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Article

Examining carry-over effects of winter habitat on breeding phenology and reproductive success in prairie warblers *Setophaga discolor*

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Winter habitat quality can influence breeding phenology and reproductive success of migratory birds. Using stable isotope ratios of carbon ($\delta^{13}\text{C}$) from bird claws and red blood cells collected in Massachusetts, USA, we assessed if winter habitat occupancy carried over to affect prairie warbler *Setophaga discolor* breeding arrival dates, body condition upon arrival, pairing success, first-egg dates and reproductive success. In two of three years (in 2011 and 2012, but not in 2013), after-second-year (ASY) males wintering in drier habitat, as indicated by enriched $\delta^{13}\text{C}$ values, arrived later on the breeding grounds. Based on the North Atlantic Oscillation index, there was likely less rainfall in the Caribbean wintering grounds during the winters of 2011 and 2012 compared to the winter of 2013, suggesting increased winter rainfall in 2013 may have diminished the influence of winter habitat occupancy on arrival date. We did not find any effects of winter habitat on breeding season phenomena for second-year (SY) males or females, but our sample sizes for these age/sex classes were relatively low. Although winter habitat quality influenced arrival dates of ASY males, there was no evidence that it affected reproductive performance, perhaps because of high rates of nest depredation in our system. Our study adds to a growing body of research that shows the influence of carry-over effects can differ among species and within populations, and also can be modulated by other environmental conditions. This information enriches our understanding of the role of carry-over effects in population limitation for migratory birds.

Keywords: carry over effects, seasonal interactions, stable isotopes

Introduction

Migratory bird populations are dependent on habitat quality at multiple sites throughout their annual cycle, and 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, Harrison et al. 2011). In the last few decades, new knowledge of these carry-over effects is becoming instrumental in better understanding the ecology



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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).

Marra et al. (1998) reported that stable isotope ratios of carbon ($\delta^{13}\text{C}$) in bird tissue could be used to link processes occurring on the wintering grounds with birds observed on the breeding grounds. A strong correlation exists between $\delta^{13}\text{C}$ in bird tissue, such as blood and claws, and winter habitat moisture (Marra et al. 1998, Norris et al. 2005, Smith et al. 2010, Akresh 2018). The correlation between moisture and $\delta^{13}\text{C}$ in birds is due to differences in the ratio of ^{13}C – ^{12}C (known as $\delta^{13}\text{C}$) in C_4 and CAM plants, which are found in dry habitats, versus C_3 plants, which are found in wet habitats (Farquhar et al. 1989, Dawson et al. 2002). In addition, $\delta^{13}\text{C}$ values differ within C_3 plants found in dry versus wet areas (Marshall et al. 2007). Carbon molecules, inherently different in the vegetation along the moisture gradient, then move up the food chain from plants to herbivorous insects, and from insects to birds (Marra et al. 1998).

Besides having a strong relationship with $\delta^{13}\text{C}$ in bird tissue, 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). Habitat and food resources can in turn influence the overwinter body condition of individuals (Brown and Sherry 2006, Studds and Marra 2007). For example, prairie warblers *Setophaga discolor* in the Dominican Republic declined in body condition while overwintering in dry scrub habitat, but body condition remained constant for birds occupying wetter habitat (Latta and Faaborg 2001); similar results were also observed in The Bahamas (Akresh 2018). 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, birds in wetter winter habitats arrive earlier and/or in better condition to migratory stop-over sites (Bearhop et al. 2004, González-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, some studies of Nearctic-Neotropical migratory passerines have failed to find significant carry-over effects of winter habitat moisture (González-Prieto and Hobson 2013, Drake et al. 2014a). For instance, no carry-over effects were observed for magnolia warblers *Setophaga magnolia* arriving to a migratory stop-over site in Ohio, USA (Boone et al. 2010). Moreover, within species, winter habitat carry-over effects can vary

among populations or among different age–sex classes. For yellow warblers *Setophaga petechia*, 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, or for any age–sex class in a population breeding in the arctic (Drake et al. 2013, 2014a). In many Nearctic-Neotropical passerine migrants, older males dominate high-quality, wetter winter habitat and force younger males and females into marginal, drier habitat (Marra 2000, Mettke-Hofmann et al. 2015, Akresh 2018); this habitat segregation may subsequently lead to differences in carry-over effects among age–sex classes (Norris et al. 2004). Lastly, winter habitat carry-over effects may vary among years, as shown by a study on Kirtland’s warblers *Setophaga kirtlandii* (Rockwell 2013). Overall, variation in carry-over effects across and within avian species is beginning to become apparent, but more studies examining carry-over effects within populations across multiple years would be useful to better understand seasonal interactions in migratory passerines.

Prairie warblers are Nearctic-Neotropical migratory passerines that winter primarily in the Caribbean and breed in shrubland habitats in the eastern United States (Nolan 1978). Based on the North American Breeding Bird Survey, prairie warblers have been declining by 1.85% per year between 1966 and 2015, and are currently considered a species of conservation concern throughout much of their breeding range (Schlossberg and King 2007, Sauer et al. 2017). Although efforts to create and maintain suitable breeding habitat are underway (Schlossberg and King 2015), these efforts could be ineffective if breeding birds are negatively influenced by marginal habitat elsewhere (Norris 2005). We tested whether winter habitat quality for prairie warblers, assessed indirectly by examining $\delta^{13}\text{C}$ in claws and red blood cells of birds captured upon arrival to the breeding grounds, carried over to drive patterns in breeding phenomena. We assessed multiple avenues in which winter habitat could influence individuals on the breeding grounds. Winter habitat carry-over effects can manifest themselves in the form of relationships between winter habitat moisture and breeding phenology, body condition upon arrival and breeding performance measures (Marra et al. 1998, Rushing et al. 2016), or alternatively, in a pathway on breeding performance through influences on breeding phenology (Norris et al. 2004, Drake et al. 2013).

Winter habitat quality for prairie warblers varies among wet and dry habitats (Latta and Faaborg 2001, Akresh 2018); therefore, we predicted that birds in wetter winter habitats would 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 overwintering in drier habitats. Additionally, we hypothesized there could be variation in carry-over effects among years, given annual variation in winter rainfall interacts with habitat to influence prairie warbler body condition during the wintering season (Akresh 2018). Lastly, we

expected variation in the strength of carry-over effects among different sex and age classes in the population, because older prairie warbler males occupy wetter winter habitats compared to younger males and females (Akresh 2018), and different age–sex classes could be influenced by different processes during the annual cycle (Norris et al. 2004, Drake et al. 2013, Rockwell 2013).

Material and methods

Study site

We conducted the study from 2009 to 2013 on the breeding grounds at the Montague Plains Wildlife Management Area (MPWMA), in western Massachusetts, USA (42°34'N, 72°31'W), as part of an ongoing project 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 MPWMA, 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 on nine plots within the study site; plots ranged in area from 4 to 29 ha (Akresh and King 2016).

Bird sampling

We monitored study plots every 2–3 d to quantify individual male arrival dates during the 2009–2013 breeding seasons. Surveys started in mid- to late April before the first prairie warbler arrived, and continued until June, at which point almost all of 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. Given that 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 d after the individual's actual arrival date, we sampled all plots 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). Using handheld global positioning system (GPS) units, we delineated territories by recording 1–10 locations of singing males during each visit, 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.

