

April 2021

Factors Influencing Stopover and Movement of Migratory Songbirds within the Silvio O. Conte National Fish and Wildlife Refuge

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**FACTORS INFLUENCING STOPOVER AND MOVEMENT OF MIGRATORY
SONGBIRDS WITHIN THE SILVIO O. CONTE NATIONAL FISH AND
WILDLIFE REFUGE**

A Thesis Presented

by

JESSICA M. TATTEN

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

MASTER OF SCIENCE

February 2021

Environmental Conservation

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ACKNOWLEDGEMENTS

I'd first like to thank my advisor, Dr. David King, for giving me the opportunity to take on this project and giving me the reassurance, support, and never-ending patience while I learned the ins and outs of this new technology. I'd also like to thank my committee members, Dr. Alex Gerson, for support with logistics regarding Motus, as well as project guidance, and Dr. Curtice Griffin for help getting this project off the ground in its initial stages. I would like to thank the field crew members, Kaya Baker, Cheryl Henke, Gillian Baird, and anyone who volunteered to come out and set up telemetry towers and help with banding when I was in need. I would also like to express my great appreciation for Aaron Hulse, who got this project up and running, and did most of the initial heavy lifting for this project, literally and figuratively. Jenny Smetzer and Zara Dowling helped teach me about this new technology and helped me along the way whenever needed, and I am grateful for the opportunity to work with you both.

I would like to thank U.S. Fish and Wildlife Service for funding this project, and seeing the potential knowledge we would gain from investing in Motus Wildlife Tracking Systems. I am also grateful for all of the collaborators who allowed us to host a tower on their properties, both public and private, such as MA D.C.R., MA Audubon Society, U.S. Fish and Wildlife Service, N.H. Department of Resources and Economic Development, Dave Hatton, and numerous others for their coordination with this project.

I would also like to thank my friends and family for keeping me sane throughout this process and being there to support my mental health when I was in need from a break from school. I'd like to thank my husband for believing in me when I didn't, and

providing support in every way, by cleaning, cooking, and tending to our dog, Porter, while I worked vigorously to finish up. I am forever grateful.

ABSTRACT

FACTORS INFLUENCING STOPOVER AND MOVEMENT OF MIGRATORY SONGBIRDS WITHIN THE SILVIO O. CONTE NATIONAL FISH AND WILDLIFE REFUGE

FEBRUARY 2021

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Most migrating songbirds are required to stopover to rest and replenish their fat reserves, and suitable stopover habitat is vitally important to their survival and success securing territories at their breeding and wintering grounds. Identifying and protecting stopover locations and movement corridors is essential to connecting all life stages of these species, yet there remain significant knowledge gaps regarding the utilization of stopover sites and fine-scale movements during migration, particularly at inland stopover areas. We investigated the factors that influence stopover duration and migration rate of ten migratory songbirds within the Silvio O. Conte National Fish and Wildlife Refuge in the Northeastern United States during two fall and spring seasons in 2015 and 2016 at 5 banding sites using automated telemetry. We expected that fat and mass would influence stopover duration and migration rate, in that birds with larger fat stores and greater masses would make shorter stopovers, and migrate faster than leaner birds. We also expected that birds would move faster in spring, and minimize time later in the season, by making shorter stopovers and migrating faster as the season progresses. A lower percentage of our focal species departed the banding sites within 24 hours compared to

other studies in coastal and urban sites, indicating that more birds made stopovers. Sixteen percent of birds made prolonged stopovers (> 7 days) in spring, and 38 % in fall, highlighting the importance of the refuge for long term refueling. Spring birds made shorter stopovers, and traveled at faster rates than fall birds, suggesting there is may be more pressure for early arrival at breeding grounds. Spring birds captured with significant fat loads made shorter stopovers, and traveled faster than leaner birds. Spring birds also appeared to employ a time minimization strategy, with birds captured later in the season making shorter stopovers. Migration rate of spring birds decreased with distance from the capture site, indicating many birds needed to make additional stopovers. Fall birds that made longer stopovers migrated at faster rates. Fall birds captured later in the season made longer stopovers, and subsequently traveled at faster rates once they departed to possibly minimize time on migration. Variation in stopover behavior was evident among sites and species and this may suggest habitat or site characteristics that affect their value for migrating birds, which should be taken into consideration when conservation planning or vulnerable species. The extensive use of this inland National fish and wildlife refuge by migratory birds, and the fact that birds are acquiring energy reserves that are facilitating successful migration suggests this region is an important corridor for migrating songbirds.

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CHAPTER 1

THE STUDY OF MIGRATION

1.1 Introduction

Songbird migration occurs twice annually as birds travel between breeding and wintering grounds. The migratory period is composed of two parts: stopover, and movement. A stopover can be defined as a period of time when birds pause migration at a location to rest, refuel for the next leg of their journey, or wait out bad weather (Smith and McWilliams 2009), and the majority of their time and energy spent on migration occurs during stopover as birds accumulate fat and energy stores (Hedenstrom and Alerstam, 1997, Wikelski et al. 2003, Bowlin et al. 2005, Seewagen et al. 2010).

Movement occurs as birds travel between stopover bouts, ultimately to reach either their breeding or overwintering grounds. Migration is often considered one of the riskiest parts of their annual life cycle, and the conditions birds experience on migration, such as resource availability, competition and predation, and weather, carry-over to affect their success at other life stages (Norris and Taylor 2006, Fischer et al. 2015, Moore 2018).

Migration is studied in order to connect all life stages of these species and better understand and meet their needs for habitat requirements year-round, however the migratory period remains of the more poorly understood life stages of birds (Faaborg et al. 2010), as its more difficult to record data on their movements and behaviors during migration. Therefore, identifying and protecting prime stopover habitat and migratory corridors along migration routes is essential to developing conservation strategies at a

time when migratory bird populations are declining at alarming rates due to habitat loss from both natural and anthropogenic causes (Rosenberg et al. 2019).

The recent development of automated tracking technologies with transmitters small enough to monitor small songbirds is one way to elucidate these questions. The Motus Wildlife Tracking System (Motus; <https://motus.org>) has been developed as a technology that allows researchers to work in combination to track small birds all over the world by way of automated radio telemetry tracking stations (Taylor et al. 2017). This technology allows for efficient, continuous data collection using a single radio frequency in which all birds fitted with transmitters (nano-tags) from any project may be detected if they are near a receiving station. The data acquired from these receivers allows researchers to collect both large and fine scale movement and stopover data to get a better look at broad scale movements as birds travel between their breeding to wintering grounds (Imlay et al. 2020, Cooper and Marra 2020), as well as local habitat use, and arrival and departure at stopover sites (Gomez et al. 2017, Bayly et al. 2018, Smetzer and King 2018, Wright et al. 2018).

1.2 Stopover

Migratory songbirds select sites for stopover that provide high quality resources for efficient refueling, in order to minimize time spent stopped over (Ktitorov et al. 2010, Woodworth et al. 2014, Gomez et al. 2017), and have shown to spend less time at low quality sites (Craves 2009, Ktitorov et al. 2010). Studies have also shown that songbirds make prolonged stopovers, exceeding the time previously thought necessary to refuel, and these sites chosen for long stopovers may provide high quality resources during migration (Gallo et al. 2013, Bayly et al. 2018, Smetzer and King 2018, Wright et al.

2018). Habitat preferences may vary seasonally, as research has found migrants utilize shrubland habitats with ample fruiting shrub species in fall (Suthers et al. 2000, Rodewald and Brittingham 2004, Mudrzynski and Norment 2013), while other studies found that forest nesters used edge-dominated mature forest (Rodewald and Brittingham 2007), and associated with hardwood forest cover (Cohen et al. 2014b) in spring for foraging. Therefore, to better protect vulnerable migratory animals, understanding their habitat preferences and factors limiting populations at multiple scales and seasons is essential.

The amount of subcutaneous fat a migrant songbird has accrued at stopover is thought to be one of the main determinants of stopover duration, as lean birds often make significantly longer stopovers than birds with higher fat scores, in order to refuel sufficiently to continue on with their migration (Goymann et al 2010, Deppe et al. 2015). Since it is advantageous for migrant songbirds to refuel quickly and efficiently, choosing high quality stopover sites is essential. The inability to accumulate fat at a stopover site may have serious fitness consequences, and impact their ability to arrive at their breeding grounds in good condition to defend territories and breed in spring (Dossman et al. 2018). Identifying key stopover sites that migratory birds use for refueling is vital, considering how impactful a single stopover site may be to their subsequent migration (Gomez et al. 2017).

Seasonal changes in stopover duration are evident, in that spring migration is often faster, with shorter stopover bouts, than fall, due to increased pressure to arrive at breeding areas to secure territories in a competitive manor (Morris et al. 1994, Marra et al. 2005, Stutchbury et al. 2009, Nilsson et al. 2013, Bennett et al. 2019). Within one

migratory season, distance to ultimate destination may also influence stopover duration. Paxton and Moore (2017) found that black and white warblers stopping over closer to their breeding grounds stayed significantly longer than those further from their destination in spring, possibly to increase their fuel stores to ensure they arrive at their breeding grounds in good condition. Along with seasonal changes in stopover, weather is also a factor that determines how long a bird stays at stopover. A bird may prolong its stopover in order to wait for the arrival of better wind conditions (Deppe et al. 2015), while another study found that long-distance migrants are less selective to local weather conditions upon departure of stopover (Packmor et al. 2020).

The duration a bird spends at stopover has also shown to vary depending on age, sex, and time of year. Hatch year birds have been observed making longer stopovers than older birds of the same species, possibly due to competition, or lack of experience navigating barriers, hence prolonging stopover (Morris et al. 1994, Yong et al. 1998, Filiberti and Perlut 2018). Birds captured later in the season at stopover sites often make shorter stops, and have a higher probability of departure in order to arrive at their destinations at the same time as earlier conspecifics (Paxton and Moore 2017, Packmor et al. 2020). Differences among sexes have also been observed, as males may migrate through a stopover area earlier than females, departed sooner, and may refuel more quickly (Yong et al. 1998, Seewagen et al. 2013). Many selection pressures, both seasonally and temporally, influence the site selection and duration of stopovers, and the continued study of migration will help fill in existing knowledge gaps, and studying the habitat requirements and preferences of songbirds during migration is key to better meeting their needs at such an influential time in their life cycle.

1.3 Migration

Neotropical migrant songbirds travel thousands of kilometers to reach their destinations each fall and spring, and threats encountered during this life stage may be responsible for steep declines of many migratory species (Newton 2006, Norris and Taylor 2006). Their route choice and rate of travel are influenced by many factors, such as departure fuel loads at stopovers (Gomez et al. 2017), distance to ultimate destination (Schmaljohann 2019), and time of year (Briedis et al 2018), that were unable to be studied in detail until the recent development of new tracking technologies. Researchers are now better able to connect the full life cycle of migratory birds and fill in knowledge gaps regarding where they go once they depart their breeding and wintering habitats to help protect prominent migratory corridors.

Birds may rely on coast lines, river valleys (Cerasale and Guglielmo 2010, Cormier et al. 2013, Kirsch et al. 2013, Fischer et al. 2015, Darrah et al. 2017) and mountain ranges (Williams et al. 2001) as corridors for navigation and refueling during migration, therefore studying stopover dynamics in a range of landscapes is important. Migrants stopped over at coastal areas have been observed relocating further inland upon initial landing in search of habitats with less competition and predation, compared to coastal landscapes, which may result in better refueling and body condition than birds captured on the coast (Akesson 1999, Smolinsky et al. 2013, Woodworth et al. 2014, Smetzer et al. 2017, Hoh et al. 2018). While the majority of energy is expended during stopover, birds may encounter many obstacles while in flight, such as increased risk of offshore and coastal wind developments and platforms (Hüppop et al. 2016, Smetzer et al. 2017, Wright et al 2018), light pollution (Poot et al. 2008, Canário et al. 2012), and

studying previously unknown migration routes will help to identify these potential threats.

Migration strategies can be studied in order to better meet the needs of species at risk, and help to understand what stopover sites may be most influential to their migration as a whole. The majority of migrants behave as time-minimizers, and carry large fuel loads, often traveling at exceedingly fast paces over long distances, while others minimize energy by making more stopovers, and carrying smaller fuel loads (Hedenstrom and Alerstam 1997, Alerstam 2011, Gomez et al. 2017, Schmaljohann 2018) and taking longer to complete their migration (McCabe et al. 2018). Gomez et al. (2017) used automated telemetry to investigate the migration strategy of a lesser studied species in this regard, the Grey-cheeked thrush (*Catharus minimus*), in Columbia, and found that they behave as time-minimizers, indicated by birds refueling at high rates quickly before departure at stopover.

Migration rate and routes taken each spring and fall may vary within and among seasons. Briedis et al. (2018) found that migrants speed up as they approach their ultimate destinations, as a possible time minimizing strategy. Individuals with shorter total migration distances have been shown to travel at a slower pace than those with more ground to cover (Schmaljohann 2019). Some migrants may also change their route seasonally, by completing a loop migration, in which they may take a more coastal migration route one season, and an overwater route the next (Stutchbury et al. 2009, Alerstam 2011, Stanley et al. 2012, Deluca et al. 2015, Bennett et al. 2019). Wind and weather may also have an effect on the speed at which migrants travel. Sjoberg et al.

(2015) found that the influence of unfavorable winds prolonged flight times of free flying songbirds undertaking a sea crossing.

1.4 Conclusion

The continued study of migration, both in flight, and at stopover, is pertinent to the survival of declining migratory songbird species. The variation among movement and stopover behaviors that has been presented by researchers will help to prioritize and focus research efforts where they are most needed. The ability to adopt and use new technologies will help uncover previously unknown migration corridors as well as vitally influential stopover areas. There is still much to learn about migratory species, and with continued research, we are able to better understand how differing migratory strategies, stopover sites, age groups, sexes, and different populations are utilizing both fine and large-scale habitats in fall and spring. Identifying and protecting key stopover sites and identifying risks along well used migration routes is an essential step in protecting these species, and using advanced tracking technologies is one way to fill in these gaps.

CHAPTER 2

FACTORS THAT INFLUENCE MIGRATORY SONGBIRD STOPOVER WITHIN THE SILVIO O. CONTE NATIONAL FISH AND WILDLIFE REFUGE

2.1 Introduction

Songbird migration is a physiologically taxing process that requires birds to pause migration and make stops to rest, refuel, and replenish depleted fat stores along their route (Smith and McWilliams 2009). The majority of the energy expended by a migrant songbird occurs not in flight, but while at stopover, as they look for suitable foraging habitats and accumulate fat stores (Wikelski et al. 2003, Bowlin et al. 2005, Seewagen et al. 2010). Understanding habitat site selection during stopover and identifying areas of high quality is a crucial step in protecting migratory birds, as they are faced with many stressors in our ever-changing environment such as habitat fragmentation, and overall loss of habitat due to urbanization along prominent migratory routes (Litwin and Lloyd-Evans 2006, Seewagen et al. 2010, Rosenberg et al. 2019).

Upon arrival of a stopover location, songbirds make assessments about the quality of the site using factors including food abundance, competition, and predation risk (Lindstrom and Alerstam 1992a, Seewagen et al. 2010). They must choose their stopover locations efficiently to maximize the amount of energy they consume by refueling in order to get to their breeding and wintering grounds quickly (Ktitorov et al. 2010). Refueling efficiently at high quality sites is a top priority for migrating birds, and these influential decisions can shape the overall outcome of their migration and affect reproductive success (Woodworth et al. 2014, Gomez et al. 2017). Success accumulating

fat stores at stopover has shown to have a direct influence and carry over effect into the breeding season (Woodworth et al. 2014), as well as the pace at which birds can travel in order to decrease time spent at stopover (Duijns et al. 2017, Gomez et al. 2017). Migrant songbirds in need of refueling resources may also depart more quickly, and spend less time in low quality sites, and make longer stopovers in higher quality ones (Craves 2009, Ktitorov et al. 2010). Recent research has found that songbirds make prolonged stopovers of 7 days or longer, a behavior previously documented in shorebirds before or after making flights over water or other ecological barriers, and is thought to surpass the time needed to refuel (Callo et al. 2013, Bayly et al. 2018, Smetzer and King 2018, Wright et al. 2018). Understanding why migratory songbirds exhibit this behavior and where exactly they are making these extended stays will shed some light on how to better protect them throughout their full annual life cycle. Some studies state these prolonged stopovers occur as migrants use these sites to congregate in large groups before or after making large over water/over barrier flights to sufficiently rest and refuel (Callo et al. 2013, Bayly et al. 2018, Smetzer and King 2018).

