The Winter Ecology and Response to Environmental Change of a Neotropical Migratory Songbird: the Swainson’s Warbler

Thesis

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Abstract

The ecological impacts of anthropogenic climate change are widespread, and rapid responses, such as shifting distributions, are being observed in many animal populations worldwide. The ability of a species to respond to these climate shifts is critical, and determining the adaptive capacity of vulnerable populations is important as weather patterns become increasingly variable. Migratory birds might provide a unique opportunity to study these responses since they experience climate change in different ways as they travel thousands of miles throughout their annual cycle. Thus far, many studies have focused on large-scale species-level responses, but since individual abilities to respond to changing conditions drive species-level adaptations, identifying behavioral plasticity at a finer-scale is important. If individuals can modify their space use and habitat utilization during changing environmental conditions, they might avoid consequences, such as declining food during periods of drought. Understanding if and how individuals can respond to seasonal changes in precipitation will help us make predictions about how long-term environmental change might impact populations.

My goal was to better understand if and how overwintering migratory birds respond to seasonal changes in precipitation and resources by modifying their home ranges and habitat utilization. In the winter of 2016 and 2017, I sought to determine how a ground foraging Neotropical migrant of conservation concern, the Swainson’s Warbler...
*Limnothlypis swainsonii*, adjusted within-season movements during dry and wet periods at Font Hill Nature Preserve in Jamaica, West Indies. I observed individuals occupying smaller home ranges in more dense habitats and modifying their home range as precipitation changed. Habitat openness had a strong effect on arthropod dry mass and denser habitats supported more arthropods on average throughout the season, although dry period prey abundance was relatively even in both mesic and xeric habitats. Swainson’s Warblers that utilized more mesic habitats shifted their home ranges farther and into denser, more xeric habitats when rainfall increased. Individuals also altered the size of their home ranges throughout the season, demonstrating plasticity in home range size with changing conditions. These results provide valuable evidence of the variable space use strategies that overwintering migratory birds can exhibit in response to fluctuating resources. My findings support the idea that some migratory birds possess the behavioral plasticity in habitat use to adjust space use strategies as seasonal environmental conditions change. Further, I found that individuals can track spatiotemporal changes in food availability while altering the structure of, but maintaining, their home ranges. By examining the behavioral plasticity of wintering migrants to track seasonal environmental change, we can better predict the implications of long-term environmental change for future populations.
Dedication

Dedicated to my parents, Peter and Star Brunner, who have instilled in me a passion for adventure, a never-ending drive to pursue what I love, and the motivation to always stand up for what I believe in. Thank you.
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Historically, climate shifts have influenced the evolution of organisms and shaped ecosystems, but post-industrial anthropogenic climate change has caused novel alterations to the structure and dynamics of ecosystems worldwide (e.g. Walther et al. 2002). There has been an increase in the frequency and magnitude of climate extremes, such as severe drought or episodes of intense rainfall (Karl et al. 1995, Smith 2011, Singh et al. 2013, Fischer et al. 2013, IPCC 2014) that can trigger an array of ecological consequences. This variability in global weather patterns alters the structure and stability of habitats (Walther et al. 2002) and influences novel spatiotemporal fluctuations in resources for many animals (e.g. Visser and Both 2005). Large-scale responses, such as phenological variation and shifting distributions, are being observed in many populations as conditions change (Walther et al. 2002). Some of the best-documented responses have been from migratory species. For instance, warming sea temperatures have influenced an increase in the migration distance of gray whales *Eschrichtius robustus* (Moore et al. 2003) and changes in winter weather are associated with shifts in nonbreeding populations of wading shorebirds, such as Ringed Plover *Charadrius hiaticula* and Sanderling *Calidris alba*, along coastal wetlands in Britain (Rehfisch 2004).

Migratory species provide a unique opportunity to study responses to environmental change because they are dependent upon the availability of suitable habitat...
during all phases of their annual cycle (i.e. breeding, migration, and nonbreeding), all of which may be affected by climate change differently (Robinson et al. 2009). Migratory passerines have undergone rapid population declines in the recent decades, many of which are upwards of 90% total population loss (Robbins et al. 1989, Ballard et al. 2003). Moller et al. (2009) found that migratory bird species with declining populations did not adjust the timing of their migration to match the temporal trend in spring phenology, whereas species with stable or increasing populations did advance their spring migration. With such examples of species-level differences in responses, determining the capacity for species to adjust to climate change is imperative.

Most research on migratory birds is conducted during the breeding season (Marra et al. 2015) but many birds spend the majority of their annual cycle on their tropical wintering grounds. For example, the Caribbean supports millions of Neotropical migratory birds during the nonbreeding season. Overwintering birds arrive during the wet season and persist through the dry season, experiencing declines in rainfall and food (Parrish and Sherry 1994, Strong and Sherry 2000, Williams and Middleton 2008). This rainfall-induced food decline is a major limiting factor for individuals during the nonbreeding stage (Brown and Sherry 2006, Studds and Marra 2007, Smith et al 2010), and these consequences impact individuals into subsequent stages, influencing migration timing, breeding success and survival (Marra et al. 1998, Sillett et al. 2000, Reudink et al. 2009, Wilson et al. 2011). Annual precipitation regimes in the Caribbean are becoming more variable overall (McLean et al. 2014), and these fluctuations in rainfall might negatively influence populations of migratory birds wintering in this region. Not only is it
important to focus on populations, but to also identify the behavioral plasticity in individual space use and habitat utilization. Flexibility in space use may allow an animal to adequately track resources as environmental conditions change. To better understand the implications for long-term climate change on populations, we must determine the abilities of vulnerable species to respond to short-term environmental change.

Global Climate Change
Evidence of anthropogenic climate change can be observed worldwide, from declining Arctic sea ice to ocean acidification. One of the most consistent changes forecast by global climate models is an increase in the frequency and magnitude of climatic extremes (Karl et al. 1995, Smith 2011, Fisher et al. 2013, Singh et al. 2013, IPCC 2014). Over the last century, the global surface temperature has warmed by approximately 0.85 °C, with the magnitude of increase differing between wet and arid regions (IPCC 2014). A more unpredictable component of climate change is the increase of global precipitation extremes caused by the intensification of the hydrological cycle (Huntington 2006, Durack et al. 2012, Marvel and Bonfils 2013). The Intergovernmental Panel on Climate Change (2014) reported that extreme global weather events have increased since 1950. For example, local heavy precipitation events have increased in more regions than they have decreased (Groisman et al. 2005, Donat et al. 2013, Westra et al. 2013). The world’s most wet and arid regions are projected to be most impacted by the modeled increases in weather extremes (Donat et al. 2016), which will likely result in major fluctuations in
annual rainfall regimes by the presence of extreme wet years contrasting with extreme dry years (Knapp et al. 2015).

A major atmospheric phenomenon driving worldwide weather is the El Niño Southern Oscillation (ENSO). ENSO is a natural cycle that disrupts global weather patterns, causing flooding, drought, cyclones and other extreme weather events (NOAA 2018). Global warming scenarios predict that El Niño occurrences could potentially occur twice as often in the future in response to warming conditions (Cai et al. 2014). ENSO can affect patterns of seasonality. For example, five decades of weather data in Puerto Rico and the Virgin Islands indicated that during ENSO events, dry season precipitation was significantly higher than neutral periods, and wet season precipitation significantly lower (National Weather Service, San Juan, PR). North America also experiences extreme weather during the El Niño and La Niña portions of ENSO; the northern United States exhibits higher than normal autumn and winter temperatures during El Niño, for instance. Because of these regionally specific shifts in temperature and precipitation patterns, projecting future change is difficult, especially in regards to the effect of climate change on animals. There is ample evidence indicating that a broad range of organisms with diverse geographical distributions has been affected by climate shifts (e.g. Wuethrich et al. 2000, McCarty 2001, Walther et al. 2001). Determining how different species respond to environmental change will help us to better understand the long-term implications climate change will have on animal populations.
Impacts of Environmental Change on Animals

Population-level Responses to Climate Change

Populations of organisms and ecological communities respond to regionally specific environmental change. Therefore, studying organisms at a local, regional scale is the most relevant in the context of ecological response to climate change (Walther et al. 2002). Many long-term studies in Europe and North America have recorded trends in seasonal dynamics of various populations, reflecting shifts in climate (e.g. Barlein and Winkel 2001, Menzel and Estrella 2001). One of the most common ways species have been observed responding to climate change is by tracking phenology, or the timing of seasonality in organisms. For instance, spring activities such as the arrival of migratory birds on the breeding grounds and choruses and spawning in amphibians have occurred progressively earlier since the 1960’s (e.g. Keeling et al. 1996, Both and Visser 2001, Parmesan and Yohe 2003).

