

ENDOGENOUS AND EXOGENOUS FACTORS INFLUENCING THE
MOVEMENT AND MIGRATORY BEHAVIORS OF A WINTERING SONGBIRD

A Dissertation

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by

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ABSTRACT

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As migratory organisms decline globally at unprecedented rates, there is a growing imperative to understand ecological and evolutionary responses to climate change – especially those that affect the availability and phenology of resources. Understanding how climate affects the behavior and population dynamics of migratory birds is challenging because migrants have complex annual cycles that extend across geographically disparate locations. How and when migrants transition between different stages of the annual cycle – in other words, their movements – can have substantial individual and population-level consequences (e.g., seasonal interactions). To date, research on movements has been constrained by our inability to track organisms at fine enough spatiotemporal resolutions, resulting in biases towards larger organisms, easily observed strategies (e.g., territoriality), and breeding-centric studies. Ultimately, a more holistic understanding of the impacts of global climate change on migratory populations requires a full annual cycle approach.

My doctoral research investigated (1) how migratory birds adjusted within-season (space use) and between-season (departure phenology and migratory movements in response to climate-associated changes in resources and phenology during the nonbreeding season and (2) the extent to which those behaviors were

shaped by the interplay between endogenous states (condition and dominance status) and exogenous conditions (resource availability). We combined new tracking technologies (2015-2020) with long-term demographic data (1995-2020) from an overwintering population of the migratory songbird, American redstart (*Setophaga ruticilla*), in Jamaica, to study individual and population-level drivers and consequences of movement behaviors.

Tracking data revealed several distinct space use behaviors that include territoriality, floating, and transience and identified the variability in space use behaviors that often blur the lines between distinct strategies that include the prevalence of secretive forays that ranged from 0 up to 8 forays per day per individual. In resource-rich years (i.e., high NDVI), birds used less space as compared to resource-poor years. Likewise, within a season, variation in weekly resource availability (i.e., weekly NDVI) had a negative influence on the prevalence of forays and the area of space utilized. Lastly, dominance status (i.e., age and sex) significantly influenced the type and plasticity of space use behaviors, with dominant classes (i.e., adult males) most likely to occupy territories and respond strongly to changing seasonal resource availability. As one of the few studies to investigate the sources of variability in space use behavior in terms of both internal and external states for overwintering migrants, this work provides evidence of the importance of the interplay between environmental conditions and individual behavior in ultimately scaling to influence the distribution of space use behaviors at the population-level. These results highlight the rich variability in space use behaviors that are typically not captured in most conventional population studies and have gone largely overlooked and

underappreciated.

Timely arrival on the breeding grounds is vitally important for individual fitness and can be delayed by poor overwintering conditions. To date, no studies have assessed how the phenology of spring departure has changed over time and in response to environmental change. In the second component of my dissertation, I assessed how the phenology of spring departure of American redstarts changed over the past 24 years (1995-2019), identified the endogenous and exogenous drivers of departure timing, and described associations among spring departure schedules, breeding origins and winter rainfall. The timing of an individual's migratory departure was shaped by both breeding latitude and winter rainfall, in addition to age and sex. Spring departure schedules were significantly earlier in wet vs. dry years and for southern vs. northern breeders. At the population level, spring departure schedules advanced at a rate of 0.21 days per year, which translated to 5 days over the past 24 years. This long-term shift in departure was better explained by the > 300-kilometer southward shift in the breeding origins of our wintering population than by rainfall, given the absence of long-term trends in precipitation at our study site. Our study is among the first to provide a nonbreeding perspective on the drivers of phenological changes in the annual cycles of migratory organisms.

Given the costs of delayed arrival on the breeding grounds, a fundamental question remains— can individuals mitigate delayed spring departure schedules by migrating at a relatively faster rate? For the final chapter of my dissertation, I focused on individual American redstarts (*Setophaga ruticilla*) that were tracked after departing their wintering grounds in Southwest Jamaica through Florida and selected

sites further north using the Motus Wildlife Tracking System. Individuals that departed relatively late migrated at a faster rate than those departing comparatively early. Importantly, delayed individuals were significantly less likely to return the following season. These results support the hypothesis that individual migrants attempt to compensate for delays in the start of spring migration and possibly incur survival costs because of these behaviors—a potential mechanism underlying differential survival during spring migration.

Through the implementation of novel technological approaches and long-term demographic data, we shed light on many subtle and difficult to observe behaviors by peering deeper into some of the commonly held assumptions on how individuals utilize space, how they respond to seasonally variable conditions, and how migratory birds mediate climate-induced changes in resource availability. Ultimately, this dissertation highlights how the endogenous states of individuals interact with exogenous conditions to shape the movement of migratory birds that has important implications on the reproductive performance of individuals breeding thousands of miles away.

BIOGRAPHICAL SKETCH

Bryant C. Dossman, born and raised in Newark, New Jersey, arrived at Cornell University after completing a B.A. in Biology and Environmental Studies at Bowdoin College (2011) and an MSc in Natural Resources from the Ohio State University (2015). He is broadly interested in the behavior, movement, and population ecology of migratory organisms, particularly regarding the linkages between animal movement and population dynamics.

His interests in the ecology of migratory birds began with his work on differential migration in a population of Savanna Sparrows at Bowdoin College with Nathaniel T. Wheelwright. He has since undertaken numerous field research positions working with the Black-throated blue warblers at Hubbard Brook Experimental Forest, the stopover ecology of passerine migrants on the Gulf Coast with the University of Southern Mississippi, to the winter ecology of American redstarts in Jamaica with the Smithsonian Migratory Bird Center. These experiences paved the way for the start of his graduate studies at the Ohio State University. He coupled his field research skills with his interests in tracking technology to establish an automated telemetry array in the western Lake Erie basin. There he was able to determine the factors that influence migratory movement dynamics across western Lake Erie and Southern Ontario, which culminated in an MSc in 2015.

Shortly after graduating with his MSc, Bryant joined the Cornell Department of Natural Resources and Cornell Lab of Ornithology to develop his interests in the movement, behavioral, and population ecology of migratory birds. Under the guidance

of Drs. Amanda Rodewald and Peter Marra (Georgetown University), he was able to return to Jamaica to conduct his research on a long-term wintering population of migratory passerine—the American redstart. While at Cornell, Bryant developed a much deeper understanding of the statistical, methodological, and technological approaches used to study animal movement. By applying some of these novel technological approaches, he was able to dive deep into the secretive and difficult to observe behaviors that underlie plastic responses of species to changing environmental conditions. Though his interests are grounded in science, Bryant is also deeply committed to teaching, mentoring, and outreach. As part of his doctoral research, Bryant mentored a total of 17 field technicians, which included students from both the U.S. and Jamaica.

After graduating from Cornell, Bryant will work as a post-doctoral fellow at Georgetown University, where he will continue his research on the movement and behavioral ecology of migratory passerines.

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I wish give special thanks to my advisor, Dr. Amanda Rodewald for her supervision, support, and encouragement. Amanda has served as a mentor since I first met her at the Ohio State University in 2012. Although she only officially began advising me when I joined her lab as a Ph.D. student in 2015, she has always been a supportive mentor, guiding my research and challenging me to think broadly about my research. Amanda's advising style fosters strong intellectual growth by providing enough guidance to ensure the success of her students while also allowing them the freedom to explore their research to the fullest. It was because of this that I was able to address a diverse range of questions for my dissertation. Amanda has also been incredibly supportive through all the challenges I have faced and has helped me in

more ways than I can count. Amanda, thank you so much for helping me grow as a scientist and as a person – I couldn't have done this without you.

I also need to thank Dr. Pete Marra, who I was fortunate enough to have as a second advisor. In many ways, Pete had guided my research since the beginning when I first started considering a career in Ecology. By chance, during one of my first weekly meetings with my undergraduate advisor Nat Wheelwright, we read through a paper by Pete. Ultimately, this paper had such an impact that it guided my initial proposal to study where our breeding population of Savannah Sparrows was wintering and has since shaped my course of research to date. Since the beginning of my PhD, Pete has been incredibly supportive and has become an important mentor to me. He has guided my research, has consistently challenged me, and continues to teach me something new every day. Pete has been instrumental in my development, and I am incredibly thankful for the support and mentorship these past several years!

I am thankful for assistance from many people who were instrumental in facilitating logistics, fieldwork, and contacts over the course of this research: Bob Reitsma, Micky Zifchock, and Joe Walkowicz. Special thanks to several folks I turned to often for helpful insights and support: Orin Robinson, Viviana Ruiz-Gutierrez, Wesley Hochachka, and André Dhondt. This work would never have been possible without the many field assistants on the project. Thanks to: Boo Curry, Jack Toriello, Kiirsti Owen, Andrew Sharp, John, and Lizzie Diener, Tara Lafabrégue-Rodkey, Emily Filiberti, Reina Galvan, Tucker Grigsby, Alex Cook, Joey Negreann, Gavin Campbell, Connor Rosenblatt, Max Witnyski, Reed Barbee, and Travenne Barnett. Special thanks to Justin Saunders, who worked for me for several years and has

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CHAPTER 1

INTRODUCTION

Background

Global climate change is reshaping the ecology of our planet as organisms respond both ecologically and evolutionarily to novel pressures (Parmesan and Yohe 2003, Parmesan 2006, Rosenzweig et al. 2008). Migratory birds, in particular, provide a useful lens to better understand the overall effects of climate change on broad patterns of their ecology, and to some degree, on the underlying mechanisms that give rise to these responses. But even for birds, we lack a sophisticated understanding of how climate fundamentally shapes the biology, ecology, and long-term persistence of these species. Because migrants have complex annual cycles that extend across geographically disparate locations, our understanding of how climate (temperature and precipitation) drive seasonal interactions to operate across the annual cycle – specifically between the breeding, migratory, and non-breeding stages. Much of our research on migratory organisms has been heavily biased towards the breeding period (Marra et al. 2015a), which resulted in a ‘blind-spot’ in our understanding of the effects of climate, and then climate change on the populations of migratory organisms (Small-Lorenz et al. 2013). Therefore, to better predict the consequences of climate change, we need to understand how climate itself acts on individuals and populations during the non-breeding and migratory periods, in addition to the breeding season (Small-Lorenz et al. 2013) and how these consequences scale up to drive population

dynamics.

From a non-breeding perspective, climate-induced drying throughout much of the Neotropics (Neelin et al. 2006, Herrera and Ault 2017) impacts migratory bird populations by limiting the resources (e.g., food) available to them. The effects of food in mediating seasonal interactions and carry-over effects have been demonstrated in a number of taxa ranging from waterfowl (Sedinger et al. 2011) and shorebirds (Gunnarsson et al. 2005) to migratory passerines (Saino et al. 2004, Reudink et al. 2009). For example, reductions in food availability during the non-breeding period (observational or manipulated) results in direct changes to the body condition (Marra et al. 1998, Brown and Sherry 2006, Studds and Marra 2007, Danner et al. 2013, Cooper et al. 2015), molt (Danner et al. 2014, Reudink et al. 2015), site persistence (Latta and Faaborg 2001, Smith et al. 2011, Danner et al. 2013, Stanley et al. 2021), and departure times (Marra et al 1998, Studds and Marra 2011, Saino et al. 2004). These effects, in turn, have been shown to carry over and influence the timing of arrival on the breeding grounds (Marra et al 1998, Norris et al. 2004, Reudink et al. 2009, Rockwell et al. 2012, McKellar et al. 2013, Haest et al. 2020), subsequent reproductive success (Norris et al. 2004, Reudink et al. 2009), abundance (Wilson et al. 2011), survival (Sillett and Holmes 2002, Rushing et al. 2017), and natal dispersal (Studds et al. 2008, Rushing et al. 2015). Sillett et al. (2000) demonstrated with the Nearctic-neotropical insectivorous migrant (Black-throated Blue warbler; hereafter BTBW) that annual survival in Jamaica (non-breeding) was largely predicted by El Nino/La Nina conditions. Following El Nino winters, survival of BTBWs declined likely owing to the increased dry-conditions and concomitant decreases in food

resources (foliar arthropods), while the opposite pattern persisted during La Nina years (Sillett and Holmes 2002, Studds and Marra 2007, 2011, Marra et al. 2015b).

Ultimately, this evidence suggests that broad and persistent drying trends throughout much of the Neotropics result in numerous direct and indirect effects on the phenology (McKellar et al. 2013, Mayor et al. 2017, Lehikoinen et al. 2019, Horton et al. 2020), abundance (Wilson et al. 2011), survival (Sillett and Holmes 2002), and fitness (Reudink et al. 2009) of several Nearctic-Neotropical migratory species. Notably, these linkages have yet to be demonstrated directly with the same individual birds and so how these carry-over effects operate through migration has yet to be directly tested and linked to long-term phenological changes observed on the breeding grounds (addressed in Chapters 3 & 4).

Even amid well-known links between resource limitation in winter and the fitness of migratory birds, individuals vary widely in the extent to which they experience or manifest these consequences. For example, because dominance hierarchies partition resources among individuals and mediate habitat occupancy during the non-breeding season (Marra 2000), dominant individuals will be comparatively buffered from declining or unpredictable food resources within habitats and/or territories (Marra and Holmes 2001, Studds and Marra 2005). Indeed, Marra et al. (2015) demonstrated that dominance-mediated habitat segregation can result in differing regulatory mechanisms operating on high quality vs. low-quality habitats— with populations (mostly males) occupying high-quality habitat being regulated by crowding, whereas populations in (mostly females) low-quality habitat being primarily limited by food availability (rainfall) resulting in a pattern of sexual habitat

segregation (Marra 2000).

Individuals also can mediate access to resources and buffer the effects of climate-induced food limitation by modifying how they use space to ensure access to resources (Brown and Long 2007, Smith et al. 2010, 2011, Stanley et al. 2021). For instance, in response to declining resources, birds may remain site faithful by simply adjusting home range (Brunner, *AR In Review*), increasing the frequency and duration of extra-territorial forays to supplement resources (Chapter 2), shifting to adjacent higher-quality territories (Brunner, *AR In Review*), or adopting alternative and non-territorial space use strategies (i.e., floating) to potentially gain access to more ephemeral and patchy resources (Brown and Orians 1970, Smith 1978, Brown and Long 2007, Brown and Sherry 2008). At a further extreme, individuals may even disperse hundreds of kilometers mid-winter into higher quality habitats (Stanley et al. 2021), thereby becoming transient as they transition between wintering sites. In fact, Cooper et al. (2015) experimentally demonstrated that individuals abandoned territoriality mid-season and likely adopted floater behavior following an 80% reduction in food availability. Further, Ruiz-Guiterrez et al. (2016) demonstrated that site persistence (a component of space use) varied latitudinally following presumed patterns of resource/habitat limitation. Collectively, this suggests that the variability in space use behaviors of a wintering population is likely to be directly tied to resource availability and, as such likely vary considerably in space and across time (Peele et al. 2015, Ruiz-Gutierrez 2016). Yet, questions remain as to the extent to which variability in space use behavior are truly driven by individuals attempting to buffer the effects of resource limitation (best of a bad job) or whether the occurrence and prevalence of

these behaviors simply reflect a lack of available habitat (see Chapter 2).

Finally, in cases where individuals cannot adjust behaviors to escape poor quality habitats, they may attempt to mitigate negative consequences by altering their migratory behavior (i.e., a delayed departure from the non-breeding grounds). There is mounting evidence that birds can increase the pace of migration (McKinnon et al. 2015, Briedis et al. 2018, González et al. 2020), though trade-offs may compromise survival (Alerstam 1991, 2011, Wingfield 2007). Given the costs of delayed arrival on the breeding grounds and the limited reproductive opportunities of many short-lived migratory songbirds, it is likely that individuals might attempt to compensate for the delays at the start of migration by migrating at a relatively faster pace. However, to date, no studies have determined, mechanistically, how non-breeding carry-over effects operate through migration and ultimately influence population dynamics of migratory organisms and whether plasticity in migratory behavior may offset the costs of poor winter conditions (see Chapter 4).

Study System

My research was conducted from 2015-2020 within the context of a long-term study (1987-*Present*) of a population of American redstarts (*Setophaga ruticilla*; hereafter redstarts) wintering at the Font Hill Nature Preserve in southwest Jamaica, West Indies. In this study system, individual redstarts have been intensively color-banded and extensively monitored throughout the mid-winter period (early January) up through spring departure (mid-May) to better understand the winter ecology of migratory songbirds.

Early work in this system revolved around understanding the role that the non-

breeding period plays in influencing the population dynamics of migratory birds through seasonal interactions such as individual-level carry-over effects (Marra et al. 1998, 2015, Norris et al. 2004). Extensive research was conducted on all aspects of the winter ecology of this migrant to better understand how external conditions (density, climate, habitat type) and internal states (dominance status) interact to influence an individual's overwintering performance (body condition change throughout the winter), migratory preparation, spring departure timing, and overall survival (within and between seasons). This foundational work shaped the way we approach the study of migratory populations and produces research that continues to support the notion that the ecology of migratory organisms must be viewed primarily from the lens of the full-annual cycle, highlighting the overlooked role that the non-breeding season plays in influencing all aspects of the ecology of migratory birds.

My research builds upon this collective body of knowledge by investigating movement behaviors that are often subtle and difficult to observe. Technological and methodological advances facilitate investigations that test commonly-held assumptions about space use by non-breeding individuals (Chapter 2), how bird movements change in response to seasonally and annual variable conditions (Chapter 2) and departure timing (Chapter 3), and ultimately their ability to potentially mediate trade-offs during the transition between the non-breeding and breeding seasons (Chapter 4) – a critical period that has important implications on the reproductive performance and survival of individuals breeding thousands of miles away.

Dissertation organization

This dissertation is comprised of three research chapters, each written as a manuscript

formatted for publication. Chapter 2 focuses on the variability in and drivers of space use behaviors at the individual and population levels within and across seasons. Chapter 3 is an evaluation of whether the timing of spring migration has advanced over a 24-year period by first investigating the drivers of individual departure schedules and then identifying which factors scale up to influence long-term patterns in spring migration timing from the non-breeding grounds. Results demonstrate that long-term advances in migration timing reflect southwards shifts in the breeding origins of this population. Building off previous chapters, Chapter 4 links how winter conditions and individual endogenous factors shape the relative timing of departure from the non-breeding grounds and how delays influence individual migration rates. Patterns reveal that tremendous variability exists in how individuals use space and populations respond to changing seasonal conditions. Ultimately, winter season movements carry over to influence the transition between the non-breeding and breeding seasons.

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CHAPTER 2

DRIVERS OF INDIVIDUAL- AND POPULATION-LEVEL SPACE USE STRATEGIES IN AN OVERWINTERING MIGRATORY BIRD

Abstract

Movement is a fundamental component of the ecology of all organisms and governs how an organism interacts with other species and the environment (hereafter space use) — ultimately underlying an individual’s fitness and survival. Yet, our understanding of space use has remained constrained by our inability to track organisms at fine enough spatiotemporal resolutions, resulting in biases towards larger organisms and easily observed strategies (e.g., territoriality). Here, using a novel automated telemetry array and extensive hand tracking, we examined the distribution of space use behaviors of a wintering population of American redstarts *Setophaga ruticilla*. We identified several distinct space use behaviors that include territoriality, floating, and transience, and identified the variability in space use behaviors that often blur the lines between distinct strategies that include the prevalence of secretive forays that ranged from 0 up to 8 forays per day per individual. In resource-rich years (i.e., high NDVI), birds exhibited more constrained space use behaviors compared to resource-poor years. Likewise, within a season, resource variability among weeks (i.e., weekly NDVI) reduced the prevalence of forays and the area of space utilized. Lastly, we determined that dominance status (i.e., age and sex) significantly influenced the space use behavior and plasticity in space use, with more dominant classes (i.e., adult

males) more likely to occupy territories and respond more strongly to changing seasonal resource availability. As one of the few studies to investigate the sources of variability in space use behavior in terms of both internal and external states for overwintering migrants, we present evidence demonstrating the importance of the interplay between environmental conditions and individual behavior in ultimately scaling to influence the distribution of space use behaviors at the population-level. Our study highlights the rich variability in space use behaviors that are typically not captured in most conventional population studies and have gone largely overlooked and underappreciated.