Migratory decisions can be influenced by many factors, such as sex, species, time of season, weather, food availability, predators, fat, etc. (Deppe et al. 2015, Smetzer et al. 2017). Temporally, birds have been shown to make shorter stopovers later in the season, in order to arrive at their breeding grounds to secure territories (Paxton and Moore 2017). Birds with larger fuel stores spend less time on stopover, per the time minimization hypothesis, which states that there is a tradeoff between refueling and getting to their ultimate destinations in an efficient manner (Lindstrom and Alerstam 1992a, Goymann et al. 2010, Deppe et al. 2015), and strategies also differ between species. Blackpoll

Warblers (*Setophaga striata*), for example, are long-distance migrants that may make fewer, longer stops in order to refuel, whereas Red-Eyed Vireos (*Vireo olivaceus*) make shorter, smaller stops more frequently (Smetzer and King, 2018).

Age and sex specific differences in songbird stopover have also been reported in that hatch-year (HY) birds have known to be out-competed by older, more established birds with regards to acquiring resources, and often make longer stopovers than older birds (Morris et al. 1994, Yong et al. 1998, Filiberti and Perlut 2018), and sometimes having lower overall body conditions than older individuals (McCabe et al. 2019). Hatch year birds have been shown to avoid barriers during initial stages of migration either because they are unfamiliar with the area, or that they decide the flights over water are not worth the risk (Brown and Taylor 2015). Stopover behavior among sexes is variable in that it differs among sites and seasons for many studies, but some have found males refuel more quickly and depart stopover sites sooner than females in order to secure territories (Yong et al. 1998, Seewagen et al. 2013). Uncovering patterns of variability in stopover behaviors within age and sex classes is informative and these habitat requirements and needs during migration are essential to include in management plans moving forward to ensure successful breeding seasons.

Many studies of stopover and migration take place at barriers such as coast lines (Covino and Holberton 2011, Deppe et al. 2015, Smetzer et al. 2017), lake shores (Goymann et al. 2010, Taylor et al. 2011, Smetzer et al. 2017, Filiberti and Perlut 2018) or urban matrices (Seewagen et al. 2010, Matthews and Rodewald 2010). These areas are characterized by concentrated populations of birds as they fuel and rest before or after

potentially migrating across a barrier, such as a large water body (Woodworth et al. 2014). Depending on the habitat and food resources in these areas, there may be intense pressure and competition for said resources, as well as increased predation with a large number of birds in one area (Hoh et al. 2018). In contrast, inland stopover sites may potentially serve migrants better due to decreased predation risk, better quality habitats for more efficient refueling, and lower mortality rates during an already trying time in their life cycles (Woodworth et al. 2014, Hoh et al. 2018), and remain understudied (Rush et al. 2014). Many coastal stopover studies near waterbodies often observe a subset of birds that move further inland before continuing their migration in search of these less congested stopover sites with potentially better foraging habitats with less competition (Akesson 1999, Smolinsky et al. 2013, Woodworth et al. 2014, Smetzer et al. 2017). It has been also observed that birds utilizing inland stopover habitats have exhibited overall better body condition when compared to a coastal site (Hoh et al. 2018).

Although migrating birds at inland sites are less concentrated than at coastal sites, they may still concentrate their movements or activities in relation to geographic features like mountain ranges (Williams et al. 2001) or river valleys (Cerasale and Guglielmo 2010, Cormier et al. 2013, Kirsch et al. 2013, Darrah et al. 2017). River valleys and mountain ranges provide birds with navigational aids to account for wind drift during migration (Akesson 1993), as well as sources of high-quality areas for refueling such as riparian or floodplain habitats surrounded by urban or arid regions lacking in food resources (Litwin and Lloyd-Evans 2006, Cerasale and Guglielmo 2010, Schoenberg and Randhir 2010, Kirsch et al. 2013, Darrah et al. 2017). Broad scale movements and stopovers within river valleys have been relatively understudied, and identifying key

patterns and factors that may drive these patterns may help shed light on previously unknown portions of this vitally important life stage of migratory songbirds.

The Connecticut River watershed is a potentially important inland migratory corridor, providing migratory songbirds with habitat for resting and refueling. The Silvio O. Conte National Fish and Wildlife Refuge encompasses the entire Connecticut river watershed, and protects over 36,000 acres of land within it (fws.gov). Past research has found that migrant songbirds concentrate at the mouth of the river on the southern end of the refuge, and that they used sites closest to the river most often (Litwin and Lloyd-Evans 2006). This study in the mid 1990's illustrated that migrants concentrate within this particular watershed during spring and that it could be an important resource for these birds due to plant phenology, and thus the abundance of insect prey, among other factors. This study was able to collect data to understand the usage of the watershed, but knowledge gaps remain with regards to site selection during stopover, as well as the factors that may influence their behaviors, and how they may vary.

Given the uncertainty that still remains in inland stopover and migration research, as well as the variability in behaviors found in birds during migration, this study hopes to gain a broad landscape level understanding of the decisions made by songbirds within a large tract of protected land. This study investigates the factors that influence the stopover duration of 10 migratory songbirds for 2 years at 5 inland stopover sites in the northeastern United States using automated VHF telemetry. The objectives of this study are to evaluate habitat quality of inland stopover sites by relating minimum stopover duration to fat upon capture, day of capture, banding site, age, sex, and species, which may elucidate previously unknown migration strategies for some species. We aim to

identify potentially important stopover sites and discuss these findings relative to the conservation of these migratory songbirds in an inland migratory corridor.

We expect that stopover duration will decrease as the season progresses given that there is a tradeoff between refueling and getting to their ultimate destinations to defend territories. We predict that stopover duration will have a negative relationship with body condition as indicated by fat and mass because fatter birds will need to spend less time refueling at sites if weather is sufficient for departure. We also expect that stopover duration will vary by site, and that sites with many prolonged stopover bouts may be prioritized as key candidates for conservation since it has been shown that birds spend less time in lower quality habitats (Ktitorov et al, 2010). There may be differences among species and ages as well due to the fact that they can differ in migration strategies as previously mentioned. We expect that hatch year birds will make longer stopovers due to inexperience and competition. The results of these analyses should also elucidate key stopover areas within the Conte National Fish and Wildlife Refuge, as well as what drives stopover behavior in this area in order to better understand and protect essential habitat needed by migrant songbirds during this vulnerable time in their annual life cycle.

2.2 Methods

2.2.1 Study Area and Telemetry

Twelve automated telemetry receivers were deployed along a 160 km segment of the Connecticut River Valley between the Fannie Stebbins unit of the Conte NFWR in Massachusetts and Mount Ascutney in Central Vermont (Fig. 1). Receivers were mounted on promontories (3), fire towers (3) and 10-meter-tall extendible steel masts (6)

in a mix of open fields and forest openings to elevate receiving antennas above the level of trees and surrounding hills to the extent possible. The first year of the study (2015), 8 receivers were erected within the study area, and in the second year in 2016, 4 more were added to expand the length of the array. We used a combination of Sensorgnome and Lotek SRX 800 receivers (Lotek Wireless, Newmarket, Ontario), anticipating minimum detection distances of 15 km (Taylor et al. 2017), however, a recent study has shown that given the topography, vegetation density, and foraging guild of the target species, the detection distance may be more like 300-500 meters. (Crewe et al. 2019). Each tower had 3-4 9 element directional Yagi antennas that allowed us to monitor hundreds of tags on one radio frequency.

Banding took place at 5 of the 12 sites that had automated telemetry receiving stations at the outer limits of the array to ensure they would travel within it as they departed each season. Banding sites included some element of shrubland habitat with open or semi-open canopy conditions and a well-developed shrub and herbaceous vegetation because mist-net captures rates and habitat use for foraging during migration are typically higher in shrubland habitats due to food availability (Suthers et al. 2000, Rodewald and Brittingham 2004, Mudrzynski and Norment 2013). The Fort River site consisted of an old field site on a sandy outwash plain and adjacent floodplain forest. Fannie Stebbins consisted of an old field with wetland margins. The Wantastiquet mountain site consisted of a 20-25 m wide powerline corridor with shrubs and saplings interspersed with herbaceous vegetation and adjacent mature forest. Hogback Mountain consisted of shrubby and herbaceous growth within an abandoned ski area and adjacent forest. The Cornish Wildlife Management Areas site consisted of a 30 m wide strip of

young forest along the Connecticut River with 100 m of cornfield separating it from the nearest inland forest. All sites are within 2 km of the Connecticut River with the exception of Hogback Mountain (20 km).

2.2.2 Capture, Banding, and Tagging

Ten to 15 mist-nets were operated at capture sites during spring (mid-April through May) at the southern end of our array of receivers, and at the northern end of our array in fall (September through mid-October) in 2015 and 2016. Mist-nets were operated from within 30-minutes of dawn to as late as 1300 hrs, weather permitting. Receivers were deployed at all capture sites. We captured birds at the Fort River unit of the Conte NWR both spring seasons, and added the Fannie Stebbins unit of the Conte NWR in Longmeadow, Massachusetts during spring 2016. Fall banding took place in 2015 at Wantastiquet Mountain in Hinsdale, New Hampshire, and Hogback Mountain in Marlboro, Vermont, and at the Cornish WMA in Cornish, New Hampshire in fall 2016.

Species fitted with nano-tags included Northeast Region Representative Species and Represented Species, as well as other candidate species identified by the CT River Pilot project team (Table 1). During spring, tagging was restricted to target species that did not breed within the study area because we were concerned birds might breed at the capture site and not fly across the array. This was illustrated with pilot tagging efforts of Red-Eyed Vireo (*Vireo olivaceus*) and Veery (*Catharus fuscescens*) in 2015, which remained at the capture site for the entire duration of the transmitters' battery life. In contrast, we tagged any target species during the fall migratory period because we were certain the species would depart on migration during the study period. White-throated sparrows (*Zonotrichia albicollis*), which winter within the study area were an exception,

and were thus only tagged in spring. Thus, opportunities for tagging were far lower during spring migratory seasons than fall.

All birds were fitted with USGS aluminum bands and aged and sexed when possible. Standard morphological measurements were taken such as mass (g), tarsus length (mm), subcutaneous fat score (0-5), culmen length (nare to tip, mm), unflattened wing cord (mm), tail length (mm), and skull ossification for aging in fall (0-6). The third retrix (R3) was sampled on monomorphic birds of which the sex could not be determined, as well as focal species fitted with nano-tags to later determine a breeding origin. Nano-tags were attached using a hand-made figure 8 leg loop harness designed to ensure minimal stress and comfortable fit to each bird species (Naef-Daenzer 2007). These lightweight tags were .29g and were < 3% of the birds' body weight to conform to USFWS regulations and ensure no harm to the bird. Depending on the burst interval of the tags, they gave off pulses to nearby receivers every 9-14 seconds, which made the life span of the tags roughly 45 days.

2.2.3 Departure Flight Classification

To ensure the individuals departed the banding site in a seasonally appropriate direction, departure direction from each banding site was recorded by using plots of signal strength vs. time during the bird's final moments at the site, and subsequent redetections when necessary if they did not show clear departure flights from the banding site. Taylor et al. (2011) studied several migratory species using automated telemetry and found that birds may make landscape scale relocations of up to 30 km while still being considered part of the same stopover bout, and thus may not be leaving the area to continue migration as they depart (Taylor et al. 2011). For this reason, departure flights

were classified as either stopover flights, probable migratory departures, or ambiguous. A probable migratory departure was a flight that occurred between civil twilight and dawn, and was in the appropriate migratory direction, given the season (Taylor et al 2011, Smetzer et al. 2017). A stopover flight was one that occurred during either day or night and in any direction with a subsequent redetection of the bird at least 1 km from where it was banded (Taylor et al 2011, Smetzer et al. 2017). The rest of the flights were put in the ambiguous category if a departure direction was not able to be established and there were no redetections, or if the bird underwent a reverse migration between sunset and sunrise (Taylor et al 2011, Smetzer et al. 2017). For our analysis, we used only probable migratory departures to ensure the birds were continuing migration.

2.2.4 Stopover Duration

We calculated stopover durations for 103 birds during the two fall and spring seasons at 5 banding sites. These stopover durations are minimum time estimates due to the fact that we cannot say for certain that we captured them as they arrived (Seewagen and Guglielmo 2010). Stopover duration was calculated after filtering out ambiguous tags that could impact the duration results, for example if the bird stayed for longer than or equal to the length of the life of the tag and/or did not show a clear departure flight or have a re-detection. Clear departure flights were characterized by looking at plots of antenna signal strength over time, in which it increases and then shows a clear decrease in a specific direction, indicating it has left the area (Taylor et al. 2011) Ambiguous detections could have been attributable to the birds' death, or loss of the tag, or issues with redetecting the tags due to topography and vegetation. Stopover duration was calculated using the timestamp of tag attachment to its last detection at the banding site

due to the lack of clear departure flights on many individuals. We then used subsequent redetections from nearby towers to confirm they had departed, although other studies use the time of maximum signal strength during a clear departure flight (Smetzer and King 2018, Taylor et al. 2011). We calculated the stopover duration at all sites within the Silvio O. Conte array, as well as for any stops made beyond our array. For detections beyond our array, we estimated stopover duration by using the minimum and maximum timestamps for each individual at each site. We had a clear cutoff in our data such that the majority of the detections were either < 100 minutes, assuming it was a sustained flight while passing by the tower, or > 100 minutes, indicating that it stopped by nearby the tower, using methods derived by Smetzer et al. (2017).

For one site, Mount Wantastiquet, the telemetry tower was at the summit of the mountain in order to collect accurate departure data with little disruption from topography and vegetation, whereas the banding site was in a powerline corridor at the mountain's base roughly 2 km away. Thus, only 9 of the 17 birds tagged at this location were picked up on the tower. However, these birds were detected at the Hogback tower 21km to the west, allowing us to estimate rough departure times using that tower. Due to technical difficulties at the fall 2016 banding site, (Cornish WMA), departure data was lost when the receiver stopped recording data on October 04, 2016 at 15:54:55 UTC for the rest of the season. Efforts were made to estimate departure time by using subsequent detections at nearby towers when possible. For birds last detected at the time the receiver failed, if they were re-detected within the array at the next closest tower (Hogback or Wantastiquet), we used distance from the banding site and time of detection (if it occurred at night assuming a departure flight that resumed migration) in order to estimate

the time it left the banding site, assuming it was a direct flight and assuming an average Blackpoll Warbler flight speed of 13 m/s (Deluca et al. 2015). If the timestamp of the last detection of the bird at the banding site was within the hour of the tower malfunction and there was no spike in signal strength indicating a departure flight, but they were no longer detected, we assumed they moved outside the range of the tower but were still nearby the study site if they were detected at a nearby tower that indicated a departure flight.

2.2.5 Statistical Analysis

Only data on tagged birds was used in order to answer questions regarding stopover duration. All data was transformed to Greenwich Mean Time for consistency, and to match the detection files. Nano-tag locational data were post processed to remove false detections due to tower noise and having multiple tags with the same id and burst interval. The data was filtered to exclude detections of tags with less than two multiples of the tags burst interval (Taylor et al. 2017). False detections can occur for a variety of reasons, one being that areas with high bird activity have simultaneous detections that can overlap and mimic an actual tag (Taylor et al. 2017). Manual filtering was then used to more finely inspect and remove unlikely detections from towers too far from a birds' previous detection, or if the bird was in two places at the same time, for example.

Mass was standardized by species in order to compare models using all species combined by scaling the masses by using mean-centering. This metric was used in place of a body condition index due to the fact that there was no linear relationship between mass and wing length or the extracted gradient using the first principal component of a PCA and mass, which was evident after looking at the R^2 values of the linear regressions, therefore, standardized mass was used moving forward (Seewagen and Guglielmo 2010).

Lack of correlation between mass and principal components could occur due to a small sample size, or that the mass of birds during migration fluctuates so that it is not correlated with other morphological size measurements. It has been shown that in mice, that using multiple regression including morphometric measurements is just as effective at predicting body fat/mass as body condition indices (Labocha et al. 2014). Fat score data was categorized as fat (4-5), moderate (2-3), or lean (0-1) for use in models (Deppe et al. 2015).