In addition to phenological changes, shifts in species distributions have also occurred across an array of taxa (e.g. Hoffman and Parsons 1997), both towards the poles and upwards in altitude. Populations are shifting into these areas as the increase in temperatures promotes greater resource availability, making polar and high-montane habitats more hospitable (Jensen et al. 2008). Chen et al (2011) found that species in regions experiencing the greatest amount of temperature warming shifted the farthest latitudinally. The authors demonstrated that from all documented species range shifts, there was an overall shift to higher latitudes at a median rate of 16.9 kms per decade, and to higher elevations at 11.0 m per decade. Range shifts have also caused an increase in
novel species interactions, with non-native species immigrating into new habitats (Walther et al. 2000). New species interactions also occur because of the variability in the rate different species respond to change (Pounds et al. 1999), and some species may have a greater adaptive capacity to respond than others (Both et al. 2009, Angert et al. 2011, Hurlbert and Liang 2012). These asymmetric responses have also been shown to cause shifts in entire community assemblages (e.g. Brown et al. 1997, Sagarin et al. 1999). Newly formed interactions between species can cause increased competition through more effective exploitation of prey (e.g. Tylianakis et al. 2008) and may lead to extinctions of native species (Davis 2003). Ultimately, individual-level abilities to respond to changing conditions drive these species-level adaptations, allowing for the persistence of populations in the face of climate change (Williams et al. 2008). Species vary greatly in their rates of response to shifting climate (Chen et al. 2011) and identifying those factors driving these differences is important. It is suggested that more dispersive individuals near range boundaries can influence fast climate change adaptation of a species (Kokko and Lopez-Sepulcre 2006) and perhaps, individuals demonstrating behavioral plasticity in space use are driving these shifts.

Space-Use Dynamics

Individual movement is a fundamental component in a species’ ability to adapt to changing climatic conditions. Understanding what factors influence animal space use is essential when researching the impacts of environmental change. Determining how species utilize space at different temporal scales can help researchers understand important drivers of survival and persistence in the environment. A major factor
influencing space use is the tendency for many animals to remain in a constrained home range (Seton 1909, Bert 1943, Borger et al. 2008). These dynamics vary based on a wide range of intrinsic and extrinsic factors such as body size, sex, and risk of predation. The factors influencing the size of any given home range can also vary on the species, population, and individual level (e.g. McLoughlin and Ferguson 2000). Factors that shift somewhat slowly, such as those associated with climate change, influence home range patterns across a population but are constrained at the individual level (McLoughlin and Ferguson 2000) as environmental change ultimately affects food availability. The utilization of resources (e.g. food) that drives home range characteristics is highly dynamic and varies based on environmental conditions that change within and between years (Mooij et al. 2002, Hovick et al. 2014, Carroll et al. 2015).

Food is a major determinant of home ranges size for individuals, and home ranges tend to decrease in size with an increase in food, as seen in a wide range of species (McLoughlin and Ferguson 2000). Constraints on this relationship can include intra- and inter-specific competition, patchy food availability on the landscape, and predation pressures (McLoughlin and Ferguson 2000). In addition to food, social interactions that increase with conspecific density might limit an individual’s space use, especially in highly territorial populations. Alternatively, some individuals of different bird or mammal species exhibit flocking or herding behaviors, while other individuals are non-territorial wanderers or floaters (e.g. Brown 1964, Winker 1979, Palombit 1999), depending on social dynamics or hierarchies in a population. There are advantages to each of these alternative space use behaviors when food abundance fluctuates, and food
may continue to become increasingly unstable with variable precipitation patterns. For instance, individuals might respond to these seasonal food declines by adjusting their space use strategy. However, very little is known about how the majority of migratory species generally utilize space during the nonbreeding season. To better understand how environmental change will impact migratory bird populations, we must first have base knowledge about species space use behaviors throughout their full annual cycle. Therefore by determining species-specific space use we can gain a better understanding about the capacity each species has to respond to adverse conditions.

Individual Responses to Environmental Change
Understanding if and how individuals can respond to short-term environmental change will help us make predictions about how long-term change might impact wildlife populations, including how and where these populations are limited (e.g. Krebs 2002, Rappole et al. 2003, Newton 2004, Flockhart et al. 2015). Many organisms must have the ability to establish populations in newly suitable habitat given the rapid rate of climate change, but species-specific research is limited on individual flexibility in this regard (Loarie et al. 2009). Behavioral plasticity in individual space use and habitat utilization is potentially advantageous, as flexibility in space use may allow an animal to adequately track resources as environmental conditions change. Individuals across different taxa have been observed altering their space use behaviors with changing resources. Large mammals, like roe deer *Capreolus capreolus*, have large range distributions and vast home ranges across the landscape that change in size with seasonal resource fluctuations (Morellet et al. 2013). Tanner et al. (2016) described how discrete ecological events such
as weekly minimum ambient temperature and thermal extremes affected Northern bobwhite *Colinus virginianus* survival and space use, respectively. Food availability has been a source of spatiotemporal resource tracking in many vertebrate species (e.g. Van Schaik et al. 1993). For instance, nonbreeding surf scoters, *Melanitta perspicillata* traveled farther and used several different smaller foraging sites in early winter compared to mid-winter when primary prey availability peaked in a large central location (Cruz et al. 2013). Extreme changes in habitat also influences space use. Habitat loss and fragmentation caused nonbreeding willow tits *Poecile montanus* to enlarge their home ranges to compensate for the reduction in suitable habitat, consequently including more open, clear-cut areas in their home ranges (Siffczyk et al. 2003). At the extreme of space use response to changing conditions, individuals have been observed completely altering space use strategies due to changes in food abundance. For example, with an experimental reduction in arthropods, several individuals from a species of insectivorous migratory birds have been observed abandoning home ranges and becoming non-territorial floater individuals (Cooper et al 2015). With ongoing land use change and rapid and increasing climate shifts, animals are forced to push the boundaries in their space use behaviors and quickly respond to drastic changes in their environment.

Nonbreeding Migratory Birds in a Changing Caribbean: The Ability of a Neotropical Migrant to Respond to Precipitation Declines

Caribbean Drying Trend

All Neotropical ecosystems are under the pressure of climatic change, as extreme weather events increase (Donat et al. 2016) and conditions become warmer and drier (Neelin
2006). In the Caribbean, seasonal drought conditions are becoming more pronounced and the mean annual wet season rainfall alone is projected to decrease up to 40% by 2080 (Kalmalkar et al. 2013). Overall variability in annual precipitation is increasing (McLean et al. 2014) and throughout the Caribbean basin, recent meteorological climate scenarios show differences in rainfall between northern and southern landmasses. For northern Caribbean islands like Cuba and Jamaica, future projections show a tendency towards more intense rainfall events (McLean et al. 2014). With these variations between regions, it is important to understand the impacts of climate change on this regional scale, especially in the context of ecological responses (Walther 2002). With the increase of drying trends and extreme weather in the Caribbean, the function and structure of these ecosystems will be considerably altered (Walther et al. 2002, Parmesan and Yohe 2003, Neelin et al. 2006, Donat et al. 2016), impacting an array of both endemic and migratory species.

Wintering Neotropical Migratory Birds
Understanding ecological responses to changing climate is of particular interest in the Caribbean, as it is a critical wintering location for millions of nonbreeding Neotropical migratory birds. Populations of migratory birds overwintering in the Neotropics have declined over the past several decades, some species experiencing upwards of 90% population loss (Robbins et al. 1989, Ballard et al. 2003) Migratory birds spend the majority of their annual cycle on their nonbreeding grounds, arriving during the wet season and persisting through the dry season. With the islands in the Caribbean basin
supporting millions of migratory birds, habitat availability and suitability is crucial for maintaining these populations.

The Caribbean experiences seasonality in rainfall similar to other tropical regions and rainfall drives much of the population dynamics of migratory birds in this region (Sherry and Holmes 1996, Sillett et al. 2000, Marra et al. 2015b). As the environment becomes increasingly dry, plant productivity slows and arthropod abundance declines (Johnson and Sherry 2000, Sherry and Holmes 1996, Smith and Robertson 2008). Thus, migratory birds already experience drastic food shortages as seasonal precipitation decreases (Parrish and Sherry 1994, Strong and Sherry 2000, Williams and Middleton, 2008). Rainfall and its influence on arthropods are major limiting factors for individual body condition during the winter period (Brown and Sherry 2006, Studds and Marra 2007, Smith et al 2010). Therefore, major shifts in rainfall regimes in the Caribbean, in addition to characteristic seasonal declines in rain, might push migratory birds beyond a threshold in their ability to respond behaviorally, ultimately having negative impacts on populations.