Introduction

Though often viewed through the lens of individuals, movement fundamentally links behavior to population dynamics. How individuals move across space governs their interactions with conspecifics, other species within the community, and the environment, all of which collectively influence survival and fitness (Pradel et al. 1997, Hines et al. 2003, Conn et al. 2011, Royle et al. 2016, Ruiz-Gutierrez et al. 2016). Our understanding of movement ecology has been, thus far, constrained technologically in ways that make it difficult to track individuals at fine spatiotemporal scales (Bridge et al. 2011, Krause et al. 2013, Kays et al. 2015), and so are biased towards conspicuous individuals and behaviors and inadequately characterize population-level distribution (Smith and Arcese 1989, Winker 1998, Brown and Long 2007, Brown and Sherry 2008). Identifying both the patterns and mechanisms underlying intraspecific variability in movement and space use is required to fully understand population limitation and regulation.

One challenge to understanding space use strategies, which are defined as the consistent manner by which an individual utilizes space (Abrahms et al. 2017, Spiegel et al. 2017, Hertel et al. 2020), is their frequent treatment as discrete movement types or categories. Space use strategies represent a continuum of behaviors across multiple spatial and temporal scales (Figure 2.1), and categorizing movements can often mask within- and among-individual variability. For instance, territoriality is one of the best-documented space use strategies where individuals defend an exclusive area of space (Brown and Orians 1970, Maher and Lott 2000), yet behaviors associated with territories vary widely among individuals over time (Ward et al. 2014, Barve et al.

2019), space (Brown and Long 2007, José-Domínguez et al. 2015), and purpose (Jirinec et al. 2016). Further, individuals may shift their behaviors across time by exhibiting variability in territory-fidelity, or potentially by abandoning territorial behavior altogether depending on the economics of territory defense (Gill and Wolf 1975, Carpenter 1987).

In addition to the temporal dynamics of territoriality and home ranges, populations may also consist of *transient* individuals, which was a term co-opted for capture-recapture studies to account for individuals that were not part of the study population and that biased survival and population estimates (Pradel et al. 1997, Hines et al. 2003, Conn et al. 2011, Royle et al. 2016, Ruiz-Gutierrez et al. 2016). Under this broad operational definition, *transients* may include individuals in the transient phase of dispersal (i.e., true transience), the periodic movements of sedentary animals (i.e., multi-territoriality, extraterritorial forays), or floaters. For instance, floaters – individuals that range broadly while in queue for an available territory or mate – are often mistaken as transients because floaters do not defend territories, are not sedentary, and often exhibit furtive behaviors (Stutchbury 1991, Winker 1998, Brown and Long 2007, Brown and Sherry 2008), which makes them less likely to be detected. Further, territorial individuals may be incorrectly classified as transients if they are detected during an extraterritorial foray or occupy multiple territories that may lie out of the study site. Ultimately, this spatiotemporal variability of individual movement behaviors likely results in substantial overlap in movement between distinct space use strategies (e.g., Figure 2.1). Hence, categorical treatments of space use behaviors, in practice, are likely to obscure the rich variability in individual space use strategies and,

at worse, bias our knowledge of the variability and population-level implications of space use strategies. Our understanding of space use will remain incomplete without an appreciation of these subtle and difficult to observe behaviors (Cooper and Marra 2020, Smith and Pinter-Wollman 2020).

Characterizing the true distribution of space use behaviors requires study designs and technologies that allow movement to be monitored at sufficiently fine spatiotemporal scales to capture variation among individuals within a population. Until recently, tracking technologies were unavailable for this application, especially for small-bodied animals like migratory songbirds (Bridge et al., 2011). We used a novel automated telemetry array coupled with more conventional radio-tracking to describe the patterns and the underlying population variability in space use behaviors of a nonbreeding, hereafter wintering, population of a Nearctic-Neotropical migratory bird – the American Redstart (*Setophaga ruticilla*, hereafter redstarts). Though most redstarts are territorial in breeding and nonbreeding stationary periods, individuals can exhibit a diverse mix of space use behaviors, including defended territories, occupation of home ranges, mixed species flocking, nocturnal roosting, and floating (Holmes et al. 1989, Lefebvre et al. 1994, Marra and Holmes 2001).

We hypothesized that space use behaviors represent individual tactics that are shaped by the interplay between individual internal states (condition, dominance status) and external conditions (habitat quality, resource availability, and conspecific density). Because migratory birds often experience unpredictable or variable food resources during winter, we predicted that movement and space use behaviors would be plastic and dependent upon environmental conditions. At the population level,

temporal variation in resource availability should shape the distribution of space use behaviors by shrinking territory and home range sizes, restricting the prevalence of extraterritorial forays, and accommodating a greater number of sedentary individuals on the landscape (Figure 2.1). Accordingly, we predicted that, within season, individuals would become more sedentary during resource-rich times than in times of resource scarcity. We further predicted that this plasticity would be constrained by social status with subordinates more likely to plastically respond to temporal variation in resource availability. Since dominant individuals disproportionately occupy the highest quality habitats, they are more likely to be buffered by changing resource availability. Lastly, we predicted that sedentary use of space would improve access to resources and thus enhance individual condition and survival as compared to less spatially and temporally predictable alternative space use strategies (e.g., floaters and transients).

Methods

Study System

This study was conducted January-May of 2016-2019 on a primarily territorial population of American redstarts (*Setophaga ruticilla*) overwintering at the Font Hill Nature Preserve (18° 02' N, 77° 57' W, < 5 m above sea level) on the southwest coast of, St. Elizabeth Parish, Jamaica.

Our study site is composed of two primary habitat types; a higher-quality mangrove forest and a lower-quality scrub forest, hereafter referred to as wet mangrove and dry scrub, respectively. The wet mangrove is dominated by Black mangrove (*Avicennia germinans*) with occasional patches of White (*Languncularia*

racemose) and Red (*Rhizophora mangle*) mangrove and tends to retain high levels of soil moisture. In this higher-quality habitat, arthropod biomass (primary food for redstarts) tends to remain consistently high throughout the winter season (Nov-Apr) as compared to the immediately adjacent dry scrub sites (Studds and Marra 2011, Wilson et al. 2013). dry scrub consisted mainly of logwood trees (*Haematoxylon campechianum*) but also had other species, including *Bursera simarubra*, *Terminalia latifolia*, and *Crescentia alata*. Unlike wet mangrove, the dry scrub forest typically retains low soil moisture and consequently tends to have less arthropod biomass that progressively declines throughout the season as conditions become drier (Studds and Marra 2011, Wilson et al. 2013). Further, annual variation in winter rainfall can compound differences in habitat quality as drought years result in substantially lower arthropod biomass and may differentially impact wet mangrove and dry scrub.

The quality of these two habitats shapes many aspects of the ecology and behavior of redstarts. For example, selection of either wet mangrove or dry scrub is mediated by behavioral dominance, with adult males occupying wetter and more food-rich mangroves (wetter and more food rich) disproportionately to subordinate females and young males (Marra 2000). This interaction between behavior and habitat quality (both within and between seasons) drives much of the variability in overwinter body condition and pre-migratory preparation, leading to substantial fitness consequences in later stages of the annual cycle (Marra et al. 1998, Norris et al. 2004, Studds and Marra 2011, Cooper et al. 2015).

To investigate the factors that underlie space use behaviors (territorial vs. floater), we classified individuals into age and sex classes using plumage and feather

characteristics. At the time of capture, we also measure standard morphometrics, including body mass (g), fat score, pectoral muscle size (Powell et al. 2021), wing chord (mm), tarsus length (mm), and used these to estimate body condition using the scaled mass index (Peig and Green 2009). We attempted to recapture as many individuals as possible throughout the season (*Mean Capture Window* = 30.68 ± 14 days) to quantify how body composition and condition changed over the winter in response to space use strategy. This allowed us to test not only how space use behaviors are distributed according to a proxy of dominance status (age and sex) but also allowed us to determine the potential consequences of these movement strategies on the maintenance of individual condition over the winter.

Movement behaviors are often tied to changes in resource availability, and to explore how flexible these movement strategies are, we attempted to link changes in the distribution of space use strategies and changes in individual movement to changing resource availability. In this system, changes in food availability mirror changes in habitat quality driven by rainfall. As droughts damage and reduce vegetation, food availability (arthropod biomass) begins to decline (Wilson et al. 2013). As such, to explore how changes in resource availability influence the distribution of movement strategies between years and influence the movement behavior of individuals within years, we utilized a satellite-derived proxy; normalized difference vegetation index (NDVI). We calculated NDVI across the study site from Sentinel-2 multispectral imagery sourced using Google Earth Engine. Sentinel-2 consists of a constellation of 2 twin satellites that capture high-resolution (10 m) multispectral imagery at an approximate weekly interval. This allowed us to estimate

the annual differences in habitat quality driven by seasonal rainfall and how individual forays varied in response to changing habitat quality seasonally at the weekly scale.

Between the winters of 2016-2019 we equipped a total of 141 redstarts ($N_{2016} = 23$, $N_{2017} = 66$, $N_{2018} = 15$, $N_{2019} = 37$) with a 0.29 g digitally coded VHF radio transmitters (NTQB1-1 & NTQB2-1, Lotek Wireless Inc., Newmarket, ON, Canada) using a modified leg-loop harness (Rappole and Tipton 1991). Transmitters operated continuously at a ~10.3-second cycle, which resulted in a battery lifespan of approximately ~30 - 45 days. Focal birds were tagged as part of two projects, one primarily for the study of pre-migratory (Apr 1 – May 15) and migratory behaviors and this study; on the space use strategies of wintering migrants.

As part of this study, we only included individuals tagged before Apr 1 of each year to avoid the effects of the pre-migratory period on individual movement behavior. Individuals were captured randomly across the study sites using a passive netting approach to avoid potentially biasing our tagged sample towards territorial individuals that are more susceptible to capture using playback approaches. A final sample of 74 individuals (39 *males*, 35 *females*) that would most accurately represent the distribution of space use behaviors were included in this study.

Tracking Individual Movement

To quantify the movement behavior of individuals, we employed two tracking methodologies: one based on manual hand tracking and another using a network of 5 automated telemetry receivers (*Sensornomes*). Hand tracking allowed us to follow individuals at a coarse temporal resolution (hourly-daily) but at a precise spatial

resolution (< 5 m). The network of automated receivers provided a very fine temporal resolution (detections every ~ 10 seconds) but the coarse spatial resolution (~ 300 m detection range of each station; presence/absence). We detail both approaches and their accompanying response variables below. Coupling both approaches allowed us to gather a more holistic understanding of both the spatial and temporal variability in movement behavior.

Manual Hand tracking

Following the initial capture and tagging, we used a standardized protocol of localizing each individual daily through a mix of triangulation and homing localization techniques using an SRX-800 (Lotek Wireless Inc., Newmarket, ON, Canada) and a 3-element yagi. To assist in the feasibility of tracking redstarts multiple times per day, we limited the number of active tags in a given tracking period to less than 15 individuals. Each day, we searched for every active tag (once per round) for approximately 5-10 minutes near the capture location or the last location the individual was detected. Upon detection, individuals were either localized via homing (identified visually), and a GPS location taken (< 1 m) or was triangulated after acquiring three bearings to the individuals' approximate location (< 5 m). Individuals were most commonly located via triangulation, but we made a concerted effort to hone in on individuals regularly to visually identify them to assess their behavior and the condition of the tag. If an individual was not detected during the initial 5-10 minute search of that round (nor opportunistically while traversing the study site between tag detections), we expanded our search to include all areas of the study site that were not originally traversed for approximately 60 minutes. Because the nanotags are digitally

encoded and transmitted on a single frequency, we were able to scan the 166.380 MHz continuously while tracking, enabling us to locate individuals as we moved through the study site opportunistically. Not only did this expedite the localization process, but it also enabled us to better search the study site without missing individuals due to frequency switches, an issue with more conventional beeper transmitters where each individual transmits at a separate frequency. Therefore, this protocol allowed us to confidently assess whether an individual was still alive, died, or departed the study site (~ 200 ha). We repeated this protocol throughout each season daily from ~ 6 am - 12 pm, which would result in an average of 26.5 locations per individual (range = 5 - 108).

Automated Telemetry

To track individuals at a fine temporal resolution across the study site, we utilized an automated radio tracking system that consisted of 5 Sensorgnome receivers (Figure 2A). All tagged individuals were initially caught within the detection range (~300m) of any given receiver ensuring that most individuals were detected consistently for at least 5 days to accurately capture space use behaviors (56/71). Each receiver was equipped with four horizontally polarized omnidirectional antennae position 9 meters high on a galvanized steel mast. Each receiver had an approximate detection range of ~300 m when individuals were moving at or below the canopy level (*BCD pers obs*). These receivers continuously collected incoming signals from any nearby transmitter and logged the tag ID, timestamp, signal strength, antenna port, and receiver ID for each detection. Data collected by the automated telemetry system was downloaded from each receiver and then uploaded to the Motus Wildlife Tracking System network

for preliminary processing, archival, and dissemination (Taylor et al. 2017). We utilized the R packages *Motus* (Brzustowski and LePage 2021) & *tidyverse* (Wickham et al. 2019) to download, filter, and analyze the data. Although detections occur approximately every 10 seconds, we summarized and smoothed the detection data at minute intervals by calculating the median signal strength from a series of consecutive detections.

Quantifying Movement Behavior

We quantified space use and the variability in movement behavior in two ways. Our first approach relied on the automated telemetry data where we quantified the daily number of forays (*detailed below*) an individual took regardless of space use tactic. This measure provided a high-resolution and temporal measure of the variability in an individual movement. The second approach relied on the manual hand tracking data, where we quantified the net square displacement of each individual throughout their tracking duration. This approach provided a quantitative measure (mean square displacement) of the scale of space utilized by the individual during its tracking duration. In general, we refrained from categorizing individuals into discrete space use tactics. However, to draw comparisons with previous work that has relied on home range size as a delineator, we used net square displacement to broadly categorize individuals into sedentary ('territorial') and alternative ('floaters' and 'transients') space use strategies.

Given our network of automated receivers, detections on multiple towers are suggestive of individual exploratory movements (hereafter forays). Conventional hand-tracking approaches do not offer the temporal resolution needed to effectively

capture these relative ephemeral movements and therefore underrepresent the diversity of movement behaviors. As such, quantifying median daily forays enabled us to quantify the extent to which individuals (territorial or floaters) explored the study site on a continuous scale at a finer temporal resolution. Moreover, these higher temporal resolution data allowed us to estimate the effect that seasonally variable conditions, such as resource availability (NDVI; *detailed below*), would have on the extent and prevalence of these movement behaviors. Therefore, although hand-tracking allows us to broadly categorize the overall space use strategies, our automated approach enabled us to dive deeper into the movement and space use behavior of each individual, uncovering largely underappreciated variation in movement behaviors.

Within a network of automated receivers, forays can be quantified in two ways: movements between one receiver and another (*Transitions*) or movements out of range of one receiver and back (*Recursions*). *Transitions* are fairly unambiguous, especially within this spatial configuration of receivers since receivers are separated by distances that are orders of magnitude larger than the average territory size of a redstart. Therefore, departures from one receiver's detection range into another's are reflective of true, relatively large-scale movements. *Recursions*, however, are more ambiguous. They can either represent the movement of individuals temporarily out of range of the receiver but still within its home range or territory, or they can represent forays outside of their respective home range but in areas not covered by our array. We distinguished between these two possibilities by filtering out movements that were <10 minutes in duration as these are more likely to occur with temporary losses in detections as opposed to movements far outside the home range but where our array

coverage is poor. Further, visual inspection of the histogram demonstrated that most *Recursions* were less than ~10 minutes in duration lending further support for this cutoff (Figure 2C) Following this approach, we proceeded to quantify the number of daily forays for each individual tracked as the number of *Transitions* plus the number of *Recursions* that were greater than 10 minutes in duration

To quantify an individual's overall occupied spatial scale, we calculated each individual's net square displacement (NSD) from the manual tracking data. NSD is a popular movement metric that captures the scale and breadth of an individual's trajectory. NSD measures the square of the Euclidean distance between the starting location of a movement path and each subsequent location. Distinct patterns in NSD time-series are theoretically expected from specific movement strategies (asymptotic NSD = home-range/territorial behavior and increasing NSD over time = nomadic movements), and parametric models have been used to classify individuals by their predominant movement (e.g., dispersal, migration, residency) strategy (Bastille-Rousseau et al. 2016, Singh et al. 2016, Imai et al. 2019). Although these studies have used non-linear models to assign individuals to movement strategies, differences in net square displacement over time were distinct enough to visually assign individuals (Appendix, Figure 2B).

Because individuals varied considerably in their space use strategies and on the duration of time spent on the study site, we chose to only include individuals that were detected at least five times after capture. This ensured that we captured the full range of variable space use strategies of all tagged individuals. However, it is important to note that by excluding individuals that were not detected (or resighted) on the study

site after tagging, we excluded true transients. Transients, by definition, represent one extreme of space use behavior that represents a dispersive phase of an individual's movement behavior as it switches between territories/home-range or even wintering locations. Given their likely limited interaction with the population of more resident individuals, we can reasonably assume that they do not constitute members of this wintering population.

Data Analysis

We fit linear models that included age class (second year and after second year) and sex (male and female) to investigate how the mean square displacement (MSD) of an individual depended on its dominance status. We also included year as a fixed effect to assess how the average space use behavior of the population differed between years. We then calculated the median NDVI (tracking period; weeks 4 – 13) of each year to quantify the relative differences in seasonal greenness and precipitation between years and related that back to the distribution of space use behaviors (MSD) for the population.

Further, we explored within-season changes in space use behavior (mean daily forays & mean daily displacement) averaged across a week using linear mixed models that included individual as a random effect and weekly NDVI as the predictor. We included age class (second-year vs. after second-year), sex (male vs. female), and habitat type (dry Scrub vs. wet mangrove) along with their respective interaction with NDVI to explore how an individual's space use response to changes in environmental conditions varied according to those factors. Both mean daily forays and mean daily displacement were log-transformed, and in the case of mean daily forays (which

included zero), we added 1 to each value. We assessed the significance of all parameter estimates using likelihood ratio tests on reduced model varieties.

Consequences of Space Use Tactics on Overwinter Condition

Overwintering condition – defined as how well an individual maintains or improves their body condition throughout the winter – is a key trait that underlies the overall performance of an individual and is inherently tied to fitness in this species through a seasonal interaction on departure time (Studds and Marra 2007, 2011). However, body condition is an inherently multifaceted trait that is difficult to measure and rarely captured with single metrics. Because we are primarily interested in the relative mass and muscle an individual accumulates or maintains throughout the season, we keyed in on the change in scaled mass index (~size corrected mass, g) (Peig and Green 2009) and change in pectoral muscle size (mm) (Bauchinger et al. 2011, Powell et al. 2021) as response variables in linear models that include space use tactic (territorial vs. floaters) as well as age, sex, and habitat type to account for their confounding effects. Of the 74 individuals tracked in this study, we recaptured 48 at least twice within a season (> 10 days apart), which allowed us to assess how space use strategy influenced overwinter condition. Key positive indicators of overwintering condition would be positive changes in scaled mass index (increases in body mass), increases in muscle size, and maintenance of fat scores. Poor performers, on the other hand, would expect to lose or maintain mass throughout the season, decrease in muscle size, and increase in fat scores as expected from a previous food-reduction experiment in this study system (Cooper et al. 2015). For all models, we assessed significance at the $\alpha = 0.05$ level.

Switches in Space Use Behaviors

We leveraged daily resight data collected every winter from 2016-2019 to assess whether individuals switched between floater and territorial tactics between years. On average, we record ~1400 resights of color-banded individuals annually that are detected on the study plots throughout the winter (Jan-May). Because all individuals were tagged within the study plots and exhibit high site fidelity to their winter territories (Holmes et al. 1989), if an individual survived and did not disperse, then it was highly likely that we would detect it the following year. We note that because floaters are highly nomadic, it is plausible that they would have a lower detection probability than territory owners and would be more likely to disperse outside of our study site, so interpretations of these data should be made cautiously.

Results

Patterns of Space Use

Space use behaviors varied widely among individuals in terms of scale and type (Figure 2.2). Space use decreased by 0.58 ha per year from 2016-2018 as winters became wetter and greener (Figure 2.2). These reductions in space use, prompted by increasing seasonal rainfall and greenness (e.g., NDVI), matched declines in the proportion of floaters in the population (2016: 54%, 2017: 42%, 2018: 33%) and declines in territory size occupied by territorial individuals (2016: 0.37 ha, 2017: 0.33 ha, 2018: 0.28 ha). Further, floaters used areas ($\overline{MSD}_{Floater} = 5.89 \text{ ha}$) that were 9.35 times larger than those used by territorial birds ($\overline{MSD}_{Territory} = 0.63 \text{ ha}$), suggesting that at least part of the population-level decline in space use distribution could be attributable to the greater proportion of territorial individuals in the population.