Missing values were interpolated as species averages. Data were visually inspected for outliers by plotting explanatory variables, and outliers were checked against field data to ensure these extreme values were not the result of data entry or other errors. Stopover duration was rounded to the nearest whole number (day) to satisfy model assumptions. Data was over dispersed, as indicated by the variance being larger than the mean, therefore, we used generalized linear mixed models with negative binomial error distribution and a log link function to test the effect of the explanatory variables (age, fat, mass, Julian date, species, season, site) on stopover duration. These models included species as a random effect due to the fact that the species assemblages varied between sites and years. To test for differences in stopover duration among species, a GLM (generalized linear model) with negative binomial errors was used, as well as a post-hoc Tukey's test to investigate all pairwise comparisons of species that had sufficient sample sizes to ensure we had enough power to correctly detect an effect. We examined models using a significance testing framework by investigating the results of univariate models, given that we have many multilevel variables, and Aicc values may misrepresent the significance of certain parameters in the top models due to the number of parameters

included in those models (Arnold 2010). We looked for seasonal and year effects using all data combined and then proceeded to conduct an analysis for spring and fall seasons separately because of the behavioral differences exhibited by migratory birds between the two seasons (Smith 2013, Wright et al. 2018). Fat upon capture was compared by site using ANOVA's and Welch's t-tests. Results of means \pm standard errors were reported in the results section below, unless noted otherwise for comparison with other studies.

2.3 Results

2.3.1 Stopover and Departure

Over the course of all four seasons, we captured and banded 2,093 birds of 58 species, and fitted 183 birds of 11 species with nano-tags. More birds were captured and tagged in the fall ($n = 132$) than the spring ($n = 51$) because of constraints on the number of migratory non-breeding species. Stopover durations were calculated for 103 birds of 10 species after filtering out ambiguous tags without any clear departure information and/or that were not redetected beyond the banding site (Table 1). We did not have any data for 14 tags, which could be the result of the tags either malfunctioning, or the tower not picking them up due to topography or vegetation.

Average spring stopover duration was 3.66 days (± 0.76 SE), spring 2015 average duration was 4.53 days (± 1.14 SE) for 13 birds, and average spring 2016 stopover duration was 3 days (± 1.02 SE) for 17 birds. Stopover durations at the banding sites ranged from 46 minutes to 16 days. Short stopovers likely reflect birds leaving the banding site to make landscape scale relocations to find different stopover habitat (Taylor et al. 2011). In spring, 30 % of migrants departed within 24 hours of capture with a mean

stopover duration of 10 hours (± 0.06 SE), and of those, 33 % of birds were fat, 11 % were lean, and 55% were moderate. Sixteen percent of spring migrants made prolonged stopovers of a week or longer at the banding sites (mean of 11.4 days ± 1.53 SE), and of those individuals, 60 % were “lean”, and 40 % had moderate fat stores, and no fat birds made prolonged stopovers.

Average fall stopover duration was 5.5 days (± 0.52 SE) among 73 birds. Average duration for fall 2015 at Wantastiquet Mountain was 9.16 days (± 1.35 SE) among 6 birds, and 3.44 days (± 0.63 SE) at Hogback Mountain among 29 birds, and the average fall 2016 stopover duration was 6.55 days (± 0.76 SE) among 38 birds. Fall stopover durations at our banding sites ranged from 72 minutes to 16 days. Sixteen percent fall of migrants departed within 24 hours of capture, with a mean stopover duration of 13 hours (± 0.10 SE), and of those, 67 % were fat, 25 % were moderate, and 8 % were lean. Twenty-seven percent of fall birds made prolonged stopovers of a week or longer with a mean of 11 days (± 0.50 SE) and of those, 65 % were considered “lean”, 26 % were moderate, and 9 % were fat.

In spring 2015, we captured 38 % AHY birds and 62 % SY or older. In spring 2016, we captured 82 % AHY birds, and 18 % SY birds. In fall 2015, 67 % of birds captured were HY birds, and 33 % were AHY at Wantastiquet, and 79 % HY birds and 21 % AHY birds at Hogback Mountain. In fall 2016, 71 % of birds captured were HY's, and 29 % AHY birds. Fat scores upon capture varied by site. In spring, we captured significantly more fat birds at Fannie Stebbins, compared to Fort River ($t = 4.00$, $df = 25.64$, $P = <0.001$). We captured zero birds with large fat stores in spring 2015, 46 % were lean, and 54 % had moderate fat stores. In spring 2016, 41 % of birds had large fat

stores at capture, while another 41 % had moderate fat, and 18 % were lean. In fall, results of an ANOVA and post-hoc Tukey's test revealed that we captured significantly more fat birds at Cornish, compared to Hogback ($P = 0.01$), and Wantastiquet ($P = 0.04$). In fall 2015, we captured zero birds with large fat stores at Hogback, 83 % of birds were lean, and 17 % were moderately fat, and in the same season at Wantastiquet, 100 % of birds were lean upon capture. In fall 2016, 57 % of birds were lean on arrival, 32 % had moderate fat, and 11 % were fat upon capture.

2.3.2 Model Results

A full list of candidate models can be found in Table 2. Using all data, with fall and spring seasons combined, we found an effect of season in that birds made shorter stopovers in spring vs. fall ($\beta = -0.49$, $P = 0.04$), and there was no significant difference in stopover duration among years. For spring data, significant models suggested a negative relationship between both mass (g) ($\beta = -0.52$, $P = 0.005$) and fat ($\beta = 1.311$, $P = 0.01$) to stopover duration at the banding sites, suggesting that leaner birds, and birds with smaller masses make longer stopovers (Fig. 2). We also found a marginally significant negative relationship between stopover duration and julian date, suggesting that birds captured later in the season made shorter stopovers in spring ($\beta = -0.36$, $P = 0.09$) (Fig. 2). There was no effect of year, banding site, age, or sex on spring stopover duration. Spring yellow-rumped warblers made marginally longer stopovers than Canada warblers ($\beta = 1.26$, $P = 0.07$), White-throated sparrows ($\beta = 1.25$, $P = 0.09$), and significantly longer stopovers than Northern waterthrush ($\beta = 1.82$, $P = 0.003$), and Swainson's thrush ($\beta = 1.55$, $P = 0.02$). Lincoln's sparrows made marginally longer stopovers than Swainson's thrush ($\beta = 1.13$, $P = 0.08$) and Northern waterthrush ($\beta =$

1.40, $P = 0.02$). Northern waterthrush made marginally shorter stopovers than White-throated sparrows ($\beta = -0.97$, $P = 0.08$) (Fig. 3).

For fall data, we found a positive relationship between stopover duration and julian date, suggesting that birds captured later in the season during made significantly longer stopovers ($\beta = 0.24$, $P = 0.029$), (Fig. 4). We tested each species separately using GLM's to look with within species effects of stopover duration on julian date. Although blackpoll warbler was the only species that had a statistically significant relationship ($\beta = 4.40$, $P = <0.001$), multiple species showed an upward trend and positive relationship between stopover and julian date that may not have been significant due to small sample size (Fig. 4). There were significant differences among banding sites that were further explored using a post-hoc Tukey's test. Stopovers were shorter at Hogback Mountain compared to Cornish state wildlife management area ($\beta = -3.10$, $P = 0.008$), and longer at Wantastiquet Mountain, compared to Hogback Mountain ($\beta = 5.72$, $P = 0.008$) (Fig. 4). In fall, both wood thrush ($\beta = 8.60$, $P = 0.006$), and yellow rumped warblers ($\beta = 6.70$, $P = 0.01$) made longer stopovers than red-eyed vireos, and Lincoln's Sparrows made marginally significantly longer stopovers than red-eyed vireos ($\beta = -6.60$, $P = 0.09$). using the results of a Tukey's test (Fig. 3).

For three fall species with large enough sample sizes ($N=11$) in fall, as indicated by a power analysis, separate analyses were conducted using negative binomial general linear models to test the effects of the independent variables on stopover duration. Of the three species tested (Ovenbird, red-eyed vireo, and Swainson's thrush), Ovenbirds were the only species to show significant results, and they made longer stopovers in fall 2016 than in fall 2015 ($\beta = 1.15$, $P = 0.03$), and they made longer stopovers at Cornish state

wildlife management area, compared to Hogback Mountain ($\beta = 1.32$, $P = 0.009$). There was no significant effect of fat, mass, year, age, or sex on fall stopover duration for these species.

2.3.3 Beyond Banding Site and Conte Array Stopover Results

Stopovers within and beyond the array differed seasonally. There were no additional stopovers recorded for spring birds once they left the array, potentially due to lack of tower coverage to the North. In fall 2015, birds made longer stopovers within the Conte (4.43 days), with only one bird making a one-day stopover beyond the array. In fall 2016, birds stopped over for similar amounts of time within and beyond the refuge, with an average duration of 6.18 days within, compared to 7.1 days outside.

After departing our banding sites, we observed several individuals make additional stopovers, both within and beyond our array. There were no additional stopovers in spring 2015 or 2016 that our data captured, but may be due to lack of tower coverage to the North. In fall 2015, we observed an ovenbird make a stop of 4 hours 53 km south of the banding site, in the area of the Bennet Meadow tower, before continuing through the Conte Refuge. This bird was then detected 5 days later making a 16-hour stopover on the New York coastline.

In fall 2016, a red-eyed vireo that departed the banding site on the day of capture was recorded making a 4-day stopover near the Hogback Mountain tower, 78 km SW of where it was tagged. In Fall 2016, two birds (wood thrush and Swainson's thrush) made stops at a nearby tower 7 km away immediately after being tagged at Cornish WMA in fall 2016 for 5 and 11 hours, possibly exhibiting exploratory flights to examine local foraging habitats, before returning to their original stopover site. Three fall 2016 birds, a

yellow-rumped warbler, and two blackpoll warblers, made stopovers near Fire Island, New York, for 3.5, 15, and 20 days. We observed a yellow-rumped warbler make a 15-day stopover at MacKay Island National Wildlife Refuge in North Carolina, which could also be its wintering grounds, since this location is within the wintering range of this species. We also observed a wood thrush making a 7-day stopover in Virginia, and a yellow-rumped warbler making a 6-day stopover in New Jersey, after flying through the Conte Refuge. And finally, a Lincoln's sparrow was recorded making a 16 hour stop on the Rhode Island coast before being redetected for a 2.5-hour stopover in Delaware 7 days later.

2.4 Discussion

Studying inland stopover during migration may help identify potentially important refueling areas for vulnerable species that rely on inland landscapes for refueling as they travel from their breeding to wintering grounds each year. This study provides further evidence suggesting that fat is an important indicator of stopover duration in spring (Goymann et al. 2010, Deppe et al. 2015), and that birds minimize time on migration, making shorter spring stopovers (Morris et al. 1994), in contrast to fall, where birds made longer stopovers (Morris et al. 1994, Stutchbury et al. 2009), later in the season, independent of body condition. Differences in stopover duration among seasons, species, time of year, and sites may also help shed light on how the needs of these migrants differ in order to make more informed decisions to better protect them during their full annual life cycle.

Birds making shorter stopovers in spring compared to fall may suggest that there is more pressure to get to their breeding grounds quickly in the spring than it is to secure

overwintering territories in the fall (Morris et al. 1994), or that spring migrants are more efficient at foraging than in fall, when there are fewer inexperienced hatch year birds (Nilsson et al. 2013). There has also been research suggesting that shifting temporal plant phenology ranges due to climate change may be affecting how long birds stay at their breeding grounds in the fall when food is still available later in the season (Cotton 2003), or that individuals with a higher body condition may stay longer to wait for favorable wind conditions (Duijns et al. 2017). Longer fall stopovers may also be attributed to an abundance of food at a stopover site, in which migrants stay longer to take advantage of that food source (Wright et al. 2018). Other studies have shown no difference in stopover duration when comparing spring and fall seasons in an urban area (Seewagen et al. 2010), and between two island sites (Suomala et al. 2012), and in these studies, birds had relatively short stopovers in both fall and spring. Our study had average stopover durations for spring similar to that of the two previously mentioned studies (Seewagen et al. 2010, Suomala et al. 2012), but our fall mean stopover durations were up to three times longer than the urban and island sites, possibly suggesting that the sites within the river valley are providing different resources for birds during fall, compared to urban and island sites.

Leaner birds, and birds with lower masses upon capture making longer stopovers in spring is consistent with other migration research (Goymann et al. 2010, Wright et al. 2018), and may suggest that leaner birds need more time to refuel at sites within our study area. Our results suggesting no relationship between fat or mass and fall stopover duration is in contrast to some studies, (Seewagen and Guglielmo 2010, Cohen et al. 2014a, Deppe et al. 2015), who reported that birds with larger fat stores made shorter

stopovers, and consistent with others (Seewagen et al. 2010, Rush et al. 2014, Liu and Swanson 2015), who found that condition at capture did not influence stopover duration. Factors other than arrival condition that may influence stopover duration include competition and predation (Seewagen et al. 2010), availability of food, and foraging guilds (McCabe et al. 2019) weather (Deppe et al. 2015), wind (Akesson and Hedenstrom 2000), or location of stopover sites, in that birds at inland stopover sites may behave differently than coastal birds at stopover that are not encountering a geographic barrier (Rush et al. 2014, Liu and Swanson 2015). Although there was no correlation between stopover duration and body condition for fall data, 65 % of birds that made prolonged stopovers were ‘lean’, and most likely remained at the stopover sites to continue accumulating fat stores, suggesting that they stayed longer than fatter birds.

The negative relationship between capture date and stopover duration for spring may suggest that birds are optimizing their time on migration with increased pressure to continue migration as the season progressed (Alerstam 1991, Lindstrom and Alerstam 1992a, Packmor et al. 2020), or that earlier birds make longer stopovers due to lower spring temperatures, possibly resulting in lower food availability earlier in spring (Cohen et al 2014a). The positive relationship between fall julian date and stopover duration is in conflict with our initial hypothesis that stopover duration would decrease as the season progressed because research has shown that birds minimize time on migration later in the season in order to arrive at their destinations and secure territories (Paxton and Moore 2017, Packmor et al. 2020). This finding could be explained by differences in breeding latitude or timing of migration. A fall 2017 study found that Purple Martins that bred at higher latitudes arrived at stopover sites later in the season and made longer stopovers

(Van Loon et al.). Conversely, Smetzer and King (2018) found that blackpoll warblers from more southern breeding latitudes made longer stopovers. This could also occur due to the phenology of migration, in that species that migrate through later in the season are making long stopovers due to migratory strategy.

Eighty-five percent of prolonged stopovers occurred in fall, highlighting the behavioral differences and usage of the river between seasons, and is consistent with other prolonged stopover research suggesting fall stopovers are longer than spring (Stutchbury et al. 2009). Our study is one of the first to highlight migrants making prolonged stopovers inland, in the absence of a geographic barrier. Prolonged stopovers occurred at all five of the banding sites in both spring and fall, but most profoundly at Cornish WMA in fall 2016, with 19 birds staying a range of 7-16 days. Since this site consisted of a small strip of riparian habitat too small for a large number of individuals to breed, we believe that the majority of these birds were migrants, and we do not think that these prolonged stops could be due to the fact that these birds could be on their breeding grounds. It has been shown that birds may make longer stopovers in sites with high quality resources in order to refuel (Craves 2009, Ktitorov et al. 2010), but conversely make longer stopovers if the habitat quality is poor because they need more time to refuel in seasons with prolonged drought (Tøttrup et al. 2012), and measuring habitat quality directly by way of refueling rates is one way to eliminate the latter assumption. Although Van Loon et al. (2017), found that stopover duration was best predicted by breeding latitude for a long-distance migrant, Purple Martin (*Progne subis*), and not habitat quality, in which birds from more northerly breeding latitudes made longer stopovers.

There was no effect of sex on stopover duration within our study. Morbey et al. (2018) also found no differences in stopover duration between sexes, and suggested stopover behavior may be variable between sexes depending on year, site, or weather effects. Beauchamp et al. (2020) also found no significant difference in stopover duration between sexes in White-Throated Sparrows in Long Point, Ontario, which could occur in areas with high habitat quality, suggesting that all birds may have refueled sufficiently. Female and males stopping for similar amounts of time within our study area in both seasons may reflect that they refueled at similar rates, and that males are not refueling more quickly than females, in contrast to results by Seewagen et al. (2013). Our sample of birds able to be sexed was very small, and thus could be an additional reason for not detecting an effect.