We captured both previously banded and unbanded males soon after their estimated arrival date during 2011–2013, using targeted mist-netting with prairie warbler song playback and a decoy. Although we primarily targeted males, we also incidentally captured some females early in the breeding season. We banded previously unbanded birds with a United States Geological Survey aluminum band and a unique combination of 2–3 plastic color bands. Upon capture, we classified birds 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 the 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.

Seventy-eight percent of claw samples used in our analyses, from males with estimated arrival dates, were sampled within three days of the estimated arrival date, 94% sampled within one week and 100% within 12 d. Claw tips represent dietary isotopic input a few weeks to a few months prior to sampling and carbon isotope ratios in claws can have a relatively long half-life (i.e. 27 d; Lourenço et al. 2015). Thus, the sampled claws of these captured males should reflect the birds' wintering habitat (Bearhop et al. 2003, Hahn et al. 2014). We recaptured 10 individual males 10–21 d (mean = 16 d) after their initial capture and re-sampled these birds by sampling different claw tips, such as the outer claws and/or the hallux. The majority (70%) of the samples from the recaptured birds had $\delta^{13}\text{C}$ values within 0.3‰ of the initial values, and almost all (90%) of the re-samples had $\delta^{13}\text{C}$ values within 0.7‰. Therefore, claws from birds captured even weeks after arrival should represent isotopic input from the wintering habitat. We could not determine female arrival dates because females were more difficult to detect on arrival, often moved among several territories early in the season, and were less likely to return to the study site as banded birds (Byers et al. 2015). Nevertheless, given the $\delta^{13}\text{C}$ half-life of claws (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.

Although claws can be effective in assessing winter habitat occupancy (Reudink et al. 2009, Rockwell 2013, Rushing et al. 2016), there are multiple sources of variation in $\delta^{13}\text{C}$ values in claws. Isotope signatures vary with distance from the base to the tip of the claw, and small differences in the length of sampled claw tips among individuals could have added variation to the $\delta^{13}\text{C}$ values (Mazerolle and Hobson 2005, Hahn et al. 2014). Moreover, some of the sampled claws may have contained a small amount of blood, depending on the wear of the claw and the location of the quick (MA personal observ.), and this could have further introduced variability because of different isotopic discrimination factors and $\delta^{13}\text{C}$ half-lives in claws versus blood

(Lourenço et al. 2015). Red blood cells (RBCs) may have less variability in $\delta^{13}\text{C}$ values compared to claws and can provide an alternative measure of winter habitat, if birds are captured soon after arrival (Norris et al. 2004, 2005, Rockwell 2013). However, carbon isotope ratios in RBC samples have a shorter half-life than claws (7–30 d in RBCs; Hobson and Clark 1993, Klaassen et al. 2010, Lourenço et al. 2015) and are metabolically active. As a result, RBCs may also represent some dietary input from migration (Norris et al. 2005, McKinnon et al. 2012). Therefore, there are limitations in using solely claws or RBCs to assess winter habitat quality, and examining both tissues allows for a more robust investigation.

We collected blood samples (up to 50 μl) for a subset of males captured in 2011 and 2012. We put blood samples on ice and then later spun them in a centrifuge for 8 min at 13 000 rpm, on the same day as sampled. Afterwards, we separated the plasma and RBCs using a Hamilton syringe and then put the blood in a freezer. Seventy-one percent of RBC samples were from males captured within 3 d of estimated arrival, 94% within one week and 100% within 9 d. The number of days between blood sampling and estimated arrival (i.e. delay in blood sampling) was not correlated with estimated arrival date (2011: $p=0.86$, 2012: $p=0.47$).

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 min between 5:30 and 14:00 every 2–4 d 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 d (Bibby et al. 1992); otherwise, they were classified as ‘non-territorial’. We located nests within territories by observing parent behavior and conducting systematic searches. We marked nests with flagging placed 10–20 m from the nest and monitored them every 2–4 d until the nestlings fledged or the contents of the nest had disappeared. We found most nests during the building stage, although we found some 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, because 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 did not assess pairing success for females because they do not hold territories and we could not track unpaired females. We determined if adults fledged young by monitoring nests, and in territories where we did not locate a successful nest, by searching territories for adults feeding fledglings. Nestlings usually fledge when

9–10 d old (Nolan 1978), and we checked almost all of the nests when the nestlings were approximately 8 d old. If the nestlings were present in the nest when 8 d old, we deemed that those nestlings fledged successfully, given that the subsequent nest check was often 2–3 d later. We also usually observed the fledglings outside of the nest or saw parents with food during the next nest check. If the nest was found empty when nestlings were 6–8 d old, we systematically searched for fledglings in the territory during visits every 2–3 d to confirm nest failure (Akresh et al. 2015). Some territories we were unable to find a nest, but just found adults feeding fledglings. For these territories, we did not know the exact number of fledglings, and 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, some plots were not surveyed extensively for reproductive success, and thus some analyses were restricted to territories only in plots that were extensively surveyed in a given year (Byers et al. 2016).

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. We soaked claws for 2 h in a 2:1 chloroform:methanol solution and dried them in a fume hood for 48 h. For RBC samples, we freeze-dried and powdered them. We then weighed all samples in tin capsules and combusted them 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 carbon 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 RBC samples from the same individual capture were replicable to within 0.2‰ ($n=4$).

Statistical analysis

Carry-over effects pathways

We explored the effects of winter habitat (assessed with $\delta^{13}\text{C}$ values) on arrival dates, body condition upon arrival, pairing success and apparent reproductive success, and also explored pathways testing if any influences of winter habitat on birds’ arrival dates then subsequently affected birds’ pairing success or reproductive output (Fig. 1a–b). We also explored a 4-step pathway examining if any influence of winter habitat on arrival dates would then affect first-egg dates, which lastly could affect reproductive output (Drake et al. 2013). We analyzed SY and ASY males separately because individuals of different age classes may winter in different habitats and exhibit distinct constraints throughout their annual

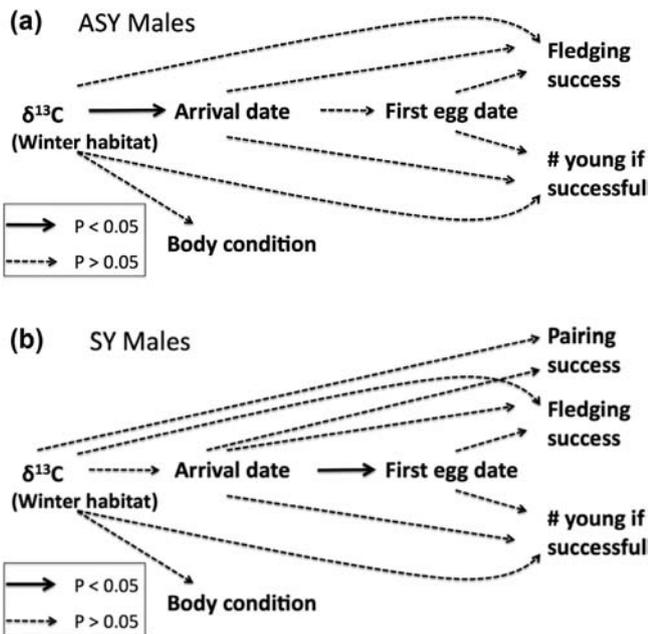


Figure 1. Analysis framework and mixed model results for (a) after-second year (ASY) and (b) second year (SY) male prairie warblers tested separately, showing effects of $\delta^{13}\text{C}$ values (as a proxy for winter habitat) on arrival date, body condition, reproductive success and pairing success (for SYs), as well as effects of breeding season phenology on reproductive success. Each arrow was tested in a separate model, often including a significant covariate of year (see Methods for more details).