Space use behavior was affected by age but not by sex. Second-year birds were more likely to exhibit floater behaviors (Prob(Floating): $\beta_{SY} = -1.894, t = -2.085, P = 0.037$) and use larger areas (Figure 3b; $\beta_{SY} = 1.067, t = 2.335, P = 0.025$) than older birds. Sex was not significantly related to the size of area used (Figure 3a; $\overline{MSD}_{Territory}: \beta_{Male} = -0.174, t = -0.417, P = 0.679$) nor the probability of being a floater (Prob(Floating): $\beta_{Male} = 0.031, t = 0.040, P = 0.968$).

A substantial portion of the population (61%) exhibited at least 1 foray. Of all the birds tagged, individuals exhibited, on average, 1.3 forays a day (range: 0 – 8). Interestingly, there was a significant interaction between habitat and sex (Figure 2.3c; $\beta_{Sex*Habitat} = , P \ll 0.001$), such that females made more forays than males ($\beta_{Sex} = , P \ll 0.001$) in dry scrub, but not in wet mangrove. Individuals occupying poorer-quality dry scrub habitat were more likely to make daily forays than birds occupying wet mangrove habitat ($\beta_{Habitat} = , P < 0.001$). Second year birds were more likely to undertake more forays than were adults (Figure 3d; $\beta_{age} = , P = 0.049$), which is consistent with second-year birds use of larger areas and greater propensity to being floaters. Within a season, birds reduced the number of daily forays as habitat quality improved (e.g., NDVI increased) (Figure 2.4). This plasticity in foray behavior was modified by a sex and habitat interaction whereby males responded to changes in NDVI in wet mangrove but not dry scrub habitat and females adjusted their foray behavior in dry Scrub but not wet mangrove habitat.

Consequences of Space Use Strategy

Overall, floaters experienced declines in body condition while territory owners either maintained or improved their condition (Figure 2.5). Floaters on average lost 0.33 grams of size corrected mass ($\beta_{Floater} = -0.331, t = -2.579, P = 0.015$) compared to territory owners over an average period of 30.6 (± 14 days). This change in mass was likely due to the significant decline in the size of the pectoral muscle ($\beta_{Floater} = -0.819, t = -2.566, P = 0.014$). Changes in condition (both muscle size and body mass) were not influenced by age (Change in Mass: $\beta_{SY} = 0.161, t = 0.106, P = 0.136$, Change in Muscle Size: $\beta_{SY} = 0.086, t = 0.301, P = 0.765$) or by sex (Δ Mass: $\beta_{Male} = -0.185, t = -1.76, P = 0.0856$, Δ Muscle Size: $\beta_{Male} = -0.460, t = -1.60, P = 0.117$). However, these physiological costs of floating were only fully realized in poor-quality dry scrub habitats. Floaters in wet mangrove habitat maintained their mass (Δ Mass: $\beta_{Floater* Mangrove} = 0.472, t = 2.115, P = 0.041$) and showed only marginal, nonsignificant changes in muscle size (Δ Muscle Size: $\beta_{Floater* Mangrove} = 1.06, t = 1.751, P = 0.088$). Of the floaters tracked in this study (N=19), only 3 individuals (16%) were resighted the following season. One individual returned for one additional year, another returned for two years, and the third returned for three additional years. Two returned and switched to a territorial space use strategy, securing and maintaining territories. The last individual returned, appeared to be a floater once again, and did not return the following year. In contrast, of the territorial individuals (N=55), 32 returned (58%) the following season, and all maintained consistent territories all winter long; we detected no territorial individuals that adopted floater strategies in a subsequent season.

Discussion

By employing a network of automated radio telemetry receivers coupled with conventional radio-tracking, we provide robust evidence that space use behaviors exhibited by a nonbreeding migratory bird are highly plastic allowing and dependent upon an individual's internal and external state. We present multiple lines of evidence in support of this conclusion, including 1) observational evidence over multiple years demonstrating a decline in the variation in the amount of space utilized with positive increases in annual rainfall, 2) declines in the prevalence of non-territorial floaters within the population coinciding with positive increases in NDVI, and 3) within-season changes by individuals adjusting their space use behavior with resource availability. Importantly, and consistent with this conclusion, we determined that floaters were unable to maintain their body condition over the nonbreeding season and who were likely to switch to territoriality in subsequent years. Taken together, our research provides strong support for the hypothesis that individual space use behavior is dependent upon resource availability during the winter and individual dominance status. With long-term trends in seasonal rainfall declining throughout the Caribbean and across much of Neotropics (Neelin et al. 2006, Herrera and Ault 2017), our study suggests that the distribution of space use behaviors, and perhaps avian social systems more generally, are likely undergoing rapid change that may result in negative carry-over effects on migration timing, reproductive success, and survival.

Space use and movement behaviors are increasingly recognized as being highly variable, especially for wintering migratory birds (Stutchbury 1994, Brotons 2000,

Brown and Sherry 2008, Peele et al. 2015, Ruiz-Gutierrez et al. 2016, Stanley et al. 2021), yet our assessment of the underlying drivers have thus far remained elusive. Here we show that resource variability (i.e., NDVI as a proxy of food availability) had a strong negative influence on the distribution of space use behaviors exhibited at the population and individual level. As resource abundance increased (high NDVI), individuals restricted the area of space utilized, exhibited a higher degree of site-fidelity (lower prevalence of forays), and the population consisted of a lower proportion of floaters. In contrast, when resource abundance decreased, individuals exhibited a higher prevalence of forays and in general the population consisted of a higher prevalence of floaters. These data collectively suggest that winter space use behaviors allow for individuals to flexibly adapt movement and space use to changing environmental conditions (Rühmann et al. 2019, Stanley et al. 2021). Our data highlight the rich spatiotemporal variability in space use behaviors that are typically not captured in most conventional population or movement studies and support the notion that discrete categorizations of space use hinder our understanding of this variability.

In fact, we determined that nearly two-thirds of all tracked individuals exhibited forays inclusive of territorial individuals suggesting that not only were forays of territorial individuals common, but that the movement of floaters also increased. Although territoriality is largely considered a fixed and sedentary space use tactic, we demonstrate substantial variation in daily movements, including extraterritorial forays. Recent genetic and technological advances have demonstrated that during the breeding season, such forays are quite common across taxonomic groups and occur for extra-

pair copulations (Churchill and Hannon 2010, Ward et al. 2014, Weiner et al. 2019), and perhaps also for prospecting for breeding sites in subsequent years (Mayer et al. 2017, Cooper and Marra 2020). Here, we provide clear evidence for the prevalence of off-territory forays during the nonbreeding season. Forays during the nonbreeding season could serve several purposes, including as an opportunity to scout resource availability in the surrounding landscape, possibly to inform a future territory upgrade. In some cases, forays might allow a bird to secure resources outside of the territory. Under the first hypothesis, juvenile individuals and individuals occupying poorer quality habitats would be more likely to go on forays as they are the most likely to abandon their territory to upgrade to a new one. Under the second hypothesis, we would expect that there should be no difference in the frequency of forays between age classes and that the frequency of forays should be higher for individuals occupying poorer quality habitats and during times when resources become scarcer (either between or within-seasons). Our evidence so far suggests that forays are most likely driven by individuals attempting to supplement their food needs when they have resource-poor territories and also during periods of resource scarcity. It is currently unclear what the costs associated with extra-territorial forays are but it could be expected that forays may expose individuals to greater predation risk and increased risk of being attacked by territorial conspecifics. However, further work is needed to identify the costs and benefits of extra-territorial forays during the non-breeding season.

The quality and quantity of winter resources are likely to change with climate, especially amid declining rainfall and increasing droughts (Neelin et al. 2006, Herrera

et al. 2018), affecting winter resource availability and habitat quality. These broad-scale climatic changes are likely to result in shifts in the distribution of space use behaviors from more sedentary and predictable behaviors to more nomadic movements that will include greater floater prevalence and declines in the territory fidelity. In fact, it has recently been demonstrated that overwinter site persistence likely follows latitudinal patterns of habitat/resource limitation (Ruiz-Gutierrez et al. 2016), suggesting that temporal patterns are expected to follow suit. The evidence presented thus far suggests that these changes are likely to have dramatic implications on migratory populations either directly through changes in survival or indirectly through seasonal interactions. Yet, because movements are not easily detected, these changes are likely to go undetected, which only further hinders our efforts at understanding the ongoing declines of migratory organisms (Rosenberg et al. 2019). Therefore, future efforts should attempt to gain a better understanding of how the distribution of space use behaviors has changed in the past to better understand their potential impacts on populations in the future.

Our study grows out of increasing interest in understanding how individual decisions about movement and use of space can scale to influence ecological and evolutionary processes (Nathan et al. 2008, Hawkes 2009, Morales et al. 2010, Allen et al. 2016, Hertel et al. 2017). As one of the few studies to investigate the sources of variability in space use behavior in terms of both internal (e.g., age, sex) and external states for overwintering migrants, we present evidence demonstrating the importance of the interplay between environmental conditions and individual behavior in ultimately scaling to influence the distribution of space use behaviors at the

population-level. Moreover, our data highlight the rich variability in space use behaviors that are typically not captured in most conventional population studies and have gone largely overlooked and underappreciated. Ultimately, the application of automated tracking approaches that allow insights into the behavior of individual animals is necessary to further our understanding of the undeniable connection between individual movement and population dynamics, especially amid ongoing climatic changes that are currently affecting the Caribbean and much of the Neotropics (Neelin et al. 2006, Herrera and Ault 2017).

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Figures

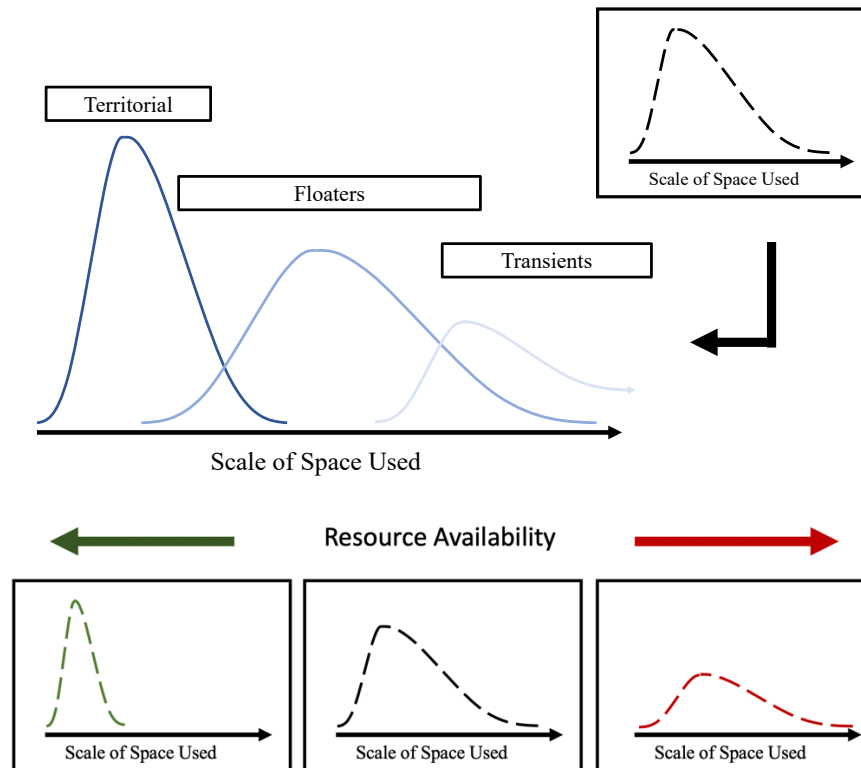


Figure 2.1. A conceptual diagram of the underlying variability between space use tactics and the proposed effect of resource availability on the distribution of space use behaviors. The top figure represents the space use distribution of a hypothetical population that consists of three space use tactics (territorial, floater, transient). Each of these behaviors are distinct but overlap substantially in space utilized. The composition of the population therefore reflects the distribution of space use behaviors. Resource availability (bottom figure) can directly influence the distribution by either changing the number of space use tactics expressed and/or by influencing the variability in movements exhibited within each tactic.

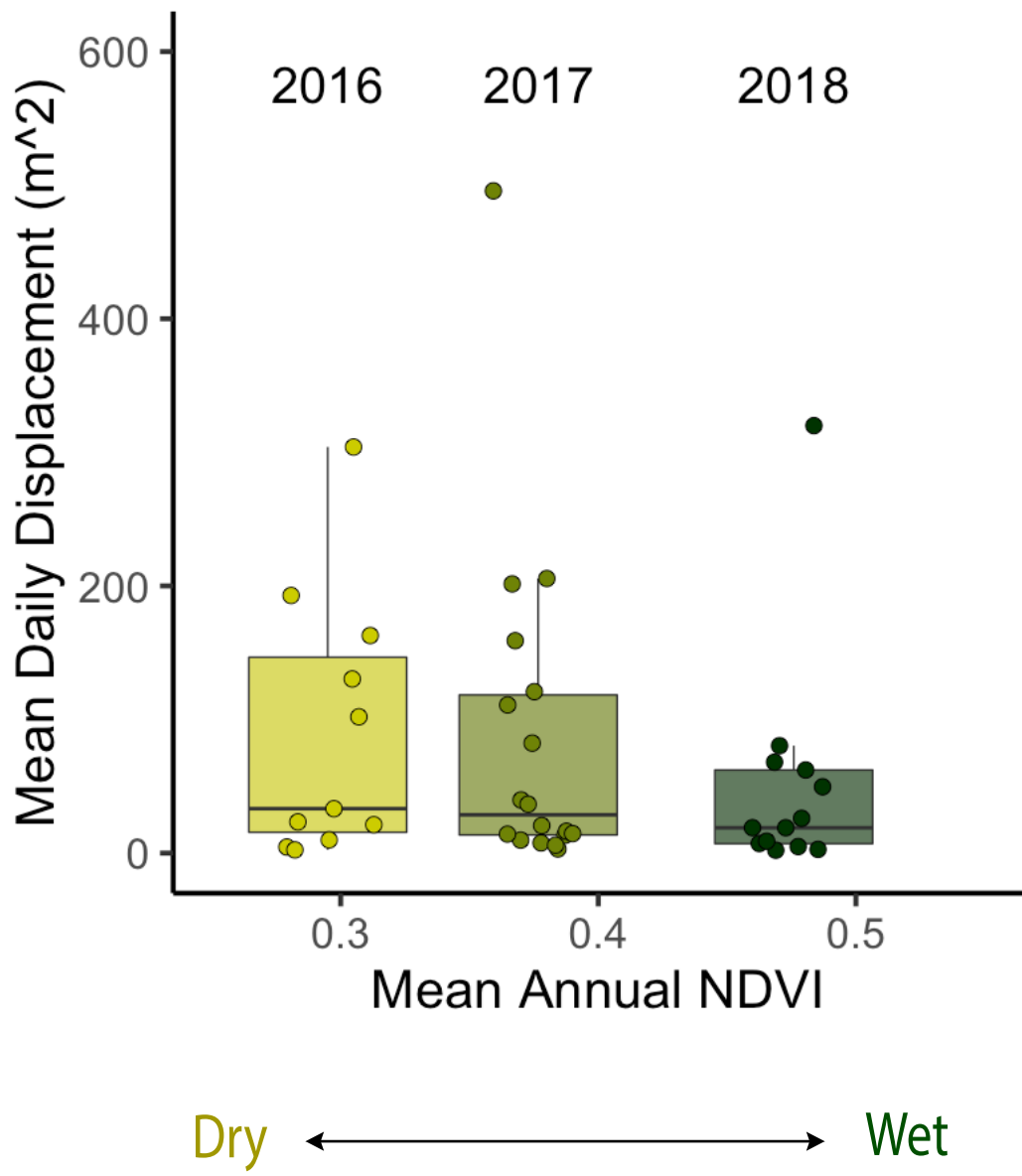


Figure 2.2. The distribution of space use behaviors (mean square displacement) varied with winter resource availability (NDVI). Overall, in wetter years with higher NDVI (darker shades of green), individuals utilized a more restricted range of space. Year is noted above each box and whisker plot.

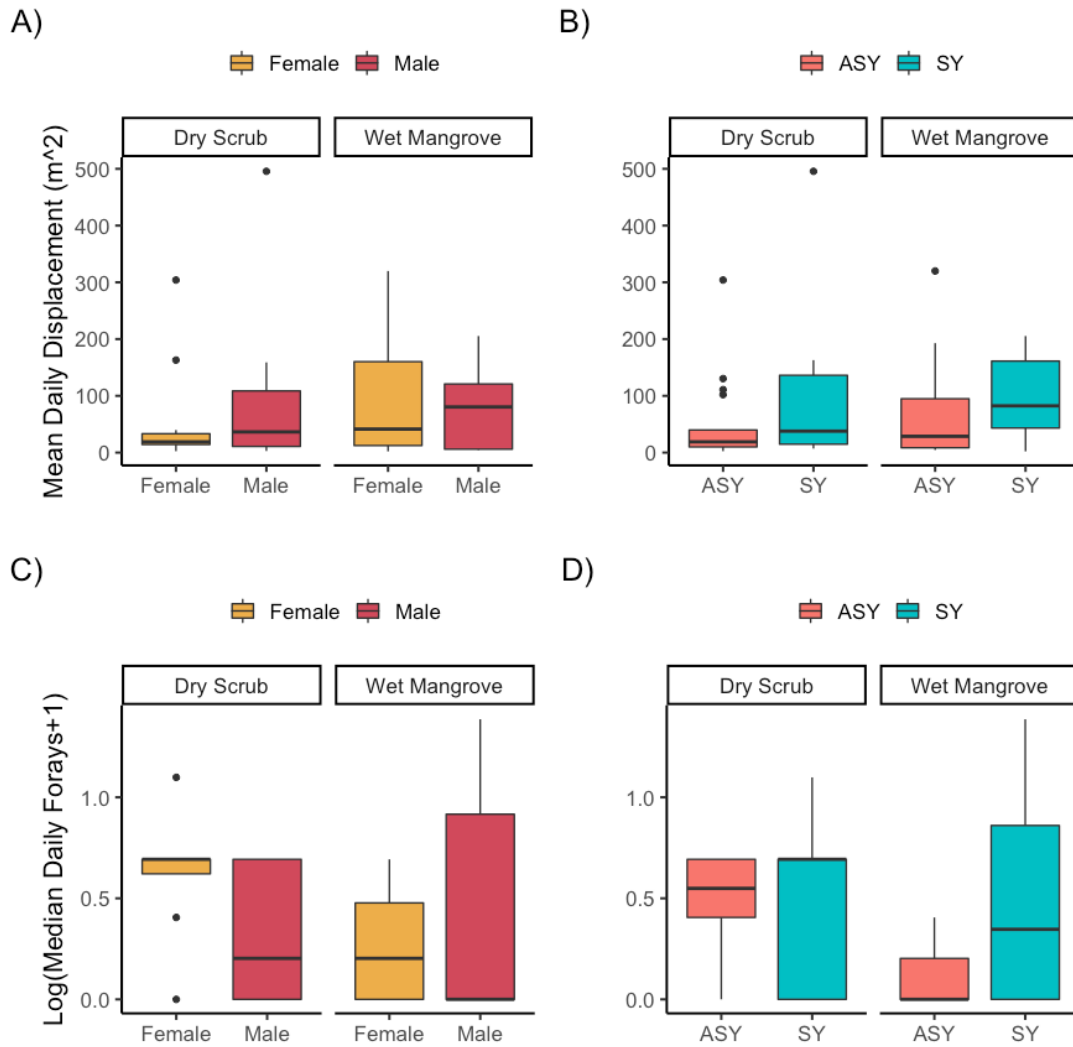


Figure 2.3. Patterns of space use behavior (median daily displacement and forays) by sex (red=males, yellow=females), age class (SY, blue = second year, ASY, pink = after-second year), and habitat (dry scrub, wet mangrove). Space use behavior was affected by age (b) but not sex (a). Second year birds used larger areas than older birds (b). There was a significant interaction between sex and habitat (c – see figure 4). Second year birds were more likely to undertake more frequent forays than adults (d).