Many studies have demonstrated the importance of environmental conditions for nonbreeding birds, and food is generally considered the most limiting factor for insectivorous overwintering migrants (Sherry et al. 2005). Winter food availability impacts individual body condition (Marra and Holberton 1998, Latta and Faaborg 2002, Studds and Marra 2005, Brown and Sherry 2006, Smith et al. 2010, Angelier et al. 2011, Cooper et al. 2015) and the progression of seasonal drying have been shown cause birds condition to decline (Johnson et al. 2006; Sherry and Holmes 1996; Strong and Sherry
2000), especially in poor-quality habitats (Marra and Holberton 1998). Since moisture influences arthropod abundance, it is also a major determinant of habitat quality for wintering birds and individuals utilizing higher-quality habitats are generally in better condition (Brown and Sherry 2006, Smith et al. 2010, Studds and Marra, 2007, Tonra et al. 2011). The late-winter dry season is a particularly important time period for migratory birds because they are preparing their bodies for spring migration (Brown and Sherry 2006, Johnson et al. 2006). Preparation for spring migration by accumulating and maintaining adequate levels of fat and large flight muscles is energetically challenging and food abundance is a critical aspect in their abilities to do so (Johnson et al. 2006; Studds and Marra 2011). Individuals occupying wetter habitats are better able to increase their body mass throughout the season, where those in drier habitats decreased in body mass (Smith et al. 2010), indicating that a wetter environment better prepares a migratory bird for subsequent spring migration. Since wetter habitats are of better quality, birds that manipulate their space use to utilize these areas benefit with greater levels of fitness.

Environmental conditions during the nonbreeding stage influence migration timing, breeding success and survival (Marra et al. 1998, Sillett et al. 2000, Reudink et al. 2009, Wilson et al. 2011). Increasingly unstable or unpredictable winter conditions may continue to impact migratory birds throughout their entire annual cycle, including individual fitness in the subsequent wintering period (Sillett et al. 2000, Rushing et al. 2016, Woodworth et al. 2017). Birds in compromised condition have been observed departing later for spring migration (Studds and Marra 2005, 2007, 2011, Cooper et al 2015) and this delay in departure impacts arrival date on the breeding grounds (Saino et
al. 2004, Balbontin et al. 2009), and subsequent breeding success (Norris et al. 2004, Reudink et al. 2009). Early arrival at the breeding grounds also enhances mate and territory acquisition and opportunities for re-nesting (Cooper et al. 2011, Tonra et al. 2011). These negative consequences on individual breeding fitness can potentially persist through multiple stages of a bird’s life cycle (Sillett et al. 2000). Sillett et al. (2000) demonstrated these impacts in a decade long study of the effects of El Niño events on the breeding and nonbreeding ecology of Black-throated Blue Warblers *Setophaga caerulescens*. They found that during the dry years of El Niño the annual survival in Jamaica was low compared to the wetter years of La Niña, and El Niño years in New Hampshire caused less lepidopteron prey items and in response, smaller fledglings (Sillett et al. 2000). Given the long-term consequences of poor wintering conditions, quantifying individual’s ability to adjust their nonbreeding space use as conditions become more adverse is important, especially with future climate projections.

### A Potential Model System for Space-Use Response

**Swainson’s Warblers: a model study species**

Swainson’s Warblers *Limnothlypis swainsonii* are a ground-foraging Neotropical migrant of conservation concern (Partners in Flight 2013). Concern for Swainson’s Warbler population status emerged in 1992 when they were identified as a species with a high degree of vulnerability due to major habitat loss throughout their breeding and nonbreeding range (Hunter 1992). Unlike most other migratory species, Swainson’s Warblers have a small distributional range, breeding in the southeastern United States.
and overwintering on islands in the Caribbean basin and throughout the Yucatan Peninsula (Anich et al. 2010). Swainson’s Warblers rely heavily on the availability of habitat in the Caribbean to support nonbreeding populations; therefore, they are an ideal species to understand the impacts of Caribbean climate change on vulnerable Neotropical migrants.

Swainson’s Warblers represent a larger guild of ground-foraging passerines that may be impacted by the increasing drought conditions in the Caribbean. Moisture levels in tropical dry forests, a major habitat type occupied by wintering ground foragers, are projected to decrease with climate change, leading to lower arthropod abundances (Toms et al. 2012). Swainson’s Warblers typically flip leaves with their large bill to access subleaf litter arthropods (Graves 1998, Strong 2000) and a certain level of soil moisture is necessary to maintain a presence of leaf litter prey. Large-scale changes in Caribbean precipitation regimes will lead to declining or unstable prey for overwintering birds.

During the breeding season, Swainson’s Warblers occupy mostly bottomland hardwood, lowland canebrakes, and rhododendron and hemlock thickets (Meanley 1971, Anich et al. 2010). Graves (2015) demonstrated behavioral plasticity in habitat selection as some breeding Swainson’s Warblers have also recently colonized seral-stage pine plantations. Nonbreeding Swainson’s Warblers have been observed in a wide range of habitat types and in Jamaica alone, they have been detected in wet and dry limestone (Graves 1996), second growth scrub and coffee plantations (Strong 2000, Strong and Sherry 2001). This behavioral plasticity in habitat utilization observed throughout their range also makes the species a great focal species to study responses to environmental change. The ability to
use new habitats might allow the species greater flexibility in space use behaviors as declining precipitation influences changes in the habitats nonbreeding birds typically utilize.

Previous research has determined that dry limestone forest is a key habitat for wintering Swainson’s Warblers, showing that birds maintain healthy body condition, owing to habitat structure and more abundant subsurface leaf litter fauna (Strong, 2000; Strong & Sherry, 2001). During breeding, Swainson’s Warbler home ranges are smaller in habitats with a dense understory, little herbaceous cover, and closed canopies (Anich et al. 2010, Benson and Bednarz 2010, Savage et al. 2010); these characteristics tend to be of high quality for Swainson’s Warblers. Using these studies, predictions can be made about how individuals may use habitats during adverse conditions. Swainson’s Warblers might have smaller home ranges in areas with dense understory and closed canopies, as these areas may sustain leaf litter prey for longer into the dry season. Since previous studies have described behavioral plasticity in habitat use, as conditions become drier, Swainson’s Warblers utilizing somewhat marginal habitats may expand into new habitats to compensate for declining resources. Studying Swainson’s Warblers winter ecology is also quite timely. Their small distributional range and low population numbers make them an overall highly vulnerable species in the face of climate change and they will most likely be greatly influenced by changing conditions. And also by determining how Swainson’s Warblers respond to changes in their environment, we might better understand how migratory species more broadly might be affected by fluctuating moisture and arthropod abundance.
Conclusion and Significance

Rapid ecosystem change is already occurring in many regions of the world (MEA 2005) due to anthropogenic climate change. The increase in the occurrence and severity of climate extremes (IPCC 2014) has caused significant ecological impacts in many regions of the world (Smith 2011). This has prompted researchers to focus on determining ecosystem responses to these extreme changes. Because of the drastic differences in climate shift between global regions, studying organisms on a regional scale better informs ecological responses to climate change (Walther et al. 2002). Individual-level responses to environmental change are fundamental in determining how a species or population will adapt to large-scale climate change. For migratory species, this requires research that encompasses all phases of the annual cycle. Behavioral plasticity in individual space use and habitat utilization may be advantageous, and animals must have the ability to establish populations in newly suitable habitat given the rapid rate of climate change, however, species-specific research is limiting (Loarie et al. 2009). Many studies focus on modeling the effect of environmental change on populations, but the nuances of population limitation may be better determined by researching individuals within these populations. If we determine how individuals may utilize space and habitats differently in changing seasonal conditions, we can better predict how long-term change might impact species-level responses.
Chapter 2. The Winter Ecology and Response to Environmental Change of a Neotropical Migratory Songbird: the Swainson’s Warbler