cycle, which could lead to differences in the importance of seasonal interactions (Drake et al. 2013, Rockwell 2013). Moreover, age class affects male arrival dates and other breeding phenomena in our study site (Akresh et al. 2015), and sample sizes between male age classes were not equal; thus, analyzing the male population as a whole may obscure within age-class patterns. We analyzed females separately from males for similar reasons; additionally, females have inherently different roles and behaviors than males during the breeding season (Norris et al. 2004, Drake et al. 2013, Rushing et al. 2016). We could not examine female age classes separately due to small sample sizes. Given that 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 ver. 3.2.1 to conduct all analyses (R Core Team), 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 $\delta^{13}\text{C}$ values in claws or RBCs as the predictor variable. Processes that affect birds in both the wintering grounds (e.g. rainfall) and the breeding grounds (e.g. nest predator abundance) often vary among years (Schmidt and Ostfeld 2003, Studds and Marra 2007); therefore, when possible we

examined annual variation in our analyses. Specifically, we first ran some exploratory models, testing for an interaction between the effect of year and $\delta^{13}\text{C}$ in claws on arrival date, to determine if winter habitat (assessed with $\delta^{13}\text{C}$ values) influenced male arrival dates differently among years. For these models with interactions, we examined a linear mixed model with a random effect of individual bird for ASY males, and a separate linear fixed-effects model for SY males. The random effect of individual was only included in models with ASY males and multiple years of data, because some ASY individuals were repeatedly surveyed in multiple years (Rockwell et al. 2012). Models with SY males only included individuals that were surveyed in their second year of life, and the random effect of individual was not applicable.

Year and $\delta^{13}\text{C}$ values in claws did significantly interact to influence arrival dates for ASY males, but based on this exploratory interaction model, we did not know if there were significant relationships between winter habitat and arrival dates within years. For ASY males, we thus analyzed data and presented results separately for each year, using linear fixed-effect models (the random effect of individual was no longer applicable because within years, individuals were only sampled once). For SY males, we did not find a significant interaction with year and $\delta^{13}\text{C}$ in claws, so we examined and presented results for SY males by combining data across all years. We still included a fixed, additive predictor variable of year in the model with SY males to account for annual variation in arrival dates, regardless of the lack of an interactive effect with winter habitat. In our exploratory examination of the data for SY males, we also noted a different trend during 2011 and 2012 compared to 2013. Thus, for SY males, we ran additional analyses separating 2013 from the other two years, but still including year as an additive covariate when examining 2011 and 2012 combined. When sufficient data were available, we also conducted the above tests using the $\delta^{13}\text{C}$ values in RBCs, instead of claws, as the predictor variable. Although isotope values in claws and RBCs from the same captured bird were correlated ($r=0.53$), there was still variation between the two types of samples. In all arrival date analyses, we omitted individuals that arrived after 1 June, as these late arrivals could have been birds immigrating into the study site from the surrounding area (Nolan 1978).

To test if $\delta^{13}\text{C}$ 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 ($n=145$, $r=0.39$, $p<0.001$; Marra et al. 1998, Boone et al. 2010, Wunderle et al. 2014). Using the body condition index as the response variable, we analyzed $\delta^{13}\text{C}$ 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. We included additional predictor variables 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. For ASY males, we additionally ran a similar mixed-effects model to test the effects of $\delta^{13}\text{C}$ values in RBCs on body condition, but the sample size of RBCs was not sufficient to run a model for SY males. In exploratory analyses, we did not find significant interactions between the effect of year and $\delta^{13}\text{C}$ values for either SY or ASY males, and therefore we pooled years in our body condition analyses. We did not examine $\delta^{13}\text{C}$ 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 an effect of $\delta^{13}\text{C}$ values in claws on male pairing success. We examined effects on pairing success only for SY males, because almost all (99%) of the territorial ASY males paired in our study site. We ran a generalized linear model (GLM) fit to a binomial distribution. We also tested for a pathway of effects of $\delta^{13}\text{C}$ on pairing success mediated through the influence of a male's arrival date (Fig. 1). As we already examined the effect of $\delta^{13}\text{C}$ on arrival dates in a previous analysis, we continued the pathway by testing if arrival date predicted pairing success for SY males, using a GLM fit to a binomial distribution. In these analyses, we excluded any plots or territories in which we did not adequately survey for reproductive success in a given year. Additionally, there were few unpaired SY males; thus, the effective sample size of the response variable in the models was low. To prevent over-fit, biased models with too many parameters relative to the number of observations (Babyak 2004), and to assist with model convergence, we completely excluded the year predictor variable and did not test for interactions with year. Therefore, unfortunately we could not account for annual variation of pairing success in these analyses.

We also assessed if first-egg date was a function of male arrival date. 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. In an exploratory analysis, we did not find a significant interaction between the effect of arrival date and year for ASY males, and we therefore did not conduct separate analyses within each year. For SY males, sample sizes were small within years. Because of problems with over-fitting and model convergence, for SY males, we pooled data across years and could not include a predictor variable of year or test for interactions with year. In all of these analyses, 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 (hereafter called 'fledging success'), and second, we examined the number of young fledged for the subset of birds that successfully fledged young (Jones et al. 2014, Byers et al. 2016). The reproduction data included a peak of zeros and was also upper-bounded (no territory produced > 5 young), and therefore did not fit a Poisson distribution (Akresh et al. 2015, Rushing et al. 2016). Moreover,

based on goodness-of-fit analyses, we found that an ordinal logistic regression fit fledgling counts that were > 0 better than a model fit to a zero-truncated Poisson. We therefore conducted a logistic regression to examine fledging success versus failure, and conducted a separate ordinal logistic regression to examine the number of young fledged, if successful, using the 'ordinal' package (Robb et al. 2008, Christensen 2015, Cade et al. 2017). For ASY males, we conducted mixed-effects models with individual as a random effect, and for SY males we conducted fixed-effects models. We separately tested the direct effect of $\delta^{13}\text{C}$ on the two reproductive performance measures, and also tested the 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 most models to account for yearly variation in reproductive performance (Akresh et al. 2015). We had small sample sizes for SY males in analyses with the number of fledglings, and to assist with model convergence we did not include year as a covariate in these analyses. For the reproduction analyses with arrival and first-egg date, we only included males in plots where we extensively examined reproductive success for every male. Given that we analyzed pairing success separately, we excluded the few territories with unpaired males.

We also examined the effects of $\delta^{13}\text{C}$ on reproduction for females, but only tested fledging success and could 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 pathways of $\delta^{13}\text{C}$ on reproductive performance mediated through breeding phenology for 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 $\delta^{13}\text{C}$ in claws, with the exception of also assessing the effects of $\delta^{13}\text{C}$ in RBCs on fledging success for ASY males.

For all analyses with $\delta^{13}\text{C}$ values or body condition upon arrival, we only used data from 2011 to 2013. We did not collect claw/blood samples or capture birds upon arrival in 2009–2010 because we had not yet considered examining carry-over effects in our population (Akresh et al. 2015). However, for analyses without $\delta^{13}\text{C}$ values or body condition (e.g. the effects of arrival on first-egg date or reproductive success), we chose to examine a broader dataset from 2009 to 2013 in order to increase sample sizes and power. Considering that we account for year in most of our analyses and examine possible yearly interactions in the data, adding data from 2009 to 2010 for these analyses should not bias our results.