There was no effect of age on stopover duration within our study, which is consistent with some studies (Seewagen et al. 2013), who found no differences in stopover duration among age classes, and in contrast to others (Morris et al. 1994, Yong et al. 1998, Filiberti and Perlut 2018), who found that younger birds made longer stopovers. The lack of effect among age classes may suggest that younger birds were not at a disadvantage compared to older birds with regards to competing for fuel resources. Jones et al. (2002) found no significant differences among refueling rates between age classes in Long Point, Ontario for most species tested, although adults of 2 species refueled more quickly than young birds, indicating that these results may be species dependent. Because our study did not occur at a geographic barrier or coastal site, compared to others that found age related differences in stopover (Morris et al. 1994, Yong et al. 1998, Filiberti and Perlut 2018), there may be less pressure or competition

among age classes, and therefore may be behaving differently inland. The proportion of young birds captured within our inland study (63 % in spring, 74 % in fall) is similar to those reported by Ralph (1981), who found 65-70 % of young birds inland, compared to 85-95 % at coastal sites. This may suggest that older, more experienced birds are selecting the inland landscape within the Conte for refueling, compared to capture rates along the coast. Although we captured a smaller proportion of HY birds inland compared to coastally, we still captured a large number of young birds, which could be why we didn't detect an effect among age classes, and that longer fall stopovers may be partly influenced by younger, inexperienced birds staying longer (Morris et al. 1994, Yong et al. 1998, Filiberti and Perlut 2018).

Spring Swainson's thrush within our study had shorter stopover durations (1.75 days; range 0-6 days), compared to an urban study in Ohio, with average stopovers of 3.7 days (Matthews and Rodewald 2010), although our sample size was small (N=4) and may not represent the entire population. This species also had shorter stopovers in our study compared to a coastal spring study in Costa Rica with mean stopovers of 3.2 and 2.3 days (Wilson et al. 2008). Fall Swainson's Thrush within our study made longer average stopovers of 5.92 days (range 0-16 days), compared to a coastal study in Columbia with average durations of 3 days (range 1-8 days; Gomez et al. 2014), and they suggest that this species migration strategy is characterized by several short stops followed by short flights. This finding highlights the flexibility in migration rates within a species, and that they may change their migration strategy as they get closer to their wintering grounds (Gomez et al. 2014).

Spring yellow-rumped warblers and Lincoln's sparrows had longer stopovers than other species within our study (8.25 and 5.4 days respectively), as well as longer stopovers than red-eyed vireos on fall. An inland fall study of yellow-rumped warblers in riparian habitat along the Missouri river in South Dakota found that birds made shorter average stopovers at two sites, of 5.9 days \pm 0.5 and 5.1 days \pm 0.3 (Liu and Swanson 2015), compared to fall birds within our study system making average stopovers of 8.85 days \pm 1.08. A fall study of Lincoln's sparrows at a reclaimed landfill in New Jersey using recaptures to estimate stopover duration reported shorter mean stopover rates of 4.7 days (Seewagen and Newhouse 2018), compared to fall Lincoln's sparrows in our study with average stopovers of 8.7 days. Yellow-rumped warblers and Lincoln's sparrows making longer stopovers at our inland sites compared to another inland study in riparian habitat, and an urban coastal study may reflect temporal availability of food resources, which may decrease later in the fall (Smith and McWilliams 2014).

A comparison between inland and coastal sites for fall migrating red-eyed vireos reveals similar stopover durations throughout New England. Average stopover durations of red-eyed vireos in fall 2015 within our study (1.9 days \pm 0.48) were similar to fall red-eyed vireos at island sites in Maine and New Hampshire (2.0 days \pm 1.6 SD, 3.3 days \pm 2.6 SD; Suomala et al. 2012), and slightly shorter than a fall study in the Gulf of Maine (3.8 days \pm 2.9 SD; Smetzer et al. 2017). Red-eyed Vireos at the island sites in Maine and New Hampshire showed positive refueling rates at these fall sites (Suomala et al. 2012), which could suggest that these stopover durations are sufficient for this species to put on fuel and depart to continue their migration. This may suggest that our inland sites provide resources similar to those at coastal sites in New England.

Fall ovenbirds banded at Cornish had longer mean stopovers (10 days) than a study at an urban stopover site in New York City, which found they made average stopovers of 2.9 days (Seewagen et al. 2010), and similar to stopover durations of ovenbirds at Hogback (2.9 days). This may suggest that Cornish provides better refueling opportunities than Hogback, possibly due to availability of riparian habitat, which has shown to be important for food resources for migrating songbirds (Schoenberg and Randhir 2010), or proximity to the river, compared to a more mountainous site like Hogback, 20 km from the river. Ovenbirds making longer stopovers in fall 2016 vs. 2015, could occur due to variability in the quality of sites, food availability and refueling rates (Suomala et al. 2012).

Average stopover duration of blackpolls at our inland study in fall at Cornish (3.5 days) was similar to findings by Smetzer et al. (2017) along the coast in the Gulf of Maine (3.5 days \pm 3.6 SD), suggesting that this species may use coastal and inland stopover habitats similarly within New England. Fall stopovers within the refuge may be influential to this species to fuel their subsequent flights to the coast in Connecticut, New York, and Massachusetts, where they made long stops to acquire fat to fuel possible long-distance overwater flights. We last detected 83 % of fall Blackpolls at the mouth of the Connecticut River, where it empties into long island sound, suggesting that many of these birds departed over water, which they have been documented to do so in fall (Deluca et al. 2015). Other studies have also shown Blackpoll warblers making long stopovers along the north-eastern coastline before presumably departing over water, making trans-oceanic flights (Smetzer et al. 2017, Deluca et al 2019), highlighting the importance of these coastal sites for refueling.

Our study had a smaller proportion of birds that departed within 24 hours of capture (30% during spring, and 16 % in fall), meaning most made stopovers of a day or more, when compared to coastal/urban stopover studies. Deppe et al. (2015) found that 85 % of their birds departed the banding site within 24 hours of capture at a coastal site. Seewagen et al. (2010) found that 48 % of spring birds, and 50 % of fall birds departed on the day of capture at an urban site near the New York Coast. Birds making shorter stopovers at coastal/urban sites may suggest that they are relocating to better habitat elsewhere, and that inland sites along river valleys could be serving as a better alternative for foraging, as research has shown some migratory songbirds at coastal sites often depart their initial stopover sites and move further inland (Akesson 1999, Smolinsky et al. 2013, Woodworth et al. 2014, Smetzer et al. 2017). However, fall birds making similar stopovers both within and beyond the Conte in 2016 could suggest that the Conte is providing similar habitat to protected coastal habitats, where we also observed our focal species making stopovers.

In spring, we captured zero birds with large fat scores (4-5), 54 % with moderate fat scores (2-3), and 46 % lean birds (0-1) from Fort River in 2015, possibly indicating that we captured many birds on or near their date of arrival with depleted fat stores, in contrast to Fannie Stebbins, where 41 % of target captures had large fat stores, and 18 % were lean upon capture. This could occur because they are using habitats differently, and migrants may be selecting Fort River for refueling. Migrants may be using Fannie Stebbins for either exploratory flights within a larger stopover landscape, as Taylor et al. (2011) has found migrants make landscape scale relocations within a single stopover bout, or resting and taking refuge from adverse weather conditions or undesirable winds.

There is also the possibility that birds with larger fat stores from Fannie Stebbins were not captured on the day they arrived, and they were able to quickly put on fat at this site to continue their migration.

Beyond our study area, other potentially important stopover sites were located at the southern end of the refuge near Long Island Sound. Here, we observed many individuals exhibit long stopovers during fall migration of as long as 20 days, and may have occurred as they were using the coastal stopover areas as staging areas to rest and refuel before making long flights south, either over water, or along the coast line after flying through the Connecticut river watershed. This area of the refuge was also highlighted as important by Litwin and Lloyd-Evans, as they found the highest concentration of migrants at the southern end of the watershed using point counts during their spring study (2006). The southern end of the refuge may be important in spring due to early leaf out, and thus more food availability, compared to sites further north with higher elevations (Litwin and Lloyd-Evans 2006), and essential for fall birds to refuel as a last stop before departing over water.

Migratory songbirds in this study were observed making prolonged stopovers both within the river valley (max. of 16 days), as well as along the coast (max. of 20 days). Because prolonged stopovers at coastal areas, or geographic barriers can be used as vital staging sites for refueling migrants before making long overwater flights (Callo et al. 2013, Bayly et al. 2018, Smetzer and King 2018), the similar maximum stopover durations both within and beyond the Conte refuge highlight importance of inland habitat as well. Although birds are likely not encountering a geographic barrier at our inland

sites, they are still utilizing the stopover habitat for prolonged periods of time, suggesting that there may be an added benefit for longer refueling at these sites.

Our finding that stopover durations of birds within the Conte Refuge were similar to other coastal studies, and longer than inland and urban studies may suggest that inland migrants in our study area may behave similarly to those in coastal landscapes. Fall birds within this study area utilized stopover sites in central Vermont and New Hampshire for prolonged stopovers to fuel their flights to the coast, where they made additional stopovers. Some species seemed to use the refuge for long term resting and refueling, like yellow-rumped warblers, while others, like blackpoll warblers, made shorter stopovers and navigated through the valley to reach the coast before making long stops there. Uncovering species specific needs for birds at stopover along declining migratory songbird routes and the influences behind their behaviors is essential to protecting habitat needed throughout the full annual life cycle of these species.

2.5 Management Applications

The extensive use of the Silvio O. Conte National Fish and Wildlife Refuge, by way of prolonged stopovers in fall, and time minimization-like strategies in spring implies that it could serve as a critical resource for songbirds during this important life stage. Because an individual's ability to accumulate sufficient fat stores efficiently during migration has a direct effect on the subsequent success of all other life stages, it is imperative we are able to understand what drives these stopovers to better protect the habitats most needed by these birds seasonally (Cormier et al. 2013).

Stopover durations of migratory songbirds were longer for ovenbirds, Lincoln's sparrows, and yellow-rumped warblers within our study area, compared to other urban

(Seewagen et al. 2010, Seewagen and Newhouse 2018), and inland stopover sites (Liu and Swanson 2015), potentially suggesting that birds are selecting these sites for prolonged fattening, possibly due to better resources than other sites. Fall Swainson's thrushes also had longer stopovers than a site in Columbia, which could indicate that fall stopover sites within our study are providing resources necessary for longer refueling bouts, and they may make shorter stopovers as they approach their wintering grounds (Gomez et al. 2014). Individuals making longer stopovers compared to other studies suggests that the Conte Refuge is an important stopover/refueling area.

Stopover durations in our study were similar to those for Blackpoll warblers and Red-eyed Vireos, compared to other coastal New England sites (Suomala et al. 2012, Smetzer et al. 2017), suggesting they employ a consistent migration strategy throughout this region, and inland and coastal stopover sites may be providing sufficient resources for these species during migration. Because inland and coastal stopover may be providing resources similarly for these two species, protecting inland habitat is critical, considering coastal development is projected to continually exacerbate habitat loss along the coast (NOAA).

The fact that species terms in models were significant may suggest that site conditions may benefit some species more than others. For example, Swainson's Thrush stayed on average twice as long at Wantastiquet (8.33 days), compared to Hogback (4.88 days), 20 km inland, during the same fall 2015 season. Longer stopovers at Wantastiquet could be explained by differing food availability at these sites. Investigations to identify site and habitat features associated with refueling and habitat use are underway to better understand how habitat use varies by species.

Some sites exhibited longer stopover than others in fall, and demonstrates that site factors influence the value of sites for stopover. Although we were not able to sample enough sites to specifically identify factors that were associated with high quality sites, it is notable that the longest stopover durations were at sites that were close to the river with riparian zones at Wantastiquet and Cornish, compared to Hogback. Since riparian habitat has shown to provide food resources and cover (Litwin and Lloyd-Evans 2006, Cerasale and Guglielmo 2010, Schoenberg and Randhir 2010, Kirsch et al. 2013, Darrah et al. 2017), these sites may be important for migratory songbirds.

Migration is a physiologically challenging part of a songbirds' annual cycle due to increased predation risk, competition for resources, and other exogenous factors like wind and weather (Norris and Taylor 2006, Deppe et al 2015, Fischer et al. 2015, Moore 2018), therefore minimizing habitat loss by protecting important habitats is imperative. The Silvio O. Conte National Fish and Wildlife Refuge provides stopover and refueling opportunities for a range of species before they continue their migrations in spring and fall, and therefore, should be prime candidates for conservation or continued study to ensure the needs of migratory landbirds are being met at this vulnerable time in their lives.

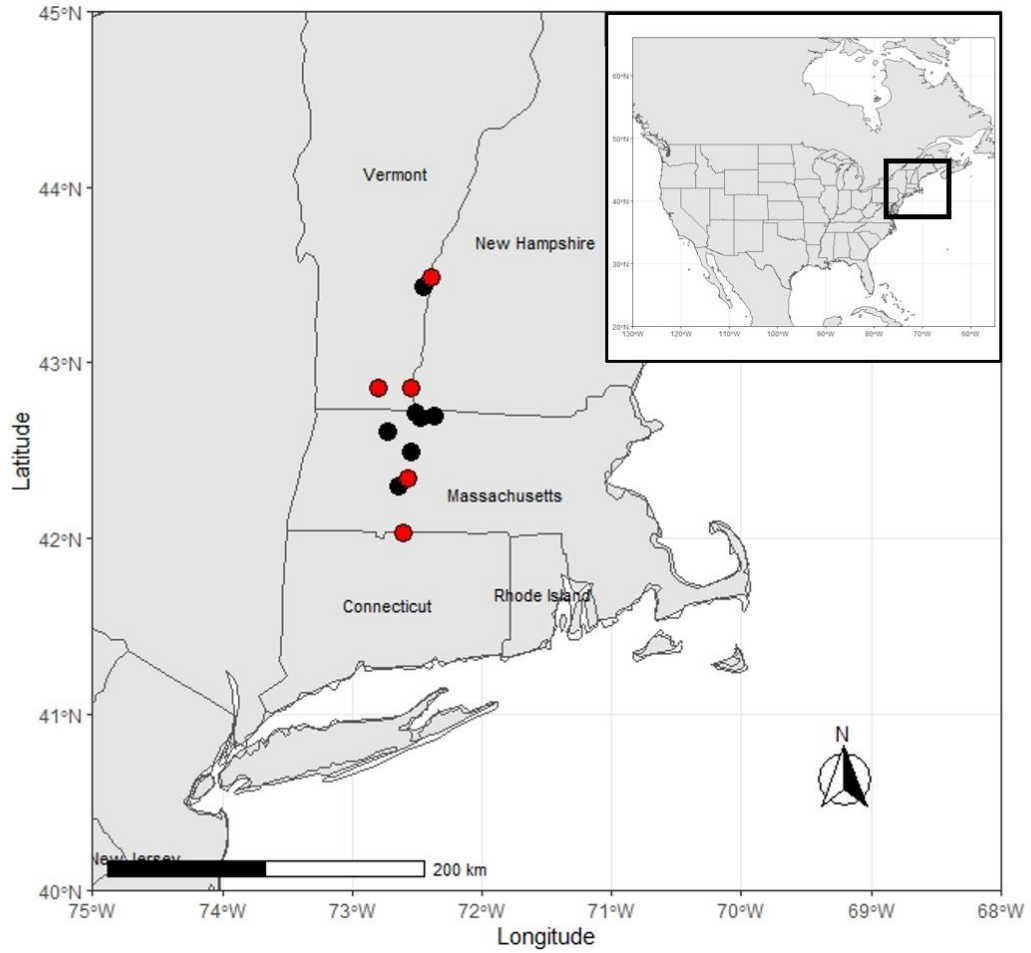


Figure 1. Map of Connecticut river automated telemetry receiving stations used for analysis in 2015 and 2016 with banding sites in red.