Introduction

The impact of climate change on animal populations is widespread, and an animal’s ability to rapidly respond to environmental change is crucial in preventing population loss. Increased variability in global weather patterns alters the structure and stability of many habitats (Walther et al. 2002) triggering novel spatial and temporal fluctuations in food sources for numerous species (e.g. Both and Visser 2001, Studds and Marra 2007). Behavioral plasticity in individual space use and habitat utilization is potentially advantageous, as flexibility in space use may allow an animal to adequately track resources as environmental conditions change. Large-scale responses, such as phenological change and shifting distributions are being observed at the species-level, yet it is also important to identify how animals respond to short-term environmental change on an individual-level. It is also imperative to assess which species may be more constrained than others as evidence suggests some species inability to respond (Both et al. 2009, Angert et al. 2011, Hurlbert and Liang 2012). Understanding if and how individuals can respond to within-season change will enable managers to incorporate predictions about the impacts of long-term environmental change, including how and where these populations are limited (Marra et al. 1998; Sillett et al. 2000; Rappole et al. 2003; Dugger et al. 2004; Newton 2004), into conservation actions.
Neotropical ecosystems are experiencing the pressure of climatic change, as extreme weather events increase (Donat et al. 2016) and conditions are becoming warmer and drier (Neelin 2006). In the Caribbean basin, mean annual wet season rainfall is projected to decrease up to 40% by 2080 (Kalmalkar et al. 2013), and annual precipitation is expected to become more variable overall (McLean et al. 2014). The Caribbean harbors an array of endemic species and is an important location for millions of nonbreeding Neotropical migratory birds that spend the majority of their annual cycle overwintering there. These migratory birds arrive in the Caribbean during the wet season and persist through the dry season, thus already experience food shortages as seasonal precipitation decreases (Parrish and Sherry 1994, Strong and Sherry 2000, Williams and Middleton, 2008). Rainfall and its influence on arthropods are major limiting factors for individual body condition during the winter period (Brown and Sherry 2006, Studds and Marra 2007, Smith et al. 2010). Therefore, major shifts in rainfall regimes in the Caribbean, in addition to characteristic seasonal declines in rain, might have drastic effects on overwintering migratory birds. These environmental conditions during the nonbreeding stage ultimately continue to impact birds into subsequent stages, influencing migration timing, breeding success and survival (Marra et al. 1998, Sillett et al. 2000, Reudink et al. 2009, Wilson et al. 2011). Therefore, an individual’s ability to respond to seasonal environmental change is critical. One way in which birds might avoid the consequences of climate change and unpredictable resources is through behavioral plasticity in space use.
Nonbreeding migratory species exhibit a variety of space use strategies (Brown 1964, Rappole and Warner 1980) depending on resource availability, as food is the primary driving factor of winter space use (Sherry et al. 2005, Brown and Sherry 2006). While some nonbreeding birds exhibit flocking behaviors or become floater individuals (non-territorial wanderers; Brown 1964, Winkler 1998), most songbirds are typically site tenacious, occupying home ranges throughout the nonbreeding season (Greenburg and Salewski, 2005). There are advantages to each of these alternative space use behaviors when food abundance fluctuates, and individuals might switch between different strategies within a given season. For instance, with an experimental reduction in arthropods, several individuals from two different species of insectivorous migratory warblers have been observed abandoning home ranges and becoming floaters (Brown et al. 2008, Cooper et al. 2015). Most individuals do not make these drastic switches in space use strategy, however, and birds could respond to changing resources by altering existing home ranges.

The availability and spatial variation of food impact distributions of wintering Neotropical migratory populations at multiple spatial scales (Johnson and Sherry 2001), as well as individual-level differences in home ranges (McLoughlin and Ferguson 2000). Birds tend to have smaller home ranges in areas with more food (e.g. Stenger 1958, Holmes 1970, Myers et al. 1979, Smith and Shugart 1987) Thus, given the influence of rainfall on food availability, individuals would be expected to expand their home ranges during the Neotropical dry season. The structural-cues hypothesis (Smith and Shugart 1987) suggests that the mechanism by which birds select habitats is cueing in on
particular habitat features that are associated with greater density of food, depending on their foraging behaviors (Wolfe et al. 2014). In ground foraging birds, for instance, Smith and Shugart (1987) proposed that home ranges are smaller in habitat types that provide a more favorable environment for leaf litter arthropods (Wallworth 1976). Leaf litter microclimate will vary between habitats (Geiger 1966) and change with the seasonal fluctuations in precipitation, so certain habitats may be more suitable for arthropods during dry periods, and others during wet periods (Silveira et al. 2010). To track both the temporal and spatial changes in food, individuals may not only respond by enlarging their home ranges, but also by shifting them into areas with a greater arthropod abundance as seasonal changes occur.

Spatial and temporal variations in food availability promote resource tracking in many vertebrate species in the tropics (Van Schaik et al. 1993). Resident animals like frugivorous birds actively track fruit sources across the landscape, following spatial variation in abundance (Whitney and Smith 1998, Powell and Bjork 2004, Holbrook 2010). Some Nearctic breeding birds have exhibited shifts in home ranges to occupy new areas during the post-breeding period, presumably prospecting for future higher-quality breeding sites (Arlt and Part 2007). Nonbreeding migratory individuals have also responded to food decline by relocating to habitats with greater moisture and higher food abundance (Smith et al 2011, Wunderle et al. 2014), abandoning their previous home ranges to make this movement. Besides complete relocation, an advantageous response for migratory birds may be a continuous shift into more suitable habitats as the availability in food changes spatially. This strategy would be a more gradual tracking of
changing resources, and these types of shifts have not been described in Neotropical migrants. Such behaviors would be evidence of behavioral plasticity in habitat use that might promote adaptation to climate change.

Neotropical migratory birds must have the adaptive capacity to alter their space use behaviors with the predicted changes in precipitation regimes, increase in extreme weather events, and the overall effect this will have on prey availability. Environmental conditions during the nonbreeding period impact population dynamics (Sherry and Holmes 1996, Sillett et al 2000, Wilson et al. 2011) and with further climate change expected in the tropics, individuals in these populations will need to modify their behaviors to avoid these consequences. Additionally, the majority of research on migratory bird space-use is conducted during the breeding period (Marra et al 2015a), and little is known about how the majority of species utilize space during the nonbreeding season. To better understand how environmental change will impact migratory bird populations, we must first have base knowledge about species space use behaviors throughout their full annual cycle. One Neotropical migrant on which limited nonbreeding research has been conducted (Graves 1996, Strong 2000, Strong and Sherry 2001) is the Swainson’s Warbler *Limnothlypis swainsonii*. Determining their overwintering space use is timely because they are a species of conservation concern (Partners in Flight 2013). Moreover, as a ground foraging species they represent a larger guild of insectivorous migrants, and knowledge gained about their space use and has further implications for other ground foraging migratory birds.
Swainson’s Warblers are an ideal focal species to study how environmental change influences migratory birds for several reasons. The species may be constrained by their small distributional range. Swainson’s Warblers breed throughout the southeastern United States and their nonbreeding range is restricted to the islands in the Caribbean basin and areas throughout the Yucatan Peninsula (Anich et al. 2010). Because of this small range, large-scale drying trends in this region could have severe effects on suitable habitat availability and food abundance for wintering Swainson’s Warblers. In addition to concerns about distributional constraints, as ground foraging species, Swainson’s Warblers might be particularly sensitive to drying. They specialize in flipping leaves with their large bill to access sub-leaf litter arthropods (Graves 1998, Strong 2000), so a certain level of soil moisture is necessary to maintain a presence of prey items.

Nevertheless, habitat use varies widely throughout their range. In Jamaica alone, Swainson’s Warblers have been detected in wet and dry limestone (Graves 1996), second growth scrub and coffee plantations (Strong 2000, Strong and Sherry 2001), and occupy other habitats throughout the winter range. Graves (2015) demonstrated behavioral plasticity in habitat use as Swainson’s Warblers have recently colonized pine plantations throughout its breeding range, which might be buffering the population from intense habitat loss in the region. This range of habitat use might be incredibly important for the species as climate change persists in the Caribbean because it may allow for individuals to respond by adjusting how they utilize space. It also gives us an opportunity to study how space use varies between individuals using diverse habitats with differing moisture and vegetation characteristics. By using Swainson’s Warblers as a model for
understanding how Neotropical migratory birds respond to seasonal changes in their environment we can better understand how species can respond to long-term climate change.

This study quantified space use behaviors of nonbreeding Swainson’s Warblers and examined the environmental drivers behind home range size and within-season changes in home range. I hypothesized that nonbreeding migratory birds will modify their space use as a result of seasonal changes in precipitation and resources. I measured soil moisture, habitat characteristics, and arthropod abundance on the home ranges of radio-tracked birds during dry and wet periods to determine the drivers of seasonal variation in space use. In order to examine seasonal variation in space use, I first needed to determine if nonbreeding Swainson’s Warblers occupied home ranges throughout the entire overwintering period. I predicted that (1) Swainson’s Warblers occupy home ranges in dry and wet periods regardless of habitat type, (2) habitat characteristics such as thick leaf litter and a dense canopy are associated with greater leaf litter arthropod abundance, (3) home ranges would be smaller in areas with a habitat structure that promotes a greater abundance of leaf-litter arthropods in both wet and dry periods, and (4) home ranges would decrease in size or shift spatially to track the increase or spatial variation of prey as precipitation increases from dry to wet period. Based on breeding season studies, I expected Swainson’s Warblers to prefer habitats with more stable soil moisture and overall denser vegetation with more exposed leaf litter (Benson and Bednarz 2010). These results will provide valuable information about the adaptive
capacity of a Neotropical migratory bird to respond to climate change by quantifying behavioral plasticity in habitat utilization and space use strategies.