Examining variation in $\delta^{13}\text{C}$ between age/sex classes and territoriality

We also explored if different age or sex classes had different $\delta^{13}\text{C}$ isotope signatures, perhaps reflecting age- or sex-specific habitat segregation on the wintering grounds. In

an exploratory analysis, we tested if $\delta^{13}\text{C}$ values in claws of females differed from those of territorial males using a linear mixed model, including interactive predictor variables of year and sex, and a random effect of individual. We observed a significant interaction between year and sex on $\delta^{13}\text{C}$ values, and therefore we examined and presented analyses for each year separately in fixed effect models (the random effect of individual was no longer applicable). For territorial males, we conducted a linear mixed model with $\delta^{13}\text{C}$ as the response variable, male age class as the predictor variable, and also included a covariate of year and a random effect of individual bird. There was no significant interaction between male age class and year in an exploratory model; therefore, we did not examine models within individual years. We only examined $\delta^{13}\text{C}$ values in claws, due to small sample sizes of RBCs.

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). To test if non-territorial males wintered in different habitats compared to territorial males, we used a linear mixed model, with a response variable of $\delta^{13}\text{C}$ values in claws, and predictor variables of territoriality (yes or no) and year, including individual as a random effect. We tested for and found no significant interaction of territoriality and year.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.hq1086p>> (Akresh et al. 2019).

Results

Winter habitat carry-over effects

The relationship between $\delta^{13}\text{C}$ values in claws or RBCs and male arrival dates varied among age classes and years (Fig. 1a–b, 2a–b). For ASY males, in 2011 there was a trend for birds using wetter winter habitats (indicated by more depleted $\delta^{13}\text{C}$ values) to arrive earlier, with claw samples ($n=49$, $\beta=1.29$, $SE=0.66$, $t=1.95$, $p=0.06$, $r^2=0.07$; Fig. 2a), and with RBC samples ($n=15$, $\beta=3.79$, $SE=1.74$, $t=2.17$, $p=0.05$, $r^2=0.27$; Fig. 2b). In 2012, the relationship between $\delta^{13}\text{C}$ values and ASY male arrival date was significant with claws ($n=39$, $\beta=1.35$, $SE=0.51$, $t=2.63$, $p=0.01$, $r^2=0.16$) and there was a trend with RBCs ($n=12$, $\beta=4.56$, $SE=2.12$, $t=2.15$, $p=0.06$, $r^2=0.32$). In 2013, there was an opposing trend of $\delta^{13}\text{C}$ in claws on ASY male arrival date, but there was no significant effect ($n=30$, $\beta=-2.27$, $SE=1.38$, $t=-1.64$, $p=0.11$). For SY males, there was no relationship between $\delta^{13}\text{C}$ values in claws and arrival dates in all years combined ($n=36$, $t=0.42$, $p=0.67$), in just 2011 and 2012 combined ($n=19$, $t=1.22$, $p=0.24$), or in just 2013 ($n=17$, $t=-0.58$, $p=0.57$). Examining $\delta^{13}\text{C}$ values in RBCs and combining across 2011 and 2012, there was a trend in which SY males arrived earlier from wetter winter habitats, but

the sample size was small and there was no significant effect ($n=7$, $\beta=11.37$, $SE=5.58$, $t=2.04$, $p=0.11$).

For ASY males, body condition upon arrival was not correlated with $\delta^{13}\text{C}$ values in claws ($n=112$, $t=1.20$, $p=0.25$), or with $\delta^{13}\text{C}$ 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. Body condition also had no relationship with $\delta^{13}\text{C}$ values in claws for SY males ($n=33$, $t=0.57$, $p=0.57$).

For SY males, $\delta^{13}\text{C}$ in claws was not correlated with pairing success ($n=34$, $z=-0.70$, $p=0.48$). For ASY males, there was no significant relationship between $\delta^{13}\text{C}$ in claws or RBCs and fledging success (claws: $n=77$, $z=-0.42$, $p=0.68$, RBCs: $n=18$, $z=1.21$, $p=0.23$) or between $\delta^{13}\text{C}$ in claws and the number of fledglings ($n=31$, $z=-0.55$, $p=0.58$). For SY males, no relationships were found between $\delta^{13}\text{C}$ in claws and fledging success ($n=23$, $z=1.43$, $p=0.15$) or the number of fledglings ($n=8$, $z=1.30$, $p=0.19$). Lastly, $\delta^{13}\text{C}$ in claws was not correlated with fledging success for females ($n=20$, $z=-0.25$, $p=0.81$).

Breeding phenology effects on reproductive performance

During 2009–2013, there was a trend in which SY males that arrived to the breeding grounds earlier had a higher probability of pairing successfully, but this trend was not significant ($n=53$, $\beta=-0.17$, $SE=0.10$, $z=-1.69$, $p=0.09$). Arrival date did not affect first-egg date for ASY males ($n=122$, $t=0.82$, $p=0.42$). In contrast to ASY males, earlier arriving SY males did significantly have earlier first-egg dates ($n=28$, $\beta=0.37$, $SE=0.17$, $t=2.12$, $p=0.04$, $r^2=0.15$).

For ASY males, there was no significant effect of arrival date on fledging success ($n=137$, $z=-1.21$, $p=0.23$), or the number of fledglings, if successful ($n=64$, $z=0.64$, $p=0.52$). There was also no significant relationship between arrival date and fledging success for SY males ($n=34$, $z=1.44$, $p=0.15$). Within the subset of successful territories, SY males that arrived later produced a higher number of fledglings ($n=16$, $\beta=0.32$, $SE=0.15$, $z=2.18$, $p=0.03$), but this relationship was influenced by two SY males that arrived relatively early and produced only one fledgling due to brood parasitism. There was still a trend after removing these two influential points, but the effect was no longer significant ($n=14$, $\beta=0.30$, $SE=0.18$, $z=1.68$, $p=0.09$).

For ASY males, there was no significant effect of first-egg date on fledging success ($n=91$, $z=-1.46$, $p=0.14$), or the number of fledglings ($n=46$, $z=1.33$, $p=0.18$). For SY males, the relationship between fledging success and first-egg date was also not significant ($n=21$, $z=-1.48$, $p=0.14$). For successful territories, there was a trend in which SY males with later first-egg dates produced more fledglings ($n=11$, $z=1.86$, $p=0.06$), but this relationship was highly influenced by one SY male that fledged one young and there was no trend after removing this data point ($n=10$, $z=0.91$, $p=0.37$).