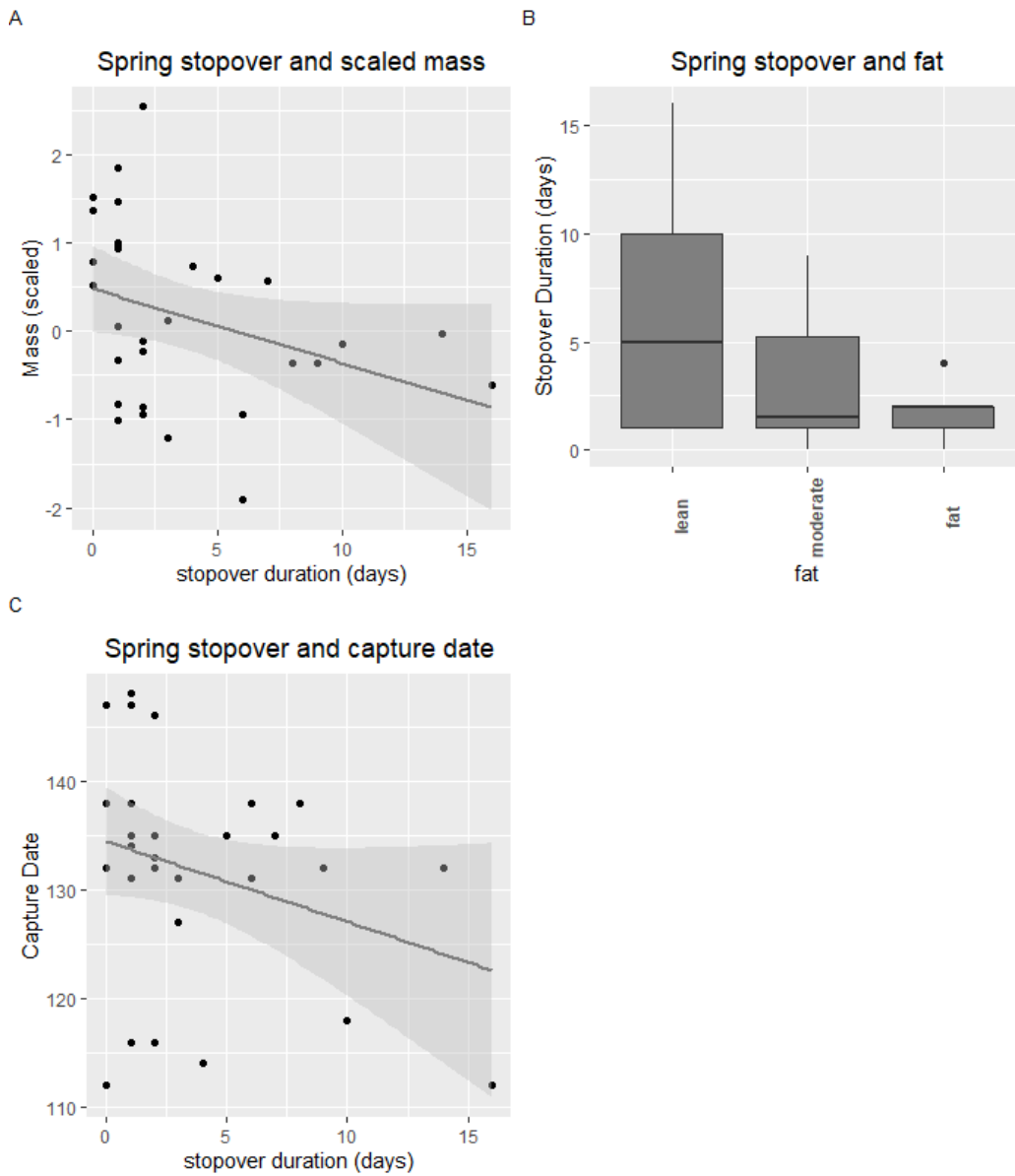
Table 1. Number of birds tagged within the Silvio. O Conte National Fish and Wildlife Refuge in fall and spring in 2015 and 2016 included in the stopover analysis.

Species	Spring 2015	Fall 2015	Spring 2016	Fall 2016	Total
Swainson's Thrush (<i>Catharus ustulatus</i>)	2	11	2	14	29
Northern Waterthrush (<i>Parkesia noveboracensis</i>)	1	0	5	1	7
Wood Thrush (<i>Hylocichla mustelina</i>)	0	3	0	1	4
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	2	0	6	0	8
Lincoln's Sparrow (<i>Melospiza lincolni</i>)	4	0	1	4	9
Ovenbird (<i>Seiurus aurocapilla</i>)	0	8	0	3	11
Blackpoll Warbler (<i>Setophaga striata</i>)	0	2	0	5	7
Canada Warbler (<i>Cardellina canadensis</i>)	2	0	1	1	4
Red-eyed Vireo (<i>Vireo olivaceus</i>)	0	11	0	2	13
Yellow-rumped Warbler (<i>Setophaga coronata</i>)	2	0	2	7	11
Total	13	35	17	38	103

Table 2. All candidate models analyzed using Negative Binomial Generalized Linear Mixed Models with species as a random effect for all data combined, spring and fall separately, as well as a Negative Binomial GLM to explore the relationship between species and stopover duration, as it is used as a random effect in all other models to account for variation among sites and seasons. Significant models are denoted with a **, indicating they reported a p-value of ≤ 0.05 , and models with * provided moderate support.

Response Variables	Overall	Spring Stopover	Fall Stopover
Candidate Models (GLMMs)	Season **	Age	Age
	Year	Sex	Sex
		Fat**	Fat
		Mass**	Mass
		Year	Year
		Julian Date*	Julian Date**
		Banding site	Banding Site**
Candidate Models (GLM)		Species**	Species**

Figure 2. Spring stopover duration was shorter for birds with lower masses (A) and leaner birds (B), and birds captured later in the season had shorter stopovers, indicating they were minimizing time on migration (C).



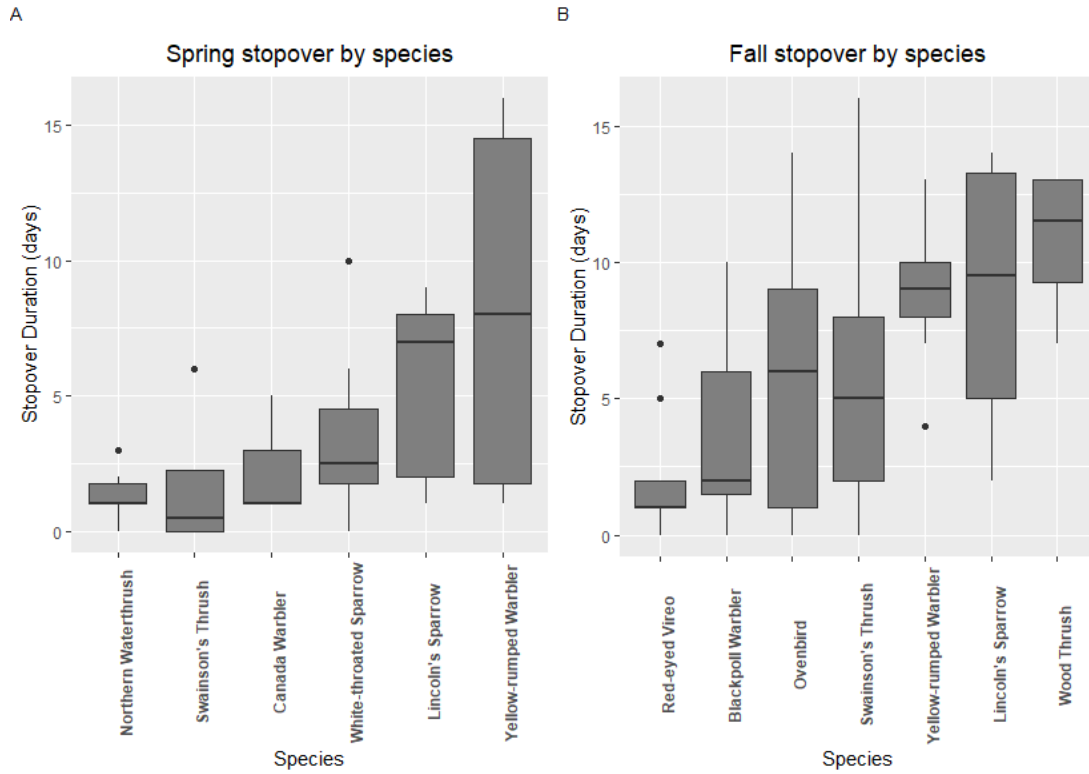


Figure 3. Stopover durations by species for spring and fall seasons within the Silvio. O. Conte National Fish and Wildlife Refuge in 2015 and 2016, with years combined.

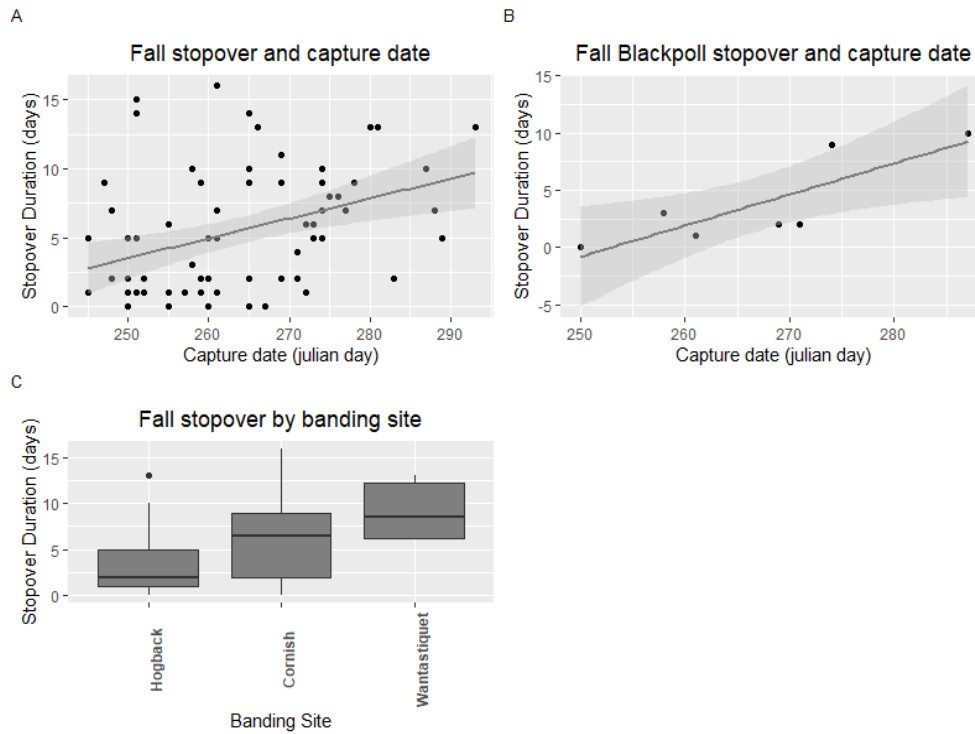


Figure 4. Fall stopover duration analysis results. Birds captured later in the season made longer stopovers (A), and Blackpoll Warblers also showed a significant relationship between capture date and stopover duration (B). Stopovers were shorter at Hogback Mountain compared to Cornish state wildlife management area ($\beta = -3.10$, $P = 0.008$), and shorter at Hogback Mountain, compared to Wantastiquet ($\beta = 5.72$, $P = 0.008$).

CHAPTER 3

FACTORS THAT INFLUENCE THE PACE OF MIGRATION WITHIN THE SILVO. O CONTE NATIONAL FISH AND WILDLIFE REFUGE

3.1 Introduction

Biannually, migratory songbirds are faced with challenging decisions about route choice in order to arrive at their breeding and over-wintering destinations in a timely manner (Lindstrom and Alerstam 1992b, Nilsson et al. 2013, Gomez et al. 2017). Migration is often considered one of the riskiest parts of the annual cycle, where the highest mortality occurs due to predation, loss of sufficient refueling habitats, and competition for resources (Fischer et al. 2015, Hewson et al. 2016, McCabe et al. 2019), and threats during migration may be responsible for steep declines of many migratory species (Newton 2006, Norris and Taylor 2006). Research conducted on stopover, breeding, and wintering habitats has shown that they can all directly impact the overall success of the migration, but knowledge of habitat utilization is still lacking within the actual migratory period. (Woodworth et al. 2014, Duijns et al. 2017, Gomez et al. 2017).

The rate at which birds travel during migration may be influenced by many factors, such as season, migratory strategy, breeding latitude, total migration distance etc., and the influence of these factors on overall success are poorly understood, yet potentially critical to populations (Bairlein 2003, Faaborg et al. 2010). It is well known that songbird migration rates vary seasonally, in that individuals can move twice as fast, and in some cases, 6 times faster in spring than fall (Marra et al. 2005, Stutchbury et al.

2009, Bennett et al. 2019). This phenomenon most likely occurs due to increased selection pressure for birds to get to their breeding grounds in the spring in order to secure territories and start breeding as early as possible, to ensure a successful season (Lindstrom and Alerstam 1992b, Nilsson et al. 2013).

Migrating birds exhibit different migration strategies, with some employing a “time minimization” strategy, in which they carry large fuel loads and travel at high speeds over long distances, versus an “energy minimization” strategy, in which birds make more frequent stops to conserve energy, prioritizing energy over speed (Hedenstrom and Alerstam 1997, Alerstam 2011, Gomez et al. 2017, McCabe et al. 2018, Schmaljohann 2018), and the choice of migration strategy may influence the pace of migration (Zhao et al. 2017, Packmor et al. 2020). Migration rate has also shown to vary within species, depending on where they are in their route, total migration distance, as well as temporally throughout the season. According to the sprint hypothesis, birds may speed up their migration as they near their ultimate destinations (Briedis et al. 2018). The total migration distance of a migrant songbird may influence their pace, in that birds with shorter total migration distances may travel at a slower pace because there is less of a rush than those traveling further to reach their ultimate destination (Schmaljohann 2019). Birds migrating later in the season may also need to travel faster in order to catch up arrive to their destinations at similar times as earlier migrants (Briedis et al. 2018, Gomez et al. 2017).

Breeding latitude, and wing morphology has also shown to affect the timing and speed of migration. A study of Blackpoll Warblers (*Setophaga striata*) in coastal Maine found that those coming from more northern breeding populations moved through their

stopover site earlier in the season (Smetzer and King 2020), while another study showed that wintering latitude affected migration timing, in that birds from more northern temperate forest wintering grounds migrated earlier, compared to birds further south in the tropics (Hagan et al. 1991). Both Bennett et al. (2019) and Smetzer and King (2020) also found that individuals of the same species with longer wing lengths traveled further distances, and that this may be an adaptive evolutionary strategy for long distance migrants. Migratory strategies are still widely unknown for some species, and how route choice and timing of migration vary between individuals within and among populations.

Individuals have also been shown to change their migratory strategy and route seasonally depending on selection pressures, with some taking offshore routes one season, and coastal routes in another (Stutchbury et al. 2009, Alerstam 2011, Stanley et al. 2012, Deluca et al. 2015, Bennett et al. 2019). Although migration research focuses on coastal movements due to large concentrations of birds using the coast as a corridor, songbirds have been shown to make inland flights during migration in search of less crowded, high quality sites to refuel, and these inland sites may be contributing to the success of their overall migration, in that inland birds have shown to have better body condition than those on the coast (Akesson 1999, Smetzer et al. 2017, Woodworth et al. 2014, Smolinsky et al. 2013, Hoh et al. 2018).

Stopover sites, where birds rest and refuel, are vital to the success of subsequent legs of migration. Research has shown that a single high-quality stopover site that results in high refueling rates can provide the necessary fuel loads needed to carry long distance migrants thousands of kilometers during non-stop flights from Columbia to Ontario, for example (Gomez et al. 2017). Coastal migration is well studied, however, research has

also shown that river valleys play an important role in migration due to increased food supply, often in riparian, or wetland habitats, as well as for navigation, and are understudied in this field (Akesson 1993, Litwin and Lloyd-Evans 2006, Cerasale and Guglielmo 2010, Kirsch et al. 2013, Fischer et al. 2015, Darrah et al. 2017). The Connecticut River valley in New England has been shown to provide habitat for migrating songbirds, but movement patterns of individual birds and habitat utilization at large scales are unknown, as well as how route choice and rate of movement are influenced by exogenous and endogenous factors within the valley (Litwin and Lloyd-Evans 2006). This research need comes at a time when neo-tropical migrants are facing steep declines due to factors like climate change and habitat loss, and loss of migratory connectivity has been shown to exacerbate migratory bird population declines (Faaborg et al. 2010, Bairlein 2016, Xu et al.2019).