Methods

Study Area

I conducted my research at Font Hill Nature Preserve located on the Southwest coast of St. Elizabeth, Jamaica (18°02’ N, 77°57’ W) during January-May 2016-2017. The habitat at Font Hill consists of dry second growth scrub forest and mangrove swamps. Dry scrub is dominated by logwood (*Haematoxylum campechianum*), and includes an array of other canopy species, such as burnwood (*Metopium brownii*) and red birch (*Bursera simabura*) with a shrubby understory. Mangrove swamps have minimal understory vegetation and are dominated by black mangrove (*Avicennia germinans*) with some areas of white (*Laguncularia racemosa*) and red (*Rhizophora mangle*) mangrove interspersed. Ecotone is a third distinct habitat type in transitional areas between mangrove and scrub, characterized by an open understory and dense canopy consisting primarily of logwood and white mangrove. This habitat gradient provided the opportunity to investigate how individuals utilize areas of different vegetation characteristics and moisture profiles.

Jamaica experiences seasonality in precipitation like most other tropical regions. The dry season at Font Hill typically commences in January with conditions becoming progressively drier through May. Although historically this pattern was observed, in both years this study was performed (2016 and 2017), precipitation increased at the end of February with large rain events continuing through May, causing an atypical increase in
wetness both years. Mangroves, which were typically flooded upon arrival to Font Hill in January, were dry with shallow pools and gradually became more flooded as rain events persisted through March in 2016-17. This atypical precipitation pattern may be attributed to a predicted shift in rainfall regimes throughout the Caribbean. Studds and Marra (2011) have described an increase in the variation in dry season precipitation in southwest Jamaica.

Field Methods
Between 5 January and 5 February, I captured 32 Swainson’s Warblers (15 in 2016, 17 in 2017) in mist nets, primarily using conspecific playback. I studied birds across a 2 km area to increase coverage and ensure I sampled individuals occupying different habitat types. I banded each individual with a U.S. Geological Survey aluminum band and equipped them with PicoPip AG376 radio transmitters (Lotek Inc. Newmarket, ON, Canada) using 0.7mm Stretch Magic jewelry cord passed through 1mm tubes and soldered for a leg loop harness attachment. Transmitters were .67 grams, or approximately five percent of each bird’s body weight. A good harness fit was confirmed by making sure I could just gently fit a pencil tip between the transmitter and the bird’s back, as I wanted the transmitter to be loose enough to accommodate body size fluctuations, but also remain snug to reduce risk of abrasion. I took standard morphological measurements (wing cord, tail, bill, and tarsus length), weighed each bird to the nearest 0.1g, scored the amount of furcular fat (Holmes et al. 1989) and obtained the shape of the pectoral muscle using a “muscle meter” device (Bauchinger et al. 2011). I took blood samples via capillary action from the brachial vein for sex determination of
birds using a commercial lab (IQ Bird Testing, Miami, FL, USA). I released individuals and thereafter hand-tracked their movements via Lotek Biotracker radio receivers and three element Yagi antennas, using triangulation to obtain location points. On average, I recorded three location points for each individual per day with at least one-hour lag between each triangulated location, tracking during different times of day to assess variations in daily movement (06:00 – 17:00).

To determine the environmental characteristics of each individual bird’s home range, I calculated home ranges with kernel density estimation (‘adehabitatHR’ R package) throughout the season to accurately assess the area utilized by each bird. After approximately 15 location points were obtained for each bird (~ one week of hand tracking), I determined the core of all home ranges, and placed an Onset HOBO Temperature/Relative Humidity data logger at each core location point housed in a PVC casing to continuously monitor soil conditions at hourly intervals. I used HOBO logger measurements for each bird to identify individual-level differences in soil moisture for each Swainson’s Warbler. To assess vegetation characteristics of each home range, I randomly selected three known Swainson’s Warbler location points to assure the birds were utilizing the areas we sampled. At each of these locations I established a five-meter diameter vegetation plot, and measured ground cover (leaves, woody debris, no cover, etc.), canopy height, visual percentage of shrub cover, and canopy cover with a spherical densiometer. At a point five meters in each cardinal direction from the center, I measured leaf litter depth (mm), leaf composition (broad or narrow leaves), total saplings (<8cm DBH), herbaceous cover, and vertical woody density using the “Wiens pole” method.
(Wiens and Rotenberry 1981). The vegetation parameters measured were determined based on previous studies of Swainson’s Warblers foraging strategy and habitat preferences (Benson and Bednarz 2010, Gerwin and Peters 2005, Strong 2000). I extended the five meter plots to 11.2 meters and recorded the DBH of all canopy trees into four groups: 0 = 8-15cm DBH, 1 = 15-25cm DBH, 2 = 25-35cm DBH, 3 = 35-45cm DBH, 4 = >45cm DBH. Basal area was then calculated from these DBH measurements using the foresters constant equation: 0.005454 x DBH².

To evaluate available prey items, I collected leaf litter from one 1m squared area at the center of the three vegetation plots using a rapid assessment hand collecting method (Snyder et al. 2006). I laid down .5 inch diameter PVC pipe as a barrier to make sure I was collecting a consistent amount of leaf litter. To ensure no arthropods escaped, I pushed all leaves into a center pile exposing the soil layer to easily see any rogue individuals and quickly scooped all litter and arthropods into a plastic trash bag, standardizing my sampling time to under two minutes. Since HOBO loggers indicated a significant increase in soil temperature after 10:00, I collected all litter samples between 06:00 and 10:00 to decrease sampling bias. Each bag of leaf litter was frozen to kill all arthropods before sorting; I then sorted litter samples by hand (Olson, 1991), separated arthropods by taxonomic order and put them into 70% isopropyl alcohol and dried and weighed the remaining leaves. Arthropod samples were later counted and dried at ~80 degrees Celsius and weighed to the nearest 0.1 mg. I focused my arthropod collection on known prey items for the species (Savage 2010, Strong 2000), which made sorting the samples more time efficient.
To assess if a bird’s home range changed with a change in environment, I split the season into two periods representing dry (5 January-20 February) and wet (21 February-10 April) conditions. To analyze changes in vegetation and food in each bird’s home range in the wet period, I resampled vegetation and arthropods in March at the same locations using identical protocols as the dry period. By doing this, I was able to capture the changes specific to an individual’s original home range and assess their response in terms of home range shifts. Two new vegetation plots were also created in the wet period home range to assess any difference in habitat and arthropods between the birds’ original dry period and ‘new’ wet period home ranges. Lastly, I recorded daily rainfall events with rain gauges to track plot-wide seasonal changes in precipitation.

Statistical Analysis

Home Range Utilization

I calculated Swainson’s Warblers home ranges (n=21 individuals with both dry and wet period home ranges) with continuous time stochastic process models (CTSP; ‘ctmm’ R package; Calabrese 2016) to estimate autocorrelated kernel density estimates (AKDE) for each individual’s dry and wet period movements. Since traditional kernel density estimates assume independence and we now recognize all tracking data is largely autocorrelated (Fleming, 2015), I used CTSP models to implement a more robust analysis of home ranges. The ‘ctmm’ workflow allowed me to visually confirm if each bird exhibited constricted space-use behavior by plotting a variogram, which reaches an asymptote if the bird is a ‘range resident’. I visually diagnosed these variograms for each individuals’ dry and wet period home range, and calculated 42 home range estimations in
total. To fit the best movement model, I performed ctmm model selection via AICc for each individual, in which there are three appropriate models for home range estimate: IID – “independent identically distributed” process, or traditional KDE; OU – “Ornstein–Uhlenbeck” process; or OUF – “Ornstein–Uhlenbeck Foraging” process. Each model accommodates different autocorrelation structures in the location data, and I selected the appropriate movement model based on the behavior of the location data for each dry and wet period home range. I used the best-fit model to calculate home range size in hectares via AKDE (Calabrese 2016). To determine the distance each individual shifted spatially from dry to wet period, I calculated the distance in meters between centroids of the core (50% utilization distribution) of each home range. I also calculated the extent of overlap of birds’ dry and wet period home ranges as another proxy for shift by using the overlap function in ‘ctmm’ package. I identified the percentage of overlap in the early and late period AKDE distributions, 0 = no overlap and 100 = complete overlap.