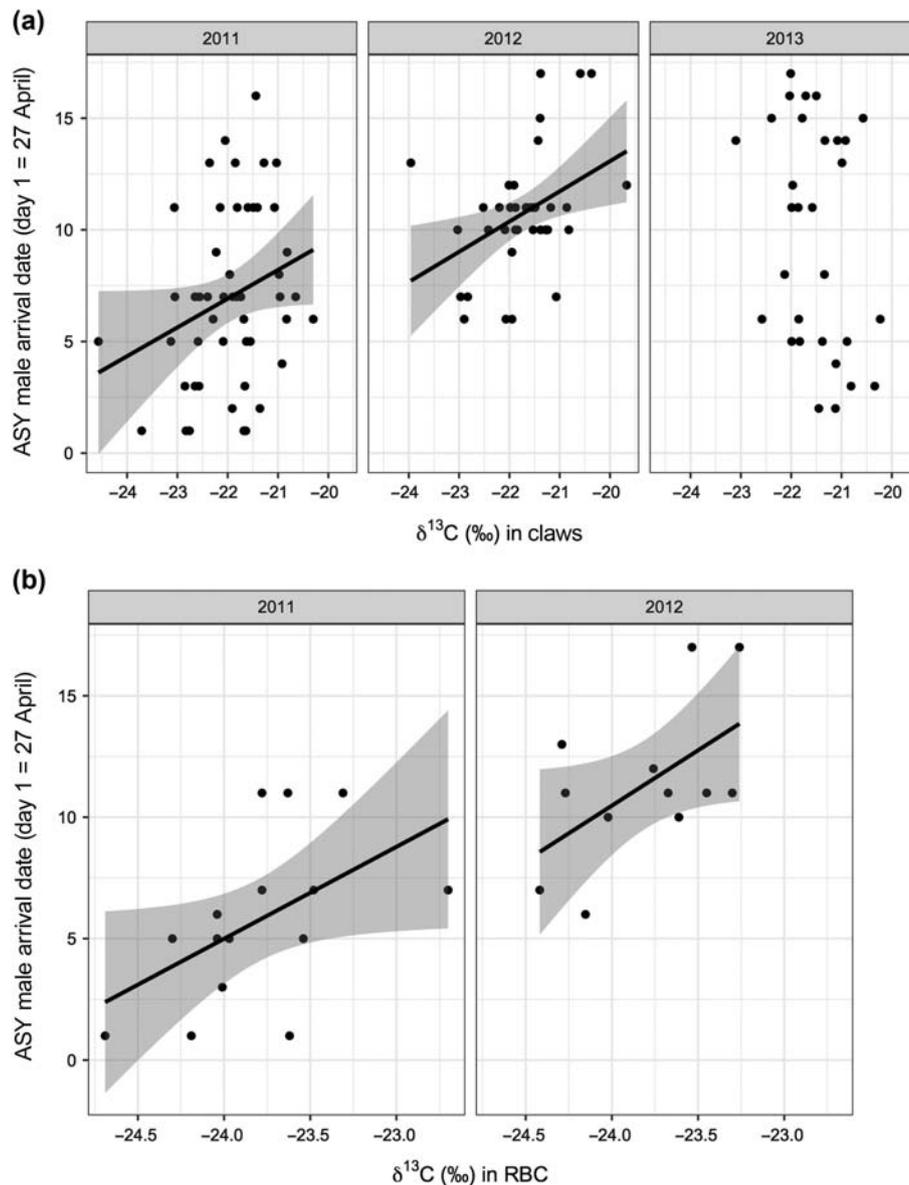


Figure 2. After-second year (ASY) male arrival dates and relationships with $\delta^{13}\text{C}$ in claws (a) or red blood cells (RBC; b) sampled on arrival to the breeding grounds in Montague, MA during 2011–2013. Points represent individual birds, black lines represent the best-fit regression lines and shading represents the 95% confidence intervals. More depleted $\delta^{13}\text{C}$ values (more negative) indicate wetter winter habitat occupancy.

Variation in $\delta^{13}\text{C}$ between sexes, male territoriality and age classes

Territorial males captured on the breeding grounds had more depleted $\delta^{13}\text{C}$ values in claws (indicating wetter winter habitat occupancy) compared to females in 2011 (males: mean = $-21.95\text{‰} \pm 0.10$ SE, females: mean = $-21.42\text{‰} \pm 0.21$ SE, $n=74$, $t=-2.10$, $p=0.04$) and in 2012 (males: mean = $-21.72\text{‰} \pm 0.10$ SE, females: mean = $-21.11\text{‰} \pm 0.33$ 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 $\delta^{13}\text{C}$ 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 ($n=171$, $t=0.37$, $p=0.71$).

Discussion

Our finding that ASY male prairie warblers occupying wetter winter habitat arrived earlier to the breeding grounds in 2011 and 2012 is consistent with observations of habitat moisture in the Caribbean influencing breeding ground arrival dates for American redstarts (Marra et al. 1998, Norris et al. 2004, Tonra et al. 2011), as well as winter habitat impacting arrival dates to migratory stop-over sites for

other passerines (Bearhop et al. 2004, González-Prieto and Hobson 2013, Paxton and Moore 2015). Our results support the hypothesis that winter habitat quality can influence arrival phenology on the breeding grounds.

Given that ASY males did not arrive earlier from wetter winter habitats in 2013, winter habitat carry-over effects are likely influenced and interact with other processes, including annual variation in rainfall on the wintering grounds. The North Atlantic Oscillation (NAO) index is negatively correlated with precipitation in the Caribbean (Malmgren et al. 1998, Jury et al. 2007), and the average monthly NAO index between January and March was lower in 2013 (mean = -0.57; <www.noaa.gov>) compared to 2011 (mean = 0.14) and 2012 (mean = 0.95). Examining the NAO index just in late winter (March), when rainfall is especially important for migratory passerines (Studds and Marra 2007, Akresh 2018), the mean NAO index was also lower in 2013 (-1.61) compared to the other two years (2011 = 0.61, 2012 = 1.27). The 2013 breeding season therefore followed a winter that likely had relatively higher precipitation. The absence of carry-over effects in 2013 is consistent with previous studies that have found elevated moisture levels in winters with more rainfall can lessen among-habitat differences in food resources, which can subsequently reduce differences in bird body condition and spring migration departure dates among wintering habitats (Brown and Sherry 2006, Studds and Marra 2007, Akresh 2018). Thus, winter rainfall and habitat quality are likely interacting to influence ASY male prairie warbler arrival dates in our study system.

Based on $\delta^{13}\text{C}$ values in claws of birds sampled on the breeding grounds, we inferred that males (ASYS and SYs combined) occupied wetter winter habitat compared to females in two of the three years, but we found no difference in habitat occupancy for ASY versus SY males. Similar to our study's Massachusetts breeding population, sex-specific habitat segregation has been observed for prairie warblers in The Bahamas (Akresh 2018) and in the Dominican Republic (Latta and Faaborg 2001). However, in contrast to our breeding population, ASY males occupied wetter habitats than SY males in The Bahamas (Akresh 2018); this was not tested in the Dominican Republic (Latta and Faaborg 2001). Preliminary analyses show that our Massachusetts breeding population is likely wintering in Haiti and the Dominican Republic (Akresh unpublished geolocator data), and therefore these contrasting results regarding male age class habitat segregation could be due to different processes occurring in disparate regions of the prairie warbler's wintering range.

We found no significant winter habitat carry-over effects on reproductive performance for any age or sex class, which contrasts with the notion that sex-based habitat segregation could lead to different carry-over effects for males compared to females (López-Calderón et al. 2017). Other studies of age- or sex-specific winter habitat carry-over effects in migratory passerines have yielded inconsistent results: reporting carry-over effects only for SY females, but not because of age- or sex-related habitat dominance (Drake et al. 2013),

stronger carry-over effects for females (Norris et al. 2004), or stronger effects for males (Rushing et al. 2016). Some of the conflicting results among studies could be related to study limitations, such as sampling claws from females late in the breeding season (Rushing et al. 2016). 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 between winter habitat and reproductive success. We additionally were unable to examine carry-over effect pathways for females (e.g. effects mediated through arrival or first-egg dates).