This study aims to uncover patterns that may exist with regards to how migratory songbirds are using an inland migratory corridor within the Atlantic flyaway, what influences those patterns, and pace of migration, compare our findings to other studies, and try to fill in gaps where our knowledge of long-distance songbird migration is lacking. We want to shed light on previously unknown areas of importance along migratory songbird routes that can be targeted for conservation. Uncovering how the stopover and banding sites within our study area prepare migrants for their subsequent migrations may help identify key characteristics about these sites that make them more or less valuable for conservation.

We expect seasonal variation in the duration of migration, and that overall spring migration rates will be faster, and the time spent on migration will be shorter. We expect that stopover duration will influence the pace of migration, in that longer stopovers may provide birds with resources to migrate faster. We also expect variation among species because migratory strategy, as well as breeding latitude, may affect their pace of migration (Van Loon et al. 2017, McCabe et al. 2018, Smetzer and King 2020). We also expect that sites with better quality resources will be indicative of faster initial movement rates due to better fuel load accumulation, and that birds captured later in the season may exhibit a time minimization strategy and travel faster than their earlier conspecifics. We expect that migration rate will decrease with migration distance, because birds will need to make stops to refuel along the way, and we are not tracking their entire migration, so shorter distances do not reflect overall migration routes. With regards to condition upon capture, as indicated by fat and mass, we expect to see a relationship between condition and migration rate in that that birds captured in poor condition will have faster migration rates once they depart if the banding site provides suitable refueling opportunities, but negative relationships at sites if they are unable to refuel sufficiently.

3.2 Methods

3.2.1 Study Area

Our study was conducted during the spring and fall of 2015 and 2016 within the Connecticut River valley within the Silvio O. Conte National Fish and Wildlife Refuge (hereafter referred to as the Conte Refuge). Banding was conducted at 5 sites, all of which encompassed a shrubland opening adjacent to mature forest. In 2015, spring

banding took place within the Fort River Unit of the Conte Refuge in Hadley, Massachusetts. The Fort River site consisted of a 4 ha shrubland opening surrounded by mixed hardwoods and floodplain forest adjacent to the Fort River (42°20', -72°33'). Fall banding took place at two sites, Hogback Mountain in Marlboro Vermont (42°51', -72°47') and Mount Wantastiquet in Chesterfield New Hampshire (42°51', -72°33'). The site at Hogback Mountain consisted of an abandoned ski area with overgrown ski trails within a matrix of mature northern hardwoods forest. The site at Mount Wantastiquet consisted of a 20-m wide powerline right-of-way within a matrix of mixed hardwoods forest adjacent to the Connecticut River.

In 2016, spring banding took place at the Fannie Stebbins Memorial National Wildlife Refuge in Longmeadow, Massachusetts (42°01', -72°36'). Fannie Stebbins consisted of a 4-ha old field site within a matrix of floodplain forest adjacent to the Connecticut River. Fall 2016 banding took place at the Cornish State Wildlife Management Area in Cornish New Hampshire. The Cornish site consisted of a 30-m wide strip of riparian forest bounded by the Connecticut River to the west and a 100-m wide cornfield to the east, beyond which was an extensive northern hardwoods forest.

Twelve automated telemetry receivers were used to monitor bird movement at sites within the study area, 8 along a 60 km segment of the river valley in 2015, and 4 additional receivers along an additional 100 km in 2016 (Fig.1). We used a mix of Lotek SRX-800 and SensorGnome receivers (Lotek Wireless, Newmarket Ontario), and each tower was equipped with 3 to 4 9-element uni-directional Yagi antennas. Nine of the receivers were located on free-standing 3-5 m tall pop-up masts in open fields (Arcadia, Bennet Meadow, Fort River and Fannie Stebbins), on a mountainside (Ascutney and

Wantastiquet), in a ski trail (Hogback), within a regenerating clear cut (Satan's Kingdom), and at a boat access point on the Connecticut river with a small strip of riparian habitat (Cornish). Three other receivers were mounted on fire towers on mountain summits (Grace, Shelburne, Toby).

3.2.2 Bird Capture and Tagging

Birds were captured and banded between mid-April and May and September through mid-October of 2015 and 2016. Each season, 10-15 mist nets were placed approximately 50 m apart within openings and forest at each banding site. Banding took place from ~30 min before sunrise to 1300 hrs. All captures were fitted with a USGS aluminum band, and standard morphological measurements taken, including unflattened wing cord (mm), tail length (mm), mass (g), tarsus length (mm), subcutaneous fat score (0-5), culmen length (nare to tip, mm), and skull ossification for aging in fall (0-6). Birds were aged and sexed when possible, and the third retrix (R3) was sampled from monomorphic birds in order to determine sex at a later date.

A subsample of focal species was fitted with NTQB-2 0.29g Lotek Nanotags (Lotek wireless, Newmarket Ontario) using handmade figure 8 leg loop harnesses (Naef-Daenzer, 2007). Nanotags are coded transmitters that individually identify tagged birds when they pass within the detection range of the stationary receivers. The anticipated detection range was ~15 km, but may have decreased depending on topography, obstructions, and foraging guild (Crewe et al 2019). Focal species selected for this study were migratory landbirds considered as representative species of the Northeast, or species that represent them, with the idea that understanding their needs may also help other

declining species (Table 1). Tags were less than 3% of the individuals' body weight to minimize effects during migration. The burst intervals of the tags were between 9 and 14 seconds, giving the tags a life span of ~ 45 days.

3.2.3 Migration Rate

Migration rate for birds in transit was calculated as the travel time between towers using the timestamp of the maximum signal strength at each site, indicating it was close to the receiver, for flybys, and used minimum and maximum detection times, which represent arrival and departure, to calculate rates for sites that birds likely stopped over nearby (Smetzer et al. 2017). We then calculated the distance of each segment and derived a migration rate (m/s) using the great circle distance and the R package *geosphere* (Hijmans et al., R Core Team 2013). We calculated an overall rate of movement from the departure of the banding site to the location of its final detection for spring and fall separately, as well as for birds tracked within our study area in the Silvio. O Conte National Fish and Wildlife Refuge by selecting movements from only those twelve towers. Since we were not able to capture the whole migration of these birds due to constraints on transmitter battery life and availability of tower coverage, these rates do not necessarily represent movements to their breeding/wintering grounds.

Data was then filtered to remove outliers in the dependent variable, to exclude migration rates that were unreasonable fast, due to towers being in close proximity to one another, and therefore providing overlapping detections. We filtered data using a cutoff of 35 m/s, where a natural break in our data occurred. Although this may be a high rate of movement for songbirds, a study of song thrushes which observed groundspeeds of 29 m/s (Sinelschikova et al. 2019). Movement rates < 5 m/s were classified as “slow

migratory movements”, and those $\geq 5\text{m/s}$ were deemed “sustained migratory flights” (Smetzer et al. 2017). Slower rates likely involved individuals making stopovers elsewhere along the route outside of tower detection radii.

3.2.4 Aerial Telemetry

In fall of 2016, we attempted to supplement the land-based automated telemetry with an aerial telemetry component to determine whether birds no longer detected within range of the receivers were still present within the landscape. On 10 June 2016 birds were tracked from a fix-wing aircraft with fixed Yagi antennas and a Lotek SRX800 receiver (Lotek Wireless, Newmarket Ontario). The flight originated at the airport in Turner's Falls, Massachusetts, and the flight path led approximately 110 km north at an altitude of 1,000 m to the Cornish Wildlife Management Area in Cornish, New Hampshire, the northern terminus of the telemetry array. The outbound and return flight paths followed trajectories 15 km east and west of the Connecticut River, which, given the ~ 15 km minimum detection distance covered a 6,600 km² area.

3.2.5 Statistical Analysis

All data were transformed to Greenwich Mean Time (G.M.T.) to match detection files. Data were manually filtered to get rid of false detections, including data with less than 2 pulses of the tags burst interval at each tower it was detected, and tags that showed no clear departure flights from banding sites that were also not subsequently redetected. Data was analyzed using generalized linear mixed models (GLMM) with a negative binomial error distribution, with species as a random effect to account for the variation in

species among seasons and sites. We tested for an effect of season using all data combined, and proceeded to analyze data for spring and fall seasons separately due to differing migratory strategies and behaviors that may vary seasonally (Marra et al. 2005, Smith 2013, Bennett et al. 2019). We tested the effect of stopover duration at our banding sites, capture date, total distance traveled (km), banding site, year, season, scaled mass upon capture, fat upon capture (0-5), and age on migration rate (m/s). We did not look for an effect of sex due to small sample sizes, with many birds unable to be sexed. We looked at differences among species and banding sites using negative binomial generalized linear models (GLM). Data was analyzed using a significance testing framework, by comparing p-values of univariate models, and reporting highly significant results with a p-value cutoff of 0.05. Migration rates were calculated for individuals overall tracked migration, from first to last detection, as well as for birds traveling within our study area in the Silvio. O. Conte National Fish and Wildlife Refuge to better understand the utilization of the river valley.

3.3 Results

3.3.1 Summary

After filtering out false detections and birds with too little movement data to calculate migration rate, we were left with 61 individuals of ten species, 16 individuals of 6 species for spring, and 45 individuals of 9 species for fall (Table 3). For the analysis within the Conte Refuge, there were 11 spring birds, and 38 fall birds with sufficient data. The mean overall migration rate using the entire tracked migration for spring was 4.31 m/s (± 5.12), and 3.84 m/s (± 6.70) for fall. The mean migration rate for birds within the

Conte Refuge for spring was 5.3 m/s (± 5.85) and 8.8 m/s (± 8.90) in fall. The maximum distance recorded during spring was a yellow-rumped warbler that traveled 1,105 km to eastern Quebec over a period of 22 days, and for fall a red-eyed vireo, and Swainson's thrush that traveled 3,897 km to Panama over a period of 40 days and 25 days respectively. The fastest observed migration rate was a fall Swainson's thrush traveling 63 km at a rate of 29 m/s within the Conte Refuge. All migration rates ≥ 15 m/s were those tracked for short distances (17-133 km), indicating that rate decreases as birds are tracked for longer distances due to stopover requirements.

3.3.2 Aerial Telemetry Results

As a result of a combination of either high winds or heavy ground layer fog aerial telemetry only took place during a single roughly 230 km flight on October 6, 2016 between Turner's Falls MA and Cornish NH. No birds were detected on the flight from Turners Falls to Cornish. Twenty birds were detected at the Cornish banding site, which were individuals that had been recently banded and were still engaged in stopover and had not yet resumed migration. By this date, 63 birds had been banded at Cornish, of which 65 % had already departed.

3.3.3 Overall Migration Rate

Spring migration rate was faster than fall ($\beta = 0.83$, $P = 0.02$; Fig. 5A), and spring migration rate decreased with total distance traveled ($\beta = -0.62$, $P = 0.06$; Fig. 5B). There was no effect of stopover, mass, fat, age, banding site, year, or capture date, on migration rate for our spring analysis. Spring Lincoln's sparrows, northern waterthrush, and white-throated sparrows had higher migration rates than yellow-rumped warblers ($\beta = -1.42$, $P =$

0.06; $\beta=-1.85$, $P = 0.03$; $\beta=-1.42$, $P = 0.06$) (Fig. 6A). In Fall, birds that made longer stopovers at Cornish WMA had subsequently faster migration rates ($\beta = 0.65$, $P = 0.02$; Fig. 5C), and birds captured later in the season at Cornish WMA moved faster ($\beta = 0.82$, $P = 0.04$) (Fig. 5D). There were no significant results among movement metrics and migration rate at Wantastiquet. Fall Swainson's thrush moved significantly faster than yellow-rumped warblers ($\beta = -3.50$, $P = 0.005$) and red-eyed vireos ($\beta = -2.59$, $P = 0.02$). Wood thrush also moved faster than yellow-rumped warblers ($\beta = -3.51$, $P = 0.02$) and red-eyed vireos ($\beta = -2.59$, $P = 0.05$) (Fig. 6B). All fall blackpoll warblers ($N=6$) traveled at extremely slow migration rates (<1 m/s) suggesting that they may have engaged in prolonged stopovers. There was no effect of fat, mass, age, banding site, or total distance traveled on migration rate for fall.

3.3.4 Migration Rate within the Silvio O. Conte National Fish and Wildlife Refuge

Average migration rates within our 160 km section of the Conte Refuge for spring birds was 5.27 m/s, and 8.84 m/s in fall, and there was no significant difference between migration rates between seasons. Spring birds with larger initial fat loads traveled faster ($\beta = 0.49$, $P = 0.03$; Fig. 7A). Birds migrating through the Conte Refuge from the southern-most site, Fannie Stebbins, traveled faster than Fort River ($\beta = 1.19$, $P = 0.02$; Fig. 7B). There was a year effect, in that spring birds in 2016 traveled at higher rates than 2015 ($\beta = 1.19$, $P = 0.02$). Spring migration rate increased with total distance traveled ($\beta = 0.61$, $P = 0.05$; Fig. 7C). There was no significant effect of species on migration rate, but could be due to very small sample sizes unrepresentative of the overall populations.

In fall, birds from Cornish that made longer stopovers had subsequently faster migration rates ($\beta = 0.88$, $P = < 0.001$; Fig 8A) and birds captured later in the season

moved faster ($\beta = 0.58$, $P = 0.01$; Fig. 8B). There were no significant results among movement metrics and migration rate at Wantastiquet, however, migration rates differed among two of the three fall banding sites, with Wantastiquet having faster migration rates than Cornish State WMA ($\beta = 0.94$, $P = 0.008$; Fig. 8C). There was no effect of fat, mass, species, or age on migration rate for fall birds within the Conte Refuge.

Upon departure of the banding site, more birds traveled at sustained paces (>5 m/s) within the refuge in fall. Fifty-five percent of fall birds exhibited sustained flights and flew through the array in < 1 hour, while 27 % of spring birds made flew through the array at a sustained pace. Seventy-three percent of spring birds, and 45 % of fall birds exhibited slow movements (<5 m/s), taking as long as 19 days to traverse the array after departing the banding site and travel through the array, suggesting they made additional stopovers within the refuge once they departed the banding site. Birds traveled slower through the Conte Refuge in spring 2015, with 88 % making slow movements, and only 12 % with sustained flights, compared to spring 2016, with 67 % making sustained flights and 33 % with slow movements, although sample sizes were very small for spring 2016 ($N= 3$). The pace of fall movements within the Conte array were similar between years (43% slow movement, 57% sustained flight versus 53% slow movement and 47% sustained flight; 2015 and 2016, respectively).

3.3.5 Direct Flights

We observed several individuals undertaking long-distance movements that we interpreted as non-stop flights based on the overall migration rate. In fall 2015 a Swainson's thrush flew 474 km from Mount Wantastiquet to Bombay Hook National Wildlife Refuge in Delaware over a 13-hour period at a rate of 10 m/s, being detected at

the receiver in Delaware at 8:49 am. This could indicate that this bird traveled at a faster pace than estimated to reach its destination before pausing migration at sunrise, and this detection could potentially be a diurnal exploratory flight while looking for potential stopover sites. A red-eyed vireo in fall 2015 traveled 422 km from northern Massachusetts to Prime Hook National Wildlife Refuge in Delaware in 11.5 hours, at a pace of 10 m/s, being last detected by tower in Delaware at 8:47 am. In fall of 2016, a Swainson's thrush was detected making a 643 km flight from Mount Wantastiquet to Virginia in 12 hours, traveling at 14 m/s, arriving at 6:57 am, where it was observed making a possible stopover nearby until it was detected that night by a tower 56 km south at 23:18. In fall 2016, a third Swainson's thrush flew 407 km in 9 hours from northern Massachusetts to Atlantic City, New Jersey at a speed of 12.5 m/s, being last detected flying by the tower in New Jersey at 4:05 am, indicating it may be continuing its flight until dawn. We observed a fall 2016 yellow-rumped warbler that traveled 430 km from Wantastiquet to southern New Jersey in 12 hours at a speed of 10 m/s, arriving in New Jersey at 6:53 am, before being detected ten days later in Delaware.