Reduction of Habitat Variables

Due to the overall small sample size and large number of habitat variables, I reduced the number of variables using a Principal Component Analysis (PCA; ‘prcomp’ function in R). I transformed all vegetation variables into principal components and the first two primary principal components, accounting for 51% of variation in the data, were ultimately included in my models. The vegetation data were square root transformed and standardized before computing the PCA. I standardized the data and calculated the PCA through the correlation matrix because the units varied between each habitat variable. To determine the percentage of xeric and mesic habitat in each bird’s dry and wet period
home range, I used the ‘intersect’ tool in QGIS. I combined ecotone and mangrove habitat into the mesic category because they have similar habitat characteristics and arthropod dry mass; dry scrub was then categorized as xeric. I calculated the area of overlap in meters between spatial habitat vectors of previously determined habitat types (Powell unpublished data; mangrove, ecotone, and dry scrub) and the AKDE home range shapefiles I calculated with ‘ctmm’.

**Arthropods and Habitat Characteristics**

To determine the relationship between leaf litter arthropods and habitat characteristics during dry and wet periods I used a linear mixed effect model. This model included the fixed effects of habitat openness (PC2) and period (dry or wet) on arthropods and an interaction between habitat openness and period. Individual bird was included as the random intercept to account for repeated sampling in each individual’s home range. I also calculated the difference in mean arthropod dry mass between xeric and mesic habitats during dry and wet periods to determine which habitat supported the greatest abundance of food during different conditions. I used the arthropod dry mass of each leaf litter sample collected next to corresponding HOBO data loggers in each individuals home range to determine if the level of soil moisture in an area also had an effect on arthropod abundance. To accomplish this, I generated linear models of the effect of mean soil relative humidity (RH), mean coefficient of variation of soil RH, and daily minimum values of soil RH on the arthropod dry mass in a given area.

**Home Range Size Model**
I generated linear mixed effect models using the lmer function in R (‘lme4’ package; Zuur et al. 2009) to determine what environmental factors predict Swainson’s Warblers home range size. The fixed effects I evaluated in these “size” models were: mean relative humidity and coefficient of variation in daytime soil moisture, total arthropod dry mass, habitat PC1/PC2, and year. I included a random intercept for each individual to account for the resampling of home range characteristics in both dry and wet periods within both years.

Home Range Change Models

I produced linear models to determine if Swainson’s Warbler home ranges change in size and shift spatially with environmental change, and if so, what factors predict these changes. I determined linear models without individual random intercepts were most appropriate for these change models because only four of the 21 individuals were tracked in both 2016 and 2017, and these disproportionate repeat observations caused issues with the model fit when I generated mixed effect models. Also, including an individual random intercept did not seem appropriate as I expected within season home range dynamics to be dependent on environmental conditions, therefore independent between years. Since I predicted that Swainson’s Warblers would adjust their home ranges by changing size or shifting spatially, linear models were generated to analyze modifications of home range with the following response variables. 1) “spatial shift”: distance of spatial shift (meters) each individual demonstrated from the dry period to the wet period and 2) “size change”: percentage of home range area change in hectares from the dry to wet.
period, either a negative or positive percent value depending if the home range increased or decreased in size.

Swainson’s Warblers may have either responded to the condition of their dry period home range or to the change in environmental conditions into the wet period, both potentially promoting a change in home range structure. Therefore, in both the “spatial shift” and “size change” linear model sets I included habitat and food variables in two classes: 1) Only variables from the dry season to determine if poor or good conditions in original home ranges are driving birds to change their space use and 2) overall change in habitat and food from dry to wet period, calculated by subtracting wet variables from dry variables, to determine if certain changes to the environment are triggering a response in birds. The environmental variables included in these two model sets are: mean daily soil relative humidity (RH) and coefficient of variation (CV) in soil moisture, total arthropod dry mass, habitat PC1 or understory density and habitat PC2 or overall habitat openness, percentage of habitat type occupied (mesic or xeric), and year.

*Determination of Final Home Range Models*

Given the small sample size and need to maximize statistical power, I sought to limit the number of explanatory variables in all of my final models. Thus, final models for “size”, “size change”, and “spatial shift” were determined by analyzing relationships between my independent and dependent variables examined in a series of univariate, additive and interaction models to assess variable importance. I iteratively removed insignificant variables from each model set to ultimately determine the most important final model for each dependent variable.
The final “size” linear mixed effect model included habitat openness with an interaction with dry/wet period, since I wanted to determine if the relationship between home range size and habitat differed during dry and wet periods. As F-tests are not appropriate for assessing statistical significance in linear mixed models, I determined the significance of each variable in my “size” model with likelihood ratio tests (Zuur et al. 2009), iteratively removing variables and comparing them to the full model to test their effects. Habitat openness was then included in my “size change” linear model to identify if this factor predicts change in area from dry to wet period. The “spatial shift” linear model included percentage of habitat type (mesic vs xeric) in each dry period home range and year. In addition to these models, to confirm that the overall change in home range size and distance of home range shift from dry to wet period was significant, I calculated a mean model for both shift distance and the absolute change in home range size. The results from each of these final models are presented with ± standard error. To describe if birds are shifting into more optimum habitats during the wet period, I also compared the characteristics between individuals’ original dry period home ranges and the new areas birds utilized during the wet period.

Results

Seasonal Precipitation

More precipitation fell in 2017 (309.5 mm) than 2016 (205.0 mm), with 2017 having a larger difference in accumulation of rain from dry (27.5 mm) to wet period (282.0 mm) than 2016 (80.5 to 124.5 mm; Figure 2.1). The intensity of rain events was also greater in 2017, with all 282 mm of wet season rain falling in 8 events; the largest event
accumulated 70 mm on March 9. Comparatively, the frequency of wet season rain events was greater in 2016 where 124.5 mm fell in 14 rain events.

Home Range Utilization
All 21 Swainson’s Warblers tracked during dry and wet periods in both years occupied nonbreeding home ranges regardless of habitat. Home ranges are exhibited by the presence of an asymptote at longer lags in the variogram for each individual’s location data (Figure A.1). While all focal individuals occupied home ranges, it should be noted that six individuals equipped with transmitters were never detected following their release. Thus, these birds may have been transients.

Principal Components Analysis of Habitat Variables
The first two primary components explained 51% of the variation within the habitat variables. Principal component one (PC1) describes the level of understory density (28% variation explained) as shrub density, herbaceous cover, and total saplings loaded negatively, while canopy height loaded positively. Principal component two (PC2) describes overall habitat openness (23% variation explained) with canopy density, basal area, leaf litter depth, and canopy height loading negatively (Table 2.1, Figure 2.2). A higher PC1 score equates to a less dense understory; a higher PC2 score equates to a more open habitat with less leaf litter.

Arthropods and Habitat Characteristics
There was overall less arthropod dry mass in more open habitats (-0.436 ± 0.138 mg SE; $df = 1$, $\chi^2 = 7.87$, $p = 0.005$), in both dry and wet periods (wet: 0.253 ± 0.217 mg; $df = 1$, $\chi^2 = 1.33$, $p = 0.25$; Figure 2.3). The average dry mass of arthropods for mesic habitats
during the dry period was 20.18 mg (± 38.96 s.d.) and 16.91 mg (± 16.17 s.d.) in the wet period. In xeric habitats, the average arthropod dry mass during the dry period was 27.99 mg (± 32.90 s.d.) and increased to 42.08 mg (±71.13 s.d.) in the wet period (Figure 2.4). The level of soil moisture does not predict arthropod dry mass, and there was no relationship between arthropods and mean soil relative humidity (0.08 ± 2.46 mg; \( p = 0.97 \), \( R^2 = 0.0007 \)), mean soil coefficient of variation (-1.07 ± 2.92 mg; \( p = 0.72 \), \( R^2 = 0.007 \)), or mean daily minimum soil relative humidity (0.41 ± 1.21 mg; \( p = 0.74 \), \( R^2 = 0.006 \)).

Home Range Area
In both wet and dry periods, Swainson’s Warblers home ranges were larger in more open habitats. We observed that with every unit increase in PC2 (habitat openness) there is an average increase in home range area of 2.72 hectares (± 1.21 ha; \( df = 1, \chi^2 = 3.37, \ p = 0.02 \)), independent of period (\( df = 1, \chi^2 = 0.09, \ p = 0.76 \); Figure 2.5) There was also no additive effect of period on home range size (-0.76 ± 1.35 ha; \( df = 1, \chi^2 = 0.37, \ p = 0.54 \)).