Small sample sizes and other study limitations may have also influenced our results when examining effects of winter habitat on arrival dates for SY males. During 2011 and 2012, the relationship between SY male arrival date and $\delta^{13}\text{C}$ values in claws did have a similar amount of variance explained ($r^2=0.11$) compared to the relationships found for ASY males in 2011 ($r^2=0.07$) and in 2012 ($r^2=0.16$), but unfortunately we cannot determine if additional samples of SY males would have had the same observed pattern and led to a significant relationship. Furthermore, our estimates of SY arrival dates likely had lower precision compared to ASY birds because 77% of territorial SY males were unbanded before capture (compared to 37% for ASY males), and this lower precision may have affected our results.

We did not find a 'direct' effect of winter habitat on pairing success, or a significant pathway of effects of winter habitat on pairing success mediated through arrival date. We observed a trend in which early-arriving SY males were more likely to pair with females; however, this relationship was driven by only five unpaired SY males. In contrast, for American redstarts, winter habitat moisture influences arrival date (Marra et al. 1998, Reudink et al. 2009), and within both age classes, earlier-arriving males are more likely to pair with females (Lozano et al. 1996). Perhaps if our study area had more marginal habitat, our population would have contained more unpaired SY males in which to detect carry-over effects on pairing success, as found in other studies (Rushing et al. 2016).

Arrival date did not affect first-egg date for ASY males, which contrasts with positive relationships found in other studies (Nolan 1978, Tonra et al. 2011, Rockwell et al. 2012, Drake et al. 2013). However, most other studies did not test relationships within age classes. Indeed, we observed a significant relationship with arrival and first-egg date when pooling male age classes (MA unpubl. data). Given that ASY males arrive weeks before females begin laying eggs, ASY males may be arriving earlier to obtain and hold higher quality breeding territories, but not necessarily to initiate earlier clutches (Morbey and Ydenberg 2001). In contrast to ASYS, earlier-arriving SY males had 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 male arrival or first-egg laid was not strongly related to prairie warbler reproductive success; thus,

birds do not appear to be limited by a later breeding start time in our study site. Our results contrast with a number of studies that have observed late arriving and late breeding males have reduced 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). Our findings could be related to specific features of our breeding 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. We observed low daily nest survival (0.958; Akresh 2012) similar to other studies on prairie warblers (Slay 2010 for review), so many of the first nests of the breeding season were depredated. Furthermore, our site in Massachusetts is at the northern edge of the prairie warbler range; early breeding could be more important farther south, where a longer breeding season permits enough time for double brooding by early-arriving individuals (Nolan 1978, Drake et al. 2014a). Finally, brood parasitism of nests by brown-headed cowbirds *Molothrus ater* influenced the reproductive success in some of the territories (Akresh 2012), and could have further added more variation in productivity in our study. We previously showed that reproductive output significantly varied among years in our site (Akresh et al. 2015); therefore, other processes on the breeding grounds that influence annual variation in reproductive output, such as food resources or predator abundance, may be more important than time constraints in our system (Rodenhouse and Holmes 1992, Clotfelter et al. 2007).

ASY males wintering in wetter habitats and arriving earlier in some years could be benefitting in other ways that we did not examine (Morbey and Ydenberg 2001, McKellar et al. 2013). For instance, early-successional breeding habitat used by prairie warblers is often destroyed naturally by wildfire or by habitat management such as mowing or prescribed burning. Returning males have been observed to 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 be an advantage to early arrival to the breeding grounds for ASY males even prior to female arrival, 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 arrive early can be ready to pair with the earliest-arriving females, who may be of higher quality (Nol and Smith 1987, McKellar et al. 2013). Lastly, earlier arrival could have improved opportunities for increased fitness through extra-pair paternity (Reudink et al. 2009). Thus, winter habitat quality may have influenced reproductive success in ways that we did not measure in our study (e.g. mediated through arrival dates and extra-pair young).

Conclusion

Our study adds to a growing body of literature on winter to breeding season carry-over effects. A number of studies report compelling and important effects (Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004, Tonra et al. 2011, Harrison et al. 2011). Nevertheless, other studies have reported varied effects among age- and sex-classes or among years (Drake et al. 2013, Rockwell 2013, López-Calderón et al. 2017, this study), or even no evidence of carry-over effects (Lourenço et al. 2011, Drake et al. 2014a, McKinnon et al. 2015). Combined, the literature suggests that the importance of carry-over effects on the ecology and fitness of birds varies across and within species. Characterizing this apparent inter- and intraspecific variance is important when including carry-over effects in population limitation models (Norris 2005, Runge and Marra 2005).

Studies such as ours are critical to determine potential sources of variation in carry-over effects, and inform future studies attempting to document and explain variation among years, age-classes, sexes and geographic localities. Many different variables on the wintering grounds, migratory sites and breeding grounds can influence breeding season phenomena and thus affect the strength of carry-over effects (Brown and Brown 2000, Rockwell 2013, Drake et al. 2014b, Finch et al. 2014). Processes occurring throughout the annual cycle can also differ in how they impact specific individuals within and among populations.

Our finding of no strong carry-over effects of winter habitat on prairie warbler reproductive performance could suggest that the winter period is not limiting for prairie warblers. Thus, breeding habitat management to increase local abundance and reproductive success of prairie warblers may support their populations irrespective of non-breeding influences, at least in our study area. However, managers should be aware that in other systems, seasonal fecundity is often correlated with arrival dates and non-breeding processes (Norris et al. 2004, Tonra et al. 2011, Rockwell et al. 2012). Moreover, regardless of reproductive success on the breeding grounds, winter habitat quality may still influence survival during spring migration (Studds and Marra 2005, Latta et al. 2016). Ultimately, full annual cycle models for migratory birds should be developed to better understand when and where population limitation occurs; this information can then be used to determine the best management and conservation approaches for declining species (Marra et al. 2015).