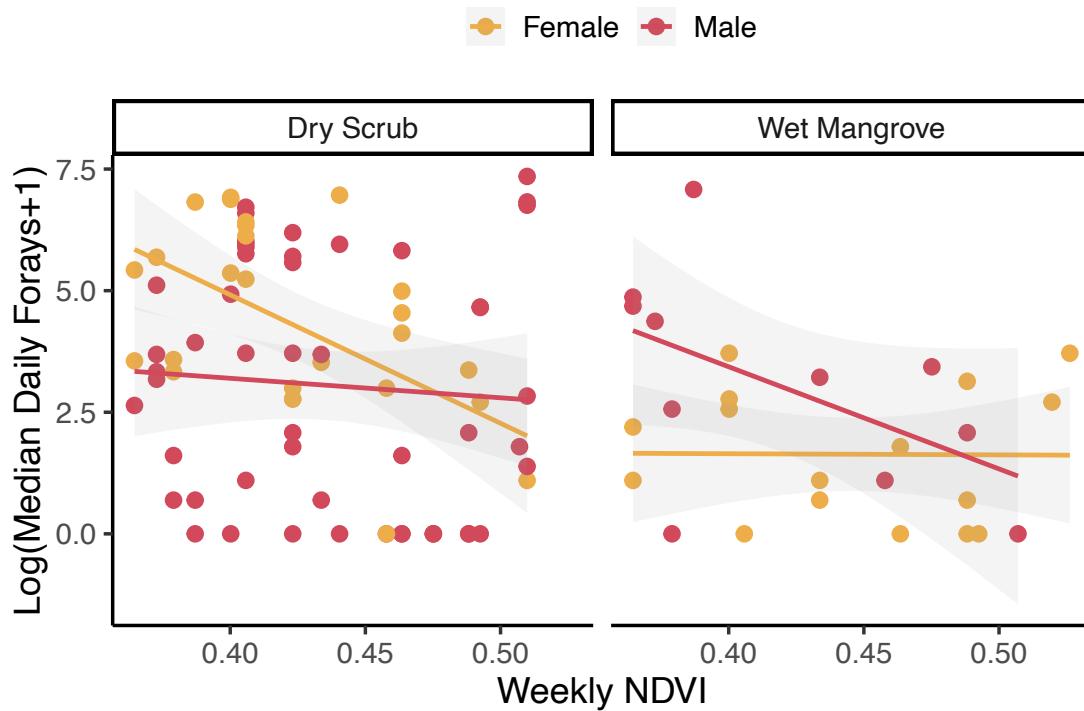


Figure 2.4. Changes in the frequency of forays in response to seasonal changes in resource availability (NDVI) by sex (yellow = females, red = males) and habitat types (dry scrub, wet mangrove). Plasticity in foray behavior was mediated by a habitat and sex interaction, such that males decreased the frequency of forays as resource availability improved in wet mangrove habitat but not dry scrub. Females on the other hand responded to increasing resource availability by decreasing their frequency of forays in dry scrub but not wet mangrove habitats.

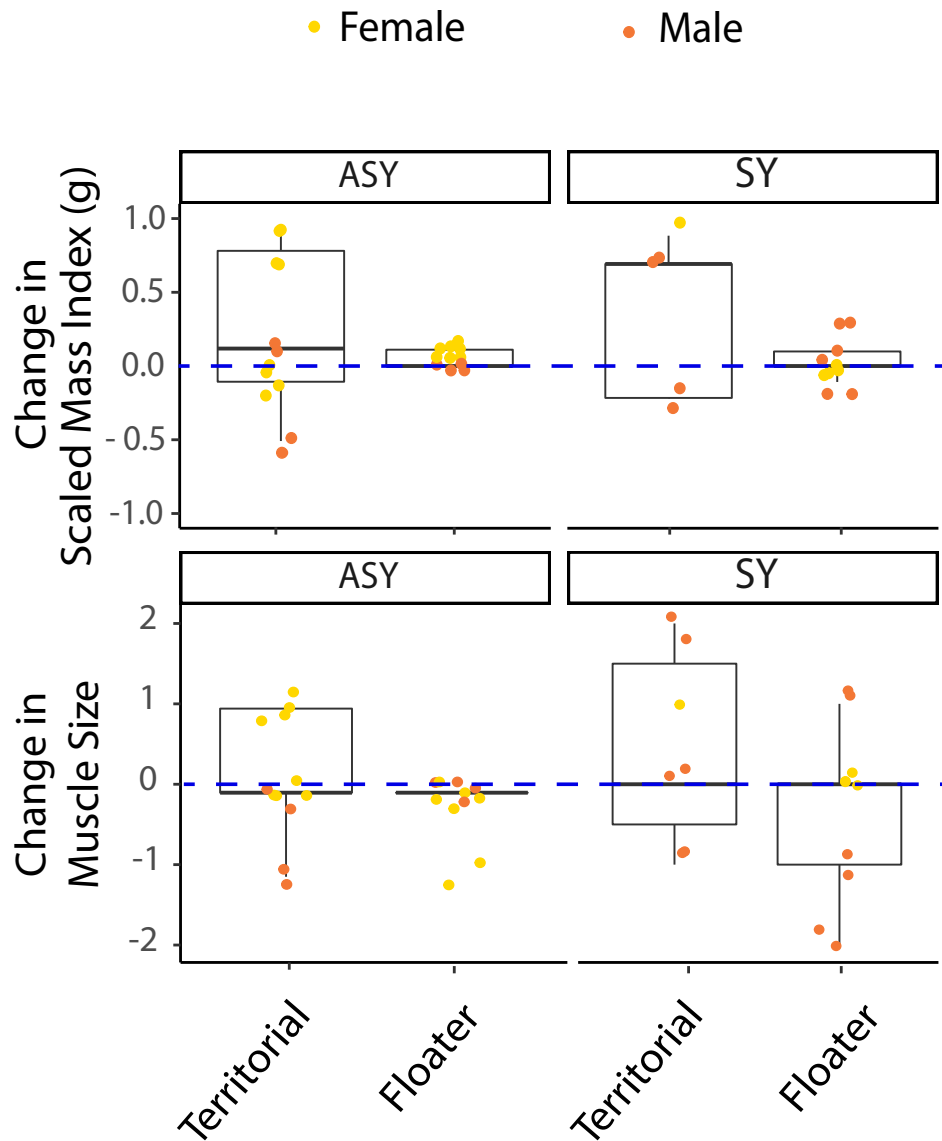


Figure 2.5. Space use tactic significantly influenced the change in body condition and composition of wintering American redstarts (*Setophaga ruticilla*) but were not influenced by sex (orange=males, yellow=females) or age class (SY = second year, ASY = after-second year). Floaters on average lost mass compared to territory owners (top row) likely due to the significant decrease in the size of pectoral muscle (Bottom row).

CHAPTER 3

EARLIER SPRING DEPARTURES OF AN OVERWINTERING SONGBIRD DRIVEN BY SOUTHWARD SHIFTS IN BREEDING ORIGINS

Abstract

A growing body of literature demonstrates how climate change can affect the annual schedules of migratory birds, and shifts towards earlier breeding are among the most commonly described. If the phenology of only certain transitions change (e.g., the timing of breeding changes but not the timing of arrival on breeding grounds), then mismatches can occur that negatively affect fitness. Here, we assess how the phenology of spring departure has changed over the past 24 years (1995-2019) in a Jamaican wintering population of American redstarts (*Setophaga ruticilla*). We further identified the primary endogenous and exogenous factors affecting departure timing, and examined links among spring departure schedules, breeding origins, and winter rainfall. We found that the timing of an individual's migratory departure was shaped by age and sex, but also by both breeding latitude and winter rainfall. Spring departure schedules were significantly earlier in wet vs. dry years, and for southern vs. northern breeders. At the population level, we demonstrate that spring departure schedules have advanced at a rate of 0.21 days per year, which translates to 5 days over the past 24 years. This long-term shift in departure was explained better by the > 300-kilometer southward shift in the breeding origins of our wintering population than by rainfall, given the absence of long-term trends in precipitation at our study site. Our study is

among the first to provide a nonbreeding perspective on the drivers of phenological changes in the annual cycles of migratory organisms.

Introduction

Climate change can profoundly affect how and when migratory birds transition among breeding, post-breeding, migratory, and nonbreeding stationary periods of the annual cycle (Both and Visser 2001a, Marra et al. 2005a, Jonzén et al. 2006, Horton et al. 2020a). One striking example is how phenological changes on the breeding grounds (Pulido 2007, Charmantier and Gienapp 2013) can prompt mismatches between the timing of breeding and insect availability, leading to reduced survival and reproductive productivity (Both et al. 2006, Møller et al. 2008, Both 2010, Saino et al. 2010, Mayor et al. 2017, Visser and Gienapp 2019). In these and other cases, the extent to which birds may face demographic consequences should be mediated by the ability of individuals to shift the timing of their arrival to the breeding grounds to match phenological changes (Both et al. 2006, Saino et al. 2010). Whether these shifts are accomplished via microevolutionary change (i.e., changes to the endogenous migratory program) or through phenotypic plasticity remains poorly understood and hotly debated (Gienapp et al. 2007, Pulido 2007, Visser 2008, Balbontín et al. 2009, Knudsen et al. 2011, Charmantier and Gienapp 2013, Gill et al. 2014a).

Disentangling the mechanisms that prompt phenological changes in the annual cycle of migrants is inherently challenging because the timing of transitions is thought to reflect interactions between an individual's endogenous circannual schedule and

external conditions it encounters throughout the year. We know, for example, that environmental conditions (e.g., winter rainfall, habitat quality) experienced during the winter affect the timing of departure (Balbontín et al. 2009, Tøttrup et al. 2010, Studds and Marra 2011, McKellar et al. 2013, Haest et al. 2020, Areta et al. 2021), much the same way that environmental conditions experienced during migration affect migration rates (Marra et al. 2005, Tøttrup et al. 2012, Drake et al. 2014, La Sorte et al. 2019, Horton et al. 2020). Adding to the complexity, interactions within and between nonbreeding and migratory periods, or “carry-over effects”, can affect migration rates (McKinnon et al. 2015a, González et al. 2020, Dossman Chapter 4) as well as the timing of arrival to the breeding grounds (Rockwell et al. 2012, Tøttrup et al. 2012, Briedis et al. 2017, Haest et al. 2018, 2020). Timing of arrival on the breeding grounds, therefore, represents a complex set of interactions across the annual cycle.

The two primary components that shape the timing of spring departure – the initiation of migration and the amount of time spent preparing for migration – are controlled by both endogenous and exogenous factors. A classic illustration is how winter habitat quality (Studds and Marra 2005, McKinnon et al. 2015b, González et al. 2020) and winter rainfall (Studds and Marra 2011, Altwegg et al. 2012, Cooper et al. 2015) influence individual departure schedules, with later departures for individuals occupying poorer quality habitats and during dry seasons. Less attention has been paid to endogenous factors like sex and age class that are thought to influence departure schedules of migrants (Gwinner 1996, Styrsky et al. 2004, Maggini and Bairlein 2012, Åkesson and Helm 2020), partly because nonbreeding phenological studies are rare (Knudsen et al. 2011, Marra et al. 2015a). Additionally, age and sex

are often confounded with habitat quality and social status (i.e., less dominant females and young males occupy poorer habitats), making it challenging to disentangle the role of endogenous factors from that of habitat (Marra 2000, Marra and Holmes 2001). Further, an underappreciated intrinsic component of an individual's annual cycle that may affect spring departure schedules is an individual's breeding origins (i.e., its migratory distance) (Conklin et al. 2010, Briedis et al. 2016a, Jahn et al. 2019). Rarely have phenological studies explicitly examined relationships with breeding or wintering origins (i.e., migratory distance) of migrants, despite evidence suggesting that climate change is leading to shorter migrations (Visser et al. 2009, Potvin et al. 2016, Rushing et al. 2020).

Here, we investigate how endogenous (i.e., age, sex, breeding latitude) and exogenous factors (habitat quality, winter rainfall, conspecific density) influenced the spring departure schedules of a migratory passerine, the American redstart *Setophaga ruticilla*, over the past 24 years (1995-2019). Our study is one of a few to provide a winter perspective on whether the climate change is affecting the timing of Spring departure schedules of migratory passerines.

Methods

Study System

This study was conducted during the winters (Jan-May) of 1995-1996 and 2003-2019 on a territorial population of American redstarts (*Setophaga ruticilla*) overwintering at the Font Hill Nature Preserve (18° 02' N, 77° 57' W, < 5 m above sea level), on the southwest coast of, St. Elizabeth Parish, Jamaica. Although departure surveys were conducted in 1995, they were terminated earlier in the season (May 1 vs. May 15) and

resulted in a large proportion of censored departure dates. We, therefore, excluded 1995 from all further analyses to limit the biased induced from censored departure dates.

The study site consists of two primary habitat types; a high-quality mangrove forest (wet mangrove) and a lower quality scrub forest (dry scrub). Plots in wet mangrove retain relatively high levels of soil moisture and arthropod availability throughout the season, even as conditions progressively dry. In contrast, the persistently low levels of soil moisture in dry scrub are associated with sparse food resources that diminish across the season. As a consequence, habitat quality (both within and between seasons) drives much of the variability into overwinter body condition and pre-migratory preparation leading to substantial fitness consequences in later stages of the annual cycle (Marra et al. 1998, Norris et al. 2004, Studds and Marra 2011, Cooper et al. 2015).

From Jan – May of each season, redstarts were systematically captured and banded with a unique color-band combination. Upon capture, age (second year and after second year) and sex (male and female) were assessed using standard plumage characteristics. We further collected standard morphometric data that included mass (g) and body size measurements (wing, tail, bill, and tarsus lengths). Lastly, we collected a tailfeather (R3) to assess approximate breeding latitude (detailed below). For a subset of individuals captured during the month of April (pre-migratory period), we estimated each individual's body condition using the scaled mass index (Peig and Green 2009). This allowed us to assess how the pre-migratory condition of our population varied over time and in response to the seasonal rainfall.

Upon release, individuals were monitored for the duration of the season through resighting and spot mapping surveys. The small territory sizes (0.16 ± 0.5 hectares) of redstarts allowed us to delineate territories quickly and reliably for each banded individual and then create a baseline map for use in departure surveys. Each year we selected up to 120 individuals that were extensively monitored over the winter and attempted to sample an equal portion of both sexes, age classes, and habitat types (~10-15 per group) to capture a representative sample of the population's spring departure schedules.

Departure Surveys

Departure surveys were conducted to assess the timing of the spring departure of color-banded individuals. Color-banded individuals were resighted every 3 days between April 1 (prior to any documented departure for this population) and May 15 (by when most birds have departed) using a standardized protocol. On the first day of the resight period, we searched for each individual within their delineated territories for 5 minutes. If a redstart is not seen on the first day of the period, it was searched for again on day two within and just beyond its territory boundaries for 10 minutes. Day three would include a 20-minute search of the territory and the surrounding areas if an individual was not detected. Finally, we concluded with playback of songs and chips on the territory for all birds not detected during the previous survey interval (see Marra et al. 1998 and Studds & Marra 2011). Because redstarts actively defend small territories that are easy to survey, we assume that individuals not detected within a 3-day period departed during the previous survey interval allowing us to be fairly confident in our assessment of individual departure timing to a 3-day period.

Over the 24-year study period, we surveyed departure schedules for 1490 individuals (mean = 83 territorial individuals per year; range: 54 - 104). We were left with a total sample size of 1398 individuals after excluding any individuals of unknown sex and age and individuals who ‘departed’ before April 15, which is a week earlier than the earliest known migratory movements in this region. These 1398 individuals consisted of 584 females and 814 males. Of those, 956 were after second years (adult), and 442 were second-year birds (juveniles) and represented individuals that occupied territories in either high quality (Mangrove; 876) or low quality (Scrub; 522) habitats (see supplementary for detailed breakdown).

To assess how breeding latitude ultimately influences the timing of departure, we sampled stable hydrogen isotopes ($\delta^2\text{H}$, detailed below) from tail feathers (R3) collected prior to departure on 422 individuals. $\delta^2\text{H}$ is incorporated into the keratin during feather growth, and because redstarts undergo a complete tail molt at the end of the breeding season, the isotopic concentration in the feather reflects the latitude where these feathers were molted. Hereafter, we refer to $\delta^2\text{H}$ as the breeding latitude.

To determine the extent to which nonbreeding conditions influence the departure schedules of individuals, we acquired monthly rainfall data from the Jamaican Meteorological Service (<http://www.metservice.gov.jm>) for a weather station located ~20 km of the study site—Burnt Savannah—for each year of the study (1995-2019). We summarized winter rainfall as the total monthly rainfall accumulated between the months of Jan – Mar for each year following (Studds and Marra 2007, Marra et al. 2015b). These previous studies demonstrate the strong linkage between winter rainfall

(Jan-Mar) and food availability (arthropod abundance) during the pre-migratory period and its direct effect on the body condition of this population of redstarts.

However, limited sample size and collinearity between habitat and rainfall on body condition (scaled mass index) precluded us from including habitat quality, rainfall, and body condition in the same models, and as such, we chose to simply include the rainfall and habitat in all further departure timing analyses. We included an analysis that demonstrated the effect of winter rainfall on mean pre-migratory condition corroborating previous studies and also assessed how rainfall and condition patterns varied temporally throughout the study period (1995-2019).

Isotope Analysis

Stable isotope analyses were conducted at the Smithsonian Institution's Stable Isotope Mass Spectrometry Laboratory in Suitland, MD, USA, although 6 of the 422 samples were run at the Cornell Stable Isotope Lab (Ithaca, NY USA) following the exact sample protocols and standards and all efforts were made to standardize all procedures and materials used between laboratories.

Tail feathers were first rinsed in a 2:1 mixture of chloroform: methanol to remove surface oils and then subsequently allowed to equilibrate for 72h at the lab. After which, a distal portion (length 3–5 mm) of each feather was sampled, weighed to 350 ± 10 ug, and placed into a 4×6 -mm silver capsule. Tissue samples were combusted in an elemental analyzer and introduced to an isotope ratio mass spectrometer via a ConFlo IV interface. One in-house standard was run for every 5 to 8 unknowns to measure accuracy and precision. The analytical error was minimal (2.65 ± 0.14 ‰) based on replicate analysis of the keratin standards ($n = 21$) and 3.89 ± 2.55 ‰ based

on replicate samples of the same feather for a subset of 39 individuals. The non-exchangeable hydrogen was determined by linear regression with calibrated in-house keratin-based standards (Caribou Hoof Keratin, -196.90 ‰; Spectrum keratin, -80.78 ‰; and Kudo Horn Keratin, -54.17 ‰). All stable hydrogen isotope ratios are in permil units (‰).

Data Analysis

We used a three-stage analysis to assess how phenology has changed on the nonbreeding grounds and the potential underlying mechanisms that drive those changes. We first determined the extent to which the spring departure schedules have advanced over the past 24 years using standard linear models with year as a predictor variable. Second, we took an individual-based approach to assess what factors influence the daily departure probability within a given year. Lastly, we determined how longitudinal changes in the factors that most strongly influenced departure dates contribute to the long-term trends. This approach allows us to leverage the long-term data on spring departure schedules to investigate potential underlying drivers of the temporal patterns we observe.

We used linear models with year and habitat (dry scrub and wet mangrove) as predictor variables to determine how spring departure phenology has changed over time. Habitat occupancy is dominance mediated in this study system (Marra 2000) and is an extremely important ecological attribute that influences everything from patterns of space use (Chapter 2), maintenance of overwintering condition, and migratory preparation, and is therefore highly important to account for when assessing patterns of phenological change.

To identify the factors that were most important in predicting individual departure probability, we modeled departure time under a time-to-event survival analysis framework, specifically using a mixed Cox Proportional Hazards model following Dossman et al. (2016) using the R packages (*coxme*). Cox Proportional Hazards models allowed us to explicitly determine how the hazard of departure varied with time-independent and time-dependent endogenous and exogenous factors (Therneau and Grambsch 2000) while accounting year as a random effect (departure data nested within year). This model estimates the hazard rate (i.e., the effect on departure time), or more commonly known as the failure rate, for an individual owing to one or more explanatory covariates. In this context, the hazard rate is analogous to the daily probability of departure. Higher hazard rates (i.e., higher daily probability of departure) are indicative of departing the wintering site early in the season, while lower hazard rates (i.e., lower daily probability of departure) are indicative of a later departure.

