

Linking events across the annual cycle, in a Neotropical migratory songbird of
conservation concern, the Prothonotary Warbler (*Protonotaria citrea*)

Dissertation

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Abstract

Migratory birds complete the stages of the annual cycle (i.e., winter, migration, breeding, molt) in areas thousands of kilometers apart and events in one location can influence subsequent events. Understanding these “carry-over effects” is fundamental to identifying seasonal variation in mortality and limits on breeding output, both of which are important components of effective conservation and management strategies. Researchers are beginning to grasp the impact of carry-over effects from winter to breeding events, however less progress has occurred in understanding carry-over effects across the rest of the annual cycle. For example, studies on carry-over effects from breeding to molt or winter are infrequent. Additionally, we still lack an understanding of how winter to breeding carry-over effects experienced by adults impact the post-fledging period, one of the most limiting times for juvenal survival and recruitment. Studying carry-over effects in migratory birds presents an enormous challenge, as many complete their annual cycles in disparate places and can be difficult to track from one season to the next, especially small (<20g) songbirds. However, we can begin to fill knowledge gaps on carry-over effects through the use of intrinsic markers (i.e., measures of physiological state) and environmental tracers (e.g., stable carbon isotopes) from tissues (e.g., feathers, claws). These techniques can span the annual cycle, and when combined with breeding metrics expand our knowledge of carry-over effects to inform conservation strategies.

The overall objective of my dissertation is to fill gaps in our knowledge of carry-over effects in order to inform conservation initiatives, and specifically how they function in a species of conservation concern, the Prothonotary Warbler (*Protonotaria citrea*). The Prothonotary Warbler is a Neotropical migrant songbird that breeds in forested wetlands across eastern North America and winters in Central and South America. They currently face threats across the annual cycle from habitat loss, habitat alteration, and global climate change. To achieve this objective, I collected extensive breeding data (i.e., arrival date, breeding effort, success, and post-fledging survival) on a population of Prothonotary Warblers, located in central Ohio, from the Spring of 2015 through 2019. Additionally, in the winter of 2017 and 2018, I traveled to Panama to document winter habitat dynamics.

Beginning with the winter stage, I assessed within-patch survival and site persistence over a six-week period as the dry season progressed using radio-tagged birds in central Panama. Additionally, I compared age and sex ratios, metrics of condition (i.e., breast muscle, fat and condition), and feather molt among habitats. Site persistence was highest in wet/mangrove habitat compared to dry/non-mangrove habitat as seasonal drying intensified; however, the probability of survival did not differ among habitats. There was no difference in condition or fat among habitats however birds in dry/non-mangrove habitat were more likely to be young males, have less breast muscle, and higher intensity body feather molt. Finally, I provide evidence for a partial prealternate molt in Prothonotary Warblers, where at least some body feathers are replaced. This study is one of the first to demonstrate habitat-dependent movement in a non-territorial

overwintering migrant songbird, and highlights the need to conserve intact, mature mangrove and lowland wet forests.

Next, I tested whether carry-over effects from winter habitat impact arrival timing, breeding phenology, and ultimately limit post-fledging survival through breeding phenology. I first validated the use of stable carbon isotopes (sampled from claw clippings) as a measure of habitat moisture (thereby quality) across a range of winter habitats in Panama and Colombia. Using this information, I then assessed the direct and indirect correlations between winter habitat, arrival timing, reproduction, and post-fledging survival. I found evidence for an interaction between winter habitat quality and climatic conditions, highlighting the importance of validating stable carbon isotope-habitat relationships as well as incorporating annual variation into studies of carry-over effects. Winter habitat quality influenced male Prothonotary Warbler arrival timing to breeding sites and indirectly predicted breeding outcomes and post-fledging survival, thus adding to the growing body of literature on carry-over effects from winter to breeding.

Finally, I investigated carry-over effects between breeding events, molt, and winter habitat. I examined the relationship between breeding, energetic effort and time investment, and physiological state, nutritional condition (i.e., feather growth rate) and stress (i.e., feather corticosterone levels) during post-breeding molt. I then tested whether nutritional condition and stress impact feather quality (i.e., feather area density) or winter habitat use (measured through stable carbon isotopes) during the spring pre-migratory period. Overall, I found that breeding events correlated with nutritional status and stress

at the time of molt, and that they subsequently predict feather quality and future winter habitat quality. However, these relationships varied between years, sexes, and in some cases age, and may be impacted by environmental conditions and/or individual quality. In male Prothonotary Warblers, high breeding effort or investment may have consequences for feather quality and winter habitat use that impact spring arrival on the breeding grounds. Females with more intense breeding effort may not experience reductions in feather quality, however they may settle in lower quality winter areas in years with moist, cool conditions.

Combined, these results highlight the importance of understanding connection across the annual cycle, as events in one stage can impact outcomes in later stages and can be mediated through variation in climate. As anthropogenic climate change and deforestation continue to alter landscapes in the Neotropics, it is likely that the repercussions will be observed on the breeding grounds of many Neotropical migratory birds. This makes it critical that conservationist act now to preserve vital habitats for these species across the annual cycle, but especially in the Neotropics. For the Prothonotary Warbler specifically, impacts from climate change across their wintering grounds (projected warming and reduced precipitation) may be particularly pronounced as they are tied to moisture across the annual cycle and my results indicate that carry-over effects from both the winter and breeding seasons can have costs in subsequent stages. Additionally, changes in breeding productivity could cause consequences in subsequent seasons that carry-over to the next breeding season.

Dedication

To my family, and the Prothonotary Warblers who have provide endless entertainment these last 6 years.

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Publications

- 1) Powell, L., **E. Ames**, J. Wright, J. Matthiopoulos, and P. Marra. 2021. Interspecific competition between resident and wintering migratory birds: Experimental evidence and consequences of coexistence. *Ecology*. 10.1002/ecy.3208
- 2) Youtz J., K. Miller, K. Bowers, S. Rogers, L. Bulluck, M. Johnson, B. Peer, K. Percy, E. Johnson, **E. Ames**, C. Tonra, and T. Boves. 2020. Bergmann's rule is followed at all stages of development in a migratory songbird, but climate change may alter this relationship. *Ecology and Evolution*. 10.1002/ece3.6721
- 3) **Ames, E.**, M. Gade, C Nieman, J. Wright, C. Tonra, A. Tutterow, C. Marroquin, and S. Gray. 2020. Striving for population-level conservation: integrating physiology across the biological hierarchy. *Conservation Physiology*. 10.1093/conphys/coaa019
- 4) Reese, J., C. Viverette, C. Tonra, N. Bayly, T. Boves, E. Johnson, M. Johnson, P. Marra, **E. Ames**, A. Caguazango, M. DeSaix, A. Matthews, A. Molina, K. Percy, M. Slevin, L. Bulluck. 2019. Using stable isotopes to estimate migratory connectivity for a patchily-distributed, wetland-associated Neotropical migrant. *Condor: Ornithological Applications*. 121.
- 5) Bulluck, L., **E. Ames**, N. Bayly, J. Reese, C. Viverette, J. Wright, A. Caguazango, C. Tonra. 2019. Habitat-dependent occupancy and movement in a migrant songbird highlights the importance of mangroves and forested lagoons in Panama and Colombia. *Ecology and Evolution*. 9.
- 6) Tonra, C., M. Hallworth, T. Boves, J. Reese, L. Bulluck, M. Johnson, C. Viverette, K. Percy, **E. Ames**, A. Matthews, M. Slevin, R. Wilson, and E. Johnson. 2019. Concentration of a widespread breeding population in few critically important

nonbreeding areas: Migratory connectivity in Prothonotary Warbler. *Condor: Ornithological Applications*. 121.

- 7) Stoeckel, J., J. Morris, **E. Ames**, D. Glover D., M. Vanni, W. Renwick, and M. González. 2012. Exposure Times to the Spring Atrazine Flush Along a Stream-Reservoir System. *Journal of the American Water Resources Association*. 48.
- 8) Cipollini, K., **E. Ames** and D. Cipollini. 2009. Amur Honeysuckle (*Lonicera maackii*) Management method impacts restoration of understory plants in the presence of white-tailed deer (*Odocoileus virginiana*). *Invasive Plant Science and Management*. 2.

Fields of Study

Major Field: Environment and Natural Resources

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Chapter 1. Introduction

The annual cycle of many organisms comprises distinct stages that occur throughout each year (Wingfield 2008). For adult Neotropical migrant songbirds, these stages include stationary non-breeding (hereafter: winter), prealternate molt (partial replacement of body feathers; not present in all species), spring migration, breeding, prebasic molt (complete replacement of all feathers), and fall migration. Each of these stages is defined by the morphological, physiological, and behavioral traits associated with the completion of critical processes for that specific stage and all are fundamentally linked and regulated by physiological processes (Ricklefs and Wikelski, 2002). The winter stage is the longest portion of the annual cycle and is focused on self-maintenance. Prealternate molt occurs within the winter stage, usually preceding spring migration, and offers an opportunity for birds to replace worn feathers and prepare for mate acquisition (e.g., adding filoplumes, Howell et al. 2003). Spring migration connects the winter and breeding areas, and migration in general often has the lowest survival of any stage throughout the annual cycle (Sillett and Holmes 2002). Breeding occurs during the peak in temperate resources (i.e., arthropod abundance) with the goal of maximizing reproduction. Breeding transitions to prebasic molt where the energetically demanding replacement of all feathers occurs (Lindstrom et al. 1993). Finally, fall migration, which

often has a slower pace than spring migration, connects the breeding and winter areas (Newton 2007).

Migratory birds complete the annual cycle in areas thousands of kilometers apart. For these birds, events in one stage can carry-over to influence individual performance in subsequent stages in seasonal interactions known as carry-over effects (Marra et al. 2015). In recent years, full annual cycle research (Faaborg et al. 2010, Hostetler et al. 2015) has sought to understand the processes and interactions that regulate the annual cycle of an organism (Marra *et al.*, 2015), such as carry-over effects, and how variation in life history traits shape those interactions. Without an understanding of these processes, elucidating the mechanisms driving variation, and ultimately limitation, in individuals and populations would not be possible (Newton, 1998). In this way, full annual cycle research helps scale from individual to population, or higher, which is a critical component to conservation action (Ames et al. 2020).

Carry-over effects remain an understudied part of the annual cycle, despite the fact that they can have important consequences for population dynamics. In songbirds, carry-over effects from winter habitat quality have been shown to affect migration phenology (i.e., timing) and ultimately reproductive condition and success (e.g., Marra et al. 1998, Tonra et al. 2011). However, we still lack an understanding of how carry-over effects experienced by adults impact the post-fledging period (the period after young leave the nest and before they depart for the winter grounds), one of the most limiting times for juvenile survival and recruitment (Cox et al. 2014). Although researchers are beginning to grasp the impact of carry-over effects from winter to breeding events,

progress in understanding carry-over effects during other portions of the annual cycle has been scant, particularly in small (i.e., <20g) songbirds. Studies examining carry-over effects from conditions experienced during breeding or molting, two energetically demanding times in the annual life cycle, onto winter are less common. However, some studies have found links between breeding and migration phenology (Stutchbury et al. 2011), winter habitat use (Latta et al. 2016), and future reproductive effort (Takaki et al. 2001). Similarly, studies examining whether non-territorial (i.e., not maintaining an exclusive home range) overwintering songbirds experience similar carry-over effects are less common or have focused on short-distance migrants. Life history characteristics, such as territoriality, likely influence carry-over effect pathways thus making it important to explore these relationships across a range of traits (Harrison et al. 2011).

Studying carry-over effects in small songbirds presents an enormous challenge as they are difficult to track from one season to the next. However, we can begin to fill the knowledge gaps described above by employing environmental tracers and measures of physiological condition (i.e., intrinsic markers) from tissues grown throughout the annual cycle (e.g., feathers, claws). For instance, stable isotope ratios (e.g., of carbon, nitrogen, hydrogen) can be measured from slow growing (i.e., claw clippings) or inert (i.e., feathers) tissues to provide an index of past habitat location or quality (Bearhop et al. 2003; Hobson and Wassenaar 2008; Reudink et al. 2009). Stable-carbon isotopes (hereafter: $\delta^{13}\text{C}$) vary naturally across a wet to dry moisture gradient in many birds using tropical habitats, due to differences in photosynthetic pathways (i.e., C3, C4, or CAM plants) and water use efficiency (i.e., transpiration due to stomata opening and closing) of

dominant plants. Thus, $\delta^{13}\text{C}$ can be used to infer quality of occupied habitats (e.g., Marra et al. 1998; Smith et al. 2010) and link quality to subsequent events, without tracking the individual across the annual cycle. In addition, measurement of feather growth rates, known as ptilochronology, can provide a useful index of nutritional condition at the time of molt (Grubb 1989). For instance, Takaki et al. (2001) found that feather growth rate during post-breeding molt (i.e., prebasic molt) predicted spring arrival time and was positively correlated to number of young fledged during the following breeding season in Styan's Grasshopper Warbler (*Helopsaltes pleskei*). Feathers can provide an integrated measure of physiological stress through incorporation of the primary avian glucocorticoid, corticosterone, into feather keratin (hereafter: fCORT ; Bortolotti et al. 2008, Jenni-Eiermann et al. 2015). For example, Latta et al (2016) found Louisiana Waterthrush (*Parkesia motacilla*) arriving to the wintering grounds with lower fCORT had higher quality winter territories (measured through insect availability) and attained better body condition as the winter season progressed. These techniques, that span the annual cycle, combined with breeding metrics, can greatly expand our knowledge of carry-over effects and provide critical information for conservation strategies for small birds that cannot carry tracking devices or are difficult to study outside the breeding season.

The Prothonotary Warbler (*Protonotaria citrea*) offers a unique opportunity to begin filling remaining gaps in our knowledge of carry-over effects in Neotropical migratory songbirds. They specialize on forested wetland habitat during both the breeding and wintering periods which provides the opportunity to better understand the

impacts from carry-over effects on habitat specialists. During the breeding season, they occupy bottomland hardwood forests and nest in cavities over flooded habitat (Petit 1999). Prothonotary Warblers have been well studied during breeding, partly due to their propensity to use nest boxes, which provides critical knowledge and background on their breeding biology allowing a deeper exploration into interactions with other stages of the annual cycle. Additionally, Prothonotary Warblers are non-territorial during winter, a life history trait that has been understudied in carry-over effects of long-distance migratory songbirds. In the winter period, they occur in highest densities in coastal mangrove and tropical riparian forests, however they also occupy secondary dry forests in lower densities (Bulluck et al. 2019). Prothonotary Warblers currently face threats to habitat across the annual cycle as bottomland hardwood forests continue to be altered and drained for development, and tropical riparian forests, especially mangroves, are being deforested at alarming rates (Sandilyan and Kathiresan 2012, Vancutsem et al. 2020). Since the 1960s, Prothonotary Warblers have experienced population declines across large portions of their breeding range (Sauer et al. 2015) with declines reaching 5.5% yr⁻¹ in some years (Ziolkowski et al. 2010). These declines are likely due to extensive loss and degradation of habitat across the annual cycle. Because of these threats the Prothonotary Warbler is on many watch lists (e.g., National Audubon Society “Priority” designation <audubon.org>) and is a species of concern both nationally (Rosenberg et al. 2016) and in many states, including Ohio (Ohio Fish and Wildlife Service <ohiodnr.gov>). Additionally, their winter habitat is expected to undergo further reduction in total area and altered species composition from climate change (Neelin et al.

2006, Ward et al. 2016). Given the extensive threats to Prothonotary Warbler populations on both the breeding and wintering grounds, it is critical that a full annual cycle approach, where we understand the links between the various stages of the annual cycle, be taken to their conservation and management. A crucial first step in reaching this goal is identifying links between seasons in this population and how those links limit breeding output.

Understanding population limitation and regulation is critical for management and conservation action. For example, if a population is limited by winter habitat quality or availability, managing breeding populations to increase reproduction, such as providing nest boxes for Prothonotary Warblers, may have little to no effect on the overall population. Therefore, having a clear picture of the full annual cycle and carry-over effects between stages is crucial for managing and conserving populations (Marra et al. 2015). This is especially true for migratory species such as the Prothonotary Warbler, which migrate between disparate places like Ohio and Panama, and thus demonstrate how habitat degradation or losses in one place can have consequences that span international boundaries. My research will help determine the capacity of these species to adapt to habitat degradation and loss in a changing climate and begin to establish conservation priorities. For example, if winter habitat quality is a limiting factor in breeding success, then preserving high quality winter habitat in locations with high densities of wintering birds, could provide the greatest overall benefit to the species. Alternatively, if these metrics are equal in perceived low quality or alternative habitats, this would imply that Prothonotary Warblers may be capable of adapting to climate

change, through shifting to these habitats. In this case, preservation of alternative habitats and enhancement for mangrove specialists should be explored as mitigation for predicted mangrove losses due to climate change. With this research I hope to aid conservation directives to stabilize Prothonotary Warbler populations and provide a model for future studies on other species where carry-over effects are little understood.

In this dissertation, I integrate field observations and intrinsic markers to elucidate understudied periods of the annual cycle and explore how carry-over effects can impact populations of the Prothonotary Warbler. I organized my dissertation to follow the annual cycle. Beginning with the winter stage in Chapter 2, I examine movement, survival, and demographic dynamics across multiple habitat types on the wintering grounds of the Prothonotary Warbler. In Chapter 3, I investigate how carry-over effects from winter habitat can impact breeding events. In Chapter 4, I explore how carry-over effects from breeding effort and investment can correlate with molt and winter habitat use. Some chapters may have redundant material, especially in methods sections, as Chapters 2-4 represent separate manuscripts that are in preparation for publication or published in part. For each of these chapters, I have used plural pronouns throughout as they will be published with coauthors, however I take full responsibility for the intellectual content of each chapter. Chapter 2 has been published in part in *Ecology and Evolution* (Bulluck et al. 2019), Chapter 3 is intended for publication in *Oecologia*, and Chapter 4 is intended for publication in *Conservation Physiology*.

Chapter 2. Habitat-dependent movement in a migrant songbird highlights the importance of mangroves and forested wetland in Panama

Introduction

Many species of migratory birds occupy mangrove and lowland riparian tropical forests during the overwintering period, as they tend to have higher prey abundance than drier habitats (e.g., Chan et al., 2008, Smith et al. 2011, Wunderle et al. 2014).

Conservation of migratory species is challenging because their shifting distributions make it difficult to identify the potentially diverse factors limiting populations at different points throughout the annual cycle (Webster et al. 2002, Runge et al. 2014, Marra et al. 2015). This is especially problematic for the overwintering period, which often encompasses the largest portion of the annual cycle and is generally when the most challenging environmental conditions are experienced (e.g., tropical dry season; Smith et al. 2010, Rushing et al. 2016). Moisture is a factor known to influence habitat quality during the overwintering period, and this is especially true for species that rely on lowland habitats such as mangroves, lagoons, and flooded riparian forests. Studies of the territorial Northern Waterthrush in Caribbean mangroves demonstrated that moisture plays a role in mass gain and spring departure date to the breeding grounds (Smith et al. 2010). Likewise, studies with territorial American Redstarts show that moisture-driven differences in habitat quality influence survival (Johnson et al. 2006) and can carry over

to influence reproductive success in the breeding season (e.g., Reudink et al. 2009). These studies highlight the importance of habitat moisture which varies widely between tropical wet and dry seasons, with the driest times often corresponding to the pre-migratory period for Neotropical migratory songbirds. Inter-annual changes in rainfall can also have a significant impact on food, mass change, and spring departure (Studds and Marra 2007). Understanding how seasonal drying influences changes in habitat-specific survival, abundance and site persistence will aid in our predictions of how birds may respond to longer term drying trends caused by climate change (Neelin et al. 2006) and will also help to prioritize conservation efforts in declining mangrove and lowland forests.

Much of our current understanding of overwintering ecology in Nearctic-Neotropical migratory songbirds has been based on studies of habitat-specific demography in *territorial* populations (e.g. American Redstart *Setophaga ruticilla*, Marra 2000; Ovenbird *Seiurus aurocapilla*, Brown and Sherry 2006). Non-territorial species (i.e., those that flock, maintain a non-exclusive home range, or are transient) represent an additional overwintering strategy that needs further study as they display more complex movement patterns than individuals maintaining an exclusive territory. As a result, effective metrics of habitat quality are likely to differ between territorial and non-territorial species. For example, differences in age/sex ratios between habitats can be the result of despotic distributions of highly territorial species (Fretwell and Lucas 1969) and may not be relevant for non-territorial species or may have different underlying causes. Density (Johnson 2007) and site persistence (Latta et al. 2012) are likely to be indicators

of habitat quality for non-territorial species. Density can be a cue for resource availability (Stamps 1991) and non-territorial birds are more likely to move out of (i.e., not persist in) habitats that decline in quality over time compared to species that have invested time in establishing a territory. Within-season movements are likely more common than previously recognized. Studies in Panama (Lefebvre et al. 1992), Belize (Gómez & Bayly 2010), and at multiple sites from Venezuela to Mexico (Ruiz-Gutierrez et al. 2016) suggest some species move between habitats/regions as the tropical dry season progresses. Recent evidence of large scale intra-tropical migration has also been observed in some species that are thought to avoid competition or track resources to increase their chances for survival (Stutchbury et al. 2016, Kolecek et al. 2018). Despite our understanding of the occurrence of within season movements of overwintering birds, few studies have examined habitat-related factors that may be driving these intra-seasonal movements (but see Smith et al. 2011, Wunderle et al. 2014).

Mangrove and tropical riparian forests are declining in area at a rate of 1-2% per year (FAO 2003) and an estimated 30-50% of mangrove forests have been lost over the last half century (Alongi 2002, Duke et al. 2007). Most of these forests occur in developing nations and the primary causes of declines are draining and conversion to agriculture/aquaculture and development (Valiela et al. 2001; Vancutsem et al. 2020). While rates of mangrove loss may be slowing in some regions (Lopez-Angarita et al. 2018), the growing palm oil industry is an additional threat to lowland riparian forests (Vargas et al. 2015, Ocampo-Peñuela et al. 2018). Mangroves are ecologically important as they sequester enormous amounts of carbon (Donato et al. 2011) and support diverse

flora and fauna, some of which are endemic and/or commercially important (Nagelkerken et al. 2009). In addition to loss of mangrove and riparian forest area, predictions of decreased rainfall in the Caribbean and Central America as a result of global climate change (Neelin et al. 2006) are expected to exacerbate the seasonality of flooding and lead to faster and more intense drying. Additional climate change related stressors including sea level rise and increased storm intensity are likely to negatively affect mangroves (Gilman et al. 2008, Ward et al. 2016). This combination of threats to mangroves and riparian forests will likely have significant impacts on the variety of species that rely on them for habitat.

In this study, we assess within-season survival, site persistence, and movement of the Prothonotary Warbler in central Panama and quantify between-habitat differences in population structure and individual condition. Our goal was to assess whether survival and site persistence varied as a function of habitat in this non-territorial species (Morton 1980, Lefebvre et al. 1994, Warkentin and Hernandez 1996). We deployed radio transmitters in habitats that varied in the level of disturbance and moisture to assess movement patterns of individuals at small temporal and spatial scales. We predict that wetter mangrove and lowland forest habitats will be of better quality to overwintering birds. Specifically, we expect individual condition and survival to be higher in wetter compared with drier habitats, and that birds will be more likely to exhibit site persistence as the dry season progresses in wetter habitats.

Methods

Focal species

The Prothonotary Warbler (Figure 1) is a Neotropical migrant songbird that breeds throughout eastern North America and overwinters in Central and northern South America. The Prothonotary Warbler population has declined by about 1% yr⁻¹ over large portions of the breeding range since the 1960s (Sauer et al. 2015) with declines reaching 5.5% yr⁻¹ in some years (Ziolkowski et al. 2010). Contemporary declines have occurred despite much of the preferred bottomland forest breeding habitat being cleared prior to 1966 (Dickson et al. 1995). However, habitat destruction of mangroves and wet lowland forests on the wintering grounds may be at least partially responsible for contemporary population declines. Because of threats due to habitat loss, continuing population declines, and relatively low population size for such a widespread species, the Prothonotary Warbler is considered a Bird of Conservation Concern in the United States (USFWS 2008).

Analysis of light-level geolocator data from Prothonotary Warblers across the breeding range indicate a large proportion overwinter in north-central Colombia, with a smaller number overwintering in Panama (Tonra et al. 2019). The Magdalena River Valley in Colombia, a previously unknown area of importance, is further inland than the coastal mangrove forests thought to be the primary overwintering habitat for Prothonotary Warblers. This suggests that both mangroves, which are being rapidly drained, filled, and developed (Lopez-Angarita et al. 2016), and inland non-mangrove habitat play a crucial role in supporting overwintering populations. Although these

geolocator data provide a useful starting point for on the ground studies assessing the relative quality of habitats are needed to help prioritize and justify conservation efforts in specific areas.

Study area

We established study areas in five locations along the Panama Canal Region of Panama (Figure 2). Two mangrove sites consisted of a majority black (Juan Diaz; 9°01'10.2"N, 79°26'40.6"W) or white (Panama Viejo; 9°00'24.2"N, 79°29'07.2"W) mangrove (*Avicennia germinans* and *Laguncularia racemosa*, respectively) with other less common mangrove species occasionally present (*Avicennia bicolor*). One mangrove site, Galeta (9°23'09.6"N, 79°52'04.8"W) on the Caribbean coast of Panama, had a higher proportion of red mangrove (*Rhizophora mangle*) with the other species present in smaller amounts. The remaining sites were a combination of habitats where Prothonotary Warblers also occur -- forested freshwater wetland associated with a river (Gamboa; 9°07'06.1"N 79°41'35.4"W) and secondary forest (Cerro Ancon; 8°57'36.3"N, 79°33'00.7"W). All sites represented a gradient of habitat moisture ranging from wet mangrove that tended to stay wet throughout the overwintering period to freshwater wetlands and secondary forests that tended to dry out as the dry season progressed (Table 1). Based on these gradients, we combined sites by habitat type (i.e., mangrove/non-mangrove) and by moisture level (i.e., wet/dry) to increase sample sizes and explore how these two habitat factors influence Prothonotary Warblers wintering in Panama.