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References

- Akresh, M. E. 2012. Prairie warbler nest-site selection, nest survival and demographic response to management in a pitch pine-scrub oak barren. – MSc thesis, Univ. of Massachusetts, Amherst, USA.
- Akresh, M. E. 2018. Using stable isotopes to examine carry-over effects during the full annual cycle of a migratory bird, the prairie warbler. – PhD thesis, Univ. of Massachusetts, Amherst, USA.
- Akresh, M. E. and King, D. I. 2016. Eastern whip-poor-will breeding ecology in relation to habitat management in a pitch pine-scrub oak barren. – *Wildl. Soc. Bull.* 40: 97–105.
- Akresh, M. E., King, D. I. and Brooks, R. T. 2015. Demographic response of a shrubland bird to habitat creation, succession and disturbance in a dynamic landscape. – *For. Ecol. Manage.* 336: 72–80.
- Akresh, M. E., King, D. I. and Marra, P. P. 2019. Data from: examining carry-over effects of winter habitat on breeding phenology and reproductive success in prairie warblers *Setophaga discolor*. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.hq1086p>>.
- Babyak, M. A. 2004. What you see may not be what you get: a brief, nontechnical introduction to overfitting in regression-type models. – *Psychosom. Med.* 66: 411–421.
- Bearhop, S., Furness, R. W., Hilton, G. M., Votier, S. C. and Waldron, S. 2003. A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material. – *Funct. Ecol.* 17: 270–275.
- Bearhop, S., Hilton, G. M., Votier, S. C. and Waldron, S. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. – *Proc. R. Soc. B* 271: S215–S218.
- Betts, M. G., Rodenhouse, N. L., Sillett, T. S., Doran, P. J. and Holmes, R. T. 2008. Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird. – *Ecography* 31: 592–600.
- Bibby, C. J., Burgess, N. D. and Hill, D. A. 1992. Bird census techniques. – Academic Press.
- Boone, A. T., Rodewald, P. G. and DeGroot, L. W. 2010. Neotropical winter habitat of the magnolia warbler: effects on molt, energetic condition, migration timing and hematozoan infection during spring migration. – *Condor* 112: 115–122.
- Brown, C. R. and Brown, M. B. 2000. Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). – *Behav. Ecol. Sociobiol.* 47: 339–345.
- Brown, D. R. and Sherry, T. W. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. – *Oecologia* 149: 22–32.
- Byers, B. E., Akresh, M. E. and King, D. I. 2015. A proxy of social mate choice in prairie warblers is correlated with consistent, rapid, low-pitched singing. – *Behav. Ecol. Sociobiol.* 69: 1275–1286.
- Byers, B. E., Akresh, M. E. and King, D. I. 2016. Song and male quality in prairie warblers. – *Ethology* 122: 660–670.
- Cade, B. S., Noon, B. R., Scherer, R. D. and Keane, J. J. 2017. Logistic quantile regression provides improved estimates for bounded avian counts: a case study of California spotted owl fledgling production. – *Auk* 134: 783–801.
- Christensen, R. H. B. 2015. ordinal – regression models for ordinal data. – R package ver. 2015.6-28, <<https://can.r-project.org/web/packages/ordinal/index.html>>.
- Clotfelter, E. D., Pedersen, A. B., Cranford, J. A., Ram, N., Snajdr, E. A., Nolan, V., Jr. and Ketterson, E. D. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. – *Oecologia* 154: 493–503.
- Dale, C. A. and Leonard, M. L. 2011. Reproductive consequences of migration decisions by Ipswich sparrows (*Passerculus sandwichensis princeps*). – *Can. J. Zool.* 89: 100–108.
- Dawson, T. E., Mambelli, S., Plamboeck, A. H., Templer, P. H. and Tu, K. P. 2002. Stable isotopes in plant ecology. – *Annu. Rev. Ecol. Syst.* 33: 507–559.
- Drake, A., Rock, C., Quinlan, S. P. and Green, D. J. 2013. Carry-over effects of winter habitat vary with age and sex in yellow warblers (*Setophaga petechia*). – *J. Avian Biol.* 44: 321–330.
- Drake, A., Martin, M. and Green, D. J. 2014a. Winter habitat use does not influence spring arrival dates or the reproductive success of yellow warblers breeding in the arctic. – *Polar Biol.* 37: 181–191.
- Drake, A., Rock, C. A., Quinlan, S. P., Martin, M. and Greer, D. J. 2014b. Wind speed during migration influences the survival, timing of breeding and productivity of a Neotropical migrant, *Setophaga petechia*. – *PLoS One* 9: e97152.
- Farquhar, G. D., Ehleringer, J. R. and Hubick, K. T. 1989. Carbon isotope discrimination and photosynthesis. – *Annu. Rev. Plant Biol.* 40: 503–537.
- Finch, T., Pearce-Higgins, J. W., Leech, D. I. and Evans, K. L. 2014. Carry-over effects from passage regions are more important than breeding climate in determining the breeding phenology and performance of three avian migrants of conservation concern. – *Biodivers. Conserv.* 23: 2427–2444.
- González-Prieto, A. M. and Hobson, K. A. 2013. Environmental conditions on wintering grounds and during migration influence spring nutritional condition and arrival phenology of Neotropical migrants at a northern stopover site. – *J. Ornithol.* 154: 1067–1078.
- Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R. and Bearhop, S. 2011. Carry-over effects as drivers of fitness differences in animals. – *J. Anim. Ecol.* 80: 4–18.
- Hahn, S., Dimitrov, D., Rehse, S., Yohannes, E. and Jenni, L. 2014. Avian claw morphometry and growth determine the temporal pattern of archived stable isotopes. – *J. Avian Biol.* 45: 202–207.
- Hobson, K. A. and Clark, R. G. 1993. Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. – *Auk* 110: 638–641.
- Jones, T. B., Drake, A. and Green, D. J. 2014. Individual quality explains association between plumage colouration, arrival dates and mate acquisition in yellow warblers (*Setophaga petechia*). – *BMC Ecol.* 14: 1.
- Jury, M., Malmgren, B. A. and Winter, A. 2007. Subregional precipitation climate of the Caribbean and relationships with ENSO and NAO. – *J. Geophys. Res.* 112: D16107.
- King, D. I., Schlossberg, S., Brooks, R. T. and Akresh, M. E. 2011. Effects of fuel reduction on birds in pitch pine-scrub oak barrens of the United States. – *For. Ecol. Manage.* 261: 10–18.