For these models, we were primarily interested in assessing the relative contributions of breeding latitude and winter rainfall in influencing the probability of departure of an individual within a given year while accounting for the effects of age, sex, and habitat type on departure probability. Because we anticipated that seasonal rainfall influences individuals residing in wet mangrove differently than dry scrub, we included a habitat x rainfall interaction term. We standardized all predictor variables for computational efficiency and to allow us to compare the relative effects of each predictor on departure probability. We created 4 models: a **null model** that included age, sex, and habitat, a **breeding latitude model** containing breeding latitude, age,

sex, and habitat, a **rainfall model** containing winter rainfall, age, sex, and habitat, and its interaction with habitat, and a **full model** containing both breeding latitude and winter rainfall along with age, sex, habitat, and the rain x habitat interaction. We compared the differences in AICc to assess the relative importance of these variables. Finally, we included year as a random effect to account for the nested nature of the departure data within years.

Finally, we determined how winter rainfall and breeding origin of the Jamaican winter redstart population has changed over the past 24 years and link those changes to the phenological patterns observed. We first model how annual winter rainfall and the mean breeding latitude of the population have changed over time. We again used linear models that include average departure date per year as the response and standardized yearly winter rainfall and standardized mean breeding latitude as predictor variables. We assessed variable importance as above by determining the amount of variance explained by each predictor to rank their importance in driving these trends

Results

Advances in Spring Departure Schedules

Over the 24 year study period, mean spring departure schedules advanced by 5 days (Figure 3.1, $\beta_{year} = -0.213$, $t = -3.042$, $p = 0.005$). Males departed on average 3.5 days earlier than females (Figure 3.1; $\beta_{sex} = -3.54$, $t = -4.253$, $p < 0.001$), but there was no significant interaction between sex and year.

Predictors of Individual Departure Timing

The timing of departure, as assessed by the hazard rate, was significantly influenced by Age, Sex, Habitat, Rainfall, Habitat x Rainfall interaction (N =1398 individuals sampled from 1996-2019). Within a given year, males departed significantly earlier than females, as indicated by a daily probability of departure twice that of females (Figure 3.2a; $HR_{Male} = 2.04 \pm 0.06$, $z = 11.17$, $P \ll 0.001$). Similarly, after-second year birds departed significantly earlier in the season than second-year birds as the daily probability of departure for after-second year birds was 2.42 times greater than second-year birds (Figure 3.2b; $HR_{ASY} = 2.42 \pm 0.07$, $z = 12.92$, $P \ll 0.001$). Birds departed earlier as winter rainfall increased ($HR_{Rainfall} = 1.34 \pm 0.09$, $z = 3.30$, $P \ll 0.001$), but this varied with habitat type ($HR_{Rainfall*Habitat} = 0.83 \pm 0.06$, $z = -3.18$, $P \ll 0.001$). More specifically, we found that the departure date was more strongly accelerated by winter rainfall for birds occupying territories in dry scrub ($HR_{Rainfall(Scrub)} = 1.34$; 95% CI {1.26, 1.42}) than for birds occupying wet mangrove ($HR_{Rainfall(Mangrove)} = 1.11$; 95% CI {1.04, 1.18}).

We fit the same model to a subsample of 442 individuals spanning from 1995 - 2019, for which we were able to estimate breeding latitude using δ^2H in tail feather tissue. As in other analyses, departure timing was significantly earlier for males than for females (Figure 3.2; $HR_{Male} = 2.38 \pm 0.10$, $z = 9.06$, $P \ll 0.001$), for after-second year birds than for second-year birds (Figure 3.2; $HR_{ASY} = 2.58 \pm 0.10$, $z = -9.33$, $P \ll 0.001$), and in wetter than in drier years (Figure 2; $HR_{Rainfall} = 1.31 \pm 0.10$, $z = 2.73$, $P = 0.006$) especially for birds in dry scrub (Figure 3.2;

$HR_{Rainfall*Habitat} = 0.67 \pm 0.09$, $z = -4.46$, $P \ll 0.001$). The similarity of parameter estimates between our complete and reduced datasets suggests that the dynamics present in the population were captured in the smaller dataset. This analysis demonstrated that breeding latitude was negatively associated with the timing of departure, such that more northerly breeders departed later in the season than did more southerly breeders (Figure 3.3; $HR_{Breeding\ Latitude} = 0.83 \pm 0.04$, $z = -4.79$, $P \ll 0.001$).

Finally, variation in individual departure timing was best explained by a model containing both breeding latitude and winter rainfall ($\Delta AICc = 0$), followed by models with only breeding latitude ($\Delta AICc = 15.87$) or only winter rainfall ($\Delta AICc = 20.76$).

Drivers of Long-term Trends of Departures at the Population Level

Over the past 24 years, the mean breeding origin of this wintering population shifted south by more than 300 kilometers miles (Figure 3.3; $\beta_{year} = 0.43$, $R^2 = 0.47$, $P = 0.002$) based upon δ^2H in tail feathers. In contrast to individual departure schedules, long-term data on population-level advances in departure were attributable to shifts in the breeding distribution rather than to winter rainfall. Mean annual breeding latitude explained a significant amount of variation annual spring departure schedules with southern breeding shifts resulting in earlier mean spring departure schedules (Figure 3.3; $\beta_{Breeding\ Latitude} = -0.61$, $T = 2.99$, $P = 0.009$). In contrast, the past 24 years saw little net change in winter rainfall, which initially decreased from 1994-2005 and

and then increased (Figure 3.4b). Despite its significant effect on individual departure timing ($HR_{Rainfall} = 1.31 \pm 0.10$, $z = 2.73$, $P = 0.006$), we did not find a significant correlation between annual winter rainfall and mean spring departure schedules at the population-level ($\beta_{Rainfall} = -0.005$, $T = -1.037$, $P = 0.317$), indicating that the advances in spring departure schedules could not be explained by temporal patterns winter rainfall. Further, if winter rainfall was driving advances in phenology, we would have observed declines in the pre-migratory condition of birds over time since departure timing is strongly affected by rainfall-limited food availability. Although we did find a significant relationship between winter rainfall and pre-migratory condition (Figure 3.4a; $\beta_{Rainfall} = 0.162$, $T = 2.431$, $P = 0.022$), we found no temporal patterns in pre-migratory condition over the study period (1995-2019; Figure 3.4c)

Discussion

We provide the first long-term evidence that spring departure schedules from the nonbreeding grounds have advanced over the past 24 years at a rate that is comparable to advances reported during migration and on the breeding grounds for other species (Saino et al. 2010, Gill et al. 2014a, Mayor et al. 2017, Horton et al. 2019). Although we show that the timing of departure for individuals is subject to a wider range of conditions, the trend towards earlier departure at the population level seems to originate from significant southward shifts in the breeding origin of our population, an explanation that is consistent with the relatively earlier departure of southern- than northern-breeding birds. Our study thus shows the importance of understanding

migration phenology through the lens of the full annual cycle.

Determinants of Individual Spring Departure Schedules

One of our key findings is that the timing of spring departure from the nonbreeding grounds is determined by an interaction between endogenous and exogenous factors. Similar to our population-level findings, we found evidence that departure timing of individuals was related to breeding latitude (i.e., migration distance), with southern-breeding birds departing significantly earlier than their northern breeding counterparts (Gwinner 1996, Styrsky et al. 2004, Gienapp et al. 2010). This aligns with several studies that demonstrate similar patterns in departure from the nonbreeding grounds (Conklin et al. 2010, McKinnon et al. 2015b, Briedis et al. 2016b, 2016a, Jahn et al. 2019) and during migration (Cohen et al. 2019). These results demonstrate the role that migratory connectivity has in structuring avian phenological responses and highlights the overlooked perspective that our understanding of how migrants will respond to climate change requires considering processes from across the annual cycle (Small-Lorenz et al. 2013).

Another important endogenous determinant of departure was sex. Males departed significantly earlier than females, which supports the notion that early arrival of males on the breeding grounds is accomplished in part through earlier initiation of migration from the nonbreeding grounds (Coppack and Pulido 2009, Schmaljohann et al. 2016, Briedis et al. 2019). These sexual differences in phenology have largely been attributed to selection for early arrival on the breeding grounds and are thought to be genetically determined (Kokko 1999, Morbey and Ydenberg 2001, Maggini and Bairlein 2012). Though the proximate mechanisms giving rise to these differences are

unclear, sex-related differences in arrival can be accomplished by males (1) wintering closer to breeding sites (e.g., differential migration), (2) initiating spring migration earlier than females, and (3) migrating at faster rates than females. Even after controlling for breeding latitude in this study, we still found persistent sex differences in the start of migration that indicate males initiate spring migration earlier than females. In a separate study (Dossman – Chapter 4), we found no significant differences in migration rates by sex. Additionally, males tend to arrive at stopover sites in the northern U.S earlier in the season than females, but their stopover behavior does not appear to differ (Dossman et al. 2016, Morbey et al. 2017). Taken together, this study demonstrates that sex differences in arrival on the breeding grounds are governed by differences in endogenous schedules and likely persist in individuals across the annual cycle (Coppack and Pulido 2009, Briedis et al. 2019).

Although the endogenous program of an individual coarsely determines its departure timing (Helm et al. 2005, Åkesson and Helm 2020), exogenous forces ultimately fine-tune the realized date of departure (Saino et al. 2004, Studds and Marra 2011, McKellar et al. 2013, Cooper et al. 2015, Haest et al. 2020). In this study, we demonstrate that some of this fine-tuning is in response to environmental conditions on the nonbreeding grounds, such as winter rainfall or even habitat quality, that affect the rate of migratory preparation and pre-migratory condition (Studds and Marra 2007, Tonra et al. 2011, Cooper et al. 2015). Indeed, even after accounting for endogenous factors (breeding latitude, sex, age), winter rainfall affected departure timing independently and in relation to habitat quality, especially for birds occupying lower quality dry scrub forests. The links among rainfall, habitat quality and food

availability collectively suggest that seasonal habitat quality mediates the ability of individuals to prepare for migration (Studds and Marra 2005, 2011, Tøttrup et al. 2010, Tonra et al. 2013, Cooper et al. 2015, González et al. 2020), though winter rainfall can improve the quality of dry scrub habitats.

Amid the discourse on whether migratory animals are more sensitive to endogenous vs. exogenous cues (Gienapp et al. 2007, Charmantier and Gienapp 2013, Gill et al. 2014b), we show that both work in tandem to determine when an individual departs the nonbreeding grounds. Endogenous cues are likely to guide the initiation of spring migration, given that the hormonal changes that facilitate migratory and breeding preparation occur weeks before departure (Wingfield 2007, Tonra et al. 2013). The realized departure date of an individual would therefore depend on how quickly an individual prepares for migration which is influenced by primarily exogenous factors (e.g., food availability). However, our understanding of migratory phenology is biased towards departure or arrival events that are easily observed. A more holistic perspective of ecological and evolutionary factors affecting transitions between annual cycle stages requires knowledge of both an individual's endogenous migratory program (i.e., when it initiates migratory preparation) and its realized date of departure. Yet, the challenge remains in determining when that migratory switch point occurs at the individual level and determining whether plasticity in migration timing is mediated by changes in the initiation of migration or during migratory preparation.

Long-term Trends in Departure Schedule and shifting Breeding Latitude

Another key finding of our study was that population-level advances in spring departure schedules were driven primarily by shifts in the breeding origin of this population. At the individual level, breeding latitude is one of the most important predictors explaining variability in departure date and that long-term southward shifts in breeding location best explain the advance in population-level spring departure schedules. Given the tight linkage between breeding timing and subsequent annual events on the breeding latitude of an individual (Slagsvold 1976, Gienapp et al. 2010, Gow et al. 2019), this result provides a relatively simple explanation for the advances in phenology we demonstrate. In fact, Coppack et al. (2003, 2008) previously suggested that shifting migratory distances could theoretically serve as a mechanism that would allow populations to respond to advancing phenology on the breeding grounds via a photoperiodic mechanism. Interestingly, despite evidence that migratory distances might be changing in response to differential shifts in breeding and wintering distributions (Visser et al. 2009, Potvin et al. 2016), no studies have attempted to account for migratory connectivity in their assessment of phenological changes, likely due to the difficulties in tracking individuals across the annual cycle.

The patterns we describe here raise the question of why the breeding origins of our wintering population are shifting southward. Previous research conducted on this population has demonstrated that the direction of natal dispersal (southward vs. northward) is tied to nonbreeding conditions, such that dry winters result in northward shifts in natal dispersal and wet winters result in southward shifts (Studds et al. 2008; Rushing et al., 2015). Considering that drought conditions are becoming more extended and pervasive throughout the Caribbean (Neelin et al. 2006, Herrera and

Ault 2017, Herrera et al. 2018), persistent northward shifts in natal dispersal would result in gradual northward shifts in breeding origins of this population. Yet, in this study, we find the opposite pattern, suggesting that natal dispersal alone cannot explain this long-term southward shift. Alternatively, given that migration is one of the riskiest periods of the annual cycle (Silleet and Holmes 2002, Rockwell et al. 2017, Rushing et al. 2017), the greater risk incurred during the migratory period could conceivably result in differential survival between northern vs. southern breeders. Indeed, our complementary work (Chapter 4) demonstrates that delays in migration due to poor nonbreeding conditions resulted in lower return rates. Although we did not specifically test for the interaction between nonbreeding conditions, breeding latitude (or migration distance), and its effect on survival, we could hypothesize that the costs of migration are likely to directly relate to migration distance. Future efforts should attempt to disentangle how migrant survival relates to migratory distance and any potentially interacting effects (e.g., carry-over effects, increased artificial light during migration, etc.).

Ultimately, our study provides a novel nonbreeding perspective on phenological advances in the annual cycles of migratory organisms. We find that the average timing of departure from the nonbreeding grounds has advanced at rates similar to those phenological advances observed during migration (Horton et al. 2020) and on the breeding grounds in other species (Both et al. 2006, Jonzén et al. 2006), but that the underlying driver of these advances can primarily be attributed to shifting breeding origins (shortening migration distance) of this population. Importantly, this finding, provides further support that care must be taken to include phenological changes from

the nonbreeding grounds (full annual perspective) in our assessment of the impacts of climate change on the phenology of migratory birds.

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Tables and Figures

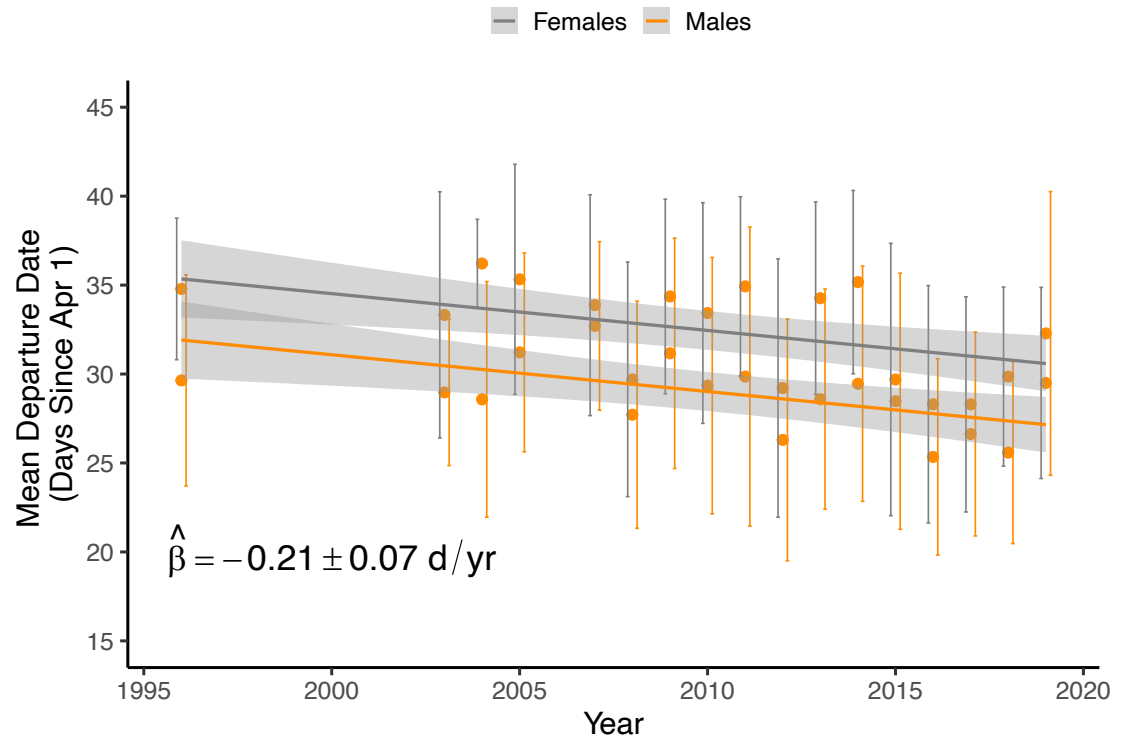


Figure 3.1. Temporal patterns in the spring departure schedules of a wintering population of American redstart (*Setophaga ruticilla*) by sex. From 1995-2019, the spring phenology of this population has advanced at a rate of 0.21 days per year. Male (orange) redstarts left significantly earlier than females (gray) but their phenological patterns did not differ over time.

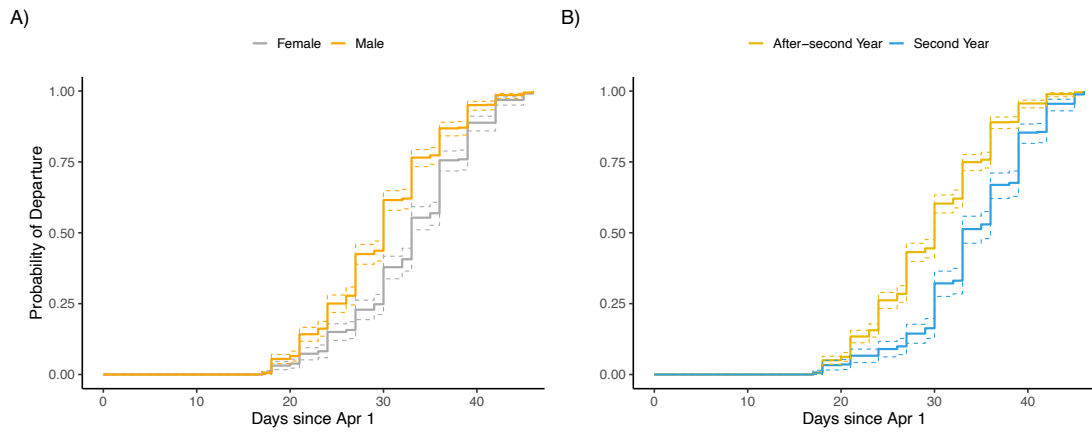


Figure 3.2. Probability of departure between (a) males and females and (b) adults (after-second year) and juvenile (second year) birds. Males (orange) were more likely to depart earlier in the season as compared to females (gray). Likewise, adults (blue) birds left significantly earlier in the season than juveniles (yellow).

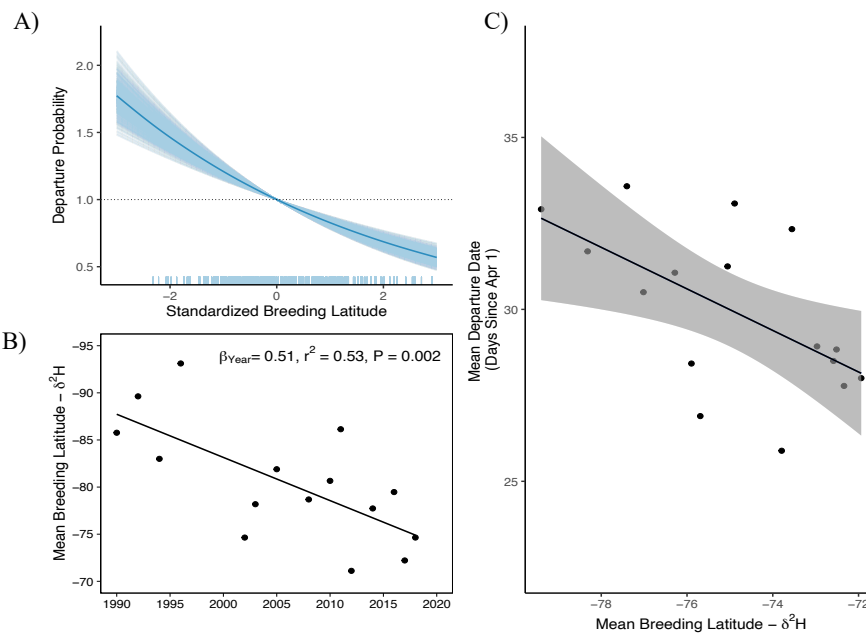


Figure 3.3. Influence of breeding latitude on the spring departure schedules of a wintering population of American redstarts (*Setophaga ruticilla*). Breeding latitude is negatively related to the daily probability of departure (a), resulting in southern breeding birds departing significantly earlier in the season than northern birds. Over the past 30 years, the mean breeding latitude of this population has shifted southward (b). On average, mean departure dates negatively correlated with the mean breeding latitude of the population suggesting that shifts in the breeding origins of this population explain the phenological advances in Spring departure timing of this population (c).