Individual movement, site persistence, and survival

We assessed movement, survival, and site persistence at five study sites in the Panama Canal Region (Figure 2) from 18 December 2016 to 7 February 2017. We used mist nets to passively and actively (distress calls and chips broadcasted) capture Prothonotary Warblers. We banded all birds with a USGS aluminum band and a unique color band combination for field identification. For each individual captured, we recorded mass ($\pm 0.01\text{g}$), structural body size (i.e., wing, tail, and tarsus length), age (young = within first year of life, or adult = after first year), sex, fat score (on a scale of zero to 7), breast muscle (on a scale of zero to 3), and body molt (on a scale of zero to 4). To control mass for structural body size and time of capture (i.e., potential time of day sampling bias), we created a scaled mass index (hereafter: SMI) using the fitted values from a linear model with wing chord, time of capture, and a wing chord*time of capture interaction term ($n = 84$, adjusted $R^2 = 0.473$). This model produced the lowest AIC value when compared to other models that included wing chord, time of capture, age, and sex (closest model was $\Delta\text{AIC} = 3.92$). We compared SMI, fat, breast muscle, and body molt between sites with a Welch's Two Sample t-test (parametric measurements) and a Kruskal-Wallis Rank Test (non-parametric measurements). To compare age and sex ratios between sites, we used the 'prop.test' function in program R (v 3.4.1; R Core Team 2017) which utilizes a Fisher's Exact probability test. We only looked at comparisons between sites combined by habitat type and moisture level to account for smaller sample sizes at the low-density sites (i.e., Cerro Ancon, Panama Viejo, and Gamboa). We

considered a level of $\alpha \leq 0.05$ to be significant throughout. However, due to small sizes for the body molt and age/sex ratios between sites we chose to report relationships with $\alpha \leq 0.1$ as trends, but we do not draw conclusions from these results.

To track warbler movements and survival, we deployed digital nanotag radio transmitters (Lotek Wireless model NTBQ-2, Inc.; tag warranty life 54 days) on individuals across the five sites. We used hand tracking (homing and triangulation) to determine overwinter survival and site persistence by visiting each site at least once every 5 days and locating tagged individuals during each visit. We exhaustively searched surrounding habitat to locate individuals when not found in the main study area. We considered a disappearance from the study area a movement, and a recovered tag with signs of predation or death to be a mortality event. In addition to hand tracking, each nanotag is individually identifiable within one VHF frequency, allowing them to be detected by Motus automated telemetry towers (Motus Wildlife Tracking System, Bird Studies Canada, <http://motus-wts.org/>; Taylor et al. 2017). We collected Motus data from four automated stations in the Panama Canal Zone to identify landscape level movements. For Prothonotary Warblers foraging in dense mangrove habitat, we estimated the detection range of the Motus stations to be reliable up to approximately 400m by using known locations of radio tagged birds (i.e. hand tracking data) to compare detections. Beyond 400m birds would likely only be detected in open habitat or exiting the forest. We filtered raw Motus data by removing detections with run lengths < 2 (run lengths of 2 were only considered with other supporting detections), pulse lengths that differed from our tags (9 seconds), unlikely locations (i.e. towers outside the winter

range), and ambiguous tags. Data were then visually inspected to ensure detections were highly plausible. To supplement nanotag tracking data, we also re-sighted individually color-marked birds at each study site. However, we did not include these in the formal analysis as most of the resighting took place incidentally while performing other tasks.

All research activities were approved by the USGS Bird Banding Lab (Permit 23941), a Scientific Research Permit from the Panama Ministry of Environment (MiAmbiente; Permit SE/A-123-16), and the Institutional Animal Care and Use Committees of the Smithsonian Tropical Research Institute (Protocol 2016-1215-2019) and the Ohio State University (Protocol 201500000028).

Statistical Analysis

Individual movement, site persistence, and survival

We used radio transmitter data to estimate site persistence and within-season survival. To do this, we combined sites by moisture level (i.e., wet= standing water was observed throughout the study; dry= either no standing water or the site dried up within three weeks) and habitat type (i.e., mangrove or non-mangrove, Table 1), and used these as predictors for statistical analyses to explore differences in survival and site persistence among habitats. Site persistence and survival were estimated using Program MARK known fate models (White and Burnham 1999). To estimate differences in both site persistence and survival rates between the two habitat types (mangrove vs non-mangrove) and sites with persistent rather than ephemeral moisture (wet vs dry), we created two models, one for habitat type and one for moisture level using a grouping variable. To estimate individual predictors, we used likelihood ratio tests to test the

significance of each predictor by removing it from the global model (i.e., grouping variable, time since tagging, age, sex, and SMI) and comparing the reduced model to the global model. Non-informative covariates in preliminary analyses (likelihood ratio test all $P > 0.071$) were removed from the final model. The inclusion of time since tagging represents a fully time-dependent model, where site persistence/survival could vary between each tracking period. We included SMI as it has been shown to indicate resource availability and impact overwinter survival (Wolfe et al. 2013). We expected birds in mangrove and wet habitat to have higher SMI and that this would positively impact survival and persistence. To explore potential differences in survival and persistence between age and sex groups, we included these variables in the models as well. For survival estimates, non-site persistent birds were right censored after departure. For site persistence estimates, we right-censored confirmed mortalities ($n=3$), recovered tags with signs of predation or death, and considered a disappearance from the study area a departure from the site.

To generate locations from triangulation data, we used LOAS software (Ecological Software Solutions LLC) and excluded locations with error $> 35\text{m}$. For each radio tagged bird, we calculated a maximum distance moved (between any two of their locations) to gauge the span of distance moved during the study period, and we calculated an average of those across all individuals at a site. We also calculated straight line travel distance for each consecutive hand tracking location (Matthews and Rodewald 2010) for each bird with > 5 locations. Due to data collection restraints, we were not able to obtain enough points to perform home range analysis. For consecutive distances, only locations

generated from tracking sessions greater than 1 day apart were used, most were 3-5 days apart, and they were not significantly correlated to length of time between tracking sessions (Pearson's correlation= 0.048, p-value= 0.52). As the raw distribution for consecutive distances was heavily right skewed, we log transformed it to achieve a normal distribution and analyzed it using generalized linear mixed effects models in a Bayesian framework with the “brms” package (Bürkner 2017) in Program R (v 3.4.1; R Core Team 2017). We constructed each model to predict distance between consecutive locations with a random effect for individual bird, and fixed effects for: habitat type or moisture level, age, sex, and SMI. Model inference was based on 15 000 Markov-chain Monte Carlo draws from four parallel chains, with uninformative priors (burn-in = 5 000; thin = 4). We used leave-one-out (LOO) cross validation and widely applicable information criterion (WAIC) to compare *a priori* models and select a best fitting model. We estimated Bayesian R squared (Bayes_R²; Gelman et al. 2019) values for each model with the “brms” package.

Results

A total of 87 Prothonotary Warblers were captured during the study (Table 2). 51% (44/87) individuals were undergoing some level of body molt at the time of capture. We found no difference between SMI ($t = 1.05$, $df = 25$, $P = 0.30$) and fat score ($\chi^2 = 1.37$, $P = 0.24$) for birds in mangrove ($n = 70$) versus non-mangrove ($n = 17$), however breast muscle score was higher in mangrove sites ($\chi^2 = 3.96$, $P = 0.047$) and body molt was higher in non-mangrove sites ($\chi^2 = 10.803$, $P = 0.001$). In wet ($n = 61$) and dry ($n = 26$)

habitat, we found no differences in SMI ($t = 1.15$, $df = 38$, $P = 0.26$), breast muscle ($\chi^2 = 0.32$, $P = 0.57$), or fat score ($\chi^2 = 0.49$, $P = 0.48$) however body molt ($\chi^2 = 10.78$, $P = 0.001$) was higher in dry habitat. We further explored the relationship between body molt and habitat by separating age and sex classes. We found that young birds exhibited more intense body molt than adults ($\chi^2 = 6.57$, $P = 0.010$) and that there was no difference in the amount of body molt between sexes ($\chi^2 = 0.03$, $P = 0.87$). Young birds had higher body molt in the dry versus wet sites ($\chi^2 = 7.71$, $P = 0.006$) and in the non-mangrove versus mangrove sites ($\chi^2 = 4.69$, $P = 0.03$). Adults trended toward higher body molt in the non-mangrove sites ($\chi^2 = 3.60$, $P = 0.058$) but not in dry habitat ($\chi^2 = 2.09$, $P = 0.15$).

With both sexes combined, non-mangrove trended toward a higher proportion of young birds compared to mangrove ($\chi^2 = 2.88$, $P = 0.090$), and wet habitat did not differ from dry habitat ($\chi^2 = 1.03$, $P = 0.31$). When males and females were examined separately, the proportion of young to adult females was not different in either mangrove ($\chi^2 = 0.00$, $P = 1$) or wet habitat ($\chi^2 = 0.00$, $P = 0.96$), however the proportion of young to adult males was higher in non-mangrove ($\chi^2 = 5.10$, $P = 0.023$) and trended higher in dry habitat ($\chi^2 = 2.72$, $P = 0.10$). Both non-mangrove ($\chi^2 = 3.62$, $P = 0.057$) and dry habitat ($\chi^2 = 3.10$, $P = 0.078$) trended toward a higher proportion of males compared to females with both young and adult birds combined. When adult and young proportions were examined separately, the proportion of adult males to females was not different in mangrove ($\chi^2 = 0.00$, $P = 1$) or wet habitat ($\chi^2 = 0.00$, $P = 1$), however dry sites ($\chi^2 = 5.28$, $P = 0.022$) and non-mangrove sites ($\chi^2 = 6.27$, $P = 0.012$) showed higher proportions of young males to females.

Site persistence and survival

We deployed nanotags on 29 individuals. We confirmed mortality for three nanotagged warblers: one in reptile scat with feathers, one mangled on the ground with plucked feathers (probable avian predator), and one mangled in a tree (unknown predator but possibly avian). Survival was generally high across all habitats and the best model predicting survival consisted solely of time since tagging (Table 3). The best model for predicting site persistence in mangrove versus non-mangrove habitat contained time since tagging, SMI, and sex. The inclusion of time since tagging in the final model suggests that site persistence varied between tracking intervals, where some intervals had higher site persistence than others. SMI was positively correlated with site persistence and females were more likely to persist than males. The estimated probability that an individual remained in mangrove habitat was 20.9% higher than in non-mangrove habitat. When comparing wet vs dry habitat, the best model for site persistence contained time since tagging and sex (again females were more likely to persist than males), and site persistence was 13.2% greater in wet than dry habitat (Table 3). In addition to the 29 tagged individuals 58 birds were color banded across all sites (Table 4) and 38% were resighted at least one week after banding.

Landscape level movement

We detected one landscape level movement with the Motus tower array. This tag was deployed on a young bird in a small secondary forest patch adjacent to the Rio

Chagres (Gamboa site) on 30 December and was subsequently detected through 9 January. After 9 January, the bird was not detected again until it was picked up by a Motus automated array 29 Km south in a large mangrove forest adjacent to the Rio Juan Diaz on 2, 9 and 28 February. Multiple detections of this individual in the same area suggest that it remained in the area for an extended period of time. No other large-scale movements (>1.5 km) were detected by the Motus towers.

Site level movement

The maximum distance moved for each individual, over the duration of the study (i.e., 6 weeks), ranged from 36 m to 1223 m. The average maximum distance moved was lowest at the two wet mangrove sites (mean= 141.44, SE= 23.16 and mean= 174.65, SE= 34.42) with the dry secondary site having an intermediate value (mean= 239.73, SE= 36.88), and highest at the dry mangrove site (mean= 418.44, SE= 102.87) and the secondary forest site (mean= 425.85, SE= 175.33). Distances between consecutive tracking locations ranged from 0 meters (i.e., individual in same location as previous observation period) to 1149 meters. Consecutive distances were lowest at the two wet mangrove sites (mean= 47.21, SE= 5.03 and mean= 71.22, SE= 6.49) with the dry secondary site having similar values (mean= 73.87, SE= 8.25), and highest at the dry mangrove site (mean= 96.45, SE= 22.06) and the secondary forest site (mean= 193.42, SE= 52.90).

The best model for consecutive distance contained moisture level as the only predictor. It explained 23% of the variation with 91.8% confidence that birds from wet

habitat were found closer to their previous location than birds in dry habitat (Bayes_ R^2 = 0.23, overlap with 0= 8.25%, β wet= -0.38, 95% credible interval {-0.95, 0.17}). On average birds in wet habitat moved 37m (95% credible interval {20.7, 65.6}) and birds in dry habitat moved 70m (95% credible interval {48.7, 103.2}) between tracking periods (Figure 3). The second-best model, which contained only habitat type as a predictor, also explained 23% of the variation for consecutive distance traveled with 88.8% confidence that birds from mangrove habitat were closer to their previous location than birds in non-mangrove habitat (Bayes_ R^2 = 0.23, overlap with 0= 11.2%, β mangrove= -0.34, 95% credible interval {-0.93, 0.22}; Figure 3).

Discussion

Multiple habitat quality indicators from this study and Bulluck et al. 2020 independently support the importance of wet, mature forests for overwintering Prothonotary Warblers. This study enhances our understanding of overwintering habitat use and movement of a non-territorial songbird. Local tracking of birds indicates that wetter habitats, specifically mangroves, are higher quality habitats for Prothonotary Warblers than drier, non-mangrove habitats. These findings suggest that overwintering habitat quality varies significantly and mediates within season movements. Our study is one of the first to demonstrate that winter site persistence, recently found to be more variable than once thought (Ruiz-Gutierrez et al. 2016), can be correlated with habitat in a non-territorial migrant songbird.

The importance of moisture to mangrove-associated species has been well established in overwintering territorial birds (Marra et al. 1998, Norris et al. 2004, Studds and Marra 2005, Johnson et al. 2006, Smith et al. 2010, McKinnon et al. 2015). This suggests that wet habitats buffer individuals against the effects of seasonal drought which is predicted to become more intense with climate change (Neelin et al. 2006). Smith et al. (2011) found that as the Caribbean dry season progressed, birds in habitats prone to drying were more likely to shift home ranges to wetter areas compared with birds in habitats less prone to drying, possibly representing a form of resource tracking. As Prothonotary Warblers are also wet forest specialists, we expected to see higher site persistence in wetter habitats. Despite our small sample size of radio-tracked birds, the best performing site persistence model supports this idea --estimated site persistence in mangrove habitat was 20.9% higher than in non-mangrove habitat. The inclusion of time since tagging in the top model indicates that site persistence varied over the course of the study, which may be indicative of varying moisture levels and drying rates in the different habitats. Birds with higher SMI when initially captured, before significant drying had occurred, had higher rates of site persistence suggesting either that their home ranges encompassed more available resources, or alternatively they were buffered against a reduction in resources (i.e., seasonal drying trends) and thus able to persist at the site longer than other birds. More information is needed to determine if the higher persistence rate of females is indicative of differing physiological requirements of the sexes, social dynamics, or other sex-specific constraints.

We did not find differences in SMI or fat for individuals between habitat type despite higher average SMI and fat in wet and mangrove habitat, however birds in mangrove habitat did show higher breast muscle scores, similar to Cooper et al. (2015). Birds utilizing habitats that undergo seasonal drying may not suffer consequences (i.e., lower SMI, breast muscle, or fat) until periods of drought (Angelier et al. 2009). Since most captures occurred over a two-week period before significant drying had occurred and sample sizes were relatively small, we may not have been able to adequately capture variation in condition. We observed some differences in age and sex ratios between the sites however given our small sample sizes once birds were partitioned by age, sex and habitat more research is needed to understand these relationships.

Interestingly, we documented a relatively high number of birds undergoing body molt on a variety of feather tracts. Previously, it had been thought that Prothonotary Warblers only replace feathers during a post-breeding prebasic molt and do not undergo a prealternate molt in the winter (Pyle 1997). However, our data suggest that they undergo a partial prealternate molt in which at least some body feathers are replaced on the crown, lores, breast, belly, rump, and flanks (unpublished data E. Ames). Previously, variation in Prothonotary Warbler plumage from fall to spring (i.e., brightening of plumage) was believed to have been from wear to olive tipped feathers grown during pre-basic molt. Recently however, other species where a similar relationship between wear and feather coloration was suggested, have been determined to undergo partial prealternate molts (Rusty Blackbird (*Euphagus carolinus*; Mettke-Hofmann et al. 2010), highlighting our still limited knowledge of molt in many bird species. Given the limited time frame of our

study it is hard to determine the extent of this molt and further research on extent and duration could broaden our understanding of this specie's winter ecology. The intensity of body molt was higher in dry compared to wet habitat and in mangrove compared to non-mangrove habitat. Additionally, young birds exhibited more intense body molt and there was no difference in intensity between sexes or adults. This suggests that there may be subtle differences in the timing of molt between habitat types (Yosef and Grubb 1992), however whether the timing is earlier or later in non-mangrove/dry habitat or mangrove/wet habitat is unclear. Limited food resources during the late winter could delay a late winter molt and contribute to delayed arrival to the breeding grounds (Cristol et al. 2014; Wright et al. 2018), especially during years where resources are particularly limited (i.e., drought in dry/non-mangrove habitat or floods in wet/mangrove habitat). Male Prothonotary Warblers with higher carotenoid (i.e., yellow pigmentation) content in body feathers acquire better nest sites in spring (Beck 2013) and females with brighter feathers produce more young (Bullock et al. 2017). Prothonotary Warblers utilizing a mature mangrove patch (high water cover) compared to a young mangrove patch (low water cover) had higher carotenoid content (estimated through feather reflectance; L. Bulluck unpublished data). This suggests either a difference in the quality of old and young mangroves or that feathers molted in those habitats vary in carotenoid content. Further research into potential difference between the timing and quality of body molt between winter habitat of varying quality could provide linkages from winter habitat to breeding phenology and success.

The importance of moisture in this system was further supported by data on movement distances of individually tracked birds across different habitat types. We found that small scale movements are likely related to habitat moisture, as birds in non-mangrove and dry sites had both greater maximum and consecutive location distances than individuals in mangrove and wet sites. There were no sex or age differences in consecutive distance traveled, suggesting that habitat impacts are consistent regardless of potential dominance hierarchies (e.g., Marra 2000). We were only able to explain 23% of the variance in our system suggesting that there are additional, unmeasured factors that influence movement patterns, such as patch size or habitat structure. We also documented two landscape level relocations (>1km), which represented 1) a movement from non-mangrove to mangrove habitat (29 km) and 2) a movement from dry non-mangrove forest to wet non-mangrove forest (1.2 km). In addition, it is likely that many of the birds that were not site persistent moved greater than 1 km from the study site as the vicinity adjacent to the study area was thoroughly searched when birds were not located during the tracking survey.

A study by Ruiz-Gutierrez et al. (2016) using banding data from a network of stations throughout Mexico, Central and South America showed that it was common for Prothonotary Warblers to be transient rather than resident between November and March. Interestingly, the trend for winter persistence varied with latitude where southerly latitudes (Panama and Colombia) were more likely to have site persistence than higher latitude sites (i.e., Belize to Nicaragua; Ruiz-Gutierrez et al. 2016). It is possible that a prolonged southerly fall migration period, which has been documented with geolocator

data (Tonra et al. 2019), could explain transient birds in more northerly latitudes. There is a need for more studies to link site persistence with habitat, as we have done here, because it provides an additional metric for ranking sites for conservation (Ruiz-Gutierrez et al. 2016).

Conclusions

Understanding Prothonotary Warbler movement patterns and habitat use during the overwintering period and identifying abundance hotspots (Bulluck et al. 2019; Tonra et al. 2019) is important for prioritizing conservation efforts for the species. Studies (Lefebvre and Poulen 1996, Calvert et al. 2010, Wolfe et. al. 2013) and citizen science data (Sullivan et al. 2009) suggest substantial population densities of Prothonotary Warblers in other countries (Colombia, Costa Rica, and Nicaragua), prompting the need for more studies in varying habitats across the known wintering range. eBird data are helpful and will inevitably play a role in our understanding of species distributions. However, mangroves and other flooded forests, due to their inaccessibility to most birdwatchers, will continue to be underrepresented and present a bias in our understanding of the true distribution of this and other mangrove-dependent species. Within Panama, our research demonstrates the importance of conserving high quality, mature mangrove forests, and other wet habitats, as abundance (Bulluck et al. 2019) and persistence was greatest in those habitats.

As the Neotropical dry season progressed, mangrove habitat retained more birds and those birds moved less than those in non-mangrove habitat. This is likely because

mangroves retain more moisture while soils and vegetation in secondary forests and freshwater wetlands dry out, leaving fewer resources (i.e., phytophagous and aquatic emergent arthropods) for birds occupying those habitats (e.g., Smith et al. 2011). Focusing conservation efforts on high quality, wet mangroves would provide habitat for the greatest number of birds; however, conserving secondary forests and freshwater wetlands, especially those adjacent to mangroves, would also provide useful habitat. Mangrove forests are facing ever increasing threats from deforestation for development, aquaculture, rising sea levels and reduced precipitation from climate change (Neelin et al. 2006), and anthropogenic changes to hydrologic regimes (Sandilyan et al. 2012). Therefore, it is imperative that conservation action be taken to preserve remaining mangroves across the Americas as they provide important overwintering habitat for Prothonotary Warblers and myriad other terrestrial and aquatic species (Nagelkerken et al. 2008).

The results presented here, coupled with those of Bulluck et al. 2019 and recent publications documenting intra-tropical migration (Stutchbury et al. 2016, Kolecek et al. 2018) and decreased residence times (Ruiz-Gutierrez et al. 2016), highlight that the ecology of overwintering migratory birds is not as simple (or stationary) as once thought. These findings are leading to a paradigm shift in how we think about the overwintering portion of the annual cycle that has been largely influenced by a focus on stationary and territorial species. Indeed, Prothonotary Warblers occupying dry forests on arrival to the overwintering grounds, may be taking advantage of seasonal abundances related to the wet season across northern Colombia and Panama (September-November), and thus

taking advantage of seasonal fluctuations in habitat suitability. The use of site persistence and residence times as measures of habitat quality is not restricted to migratory birds; indeed, studies from butterflies (Shahabuddin et al. 2000) to chimpanzees (Foerster et al. 2016) have found similar relationships. Full life cycle models will need to incorporate the transient nature of species if they are to effectively identify priority areas for conservation (Stutchbury et al. 2016), and further research is required to determine the benefits/disadvantages of occupying more than one habitat.



Figure 1 Prothonotary Warbler captured and tagged with a nanotag in Panama in December 2016.

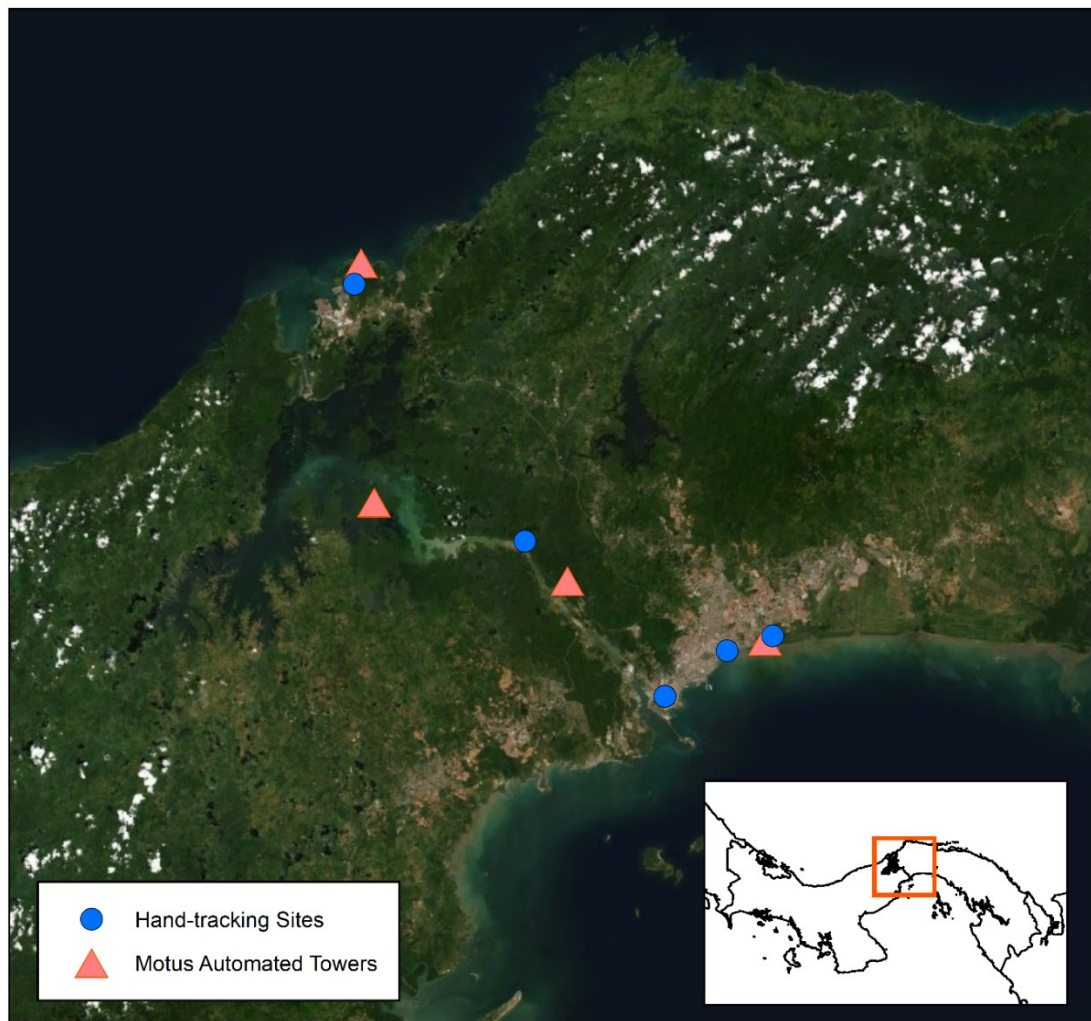


Figure 2 Location of sites in the Panama Canal Region where we tracked individual Prothonotary Warblers using VHF tags and Motus towers that could detect larger scale movements of these same tagged birds.