In spring 2015, 29 % of birds flew in a north-east trajectory to Nova Scotia and New Brunswick, while one bird continued north to eastern Quebec, and in 2016, 15 % of birds were detected in Nova Scotia, where they most likely bred. The rest of the birds from these seasons were either detected on the Massachusetts coast, or were not redetected beyond the Conte array. Very few birds followed the river once they departed the banding site, and only one of the birds tagged in spring 2015 was detected at the northern most tower, and in 2016, two birds were detected mid-way through the array in

southern Vermont, indicating that most birds took a coastal route, rather than continuing North following an inland trajectory.

A higher percentage of birds followed the Connecticut river valley in fall than spring, in that 13 % of birds banded were detected at the southern-most tower within our array in fall 2015, and 19 % in fall 2016, indicating that they flew through our entire array. In fall 2015, nearly half of our birds (47%) were detected as far south as Delaware and Virginia, 20 % of birds were last detected on the New York and Connecticut coast line at the mouth of the Connecticut river, and the remainder were not redetected beyond our array. In fall of 2016, 60 % of birds were detected moving along the coast line in Delaware, Virginia, and as far as South Carolina, ~1300 km from the banding site. The other 40 % were detected either not detected beyond our array or on the coast line at the mouth of the river. The birds not detected beyond the coast may have likely either departed over water to continue their southward migration, continued in a trajectory in a route with that lacked tower coverage, or had tag malfunctions. Forty-nine percent of fall birds utilized the southern end of the Conte Refuge and Connecticut river as it empties into Long Island Sound, which could serve as an important staging area before or after making overwater or long over land flights.

3.4 Discussion

While understanding the needs of migratory birds during their full annual life cycle is essential to protecting these declining species, there is still much we don't know about migration (Faaborg et al. 2010). Annual movements from breeding to wintering grounds are now able to be studied in much finer detail due to the development of new tracking technologies. Inland migration is understudied (Rush et al. 2014), and because

research has found evidence of coastal birds making inland flights to find stopover habitat potentially more suitable for their needs (Akesson 1999, Smetzer et al. 2017, Woodworth et al. 2014, Smolinsky et al. 2013, Hoh et al. 2018), understanding the influences of inland stopover and movement is essential, in the absence of a geographic barrier, because behavior may differ from coastal migration (Rush et al. 2014, Liu and Swanson 2015). For example, Rush et al. (2014), found no relationship between stopover duration and fat upon capture for Tennessee Warblers (*Oreothlypis peregrina*) at an inland site in Tennessee, possibly suggesting that they are not refueling at the same rates as coastal sites, while coastal studies did find relationships for a variety of species (Lindstrom and Alerstam 1992a, Goymann et al. 2010, Deppe et al. 2015).

Birds within this study system utilized the watershed in different ways seasonally. Birds seemed to utilize the river valley for navigation, long term refueling, or a combination of both, more often in fall, as a larger portion of fall birds were detected moving through the entire 160 km array (13 % fall 2015, 19 % fall 2016), with 49 % of birds detected at the coast in Long Island Sound. In spring, migrants were most often detected at the southern end of the refuge, in southern Massachusetts, before departing in a northeastern trajectory to the coast, with very few birds detected flying through the whole array (1 bird in 2015, 0 birds in 2016). This observation may reflect findings from Litwin and Lloyd-Evans (2006), who noted spring migrants utilized the southern portion of the Connecticut river most often, and spread out as they moved North, utilizing habitats both close and further from the river similarly.

The majority of spring birds made slow movements once they left the banding site (73 %), suggesting they made other stopovers within the refuge that we could not record

due to lack of tower coverage. Fall birds made more sustained flights (56 %) upon departure of the banding sites, and moved quickly through the refuge. This may suggest that spring birds made shorter, more frequent stops within the Conte Refuge, because they moved unrealistically slow ($< 5\text{m/s}$), indicating additional stopovers, and fall birds made long stopovers at the banding sites, followed by fast movements through the refuge, with most refueling at the banding site alone, and not making additional stopovers until they reached the coast.

Seasonally, birds traveling faster in spring than fall is consistent with other studies, suggesting that they may be behaving as time minimizers, trying to reach their breeding grounds quickly to secure territories, while that strategy is more relaxed in fall, as there is less pressure to reach wintering grounds (Lindstrom and Alerstam 1992b, Nilsson et al. 2013, Gomez et al. 2017, McCabe et al. 2018). Shorter stopover durations during spring has shown to be a main influence in the seasonal differentiation of migration rate (Schmaljohann, 2018). Studies have also shown that individuals may change their strategies and routes between fall and spring (Stutchbury et al. 2009, Stanley et al. 2012, Deluca et al. 2015), which may ultimately influence the duration of migration. Although there was no significant difference between spring and fall migration within the Conte Refuge, the mean migration rate for fall was almost double that of spring (spring $5.3\text{ m/s} \pm 5.85$; fall $8.8\text{ m/s} \pm 8.90$), illustrating that migration rates may not be constant throughout the season (Briedis et al. 2018).

Fall migrants moving faster through the Conte Refuge could be due to the fact that they made prolonged stopovers at the banding sites where they were able to refuel sufficiently, and moved through the study area quickly to reach the coast for additional

refueling before continuing to the next leg of their journeys, either over water or along the coast line. For example, we observed a blackpoll warbler tagged at our 2016 northern most banding site make a prolonged stopover of 9 days, fly through the Conte array in two hours, and make an additional stopover of 14 days in Fire Island, NY, but was not redetected after that. This may indicate that the tag malfunctioned, the bird was predated, or most likely, that it made an overwater flight because it was not redetected on the coast line with ample tower coverage. Inspection of fine scale departure data did show a clear departure flight, so we assume that it continued its migration, given than Blackpolls making over water flights during fall is documented (Deluca et al. 2015).

Spring birds showing a negative relationship with migration distance may suggest that the majority of the birds did not make direct non-stop flights, and needed to make additional stopovers along their route, as expected. We did not track these birds for their entire migration due to lack of tower coverage and transmitter battery life, and while we found a negative relationship with distance in spring, another study found that migrants with longer migration distances traveled faster than short-distance migrants (Schmaljohann 2019). This could indicate that migration speed varies along the route, as one study has found (Briedis et al 2018), and our data represents a smaller scale of a birds' entire migration. The lack of a relationship between distance and migration rate in fall suggests that birds tracked for longer distances traveled at a variety of paces, which may speak to different migratory strategies. Short-distance migrants may migrate slower than a long-distance migrant to the same stopover location (Schmaljohann 2019).

Conversely, birds that traveled further distances migrating at faster paces during spring within the Conte Refuge could be explained by effects of banding site, year, and

fat scores upon capture. Birds captured from Fannie Stebbins in 2016 had larger fat stores upon capture, compared to Fort River in 2015, and they traveled faster and further than birds in 2015. Birds migrating faster from Fannie Stebbins could be an indicator of higher refueling rates associated with better habitat quality. The birds captured at Fannie Stebbins with large fat stores may reflect conditions at their previous stopover site, however it is also possible they had gained their fuel loads at the capture site. It should also be noted that our Motus array expanded in 2016, increasing our array an extra 100 km North, therefore we had the ability to track birds for longer distances in 2016, and may influence results. Because results of our study suggested that birds with faster migration rates had larger fat stores, fat upon capture is likely why birds moved faster from Fannie Stebbins, given that fuel loads have shown to affect migration rate (Gomez et al. 2017). A multi-year study with repeated banding at these stopover sites would be necessary to determine the year and site effects.

Fall birds captured later in the season traveling faster than earlier migrants may suggest these birds are minimizing time on migration, which has been shown in other research (Gomez et al. 2017, Briedis et al. 2018, Smetzer and King 2018). Migrants were also observed making longer stopovers, later in the season, as we found from a previous analysis of stopover within this study area, and could be explained by the positive relationship between stopover length and migration rate. The availability of food at stopover sites may vary temporally throughout the migratory period (Bayly 2007) and influence the fuel loads of migrants, which may subsequently influence their pace (Gomez et al. 2017). Populations within a species breeding at different latitudes may also be influencing this relationship. Smetzer and King (2020) found that blackpoll warblers

breeding at higher latitudes migrated through their coastal Maine stopover sites earlier in the season, and had longer wing lengths. A separate analysis of our fall 2016 blackpoll warbler banding data showed a moderately significant relationship (linear regression, $\beta = -0.24$, $P = 0.07$, Fig. 9) between capture date and wing length, in that the individuals with longer wing lengths moved through earlier in the season, similar to findings in Maine. This could indicate that the birds moving faster, and stopping longer, may have been more local to the area than the earlier migrants.

Our results suggesting that longer fall stopovers are related to faster migration rates both within and beyond our study system speak to the influence a single stopover site can have on a migration. While we saw a positive relationship in our fall data, our results were not significant for spring, possibly because spring birds attempt to minimize their time spent at stopover in order to speed up their migration. Studies of the influence of stopover duration on migration pace are lacking, and here we provide some support that there is a positive influence in fall. Since our fall data showed that birds made longer stopovers, and moved faster later in the season, although we were unable to measure refueling rates, we may infer that longer stopovers could potentially suggest better refueling opportunities for some migrants, because other studies have shown birds spend more time in high quality stopover habitats compared to lower quality ones (Craves 2009, Ktitorov et al. 2010).

There were site effects in that birds from Wantastiquet moved faster than from Cornish. This could be a result of better habitat quality, possibly resulting in higher refueling rates for birds at Wantastiquet. One alternative explanation for these results could be that the average capture date for birds at Wantastiquet was 10 days later than

Cornish, and because our analysis of Cornish showed that birds captured later in the season moved faster than earlier captures, birds from Wantastiquet may be moving faster in relation to when in the season they were captured, and minimizing time on migration as the season progressed.

All blackpoll warblers within this study had migration rates of 0 m/s, which may indicate that they engaged in prolonged stopovers in order to refuel, presumably before making long overwater flights. All but one blackpoll warbler was tracked to the coastline in New York and Massachusetts before departing with clear departure flights in probable overwater flights. Since the coast line had ample tower coverage with a high probability of detection if they took a coastal route, we assume that these birds detected on the coast engaged in over water flights. Smetzer and King (2018) also found that blackpoll warblers had very slow migration rates in fall, attributed to prolonged stopovers before making possible overwater.

Yellow-rumped warblers moved significantly slower than many other species in both seasons, and this may reflect that some populations of yellow-rumped warblers are short distance migrants. They may be breeding closer to the spring capture sites than other species, or wintering further north closer to the fall capture sites than other species, and may be moving more slowly than longer distance migrants (Schmaljohann 2019). Although yellow-rumped warblers were among the slowest average migration rates in spring ($1.3 \text{ m/s} \pm 0.57$), they were also tracked the furthest total distances in spring (1,105 km). Birds traveling longer distances must make stopovers to refuel, and so additional stopovers may influence their pace, traveling slower than birds that we tracked for shorter distances.

Red-eyed Vireos migrated slower than other species in fall within this study, and also made the shortest stopovers among all other species tested (Chapter 2). This may suggest they adopt a migration strategy in which they make more frequent, shorter stopovers, possibly minimizing energy expenditure (Alerstam 2011). Red-eyed vireos have also been shown to avoid over water flights (Deppe et al. 2015), and traveling around barriers may prolong the duration of migration, although they may depart over water, or barriers later in the season (Smetzer and King 2018, Smetzer et al. 2017).

Fall Swainson's thrush made relatively long stopovers at the banding sites (mean stopover 6.37 days, chapter 2), followed by faster migration rates, compared to other species. This could speak to their migration strategy, suggesting they make long stopovers, followed by long flights between stops, because Swainson's thrush also exhibited more direct flights than other species. For example, a fall 2016 Swainson's thrush was detected 480 km from its banding site 11 hours after departure after making a ten-day stopover, compared to a yellow-rumped warbler traveling to the same location in a time frame of 11 days. The difference in travel time between these two species could reflect differing strategies between long and short distance migrants (Schmaljohann 2019).

Wind is undoubtedly known to influence the departure of migrants as they decide to initiate or resume migration, given that they can drastically reduce energy expenditure and increase flight speed (McCabe et al. 2018, Sinelschikova et al. 2019). However, it has also been shown that long distance migrants are less selective when it comes to wind on departure of stopover sites (Packmor et al. 2020).

Understanding where migratory songbirds concentrate their movements, and what influences their behaviors is crucial to protecting prime habitat used during their migration for navigation and refueling. Birds within our study system utilized the Conte Refuge differently in spring and fall, and species exhibited behaviors consistent with differing migratory strategies. Protecting critical habitat used within the refuge is essential to help mediate habitat loss for these declining species and ensure they are able to carry out successful migrations.

3.5 Management Applications

The staggering decline of migratory birds since the 1970's (Rosenberg et al. 2019) further exacerbates the need for continued research on the influences of migratory decisions to help promote migratory connectivity and uncover where resources are best suited. Because inland movements from coastal landscapes have been documented, as a possible adaptive strategy to seek high quality habitat with decreased predation and competition compared to coastal sites (Akesson 1999, Smolinsky et al. 2013, Woodworth et al. 2014, Smetzer et al. 2017, Hoh et al. 2018), the study of inland migration should be a top priority.

Our results suggest that the Silvio O. Conte National Fish and Wildlife Refuge may be an important inland migratory corridor for birds moving through in fall and spring. In our study, birds exhibited fidelity to the southern portion of the river valley in spring, and dispersed as they moved north, consistent to findings from Litwin and Lloyd Evans (2006), in contrast to fall, where a larger portion of birds followed the river south from Vermont and New Hampshire to the mouth of the river in Long Island Sound. These sections of the river valley may be vital to individuals making inland flights seeking

additional refueling opportunities. The seasonal utilization of the river valley could speak to species breeding locations. Spring birds traveling North were last detected in Nova Scotia and Eastern Quebec, therefore traveling over land, through the refuge may not be the most direct route, especially while spring birds prioritize minimizing time on migration (Lindstrom and Alerstam 1992b, Nilsson et al. 2013, Gomez et al. 2017, McCabe et al. 2018). Fall birds moving through the Conte refuge may be breeding in a more central location, in central Quebec or Ontario, for example, compared to spring birds tracked to the Northeast in Nova Scotia. The refuge may be supporting different breeding populations seasonally, and therefore loss of habitat in this region may pose a significant threat to migrants breeding throughout a wide range of areas to the North. Although we did not incorporate data on breeding origins, analysis of stable isotope markers could answer these questions (Smetzer and King 2020).

Stopover duration and fat upon capture affected migration rate, which may reflect habitat quality at these sites, although measuring refueling rates directly is one way to confirm high quality habitats, and is underway as part of a subsequent analysis. Fall birds that made longer stopovers at Cornish WMA, the fall 2016 site, traveled faster, suggesting that this site may provide quality resources for migrants to refuel, and may influence their subsequent migration success. Birds at Fannie Stebbins in spring 2016 with larger fat upon capture migrated more quickly than those from Fort River with lower fat stores. This may suggest that birds were able to sufficiently refuel at Fannie Stebbins, compared to Fort River, where birds captured with lower fat stores made more slow movements than birds at Fannie Stebbins upon departure. Birds from Fort River most likely needed to make additional stopovers within the refuge, considering individuals

moved more slowly through the valley, and therefore may have been seeking additional refueling opportunities elsewhere in the refuge.

Although this study was not designed to compare sites, the sites with the fastest migration rates were the southern-most Massachusetts site in spring, characterized by floodplain forest, and a southern New Hampshire site in fall, with powerline corridors at the base of Mount Wantastiquet, both on the banks of the Connecticut river. Spring birds may be refueling more quickly at southern most sites, due to increased food availability due to early leaf out, closer to the river, and moving more quickly to reach their breeding destinations, compared to birds captured further north, where food may be less available early in the spring (Litwin and Lloyd- Evans 2006).

Species differ with respect to their migration strategies, and therefore have differing needs in their vulnerability to stopover habitat quality. Thus, caution should be exercised in extrapolating between studies of different species, as well as timing of passage. Yellow-rumped warblers moved through the study sites later in the season, moved slowly, and made long stopovers at the banding site, whereas fall red-eyed vireos moved through earlier in the season, made short stopovers, while also migrating slowly. These two species both migrated at slower paces than other species in our study, while employing different migration strategies. This may suggest that red-eyed vireos rely on more of the landscape for refueling, suggesting they may make several short stopovers, whereas yellow-rumped warblers may make fewer, longer stopovers, and rely on those habitats for prolonged refueling.