- Klaassen, M., Piersma, T., Korthals, H., Dekinga, A. and Dietz, M. W. 2010. Single-point isotope measurements in blood cells and plasma to estimate the time since diet switches. – *Funct. Ecol.* 24: 796–804.
- Latta, S. C. and Faaborg, J. 2001. Winter site fidelity of prairie warblers in the Dominican Republic. – *Condor* 103: 455–468.
- Latta, S. C. and Faaborg, J. 2002. Demographic and population responses of Cape May warblers wintering in multiple habitats. – *Ecology* 83: 2502–2515.
- Latta, S. C., Cabezas, S., Mejia, D. A., Paulino, M. M., Almonte, H., Miller-Butterworth, C. M. and Bortolotti, G. R. 2016. Carry-over effects provide linkages across the annual cycle of a Neotropical migratory bird, the Louisiana waterthrush *Parkesia motacilla*. – *Ibis* 158: 395–406.
- López-Calderón, C., Hobson, K. A., Marzal, A., Balbontín, J., Reviriego, M., Magallanes, S., García-Longoria, L., de Lope, F. and Møller, A. P. 2017. Wintering areas predict age-related breeding phenology in a migratory passerine bird. – *J. Avian Biol.* 48: 631–639.
- Lourenço, P. M., Kentie, R., Schroeder, J., Groen, N. M., Hooijmeijer, J. C. E. W. and Piersma, T. 2011. Repeatable timing of northward departure, arrival and breeding in blacktailed godwits *Limosa l. limosa*, but no domino effects. – *J. Ornithol.* 152: 1023–1032.
- Lourenço, P. M., Granadeiro, J. P., Guilherme, J. L. and Cury, T. 2015. Turnover rates of stable isotopes in avian blood and toenails: implications for dietary and migration studies. – *J. Exp. Mar. Biol. Ecol.* 472: 89–96.
- Lozano, G. A., Perreault, S. and Lemon, R. E. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. – *J. Avian Biol.* 27: 164–170.
- Malmgren, B. A., Winter, A. and Chen, D. 1998. El Niño-southern oscillation and North Atlantic oscillation control of climate in Puerto Rico. – *J. Clim.* 11: 2713–2717.
- Marra, P. P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the non-breeding season. – *Behav. Ecol.* 11: 299–308.
- Marra, P. P., Hobson, K. A. and Holmes, R. T. 1998. Linking winter and summer events in migratory bird by using stable-carbon isotopes. – *Science* 282: 1884–1886.
- Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E. and Tonra, C. M. 2015. A call for full annual cycle research in animal ecology. – *Biol. Lett.* 11: 20150552.
- Marshall, J. D., Brookes, J. R. and Lajtha, K. 2007. Sources of variation in the stable isotopic composition of plants. – In: Michener, R. and Lajtha, K. (eds), *Stable isotopes in ecology and environmental sciences*. Blackwell Publishing, pp. 22–50.
- Mazerolle, D. F. and Hobson, K. A. 2005. Estimating origins of short-distance migrant songbirds in North America: contrasting inferences from hydrogen isotope measurements of feathers, claws and blood. – *Condor* 107: 280–288.
- McKellar, A. E., Marra, P. P. and Ratcliffe, L. M. 2013. Starting over: experimental effects of breeding delay on reproductive success in early-arriving male American redstarts. – *J. Avian Biol.* 44: 495–503.
- McKinnon, E. A., Fraser, K. C., Diamond, A. W., Rimmer, C. C. and Townsend, J. M. 2012. Stable-hydrogen isotope turnover in red blood cells of two migratory thrushes: application to studies of connectivity and carry-over effects. – *J. Field Ornithol.* 83: 306–314.
- McKinnon, E. A., Stanley, C. Q. and Stutchbury, B. J. 2015. Carry-over effects of nonbreeding habitat on start-to-finish spring migration performance of a songbird. – *PLoS One* 10: e0141580.
- Mettke-Hofmann, C., Hamel, P. B., Hofmann, G., Zenzal, T. J., Jr., Pellegrini, A., Malpass, J., Garfinkel, M., Schiff, N. and Greenberg, R. 2015. Competition and habitat quality influence age and sex distribution in wintering rusty blackbirds. – *PLoS One* 10: e0123775.
- Morbey, Y. E. and Ydenberg, R. C. 2001. Protandrous arrival timing to breeding areas: a review. – *Ecol. Lett.* 4: 663–673.
- Motzkin, G., Ciccarello, S. C. and Foster, D. R. 2002. Frost pockets on a level sand plain: does variation in microclimate help maintain persistent vegetation patterns? – *J. Torrey Bot. Soc.* 129: 154–163.
- Nol, E. and Smith, J. N. M. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. – *J. Anim. Ecol.* 56: 301–313.
- Nolan, Jr., V. 1978. The ecology and behavior of the prairie warbler *Dendroica discolor*. – *Ornithol. Monogr.* 26. American Ornithologists' Union.
- Norris, D. R. 2005. Carry-over effects and habitat quality in migratory populations. – *Oikos* 109: 178–186.
- Norris, D. R. and Marra, P. P. 2007. Seasonal interactions, habitat quality and population dynamics in migratory birds. – *Condor* 109: 535–547.
- Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W. and Ratcliff, L. M. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds of a migratory bird. – *Proc. R. Soc. B* 271: 59–64.
- Norris, D. R., Marra, P. P., Kyser, T. K. and Ratcliff, L. M. 2005. Tracking habitat use of a long-distance migratory bird, the American redstart *Setophaga ruticilla*, using stable-carbon isotopes in cellular blood. – *J. Avian Biol.* 36: 164–170.
- Paxton, K. L. and Moore, F. R. 2015. Carry-over effects of winter habitat quality on en route timing and condition of a migratory passerine during spring migration. – *J. Avian Biol.* 46: 495–506.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and R Core Team 2015. nlme: linear and nonlinear mixed effects models. – R package ver. 3.1-120, <<http://CRAN.R-project.org/package=nlme>>.
- Pyle, P. 1997. Identification guide to North American birds. Part I Columbidae to Ploceidae. – Slate Creek Press.
- Reudink, M. W., Marra, P. P., Kyser, T. K., Boag, P. T., Langin, K. M. and Ratcliffe, L. M. 2009. Non-breeding season events influence sexual selection in a long-distance migratory bird. – *Proc. R. Soc. B* 276: 1619–1626.
- Robb, G. N., McDonald, R. A., Chamberlain, D. E., Reynolds, S. J., Harrison, T. J. and Bearhop, S. 2008. Winter feeding of birds increases productivity in the subsequent breeding season. – *Biol. Lett.* 4: 220–223.
- Rockwell, S. M. 2013. Carry-over effects from the non-breeding season influence spring arrival dates, reproductive success and survival in an endangered migratory bird, the Kirtland's warbler (*Setophaga kirtlandii*). – PhD thesis, Univ. of Maryland, USA.
- Rockwell, S. M., Bocetti, C. I. and Marra, P. P. 2012. Winter climate on non-breeding grounds explains spring arrival date and reproductive success in an endangered migratory bird, the Kirtland's warbler (*Setophaga kirtlandii*). – *Auk* 129: 744–752.
- Rodenhouse, N. L. and Holmes, R. T. 1992. Results of experimental and natural food reductions for breeding black-throated blue warblers. – *Ecology* 73: 357–372.
- Runge, M. C. and Marra, P. P. 2005. Modeling seasonal interactions in the population dynamics of migratory birds. – In: Greenberg,

- R. and Marra, P. P. (eds), Birds of two worlds: the ecology and evolution of migration. John Hopkins Univ. Press, pp. 375–389.
- Rushing, C. S., Marra, P. P. and Dudash, M. R. 2016. Winter habitat quality but not long-distance breeding dispersal influences apparent reproductive success in a migratory bird. – *Ecology* 97: 1218–1227.
- Sauer, J. R., Niven, D. K., Hines, J. E., Ziolkowski, D. J., Jr., Pardieck, K. L., Fallon, J. E. and Link, W. A. 2017. The North American breeding bird survey, results and analysis 1966–2015. Ver. 2.07.2017. – USGS Patuxent Wildlife Research Center, Laurel, MD.
- Schlossberg, S. and King, D. I. 2007. Ecology and management of scrub-shrub birds in New England: a comprehensive review. Report. – USDA Natural Resources Conservation Service Resource Inventory and Assessment Division.
- Schlossberg, S. and King, D. I. 2015. Measuring the effectiveness of conservation programs for shrubland birds. – *Global Ecol. Conserv.* 4: 658–665.
- Schmidt, K. A. and Ostfeld, R. S. 2003. Songbird populations in fluctuating environments: predator responses to pulsed resources. – *Ecology* 84: 406–415.
- Senner, N. R., Hochachka, W. M., Fox, J. W. and Afanasyev, V. 2014. An exception to the rule: carry-over effects do not accumulate in a long-distance migratory bird. – *PLoS One* 9: e86588.
- Slay, C. 2010. An evaluation of reproductive success, adult survivorship and habitat use of shrubland birds on conservation-managed fields in western Connecticut. – PhD thesis, Univ. of Arkansas, USA.
- Smith, J. A., Reitsma, L. R. and Marra, P. P. 2010. Moisture as a determinant of habitat quality for a nonbreeding Neotropical migratory songbird. – *Ecology* 91: 2874–2882.
- Studds, C. E. and Marra, P. P. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. – *Ecology* 86: 2380–2385.
- Studds, C. E. and Marra, P. P. 2007. Linking fluctuations in rainfall to non-breeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. – *Clim. Res.* 35: 115–122.
- Tonra, C. M., Marra, P. P. and Holberton, R. L. 2011. Migration phenology and winter habitat quality are related to circulating androgen in a long-distance migratory bird. – *J. Avian Biol.* 42: 397–404.
- Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S. and Holmes, R. T. 2002. Links between worlds: unraveling migratory connectivity. – *Trends Ecol. Evol.* 17: 76–83.
- Wunderle, Jr., J. M., Lebow, P. K., White, J. D., Currie, D. and Ewert, D. N. 2014. Sex and age differences in site fidelity, food resource tracking and body condition of wintering Kirtland's warblers (*Setophaga kirtlandii*) in The Bahamas. – *Ornithol. Monogr.* 80: 1–62.
- Zack, S. and Stutchbury, B. J. 1992. Delayed breeding in avian social systems: the role of territory quality and 'floater' tactics. – *Behaviour* 123: 194–219.