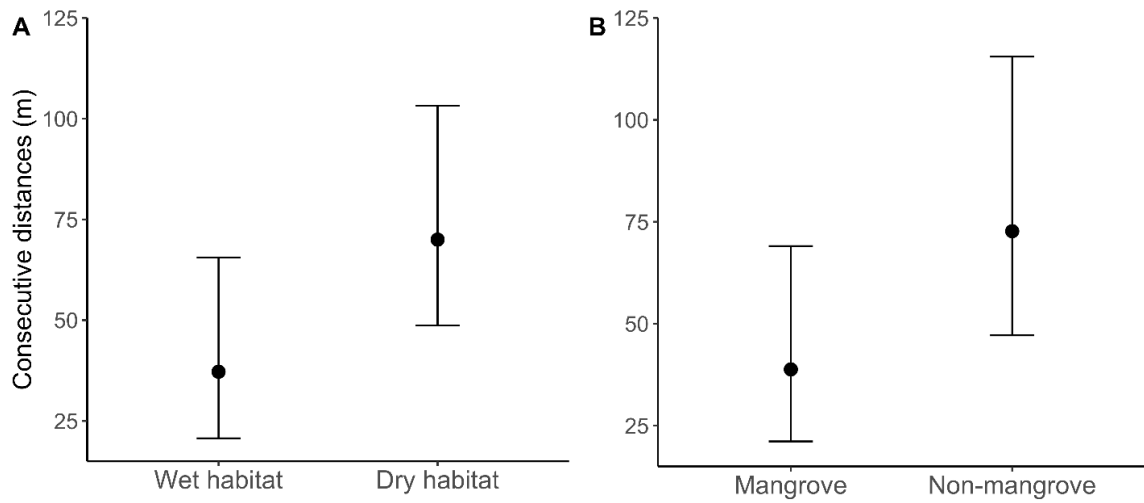


Figure 3 Predicted consecutive distances (meters) between locations for Prothonotary Warblers wintering in Panama, from late December 2016 to early February 2017, for the two best Bayesian linear mixed effects models from leave-one-out cross-validation. A) The wet habitat model and B) The mangrove habitat model. Error bars represent 95% credible interval.

Table 1 Habitat features of Prothonotary Warbler study sites across the Panama Canal region of Panama. Sites were monitored from late December 2016 to early February 2017.

Site	Habitat Type	Moisture level	Disturbance level	Approximate Patch size
Juan Diaz (JUDI)	Black Mangrove	High	Medium	2.0 Km ²
Galeta Res. Sta. (GALE)	Mixed Mangrove	High	Low	6.7 Km ²
Panama Viejo (PAVI)	White Mangrove	Low	High	0.2 Km ²
Cerro Ancon (CEAN)	Secondary	None	High	0.5 Km ²
Gamboa Resort (GARD)	Secondary/Riparian	Low	Medium	0.6 Km ²

Table 2 Protonotary warblers captured along the Panama Canal region of Panama from late December 2016 to early February 2017 by age, sex, site, and habitat type. Number captured represents the total number of individuals captured in each location and for all other columns numbers outside parentheses represent percent and within parentheses represent number of individuals.

Site	Number captured	Male	Female	Young Male	Adult Male	Young Female	Adult Female
Juan Diaz	36	56 (20)	44 (16)	22 (8)	33 (12)	22 (8)	22 (8)
Galeta	25	32 (8)	68 (17)	16 (4)	16 (4)	44 (11)	24 (6)
Panama Viejo	9	56 (5)	44 (4)	22 (2)	33 (3)	22 (2)	22 (2)
Cerro Ancon	9	67 (6)	33 (3)	67 (6)	0 (0)	22 (2)	11 (1)
Gamboa	8	86 (7)	14 (1)	63 (5)	25 (2)	0 (0)	13 (1)
Total	87	53 (46)	47(41)	29 (25)	24 (21)	26 (23)	21 (18)
Mangrove Habitat	70	47 (33)	53 (37)	20 (14)	27 (19)	30 (21)	23 (16)
Non-Mangrove Habitat	17	76 (13)	24 (4)	64 (11)	12 (2)	12 (2)	12 (2)
Wet Habitat	61	46 (28)	54 (33)	20 (12)	26 (16)	31 (19)	23 (14)
Dry Habitat	26	69 (18)	31 (8)	50 (13)	19 (5)	15 (4)	15 (4)

Table 3 Prothonotary Warbler site persistence estimates and survival estimates along the Panama Canal region of Panama, from late December 2016 to early February 2017, using the best fitting model for mangrove vs. non-mangrove habitat and wet vs. dry habitat, with lower 95% confidence interval (LCI 95%) and upper 95% confidence interval (UCI 95%).

Parameter	Site Persistence Estimate	LCI 95%	UCI 95%	Survival Estimate	LCI 95%	UCI 95%
Mangrove Habitat	0.831	0.559	0.951	0.827	0.508	0.956
Non-Mangrove Habitat	0.622	0.292	0.868	0.903	0.541	0.987
Wet Habitat	0.809	0.468	0.953	0.884	0.487	0.984
Dry Habitat	0.677	0.402	0.868	0.848	0.553	0.964

Table 4 Summary of the number of color banded Prothonotary Warblers (# color banded) at each site along the Panama Canal region of Panama. Total resighted is the percent of color banded individuals resighted during the study period with number of individuals in parentheses. The Day columns represent the number of individuals resighted after that many days after banding.

Site	No. Color banded	Total resighted	Day 7	Day 14	Day 21	Day 28	Day 35
Juan Diez	31	35% (11)	11	10	7	2	0
Galeta	20	50% (10)	10	10	6	2	2
Panama Viejo	4	25% (1)	1	0	0	0	0
Cerro Ancon	3	0	na	na	na	na	na
Gamboa	0	na	na	na	na	na	na
Total	58	38%(22)	22	20	13	4	2

Chapter 3 Linking winter habitat, arrival dynamics, breeding phenology, and post-fledgling survival in a Neotropical migrant songbird of conservation concern

Introduction

For long-distance migratory birds, suitable breeding conditions occur in a narrow window of the annual cycle making timely arrival to the breeding grounds critical for maximizing breeding success (Aebischer et al. 1996). Events preceding this narrow window of opportunity can carry-over to impact breeding outcomes (e.g., Marra et al. 1998; Gunnarsson et al. 2006) and cause seasonal interactions where events during the preceding season impacts the processes or outcomes of another (Marra et al. 2015). Spring arrival timing can be a strong determinant of reproductive output as early arrival allows for optimal habitat and mate selection (e.g., Gunnarsson et al. 2005), a longer breeding period, and the opportunity for more brood attempts (i.e., double brooding; Ogden and Stutchbury 1996). Nest initiation date, a corollary of spring arrival, often predicts clutch size (Petit 1989), with later initiation resulting in smaller clutches, and rates of double brooding can drive annual variation in reproduction (Nagy and Holmes 2005), predict site fidelity (Hoover 2003), and increase lifetime reproductive success (Gillis et al. 2008; Petit and Petit 1996). A delay in spring arrival can have a cascading effect on breeding events resulting in reduced or failed reproduction (e.g., Gunnarson et al. 2005; Reudink et al. 2009; Tonra et al. 2011). Thus, events during the non-breeding

stationary period (hereafter: winter) that delay spring arrival can carry-over to limit reproductive output (Saino et al. 2004, Norris et al. 2004).

Carry-over effects can act as important drivers of population dynamics and understanding them is critical for effective conservation planning and population management (Harrison et al. 2010). However, we still lack an understanding of how carry-over effects experienced by adults impact more limiting aspects of breeding success, beyond the nest, which can determine recruitment and productivity. Among these is offspring survival during the post-fledging period (the period after leaving the nest and prior to dispersal/migration), one of the most limiting times for juvenile survival and recruitment (Cox et al. 2014). Despite evidence that population growth rates are sensitive to annual survival of young birds (e.g., Donovan et al. 1995, Rushing et al. 2017) it remains one of the most understudied periods of the annual cycle in avian populations (Cox et al. 2014). The time of season when fledging occurs (i.e., fledge date) has been highlighted as an important predictor of post-fledging survival, where earlier fledging increases survival probability and recruitment (McKim-Louder et al. 2013; Schmidt et al. 2008, Vitz and Rodewald 2011). If carry-over effects from winter habitat delay spring arrival, it could cause later fledging dates and thus lower post-fledging survival and recruitment. Additionally, studies of carry-over effects often rely on measures of breeding success that are misleading when rates of post-fledging survival are low, despite high rates of nest success (e.g., Balogh et al. 2011). High mortality in late fledglings could impose high costs on late arriving individuals and reduced possibilities for producing multiple broods. Therefore, our understanding of carry-over effects in

migratory birds is incomplete without elucidating potential impacts of nonbreeding conditions on post-fledging survival.

A major driver of carry-over effects in migratory songbirds is winter habitat quality, which can impact pre-alternate molt (Cristol et al. 2014), migratory preparation (Studds and Marra 2005), departure date, migratory condition (Bearhop et al. 2004), arrival timing and body condition at the breeding grounds (Marra et al. 1998), hormonal breeding preparedness (Tonra et al. 2011), and total breeding output for the season (Reudink et al. 2009). However, quantifying winter habitat quality can be challenging, especially for small migratory songbirds that are difficult to track across the full annual cycle. Measures of winter habitat moisture can be used to infer habitat quality, in some species, and link it to spring arrival timing when tracking is too costly or not feasible, as it is a major determinant of habitat quality in Neotropical migratory birds (e.g., Studds and Marra 2007, Smith et al. 2010). Winter habitat moisture has been shown to drive changes in body mass (Smith et al. 2010), time of migratory departure (Studds and Marra 2011), arrival to the breeding grounds (McKellar et al. 2013), and both annual and within season survival (Johnson et al. 2006; Wolfe et al. 2013). Stable-carbon isotopes (hereafter: $\delta^{13}\text{C}$), which are transferred up the food chain from plants to insects and ultimately the tissues of vertebrate consumers, offer a useful index of the moisture of habitats previously utilized by birds. $\delta^{13}\text{C}$ varies naturally across habitats due to differences in photosynthetic pathways (i.e., C3, C4, or CAM plants) and water use efficiency (i.e., transpiration rates due to stomata opening and closing) of dominant plants. This variation can be observed in tropical habitats and is reflected in the tissues of

birds using those habitats, where birds using mesic habitats tend to show more depleted $\delta^{13}\text{C}$ than those in more xeric habitats (Marra et al. 1998, Smith et al. 2010). $\delta^{13}\text{C}$ can be measured from multiple tissues in birds including blood, claws, and feathers (Hobson and Clark 1992; Bearhop et al. 2003), however claws are particularly useful because they have slow turnover rates (~6 weeks; Bearhop et al. 2003, Reudink et al. 2009). Thus, claws collected from birds arriving to breeding grounds can be used to estimate $\delta^{13}\text{C}$ of winter habitat, and thereby quality, and link it to subsequent breeding events.

Winter habitat may be of particular importance to specialists who are limited by habitat availability and may be more sensitive to small changes in quality, such as moisture levels (e.g., Smith et al. 2010). For instance, wetland specialists, that are limited to relatively mesic habitats (e.g., mangrove forest) on the wintering grounds, may be particularly vulnerable to annual variation in precipitation, as this can limit the amount and quality of available habitat (Soriano-Redondo et al. 2016). This is currently of particular concern in the Neotropics under anthropogenic climate change, as seasonality and annual variation in precipitation are becoming more extreme (e.g., Neelin et al. 2006). Understanding whether carry-over effects from winter habitat impact breeding dynamics in these species and how they fluctuate in intensity annually are critical for understanding the sensitivity of these species to climate change and other stressors across the annual cycle (Small-Lorenz et al. 2013, Culp et al. 2017).

We tested whether carry-over effects from winter habitat impact arrival timing, breeding phenology, and ultimately limit post-fledging survival through phenology, in a neotropical migratory songbird of conservation concern, the Prothonotary Warbler

(*Protonotaria citrea*). We predicted that Prothonotary Warblers wintering in more mesic (i.e., higher quality) habitat, measured from $\delta^{13}\text{C}$ in claws, would arrive earlier to the breeding grounds, breed sooner, and fledge more young, than birds wintering in more xeric (i.e., lower quality) habitat. Additionally, we predicted late arriving birds who fledge young later in the breeding season, would have lower rates of post-fledging survival and recruitment than earlier arriving birds. To validate their use as a measure of habitat moisture in Prothonotary Warblers, we first quantified $\delta^{13}\text{C}$ (sampled from claws) across a range of winter habitats in Panama and Colombia. Using this information, we then assessed the impacts of winter habitat on arrival timing and reproduction. Since carry-over effects from winter habitat have been shown to manifest both directly and indirectly on breeding phenology and performance, we tested multiple direct and indirect pathways that might connect winter habitat to breeding events and ultimately post-fledging survival and recruitment.

Methods

Study Species

The Prothonotary Warbler is Neotropical migratory songbird that specializes on mesic habitats across the annual cycle. During the breeding season, they utilize wet forest habitats including swamps, bottomland hardwood forests, and riparian corridors (Petit 1999) where they nest in tree cavities over flooded habitat. Largely due to their propensity to also use nest boxes, they are well studied on the breeding grounds offering a solid understanding of their breeding ecology. However, our knowledge of the winter

period (but see Lefebvre and Poulin 1996, Wolfe et al. 2013, Bulluck et al. 2019), and interactions with other stages in the full annual cycle remain incomplete. Spring arrival dynamics have been studied in relation to the timing of arrival (Petit 1989) and both habitat and nest site selection upon arrival (Petit and Petit 1996) however, to date no study has examined the link between winter habitat quality and arrival timing. Early arrival to the breeding grounds may be particularly important for this species as intra- and inter-species competition for cavities can drive population dynamics (Newton 1998).

Prothonotary Warblers occur in highest densities in coastal mangrove and tropical riparian forests during winter, however they also occupy secondary dry forests at lower densities (Bulluck et al. 2019). Within these habitats they occur solitarily or in mixed species flocks and many maintain home ranges even as seasonal drying occurs (83%-62% were site persistent; Chapter 2). Variation in population density (Bulluck et al. 2019) and movement patterns (Chapter 2) among habitats suggests that habitat quality may play a role in winter dynamics and potentially carry-over effects to breeding outcomes.

Prothonotary Warblers currently face threats to habitat across the annual cycle as bottomland hardwood forests continue to be altered and drained for development, and tropical riparian forests, especially mangroves, are deforested at alarming rates (Sandilyan and Kathiresan 2012). Since the 1960s, Prothonotary Warblers have experienced population declines across large portions of the breeding range (approximately 1% yr⁻¹; Sauer et al. 2015) with declines reaching 5.5% yr⁻¹ in some years (Ziolkowski et al. 2010). Due to the declining population, likely caused by extensive loss and degradation of both breeding and wintering habitat, the Prothonotary Warbler is on

many watch lists (e.g., National Audubon Society) and is a species of concern both nationally (U.S. Fish and Wildlife Service; Partners in Flight) and in many states, including Ohio. Additionally, their winter habitat is expected to undergo further degradation from climate change (e.g., reduced precipitation, rising sea levels and increased storm frequency; Neelin et al. 2006, Ward et al. 2016). Given the extensive threats to Prothonotary Warbler populations on both the breeding and wintering grounds, it is critical that a full annual cycle approach, where we understand the links between the various stages, be taken to their conservation and management.

Study Site

We conducted our research from 2016 to 2019, at the Hoover Nature Preserve, Galena, OH, USA (40.1990° N, 82.8852° W), which consists of 925 acres of upland forest, ephemerally flooded forest, and forested wetland along the shoreline of the Hoover Reservoir and two river corridors. The site hosts a large breeding population of Prothonotary Warblers and contains a network of nest boxes. The boxes, established and maintained, but not monitored, by a volunteer private citizen, are mounted on trees and do not have mechanisms to exclude predators. Thus, boxes have much lower success (i.e., fledging at least one young) compared to cavities in trees (box nests were successful 12.5% n= 96 and natural cavities were successful 38.2% n= 225) in this system. Dominant tree and shrub species include eastern cottonwood (*Populus deltoids*), American sycamore (*Platanus occidentalis*), boxelder (*Acer negundo*), green ash

(*Fraxinus Pennsylvania*; mostly dead or dying due to *Agrilus planipennis*), and buttonbush (*Cephalanthus occidentalis*).

Arrival surveys and captures

We conducted arrival surveys every two days, beginning in early to mid-April each year which ensured Prothonotary Warblers were not present during the first survey (in most cases no males arrived until after the 3rd survey). During each survey, we walked pre-established transects and used visual and auditory cues to detect and identify individuals. Males captured in previous years were identified by color bands. For males without bands, we used unique external features (i.e., extent of green on nape and forehead, residue from sap on forehead, extent of yellow on belly/vent) to identify them until captured. Arrival dates were recorded relative to the earliest arrival date within year and between years (i.e., first bird arrived on Day 1). Males that arrived >35 days after the first arrival were excluded as it was possible they were local relocations rather than arrivals from the non-breeding grounds. Individuals were captured as soon as possible after arrival using conspecific playback and mist nets. We banded each new bird with a unique combination of a USGS aluminum band and three plastic color bands. For stable isotope analysis, we collected claw clippings (~2mm) from the center toe on each foot. Only claw samples collected within 7 days of an individual's arrival to the breeding grounds were used for further analysis to reduce the likelihood that samples contained stable carbon signatures from migration or breeding (Reudink et al. 2009, Tonra et al. 2011). Additionally, we recorded sex, age (young = within first year of life, or old = > 1

year old), mass (± 0.01 g), and structural body size (i.e., wing and tail to nearest mm, and tarsus length to nearest 0.1mm).

Nest monitoring

Concurrently with arrival surveys, we monitored each territory, identified by the territorial male, for pairing success (i.e., female consistently on territory) and nesting behavior. We had a small number of males that did not pair during the full breeding season since females often switch territories after nest failure allowing initially unpaired males to eventually attract a female. To increase sample size of our initial pairing success variable, we counted males that did not pair with females in the first round of nesting (i.e., before June 1st) or paired with a female who had a previous nest attempt with another male, as unpaired. Therefore, the initial pairing success variable represents pairing in the first round of breeding not for the whole season. We located nests using adult behavior and systematic searching for both natural cavity and artificial box nests and monitored them every 2-5 days to determine first egg date (i.e., date of first egg laid on male's territory) and fledge date. Both first egg date and fledge date were recorded relative to the earliest date within year and between years. We checked nest contents and determined nestling age with a handheld nest camera (Explorer Premium, model 8803AL), which we mounted on an extension pole for nests over 3 meters. We considered the first egg date for a male to be the first date an egg was laid in his territory so in some cases the female of the nest may have an earlier first egg date from a previous attempt. We chose to make this distinction since our pathway was focused on the male

(see below). We removed males ($n=4$) with dates greater than 34 days after the earliest first egg date and territories where we knew based on behavior that a previous nesting attempt was not found before failure. Following the completion of each nest attempt, either due to fledging or failure, we monitored the territory to find subsequent nesting attempts and determine final breeding status (i.e., number fledged in each attempt and total fledged for breeding season).

Post-fledging survival

We banded nestlings between day 7-10 of the nestling period with a USGS aluminum band and three plastic color bands. During the 2016 and 2017 breeding seasons, we estimated post-fledgling survival by deploying a radio transmitter (Model A2415; Advanced Telemetry Services, Inc.) on one randomly selected nestling from each brood. We attached transmitters using a leg loop harness (Rappole and Tipton 1991) made of elastic bead chord. Transmitters were $<5\%$ of nestling body mass and had a battery life of approximately 45 days. We tracked each fledgling by homing until visually detected at least once every two days to determine survival. Following each mortality event, we attempted to identify cause of mortality by examining remaining body parts, transmitter condition, and location (Shiple et al. 2013).

Winter isotope analysis

To validate the use of stable-carbon isotopes as a measure of winter habitat, we collected claw samples from five sites, representing lowland forest (i.e., broadleaf non-

mangrove forests), freshwater wetland, black mangrove, white mangrove, and red mangrove (see Chapter 2 for habitat specific details), along the Panama Canal Region, Panama from December 2016 to February 2017 and at two sites, representing freshwater wetlands and mixed red mangrove habitat, in northeastern Colombia. We used mist nets to passively and actively (using distress calls and chips) capture Prothonotary Warblers and collected claw samples as described above.

Stable isotope analysis

We prepared all winter and arrival claw samples for isotope analysis by washing them in 2ml of 2:1 chloroform to methanol for 2 hours to remove foreign material and then allowed them to dry for 48 hours. After drying, we weighed and packed each sample into tin capsules and transported them to the Smithsonian MCI Stable Isotope Mass Spectrometry Lab for analysis. All samples were run on a Thermo Delta V Advantage mass spectrometer in continuous flow mode coupled to an Elementar vario ISOTOPE Cube Elemental Analyzer via a Thermo Conflo IV and calculations of raw isotope values were performed with Isodat 3.0 software. Carbon isotope ratios ($^{13}\text{C}/^{12}\text{C}$) are reported in delta (δ) notation in per-mil units (‰) as deviation from the Vienna Pee Dee belemnite standard. All runs included a set of reference materials (i.e., include Costech Acetanilide [calibrated to USGS40 (L-glutamic acid) and USGS41 (L-glutamic acid)] and USGS66 (glycine)) for every 10-12 samples and reproducibility of reference materials was $\pm 0.2\text{‰}$.

Statistical analysis

We compared $\delta^{13}\text{C}$ values sampled from the seven winter habitats with the “anova” function in program R (v 4.0.3, R Core Team, 2020) followed by a Tukey HSD test. We used a Welch Two Sample t-test to determine if male arrival date varied by age with means and standard errors. Following Drake et al. (2013) and Akresh et al. (2019), to examine potential carry-over effects from winter on breeding season events, we analyzed direct and indirect relationships between claw $\delta^{13}\text{C}$ and each subsequent breeding event starting with arrival timing to the breeding grounds (Figure 4). Each step in the *a priori* pathway was modeled individually to maximize sample size and to increase statistical power by reducing the number of parameters in each model. This was important as difficult capture conditions (i.e., deep water, spring weather, and repeated capturing across years) limited usable carbon samples (i.e., sampled in <8 days post-arrival) and we were not always able to collect every breeding parameter for each bird (e.g., occasional nest on private property). We used linear mixed-effects models with a random intercept for individual to account for repeated samples across years and in some cases (i.e., clutch initiation date) repeated samples within years. For each step in the pathway, the dependent variable was the variable to the right of the arrow in Figure 4, and we started with a full model that included: the explanatory variable of interest (i.e., the variable to the left of the arrow in Figure 4), interaction terms with year and age, and removed non-significant predictors in a stepwise fashion (excluding the variable of interest). We first removed the year interaction if not statistically significant ($P>0.05$) followed by year ($P>0.05$) and finally age ($P>0.10$). We were more conservative when

removing age from our models as sample sizes for young males was considerably smaller than older males and age is an important factor in breeding outcomes. If there was a year interaction, we ran each year separately using a linear fixed-effects model, since individuals were no longer repeated, and followed the same procedure outlined above.

We used program R (v 4.0.3, R Core Team, (2020) to conduct analyses in the carry-over pathway (Figure 4) except for the post-fledging models (see below). For models with arrival date, first egg date, and fledge date as the dependent variable, we used the R package “nlme” to build gaussian linear mixed-effects models (Pinheiro et al. 2015). We used the R package “lme4” to construct binomial mixed-effects models for initial pairing success, nest type (box versus natural cavity), nest success (i.e., did the nest fledge at least one prothonotary warbler), Brown-headed Cowbird (*Molothrus ater*) nest parasitism, and recruitment. For the arrival date to nest type model, we only used the nest type of the first attempt.

We used the R package “ordinal” to fit cumulative link mixed-effects models (Christensen 2012) with number fledged for a given nest attempt (i.e., 1-6) or total number fledged for the year (i.e., sum of young produced from all attempts within a year) as the dependent variables. For total number fledged, we created an ordinal variable where we grouped males that fledged less than average (i.e., 1-3 young), average (i.e., 4-6 young) and above average (i.e., 7-10 young) as low and high categories were rank deficient and prevented model convergence without grouping. Additionally, we included a binary variable to account for Brown-headed Cowbird parasitism in the total fledged model. We used clutch initiation date rather than first egg date for the pathway from first

egg date to number fledged to increase sample size and excluded parasitized nests rather than fitting an additional Brown-headed Cowbird variable as it was rank deficient. When modeling Brown-headed Cowbird parasitism to number fledged we could not include age as a covariate because only 2 parasitized young male nests successfully fledged Prothonotary Warblers. We considered a level of $\alpha \leq 0.05$ to be significant in final models throughout. However, we report relationships with $\alpha \leq 0.1$ as trends to account for small sample sizes but have avoided drawing conclusions from these results.