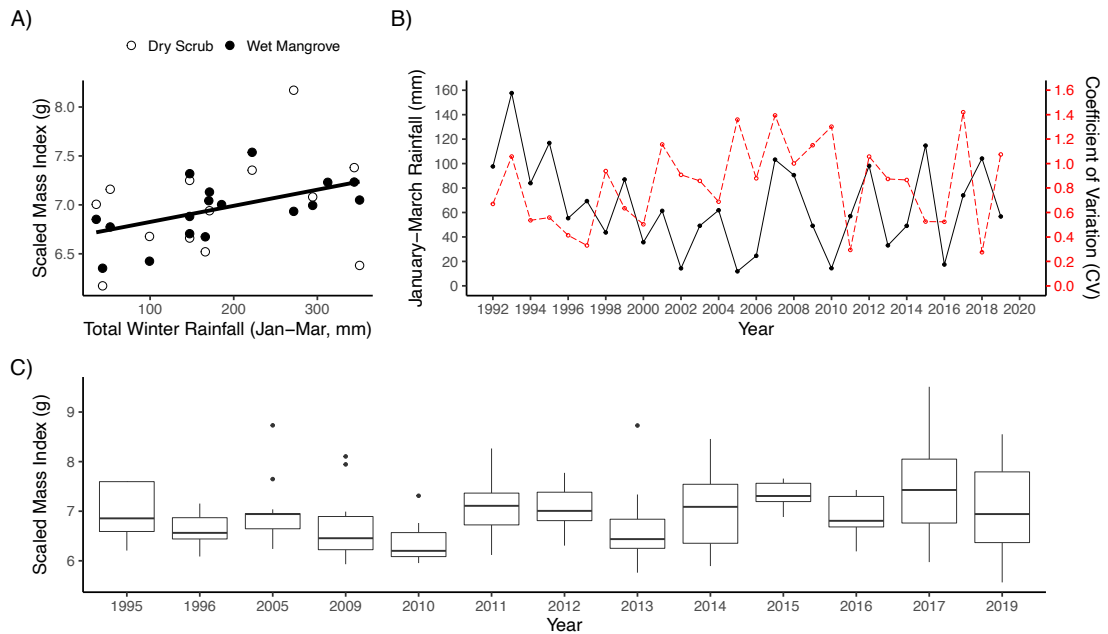


Figure 3.4. Patterns in winter rainfall and pre-migratory condition (April scaled mass index) over a 24-year period (1995-2019) of a wintering population of American redstarts (*Setophaga ruticilla*). Winter rainfall significantly influenced the mean pre-migratory condition of the population with average condition being higher during wet than dry years (a). Overtime, winter rainfall (black) has varied considerably but no significant trend was apparent across the entire 24-year period (b). As a consequence, we found no temporal trends in pre-migratory condition that would have otherwise reflected a trend in seasonal rainfall given the tight linkage between winter rainfall, food availability, and pre-migratory condition(c).

CHAPTER 4

SONGBIRDS WITH DELAYED SPRING DEPARTURE MIGRATE FASTER BUT PAY THE CONSEQUENCES

Abstract

Timely arrival on the breeding grounds is vitally important for individual fitness, and delays in arrival have largely been attributed to poor overwintering conditions. Despite the importance of this carry-over effect, few studies have investigated the extent to which individuals can modify their migratory behaviors to compensate for delayed departure from the overwintering grounds. Given their limited reproductive opportunities facing short-lived migratory passerines, it follows that these species should attempt to compensate for delays at the start of spring migration by migrating at faster rates. Since migrants make trade-offs among time, energy, and safety, accelerating migration to compensate for delays is likely to incur survival costs – yet the potential reproductive advantages may outweigh these consequences. To investigate these hypotheses, we tracked individual American redstarts (*Setophaga ruticilla*) departing their wintering grounds in Southwest Jamaica up through Florida and selected sites further north using the Motus Wildlife Tracking System. We combined long-term data on departure timing and annual return rates to quantify the relative departure dates (early vs. delayed) of tagged individuals, which we then related to individual migration rates and annual survival. We found that individuals that departed relatively late migrated at a faster rate than individuals that departed relatively early. Further, those delayed individuals were significantly less likely to

return the following season. Our study supports the hypothesis that individual migrants attempt to compensate for delays in the start of spring migration and possibly incur survival costs because of these behaviors—a potential mechanism underlying differential survival during spring migration.

Introduction

Migratory species are declining at unprecedented rates (Bolger et al. 2008, Wilcove and Wikelski 2008, Rosenberg et al. 2019), yet progress towards identifying the drivers of declines remains slow due to the complex nature of annual migratory cycles (Marra et al. 2015a, Rosenberg et al. 2019). The migratory period is a vulnerable stage in the annual cycle. Birds face a high risk of mortality as they travel thousands of kilometers through unfamiliar terrain and are exposed to numerous threats (e.g., predators, adverse weather, building collisions). At the same time, birds are under selective pressure to complete these journeys and arrive on breeding grounds as quickly as possible (Kokko 1999, Morbey and Ydenberg 2001). Optimal migration theory predicts trade-offs among time-minimization, energy accumulation, and predation risk that ultimately influence survival (Alerstam 2011). Migratory behavior demands that birds negotiate a balance between the overall rate of migration and survival. Key to understanding one of the main limiting stages in the annual cycle of migratory organisms requires that we determine what factors shape these migratory trade-offs.

Migration is one of the riskiest periods of the annual cycle for birds (Sillert and Holmes 2002, Paxton et al. 2017, Rockwell et al. 2017, Rushing et al. 2017) and one

that can profoundly affect population dynamics (Sillett and Holmes 2002, Paxton et al. 2017, Rockwell et al. 2017, Rushing et al. 2017). Monthly mortality rates are estimated to be almost 15 times higher during migration than during stationary breeding and non-breeding periods (Sillett and Holmes 2002) and higher during spring than fall migration (Klaassen et al. 2014, Lok et al. 2015, Rushing et al. 2017). One hypothesis for the comparably lower survival rates during spring versus fall migration is the pressure to arrive early on the breeding grounds may force them to adopt riskier migratory strategies and migrate at relatively faster speeds in the spring as compared to the fall (Nilsson et al. 2013, Sorte et al. 2013, Horton et al. 2016, Schmaljohann 2018). Therefore, survival during migratory periods is likely to be influenced by selective forces operating throughout the annual cycle.

Seasonal interactions play critical roles in population dynamics and individual fitness of migratory species (Marra et al. 1998, Norris and Marra 2007). For example, poor conditions experienced during non-breeding stationary periods can delay migration and reduce reproductive success on the breeding grounds – a situation commonly termed “carry over effects” (Marra et al. 1998). For example, drought-related declines in food availability can delay spring departure schedules of migratory birds by as much as a week (Studds and Marra 2011), which in turn carry over to delay arrival on the breeding grounds (Norris and Marra 2007, Tøttrup et al. 2012, Ouwehand and Both 2017) and reduce the number of offspring produced (Reudink et al. 2009, Rockwell et al. 2012, McKellar et al. 2013b). Given the costs of delayed arrival on the breeding grounds, a fundamental question remains: can individuals mitigate delayed spring departure schedules by migrating at a relatively faster rate?

There is mounting evidence that birds can increase the rate of migration (McKinnon et al. 2015a, Briedis et al. 2018, González et al. 2020), but doing so is expected to require trade-offs that may compromise survival (Alerstam 1991, 2011, Wingfield 2007). Empirical evidence suggests that trade-offs may include navigating across rather than traveling around geographic barriers while in flight (Alerstam 2001, Deppe et al. 2015, Dossman et al. 2016, Ward et al. 2018), decreasing the total number of stopovers by extending the flight duration between successive stopover bouts (Hedenström and Alerstam 1997, Erni et al. 2002, Alerstam 2011, Gómez et al. 2017), or decreasing stopover duration by spending more time re-fueling rather than avoiding predators during stopover (Moore 1994, Lank et al. 2003, Cimprich et al. 2005, Schmaljohann and Dierschke 2005, McCabe and Olsen 2015) – any of which may accrue additional energetic cost and/or risk.

Here, we combine data from a long-term study of wintering American redstarts *Setophaga ruticilla* in Jamaica with independent tracking data to evaluate the hypothesis that plasticity in migratory behavior can mitigate the delays at the start of spring migration brought upon by non-breeding season carry-over effects. We predicted that individuals delayed on spring departure from the non-breeding grounds will compensate by migrating faster than individuals leaving earlier. However, because increasing migration rate is energetically demanding and may expose birds to greater risk (Alerstam and Lindström 1990, Alerstam et al. 2003a), we also predicted a lower return rate (as an index of survival) for late-departing individuals that migrate at faster rates compared to those that did not.

Methods

Study System

Our research focused on a wintering population of American redstarts (*Setophaga ruticilla*) that have been studied continuously since 1987 at the Font Hill Nature Preserve (18° 02' N, 77° 57' W, < 5 m above sea level), about 13 km west of Black River, St. Elizabeth Parish, Jamaica (e.g. (Holmes et al. 1989, Marra and Holmes 2001). American redstarts are a small-bodied Nearctic-Neotropical migratory passerine that is primarily insectivorous throughout the annual cycle. During the non-breeding season, redstarts actively defend small territories in habitats that are occupied at relatively high densities (3-7 birds ha⁻¹) (Marra et al. 2015b). Habitat selection is primarily mediated by dominance hierarchies, with adult males occupying higher quality habitats (wetter and food rich) disproportionately to subordinate females and young males (Marra 2000). Our study site comprises of two primary habitat types: a wet higher-quality mangrove forest (wet mangrove) and a drier lower-quality scrub forest (dry scrub). The wet mangrove is dominated by Black mangrove (*Avicennia germinans*) with occasional patches of white (*Languncularia racemose*) and red (*Rhizophora mangle*) mangrove and tends to retain high levels of soil moisture. Dry scrub consists mainly of Logwood trees (*Haematoxylon campechianum*) with scattered *Bursera simarubra*, *Terminalia latifolia*, *Crescentia alata*, and other species. Unlike wet mangrove, dry scrub forests are characterized by low soil moisture and comparably lower arthropod biomass, both of which decline as conditions become drier throughout the season (Nov-Apr) (Studds and Marra 2011, Wilson et al. 2013). The consistently greater arthropod biomass (primary food for redstarts) in wet

mangrove than adjacent dry scrub (Studds and Marra 2011, Wilson et al. 2013) is mirrored by the greater densities of redstarts in those habitats (Marra et al. 2015).

The quality of habitat during the non-breeding season plays a central role in the ecology of redstarts (Marra et al. 2015b) and shapes not only individual condition (Studds and Marra 2007, Cooper et al. 2015) and its ability to prepare for migration (Studds and Marra 2011, Tonra et al. 2011) but also influences reproductive success and survival in subsequent seasons (Marra et al. 1998, Marra and Holmes 2001, McKellar et al. 2013b). Redstarts that occupy wet mangrove tend to improve or maintain condition throughout the season, prepare for migration sooner, and ultimately depart the non-breeding grounds earlier than individuals occupying dry scrub.

Quantifying Relative Spring Departure and Migration Rate

Individual spring departure schedules of non-tagged birds were estimated following a standardized departure survey protocol. These surveys began on April 1 (before any documented migration occurs in this region) and continue through to May 15 by when the majority of the population has already departed. Color-banded individuals are resighted every three days as part of a standardized protocol that concludes with playback surveys if not detected sooner (see Dossman Chapter 3 for detailed description). The probability of resighting a color-banded individual is relatively high and comparable among habitats because redstarts actively defend small territories (0.16 ± 0.5 hectares) that are easy to survey. Therefore, individuals not detected within three days are assumed to have departed on the last night of the survey period. We excluded the rare cases where an individual abandoned a territory before April 15, a

week before the earliest migratory departures.

We utilized the Motus Wildlife Tracking System (motus.org; Taylor et al. 2017) to track the movements of individual redstarts upon departure from Jamaica. Between the winters (Jan-May) of 2016-2019, we equipped 57 redstarts (39 *males*, 18 *females*) with a 0.29 g digitally coded VHF radio transmitter (NTQB2-1, Lotek Wireless Inc., Newmarket, ON, Canada) using a modified leg-loop harness (Rappole and Tipton 1991). Transmitters operated continuously at either a 10.3- or 14.9-second cycle, which resulted in a battery lifespan of approximately 45 and 69 days, respectively. Because the mean departure date was May 3 (7 SE) for our population, individuals were tagged after April 1 to ensure that tags were operational during at least a portion of an individual's spring migration (Studds and Marra 2011).

Briefly, the broader Motus network consists of several hundred receiver stations located across the world, with a particularly high concentration of receivers located in the Eastern United States. These stations passively record all received detections of radio-tagged migrants at the 166.38 MHz frequency allowing researchers to track migrants at unprecedented scales using ultra-lightweight transmitters (Taylor 2017). To supplement the existing Motus network, we established one local array that encompassed our wintering study site in Jamaica and allowed us to precisely quantify the timing of departure and the start of spring migration. We established a second array across Northern Florida in a 'turnstile' configuration that consisted of 6 receiving stations that spanned the width of Florida to ensure that we could detect individuals passing through this migratory corridor as they departed their wintering grounds in Jamaica. Together these arrays – coupled with other stations in the Florida

& Georgia region—enabled us to estimate the migration rate for 15 of 57 individuals tagged.

The local array in Jamaica consisted of 5 automated telemetry stations outfitted with a *Sensorgnome* receiver (www.sensorgnome.org) and four horizontally polarized omnidirectional antennas positioned 9 meters high on a galvanized steel mast. One receiver was affixed with four 3-element directional Yagi antennas (oriented 90, 180, 270, and 0 degrees) and was situated on the northwest corner of the field site. The 3-element yagis provided better detection distances once birds were aloft and allowed for increased detection of birds and fine-scale assessment of individual trajectories upon departure.

The array located in northern Florida consisted of 6 *Sensorgnome* based automated telemetry towers, each affixed with at least two 9-element directional yagi's (PLC 1669, Laird Technologies) oriented East and West, respectively. The detection range of each tower was approximately 15 km but up to 25 km under ideal conditions with a clear line of sight between the radio-tag and antennas (Mitchell et al. 2012, Taylor et al., 2017). By positioning these stations (approximately 30 km apart) across the narrowest point in Florida, we covered most of the migratory corridor used by our tagged birds.

Data collected by the automated telemetry system were uploaded to the Motus Wildlife Tracking System network for preliminary processing, archival, and dissemination (Taylor et al. 2017). We used the R packages *Motus* (Brzustowski and LePage 2021) & *tidyverse* (Wickham et al. 2019) to download, filter, and analyze the

data. Time of departure was determined by visually inspecting the departure signals (dB overtime prior to departure) for peak signal strength before its rapid decline and eventual loss (c.f. (Dossman et al. 2016)). The same approach was used to quantify individuals' 'crossing time' as they passed Motus towers in Florida or Georgia. With the precise time of departure from Jamaica and with at least one detection in Florida/Georgia, we were able to quantify the exact amount of time it took an individual to migrate (hours). We divided that time by the great circle distance (kilometers) between the centroid of our study site and the receiver's location during migration to estimate a rate of migration in kilometers per hour.

Light-level Geolocator Analysis

As part of a separate study, 45 (9-2017, 36-2019) individuals were equipped with a 0.32 g light-level geolocator (Intigeo-W30Z11-DIP, Migrate Technologies LTD., Cambridge, UK) using a modified leg-loop harness using stretch magic material. Of those deployed (2017 and 2019), four were recovered in 2018 and 11 recovered in 2020 on the study site a year after deployment allowing us to assess breeding destinations and their spring/fall migratory routes and duration.

We followed the methods outlined Lisovski et al. (2019) and the R package (*GeolocTools*) to analyze our light-level geolocator data. Data were downloaded, twilights were annotated using a threshold adjusted for each individual and manually annotated to conservatively mark outliers for exclusion in final analyses. Analysis of the movement tracks and stationary distributions were conducted in the *flightR*

package. Calibrations were made with light-level data collected on tagged birds in the weeks prior to departure, which, for most birds, occurred after April 20. Calibration periods ranged from 10 – 46 days. We set the spatial extent for our models to -90 – -120 degrees longitudinally and 18 – 55 degrees latitudinally. This extent conservatively captured our population’s breeding and migratory distribution and improved computation efficiency for the particle filter. Particle filter runs were conducted with a million particles, and the breeding origins of these individuals were estimated by this model (*Supplementary Material – SI*).

Stable Isotope Analysis

As a proxy for breeding latitude, we used the isotopic concentration of stable-hydrogen isotopes in tail feathers (3rd rectrix) known to be molted on the breeding grounds. Isotope analyses were conducted primarily at the Smithsonian Institution’s Stable Isotope Mass Spectrometry Laboratory in Suitland, MD, USA. However, six samples were run at the Cornell Stable Isotope Lab (Ithaca, NY USA), following the exact sample protocols and standards. Efforts were made to standardize all procedures and materials used between laboratories.

Tail feathers were first rinsed in a 2:1 mixture of chloroform: methanol to remove surface oils and then subsequently allowed to equilibrate for 72h at the lab. Each feather’s distal portion (length 3–5 mm) was sampled, weighed to $350 \pm$ ten ug, and placed into a four × 6-mm silver capsule. Tissue samples were combusted in an elemental analyzer and introduced to an isotope ratio mass spectrometer via a Conflo

IV interface. One in-house standard was run for every 5 to 8 unknowns to measure accuracy and precision. The analytical error was minimal ($XX \pm xx \text{‰}$) based on replicating the same tissue samples ($n = XX$). The non-exchangeable hydrogen was determined by linear regression with calibrated in-house Keratin-based standards (Caribou Hoof Keratin, -196.90‰ ; Spectrum Keratin, -80.78‰ ; and Kudo Horn Keratin, -54.17‰). All stable hydrogen isotope ratios are in per mil units (‰).

Quantifying Relative Migratory Timing

Departure schedules vary widely among years according to exogenous (e.g., habitat quality, food availability; Saino et al. 2004, Studds and Marra 2011, Haest et al. 2020) as well and endogenous factors (e.g., breeding latitude, sex). Over contemporary and evolutionary time scales, these factors collectively shape an endogenous migratory schedule (or program) governed by circannual rhythm (Gwinner 1996a, Helm et al. 2005, Wikelski et al. 2008, Conklin et al. 2010, Åkesson and Helm 2020). Non-breeding populations of migratory birds represent a mix of individuals that originate from different breeding areas with different phenological schedules— with southern breeding birds typically commencing migration earlier than their more northern counterparts (Nicolau 2021, Briedis 2016). Further, it is well understood that differences in selective pressures operating on breeding arrival between males and females promote differences in migratory behavior (Morbey 2001, Morbey 2017, Chapter 3). Understanding how delays in spring departure schedules carry over and influence an individual's migration rate requires accounting for known phenological

differences in departure dates. Following this, we estimated an *expected departure date* for each individual, allowing us to standardize departure date based on each individual's breeding latitude and sex—precursors of the endogenous program. Therefore, variation around the *expected departure date* – driven by annual variation in winter food availability or habitat quality – would determine whether that individual is relatively early, on-time, or delayed (hereafter *relative migratory timing*).

The expected departure date for each individual was estimated with a predictive model based on factors previously demonstrated to govern an individual's endogenous departure schedule (Studds and Marra 2011, Chapter 3). Utilizing a subset of a long-term departure data (2010-2020) for the same individuals, we fit a Bayesian linear mixed model that included δD_F (a proxy for breeding latitude), sex, and standardized total winter rainfall (Jan-Mar) as fixed effects and included individual as a random effect. We then applied this fitted model to our dataset of radio-tagged individuals to predict their expected departure date for an average winter (standardized mean rainfall 2010-2020) given its respective breeding latitude and sex. The difference between expected and observed departure dates quantified using the automated telemetry array gave an estimate of an individual's relative migratory timing (early = negative values, late = positive values). The Bayesian framework enabled us to propagate the uncertainty in the expected departure date through the migration rate model. An effect was considered significant when 95% Bayesian credible intervals did not overlap zero.