Change in Home Range Size
Overall, the size of Swainson’s Warblers home ranges spanned from 2.4 – 23.6 ha and 1.9 – 16.8 ha in the dry and wet periods respectively, with an average decrease in size of 1.28 hectares (± 1.12 ha) in the wet period. Although there was an overall average decrease in home range size, variations in magnitude and direction of size change were evident. The average absolute change in size of home ranges between dry and wet periods was significant (3.93 ± 0.75 ha / \( p < .001 \)), with some birds decreasing their dry period home ranges up to 62% while others increased up to 170% into the wet period.
Because of this individual variation in the change in home range size, period is not a predictor for home range area (see *Home Range Area*). Habitat openness predicts the average home range size of individuals, but dry season habitat does not predict the change in home range size from dry to wet period (10.10% change in HR; $p = 0.55$, $R^2 = 0.02$). The overall large home ranges and disparity in size between individual Swainson’s Warblers are consistent with breeding home ranges (Anich et al. 2010).

**Spatial Shift of Home Range**

The individuals that shifted their core home ranges the farthest from dry to wet period utilized a higher percentage of mesic habitat when conditions were drier. On average, with every one percent increase in mesic habitat occupied during the dry period, Swainson’s Warblers core home ranges shift 2.08 meters ($\pm 0.54$ m; $p = 0.001$, $R^2 = 0.46$) in the wet period. We observe a clear difference in the average distance birds shifted home range and primary habitat type occupied in the dry period (Figure 2.6). Individuals utilizing mesic habitat during the dry period shifted their core home range on average 177.93 m more than birds utilizing xeric habitat ($\pm 31.86$ m; $p < .001$, $R^2 = 0.62$).

Although the overall mean home range shift distance was greater in 2017 (127.18m) than in 2016 (96.33m), year does not predict home range shift (2017: $48.9 \pm 33.57$ m; $p=0.16$, $R^2 = 0.46$). The home range shift for individuals was not just out of mesic areas, but also into denser habitats. Swainson’s Warblers with home ranges that shifted more than 150 meters, on average, shifted into areas with habitat pc scores that were 0.821 lower than their original home range. Birds who shifted less also experienced less of a change in habitat density; with the difference in habitat pc scores being only 0.04 lower.
Discussion

Determining if and how migratory birds can respond to seasonal fluctuations in precipitation and food can help us understand how they might cope with long-term drying trends or variability in precipitation regimes. In this study, I demonstrate the ability of a ground foraging Neotropical migratory bird to respond to seasonal changes in precipitation, habitat, and availability in resources through altered space use. In both wet and dry periods, Swainson’s Warblers occupied restricted home ranges that were smaller in habitats with dense trees, higher canopy and a thick leaf litter layer. These denser habitats also had a greater amount of leaf litter arthropods in both dry and wet periods. The size of individuals’ home ranges significantly differed between dry and wet periods, but I observed no effect of environmental characteristics on these changes. However, many individuals shifted their home ranges spatially out of potentially less favorable habitats as precipitation and food availability increased. These findings suggest that Swainson’s Warblers are cueing into habitat structure that promotes a greater abundance of arthropods and the size of their home ranges reflect this availability of food. Furthermore, individuals are exhibiting behavioral plasticity in habitat utilization by adjusting their home ranges, and appear to shift spatially to respond to changing resources.

A combination of environmental factors explains Swainson’s Warblers nonbreeding space use. I observed that more open areas are negatively associated with leaf litter arthropods and that habitat openness has the largest effect on the size of an
individual’s home range. These results suggest birds utilize structural cues to determine high-quality foraging sites. Although it is assumed that a primary factor influencing home range size is food, multiple studies have found a stronger link between structural habitat characteristics indicative of quality (i.e. prey availability) and home range size (Marshall and Cooper 2004, Vagras et al. 2011). For example, Marshall and Cooper (2004) observed that foliage density influences caterpillar abundance in temperate deciduous forests, and breeding Red-eyed Vireos *Vireo olivaceous* home ranges decrease in size in areas with denser foliage. They observed variable caterpillar abundance among trees species and habitat patches, and the authors concluded that foliage density was highly predictive of caterpillars during the nestling stage and birds are most likely cueing in on these characteristics because of this temporal relationship. In my study, increase in precipitation throughout the season influenced spatial and temporal variation in habitat structure and arthropod abundance, but the negative relationship between habitat openness and arthropod dry mass was consistent in both dry and wet periods. This supports Smith and Shugart’s (1987) idea that the relationship between habitat structure and arthropods is predictable, and most likely what drove evolution of habitat selection on the basis of structural cues in birds. Swainson’s Warblers are most likely selecting for denser habitats as they have recognized these areas support the highest average arthropod abundance. Moreover, even though food declines during the dry season, these dense habitats most likely remain of higher quality throughout these adverse periods, regardless of moisture content.
When conditions were dry, some Swainson’s Warblers made use of habitats that are typically marginal during wet seasons to compensate for limited prey. Individuals that occupied a higher percentage of mesic habitats during the dry period exhibited a greater spatial shift in home range when precipitation increased. Typically during the dry season, these mesic habitats become increasingly available to ground foraging birds as standing water recedes and leaf litter becomes accessible. As the field seasons progressed, I measured a 76% increase in precipitation on average from dry to wet period (Brunner unpublished data). Although this influx in moisture caused mangroves to partially flood, this primarily impacted deep pools and did not restrict the habitat edges Swainson’s Warblers utilized. Therefore, the shift out of mesic habitats was most likely influenced improving conditions in areas of dry scrub birds were shifting into. Xeric habitat exhibited an increase in arthropod dry mass during the wet period and had on average 65% more beetles and 47% more spiders (the main prey items for Swainson’s Warblers; Strong 2000) than mesic habitats, which did not experience a change in arthropods. These habitats therefore provide a more consistent availability of prey on average throughout the winter season. Dry-scrub with a denser canopy and thicker leaf litter is also higher quality for ground foragers than dry-scrub with a more open structure. Deeper leaf litter provides a protective environment for arthropods longer during drought conditions (Leving and Windsor 1982, Strong 2000), buffering these areas from a depletion of food. We observed individuals that occupied habitats which experienced little structural change from dry to wet period shift less, supporting the concept of structural-cues as these areas most likely maintained an overall dense structure throughout the dry season.
In contrast to other wintering migratory songbird studies (Brown and Long 2007, Brown and Sherry 2008, Cooper et al. 2015), I found that as environmental conditions change, birds shift spatially while maintaining restricted home ranges and/or adjusting home range size. As I predicted, Swainson’s Warblers altered the size of their home range as precipitation increased throughout the season, but I observed substantial variation in the direction of change between individuals. This is most likely due to some birds taking advantage of the opportunity to perform a spatial shift into new areas and not attempt to expand home range size simultaneously. Therefore, the changes I observed in Swainson’s Warblers home range size might be related to individuals utilizing multiple strategies to adjust their space use. Individuals that shift might be focusing efforts on searching for prey in different habitats, as some birds shift while maintaining the size of their home range, and others shift while exhibiting a size change.

These observations provide evidence that there are multiple ways Swainson’s Warblers adjust their space use, and individuals either alter 1) the size, 2) the location or 3) both the size and location of their home range. In contrast to these findings, studies where prey was experimentally reduced found no changes in home ranges. For example, two ground foraging species, Ovenbirds *Seiurus aurocapillus* and Hermit thrushes *Catharus guttatus*, birds did not expand home ranges to compensate for declining food (Brown and Long 2006, Brown and Sherry 2008). American Redstarts *Setophaga ruticilla* also did not display any flexibility in their home range size, but some individuals became transients with experimental prey reduction (Cooper et al. 2015). The authors determined that these observations are most likely because of social constraints in these
particular populations, dynamics that might not be present in our study species.
Populations of birds that are highly territorial are limited by the energetic demands of defending resources, and expanding or shifting territories could increase agonistic encounters, making these movements energetically costly (e.g. Brown and Long 2006, Cooper et al. 2015). We observed Swainson’s Warblers having overall large home ranges (1.9 to 23.7 hectares) that overlapped substantially with conspecifics. We could presume these birds may not be territorial, but since we did not study territoriality we cannot speak to these dynamics directly. In fact, many Swainson’s Warblers responded aggressively to conspecific playback (Brunner personal observation), which may be evidence to suggest they are potentially defending a core area of their home ranges similar to wintering Ovenbirds (Brown and Sherry 2008).

Social consequences may also be observed in different habitats with contrasting levels of quality, or prey availability. Strong and Sherry (2001) determined that in Jamaica, dry second growth scrub is of lesser quality for Swainson’s Warblers than other habitats, such as dry limestone forest. Food availability drives distributions of overwintering warblers spatially and temporally throughout different habitats (Johnson and Sherry 2001), thus, we expect individuals experience variable conspecific density depending on the wintering site they occupy (e.g. Marra et al. 2015). Our study site consisted of second-growth scrub and adjacent mesic habitats, thus greater conspecific density in other nonbreeding habitats may alter some of the observed relationships we observed. We might expect a greater density of birds in higher quality habitats and if the conditions in those habitats deteriorate with increased drying, competition between
conspecifics might increase. Therefore, the flexibility in space use Swainson’s Warblers exhibited in our study may be minimized in higher density populations.