We estimated post-fledging survival with Program MARK (White and Burnham 1999) known-fate models, which utilize a Kaplan-Meier approach (Kaplan-Meier 1958). To reduce model complexity, we first constructed a base model by assessing important known predictors of post-fledging survival prior to testing predictions based on phenology variables. We included models for fledgling age (i.e., time since fledging), year, fledgling sex (Maness and Anderson 2013), parental male age (young or old), brood (i.e., first or second successful brood), and number fledged (i.e., number of siblings). To build the base model, we constructed single variable models for each covariate listed above, as well as an additive and interaction model with fledgling age. We assessed potential predictors using Akaike's Information Criterion corrected for small sample size (AIC_c ; Akaike 1973, Burnham and Anderson 2002). We investigated potential interactions between fledgling age and other covariates as it is one of the most important predictors of survival for passerines (Cox et al. 2014). Covariates from models ranked $\leq 2 \Delta AIC_c$ were included in the final base model, and we further tested the importance of each covariate with a likelihood ratio test between the final base model and a reduced

model with each covariate removed independently. By building the base model, we hope to control for factors that influence post-fledging survival but that are not directly related to our carry-over pathway.

Once the base model was constructed, we tested the importance of each phenology variable (i.e., arrival date, first egg date, and fledge date) in our pathway individually by performing a likelihood ratio test between the final base model (i.e., the reduced model) and a model that consisted of the base model with the added phenology variable (i.e., the full model).

Results

Spring Arrival

We recorded 158 arrival dates for 95 individual male Prothonotary Warblers during spring 2016-2019. The earliest arrival across all 4 years was 14 April 2017. Old males arrived to breeding sites on average 2.5 days earlier than young males ($t= 2.30$, $df= 96$, 95% CI= 0.34-4.6, $P=0.024$). Winter $\delta^{13}\text{C}$ values ranged from -26.1 to -22.8 (Table 5). Young males arriving at the breeding grounds showed significantly more enriched $\delta^{13}\text{C}$ values (-24.25 ± 0.10 ; indicative of non-mangrove or red mangrove habitat) compared to old males (-23.91 ± 0.12 ; $t= -2.30$, $df= 93$, 95% CI= -0.65- -0.05, $P= 0.025$).

Carry-over effects pathway

For Prothonotary Warblers wintering in Panama and Colombia, we found that individuals utilizing lowland forests and freshwater wetlands showed depleted $\delta^{13}\text{C}$

signatures similar to individuals utilizing red mangroves and that black and white mangroves showed more enriched $\delta^{13}\text{C}$ (Figure 5, Table 5). The relationship between winter habitat, estimated through $\delta^{13}\text{C}$, and arrival date was dependent on year (Figure 6), so we modeled years separately. Males with more enriched $\delta^{13}\text{C}$ (representing black and white mangrove habitat) arrived earlier than those with more depleted $\delta^{13}\text{C}$ (representing non-mangrove or red mangrove habitat) in 2016 ($n=21$, $\beta=-3.60$, $\text{SE}=1.65$, $t=-2.19$, $P=0.042$, $r^2=0.20$) and in 2019 ($n=25$, $\beta=-3.34$, $\text{SE}=1.51$, $t=-2.21$, $P=0.037$, $R^2=0.14$). There was no relationship between arrival and $\delta^{13}\text{C}$ ($n=21$, $\beta=1.639$, $\text{SE}=2.08$, $t=0.79$, $P=0.44$, $R^2=0.03$) in 2017. In 2018, males with more depleted $\delta^{13}\text{C}$ arrived earlier than males with more enriched $\delta^{13}\text{C}$ ($n=30$, $\beta=1.32$, $\text{SE}=0.61$, $t=2.16$, $P=0.04$, $R^2=0.36$) and old males arrived earlier ($n=30$, $\beta=3.80$, $\text{SE}=1.14$, $t=3.34$, $P=0.002$, $R^2=0.36$) than young males. We did not find evidence for a direct effect of $\delta^{13}\text{C}$ on initial pairing success ($n=95$, $\beta=-0.12$, $\text{SE}=0.36$, $z=-0.35$, $P=0.73$), nest success ($n=98$, $\beta=0.38$, $\text{SE}=0.24$, $z=1.59$, $P=0.11$), first egg date ($n=61$, $\beta=-0.31$, $\text{SE}=0.88$, $t=-0.35$, $P=0.73$), or fledge date ($n=42$, $\beta=1.29$, $\text{SE}=2.41$, $t=0.54$, $P=0.62$).

We documented the lowest rates of unpaired males in 2016 (12.2%) and 2019 (12.9%) followed by 2017 (19.6%), and finally 2018 (27.8%). With all years combined 9.6% ($n=104$) of old males and 34.7% ($n=49$) of young males were not paired during the initial nesting period and 3.8% of old males and 26.5% of young males did not acquire a mate for at least one entire breeding season. Arrival date ($n=153$, $\beta=-0.53$, $\text{SE}=0.24$, $z=-2.23$, $P=0.026$) and age ($n=153$, $\beta=-1.46$, $\text{SE}=0.46$, $z=-3.19$, $P=0.001$) predicted initial pairing success where old and earlier arriving males were more likely to acquire a

female during the first round of nesting. Early arriving males were more likely to successfully fledge at least one young ($n=146$, $\beta = -0.07$, $SE = 0.03$, $z = -2.32$, $P = 0.021$) independent of age. Arrival date did not predict nest type (box or cavity) for the first nest attempt ($n=134$, $\beta = 0.04$, $SE = 0.04$, $z = 1.02$, $P = 0.31$). Arrival date predicted first egg date when controlling for year and age, where early arriving males had earlier first egg dates ($n=107$, $\beta = 0.32$, $SE = 0.09$, $t = 3.73$, $P < 0.001$) and young males had later first egg dates than older males ($n=107$, $\beta = 3.56$, $SE = 1.20$, $t = 2.98$, $P = 0.005$).

Nests with earlier first egg dates were more likely to be successful (i.e., fledge at least one young; $n=120$, $\beta = -0.08$, $SE = 0.03$, $z = -2.45$, $P = 0.013$). First egg date ($n=64$, $\beta = 0.67$, $SE = 0.29$, $t = 2.35$, $P = 0.041$) predicted fledge date of the first successful nest (not necessarily the same nest attempt as the first egg date) and young males showed a trend toward only fledging earlier attempts ($n=64$, $\beta = -8.24$, $SE = 4.24$, $t = -1.94$, $P = 0.058$). Clutch initiation date ($n=75$, $\beta = -0.06$, $SE = 0.02$, $z = -3.90$, $P < 0.001$) and age ($n=75$, $\beta = -1.67$, $SE = 0.54$, $z = -3.11$, $P < 0.001$) predicted the number fledged per attempt where earlier nests and older males produced more young. We found that males with earlier first egg dates, whether young or old, trended toward higher numbers of total young for the year ($n=65$, $\beta = -0.11$, $SE = 0.06$, $z = -1.82$, $P = 0.07$) when Brown-headed Cowbird parasitism was accounted for ($n=65$, $\beta = -2.16$, $SE = 1.13$, $z = -1.92$, $P = 0.06$). We did not find evidence that fledge date impacted recruitment ($n=229$, $\beta = -0.26$, $SE = 0.24$, $z = -1.08$, $P = 0.28$), however our effective sample size was relatively small with only 10.9% of banded nestlings returning as breeders over the three-year period.

Brown-headed Cowbird parasitism reduced the number of young fledged per nest attempt ($n=88$, $\beta= -1.67$, $SE= 0.68$, $z= -2.45$, $P= 0.01$). We found that nests in boxes tended to have fewer instances of Brown-headed Cowbird parasitism ($n=88$, $\beta= -0.86$, $SE= 0.51$, $z= -1.70$, $P= 0.09$), however boxes did not completely prevent parasitism due to large entrance holes. Despite a reduction in parasitism, box nests were significantly less likely to be successful (i.e., fledge at least one prothonotary warbler) compared to cavities ($n=306$, $\beta= -1.57$, $SE= 0.38$, $z= -4.16$, $P< 0.001$) for both old and young males.

Post-fledging survival

We tracked survival of 46 fledglings (2016: $n=22$, 2017: $n=24$) and documented 17 mortality events (2016: $n=9$, 2017: $n=8$) all of which occurred in the first 8 days after fledging. The base model for predicting post-fledging survival consisted of fledgling age, sex, an age sex interaction, and number fledged. Overall survival probability increased as fledgling age (i.e., time since fledging; $\chi^2= 32.98$, $df= 4$, $P< 0.001$) increased and more females survived overall than males ($\chi^2= 7.94$, $df= 1$, $P= 0.019$). However, age and sex interacted ($\chi^2= 5.70$, $df= 1$, $P= 0.017$) to impact survival where mortality in females occurred shortly after fledging but male mortality consistently decreased with age. Survival also varied by the number of young fledged from the nest ($\chi^2= 4.59$, $df= 1$, $P= 0.032$) where the more young that fledged the greater the probability of survival for the tagged nestling. Arrival date ($\chi^2= 0.43$, $df= 1$, $P= 0.51$), first egg date ($\chi^2= 0.28$, $df= 1$, $P= 0.60$), and fledge date ($\chi^2= 1.65$, $df= 1$, $P= 0.20$) did not influence post-fledgling survival. Four mortalities were attributed to avian predation, three mortalities were

attributed to mammal predation, one was attributed to weather (i.e., severe storm), one was found inside a gray rat snake (*Pantherophis spiloides*), one was likely predated by a turtle or fish (unknown species) either before or after drowning and seven had unknown mortality.

Discussion

Carry-over effects can act as important drivers of population dynamics and understanding them is critical for effective conservation planning and population management. However, we still lack a complete understanding of how carry-over effects limit aspects of breeding success, especially in habitat specialist like the Prothonotary Warbler. To address these knowledge gaps, we studied the impact of carry-over effects from winter habitat quality on nesting success and post-fledgling survival in a population of Prothonotary Warblers breeding in Ohio. We found that winter habitat quality, estimated from $\delta^{13}\text{C}$ in claws, impacts arrival timing in some years on the breeding grounds of male Prothonotary Warblers adding to the growing body of literature on carry-over effects from winter to breeding. The relationship between winter habitat and arrival varied between years, similar to other studies (Rockwell et al. 2013, Akresh et al. 2019), suggesting that the strength of these relationships may be related to broad scale climatic events. Additionally, we found multiple pathways through which winter habitat quality may indirectly impact breeding outcomes through arrival date.

Prothonotary Warblers wintering in lowland forests and freshwater wetlands showed depleted $\delta^{13}\text{C}$ signatures similar to red mangroves, however black and white

mangroves showed more enriched $\delta^{13}\text{C}$ (Figure 5). This was contrary to the expected relationship between presumed habitat moisture and $\delta^{13}\text{C}$. Other species have shown similar $\delta^{13}\text{C}$ patterns among habitats, where birds using lowland forest (presumably drier than mangroves) show depleted $\delta^{13}\text{C}$ compared to mangroves. For example, Northern Waterthrush (*Seiurus noveboracensis*) wintering Puerto Rico showed more depleted signatures in dry lowland forests compared to black mangroves (Smith et al. 2010) and American Redstarts (*Setophaga ruticilla*) wintering in wet lowland forests in both Jamaica and Honduras showed more depleted $\delta^{13}\text{C}$ compared to black mangrove (both habitats were more depleted than coastal scrub habitat; Marra et al. 1998). Most studies that have validated winter $\delta^{13}\text{C}$ in warblers have been based on Caribbean islands (Marra et al. 1998, Bearhop et al. 2004, Akresh et al. 2019) or the northern continental Caribbean coast (Marra et al. 1998; but see Drake et al. 2013) and focused on species where a substantial proportion of the population utilizes coastal scrub (but see Smith et al. 2010) during the winter. González-Prieto and Hobson 2013 tested the generality of the xeric-mesic $\delta^{13}\text{C}$ gradient by examining arrival and condition in multiple species and found that it may not be applicable for species wintering outside the Caribbean, not using scrub in high proportions, with specific habitat requirements, or for some populations of a species. They cautioned against using this paradigm with species that deviate from the norm without first quantifying $\delta^{13}\text{C}$ habitat relationships *in situ*. For example, Alder Flycatchers (*Empidonax alnorum*) with enriched $\delta^{13}\text{C}$ (i.e., presumably more xeric habitat) arrived earlier than those with more depleted $\delta^{13}\text{C}$ (González-Prieto and Hobson 2013). Similarly, Imlay et al. (2019), found male Bank Swallows (*Riparia riparia*) with

depleted winter $\delta^{13}\text{C}$ were associated with higher nestling survival but male Cliff swallows (*Petrochelidon pyrrhonota*) had lower nestling survival associated with depleted $\delta^{13}\text{C}$. *In situ* validation of $\delta^{13}\text{C}$ -habitat relationships is critical for these and other studies to confirm not only the nature of variation in $\delta^{13}\text{C}$ among habitat types, but the relative quality of such habitats to overwintering birds (e.g., Marra 2000, Smith et al. 2010, Bulluck et al. 2019). Our results further highlight the importance of validating $\delta^{13}\text{C}$ in a variety of habitats for species outside of the well-established paradigm in order to better understand the $\delta^{13}\text{C}$ gradient and carry-over effects.

Early arriving male Prothonotary Warblers originated from habitats similar in $\delta^{13}\text{C}$ to lowland forests, freshwater wetlands, or red mangroves in 2018 but originated from habitats similar in $\delta^{13}\text{C}$ to black or white mangrove in 2016 and 2019. Previous research on the wintering grounds of Prothonotary Warblers provides evidence that lowland forests and freshwater wetlands are of lower quality compared to mangroves (Chapter 2, Bulluck et al. 2020), leading to our prediction that early arriving birds would originate from wet mangrove habitat. As a wet habitat specialist on both the breeding and winter grounds, Prothonotary Warblers may be particularly sensitive to variation in moisture (i.e., precipitation or tidal levels). Thus, broad scale weather patterns, such as the El Niño-Southern Oscillation (hereafter: ENSO), could introduce variability in habitat quality (through variation in rainfall), and thus arrival patterns, among years. Across the Prothonotary Warbler's winter range, ENSO drives annual moisture and temperature patterns and is monitored through the Oceanic Niño Index (ONI; 3 month running mean for January to March, <noaa.gov>), where El Niño years (i.e., hot and dry) are

represented by more positive values and more negative values represent La Niña years (i.e., cool and moist). In 2016, there was an extreme El Niño event (mean= 2.1 ONI) and in 2019 there was another weaker El Niño event (mean= 0.9 ONI). In comparison, 2018 experienced La Niña conditions (-0.9 ONI) and 2017 was considered neutral (-0.2 ONI).

Interestingly, ENSO events across the four winters of our study fit what one might predict in terms of how climatic conditions may alter habitat quality variably among habitats, based on our observed variation in the arrival $\delta^{13}\text{C}$ relationships. The disproportionate impact of hot dry winter conditions on more depleted habitats (i.e., lowland forests or freshwater wetlands) could have led birds from more enriched habitats (i.e., black, white, or mixed mangrove) to arrive earlier at the breeding grounds. In contrast to mangroves, lowland forest areas can be more prone to seasonal drying as many of their canopy species are facultatively deciduous during periods of drought, and therefore are more likely to experience reductions in arthropod abundance (Richards and Windsor 2007; Studds and Marra 2007). This is especially true for younger, more disturbed forests that have shallower root systems (Cheng et al. 2020) and make up a considerable portion of lowland forests (Vancutsem et al. 2020). Additionally, open or sparsely canopied freshwater wetlands that follow seasonal wet-dry cycles may be completely devoid of water during dry extremes or normal seasonal dry cycles (due to evaporation and lower freshwater input) but in wet years may undergo minimal drying (Junk 1997; Mitsch and Gosselink 2007; Reddy and DeLaune 2008). In contrast, following cool, moist winter conditions in 2018 birds from more depleted $\delta^{13}\text{C}$ habitats (i.e., lowland forest, fresh wetlands, or red mangroves) arrived earlier. Mangroves,

which appear more buffered against dry years (e.g., Studds and Marra 2007) could experience some changes in quality when precipitation is very high. Inundation (i.e., due to flooding, tidal surges, or severe coastal storms) could reduce habitat quality from high water creating more competition for limited resources. Prothonotary warblers often forage low to the ground during the winter (Lefebvre et al. 1992), specifically on and around pneumatophores in mangrove habitats, which could function to reduce intra or inter specific competition from resident or migrants who forage higher up (Powell et al. 2021). However, during high rainfall events these areas can quickly become flooded reducing foraging opportunities (e.g., pneumatophores and mud availability) and increasing competition. These differences in habitat responses to annual variation in precipitation could alter the dynamic between habitat type and quality for overwintering migrants. For example, differences in arthropod biomass between lowland dry forests and mangrove can disappear in wetter years, reducing differences in avian body condition and spring departure dates between habitat types observed in drier years (Studds and Marra 2007). Here we observed a reversal of the relationship between winter habitat and spring arrival date in La Niña versus El Niño years. While more long-term study is needed, our results highlight the importance of studies that encompass a variety of climatic conditions to capture the potentially complex interactions between climatic cycles and the nature of carry-over effects from winter habitat.

An alternative explanation for the annual variation in the $\delta^{13}\text{C}$ -arrival date relationship is that, because Prothonotary Warblers are non-territorial on the wintering grounds, some of the between year variation might be attributable to birds moving

between habitats. Small scale spatial shifts in habitat have been documented in another wet habitat specialist (Northern Waterthrush, Smith et al 2010). However, Prothonotary Warblers wintering in Panama showed high rates of site persistence (83% in mangroves and 62% in non-mangroves) as the dry season progressed, and it is not clear if movements tended to be within or between habitats (Chapter 2). Thus, additional intensive tracking of individuals (potentially including additional habitats; e.g., cienagas in Colombia; Tonra et al. 2019; Bullock et al. 2020) throughout the winter is needed to better understand responses to annual variation in moisture, and its potential relationship to migration phenology.

We did not find evidence for direct carry-over effects from winter habitat on breeding phenology or success beyond arrival date. However, we did find evidence for multiple pathways through which winter habitat quality may indirectly impact breeding outcomes through arrival date. Arrival date negatively correlated with initial pairing success and nest success where early arrival favored early pairing and successfully fledging young. Early spring arrival to the breeding grounds allows for optimal habitat and mate selection in Prothonotary Warblers which could be particularly important for this population as high-quality territories over water are limited (Blem and Blem 1991) and predation is high (E. Ames unpublished data). Other studies have also found that the benefits of early arrival may be mediated by territory or resource acquisition, which is likely linked to individual quality in addition to arrival timing (McKeller et al. 2013). In our system, it is likely that nest type (i.e., box or tree cavity) is not driving the observed relationship as early arrival did not predict nest type (i.e., box or cavity). However, nest

type strongly predicted fledging success, where nests in cavities were approximately 5 times more likely to fledge young. In this system, boxes are used less frequently (see description in methods) than natural cavities, unlike other similar populations (i.e., Slevin et al. 2018, Mueller et al. 2019), potentially due to high predation pressure associated with boxes mounted on trees (Bailey and Bonter 2017). Similar to Petit and Petit (1996), we found that clutch initiation date was positively correlated with number of young fledged if successful and earlier first egg dates correlated with earlier fledge dates. Given our results and coupled with similar studies (i.e., Gunnarsson et al. 2005, Drake et al. 2013, Akresh et al. 2019), it seems that carry-over effects from winter habitat on breeding outcomes most often operate through indirect pathways.

Beyond the nesting period, we did not find evidence for a direct effect of winter habitat on post-fledging survival or a phenological link between fledge date and post-fledging survival or recruitment as predicted. However, number of nestlings fledged positively impacted post-fledgling survival and was linked through first egg date and arrival date to winter habitat. We may not have been able to detect a signal from fledge date due high predation rates which causes many first attempts to fail and spread fledge dates throughout the breeding season (E. Ames unpublished data). The number fledged may have improved survival by reducing the odds of being eaten by a predator when there are more siblings (Newton 1998), however it may be more likely that parents who produce more young are better quality or have a better quality territory (i.e., food resources or cover, Germain and Arcese 2014). We did not examine territorial habitat quality; however, it can be a strong predictor of post-fledging survival (Cox et al. 2014)

and can be impacted through arrival timing (e.g., Lundberg et al. 1981). Additionally, in another Prothonotary Warbler population in Illinois fledge date was negatively correlated with annual juvenal survival suggesting that spring arrival timing, and therefore winter habitat quality, likely impact these factors (McKim-Louder et al. 2013). Capturing the impacts of winter habitat quality on post-fledgling survival or recruitment may also be inherently challenging as each stage of breeding adds random and patterned variation that may obscure or negate the signal of a winter habitat effect. This is likely the case in systems that experience high rates of nest predation, assuming nest predation is not related to winter habitat quality through arrival date. Thus, studies that experimentally, or otherwise, limit predation (e.g., nest boxes with predator guards, Bailey and Bonter 2017) may be more suited to isolate the effects of winter habitat onto the post-fledging period.

Our findings contribute to the growing body of literature on carry-over effects in songbirds. We found that carry-over effects from winter habitat can carry-over to impact breeding success and post-fledging survival in a wet habitat specialist, the Prothonotary Warbler. We provide evidence for an interaction between winter habitat quality and climatic conditions, highlighting the importance of incorporating annual variation into studies of carry-over effects, particularly given projected climate variability in the future (Neelin 2006). Climate change is projected to cause continued decreased rainfall and increased temperatures across the wintering range of Prothonotary warblers, and many other Nearctic-Neotropical migrants. Additionally, tropical moist forests are undergoing rapid and vast deforestation across the tropics (Vancutsem et al. 2020) making it critical

that their preservation be prioritized. As deforestation and anthropogenic climate change continue to alter landscapes in the Neotropics, it is likely that the repercussions will be observed on the breeding grounds of many Neotropical migratory birds. This makes it critical that we act now to preserve remaining important habitats for these species (Rosenberg et al. 2016).

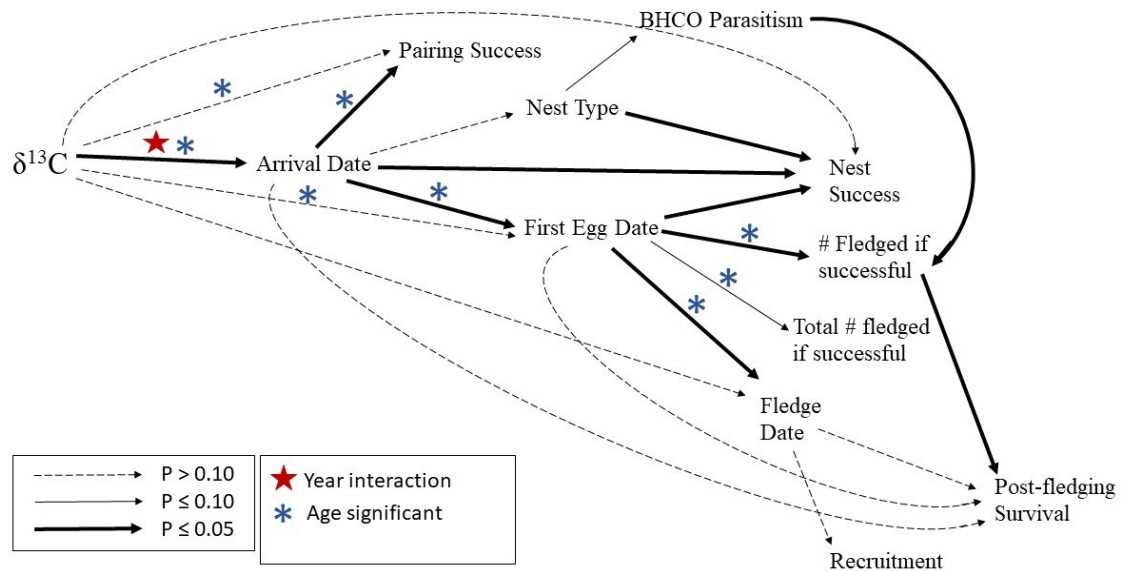


Figure 4 Analysis framework and mixed model results for carry-over effects from winter habitat quality (measured through $\delta^{13}\text{C}$) on male breeding parameters in a central Ohio population of Prothonotary Warblers from 2016-2019. Variables to the left of the arrows represent independent variable and those to the right represent dependent variables (see methods for model more details).