Assessing Annual Return Rate

We sought to determine whether compensatory migratory behaviors incurred costs on survival given the trade-offs involved in accelerating the rate of migration. A low sample size of radio-tagged individuals precluded a direct assessment of the effect of migration rate on survival, so as an alternative, we utilized return rates of color-banded individuals with known departure. High winter site fidelity coupled with relatively small territories allowed us to indirectly infer survival from annual return data of color-banded individuals. As such, we modeled the probability of return using a logistic regression accounting for habitat and sex differences. We included *relative migratory timing* (as estimated above) as a predictor to assess the impact that migratory timing would have on the probability of survival.

Wind Conditions and Tailwind Assistance

Wind assistance can influence the overall rate and survival during migration (Able 1973, Liechti and Schaller 1999, Kemp et al. 2013, Drake et al. 2014, Clipp et al. 2020). We accounted for these confounding effects by first assessing how wind conditions varied across the departure window for this population of redstarts (April 21 – May 12). Averaged daily wind data presented in their easterly and northerly vector components (u & v, respectively) were acquired from the NCEP-DOE Reanalysis 2 (Kanamitsu et al. 2002) using the *RNCEP* package in R (Kemp et al. 2012) at a spatial resolution of 2.5° x 2.5° degrees. We constrained the spatial extent of

our wind data to 20 - 27.5° N and 75 – 82.5°W corresponding to the region between Jamaica and Northern Florida and the likely airspace used by this population. Wind velocities are averaged across pressure-levels ranging from 1000 hPa (100 m.a.s.l) and 10 hPa (~26000 m.a.s.l) with the two relevant pressure levels for migratory passerines in flight being 925 hPa (760 m.a.s.l) and 850 hPa (1450 m.a.s.l). For simplicity and because wind conditions tend to be correlated at these lower altitudes (Gauthreaux et al. 2006), we used wind data from the 925 hPa pressure level (~760 m.a.s.l.), which is closer to the average for migratory passerines (< 1km m.a.s.l.) experiencing favorable wind conditions (e.g., tailwinds) at lower elevations (Dokter et al. 2011, Kemp et al. 2013). We used a simple vector model to estimate the tailwind assistance from the U and V components of wind velocity for a bird migrating at a bearing of 340° (towards Central Florida), which is the approximate average of bearings from individual tracks (range 336° - 344°). For each individual, we calculated the mean daily tailwind components experienced while migrating between Jamaica and Florida. For individuals not detected in Florida, we divided their migration rate by the distance between Jamaica and Florida/Georgia turnstile and used those days to calculate a mean tailwind component. This allowed us to directly model the tailwind effect allowing us to disentangle its effect on migration rate from that of departure time.

Results

Spring Departure Schedules and Expected Departure Date

Birds with more northern breeding origins departed later than more southern breeders (Fig 4.2A; β_{lat} = - 0.13, 95% CRI: - 0.20, - 0.06), and males departed an average of 4 days earlier than females after controlling for breeding latitude (Fig 4.2A; β_{sex} = - 4.27,

95% CRI: - 6.36, - 2.12). The influence of weather depended upon habitat type ($\beta_{\text{Rainfall}*\text{Habitat}} = 1.87$; 95% CRI: 0.26, 3.49), such that birds in dry scrub departed on average 3.82 days earlier for every 1 standard deviation increase in total winter rainfall ($\beta_{\text{Rainfall}*\text{Logwood}} = - 3.82$; 95% CRI: - 6.59, -1.10). In contrast, departure schedules of individuals in wet mangrove did not change in response to rainfall ($\beta_{\text{Rainfall}*\text{Mangrove}} = - 1.95$; 95% CRI: - 4.72, 0.77).

Relative Migration Timing and Subsequent Migration Rate

Using an automated telemetry array on our Jamaican study sites, the average departure date of radio-tagged individuals was May 2 \pm 7 days. Relative departure timing ranged from 3 days earlier (advanced) to 15 days later than expected (delayed) for any given individual and was positively correlated with migration rate ($\text{km} * \text{hr}^{-1}$) (Fig 4.2B; $\beta_{\text{RelativeMigrationTiming}} = 0.19$; 95% CRI: 0.01, 0.38), which increased by 0.19 $\text{km} * \text{hr}^{-1}$ for every day delayed. Assuming a bird left on the expected day of departure (relative migration timing = 0), the average migration rate was approximately 4.5 \pm 1.38 $\text{km} * \text{hr}^{-1}$ (108 $\text{km}*\text{d}^{-1}$). In comparison, a delay of 10 days would result in an increase of migration rate to 6.35 $\text{km} * \text{hr}^{-1}$ (152.4 $\text{km}*\text{d}^{-1}$) or approximately a 43% increase. We estimated that individuals that occupied dry scrub habitat departed relatively later and migrated 79% faster than individuals occupying wet mangrove (6.09 \pm 0.47 $\text{km}*\text{hr}^{-1}$ in dry scrub vs. 3.41 \pm 0.78 $\text{km}*\text{hr}^{-1}$ in wet mangrove).

Tailwind did not influence the overall rate of migration between Jamaica and Northern Florida for our birds ($\beta_{\text{tailwind}} = 12.00$, 95% CRI: - 3.57, 26.73). However, our failure to detect a relationship might reflect the fact that wind conditions are generally

favorable and from the South in our region during Spring migration impacting early and late birds equally (Fig 4.1C; mean wind speed 2.14 ± 0.72 m/s SD).

Overall, geolocator-derived migration across the entire migratory path (7.79 ± 3.5 km * hr⁻¹) were comparable to those calculated using partial tracks generated with the automated radio telemetry array (5.37 ± 1.95 km * hr⁻¹). After accounting for breeding latitude, late-departing birds migrated at a faster rate than those departing earlier ($\beta_{\text{departure date}} = 0.29$, $T = 4.096$, $P = 0.001$, $N = 15$), consistent with the positive relationship found (in our independent sample of radio-tagged birds (Appendix 4 Figure 4B).

Migratory Delays and Annual Return Rates

Redstarts that delayed spring migration and likely compensated with faster speeds were less likely to return to Jamaica the following year although this effect was only marginally significant (Fig 4.3; $\beta = -0.073$, $P = 0.051$). Independent of their relative migration timing, females were less likely to return (survive) from one year to the next ($\beta = 1.24$, $P = 0.002$).

Discussion

Although seasonal interactions are known to affect phenology, reproductive success, and survival of migratory species (Marra et al. 1998, Saino et al. 2004, Norris and Marra 2007, Tøttrup et al. 2010, McKellar et al. 2013a, Rockwell et al. 2017), the extent to which individuals compensate for those effects have not been demonstrated until now. Here we provide two independent lines of evidence (automated radio

telemetry and light-level geolocators) that migratory birds attempt to compensate for delays in spring departure by migrating at a relatively faster rate. In addition, we demonstrate that this compensation appears to carry a cost, such that late-departing individuals that migrated more quickly were less likely to return to Jamaica the subsequent year. We suggest that this compensatory behavior is likely widespread amongst migratory passerines and might serve as a potential mechanism underlying variation in survival during migration.

In this study, we present strong evidence demonstrating the importance of both endogenous and exogenous factors in driving spring departure schedules. An individual's internal circannual schedule largely predicts when an individual will begin preparing for migration and, as such, determines its relative departure time within a season (Coppack and Both 2002, Alerstam et al. 2003b, Bartell and Gwinner 2005, Åkesson et al. 2017, Åkesson and Helm 2020). These circannual schedules are suspected of being set on the breeding grounds such that the timing of annual events is synced to local breeding phenology (Gwinner 1996b, 1996a, Briedis et al. 2016). A latitudinal gradient in breeding phenology (Nicolau et al. 2021) would suggest that populations of wintering migrants – comprised of individuals from across a species breeding range – would exhibit a high degree of variability in their endogenous schedules, and thus their spring departure schedules would reflect that variability. Consistent with this, we found that breeding latitude was an important predictor of spring departure schedules from winter grounds, with birds originating from more southerly breeding latitudes departing earlier in the season than those from more northerly breeding sites. We also found that sex played an important role in

determining spring departure timing, consistent with other studies (REFS) and the idea that differences in selective pressures in arrival on the breeding grounds influence migratory behavior (Kokko 1999, Morbey and Ydenberg 2001, Dossman et al. 2016, Schmaljohann et al. 2016, Morbey et al. 2017). These results allowed us to predict the expected departure date of an individual based on an approximation of its endogenous schedule

Although the endogenous schedule determines when a bird should begin preparing for migration, it is ultimately exogenous forces that fine-tuned departure date by influencing the rate at which individuals can prepare. Numerous studies have demonstrated the importance of non-breeding season habitat quality and environmental conditions in influencing spring departure dates for various avian species (Marra et al. 1998, Norris et al. 2004, Saino et al. 2004, Gunnarsson et al. 2006, Studds and Marra 2011). Individuals that occupy high-quality habitat improve body condition through the winter (Marra and Holmes 2001, Studds and Marra 2005, Cooper et al. 2015), prepare for migration sooner (Tonra et al. 2011), and ultimately depart earlier (Studds and Marra 2005, Cooper et al. 2015, McKinnon et al. 2015b). In fact, any factor that influences habitat quality (e.g., winter rainfall) can result in similar patterns over space and time, as indicated by later departures in dry versus wet years (Saino et al. 2004, Studds and Marra 2007, 2011). Our study builds upon this research by further demonstrating the importance of non-breeding environmental conditions directly influencing the departure schedules of birds at the individual level. Collectively, these results support the hypothesis that departure date alone is insufficient to determine whether an individual migrant is delayed for the start of

migration. By accounting for an individual's expected departure date, based on its sex, its likely breeding latitude, and winter rainfall, we provide a direct measure of whether an individual is delayed at the start of migration. This measure of relative migration timing serves as the basis for determining whether individuals can mitigate these carry-over effects by adjusting their subsequent migratory behavior.

We predicted that individuals would adjust their rate of migration to compensate for delays in spring departure given that even relatively small delays in departure from the non-breeding grounds can have severe fitness consequences (Marra et al. 1998, Norris et al. 2004, Reudink et al. 2009, Rockwell et al. 2012). In fact, delayed migrants are less likely to secure high-quality territories and mates (McKellar et al. 2013b), sire genetic offspring both within-pair and via extra-pair copulations (Reudink et al. 2009), or have opportunities to re-nest or replace failed clutches (Morrison et al. 2019). For instance, an approximate 10-day difference in arrival brought upon by occupying poor-quality dry scrub vs. high-quality wet forest habitat resulted in a ~25% reduction in total fledging success (Reudink et al. 2009). Such fitness consequences suggest that there are likely strong selective pressures acting on the timing of arrival (Kokko 1999, Morbey and Ydenberg 2001, Reudink et al. 2009) that would favor compensatory behavior in short-lived and time-constrained migrants. In direct support, we found a strong positive relationship between an individual's relative departure date and its subsequent migration rate, with delayed individuals migrating at a substantially faster rate. These results support recent evidence suggesting that late departing migrants potentially compensate for delays by migrating faster (McKinnon et al. 2015b, Briedis et al. 2018, González et al. 2020). Despite the potential for these

compensatory behaviors to allow individuals to make up lost time, our estimates of migration rates coupled with estimates of migratory distances assessed via light-level geolocators suggest that these behaviors would only result in a partial compensation (*Supplementary Material – S2*).

Despite the expected fitness benefits of even partial compensation, facilitating these compensatory behaviors require trade-offs during migration that might result in greater risks. According to optimal migration theory (Alerstam et al. 2003b, Alerstam 2011), trade-offs are expected among time-minimization, energy accumulation, and predation risk, such that increases in migration rate are likely to incur costs that influence survival (Alerstam 2011). In support of this prediction, we demonstrate that these compensatory behaviors come at the cost of reduced survival. Late departing birds that likely migrated at a faster rate were less likely to return the following season. Redstarts delayed in their departure from Jamaica may try to compensate by shifting from risk-averse to risk-prone migratory behaviors (Alerstam and Lindström 1990, Alerstam 2011, Nilsson et al. 2013), such as extending the length of flight bouts (Alerstam 1991, Hedenström and Alerstam 1997), avoiding detours around geographic barriers (Alerstam 2001, 2011), and/or shortening the time spent at stopover sites (Dossman et al. 2016). Given that stopovers account for most of the time and energy spent on migration (Hedenström and Alerstam 1997, Wikelski et al. 2003), it is more likely that individuals hasten their migration through adjustments in their stopover behavior. For example, individuals may increase their foraging rate at stopover sites which would increase their fuel deposition rate but would come at the cost of less time being devoted to avoiding predators (Cimprich et al. 2005, McCabe and Olsen 2015).

Ultimately, intraspecific differences in survival during migration reflect that individual adjust their migration rate in response to various ecological constraints. For instance, its well understood that rates of migration tend to be faster in the spring than they are in the fall (Nilsson et al. 2013, Horton et al. 2016), presumably due to selection for arrival to breeding areas (Kokko 1999, Morbey and Ydenberg 2001). As a consequence, survival also tends to be significantly lower during spring migration compared to fall (Rushing et al. 2017). The assumed differences in selective pressures operating on breeding rather than winter arrival necessitate faster migrations which require shifting migratory behaviors to minimize time spent on migration.

In conclusion, our study provides insights into how migratory birds attempt to compensate for the effects of non-breeding carry-over effects by adjusting their rate of migration to compensate for delays at the start of migration. We further demonstrate that these compensatory behaviors may come at a survival cost, likely due to trade-offs in optimization criteria during migration. Ultimately, this study sheds light on individual-level plasticity in migratory behavior with potential consequences for our understanding of how seasonal interactions manifest themselves across the annual cycle and how species might respond to changing climates. Further work should explore the potential link between life history and these compensatory behaviors, especially as they relate to trade-offs between migration rate, arrival timing, reproductive success, and survival. Experimental manipulations of departure schedules of migratory birds, in particular, might provide a powerful opportunity to directly link individual migration rates to mortality risks.

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Figures

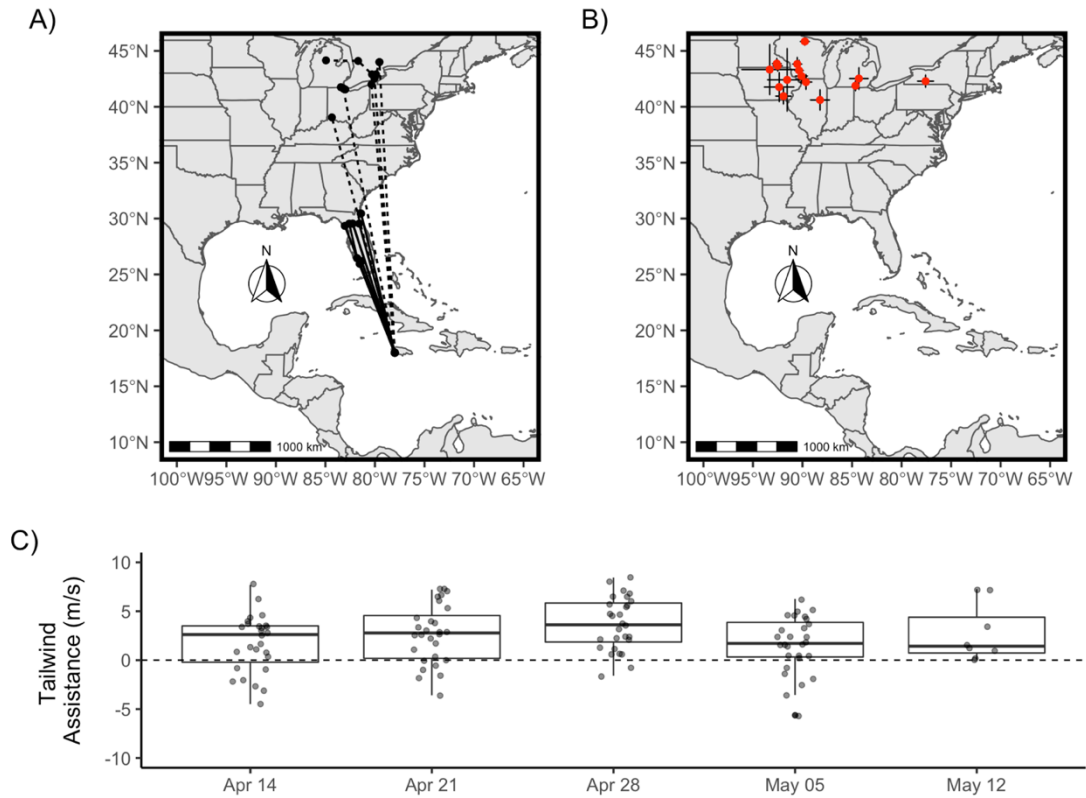


Figure 4.1. Migratory routes, breeding origins, and predominant wind conditions encountered for a sample of American redstarts *Setophaga ruticilla* captured and marked at the long-term study site in Southwest Jamaica, and the Font Hill Nature preserve. Map of the migratory tracks of 15 redstarts tracked using the Motus wildlife tracking system (A). Map of approximate breeding origins of an independent set of 15 American redstarts *Setophaga ruticilla* tracked using archival light-level geolocators and tagged on their wintering grounds in Jamaica (B). Points represent median breeding coordinates with error bars representing \pm one standard deviation in breeding origins. The primary breeding origin of this wintering population appears to be centered in the Midwest of the United States (Iowa, Illinois, Wisconsin, and Minnesota). Predominant wind conditions during the migratory period for this wintering population (Apr 15 – May 15) are primarily out of the South, indicating that most migrants experience favorable tailwinds during their migration from Jamaica back to the US (C; 2.14 ± 0.72 m/s).

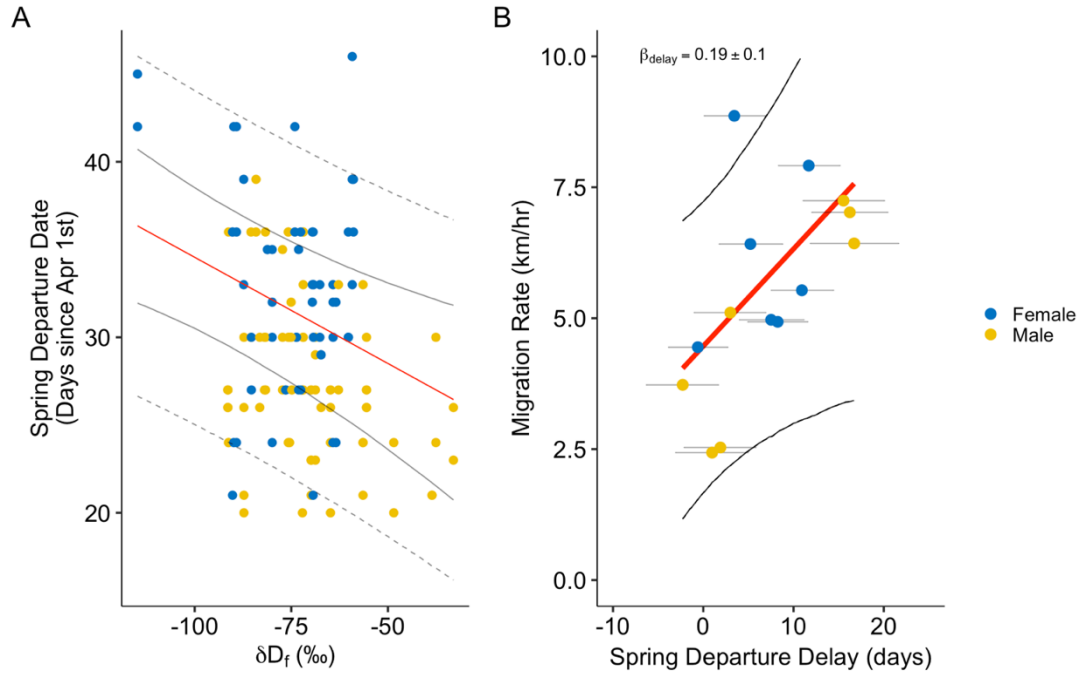


Figure 4.2. American redstarts *Setophaga ruticilla* breeding at more northern latitudes depart relatively later in the season than individuals with southern breeding origins, as demonstrated in the significant negative relationship between breeding latitude ($\delta D_{\text{feather}}$) and mean departure date (A). After accounting for breeding latitude, relative migration timing was positively related to migration speed (B). Individuals compensate for delays in the start of migration by migrating at overall faster rates.

