that better-quality males obtain habitat with more moisture additionally during spring migration.

In our study population, we found little evidence for full-cycle or intergenerational COEs, in this study or in combination with our previous findings examining winter to breeding COEs (Chapter 2). For juvenile males, nestling hatch date
affected winter habitat acquisition, but winter habitat did not subsequently affect SY males’ arrival dates or reproductive success, although small sample sizes within years may have limited our ability to observe significant results (Chapter 2). Also, the dominant vegetation leafed out relatively late in our pitch pine-scrub oak barren study site, which could have influenced prairie warbler nest survival early in the season and complicated temporal relationships (i.e., between arrival date, lay date, and hatch date) and relationships with birds’ reproductive success (Akresh 2012, Akresh et al. 2015). With both juvenile and adult males combined, we did observe birds arrived to the breeding grounds earlier from wetter winter habitats in some years (Akresh unpublished data), but this relationship was likely driven primarily by adult males. Combining juvenile and adult males, early-arriving birds had higher pairing success compared to late-arriving birds in our study site, but only a small percentage of the population (3%) was unpaired. Overall, the lack of strong full cycle effects in our study was likely due to the local breeding environment and age structure of the breeding population, and strong full cycle effects may exist for other passerine species, in populations with stronger winter to breeding COEs, and in populations with more unpaired SY males (Norris et al. 2004, Rushing et al. 2016).

**Conclusion**

Understanding the full annual cycle of migratory animals and interactions that occur between seasons is important to determine the limiting factors of declining populations and identify and conserve the most valuable habitats. Our study and others show that wetter wintering habitat in the Caribbean is selected for and is important to
conserve for migratory passerines (Chapter 1, Marra et al. 1998, Smith et al. 2010). Additionally, conservation of high-quality ‘source’ breeding habitat is necessary to sustain populations and increase population growth rates (Runge and Marra 2005). Given our findings of developmental COEs, breeding habitat quality should not be based solely on reproductive output and post-fledgling survival, but one should also consider whether or not birds reproduced early the breeding season. Moreover, habitats that experience higher nest depredation rates are likely poorer-quality as juveniles fledge later in the season in these areas (Morris et al. 2015).

Our findings have implications for migratory birds in a changing climate. Studies have found migratory birds are arriving earlier on the breeding grounds, as well as having earlier mean laying dates, due to climate change (Dunn and Winkler 1999, Jonzén et al. 2006, Gill et al. 2014). Earlier breeding phenology could affect hatch dates and thus influence interactions on the wintering grounds between early-arriving juveniles and older individuals. Furthermore, the Caribbean wintering grounds are predicted to have less rainfall due to climate change (Neelin et al. 2006), which based on our and others’ findings, will likely impact the importance and strength of carry-over effects occurring throughout the annual cycle (Rockwell et al. 2012). Overall, more research is needed examining effects of climate change, seasonal interactions, and full annual cycles in migratory animals to provide the best management tools and conservation actions for declining and threatened species (Marra et al. 2015b).
Figure 3.1. Relationships between $\delta^{13}$C values in prairie warblers’ claws (indicating winter habitat moisture) and the effect of the following variables: a) Nestling hatch date on the breeding grounds, separately for males and females, and b) during dry (‘normal’) versus wet winters based on the mean winter NAO index, c) nestling body condition, separately for males and females, and d) during dry (‘normal’) versus wet winters. More negative $\delta^{13}$C values indicate wetter winter habitats. Solid lines represent regression line, while grey shading represents the 95% CI.
Figure 3.2. Relationship between $\delta^{13}C$ values of claws in male prairie warblers as a function of the males’ fledging success during the previous breeding season. More negative $\delta^{13}C$ values indicate wetter winter habitats. Points represent means and error bars are $\pm 1$ standard error.
Figure 3.3. Correlation between the $\delta^{13}$C values in claws (indicating winter habitat moisture) of prairie warblers captured as SY birds and the $\delta^{13}$C values of the same individuals captured in a following year. The solid line represents the regression line, while the grey shading represents the 95% CI.
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