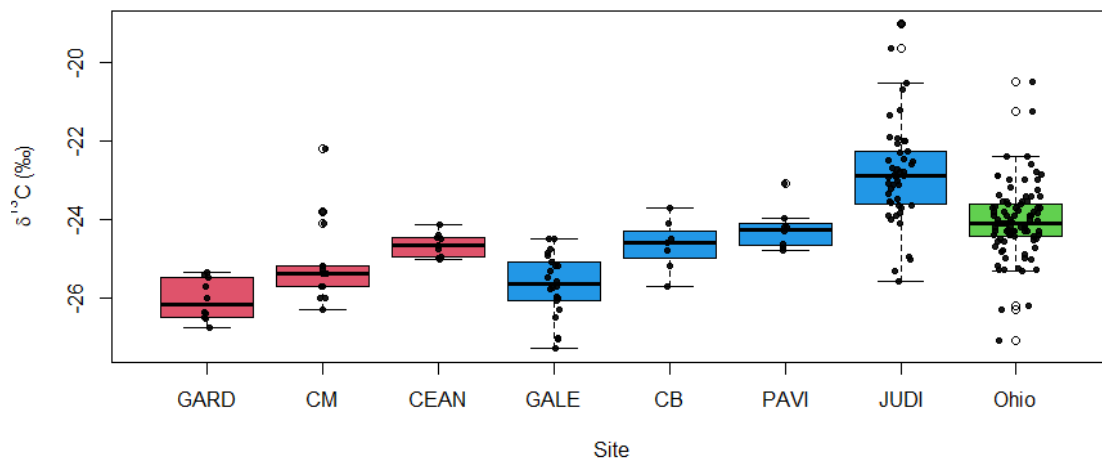


Figure 5 Stable carbon isotope ($\delta^{13}\text{C}$) values from Prothonotary Warbler claw clippings collected in Panama and Colombia by site. Birds were captured from December 2016 to February 2017 and January 2018 in Panama, and January 2016 in Colombia. Gamboa Resort (GARD), Marimonda (CM), Cerro Ancon (CEAN), Galeta Res. Sta. (GALE), Bocas del Atrato (CB), Panama Viejo (PAVI), Juan Diaz (JUDI). Red boxes represent non-mangrove habitat, blue boxes represent mangrove habitat and the one green box represents samples collected from males arriving in Ohio in during spring 2016-2019.

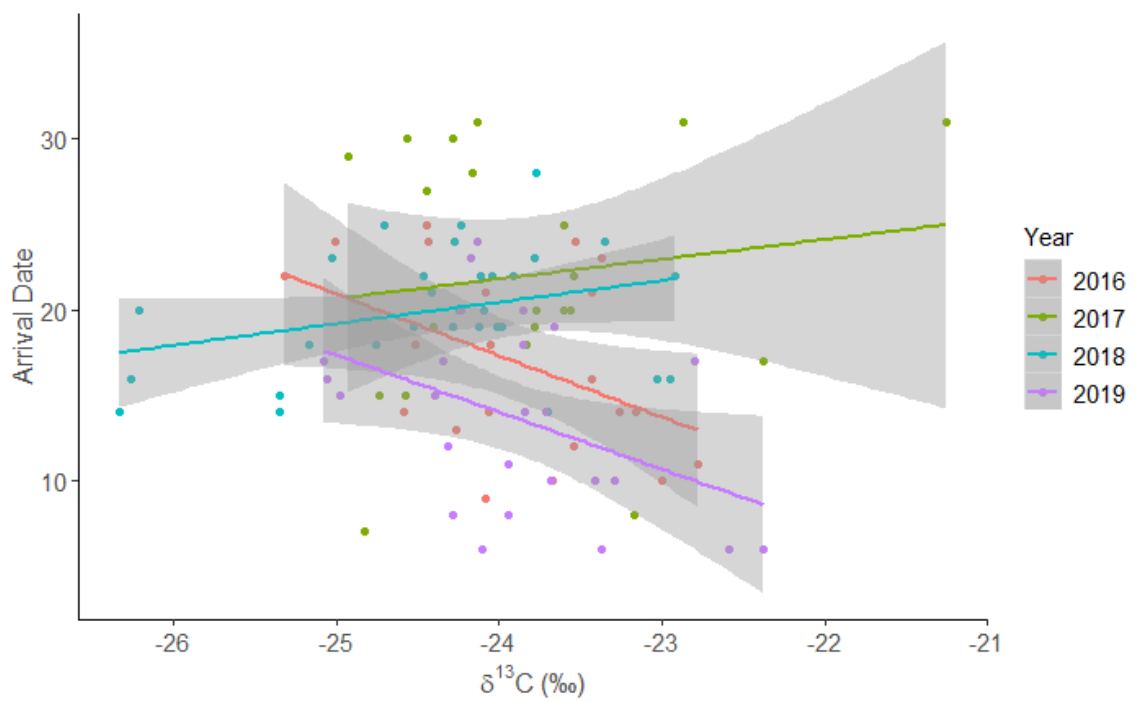


Figure 6 Spring arrival date and stables carbon isotope ($\delta^{13}\text{C}$) relationships in male Prothonotary Warblers arriving breeding at the Hoover Nature Preserve, in central Ohio, from 2016 to 2019. $\delta^{13}\text{C}$ was sampled from claw clippings collected within 7 days of arrival. Each year is displayed separately with shaded areas representing 95% confidence intervals. Arrival day 1= April 14th.

Table 5 Stable carbon isotope ($\delta^{13}\text{C}$) values from Prothonotary Warbler claw clippings collected in Panama and Colombia. Birds were captured from December 2016 to February 2017 and January 2018 in Panama, and January 2016 in Colombia. Site names and abbreviated location codes, general habitat type, $\delta^{13}\text{C}$, standard error (SE), and letters representing significant difference calculated from an anova followed by a TukeyHSD test (see methods for details).

Site	Habitat Type	$\delta^{13}\text{C}$	SE	TukeyHSD
Gamboa Resort (GARD)	Freshwater wetland	-26.1	0.53	a
Marimonda (CM)	Freshwater wetland	-25.1	1.12	ab
Cerro Ancon (CEAN)	Lowland Forest	-24.7	0.30	ab
Galeta Res. Sta. (GALE)	Red mangrove	-25.7	0.17	a
Bocas del Atrato (CB)	Red/mixed mangrove	-24.7	0.25	ab
Panama Viejo (PAVI)	White Mangrove	-24.2	0.20	b
Juan Diaz (JUDI)	Black mangrove	-22.8	0.19	c

Chapter 4 Breeding effort and investment influence events during post-breeding molt and winter in the Prothonotary Warbler

Introduction

For many organisms, seasonal cycles in climate impose constraints on the duration of life history stages and limit resources across the full annual cycle. This is especially true for migratory birds who are constrained by the need to escape temperate breeding areas before harsh conditions impact current or future survival (Newton 2007). Timing constraints may be mitigated by overlapping portions of the annual cycle, but this can result in trade-offs (Wingfield 2008). For instance, at the end of the temperate growing season, resources and time must be balanced between reproduction, molt (the annual replacement of feathers) and migratory preparation, which may require sacrifices to one or more of these critical events (Ramenofsky and Wingfield 2007). Costs of these trade-offs can carry-over to subsequent stages of the annual cycle, such as migration and the stationary non-breeding period (hereafter: winter) and impact outcomes in those stages (Harrison et al. 2011). For instance, extending reproduction for as long as possible within the breeding season can increase reproductive success (Newton 1998) but could come at the cost of survival on migration or during winter (Ricklefs 1977). Identifying these carry-over effects is fundamental to understanding seasonal variation in mortality and limits on breeding output, which is critical to effective conservation strategies of migratory populations (Faaborg et al. 2010).

When reproduction is extended into the annual prebasic molt (i.e., post-breeding molt; Humphrey and Parkes 1959, Howell et al. 2003), individuals must either overlap the two stages, delay molt in favor of breeding effort, or abandon breeding effort. If resources are abundant, both rearing of young and molting feathers may be the most beneficial to both processes. However, even with abundant resources, reduced energetic condition associated with simultaneously rearing young and molting can lead to increased foraging effort, decreased survival of young (Svensson and Nilsson 1997), reduced body condition, mismatches in endocrine states (Williams 2012), slower feather growth (Echeverry-Galvis and Hau 2012), and protracted or delayed molt (Ogden and Stutchbury 1996). Delaying molt until young are independent might cause molt to occur during a more limited time in seasonal resources (Newton 1998), make it necessary to increase the pace of molt, or cause overlaps between molt and migratory preparation. Both molt and migratory preparation are energetically demanding (Lindstrom et al. 1993, Newton 2007) and limited late summer food resources, due to environmental conditions (i.e., reduced precipitation, temperature, or leaf senescence), can impact late breeding effort and molt (Siikamäki 1998, Verhulst and Nilsson 2008). Molting more feathers simultaneously and quickly can shorten molt duration potentially avoiding the need to overlap molt and migration (i.e., molt-migration; Tonra and Reudink 2018), but can also reduce feather quality (i.e., feather density and stiffness; Dawson et al. 2000), and thermal tolerance (Vágási et al. 2012). In either case, the consequences of shortening molt duration in order to extend reproduction can carry-over to impact migration phenology (Heckscher et al. 2017) and winter habitat quality (Latta et al. 2016). Alternatively, abandoning current

reproduction to devote energy toward molting would maximize survival probability (e.g., Mumme 2018) and reduce potential carry-over effects in subsequent stages but at the cost of current reproduction.

Researchers have made considerable progress in understanding winter to breeding carry-over effects in songbirds (Harrison et al. 2010). However, carry-over effects from breeding to nonbreeding stages (i.e., molt, migration, winter) have received considerably less attention, particularly for small (<20g) migratory songbirds (but see Latta et al. 2016). A major challenge in understanding carry-over effects in small migratory birds is the difficulty in tracking them across the annual cycle, especially during periods when direct observation or capture are difficult such as molt, when birds reduce visibility to decrease predation risks (Jenni and Winkler 2020). This challenge can be somewhat overcome by utilizing intrinsic markers (e.g., feathers and claws) that carry indicators of physiological condition, such as stress (Madliger 2018) or nutritional state (Grubb 2006), and habitat use (i.e., stable isotopes, Bearhop et al. 2003) from tissues grown in preceding stages.

In birds, feathers can provide a relatively non-invasive method for studying carry-over effects from breeding to nonbreeding periods, as they capture information as they are grown, and since feather tissue is inert, the bird carries this information until the following molt cycle. Feathers from post-breeding prebasic molt can be collected during the winter or upon return to the breeding grounds the following year to determine the physiological state of an individual during the preceding season (Hansen et al. 2016, Latta et al. 2016, Romero and Fairhurst, 2016). Corticosterone (hereafter: CORT), the

primary avian glucocorticoid, can be measured from such feathers to provide an estimate of stress levels during the time the feather was grown (Madliger et al. 2018). Feather corticosterone (fCORT) provides an integrated measure of circulating CORT (Bortolotti et al. 2008, Jenni-Eiermann et al. 2015). Latta et al. (2016) found Louisiana Waterthrush (*Parkesia motacilla*) arriving to the wintering grounds with lower fCORT had higher quality winter territories, measured through insect availability, and attained better body condition as the winter season progressed. This suggests that stressors experienced during molt can carry-over to impact performance on the wintering grounds. Although CORT can represent stressful environmental conditions (i.e., poor nutritional state) and correlate to fitness consequences such as feather quality (DesRochers et al. 2009), it can vary depending on the stage of the annual cycle, age, and sex. For instance, elevated CORT is adaptive in facilitating hyperphagia during migratory preparation (Holberton 1999).

Feathers collected during the winter or following spring can also provide a useful index of nutritional condition during post-breeding molt by measuring feather growth rate (i.e., ptilochronology, Grubb 2006). When feather keratin is laid down during growth a series of light and dark bands are produced that represent periods of day and night in songbirds (Grubb 2006). By measuring the width of these bands, we can estimate feather growth rate (i.e., mm/day; hereafter: FGR) for an individual at the time that the feather was grown. FGR can provide a useful measure of nutritional status at the time of growth (Grubb 2006) and correlates to within season reproductive effort (White et al. 1991), future reproductive effort (Takaki et al. 2001), molt duration (De La Hera et al. 2011),

and migration phenology (Stutchbury et al. 2011). However, growing feathers too quickly, especially when nutrients are limited, can result in lower feather quality (i.e., mass and length; Dawson et al. 2000, De La Hera et al. 2009) which could have consequences for long-term feather wear, flight performance, and thermoregulation.

By combining measures of breeding effort, fCORT , FGR, and measures of feather quality, we can gain a more comprehensive understanding of how breeding impacts post-breeding molt. However, to determine whether these events carry-over to impact future events individuals must be tracked beyond the breeding grounds which can be challenging for small passerines that cannot carry long-lasting tracking devices (i.e., GPS or satellite tags, Mckinnon et al. 2018). Intrinsic markers also provide a potential solution, specifically using stable carbon isotope ratios (hereafter: $\delta^{13}\text{C}$) to estimate winter habitat quality. Due to stomatal limitation and photosynthetic pathways in dominant plants, $\delta^{13}\text{C}$ varies naturally across a wet to dry moisture gradient in tropical habitats (e.g., Marra et al. 1998; Smith et al. 2010). Birds using these habitats incorporate $\delta^{13}\text{C}$ from the diet into their tissues, and slow growing tissues (i.e., claw clippings) collected at arrival to the breeding grounds can provide a useful index of past habitat quality (e.g., Bearhop et al. 2003, Reudink et al. 2009). Thus, we can determine if physiological state during the post-breeding period impacts subsequent winter habitat use by combining multiple intrinsic markers ($\delta^{13}\text{C}$, FGR, and fCORT) collected at one time in the annual cycle. If events during post-breeding molt impact winter habitat use it could represent a negative feedback loop on reproductive limits, as winter habitat can

subsequently impact arrival on the breeding grounds, leading to later fledging dates, and fewer opportunities for double brooding (Ogden and Stutchbury 1996).

In this study, we aim to expand knowledge of carry-over effects by examining links between breeding events, molt, and winter habitat, and specifically how they function in a species of conservation concern, the Prothonotary Warbler (*Protonotaria citrea*). First, we explore the relationship between energetic effort and time investment during breeding to determine if they impact nutritional condition (i.e., FGR) and stress (i.e., fCORT) during the post-breeding molt. We predict that late breeders will have lower FGR, due to the higher nutritional demands of overlapping breeding and molt, and higher fCORT due to increased stress from breeding activities and migratory preparation, which adaptively increases fCORT (Lohmus et al 2003). Second, we test whether FGR and fCORT impact feather quality (i.e., feather area density) and predict that high fCORT and a fast FGR will produce lower quality feathers. Third, we test whether FGR, fCORT , and feather quality impact winter habitat use (measured through $\delta^{13}\text{C}$) during the spring pre-migratory period. We predict that birds with higher fCORT and slower growth rates will utilize lower quality winter habitat. To test these predictions, we collected feathers and claws from two groups of Prothonotary Warblers: birds returning to breeding areas that were monitored for breeding metrics the previous year, and birds occupying multiple habitats on the wintering grounds in Panama.

Methods

Study species

The Prothonotary Warbler is a Neotropical migratory songbird that specializes on forested wetland habitat during both breeding and winter (Petit 1999). During the breeding season, they occupy swamps, bottomland hardwood forests, and riparian corridors across the eastern half of North America. They are unique among wood warblers as they are one of only two species that are secondary cavity nesters and the only one in eastern North America. They also readily use nest boxes when placed in acceptable habitat and much of the research on breeding has been on populations using boxes (e.g., Blem and Blem 1991). Nest initiation date has been shown to correlate with clutch size and rates of double brooding (producing two sets of offspring in a single breeding season), with later initiation resulting in smaller clutches and reduced rates of double brooding (Petit and Petit 1996). Prothonotary Warblers regularly double brood (Petit 1999), and double brooding in other songbird species has been shown to be a driver of lifetime reproductive success (Gillis et al. 2008), as well as annual reproductive output (Nagy and Holmes 2005).

At the end of the breeding season, adult Prothonotary Warblers undergo a complete prebasic molt, replacing all flight (i.e., wing, tail) and body feathers (Pyle 1997). During the late winter months, before spring migration, they also complete a partial prealternate molt which includes only some body feathers (Chapter 2). Since they retain their flight feathers across the full annual cycle, we can collect feathers from known individuals returning to the breeding grounds and relate intrinsic markers to reproduction and molt in the previous season. Prothonotary Warblers depart the breeding grounds in late July through late August, depending on breeding location, and arrive on

the stationary non-breeding grounds in late September to late October (Tonra et al. 2019). During this period, they utilize a range of wet forest habitats as well as alternative habitats such as upland broadleaf forests, city parks and gardens. They are most abundant in mangroves – one of the rarest and most endangered forest types globally (Sandilyan and Kathiresan 2012) – and inland freshwater wetlands in Colombia (Bulluck et al. 2019). $\delta^{13}\text{C}$ signatures from these habitats can be used to approximate general habitat type and quality (see Chapter 3). Due to recent population declines, likely caused by extensive loss and degradation of both breeding and wintering habitat, the Prothonotary Warbler is a species of concern both nationally and in many states, including Ohio (<ohiodnr.gov>). Given the threats to Prothonotary Warbler populations on both wintering and breeding grounds, it is critical that a full annual cycle approach be taken to their conservation and management.

Field data collection

From 2016-2019, we studied the Prothonotary Warbler population at the Hoover Nature Preserve, which consists of 925 acres of forested wetland surrounding the Hoover Reservoir, Galena, OH (40.1990° N, 82.8852° W; for more details on the field site see Chapter 3). Early every spring, before Prothonotary Warblers arrived, we conducted arrival surveys (two-day intervals) by walking pre-established transects and identifying individuals using visual and auditory cues. We identified all previously captured individuals with color bands and for new individuals we used unique external features to identify them until capture. We were not able to accurately determine arrival dates for

most females as they often visit multiple territories before settling. We attempted to capture all birds as soon as possible after detection using conspecific playback and mist nets. Females were less responsive to target netting so often were not captured until incubation began and they could be captured off the nest. Each newly captured bird received a unique combination of three plastic color bands and a USGS aluminum band. For both new captures and recaptures, we recorded sex, age (older = feathers grown at the end of second or later breeding season, younger = feathers grown at the end of their first breeding season), mass ($\pm 0.01\text{g}$), wing ($\pm 0.1\text{mm}$), tail ($\pm 0.1\text{mm}$), and tarsus ($\pm 0.1\text{mm}$). We collected the right outer most rectrix (6th tail feather) because growth bars appeared more visible on this feather and other studies have struggled to visualize growth bars on other warbler species (Ruhs et al. 2019). We avoided collecting adventitiously replaced feathers (i.e., flight feathers replaced between post-breeding molt and spring arrival) by checking that feathers did not appear fresher or less worn than other rectrices. Additionally, we collected claw clippings ($\sim 2\text{mm}$ from each central toenail) for $\delta^{13}\text{C}$ analysis from each male with a known arrival date. We only used samples collected within 7 days of an individual's arrival to reduce the likelihood that samples contained signatures from migration or the breeding grounds (Reudink et al. 2009, Tonra et al. 2011).

We monitored breeding effort and time investment for each individual following their arrival to the breeding site. We used systematic searching and adult behavior to locate both natural cavity and artificial box nests. We checked nests regularly (every 2-5 days) to determine first egg date, number of eggs, nestlings, and fledglings, and date of

fledging using a handheld nest camera (Explorer Premium, model 8803AL) mounted on a pole (for nests over 3 meters). We monitored each territory for subsequent nest attempts after fledging or failure. Since females often switched mates after a failed attempt or occasionally after successfully fledging a first brood, we followed each individual to determine their final breeding status (i.e., completion date and total fledged for breeding season).

We considered breeding parameters that represented either an energy or time investment. We considered total number of eggs, eggs laid per nest attempt, total number of nestlings, nestlings per attempt, and total number fledged for the season to be estimates of energy investment during the breeding season. To estimate time invested in reproduction, we used date of breeding completion (i.e., failure or fledge date of last nest attempt), arrival date to completion date (males only), and first egg date to completion date (females only). All dates were expressed as ordinal dates. Due to extenuating circumstances (e.g., floods, nests on private property) and high predation rates, we were not able to collect all breeding parameters for each individual. When this occurred, we only included parameters that were complete for that individual. For example, a female with accurate first egg and completion dates but an attempt with an unknown egg count (due to predation) would not be included in the total eggs or eggs per attempt models but in all the other models. At the end of the 2019 breeding season, we documented the degree of molt for adults still present at the study sites by systematically searching territories and conducting playback. When birds were located, we documented the progression of molt through high resolution photographs, intensive visual observation, or

both; however, since we did not capture all of them the molt scores we assigned are estimates. Molt of body feathers was recorded on a scale from 0-4 (0= no molt visible, 1= >0< %5 feathers in molt, 2= >5< 20% feathers in multiple feather tracts, 3= >20%<50% feathers in multiple feather tracts, 4= >50% from many tracts), however this measure only estimated visible molt so molt may have been higher in some areas where molt is less visible. Wing and tail molt were also recorded on a scale of 0-4 (0= no molt visible, 1= ~1 feather in molt, 2= 2-3 feathers in active molt, 3= 4-5 feathers in active molt, 4= >5 feathers in active molt and less than halfway grown with large gap visible or no tail present). Unfortunately, due to the global pandemic in 2020 we were not able to collect feathers from returning birds to explore how molt intensity or timing impacted FGR or fCORT .

In addition to collecting samples on the breeding grounds, we also captured Prothonotary Warblers at five sites along the Panama Canal Region, Panama from December 2016 to February 2017 (see Chapter 2 for a full description of each habitat). We used mist nets to passively and actively (using distress calls and chips) capture Prothonotary Warblers and collected claw and feather samples as described above. These samples were used along with breeding samples to explore the relationship between fCORT , FGR, feather density, and winter habitat (i.e., $\delta^{13}\text{C}$). Since breeding data was unknown for these individuals, they were not included in any of the models that investigated the impact of breeding on fCORT or FGR.

Feather growth rate and area density

In order to determine the impact of breeding on FGR, we used feathers from returning individuals with breeding history from the previous season. We calculated FGR by attaching each feather to black card stock with a small amount of mounting putty attached to the calamus. A set of feathers were then placed feather side down on a scanner (HP ENVY 4500 Series) with a small square of grid paper or flat ruler for scale and scanned (gray scale, 300dpi, low compression). FGR was calculated by measuring a segment containing 2-5 growth bars using the program ImageJ (Schneider et al. 2012, Ruhs et al. 2019) and then dividing by the number of growth bars within the segment (Ptilochronology; Grubb 2006). Thus, FGR represents average daily feather growth (0.01mm) and higher values can be interpreted as having been grown faster. Although measuring a greater number of growth bars may represent a more complete understanding of an individual's condition during feather replacement, we limited the number of growth bars measured to 2-5 as this was the number visible on most individuals and represented approximately one third of feather growth (Results). Additionally, the area of each feather was calculated in ImageJ by tracing the feather outline with the polygon tool (cm^2). Feather area density (hereafter: density) was then calculated by dividing the mass ($\pm 0.01\text{mg}$) by the area ($\pm 0.001\text{cm}^2$) and is reported as mg/cm^2 . To reduce bias, all samples were measured by the same observer (E. Ames).

Corticosterone analysis

We measured fCORT using a methanol-based extraction, modified from Bortolotti et al. (2008), and a commercial ELISA kit (Corticosterone ELISA kit; Neogen

Corporation, Ayr, UK) as validated by Carbajal et al. (2014). For each feather, we recorded the mass (± 0.001 mg) and length (± 0.1 mm) before removing the distal portion of the calamus, mincing the feather, and storing in a glass vial for methanol extraction. The methanol extraction was achieved by incubating the minced feather in methanol overnight, vacuum filtration, and evaporating under N₂ gas. Samples were then reconstituted following the Corticosterone ELISA kit directions. Assay recovery was assessed by adding 20 μ L of tritium-labeled CORT to each sample. Across all assays, extraction efficiency was >92%. Inter-assay variation based on the coefficient of variation (%CV) of relative binding of kit standards was 9.1% and intra-assay variation based on the average %CV between the duplicate unknown samples was 4.1%.

Stable carbon isotope analysis

Breeding and winter claw samples were prepared for analysis at the Tonra Lab for Avian Ecology at The Ohio State University. Samples were washed with 2 ml of 2:1 chloroform to methanol for 2 hours to remove superficial contaminants and allowed to dry for 48 hours. We then recorded the mass (± 0.0001 mg) and packed each sample into tin capsules. We used a Thermo Delta V Advantage mass spectrometer in continuous flow mode coupled to an Elementar vario ISOTOPE Cube Elemental Analyzer via a Thermo ConFlo IV located at the Smithsonian MCI Stable Isotope Mass Spectrometry Lab to analyze all samples, and calculations were performed in Isodat 3.0 software. All runs included a set of reference materials (i.e., include Costech Acetanilide [calibrated to USGS40 (L-glutamic acid) and USGS41 (L-glutamic acid)] and USGS66 (glycine)) for

every 10-12 samples and reproducibility of reference materials was $\pm 0.2\%$. Carbon isotope ratios ($^{13}\text{C}/^{12}\text{C}$) are reported in delta (δ) notation in per-mil units (‰) as deviation from the Vienna Pee Dee belemnite standard.

Statistical analysis

We assessed the impact of breeding effort and time investment on FGR and ρCORT in program R (v 4.0.3, R Core Team 2020) using linear mixed-effects models (males) built in the “nlme” package (Pinheiro et al. 2015) and linear fixed-effects models (females) built using the “lm” function. We log transformed ρCORT for females in the breeding models to meet normality assumptions but not females in the broader models or males as they fit normality assumptions without transformation. We included a random intercept in each male model to account for individuals that were sampled more than once across years. We did not include a random intercept for individual in the female models as only 2 females were sampled in more than one year causing convergence failure when year was included. For each model, we started with a full model that included: the explanatory breeding variable of interest (Figure 7), year, age, and a three-way interaction term. We removed non-significant predictors ($P > 0.10$) in a stepwise fashion (excluding the variable of interest) starting with the least significant interaction terms. We included age in our breeding effort and investment models as inexperienced Prothonotary Warblers (i.e., those in their first breeding season) often have fewer attempts and reduced breeding effort (E. Ames unpublished data) and are undergoing their first pre-basic molt. For models with a significant interaction, we performed a *post-*

hoc analysis using the “emtrends” function in the “emmeans” package to determine if the slope of the variable of interest was significantly different from zero at each level of the interaction (e.g., male or female) and reported confidence intervals for each level.