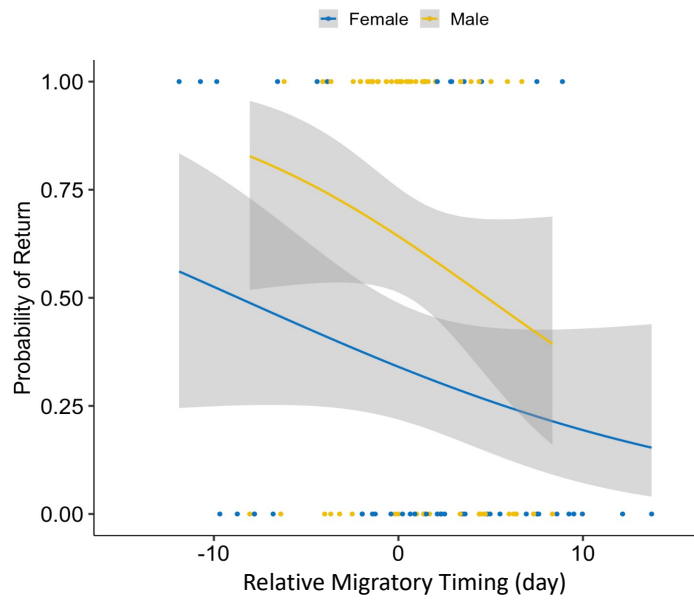


Figure 4.3. Relative migratory timing was negatively associated with the probability of return for American redstarts *Setophaga ruticilla* wintering in Jamaica, suggesting that delayed migrants had a lower return rate. Independent of timing, females had significantly lower return probabilities than males.

CHAPTER 2 APPENDIX

This appendix contains supplementary materials affiliated with Chapter 2 and contains the following elements:

- Figure 2A – Map of study site highlighting the locations (white dots) of each receiver in the automated telemetry array. White opaque circles represent average detection range (300m) of each receiver when a tag is below the canopy.
- Figure 2B – Example of differences in net square displacement over time for a subset of individual American Redstarts *Setophaga ruticilla* tagged in 2017. Left figures depict the spatial positions of tagged individuals across the study period. The right figures are complementary net square displacement curves for those same individuals. Top 2 rows represent classic territorial pattern in net square displacement while the bottom row represents likely floater individuals.
- Figure 2C – Distribution of the time (minutes) spent outside of the detection range of the automated telemetry array for *recursions*. The majority of *recursions* were < 10 minutes in duration (dashed line) lending support to the idea that these movements weren't true forays but rather boundary movements of birds in and out of the detection range of receivers.

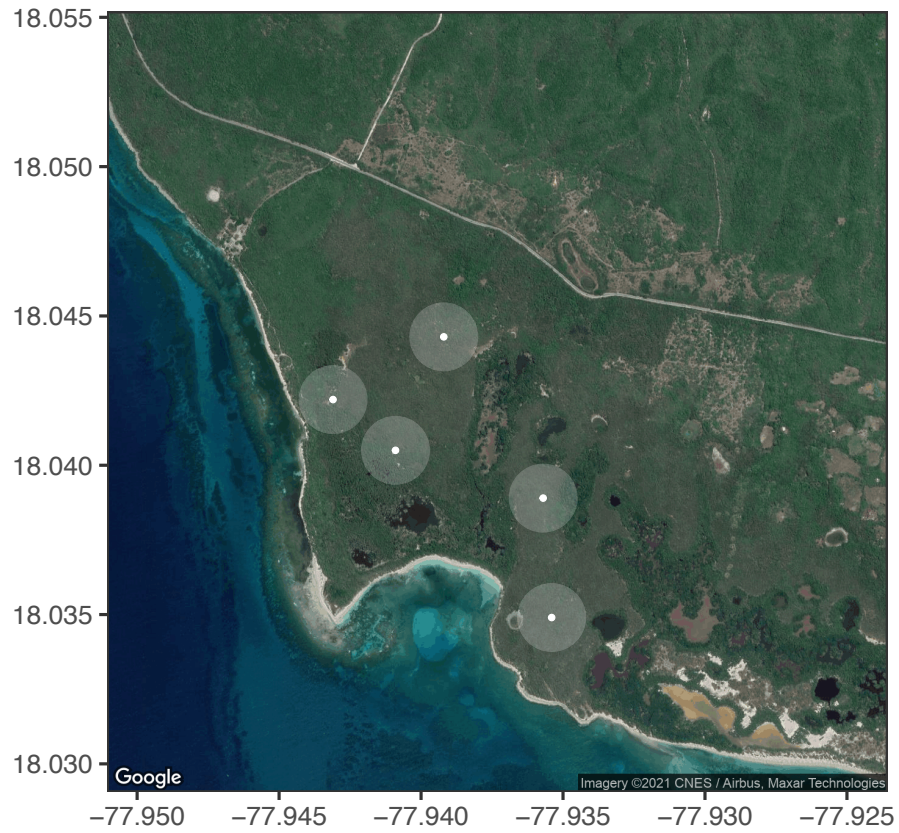


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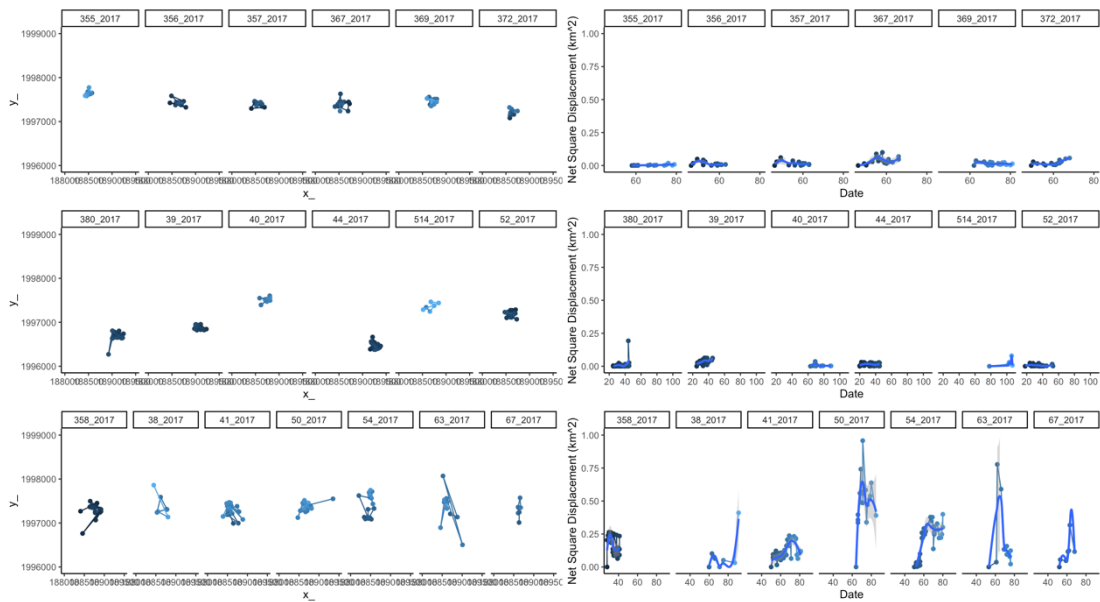


Figure 2B - Example of differences in net square displacement over time for a subset of individual American Redstarts *Setophaga ruticilla* tagged in 2017. Left figures depict the spatial positions of tagged individuals across the study period. The right figures are complementary net square displacement curves for those same individuals. Top 2 rows represent classic territorial pattern in net square displacement while the bottom row represents likely floater individuals.

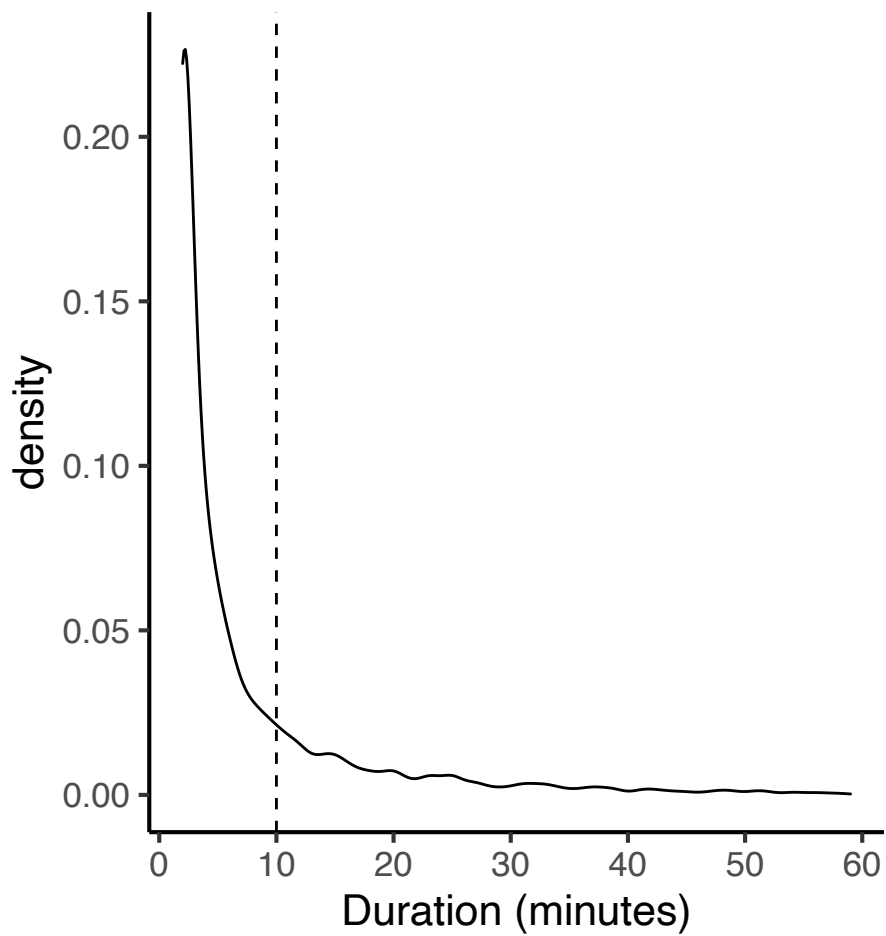


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CHAPTER 3 APPENDIX

This appendix contains supplementary materials affiliated with Chapter 3 and contains the following elements:

- Table 3A - Sample size by age (after-second year, second year), sex (male, female), and habitat type (mangrove, scrub). Values represent the number of individual American Redstarts *Setophaga rutcilla* sampled in each group.
- Table 3B - Number of individual American Redstarts *Setophaga rutcilla* sampled in each year of the study at Font Hill, Jamaica.

Mangrove

| | Male | Female |
|--------------------------|-------------|---------------|
| After-second Year | 359 | 198 |
| Second Year | 218 | 63 |

Scrub

| | Male | Female |
|--------------------------|-------------|---------------|
| After-second Year | 113 | 247 |
| Second Year | 77 | 65 |

Table 3A - Sample size by age (after-second year, second year), sex (male, female), and habitat type (mangrove, scrub). Values represent the number of individual American Redstarts *Setophaga ruticilla* sampled in each group.

| Year | # of Individuals |
|-------------|-------------------------|
| 1995 | 57 |
| 1996 | 80 |
| 2003 | 70 |
| 2004 | 51 |
| 2005 | 73 |
| 2007 | 73 |
| 2008 | 60 |
| 2009 | 100 |
| 2010 | 72 |
| 2011 | 85 |
| 2012 | 84 |
| 2013 | 67 |
| 2014 | 91 |
| 2015 | 97 |
| 2016 | 70 |
| 2017 | 77 |
| 2018 | 48 |
| 2019 | 85 |

Table 3B - Number of individual American Redstarts *Setophaga ruticilla* sampled in each year of the study at Font Hill, Jamaica.

CHAPTER 4 APPENDIX

This appendix contains supplementary materials affiliated with Chapter 4 and contains the following elements:

- Table 4A – Breeding origins of each individual American Redstart *Setophaga rutcilla* tagged with a light-level geolocator at Font Hill, Jamaica
- Figure 4A – Map of each individual American Redstart's *Setophaga rutcilla* breeding origin superimposed on a map of relative abundance derived from eBird.
- Figure 4B – Migration rates estimated via automated telemetry (A; 5.37 ± 1.95 km * hr⁻¹) and light-level geolocators (B; 7.79 ± 3.5 km * hr⁻¹). Migration rate estimated from an independent sample (N=15) of radio-tagged birds was found to be positive related to departure date (days since Apr 1). Similarly, migration rate estimated for a separate group (N=15) of individuals tagged with light-level geolocators was positively related to departure date (days since Apr 1).

| ID | SEX | AGE | BREEDING LATITUDE | BREEDING LONGITUDE | WINTER DEPARTURE | BREEDING ARRIVAL | MIGRATION DURATION | MIGRATION DISTANCE | MIGRATION RATE |
|-------|-----|-----|----------------------|-----------------------|---------------------|---------------------|-----------------------|-----------------------|-------------------|
| BQ700 | SY | M | 42.52404 | -84.31188 | 5/17/19 | 5/25/19 | 8 | 2780.34 | 14.4809375 |
| BQ702 | SY | M | 42.40735 | -91.55355 | 5/2/19 | 5/23/19 | 21 | 2993.08 | 5.93864087 |
| BQ703 | SY | M | 43.24823 | -90.34288 | 5/10/19 | 5/24/19 | 14 | 3028.85 | 9.0144256 |
| BQ715 | SY | M | 42.74727 | -90.10783 | 5/7/19 | 5/30/19 | 23 | 2970.49 | 5.3813279 |
| BQ716 | SY | M | 41.88076 | -84.65108 | 5/9/19 | 5/23/19 | 14 | 2718.6 | 8.09105952 |
| BQ719 | SY | M | 40.60681 | -88.23233 | 5/15/19 | 5/23/19 | 8 | 2688.68 | 14.0035521 |
| BQ731 | SY | M | 45.83728 | -89.76698 | 5/6/19 | 5/29/19 | 23 | 3270.4 | 5.9246413 |
| BQ737 | SY | M | 43.85692 | -92.59539 | 5/7/19 | 5/30/19 | 23 | 3174.93 | 5.75167754 |
| BQ738 | SY | M | 40.94955 | -91.92451 | 5/19/19 | 6/1/19 | 13 | 2869.77 | 9.19797115 |
| BQ740 | SY | M | 43.82161 | -90.53147 | 5/18/19 | 6/2/19 | 15 | 3092.67 | 8.59074167 |
| BQ741 | SY | M | 42.20788 | -89.65248 | 5/15/19 | 5/25/19 | 10 | 2900.19 | 12.0841208 |
| BD622 | ASY | M | 43.66348 | -92.50675 | 4/27/17 | 5/26/17 | 29 | 3152.77 | 4.52983477 |
| BD624 | ASY | M | 43.32939 | -93.31253 | 4/24/17 | 5/13/17 | 19 | 3154.75 | 6.91831579 |
| BD626 | ASY | M | 41.76078 | -92.35556 | 4/27/17 | 6/9/17 | 43 | 2965.32 | 2.87337209 |
| BD628 | ASY | M | 42.28853 | -77.57697 | 4/25/17 | 5/22/17 | 27 | 2688.19 | 4.14843673 |

Table 4A – Breeding origins of each individual American Redstart *Setophaga ruticilla* tagged with a light-level geolocator at Font Hill, Jamaica.

Jamaican AMRE Breeding Origins

Ebird Relative Abundance
Week of June 7

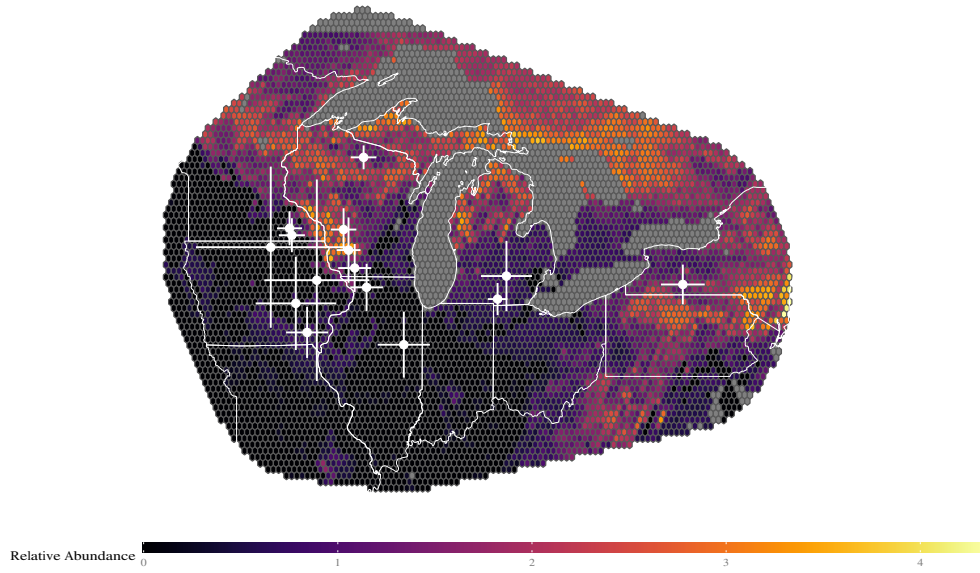


Figure 4A - Map of each individual American Redstart's *Setophaga rutcilla* breeding origin superimposed on a map of relative abundance derived from eBird.

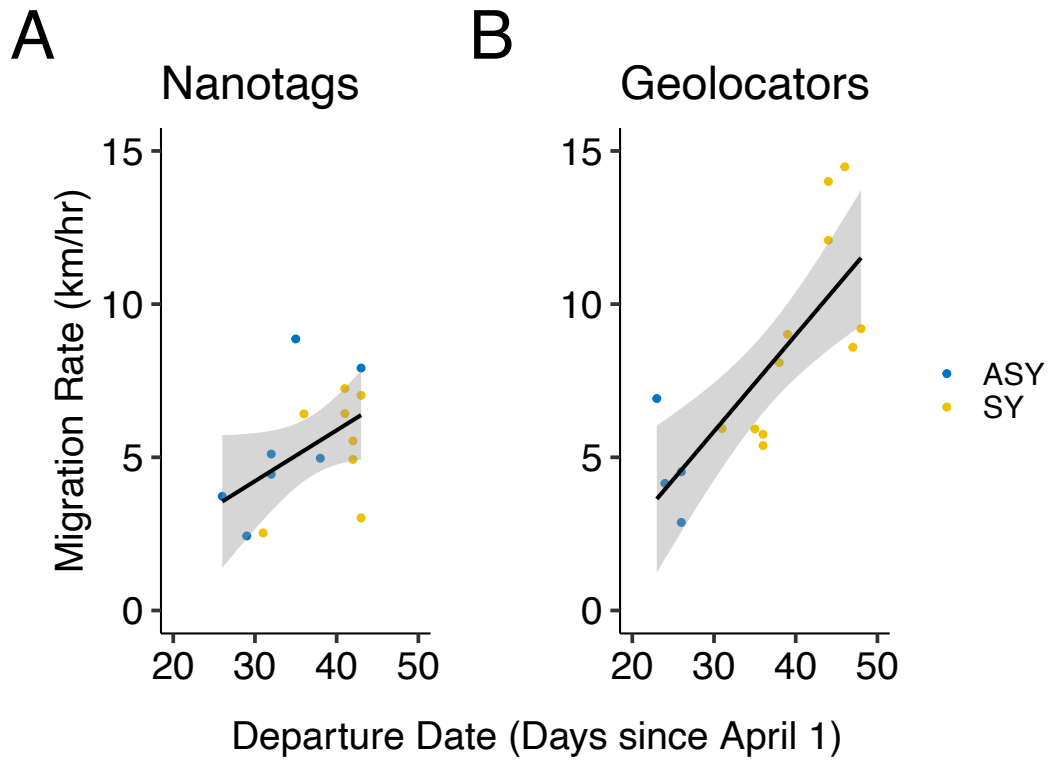


Figure 4B – Migration rates estimated via automated telemetry (A; $5.37 \pm 1.95 \text{ km} * \text{hr}^{-1}$) and light-level geolocators (B; $7.79 \pm 3.5 \text{ km} * \text{hr}^{-1}$). Migration rate estimated from an independent sample (N=15) of radio-tagged (nanotag) birds was found to be positive related to departure date (days since Apr 1). Similarly, migration rate estimated for a separate group (N=15) of individuals tagged with light-level geolocators was positively related to departure date (days since Apr 1).