Understanding the variation in stopover and movement behavior among seasons, years, individuals, and species may help add to a better understanding of the full life

cycle of migrant songbirds. Spring birds within this study may rely more on the coastal landscape for refueling and navigation as they move north, but initially may use the southern portion of the Conte refuge to refuel and escape from crowded coastal areas with potentially more competition and predation, before continuing on, taking a more coastal route. Fall birds captured within the Conte Refuge seem to utilize the river more for prolonged stopover bouts to rest and refuel, as well as for navigation to the coast line, whether to continue to follow a coastal route south, or depart over water. The Conte Refuge is providing habitat seasonally for these birds, whether for refueling upon initial landing after a long strenuous flight in spring, or to accumulate large fat stores before making long flights in the early legs of migration in fall. Overall, protecting and conserving habitat close to the river that may be used for prolonged stopover bouts for refueling may be an essential part of a successful migration for these species, especially at the southern terminus of the Connecticut River, where there may be more urbanization.

Table 3. Number of tagged birds included in the migration rate analysis by season and year.

Species	2015		2016		Total
	Spring	Fall	Spring	Fall	
Swainson's Thrush (<i>Catharus ustulatus</i>)	1	7	1	12	21
Red-eyed Vireo (<i>Vireo olivaceus</i>)	0	3	0	1	4
Ovenbird (<i>Seiurus aurocapilla</i>)	0	2	0	1	3
Yellow-rumped Warbler (<i>Setophaga coronata</i>)	2	0	1	6	9
Lincoln's Sparrow (<i>Melospiza lincolnii</i>)	4	0	0	2	6
Northern Waterthrush (<i>Parkesia noveboracensis</i>)	1	0	1	1	3
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	2	0	2	0	4
Blackpoll Warbler (<i>Setophaga striata</i>)	0	1	0	5	6
Canada Warbler (<i>Cardellina canadensis</i>)	1	0	0	1	2
Wood Thrush (<i>Hylocichla mustelina</i>)	0	2	0	1	3
Total	11	15	5	30	61

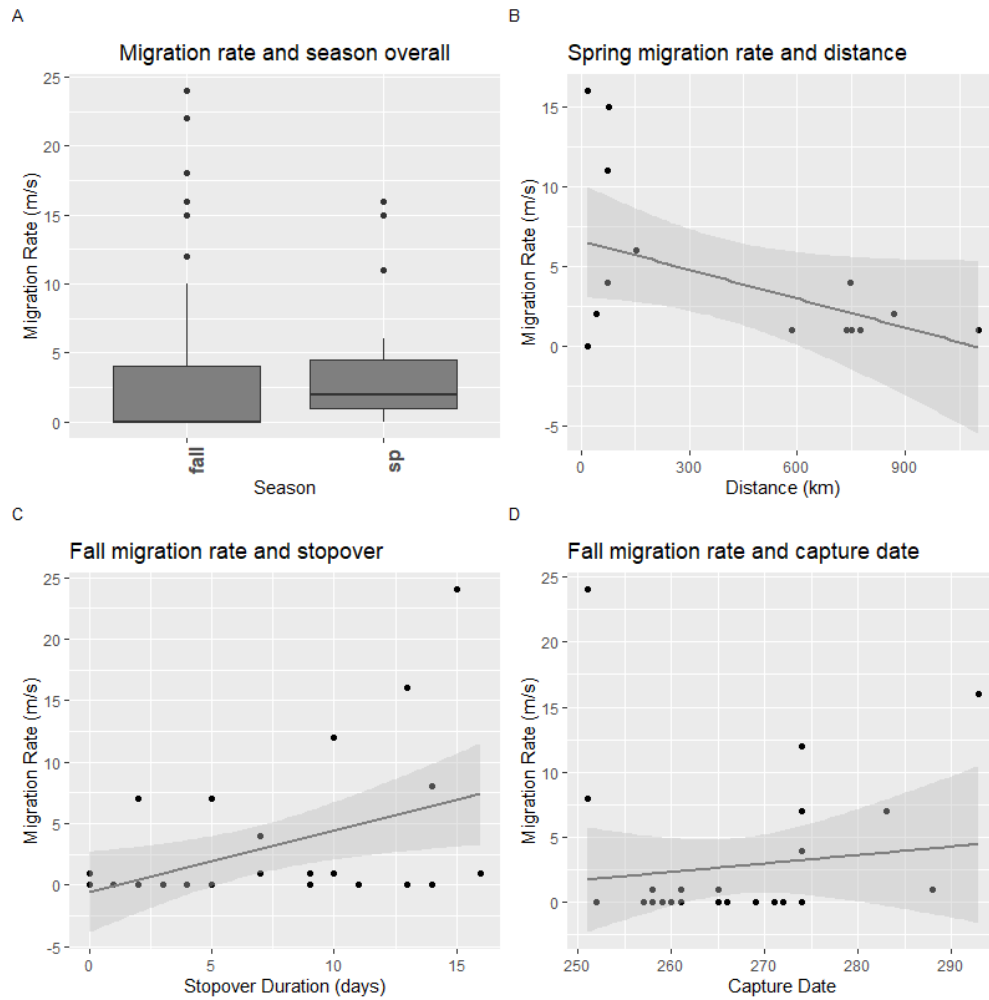


Figure 5. The results of our analysis of overall migration rate using movement data from the banding site departure to the last detection, which may not reflect breeding or wintering grounds because of tracking capabilities. Migration rate was faster in spring than fall (A), migration rate decreased with distance in spring (B), fall birds with longer stopovers at Cornish had faster migration rates (C), and fall birds captured later in the season at Cornish had faster migration rates (D).

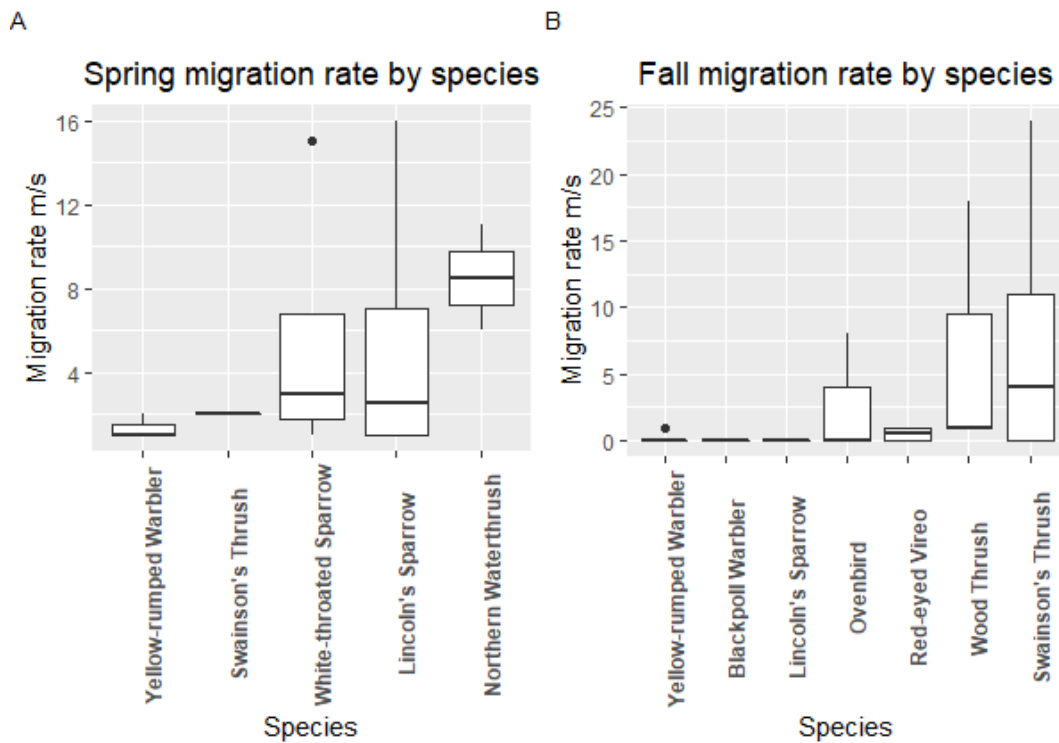


Figure 6. Analysis of seasonal migration rate by species. Spring Lincoln's sparrows, northern waterthrush, and white-throated sparrows had higher migration rates than yellow-rumped warblers (A). Fall Swainson's thrush moved significantly faster than yellow-rumped warblers ($\beta = -3.50$, $P = 0.005$) and red-eyed vireos ($\beta = -2.59$, $P = 0.02$). Wood thrush also moved faster than yellow-rumped warblers ($\beta = -3.51$, $P = 0.02$) and red-eyed vireos ($\beta = -2.59$, $P = 0.05$) (B).

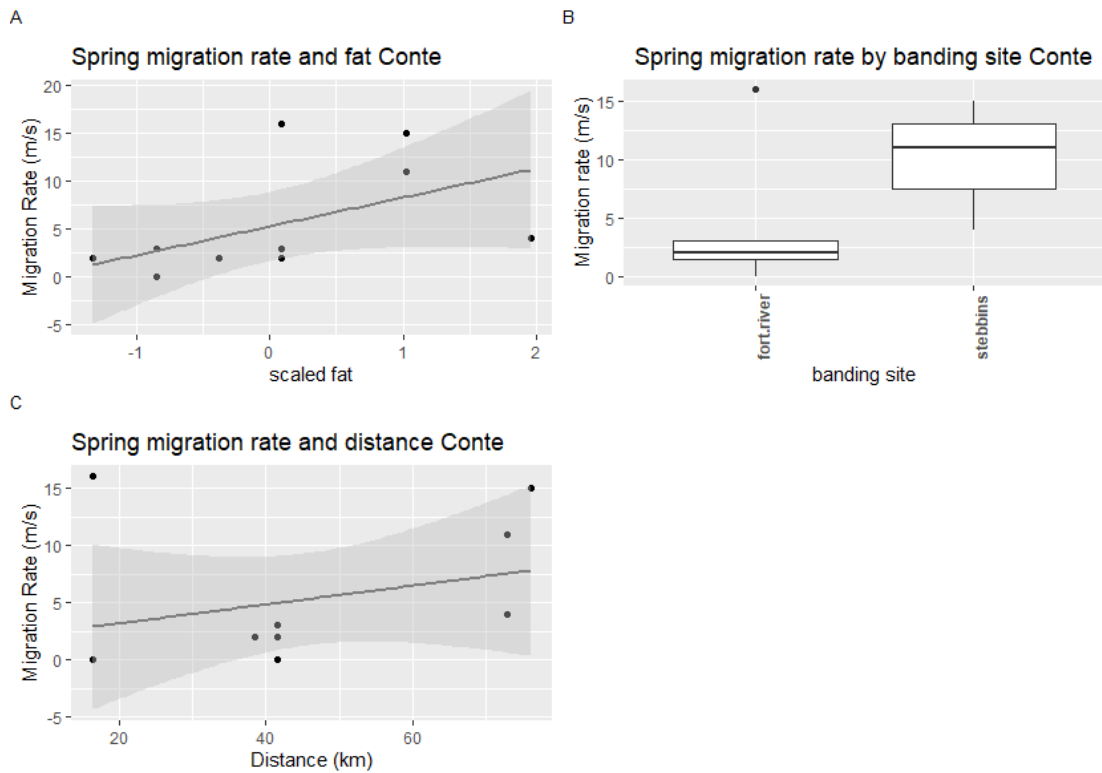


Figure 7. Results from the spring analysis of migration rate within the Conte Refuge. Birds with larger initial fat stores traveled faster (A), the spring 2016 site, Fannie Stebbins, had faster migration rates (B), and migration rate increased with total distance moved within the Refuge (C).

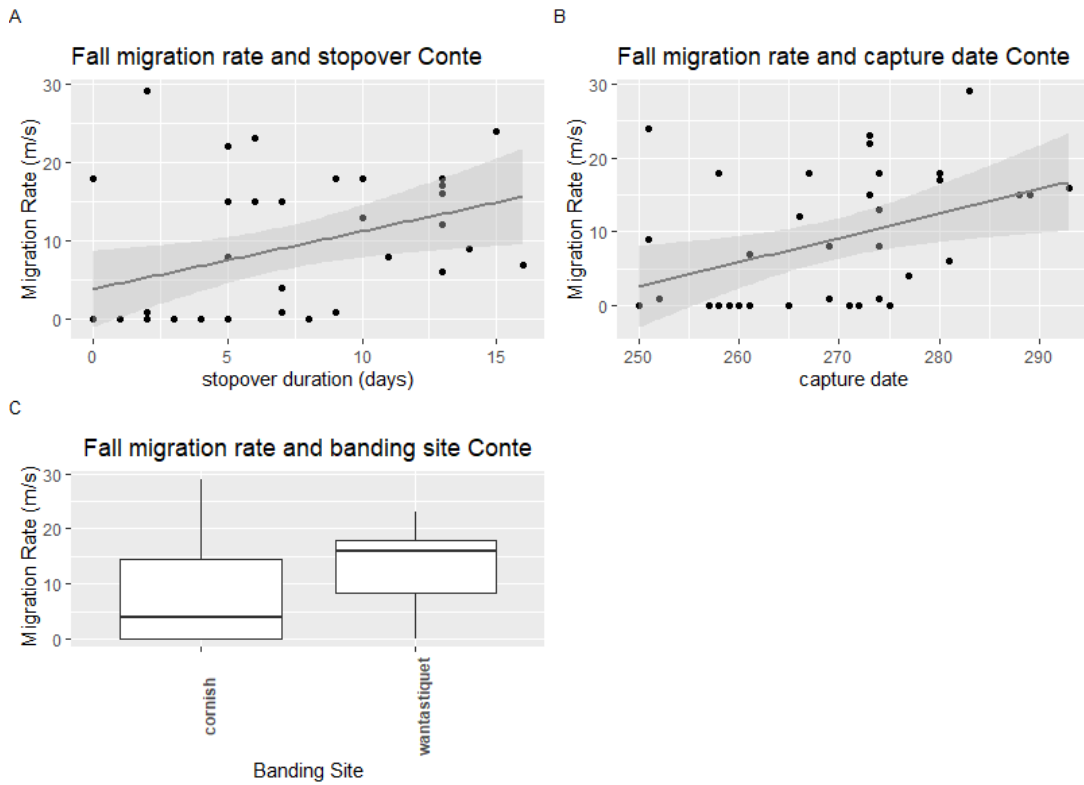


Figure 8. Results from the fall analysis within the Conte Refuge. Birds that made longer stopovers traveled at faster rates (A), birds captured later in the season traveled faster (B), and birds from the 2015 banding site, Wantastiquet, moved at higher rates (C).

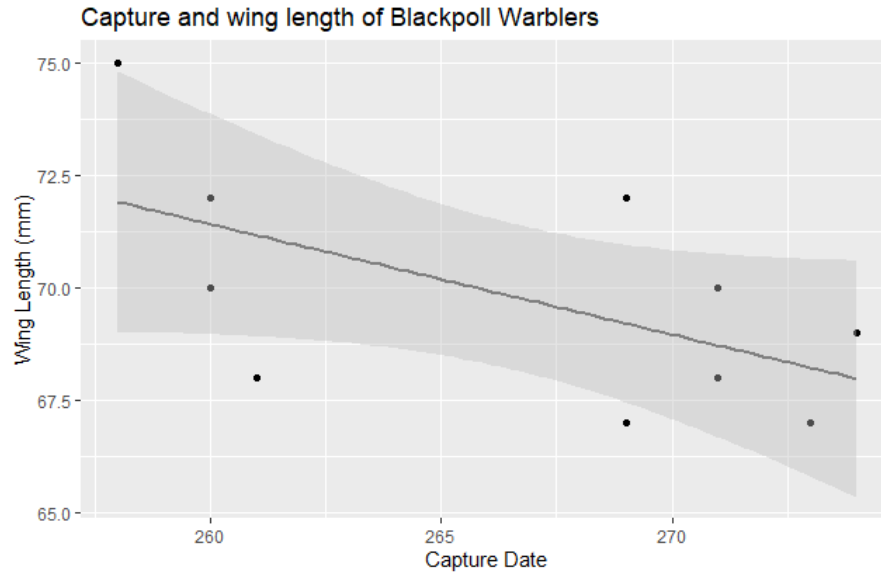


Figure 9. Results of a linear regression of blackpoll warbler wing length and capture date for Fall 2016 birds N=10 indicating that birds with longer wing lengths were captured earlier in the season at the banding site.

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