Results

We collected feathers from 41 males (30 older, 11 younger) and 19 females (12 older, 7 younger) with known breeding history the previous year. We measured FGR on 136 males and 110 females (with or without previous breeding histories). Growth bars were visible across the whole feather for 11 males (mean # of bars = 14.27 ± 0.33) and 13 females (15.38 ± 0.36). During late July and early August of 2019, we located 33.3% of color-banded males (11/29 older and 2/10 younger) still on or near (within 300m) their breeding territories and 12.0% of color-banded females (2/18 older and 1/7 younger). Simultaneous rectrix molt, where the whole tail was missing or growing simultaneously, was observed in 38% of remaining males (5/13) and no females (0/3).

Breeding energetic effort and feather growth rate

FGR did not vary between younger (mean= 2.72) and older (mean= 2.66) males ($t = -1.06$, $df=25$, 95% CI= -0.18-0.06, $P = 0.30$) or between younger (mean= 2.53) and older (mean= 2.48) females ($t = -0.46$, $df=20$, 95% CI= -0.26-0.17, $P = 0.65$), however it was lower for females (mean= 2.50) compared to males (mean= 2.67; $t = -2.90$, $df=37$, 95% CI= 0.05-0.29, $P = 0.006$).

The number of eggs produced during the breeding season did not correlate with FGR in females or males and FGR varied by year in males (Table 6). FGR also varied between years for males and did not show a relationship with number of eggs produced per attempt (Table 6). However, females who produced more eggs per nest attempt had slower growth, with younger females showing faster growth than older females and growth varying by year (Table 6). The number of nestlings produced did not relate to FGR in males and feather growth varied by year (Table 6). However, in females, producing more nestlings correlated with slower growth. In males, FGR showed no relationship with number of nestlings produced per attempt and FGR varied by year (Table 6). The relationship between nestlings per attempt and FGR in females depended on year (Table 6). In post-hoc analysis, FGR and number of nestlings per attempt had a negative relationship in 2016 ($\beta = -0.08$, $SE = 0.03$, 95% CI = -0.1431 - -0.0145) and non-significant relationships in the other two years (2017: $\beta = -0.07$, $SE = 0.05$, 95% CI = -0.18 - 0.04; 2018: $\beta = 0.09$, $SE = 0.04$, 95% CI = -0.01 - 0.18), suggesting that in 2016 only, producing more nestlings resulted in slower feather growth. The total number of young fledged was not related to FGR in females or males and FGR varied by year in males (Table 6).

Breeding time investment and feather growth rate

For males, the relationship between breeding completion date and FGR varied with year (Table 6). Late breeding males grew their feathers faster in 2017 ($\beta = 0.006$, $SE = 0.002$, 95% CI = 0.002 - 0.01) and there was no relationship in 2018 ($\beta = -0.0008$,

SE= 0.002, 95% CI= -0.007-0.005). FGR was not correlated with completion date in females (Table 6). Similar to completion date, for males FGR and the amount of time between arrival and breeding completion was dependent on year (Table 6), and only 2017 showed a significantly positive relationship (2017: β = 0.008, SE= 0.002, 95% CI= 0.004-0.01; 2018: β = 0.0001, SE= 0.002, 95% CI= -0.005- 0.006). The time between first egg date and completion date for females was negatively correlated with FGR (Table 6), suggesting that the more time a female devotes to breeding the slower they grow their feathers during the post-breeding molt. However, this relationship is based on a small number of females so caution should be used in interpreting these results.

Breeding energetic effort and feather CORT

r CORT did not vary by male age (young mean= 6.45, old mean= 5.76; t = -1.27, df =22, P = 0.22) or female age (young mean= 6.93, old mean= 7.45; t = 0.42, df =19, P = 0.68). The number of eggs produced across the breeding season showed no relationship with feather CORT for males or females and CORT varied between years for females (Table 7). In both males and females, the number of eggs produced per nest attempt did not correlate with r CORT and females showed higher r CORT in both 2017 and 2018 compared to 2016 (Table 7). The relationship between r CORT during the post-breeding molt and number of nestlings differed between year in males (Table 7), where 2016 (β = -0.21, SE= 0.12, 95% CI= -0.46- 0.04) and 2018 (β = 0.04, SE= 0.20, 95% CI= -0.39-0.46) showed no relationship, and in 2017 (β = 0.41, SE= 0.18, 95% CI= 0.03- 0.79) males that produced more nestlings throughout the breeding season had higher r CORT

during post-breeding molt. For females, the relationship between r CORT and the number of nestlings produced was not significant and r CORT varied between years. Similarly, the correlation between r CORT and number of nestlings per attempt was dependent on year for males (Table 7) with only 2017 ($\beta = 0.60$, $SE = 0.23$, 95% $CI = 0.11 - 1.09$) showing increased r CORT in males that produced more nestlings per attempt (2016: $\beta = -0.06$, $SE = 0.20$, 95% $CI = -0.49 - 0.38$; 2018: $\beta = 0.13$, $SE = 0.30$, 95% $CI = -0.49 - 0.77$). The number of nestlings per attempt did not predict r CORT for females and r CORT varied by year (Table 7). For males, the relationship between number fledged and r CORT, like number of nestlings and nestlings per attempt, was dependent on year (Table 7) where only 2017 showed a positive relationship ($\beta = 0.45$, $SE = 0.17$, 95% $CI = 0.08 - 0.81$) and the other two years showed no relationship (2016: $\beta = -0.02$, $SE = 0.16$, 95% $CI = -0.36 - 0.31$; 2018: $\beta = 0.21$, $SE = 0.20$, 95% $CI = -0.21 - 0.63$). r CORT and number fledged were not correlated in females and varied between year.

Breeding time investment and r CORT

For males, the relationship between r CORT and completion date depended on year, with only 2016 having a negative relationship (2016: $\beta = -0.07$, $SE = 0.02$, 95% $CI = -0.13 - -0.02$; 2017: $\beta = 0.02$, $SE = 0.02$, 95% $CI = -0.03 - 0.06$; 2018: $\beta = 0.01$, $SE = 0.03$, 95% $CI = -0.06 - 0.07$; Table 7). In females, the relationship between r CORT and completion date was dependent on age and r CORT varied by year (Table 7). Older females that finished breeding earlier had higher r CORT ($\beta = -0.02$, $SE = 0.007$, 95% $CI = -$

0.03- -0.005) and younger females did not show a significant relationship ($\beta = 0.002$, $SE = 0.008$, 95% $CI = -0.02 - 0.02$).

The relationship between $fCORT$ and the time from arrival to completion date in males was dependent on year where only 2016 showed a negative relationship (2016: $\beta = -0.07$, $SE = 0.03$, 95% $CI = -0.13 - -0.02$; 2017: $\beta = 0.04$, $SE = 0.02$, 95% $CI = -0.02 - 0.09$; 2018: $\beta = 0.02$, $SE = 0.03$, 95% $CI = -0.05 - 0.09$; Table 7). For females, the relationship between first egg date to completion date and $fCORT$ depended on female age and $fCORT$ varied by year (Table 7). In this case, only older females showed a significant relationship between first egg date to completion date and $fCORT$ (Old: $\beta = -0.02$, $SE = 0.008$, 95% $CI = -0.03 - 0.0007$; young: $\beta = 0.01$, $SE = 0.01$, 95% $CI = -0.01 - 0.03$), where older females that ended breeding early had higher $fCORT$ than late breeders.

Feather growth rate, density, and winter habitat

FGR negatively predicted feather density (i.e., fast grown feathers were less dense) with males having more dense feathers than females, however FGR did not predict winter habitat $\delta^{13}C$ (Table 8).

$fCORT$, feather density and winter habitat

The relationship between $fCORT$ and density differed between sexes and varied by year, where females showed a non-significant relationship that trended positive, and males had a significant negative relationship (Table 8). Birds with higher $fCORT$ wintered in habitats with more enriched (i.e., positive) $\delta^{13}C$ (e.g., black or white

mangrove) with 2017 and 2018 generally showing more negative $\delta^{13}\text{C}$ compared to 2016 and 2019 (Table 8).

Discussion

Identifying carry-over effects is fundamental to understanding seasonal variation in mortality and limits on breeding output, and in turn developing effective conservation strategies for migratory populations. Although progress has been made in understanding winter to breeding carry-over effects in songbirds, we still lack a clear understanding of carry-over effects from breeding to nonbreeding, especially for small migratory songbirds. In this study, we examined links between breeding events, molt, and winter habitat utilization in a breeding and wintering population of Prothonotary Warblers. We found evidence breeding events correlate with post-breeding stress (i.e., rCORT) and nutritional condition (i.e., FGR), suggesting that breeding can carry-over to the post-breeding period. Additionally, we found that an individual's nutritional condition during post breeding molt predicts future feather quality (i.e., density) and stress levels during molt correlate with future winter habitat use. These results suggest that events during breeding (i.e., effort or investment) can carry-over to the molt and winter stages in the Prothonotary Warbler. However, we found considerable variation in relationships between years, sexes, and, in some cases, age. This highlights the need for further investigation into the underlying mechanisms causing this variation.

Males

For male Prothonotary Warblers, we did not find evidence that breeding effort (i.e., numbers of eggs, nestlings, or young fledged) influenced FGR during post-breeding molt. However, time investment correlated with FGR, where late breeding males grew feathers faster. This relationship was only observed in 2017 and did not fit our prediction that late breeding males would grow their feathers slower due to increased nutritional demands from overlapping breeding and molting. This suggests that annual variation, such as environmental conditions on the breeding grounds or survival during the non-breeding period, can either mitigate, exacerbate, or obscure the consequences of late breeding on FGR. Although we predicted late breeders would overlap breeding and molt, we did not directly document an overlap between the two (but see 2019 molt results). Rather than overlapping the two stages, the majority of male Prothonotary Warblers may delay molt or abandon breeding effort. The speed of molt, which is controlled by FGR and intensity (i.e., number of feathers molting at once) can be correlated with photoperiod, where molt speed increases as photoperiod decreases (Dawson et al. 2000). However, this relationship may be based largely on intensity rather than FGR (Rohwer and Rohwer 2013). Additionally, Mumme et al. (2021) found evidence that shorter photoperiod was associated with slower molt speed in 13 Parulid warblers and suggested this is related to resource availability, however they did not separate the effect of FGR and intensity. Given that photoperiod would not account for the variability between years and that Parulid warblers show slower speed later in the seasons, it is unlikely that it explains our highly variable results. It is possible that individual male quality could drive higher FGR in Prothonotary Warblers, as higher quality males have more breeding

opportunities and acquire wetter (i.e., higher quality) territories with more abundant or consistent resources (Petit and Petit 1996, Blem and Blem 2013, Bulluck et al. 2017). Given this unexplained variability, it seems likely that individual male quality or environmental conditions (see below for further discussion) could be driving these relationships and warrant further investigation.

Similar to other studies (i.e., de la Hera et al. 2009, Vagasi et al. 2012) and as predicted, we found that faster FGR correlated with less dense feathers for male Prothonotary Warblers. Given that breeding events can impact FGR, at least in some years, and that FGR reduces feather quality, it appears likely that carry-over effects from breeding could impact later stages of the annual cycle in Prothonotary Warblers. However, it is unclear how these carry-over effects would manifest, given that we did not observe a correlation with winter habitat use. Less dense feathers may degrade more quickly from normal wear (Møller and Nielsen 2018) and reduce flight performance (Echeverry-Galvis and Hau 2013), however consequences from reduced density may not be apparent until feathers have aged and worn considerably. If this is the case, non-lethal carry-over effects from FGR may not be evident until spring migration (i.e., speed of migration) or breeding (i.e., mate acquisition) which we did not quantify in this study. Annual variation in weather conditions during both post-breeding molt and winter, which can drive events such as molt-migration (Pageau et al. 2020), may influence these relationships through abundance of resources or foraging efficiency. The post-breeding period in July 2017 was unseasonably stormy and had almost double the total rainfall of 2018, yet August 2018 was wetter than August 2017. Thus, rainfall dependent food

availability (Newton 1998) or available habitat (i.e., flooding) during the post-breeding molt may have produced some of the annual variation observed in our study.

We found support for our prediction that males who invest more effort in breeding would show higher fCORT , similar to other studies of breeding effort and CORT (Done et al. 2011, Crossin et al. 2013). However, similar to FGR and breeding investment, this relationship was only apparent in 2017, suggesting that environmental conditions that year or individual quality, potentially in conjunction with environmental conditions, may have influenced stress and nutritional condition. Other studies have documented relationships between CORT and environmental conditions, such as habitat quality (i.e., moisture, Marra and Holberton 1998), noise pollution (e.g., Kleist et al. 2018), high temperatures (Newberry and Swanson 2018) and disease outbreaks (Harms et al. 2015). However, responses to environmental conditions may not always be detectable especially when conditions don't elevate stress levels above normal operating levels (Madliger et al. 2015), potentially explaining why we only detected a relationship in a year with extreme weather conditions. We also found evidence that time investment in breeding impacts fCORT , however it was in the opposite direction as predicted, where breeding late correlated with reduced fCORT and was only observed in 2016.

Unfortunately, we do not have FGR for 2016 and thus cannot make comparisons with fCORT , but compared to 2017, weather conditions in 2016 were relatively mild with a wetter August. This highlights the context-dependent nature of fCORT (Aharon-Rotman et al. 2017) and suggests that further investigation is needed to understand drivers of these relationships. Similar to FGR, increased fCORT correlated with reduced feather

density, supporting the idea that there are trade-offs between elevated fCORT and feather quality (DesRochers et al. 2009, Lattin et al. 2011). The potential consequences of decreased feather quality from high fCORT would likely manifest similarly to those of FGR described above, where events such as winter survival or migratory speed might be impacted. Finally, as predicted, we found that fCORT was positively related to $\delta^{13}\text{C}$ from the wintering grounds, where males with higher fCORT wintered in habitats with more enriched $\delta^{13}\text{C}$ (i.e., black or white mangrove, Chapter 3). However, given our findings in Chapter 3, that winter $\delta^{13}\text{C}$ does not always follow a clear quality gradient in Prothonotary Warblers, interpreting this relationship may not be straightforward. Interestingly, the relationship between fCORT and winter habitat did not vary between year like it did for arrival date and habitat (Chapter 3), suggesting that in some years (i.e., low precipitation) having higher fCORT may be beneficial in relation to wintering location.

Females

For females, greater breeding effort (i.e., number of eggs per attempt, nestlings, and nestlings per attempt) correlated with slower FGR, as predicted, but only in 2016. In addition, length of breeding investment (i.e., first egg date to completion date but not completion date) of females was correlated with slower FGR in both years. Combined, these results support our prediction that the more effort and time a female devotes to breeding the slower they grow their feathers during the post-breeding molt. Breeding is especially nutritionally demanding for females (Perrins 1970), particularly in species like

the Prothonotary Warblers where they not only produce eggs but also incubate and brood young. Additionally, the cost of egg production and incubation in females has been shown to have future reproduction and fitness costs (Newton 1998), such as survival (Visser and Lessers 2001). Females may be less likely to abandon young compared to males, more likely to delay molt in favor of breeding, initiate molt later (E. Ames unpublished data for Prothonotary Warblers), and have longer molt duration for some species (e.g., Hooded Warbler; Ogden and Stutchbury 1996, Mumme 2018). Slow FGR correlated with denser feathers for both male and female Prothonotary Warblers, however females had less dense feathers in general compared to males. Given our observed lower feather density in females compared to males and that females of some species take longer to molt (Mumme 2018), this could suggest that a slower FGR is an adaptive response to preserve feather integrity across the annual cycle. However, this relationship needs further clarification. Similar to males, FGR did not correlate with winter habitat for females, however female $\delta^{13}\text{C}$ samples were only collected on the wintering grounds. Given our small sample sizes for females and annual variation, further research into the nature of these relationships is warranted before they can be applied in a conservation or management context.

Contrary to our predictions, we found no evidence that breeding effort in females impacted fCORT . However, 2017 had higher levels of fCORT in general. This provides further support to the idea that conditions during the 2017 breeding or post-breeding periods affected fCORT relationships in males (see above) and suggests that environmental conditions can act on populations as a whole to contribute to annual

differences in stress (Romero et al. 2000). However, although females showed higher fCORT in 2017, we had very few samples that year, suggesting either return rates (due to survival or dispersal) were low or that our sampling was biased between years. Further investigation into overall return rate (i.e., not just recaptured females) to account for over-winter mortality could help clarify this relationship to determine the role of environmental conditions. Younger Prothonotary Warbler females have shorter breeding seasons and double brood less frequently than older females (Bulluck et al. 2013, E. Ames unpublished data). This could potentially explain why we found that time investment in breeding correlated with fCORT for older but not younger females, where older females that bred late had lower fCORT . This contrasts with our results for late breeding males; however, CORT has been shown to be context-dependent (i.e., age, sex, and population; Aharon-Rotman et al. 2017, Madliger et al. 2015, Madliger et al. 2018) and can vary based on differences in life history timing, as males of some species molt earlier than females (e.g., Hooded Warbler, Mumme 2018). fCORT did not impact feather density in females, unlike males who showed reduced density in feathers with higher fCORT . Similar to males, females with lower fCORT used areas that were more depleted in $\delta^{13}\text{C}$ during the winter period, however $\delta^{13}\text{C}$ for females was limited to winter grounds samples as arrival date and early capture on arrival to the breeding grounds is difficult for female Prothonotary Warblers in our population.

Conclusions

In addition to non-lethal effects, higher reproduction or feather quality could result in carry-over effects onto survival probability in subsequent seasons (Verhulst 1995, Nilsson and Svensson 1996, Harms et al. 2015). Given our methodology (i.e., only collecting feathers from returned individuals), we did not measure lethal effects, for example during fall migration, winter, or spring migration. Thus, it is possible we failed to detect the full magnitude of carry-over effects from breeding or that they were obscured by seasonal mortality. For instance, migration is known to have the highest mortality during the annual cycle for many species (Sillett and Holmes 2002, Rushing et al. 2017, Ward et al. 2018), and feather quality can impact flight performance (Echeverry-Galvis and Hau 2013). This suggests that birds with reduced feather quality may be less likely to survive challenging conditions on migration. Additionally, feather quality may impact foraging efficiency (Matyjasiak et al. 2018) and predation avoidance (Swaddle et al. 1999, Møller and Neilsen 2018), potentially affecting over-winter survival or causing delays to spring arrival on the breeding grounds due to migration timing or speed (Stutchbury et al. 2011), which has been shown to correlate with breeding outcomes (Chapter 3). More *in situ* studies that relate feather quality to winter survivorship and migration parameters could help clarify these relationships and further our understanding of how breeding carry-over effects impact subsequent seasons.

Trade-offs between reproduction, molt, and migration can be costly for migratory songbirds and lead to carry-over effects in subsequent stages of the annual cycle (Newton 2007, Marra et al. 2015). We set out to explore these relationships and specifically how they impact the Prothonotary Warbler, a species of conservation concern. Overall, we

found that breeding events correlated with FGR and f CORT, that FGR and f CORT predict feather quality, and that f CORT predicts future winter habitat quality. However, these relationships varied between years, sexes, and in some cases age, and may be impacted by environmental conditions and/or individual quality, similar to other studies (Madliger et al. 2015, Harris et al. 2016, Madliger and Love, 2016, Romero and Fairhurst, Imlay et al. 2019). Further research into these relationships that document frequency of breeding-molt overlap, molt timing, and the consequences for migration and winter survival could help broaden our understanding of these carry-over effects.

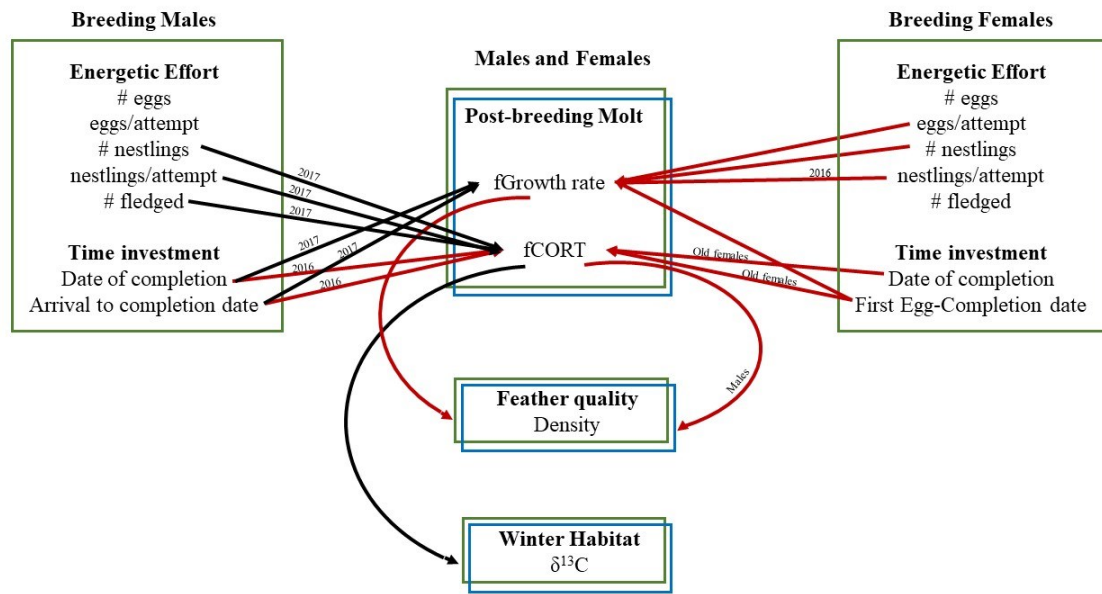


Figure 7 Analysis framework for examining carry-over effects from breeding effort and investment to feather quality and winter habitat, measured through stable carbon isotopes ($\delta^{13}\text{C}$), for male and female Prothonotary Warblers in Ohio during 2016-2019. Black (positive) and red (negative) arrows depict a significant relationship from mixed model (see methods for more details). For models where only one year, sex, or age class were significant, the significant year or class is denoted above the line. Green boxes denote breeding grounds data and blue boxes wintering grounds data.

Table 6 Final mixed effects (males) and linear (females) models for breeding parameters predicting feather growth rate (FGR) in Prothonotary Warblers breeding in central Ohio from 2016-2019. Bolded variables represent the main explanatory variable of interest and “Var x” before another variable represents an interaction with the variable of interest.

Model group	Explanatory variables	Males					Females					
		Estimate	SE	<i>t</i>	<i>P</i>	<i>n</i>	Estimate	SE	<i>t</i>	<i>P</i>	df	R ²
FGR by breeding energetic effort												
	Intercept	2.490	0.07	33.90	<0.001	39	2.660	0.10	26.65	<0.001	15	0.05
	No. of eggs produced	0.020	0.01	2.07	0.070		-0.008	0.01	-0.87	0.400		
	Year ₂₀₁₈	0.140	0.05	2.93	0.017							
	Intercept	2.570	0.11	23.14	<0.001	38	3.170	0.18	17.86	<0.001	12	0.6
	No. of eggs per attempt	0.010	0.02	0.49	0.640		-0.160	0.04	-3.8	0.003		
	Age _{Young}						0.160	0.06	2.44	0.031		
	Year ₂₀₁₇						0.160	0.08	1.95	0.075		
	Year ₂₀₁₈	0.120	0.05	2.16	0.060		0.060	0.07	0.94	0.370		
	Intercept	2.570	0.06	43.02	<0.001	39	2.730	0.08	32.35	<0.001	16	0.24
	No. of nestlings produced	0.020	0.01	1.27	0.230		-0.040	0.02	2.27	0.038		
	Year ₂₀₁₈	0.130	0.05	2.51	0.030							
	Intercept	2.620	0.06	44.57	<0.001	38	2.740	0.09	30.8	<0.001	12	0.54
	No. of nestlings per attempt	0.002	0.02	0.13	0.900		-0.080	0.03	-2.67	0.020		
	Year ₂₀₁₇						0.070	0.17	0.42	0.680		
	Year ₂₀₁₈	0.120	0.06	2.05	0.070		-0.440	0.16	-2.74	0.018		
	Var x Year ₂₀₁₇						0.010	0.06	0.19	0.850		
	Var x Year ₂₀₁₈						0.160	0.05	3.12	0.009		
	Intercept	2.620	0.05	52.50	<0.001	40	2.640	0.07	36.55	<0.001	16	0.11
	No. of young fledged	0.002	0.01	0.19	0.850		-0.030	0.02	-1.39	0.180		
	Year ₂₀₁₈	0.110	0.05	2.12	0.060							
FGR by breeding time investment												
	Intercept	1.560	0.29	5.35	<0.001	36	3.580	0.55	6.49	<0.001	16	0.18
	Breeding completion date	0.006	0.002	3.73	0.010		-0.005	0.003	-1.85	0.080		
	Year ₂₀₁₈	1.350	0.45	2.97	0.025							
	Var x Year ₂₀₁₈	-0.007	0.002	-2.64	0.039							
	Intercept	2.150	0.10	21.06	<0.001	35	2.770	0.11	24.91	<0.001	15	0.24
	Total breeding time*	0.008	0.002	4.95	0.003		-0.005	0.002	-2.19	0.045		
	Year ₂₀₁₈	0.590	0.13	4.49	0.004							
	Var x Year ₂₀₁₈	-0.008	0.002	-3.15	0.020							

* Total breeding time for males = arrival date to completion date; for females = first egg date to completion date, where completion date is fledged or fail date of last nest attempt

Table 7 Final mixed effects (males) and linear (females) models for breeding parameters predicting feather corticosterone (fCORT) in Prothonotary Warblers breeding in central Ohio from 2016-2019. Bolded variables represent the main explanatory variable of interest and “Var x” before another variable represents an interaction with the variable of interest.