Precipitation is a major driver of overall food availability for overwintering Neotropical migrants (e.g. Smith et al. 2010, Studds and Marra 2011). Therefore, we would expect Swainson’s Warblers food (leaf litter arthropod) abundance to be positively correlated with soil moisture and have a negative relationship with home range size. However, we did not find any effect of soil moisture characteristics on home range size, and a high level of soil moisture does not seem to necessarily predict high leaf litter arthropod abundance. On average, arthropod dry mass increases in dry scrub during wet periods even though mesic habitats have higher levels of soil moisture, thus the level of moisture may not be a determinant of habitat quality for Swainson’s Warblers. This is contrary to research conducted by Smith et al. 2010 on another ground foraging warbler, the Northern Waterthrush *Parkesia noveboracensis*, where they determined wetter habitats have a higher leaf litter food abundance. In American Redstarts *Setophaga Ruticilla* this difference in habitat quality impacts correlates of fitness, and birds utilizing mangroves are in better condition and depart earlier for spring migration (Marra and Holberton 1998, Studds and Marra 2005, 2007). Our results show that arthropod abundance is greater with a dense canopy and thick leaf litter. Thus, these habitat characteristics appear to be the most important factors in sustaining leaf litter arthropods, as opposed to moisture. However, it is possible we did not detect an effect of soil moisture due to high spatial variability in moisture levels across the landscape, and
moisture may influence arthropods in habitat patches. These nuances may be difficult to detect without more intensive monitoring throughout the study area.

Increasingly unstable or unpredictable winter conditions may impact migratory birds not only during the nonbreeding season, but throughout their entire annual cycle (Sillett et al. 2000, Rushing et al. 2016, Woodworth et al. 2017). Because of these seasonal interactions it, studying winter ecology and the response to climate change in the Caribbean is increasingly important. Winter food availability impacts individual body condition (Marra and Holberton 1998, Latta and Faaborg 2002, Studds and Marra 2005, Brown and Sherry 2006, Smith et al. 2010, Angelier et al. 2011, Cooper et al. 2015) and birds in compromised condition have been observed departing later for spring migration (e.g. Studds and Marra 2005, 2007, 2011, Cooper et al. 2015). This delay in departure impacts arrival date on the breeding grounds (Saino et al. 2004, Balbontin et al. 2009), and subsequent breeding success (Norris et al. 2004, Reudink et al. 2009). These negative consequences on fitness can potentially influence an individual through multiple stages of its life cycle (Sillett et al. 2000). In order to persist, birds must respond behaviorally as precipitation becoming more variable in the tropics. My results demonstrate the potential some vulnerable birds may have to actively adjust their space use in response to changing conditions. This study also directly demonstrated how annual precipitation is becoming more variable and unpredictable because we observed the complete reverse trend in seasonal rainfall. This uncharacteristic increase in precipitation is not typically what migratory birds experience during their pre-migratory period. My study took advantage
of this pattern to help determine how fast birds may respond to these unpredictable changes in precipitation and resources.

Overall, additional studies are needed to determine if these shifting home ranges allowed individuals to maintain their phenological schedules (e.g. migratory departure timing) and body condition throughout the season. This information will allow for us to better understand if these responses are truly beneficial to individual nonbreeding fitness. Because we know very little about how food availability impacts most nonbreeding migratory bird species, it is critical to focus extensively on how species utilizing habitats of varying quality, in low and high density populations, respond to seasonal changes in resources. These responses will benefit the populations only if environmental conditions do not shift faster than the rate birds’ can feasibly respond. Habitat loss may also inhibit the extent species can shift their space use and range distributions, so preserving habitats for both resident and migratory birds will be crucial as the climate continues to change.

Our results provide valuable evidence of the variable space use strategies that overwintering migratory birds can exhibit in response to fluctuating resources. Our findings support the idea that some migratory birds possess the behavioral plasticity in habitat use to adjust space use strategies as seasonal environmental conditions change. Further, we found that individuals can track spatial and temporal changes in food availability while altering the structure of, but maintaining, their home ranges. By examining the behavioral plasticity of wintering migrants to track seasonal environmental change, we can better predict the implications of long-term environmental change for future populations.
Table 2.1- Principal Component Analysis factor loadings and summary for all habitat characteristics in each individual’s home range.

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
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<tr>
<td>Standard deviation</td>
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<td>1.2689</td>
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<tr>
<td>Proportion of Variance</td>
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<td>Cumulative Proportion</td>
<td>0.2802</td>
<td>0.5102</td>
<td>0.6452</td>
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**Factor Loadings**

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<th>Habitat Characteristic</th>
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<th>PC2</th>
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<tr>
<td>Litter Depth</td>
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<td>-0.4671175</td>
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<td>Canopy Density</td>
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<td>Canopy Height</td>
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<td>Herbaceous Cover</td>
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<td>Basal Area</td>
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<td>Saplings</td>
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<td>-0.2005535</td>
<td>-0.04253249</td>
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Figure 2.1: The difference in total accumulated precipitation between the dry (early) and wet (late) periods and across years (2016 and 2017) at Font Hill Nature Preserve, Jamaica, W.I. More precipitation fell in 2017 (309.5 mm) than 2016 (205.0 mm), with 2017 having a larger difference in accumulation of rain from dry (27.5 mm) to wet period (282.0 mm) than 2016 (80.5 to 124.5 mm).
Figure 2.2: Principal Component Analysis loadings for the habitat characteristics measured in each individual Swainson’s Warblers dry and wet period home range during the winter of 2016 and 2017 in Jamaica, W.I. Vegetation characteristics include: shrub density, saplings, herbaceous cover, leaf litter depth, canopy density, canopy height, and basal area. A higher PC1 score equates to a less dense understory; a higher PC2 score equates to a more open habitat with less leaf litter.
Figure 2.3: The relationship between habitat openness and amount of log arthropod dry mass in mesic and xeric habitats in Font Hill Nature Preserve, Jamaica, W.I. during both wet and dry periods in 2016 and 2017. There was overall less arthropod dry mass in more open habitats (-0.436 ± 0.138 mg; \( df = 1, \chi^2 = 7.87, p = 0.005 \)), in both dry and wet periods (wet: 0.253 ± 0.217 mg; \( df = 1, \chi^2 = 1.33, p = 0.25 \)).
Figure 2.4: The difference in arthropod dry mass between mesic and xeric habitats in the dry period versus the wet period in both 2016 and 2017. Vertical error bars represent the standard error of each sample. The average dry mass of arthropods for mesic habitats during the dry period was 20.18 mg and 16.91 mg in the wet period. In xeric habitats, the average arthropod dry mass during the dry period was 27.99 mg and increased to 42.08 mg in the wet period.
Figure 2.5: The relationship between habitat openness and Swainson’s Warblers home range size in both dry and wet periods during the nonbreeding season of 2016 and 2017 in Jamaica, W.I. With every unit increase in habitat openness there is an average increase in home range area of 2.72 hectares (± 1.21 ha; df = 1, $\chi^2 = 3.37, p=0.02$), independent of period (late: df = 1, $\chi^2 = 0.09, p = 0.76$).
Figure 2.6: The difference in the average distance individuals shifted core home ranges between mesic and xeric habitat types. Individuals utilizing mesic habitat during the dry period shifted their core home range on average 177.93 m more than birds utilizing xeric habitat (±31.86 m; \( p < .001 \), \( R^2 = 0.62 \)).
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Appendix A: Supplementary Materials

Figure A.1: Location of the study site, Font Hill Nature Reserve, on the coast of southwest Jamaica, West Indies.
Figure A.2: Autocorrelated kernel density utilization distributions for all individual Swainson’s Warblers tracked during 2016 and 2017 field seasons.
Figure A3: Variograms generated to determine if each individual Swainson’s Warbler occupied a bounded home range in both the dry and wet period. Range residents are determined by the presence of an asymptote in each variogram.
Figure A.3 continued
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Figure A.3 continued
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<td>10.86 ha</td>
<td>8.25 ha</td>
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Figure A.3 continued
Figure A.3 continued
Figure A.4: Demonstration of different space use strategies in response to changing environmental conditions. Swainson’s Warblers can adjust 1) size, 2) location or 3) size and location of their home ranges from dry to wet period. Individuals utilizing a greater percentage of mesic habitat in the dry period shifted further into the wet period.