Model group	Explanatory variables	Males					Females					df	R ²
		Estimate	SE	t	P	n	Estimate	SE	t	P			
fCORT by breeding energetic effort													
	Intercept	6.61	0.61	10.84	<0.001	49	1.93	0.26	7.47	<0.001	15	0.39	
	No. of eggs produced	-0.08	0.07	-1.17	0.260		-0.02	0.02	-0.67	0.510			
	Year ₂₀₁₇						0.65	0.24	2.76	0.015			
	Year ₂₀₁₈						0.07	0.20	0.36	0.720			
	Intercept	4.17	0.97	4.31	<0.001	49	1.27	0.49	2.62	0.019	15	0.42	
	No. of eggs per attempt	0.43	0.21	2.02	0.057		0.11	0.11	1.05	0.310			
	Year ₂₀₁₇						0.67	0.23	2.98	0.009			
	Year ₂₀₁₈						0.12	0.19	0.67	0.510			
	Intercept	6.83	0.62	10.94	<0.001	49	1.67	0.89	8.81	<0.001	16	0.39	
	No. of nestlings produced	-0.21	0.12	-1.78	0.094		0.02	0.03	0.65	0.520			
	Year ₂₀₁₇	-2.46	0.91	-2.69	0.016		0.71	0.23	3.14	0.006			
	Year ₂₀₁₈	-0.75	0.96	-0.78	0.490		0.09	0.18	0.53	0.600			
	Var x Year ₂₀₁₇	0.62	0.20	3.08	0.007								
	Var x Year ₂₀₁₈	0.25	-0.24	1.02	0.320								
	Intercept	6.12	0.60	10.12	<0.001	49	1.61	0.16	10.18	<0.001	16	0.43	
	No. nestlings per attempt	-0.06	0.20	-0.28	0.780		0.06	0.05	1.30	0.210			
	Year ₂₀₁₇	-1.69	0.84	-2.01	0.062		0.71	0.22	3.27	0.005			
	Year ₂₀₁₈	-0.23	0.89	-0.26	0.800		0.07	0.17	0.44	0.660			
	Var x Year ₂₀₁₇	0.66	0.29	2.24	0.040								
	Var x Year ₂₀₁₈	0.19	0.37	0.52	0.610								
	Intercept	6.03	0.50	12.15	<0.001	49	1.62	0.14	11.63	<0.001	16	0.45	
	No. of young fledged	-0.02	0.16	-0.14	0.890		0.06	0.04	1.53	0.145			
	Year ₂₀₁₇	-1.18	0.67	-1.76	0.097		0.71	0.21	3.32	0.004			
	Year ₂₀₁₈	-0.34	0.79	-0.44	0.670		-0.04	0.18	-0.21	0.830			
	Var x Year ₂₀₁₇	0.47	0.21	2.21	0.042								
	Var x Year ₂₀₁₈	0.23	0.25	0.92	0.370								
fCORT by breeding time investment													
	Intercept	18.84	4.44	4.25	<0.001	45	5.45	1.32	4.12	0.001	14	0.60	
	Breeding completion date	-0.07	0.02	-2.93	0.012		-0.02	0.01	-2.80	0.014			
	Age _{Young}						-3.96	1.95	-2.04	0.060			
	Var x Age _{Young}						0.02	0.01	2.03	0.060			
	Year ₂₀₁₇	-15.53	5.66	-2.74	0.012		0.87	0.20	4.28	<0.001			
	Year ₂₀₁₈	-13.20	7.58	-1.74	0.110		-0.04	0.16	-0.23	0.820			
	Var x Year ₂₀₁₇	0.09	0.03	2.80	0.015								
	Var x Year ₂₀₁₈	-0.08	0.04	1.82	0.092								
	Intercept	10.14	1.50	6.74	<0.001	44	2.52	0.42	6.03	<0.001	12	0.58	
	Total breeding time*	-0.07	0.03	-2.84	0.015		-0.02	0.01	-2.09	0.058			
	Age _{Young}						-1.14	0.55	-2.09	0.058			
	Var x Age _{Young}						0.02	0.01	2.13	0.054			
	Year ₂₀₁₇	-6.22	2.06	-3.02	0.011		0.95	0.26	3.70	0.003			
	Year ₂₀₁₈	-4.51	2.43	-1.85	0.090		0.07	0.20	0.33	0.750			
	Var x Year ₂₀₁₇	0.11	0.03	3.24	0.007								
	Var x Year ₂₀₁₈	0.09	0.04	2.08	0.060								

* Total breeding time for males = arrival date to completion date; for females = first egg date to completion date, where completion date is fledge or fail date of last nest attempt

Table 8 Final mixed effects models for feather corticosterone (fCORT) or feather growth rate (FGR) predicting feather density or winter habitat quality ($\delta^{13}\text{C}$) in male and female Prothonotary Warblers breeding from 2016-2019 in central Ohio. Bolded variables represent the main explanatory variable of interest and “Var x” before another variable represents an interaction with the variable of interest.

Response	Explanatory variables	Estimate	SE	<i>t</i>	<i>P</i>	<i>n</i>
Feather density						
	Intercept	2.14	0.13	16.45	<0.001	157
	FGR	-0.11	0.05	-2.19	0.035	
	Sex _{Male}	0.11	0.03	4.04	<0.001	
	Intercept	1.82	0.06	30.00	<0.001	122
	fCORT	0.007	0.007	0.92	0.365	
	Sex _{Male}	0.27	0.08	3.48	<0.001	
	fCORT x Sex _{Male}	-0.03	0.01	-2.40	0.021	
	Year ₂₀₁₇	-0.08	0.04	-2.33	0.020	
	Year ₂₀₁₈	0.04	0.04	1.02	0.310	
	Year ₂₀₁₉	0.01	0.04	0.27	0.790	
Winter habitat ($\delta^{13}\text{C}$)						
	Intercept	-26.25	1.55	-16.90	<0.001	90
	FGR	0.87	0.59	1.47	0.160	
	Intercept	-24.19	0.55	-43.85	<0.001	63
	fCORT	0.20	0.06	3.15	0.010	
	Year ₂₀₁₇	-1.28	0.50	-2.56	0.028	
	Year ₂₀₁₈	-1.50	0.50	-3.02	0.013	
	Year ₂₀₁₉	-0.94	0.54	-1.75	0.110	

Chapter 5 Conservation Implication

As a wet forest specialist, the Prothonotary Warbler is particularly vulnerable to habitat loss and degradation across the annual cycle making it imperative that managers and conservationists use a full annual cycle approach when developing conservation strategies for the species (Vargas et al. 2015, Rosenberg et al. 2016, Vancutsem et al. 2020). This dissertation provides evidence for carry-over effects from winter habitat to breeding and from breeding to molt and winter habitat. This suggests that in order to conserve the Prothonotary Warbler, we need to actively consider processes and events across the annual cycle in decision making and planning (Marra et al. 2015; Rosenberg et al. 2016). This may be challenging as breeding, migration (i.e., stopover sites), and winter areas span multiple states and countries, all with different conservation priorities and socio-economic considerations. However, through range-wide collaborative efforts, such as the Prothonotary Warbler Working Group and others, we can begin to bridge geographic divides to conserve this species and other wet habitat specialists that rely on the same habitats.

Winter habitat quality can be a limiting factor in breeding success of Prothonotary Warblers, especially during hot dry winter conditions (Chapter 3). Given this finding, it is critical that conservation strategies incorporate preservation of winter habitat. In areas where climate models predict decreased rainfall and increased temperatures, such as

along the northern Colombian coast (Neelin et al. 2006), preserving undisturbed mature mangroves with high Prothonotary Warbler concentrations may provide the most benefit per conservation dollar. In areas that are projected to experience more variable weather (i.e., increased storm frequency and intensity) preserving freshwater wetlands and moist lowland forests with modest densities in addition to mangroves could also benefit the species as birds utilizing them in extreme wet years may perform better. My research and that of others have demonstrated individual variation in responses to annual fluctuations in winter conditions in songbirds around Spring migration (Chapter 3, Studds and Marra 2011). Therefore, further long-term research into winter habitat dynamics is necessary in this guild to identify the role of annual variation in full annual cycle population dynamics.

Carry-over effects from breeding to molt and winter habitat use may also play a role in limiting populations, however more research is needed to further clarify these relationships and the contexts in which they may be most impactful on the species. For example, we found that high breeding effort or investment in male Prothonotary Warblers may have consequences for feather quality and winter habitat in some years (Chapter 4), which in turn can impact spring arrival in subsequent years (Chapter 3). However, these consequences may be mediated by environmental conditions on the breeding or wintering grounds. Environmental conditions on the breeding grounds can impact molt strategies (Pageau et al. 2020), presumably by limiting resources for molt. Therefore, intensive breeding followed by poor weather conditions (e.g., storms or drought) during post-breeding could result in individuals occupying black or white mangroves on the wintering

grounds. During hot, dry winters those habitats, potentially through stability of resources, may increase the probability of arriving early to the breeding grounds, however in moist, cool winters those habitats may delay arrival (Chapter 3). Females with more intense breeding effort may not experience reductions in feather quality, however they may settle in lower quality winter areas in winters with moist, cool conditions. Thus, the consequences of breeding effort likely depend on conditions across the annual cycle and vary between male and female Prothonotary Warblers, making it critical that we further research these connections to determine if conservation action during the post-breeding period is of high priority.

Managers on the breeding grounds can attempt to mitigate negative carry-over effects from winter conditions (i.e., late arrival to the breeding grounds) by maximizing breeding success and habitat quality. For Prothonotary Warblers, and other cavity nesting species, nest boxes can increase reproduction through reduction in predation and parasitism, and if nest sites are limited boxes can increase breeding densities. Reducing predation with boxes could help mitigate the cascading impact of late arrival on breeding phenology by increasing fledging success in early breeders and providing more opportunities to produce a second brood. However, when box programs are not properly designed or monitored, they can have negative consequences for populations, such as high nest predation (Chapter 3, Bailey and Bonter 2017). For example, at our central Ohio sites boxes, deployed by a local citizen, are mounted on trees with out devices to prevent predation and many have openings large enough for Brown-headed Cowbirds to parasitize nests. We found that tree mounted boxes are 5 times more likely to be

predated than natural cavities. Through a concurrent project funded by the Columbus Audubon Society (unpublished data), we found that boxes mounted on poles with predator exclusion devices increased nest success above that of natural cavities demonstrating the importance of proper nest box design and implementation. Strategic placement of boxes within habitat will also likely play an important role in nest success and box use as Prothonotary Warblers prefer nest locations over water and with canopy cover (Slevin et al. 2018) and predation can be lower over deep water (Hoover 2006). Ultimately, box programs should only be considered as a conservation strategy when properly designed and monitored for long term success otherwise they may do more damage than good.

Beyond nesting sites, managers can work to maximize habitat quality to support breeding efforts and reduce carry-over effects from breeding to molt and winter habitat use through restoration of water resources and native plant communities. Management of water resources is often driven by human consumptive needs (i.e., in reservoir systems) and agricultural demands, however steps to restore natural water regimes can benefit Prothonotary Warblers, as well as other species of wildlife. For example, reducing flooding from upstream agricultural and urban runoff through stream re-meandering (i.e., dechannelizing) or wetland buffers could reduce flash flood events that destroy nests and reduce foraging areas (Hoover 2009, Hienrich et al. 2014). Controlling region specific non-native plant species, such as bush honeysuckle in Ohio, and increasing important native species, such as buttonbush, can help increase food resources (i.e., caterpillars and other insects) for young and adults, as well as provide important structural habitat for

concealment during the vulnerable molting period (Burghart et al. 2009). Maximizing high quality habitat in these ways could help to offset negative impacts from late or intense breeding on post-breeding condition (i.e., stress and nutrition) and on winter habitat use. Further study into habitat requirements during the post-fledging and molting periods could provide concrete habitat management strategies to support populations during these critical times.

Future research priorities for Prothonotary Warblers should focus on further understanding how the stages of the annual cycle are linked. Specifically, how annual environmental variation on both the breeding and wintering grounds impact carry-over effects to advance understanding of the consequences of climate change for the species. Investigating winter survival, site persistence, and movement dynamics (Chapter 2) over longer time periods, in more diverse habitats and across the landscape, may help to determine how broad scale climactic events will continue to impact the species and further highlight critical habitats. It may be particularly relevant to focus on the impacts to females as they may suffer higher mortality during the breeding season (i.e., nest predation) and appear to be limited in some populations- all females had breeding attempts in our study but not all males. Additionally, in general females have received less study in avian ecology than males and recent literature has highlighted the need to better understand their annual cycle ecology and how it differs from males (Haines et al. 2020). As females are generally considered to be the more limiting sex in bird populations and the majority of studies on carry-over effects have focused almost exclusively on males (e.g., Reudink et al. 2009; Tonra et al. 2011), it is imperative we

better understand more aspects of their full annual cycle in species of conservation concern, like the Prothonotary Warbler. In addition, we still lack an understanding of species-specific habitat requirements during the post-fledging period, molt, and migration, which may vary from breeding habitat (Cox et al. 2014). Clarifying important habitat features during these time periods could help managers reduce impacts from carry-over effects and increase survival. Finally, incorporating data from across the annual cycle, including the impact of carry-over effects and environmental variation provided here, into integrated population models could help elucidate Prothonotary Warbler population trajectories and continued consequences of climate change.

Bibliography

- Aebischer A, Perrin N, Krieg M, Studer J, Meyer DR (1996) The Role of Territory Choice, Mate Choice and Arrival Date on Breeding Success in the Savi's Warbler *Locustella luscinioides*. *Journal of Avian Biology* 27: 143–152.
- Aharon-Rotman Y, Buchanan KL, Klaassen M, Buttemer WA (2017) An experimental examination of interindividual variation in feather corticosterone content in the house sparrow, *Passer domesticus* in southeast Australia. *General and Comparative Endocrinology* 244: 93–100.
- Akresh ME, King DI, Marra PP (2019a) Examining carry-over effects of winter habitat on breeding phenology and reproductive success in prairie warblers *Setophaga discolor*. *Journal of Avian Biology* 50. doi:10.1111/jav.02025
- Akresh ME, King DI, Marra PP (2019b) Rainfall and habitat interact to affect the condition of a wintering migratory songbird in The Bahamas. *Ecol Evol* 9: 8042–8061.
- Alongi DM (2002) Present state and future of the world's mangrove forests. *Envir Conserv* 29: 331–349.
- Ames EM, Gade MR, Nieman CL, Wright JR, Tonra CM, Marroquin CM, Tutterow AM, Gray SM (2020) Striving for population-level conservation: integrating physiology across the biological hierarchy. *Conservation Physiology* 8. doi:10.1093/conphys/coaa019
- Anderson DR, Burnham KP (2002) Avoiding Pitfalls When Using Information-Theoretic Methods. *The Journal of Wildlife Management* 66: 912–918.
- Angelier F, Holberton RL, Marra PP (2009) Does Stress Response Predict Return Rate in a Migratory Bird Species? A Study of American Redstarts and Their Non-Breeding Habitat. *Proceedings: Biological Sciences* 276: 3545–3551.
- Bailey RL, Bonter DN (2017) Predator guards on nest boxes improve nesting success of birds. *Wildlife Society Bulletin* 41: 434–441.
- Balogh AL, Ryder TB, Marra PP (2011) Population demography of Gray Catbirds in the suburban matrix: sources, sinks and domestic cats. *Journal of Ornithology* 152: 717–726.

- Bearhop S, Furness RW, Hilton GM, Votier SC, Waldron S (2003) A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material. *Functional Ecology* 17: 270–275.
- Bearhop S, Hilton GM, Votier SC, Waldron S (2004) Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. *Proceedings of the Royal Society of London B: Biological Sciences* 271: S215–S218.
- Beck ML (2013) Nest-Box Acquisition is Related to Plumage Coloration in Male and Female Prothonotary Warblers (*Protonotaria citrea*). *The Auk* 130: 364–371.
- Blem CR, Blem LB (1991) Nest-Box Selection by Prothonotary Warblers (Selección de Cajas para Anidar por Parte de *Protonotaria citrea*). *Journal of Field Ornithology* 62: 299–307.
- Bortolotti GR, Marchant TA, Blas J, German T (2008) Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. *Funct Ecol* 22: 494–500.
- Brown DR, Sherry TW (2006) Food supply controls the body condition of a migrant bird wintering in the tropics. *Oecologia* 149: 22–32.
- Bulluck L, Ames E, Bayly N, Reese J, Viverette C, Wright J, Caguazango A, Tonra C (2020) Habitat-dependent occupancy and movement in a migrant songbird highlights the importance of mangroves and forested lagoons in Panama and Colombia. *Ecology and Evolution* 9: 11064–11077.
- Bulluck L, Huber S, Viverette C, Blem C (2013) Age-specific responses to spring temperature in a migratory songbird: older females attempt more broods in warmer springs. *Ecol Evol* 3: 3298–3306.
- Bulluck LP, Foster MJ, Kay S, Cox DE, Viverette C, Huber S (2017) Feather carotenoid content is correlated with reproductive success and provisioning rate in female Prothonotary Warblers. *The Auk* 134: 229–239.
- Burghardt KT, Tallamy DW and Shriver GW (2009) Impact of Native Plants on Bird and Butterfly Biodiversity in Suburban Landscapes. *Conservation Biology* 23: 219–224.
- Bürkner P-C (2017) brms : An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software* 80. doi:10.18637/jss.v080.i01
- Calvert AM, Woodcock J, McCracken JD (2010) Contrasting Seasonal Survivorship of Two Migratory Songbirds Wintering in Threatened Mangrove Forests. *Avian Conservation and Ecology* 5: 2.

- Carbajal A, Tallo-Parra O, Sabes-Alsina M, Mular I, Lopez-Bejar M (2014) Feather corticosterone evaluated by ELISA in broilers: A potential tool to evaluate broiler welfare. *Poultry Science* 93: 2884–2886.
- Chan EKW, Yu Y-T, Zhang Y, Dudgeon D (2008) Distribution Patterns of Birds and Insect Prey in a Tropical Riparian Forest. *Biotropica* 40: 623–629.
- Cheng Y, Leung LR, Huang M, Knox RG, Koven C, Bisht G, Bretfeld M, Detto M, Fisher R, Shuman JK, *et al.* (2020) Dry season soil moisture dynamics along secondary forest succession in Panama: impacts of soil hydraulic properties vs. tree root profile 2020: B127-04.
- Christensen RHB (2012) Cumulative Link Models for Ordinal Regression with the R Package ordinal 40.
- Cooper NW, Sherry TW, Marra PP (2015) Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. *Ecology* 96: 1933–1942.
- Cox WA, Thompson FR, Cox AS, Faaborg J (2014) Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. *Journal of Wildlife Management* 78: 183–193.
- Cristol DA, Johnson KM, Jenkins KD, Hawley DM (2014) Timing of feather molt related to date of spring migration in male white-throated sparrows, *Zonotrichia albicollis*. *J Exp Zool A Ecol Genet Physiol* 321: 586–594.
- Crossin GT, Phillips RA, Lattin CR, Romero LM, Williams TD (2013) Corticosterone mediated costs of reproduction link current to future breeding. *General and Comparative Endocrinology* 193: 112–120.
- Culp LA, Cohen EB, Scarpignato AL, Thogmartin WE, Marra PP (2017) Full annual cycle climate change vulnerability assessment for migratory birds. *Ecosphere* 8: e01565.
- Dawson A, Hinsley SA, Ferns PN, Bonser RHC, Eccleston L (2000) Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proc R Soc Lond B* 267: 2093–2098.
- DE LA HERA I, PÉREZ-TRIS J, TELLERÍA JL (2009) Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird. *Biological Journal of the Linnean Society* 97: 98–105.
- DesRochers DW, Reed JM, Awerman J, Kluge JA, Wilkinson J, van Griethuijsen LI, Aman J, Romero LM (2009) Exogenous and endogenous corticosterone alter feather quality. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 152: 46–52.

- Dickson, JG, Thompson FR, Conner RN, Franzreb KE (1995) Silviculture in central and southeastern oak-pine forests. *In: Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues.* (Martin, TE and DM Finch, Eds.) pp. 245-266. Oxford Univ. Press, NY, USA.
- Donato DC, Kauffman JB, Murdiyarso D, Kurnianto S, Stidham M, Kanninen M (2011) Mangroves among the most carbon-rich forests in the tropics. *Nature Geosci* 4: 293–297.
- Done T, Gow EA, Stutchbury BJM (2011) Corticosterone stress response and plasma metabolite levels during breeding and molt in a free-living migratory songbird, the wood thrush (*Hylocichla mustelina*). *General and Comparative Endocrinology* 171: 176–182.
- Donovan TM, Thompson FR III, Faaborg J, Probst JR (1995) Reproductive Success of Migratory Birds in Habitat Sources and Sinks. *Conservation Biology* 9: 1380–1395.
- Drake A, Rock C, Quinlan SP, Green DJ (2013) Carry-over effects of winter habitat vary with age and sex in yellow warblers *Setophaga petechia*. *Journal of Avian Biology* 44: 321–330.
- Duke NC, Meynecke J-O, Dittmann S, Ellison AM, Anger K, Berger U, Cannicci S, Diele K, Ewel KC, Field CD, *et al.* (2007) A World Without Mangroves? *Science* 317: 41–42.
- Echeverry-Galvis MA, Hau M (2012) Molt–breeding overlap alters molt dynamics and behavior in zebra finches, *Taeniopygia guttata castanotis*. *Journal of Experimental Biology* 215: 1957–1964.
- Echeverry-Galvis MA, Hau M (2013) Flight Performance and Feather Quality: Paying the Price of Overlapping Moulting and Breeding in a Tropical Highland Bird. *PLOS ONE* 8: e61106.
- Faaborg J, Holmes RT, Anders AD, Bildstein KL, Dugger KM, Gauthreaux SA, Heglund P, Hobson KA, Jahn AE, Johnson DH, *et al.* (2010) Recent advances in understanding migration systems of New World land birds. *Ecological Monographs* 80: 3–48.
- FAO, (2003) Status and trends in mangrove area extent worldwide. By Wilkie, M. and Fortuna, S. Forest Resources Assessment Working Paper No. 63. Forest Resources Division. FAO, Rome.
- Foerster S, Zhong Y, Pintea L, Murray CM, Wilson ML, Mjungu DC, Pusey AE (2016) Feeding habitat quality and behavioral trade-offs in chimpanzees: a case for species distribution models. *Behavioral Ecology* 27: 1004–1016.
- Fretwell SD, Lucas HL (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor* 19: 16–36.

- Gelman A, Goodrich B, Gabry J, Vehtari A (2019) R-squared for Bayesian Regression Models. *The American Statistician* 73: 307–309.
- Germain RR, Arcese P (2014) Distinguishing individual quality from habitat preference and quality in a territorial passerine. *Ecology* 95: 436–445.
- Gillis EA, Green DJ, Middleton HA, Morrissey CA (2008) Life history correlates of alternative migratory strategies in american dippers. *Ecology* 89: 1687–1695.
- Gilman EL, Ellison J, Duke NC, Field C (2008) Threats to mangroves from climate change and adaptation options: A review. *Aquatic Botany* 89: 237–250.
- Gómez-Montes C, Bayly NJ (2010) Habitat use, abundance, and persistence of Neotropical migrant birds in a habitat matrix in northeast Belize. *Journal of Field Ornithology* 81: 237–251.
- González-Prieto AM, Hobson KA (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.
- Grubb T (1989) Ptilochronology - Feather Growth Bars as Indicators of Nutritional-Status. *AUK* 106: 314–320.
- Grubb T (2006) Ptilochronology: Feather Time and the Biology of Birds. Oxford University Press, Oxford, New York.
- Gunnarsson TG, Gill JA, Atkinson PW, Gélinaud G, Potts PM, Croger RE, Gudmundsson GA, Appleton GF, Sutherland WJ (2006) Population-scale drivers of individual arrival times in migratory birds. *Journal of Animal Ecology* 75: 1119–1127.
- Gunnarsson TG, Gill JA, Newton J, Potts PM, Sutherland WJ (2005) Seasonal Matching of Habitat Quality and Fitness in a Migratory Bird. *Proceedings: Biological Sciences* 272: 2319–2323.
- Haines CD, Rose EM, Odom KJ, Omland KE (2020) The role of diversity in science: a case study of women advancing female birdsong research. *Animal Behaviour* 168:19–24.
- Hansen WK, Bate LJ, Landry DW, Chastel O, Parenteau C, Breuner CW (2016) Feather and faecal corticosterone concentrations predict future reproductive decisions in harlequin ducks (*Histrionicus histrionicus*). *Conserv Physiol* 4. doi:10.1093/conphys/cow015
- Harms NJ, Legagneux P, Gilchrist HG, Bêty J, Love OP, Forbes MR, Bortolotti GR, Soos C (2015) Feather corticosterone reveals effect of moulting conditions in the autumn on subsequent reproductive output and survival in an Arctic migratory bird. *Proceedings of the Royal Society B: Biological Sciences* 282: 20142085.

Harris CM, Madliger CL, Love OP (2016) Temporal overlap and repeatability of feather corticosterone levels: practical considerations for use as a biomarker. *Conserv Physiol* 4. doi:10.1093/conphys/cow051

Harrison TJE, Smith JA, Martin GR, Chamberlain DE, Bearhop S, Robb GN, Reynolds SJ (2010) Does food supplementation really enhance productivity of breeding birds? *Oecologia* 164: 311–320.

Heckscher CM, Ramirez MG, Kneidel AH (2017) Reproductive outcomes determine the timing of arrival and settlement of a single-brooded Nearctic–Neotropical migrant songbird (*Catharus fuscescens*) in South America. *tauk* 134: 842–856.

Heinrich KK, Whiles MR and Roy C (2014) Cascading Ecological Responses to an In-Stream Restoration Project in a Midwestern River. *Restoration Ecology*. 22: 72-80.

Hera IDL, Schaper SV, Díaz JA, Pérez-Tris J, Bensch S, Tellería JL (2011) How Much Variation in the Molt Duration of Passerines Can Be Explained By the Growth Rate of Tail Feathers? *The Auk* 128: 321–329.

Hobson K, Wassenaar L (2008) Tracking Animal Migration with Stable Isotopes. Terrestrial Ecology Series 2. pp xi, 1.

Hobson KA, Clark RG (1992) Assessing Avian Diets Using Stable Isotopes I: Turnover of ¹³C in Tissues. *The Condor* 94: 181–188.

Holberton RL (1999) Changes in Patterns of Corticosterone Secretion Concurrent with Migratory Fattening in a Neotropical Migratory Bird. *General and Comparative Endocrinology* 116: 49–58.

Hoover JP (2003) Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology* 84: 416–430.

Hoover JP (2006) Water depth influences nest predation for a wetland-dependent bird in fragmented bottomland forests. *Biological Conservation* 127: 35–47.

Hoover JP (2009) Effects of hydrologic restoration on birds breeding in forested wetlands. *Wetlands*. 29: 563–573.

Hostetler JA, Sillett TS, Marra PP (2015) Full-annual-cycle population models for migratory birds. *The Auk* 132: 433–449.

Howell SNG, Corben C, Pyle P, Rogers DI (2003) The First Basic Problem: A Review of Molt and Plumage Homologies. *The Condor* 105: 635–653.

Humphrey PS, Parkes KC (1959) An Approach to the Study of Molts and Plumages. *The Auk* 76: 1–31.

- Imlay TL, Angelier F, Hobson KA, Mastromonaco G, Saldanha S, Leonard ML (2019) Multiple intrinsic markers identify carry-over effects from wintering to breeding sites for three Nearctic–Neotropical migrant swallows. *The Auk* 136. doi:10.1093/auk/ukz053
- Jenni L, Winkler R (2020) *The Biology of Molt in Birds*, 1st edition. Edition. Helm.
- Jenni-Eiermann S, Helfenstein F, Vallat A, Glauser G, Jenni L, Fisher D (2015) Corticosterone: effects on feather quality and deposition into feathers. *Methods in Ecology & Evolution* 6: 237–246.
- Johnson MD (2007) Measuring habitat quality: a review. *The Condor* 109: 489–504.
- Johnson MD, Sherry TW, Holmes RT, Marra PP (2006) Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. *Conserv Biol* 20: 1433–1444.
- Junk WJ (2013) *The Central Amazon Floodplain: Ecology of a Pulsing System*. Springer Science & Business Media.
- Kaplan EL, Meier P (1958) Nonparametric Estimation from Incomplete Observations. *Journal of the American Statistical Association* 53: 457–481.
- Kleist NJ, Guralnick RP, Cruz A, Lowry CA, Francis CD (2018) Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. *PNAS* 115: E648–E657.
- Koleček J, Hahn S, Emmenegger T, Procházka P (n.d.) Intra-tropical movements as a beneficial strategy for Palearctic migratory birds. *Royal Society Open Science* 5: 171675.
- Latta SC, Cabezas S, Mejia DA, Paulino MM, Almonte H, Miller-Butterworth CM, Bortolotti GR (2016) Carry-over effects provide linkages across the annual cycle of a Neotropical migratory bird, the Louisiana Waterthrush *Parus motacilla*. *Ibis* 158: 395–406.
- Latta SC, Howell CA, Dettling MD, Cormier RL (2012) Use of Data on Avian Demographics and Site Persistence during Overwintering to Assess Quality of Restored Riparian Habitat. *Conservation Biology* 26: 482–492.
- Lattin CR, Reed JM, DesRochers DW, Romero LM (2011) Elevated corticosterone in feathers correlates with corticosterone-induced decreased feather quality: a validation study. *Journal of Avian Biology* 42: 247–252.
- Lefebvre G, Poulin B (1996) Seasonal Abundance of Migrant Birds and Food Resources in Panamanian Mangrove Forests. *The Wilson Bulletin* 108: 748–759.

- Lefebvre G, Poulin B, McNeil R (1992) Abundance, Feeding Behavior, and Body Condition of Nearctic Warblers Wintering in Venezuelan Mangroves. *The Wilson Bulletin* 104: 400–412.
- Lefebvre G, Poulin B, McNeil R (1994) Spatial and social behaviour of Nearctic warblers wintering in Venezuelan mangroves. *Can J Zool* 72: 757–764.
- Lindström Å, Visser G, Daan S (1993) The Energetic Cost of Feather Synthesis Is Proportional to Basal Metabolic Rate. *Physiological Zoology* 66: 490–510.
- Löhmus M, Sandberg R, Holberton RL, Moore FR (2003) Corticosterone Levels in Relation to Migratory Readiness in Red-Eyed Vireos (*Vireo olivaceus*). *Behavioral Ecology and Sociobiology* 54: 233–239.
- López-Angarita J, Roberts CM, Tilley A, Hawkins JP, Cooke RG (2016) Mangroves and people: Lessons from a history of use and abuse in four Latin American countries. *Forest Ecology and Management* 368: 151–162.
- López-Angarita J, Tilley A, Hawkins JP, Pedraza C, Roberts CM (2018) Land use patterns and influences of protected areas on mangroves of the eastern tropical Pacific. *Biological Conservation* 227: 82–91.
- Lundberg A, Alatalo RV, Carlson A, Ulfstrand S (1981) Biometry, Habitat Distribution and Breeding Success in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica (Scandinavian Journal of Ornithology)* 12: 68–79.
- Madliger CL, Love OP (2016) Employing individual measures of baseline glucocorticoids as population-level conservation biomarkers: considering within-individual variation in a breeding passerine. *Conservation Physiology* 4. doi:10.1093/conphys/cow048
- Madliger CL, Love OP, Hultine KR, Cooke SJ (2018) The conservation physiology toolbox: status and opportunities. *Conserv Physiol* 6. doi:10.1093/conphys/coy029
- Madliger CL, Semeniuk CAD, Harris CM, Love OP (2015) Assessing baseline stress physiology as an integrator of environmental quality in a wild avian population: Implications for use as a conservation biomarker. *Biological Conservation* 192: 409–417.
- Maness, T., Anderson, D. (2013) Predictors of Juvenile Survival in Birds. In: Ornithological Monographs No. 78. American Ornithologists' Union, pp 1–55.
- Marra PP (2000) The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behavioral Ecology* 11: 299–308.

- Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM (2015) A call for full annual cycle research in animal ecology. *Biology Letters* 11: 20150552.
- Marra PP, Hobson KA, Holmes RT (1998) Linking Winter and Summer Events in a Migratory Bird by Using Stable-Carbon Isotopes. *Science* 282: 1884–1886.
- Matthews SN, Rodewald PG (2010) Movement behaviour of a forest songbird in an urbanized landscape: the relative importance of patch-level effects and body condition during migratory stopover. *Landscape Ecology; Dordrecht* 25: 955–965.
- Matyjasiak P, Boniecki P, Fuszara M, Okołowski M, Olejniczak I (2018) Feather holes and flight performance in the barn swallow *Hirundo rustica*. *Anim Cells Syst (Seoul)* 22: 124–131.
- McKellar Ann E, Marra PP, Hannon SJ, Studds CE, Ratcliffe LM (2013) Winter rainfall predicts phenology in widely separated populations of a migrant songbird. *Oecologia* 172: 595–605.
- McKellar Ann E., Marra PP, Ratcliffe LM (2013) Starting over: experimental effects of breeding delay on reproductive success in early-arriving male American redstarts. *Journal of Avian Biology* 44: 495–503.
- McKim-Louder MI, Hoover JP, Benson TJ, Schelsky WM (2013) Juvenile Survival in a Neotropical Migratory Songbird Is Lower than Expected. *PLoS ONE* 8: e56059.
- McKinnon EA, Rotenberg JA, Stutchbury BJM (2015) Seasonal change in tropical habitat quality and body condition for a declining migratory songbird. *Oecologia* 179: 363–375.
- Mettke-Hofmann C, Sinclair PH, Hamel PB, Greenberg R (2010) Implications of Prebasic and a Previously Undescribed Prealternate Molt for Aging Rusty Blackbirds. *The Condor* 112: 854–861.
- Mitsch W, Gosselink J (2000) *Wetlands*, 3rd Edition.
- Møller AP, Nielsen JT (2018) The trade-off between rapid feather growth and impaired feather quality increases risk of predation. *J Ornithol* 159: 165–171.
- Morton, ES (1980) Adaptation to seasonal changes by migrant land birds in the Panama Canal Zone. In *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution and Conservation*. (A. Keast and E. S. Morton, eds.) Smithsonian Institution Press. Washington, D.C. 437–453.
- Mueller AJ, Twedt DJ, Bowers EK (2019) Rapid adoption of nestboxes by Prothonotary Warblers (*Protonotaria citrea*) in mesic deciduous forest. *Canadian Journal of Zoology*.

- Mumme RL (2018) The trade-off between molt and parental care in Hooded Warblers: Simultaneous rectrix molt and uniparental desertion of late-season young. *Auk: Ornithological Advances* 135: 427–438.
- Mumme RL, Mulvihill RS, Norman D (2021) High-intensity flight feather molt and comparative molt ecology of warblers of eastern North America. *Ornithology* 138. doi:10.1093/ornithology/ukaa072
- Nagelkerken I, Blaber SJM, Bouillon S, Green P, Haywood M, Kirton LG, Meynecke J-O, Pawlik J, Penrose HM, Sasekumar A, *et al.* (2008) The habitat function of mangroves for terrestrial and marine fauna: A review. *Aquatic Botany* 89: 155–185.
- Nagy LR, Holmes RT (2005) Food Limits Annual Fecundity of a Migratory Songbird: An Experimental Study. *Ecology* 86: 675–681.
- Neelin JD, Münnich M, Su H, Meyerson JE, Holloway CE (2006) Tropical Drying Trends in Global Warming Models and Observations. *Proceedings of the National Academy of Sciences of the United States of America* 103: 6110–6115.
- Newberry GN, Swanson DL (2018) Elevated temperatures are associated with stress in rooftop-nesting Common Nighthawk (*Chordeiles minor*) chicks. *Conserv Physiol* 6: coy010.
- Newton I (1998) Population Limitation in Birds. Elsevier.
- Newton I (2007) The Migration Ecology of Birds. *The Migration Ecology of Birds*. doi:10.1016/B978-0-12-517367-4.X5000-1
- Nilsson J-Åke, Svensson E (1996) The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proceedings of the Royal Society of London Series B: Biological Sciences* 263: 711–714.
- Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM (2004) Tropical Winter Habitat Limits Reproductive Success on the Temperate Breeding Grounds in a Migratory Bird. *Proceedings: Biological Sciences* 271: 59–64.
- Ocampo-Peñuela N, Garcia-Ulloa J, Ghazoul J, Etter A (2018) Quantifying impacts of oil palm expansion on Colombia's threatened biodiversity. *Biological Conservation* 224: 117–121.
- Ogden LJE, Stutchbury BJM (1996) Constraints on Double Brooding in a Neotropical Migrant, the Hooded Warbler. *The Condor* 98: 736–744.
- Pageau C, Tonra CM, Shaikh M, Flood NJ, Reudink MW (2020) Evolution of moult-migration is directly linked to aridity of the breeding grounds in North American passerines. *Biology Letters* 16: 20200155.

- Perrins CM (1970) The Timing of Birds' Breeding Seasons. *Ibis* 112: 242–255.
- Petit LJ (1989) Breeding Biology of Prothonotary Warblers in Riverine Habitat in Tennessee. *The Wilson Bulletin* 101: 51–61.
- Petit LJ (1999) Prothonotary Warbler (*Protonotaria citrea*). *The Birds of North America Online*. doi:10.2173/bna.408
- Pinheiro J, Bates D, DebRoy SS, Sarkar D (2013) Nlme: Linear and Nonlinear Mixed Effects Models. *R package version 3.1-110* 3: 1–113.
- Powell LL, Ames EM, Wright JR, Matthiopoulos J, Marra PP (2021) Interspecific competition between resident and wintering birds: experimental evidence and consequences of coexistence. *Ecology* 102: e03208.
- Pyle P (1997) Identification Guide to North American Birds, Part I: Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.
- R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Ramenofsky M, Wingfield JC (2007) Regulation of Migration. *BioScience* 57: 135–143.
- Rappole JH, Tipton AR (1991) New Harness Design for Attachment of Radio Transmitters to Small Passerines (Nuevo Diseño de Arnés para Atar Transmisores a Passeriformes Pequeños). *Journal of Field Ornithology* 62: 335–337.
- Reddy KR, DeLaune RD (2008) Biogeochemistry of Wetlands: Science and Applications. CRC Press, Boca Raton.
- Reudink MW, Marra PP, Kyser TK, Boag PT, Langin KM, Ratcliffe LM (2009) Non-Breeding Season Events Influence Sexual Selection in a Long-Distance Migratory Bird. *Proceedings: Biological Sciences* 276: 1619–1626.
- Richards LA, Windsor DM (2007) Seasonal variation of arthropod abundance in gaps and the understorey of a lowland moist forest in Panama. *Journal of Tropical Ecology* 23: 169–176.
- Ricklefs RE (1977) On the Evolution of Reproductive Strategies in Birds: Reproductive Effort. *The American Naturalist* 111: 453–478.
- Ricklefs RE, Wikelski M (2002) The physiology/life-history nexus. *Trends in Ecology & Evolution* 17: 462–468.

Rockwell SM, Bocetti CI, Marra PP (2012) Carry-Over Effects of Winter Climate on Spring Arrival Date and Reproductive Success in an Endangered Migratory Bird, Kirtland's Warbler (*Setophaga kirtlandii*). *The Auk* 129: 744–752.

Rohwer VG, Rohwer S (2013) How do birds adjust the time required to replace their flight feathers? - ¿Cómo Ajustan las Aves el Tiempo Requerido para Reemplazar sus Plumas de Vuelo? *The Auk* 130: 699–707.

Romero LM, Fairhurst GD (2016) Measuring corticosterone in feathers: Strengths, limitations, and suggestions for the future. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 202: 112–122.

Romero LM, Reed JM, Wingfield JC (2000) Effects of Weather on Corticosterone Responses in Wild Free-Living Passerine Birds. *General and Comparative Endocrinology* 118: 113–122.

Rosenberg, KV, Kennedy JA, Dettmers R, Ford RP, Reynolds D, Alexander JD, Beardmore CJ, Blancher PJ, Bogart ER, Butcher GS, et al. (2016) Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States. Partners in Flight Science Committee 199. <http://www.partnersinflight.org/wp-content/uploads/2016/08/pif-continental-plan-final-spread-single.pdf>

Ruhs EC, Borden DM, Dallas T, Pitman E (2019) Do feather traits convey information about bird condition during fall migration? *wils* 131: 693–701.

Ruiz-Gutierrez V, Kendall WL, Saracco JF, White GC (2016) Overwintering strategies of migratory birds: a novel approach for estimating seasonal movement patterns of residents and transients. *Journal of Applied Ecology* 53: 1035–1045.

Runge CA, Martin TG, Possingham HP, Willis SG, Fuller RA (2014) Conserving mobile species. *Frontiers in Ecology and the Environment* 12: 395–402.

Rushing CS, Hostetler JA, Sillett TS, Marra PP, Rotenberg JA, Ryder TB (2017) Spatial and temporal drivers of avian population dynamics across the annual cycle. *Ecology* 98: 2837–2850.

Rushing CS, Ryder TB, Marra PP (2016) Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. *Proc R Soc B* 283: 20152846.

Saino N, Szép T, Romano M, Rubolini D, Spina F, Møller AP (2004) LETTER Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecology Letters* 7: 21–25.

Sandilyan S, Kathiresan K (2012) Mangrove conservation: a global perspective. *Biodiversity & Conservation* 21: 3523–3542.

- Schmidt KA, Rush SA, Ostfeld RS (2008) Wood Thrush Nest Success and Post-Fledging Survival across a Temporal Pulse of Small Mammal Abundance in an Oak Forest. *Journal of Animal Ecology* 77: 830–837.
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9: 671–675.
- Shahabuddin G, Herzner GA, Aponte CR, del Gomez MC (2000) Persistence of a frugivorous butterfly species in Venezuelan forest fragments: the role of movement and habitat quality. *Biodiversity and Conservation* 9: 1623–1641.
- Shipley AA, Murphy MT, Elzinga AH (2013) Residential Edges as Ecological Traps: Postfledging Survival of a Ground-Nesting Passerine in a Forested Urban Park. *The Auk* 130: 501–511.
- Siikamäki P (1998) Limitation of Reproductive Success by Food Availability and Breeding Time in Pied Flycatchers. *Ecology* 79: 1789–1796.
- Sillett TS, Holmes RT (2002) Variation in Survivorship of a Migratory Songbird throughout Its Annual Cycle. *Journal of Animal Ecology* 71: 296–308.
- Slevin MC, Matthews AE, Boves TJ (2018) Prothonotary Warbler demography and nest site selection in natural and artificial cavities in bottomland forests of Arkansas, USA. *Avian Conservation & Ecology* 13: 1–18.
- Small-Lorenz S, A Culp L, Ryder T, Will T, Marra P (2013) A blind spot in climate change vulnerability assessments. *Nature Climate Change* 3. doi:10.1038/nclimate1810
- Smith JAM, Reitsma LR, Marra PP (2010) Moisture as a determinant of habitat quality for a nonbreeding Neotropical migratory songbird. *Ecology* 91: 2874–2882.
- Smith JAM, Reitsma LR, Marra PP (2011) Influence of Moisture and Food Supply on the Movement Dynamics of a Nonbreeding Migratory Bird (*Parkesia noveboracensis*) in a Seasonal Landscape. *The Auk* 128: 43–52.
- Soriano-Redondo A, Bearhop S, Cleasby IR, Lock L, Votier SC, Hilton GM (2016) Ecological Responses to Extreme Flooding Events: A Case Study with a Reintroduced Bird. *Sci Rep* 6: 28595.
- Stamps JA (1991) The effect of conspecifics on habitat selection in territorial species. *Behav Ecol Sociobiol* 28: 29–36.
- Studds CE, Marra PP (2005) Nonbreeding Habitat Occupancy and Population Processes: An Upgrade Experiment with a Migratory Bird. *Ecology* 86: 2380–2385.

Studds CE, Marra PP (2007) Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. *Climate Research* 35: 115–122.

Studds CE, Marra PP (2011) Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proceedings: Biological Sciences* 278: 3437–3443.

Stutchbury BJM, Siddiqui R, Applegate K, Hvenegaard GT, Mammenga P, Mickle N, Pearman M, Ray JD, Savage A, Shaheen T, *et al.* (2016) Ecological Causes and Consequences of Intratropical Migration in Temperate-Breeding Migratory Birds. *The American Naturalist* 188: S28–S40.

Stutchbury Bridget J. M., Gow Elizabeth A., Done Tyler, MacPherson Maggie, Fox James W., Afanasyev Vsevolod (2011) Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proceedings of the Royal Society B: Biological Sciences* 278: 131–137.

Sullivan B, Wood C, Iliff M, Bonney R, Fink D, Kelling S (2009) eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation - BIOL CONSERV* 142: 2282–2292.

Svensson E, Nilsen J-Å (1997) The trade-off between molt and parental care: a sexual conflict in the blue tit? *Behavioral Ecology* 8: 92–98.

Swaddle JP, Williams EV, Rayner JMV (1999) The Effect of Simulated Flight Feather Molt on Escape Take-Off Performance in Starlings. *Journal of Avian Biology* 30: 351–358.

Taylor, PD, Crewe T, Mackenzie S, Lepage D, Aubry Y, Crysler Z, Finney G, Francis CM, Guglielmo CG, Hamilton DJ, Holberton RL, Loring PH, Mitchell GW, Norris D, Paquet J, Ronconi RA, Smetzer J, Smith PA, Welch LJ, and Woodworth BK (2017) The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology* 12:8.

Takaki Y, Eguchi K, Nagata H (2001) The growth bars on tail feathers in the male Styan's Grasshopper Warbler may indicate quality. *J Avian Biol* 32: 319–325.

Tonra CM, Reudink M (2018) Expanding the traditional definition of molt-migration. *The Auk* 135: 1123–1132.

Tonra CM, Hallworth MT, Boves TJ, Reese J, Bulluck LP, Johnson M, Viverette C, Percy K, Ames EM, Matthews A, *et al.* (2019) Concentration of a widespread breeding population in a few critically important nonbreeding areas: Migratory connectivity in the Prothonotary Warbler. *Condor*. doi:10.1093/condor/duz019

- Tonra CM, Marra PP, Holberton RL (2011a) Migration phenology and winter habitat quality are related to circulating androgen in a long-distance migratory bird. *Journal of Avian Biology* 42: 397–404.
- Tonra CM, Marra PP, Holberton RL (2011b) Early elevation of testosterone advances migratory preparation in a songbird. *Journal of Experimental Biology* 214: 2761–2767.
- Vágási CI, Pap PL, Vincze O, Benkő Z, Marton A, Barta Z (2012) Haste Makes Waste but Condition Matters: Molt Rate- Feather Quality Trade-Off in a Sedentary Songbird. *PLoS ONE* 7: 1–9.
- Valiela I, Bowen JL, York JK (2001) Mangrove Forests: One of the World's Threatened Major Tropical Environments. *BioScience* 51: 807.
- Vancutsem C, Achard F, Pekel J-F, Vieilledent G, Carboni S, Simonetti D, Gallego J, Aragao L, Nasi R (2020) Long-term (1990-2019) monitoring of tropical moist forests dynamics. *bioRxiv* 2020.09.17.295774.
- Vargas LEP, Laurance W, Clements GR, Edwards W (2015) The Impacts of Oil Palm Agriculture on Colombia's Biodiversity: What We Know and Still Need to Know. *Tropical Conservation Science* 8: 828–845.
- Verhulst S, Balen JH van, Tinbergen JM (1995) Seasonal Decline in Reproductive Success of the Great Tit: Variation in Time or Quality? *Ecology* 76: 2392–2403.
- Verhulst S, Nilsson J-Å (2008) The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philos Trans R Soc Lond B Biol Sci* 363: 399–410.
- Visser ME, Lessells CM (2001) The costs of egg production and incubation in great tits (*Parus major*). *Proceedings of the Royal Society of London Series B: Biological Sciences* 268: 1271–1277.
- Vitz AC, Rodewald AD (2011) Influence of Condition and Habitat use on Survival of Post-Fledging Songbirds. *The Condor* 113: 400–411.
- Ward MP, Benson TJ, Deppe J, Zenzal TJ, Diehl RH, Celis-Murillo A, Bolus R, Moore FR (2018) Estimating apparent survival of songbirds crossing the Gulf of Mexico during autumn migration. *Proceedings of the Royal Society B: Biological Sciences* 285: 20181747.
- Ward RD, Friess DA, Day RH, Mackenzie RA (2016) Impacts of climate change on mangrove ecosystems: a region by region overview. *Ecosystem Health and Sustainability* 2: e01211.

- Warkentin IG, Hernández D (1996) The conservation implications of site fidelity: A case study involving nearctic-neotropical migrant songbirds wintering in a Costa Rican mangrove. *Biological Conservation* 77: 143–150.
- Webster M, Marra P, Haig S, Bensch S, Holmes R (2002) Links Between Worlds: Unravelling Migratory Connectivity. *Trends in Ecology & Evolution* 17: 76–83.
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: S120–S139.
- Williams TD (2012) Hormones, life-history, and phenotypic variation: opportunities in evolutionary avian endocrinology. *Gen Comp Endocrinol* 176: 286–295.
- Wingfield JC (2008) Organization of Vertebrate Annual Cycles: Implications for Control Mechanisms. *Philosophical Transactions: Biological Sciences* 363: 425–441.
- Wolfe JD, Johnson MD, Ralph CJ (2013) Greater Mass Increases Annual Survival of Prothonotary Warblers Wintering in Northeastern Costa Rica. *The Condor* 115: 163–167.
- Wright J, Tonra C, Powell L (2018) Prealternate molt-migration in Rusty Blackbirds and its implications for stopover biology. *The Condor* 120: 507–516.
- Wunderle JM, Lebow PK, White JD, Currie D, Ewert DN (2014) Sex and age differences in site fidelity, food resources tracking, and body condition of wintering Kirtland's Warblers (*Setophaga kirtlandii*) in the Bahamas. *Ornithological Monographs No 80* 1.
- Yosef R, Grubb TC (1992) Territory Size Influences Nutritional Condition in Nonbreeding Loggerhead Shrikes (*Lanius ludovicianus*): A Ptilochronology Approach. *Conservation Biology* 6: 447–449.